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## THE PAIR-FORMATION DISPLAYS OF THE WESTERN GREBE

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**ABSTRACT.**—In this paper we describe and illustrate the pair-formation displays of the Western Grebe (*Aechmophorus occidentalis*), examining their structural variation, social contexts, and probable evolutionary origins and functions. Most displays are performed mutually by two or more individuals and occur in elaborate and predictable sequences or “ceremonies.” One of these, the “Rushing Ceremony” is performed by either two males, a male and a female, or several males and a female. The “Weed Ceremony,” on the other hand, occurs later in the pairing sequence and always involves a male and a female. Finally, the “Greeting Ceremony,” used by pairs coming together after being separated, appears to be an abbreviation of the above two ceremonies with the energetic, core displays left out. We examine the temporal and spatial coordination between individuals involved in each of these ceremonies.

Most displays and ceremonies of Western Grebes differ greatly from those described for other grebe species, which supports morphological evidence for retaining the Western Grebe in a separate genus. The similarity of the Weed Ceremony to that of some species of *Podiceps* supports morphological evidence for considering the Western Grebe more closely related to that genus than to any other.

The spectacular courtship displays of the Western Grebe (*Aechmophorus occidentalis*) have aroused considerable attention, yet, surprisingly, no detailed description of them has been published. The only available summary for the species (Palmer 1962:100–102), though based largely on excellent information provided by R. W. Nero (1959), is much condensed and includes many inaccuracies from the earlier literature.

Western Grebes are gregarious at all times of the year and usually nest in colonies. On the breeding grounds, however, unpaired birds are highly aggressive and males frequently use their long, pointed bill to stab other individuals from below the water surface (“torpedoing”). Two courting males often perform elaborate mutual displays in front of nearby females. Many observers have misinterpreted these displays, mistaking such rival males for courting male-female dyads (but see Nero 1959).

The aim of this paper is to name, describe, and illustrate displays used by Western Grebes during pair-formation. Under each display the

description of a typical performance is followed by comments on variability from one performance to the next, the degree and nature of coordination and orientation among displaying individuals, and its social contexts. Probable functions, evolutionary design, origins, and comparisons with displays of other grebes are then discussed.

### DISPLAY TERMINOLOGY

A display is usually defined as a behavioral pattern or posture that is ritualized or adapted for signal function (Moynihan 1955). Therefore, there is a basic functional dichotomy between display behavior and other daily activities such as feeding, locomotion, and comfort movements. This definition, however, does not specify how far behavior in a display should be combined or subdivided. In this paper we define a “display” as the largest unit of ritualized behavior that, in all contexts, is typically reproduced intact from one performance to the next (barring outside interference). The beginning and end of each display,



Rushing by a pair of Western Grebes. The male is on the left.

therefore, are determined by natural breaks occurring within longer chains of courtship activity. For example, if components A and B of an observed sequence of ritualized movements (ABCDE) are, in other contexts, reordered or broken apart (e.g., observed sequences of ACDB, BACD, or AE), they should be considered separate displays. On the other hand, if D follows C in all contexts, the two components should be combined and considered a single display. This provides a useful definition of a display as a "basic unit of ritualized behavior," somewhat analogous to Williams' (1966) and Dawkins' (1976) definitions of a gene. A display frequently incorporates both vocal and visual components, and we often include the vocalization in the display name (e.g., "Tick-pointing") and illustration. This avoids having separate terms for visual and vocal components. Grebe displays are often organized into highly stereotyped sequences called "ceremonies," here defined as formalized interactions involving two or more birds and a combined performance of two or more displays in a predictable sequence (Smith 1977). Names of displays and ceremonies are capitalized to distinguish them from non-signal action patterns, as in Moynihan (1955).

The photographs, drawings, and sonograms should not be considered representative of all species members or display performances. Variations in the form, frequency, and duration of displays occur and many of these variations appear to have functional significance (Beer 1975).

#### STUDY AREAS, METHODS AND MATERIALS

Nuechterlein studied Western Grebes in Manitoba (1973–1979) and in Utah, Oregon, and California (1978–1979). He observed display behavior most intensively at Marshy Point (50°30'N, 98°5'W) and in the Delta Marsh (50°15'N, 98°15'W), Lake Manitoba. Both are extensive, wind-tide marshes, free from human disturbance during the breeding season. During three seasons at Marshy Point (1976–1978), the senior author lived in an abandoned trapper's cabin located at the outer edge of a Western Grebe colony numbering several hundred individuals. A tower constructed on the roof of the cabin provided a broad view of the colony.

Nuechterlein used a small floating blind (constructed from an inner tube) disguised as a muskrat house to observe, photograph and tape-record courting birds at close range inside colonies (Nuechterlein 1980). Incubating birds in part of the colony were individually marked by slowly approaching them in a floating blind

and squirting them with dye from a pressurized tree-sprayer. Black (Nyazol) or yellow (picric acid) dyes were used. Other birds were captured in funnel traps set in channels leading from the colony to open bays of the marsh. In most instances sexes could be distinguished, both in the hand and at a distance (aided by a spotting scope) by the male's larger body and stouter, more massive bill (Palmer 1962). Where morphological differences were not evident, sex differences in the Advertising call were used.

Details of display structure were extracted from approximately 110 h of sound recordings and 12,000 m of 16-mm film. From these samples, segments of particular interest were analyzed using a Spectral Dynamics real-time analyzer, Kay Electric Sonograph and L-W Analyst projector. Interactions not recorded on film were dictated into a cassette recorder and later transcribed onto "time-line" sheets. Most of the quantitative temporal data in this paper are derived from films and from these sheets.

Storer observed Western Grebes mostly in Utah, North Dakota, Oregon, and Saskatchewan. His data were obtained from direct observation, 2,000–3,000 m of 16-mm film, and several hours of sound recording. Between 1952 and 1976, he also gained field experience with all but 2 of the 19 known species of grebes; not seen were the Madagascar Little Grebe (*Tachybaptus pelzelni*) and the Atitlán Grebe (*Podilymbus gigas*). Comparative data, drawn from his observations and the literature, range from extensive for most of the species of *Podiceps* to negligible for some of the species of *Tachybaptus*.

#### SOCIAL COURTSHIP DISPLAYS

##### ADVERTISING

*Typical performance.* While swimming or resting on the water, a Western Grebe raises its crest and emits several loud, one- or two-noted calls: "creet" or "cree—creet." The posture is variable and often differs little from the usual swimming posture (Fig. 1). The display usually includes from one to six calls 0.5–1.0 s apart. During extended calling bouts, the bill remains open and the crest is kept raised throughout. Advertising calls of different birds are often so distinctive and consistent that one can easily learn to recognize individuals by their calls.

Spectrographic analysis of call variations shows distinct sex differences, correlation with color phase, individual variation, and variation with respect to pairing status (Nuechterlein 1981a). In both color phases (Storer 1965), calls of males are longer and of lower frequency than those of females. Calls of light-phase birds

usually consist of a single note ("creet") whereas those of dark-phase birds have two notes ("cree-creet") separated by a 20–200 ms gap (Fig. 1). Paired birds tend to give fewer calls per bout than unpaired birds (paired birds:  $\bar{x} = 1.7$  calls/bout; unpaired birds:  $\bar{x} = 3.4$  calls/bout; Nuechterlein 1981a).

**Orientation and coordination.** Lone, actively courting birds repeatedly answer (within 1–5 s) Advertising calls given by other unpaired birds in the vicinity. Usually, two birds calling to one another are not in visual contact, and they may be 100–200 m apart. Calling often occurs in bursts, apparently caused by many males responding simultaneously to Advertising by a female.

**Social contexts.** This is the only courtship display that is regularly performed by lone individuals. Unpaired males and females Advertise "spontaneously" while swimming restlessly from one open water area to the next in search of a mate. On hearing the call, interested birds of the opposite sex respond by approaching and Advertising in reply. Back-and-forth calling continues at intervals until eventually two or more individuals come together and engage in mutual display sequences.

Later in the season, paired birds use the Advertising call for individual recognition when mates or parents and offspring become separated. Thus, this call is given both in the colony and on the feeding grounds, at night and during the day, and in all seasons of the year.

**Discussion.** Advertising is the call most often associated with the species and is, for most ornithologists, diagnostic for species identification. It is very frequently given, probably because in Western Grebes the display has taken on a variety of functions related not to territorial Advertisement, but to maintenance of individual contact within large colonies. (In most of these contexts the term "Advertising" is actually inappropriate, but it is widely used in the grebe literature and is retained here as a label only.) Advertising also plays an important role in reproductive isolation of the two color phases of Western Grebe (Nuechterlein 1981b). Playback experiments indicate that unpaired males readily respond only to calls of unpaired members of the same color phase and opposite sex. Once paired, birds appear to narrow even further this response to the individual call pattern of their mate (Nuechterlein 1981a).

**Advertising in other grebes.** While Advertising is probably used by all species of grebes, it is best known in the genus *Podiceps*. It was first named and described by Simmons (1954)

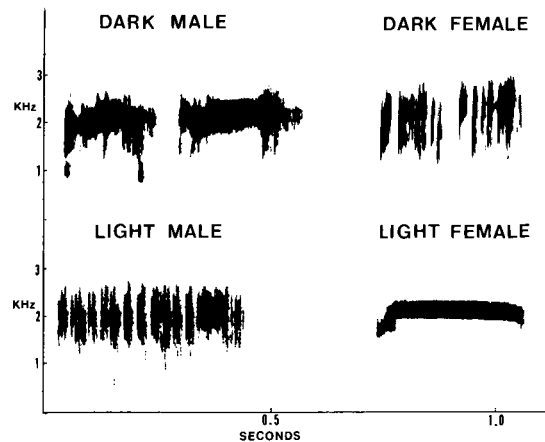


FIGURE 1. Advertising by a male. Calls of females are shorter and higher pitched. Advertising calls of dark-phase birds are two-noted; those of light-phase birds, one-noted.

for the Great Crested Grebe (*P. cristatus*) and subsequently for the Eared Grebe (*P. nigricollis*; McAllister 1958), the Great Grebe (*P. major*; Storer 1963a), and the Horned Grebe (*P. auritus*; Storer 1969). The last paper also includes a briefer account of this display in the Red-necked Grebe (*P. grisegena*), the Silvery Grebe (*P. occipitalis*), and Puna (Taczanowski's) Grebe (*P. taczanowskii*). In addition, Advertising is frequently performed by the Hooded Grebe (*P. gallardoi*; Storer 1982). Outside *Podiceps*, Advertising is known for Rolland's Grebe (*Rollandia rolland*; Storer 1967), the Least Grebe (*Tachybaptus dominicus*; Storer 1976), and the Little Grebe (*T. ruficollis*; Cramp and Simmons 1977). LaBastille (1974) thought the "Cuh-cuh call" of females of the Atitlán Grebe might "be akin to Advertising," but this has not been demonstrated for it or for the Pied-billed Grebe (*Podilymbus podiceps*).

Individual differences in Advertising calls have been suspected for *P. nigricollis* and shown for *P. auritus* (Storer 1969), *P. gallardoi* (Storer 1982), and *A. occidentalis* (Nuechterlein 1981a). Such differences are presumably to be found in all grebes, although they are probably greatest in species that nest colonially

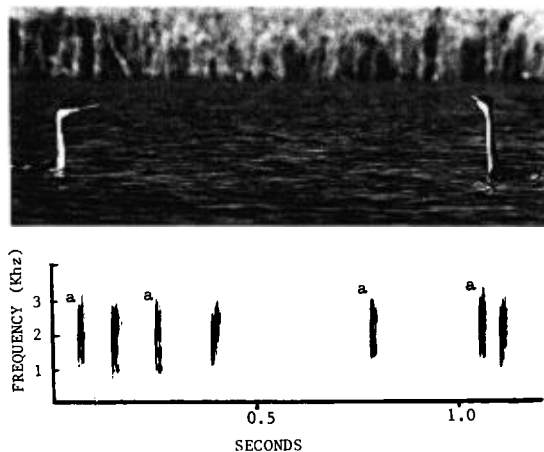


FIGURE 2. Tick-pointing by two males. Sonogram shows the closely interspersed, irregularly spaced "ticks" of two different birds (a = one bird).

or on bodies of water with extensive areas of emergent vegetation where visibility is reduced.

In unpaired birds and newly-paired birds separated from their mates, the display tends to be given in the characteristic upright posture, often with some of the ornamental plumes spread. In species such as *A. occidentalis* and *P. nigricollis*, which nest in colonies, the display is also frequent long after the young have hatched and is used to locate mates and offspring. During this period, there is increased emphasis on the call and de-emphasis on the visual aspects of the display. On the other hand, solitary nesters or those with large territories tend to Advertise most frequently early in the pairing season and seldom afterward.

Fjeldså (1973) described and illustrated variants of Advertising in the Horned Grebe (*P. auritus*) involving different contexts, different postures, and differences in the ways in which the nuptial plumes are spread. In Advertising of unpaired birds, the black tippets, as well as the buffy ear tufts are spread, the tail is cocked, and the white of the anterior underparts shows well above the water. These give maximum conspicuousness to the displaying bird. After pair formation, other versions appear in which the head is held forward and the ear tufts, but not the tippets, are spread. Whereas the call is the same, the different postures and lack of spreading of the tippets, along with the difference in pairing status, suggest that the signal function differs from that of unpaired birds. Although not named, these variants of Advertising near the nest were described and illustrated much earlier by Hosking (1939).

The Pied-billed and Atitlán grebes (*Podilymbus*) have a territorial "song" given by the

male, often in duet with the female, whose corresponding call resembles the first part of the male's call but lacks the final series of "cow" notes characteristic of the male's call. The duets, without the "cow" ending, are the usual greeting of a pair of Pied-bills as they come together, turn, and swim side by side. The Least Grebe, Little Grebe, and the Australian Dabchick (*Tachybaptus novaehollandiae*) have similar trills, which appear to serve the same function. In both genera, the trilling appears to be related to and possibly derived from a Triumph Ceremony like that of *Podiceps auritus* (Storer 1969), and therefore is probably not homologous with Advertising.

#### TICK-POINTING

*Typical performance.* The bird sleeks the feathers on its body and crest and assumes a rigid, head-erect posture with tail cocked vertically and bill tilted slightly upwards, 10°–30° above the horizontal (Fig. 2). At 3–5-s intervals, it repeatedly jerks its head to one side, then the other, and emits a series of sharp, irregularly spaced "ticks" (0.1–3.0 s apart). The head movements are very regular, each bird maintaining its own individual rhythm. Tick-pointing bouts often last up to several minutes, but vary greatly in duration.

*Orientation and coordination.* Once begun, mutual Tick-pointing bouts are highly contagious, and four or five birds are frequently drawn into the display performance. Two birds usually begin Tick-pointing while 5–15 m apart and facing one another. Then as they slowly approach one another they begin "ticking" more rapidly.

*Social contexts.* Lone birds appear to use Tick-pointing as a rare alternative to Advertising for attracting attention and initiating courtship interactions. Unlike Advertising, Tick-pointing usually involves birds that already see each other, and bouts frequently include four or more participants. Unpaired birds of both sexes participate, although males tend to predominate. Tension mounts as members of the group slowly converge, "ticking" more and more rapidly, then suddenly two or more birds may break into a parallel Rush (see frontispiece).

*Discussion.* Tick-pointing is probably derived from the alert posture. In alarm situations, parents with offspring raise their heads high and give several sharp, widely-spaced "ticks." The vocalization during Tick-pointing is identical, except that the "ticks" are much more numerous and closely spaced. Also, the alarm posture lacks the regular head-turning movements and slight upward pointing of the bill seen during Tick-pointing. Presumably

because of their ability to draw attention, alarm postures frequently provide a source for display postures in waterbirds (McKinney 1975). In this new context, however, selection for "ticks" that are widely spaced and difficult to localize has apparently been relaxed, and Tick-pointing birds give a much longer, more rapid series of calls than do alarmed individuals.

Tick-pointing seems to have retained some of its original functional association with mild alarm situations. On several occasions, for example, bursts of mutual Tick-pointing and Rushing occurred after mild disturbances created by Forster's Terns (*Sterna forsteri*) giving alarm calls as they flew by an observation tower. Such alarm cries usually elicited alert, head-erect postures from nearby grebes. On several occasions grebes facing one another in mutual alarm posture then began raising their bills to engage in Tick-pointing as the terns flew off. They sometimes reacted similarly when airplanes flew low overhead.

Tick-pointing has no known homologue in the behavioral repertoire of other grebes, but various movements of the head, including turning, are performed by most, if not all, grebes. Pairs of the New Zealand Dabchick (*Poliiocephalus rufopectus*) perform a somewhat similar Head Turning display, in which the body, as well as the head, is turned (Storer 1971) and the Great Grebe has an even more elaborate Turning Ceremony (Storer 1963a). These displays may not be accompanied by vocalizations, and in context, they lack the similarity to Advertising found in Tick-pointing.

**RATCHET-POINTING (MENACING, THREAT-POINTING:** Nero 1959, Palmer 1962)

*Typical performance.* With head low, crest raised forward and throat bulging, the grebe points its bill and stares at another bird and emits a harsh, 0.2–2-s ratchet-like call. The body is held low on the water with tail feathers cocked (Fig. 3). Intensity and duration of the display are variable, and depend on the sex and responsiveness of other displaying individuals. In general, staring bouts involving two males are more intense and more likely to break out into overt aggression than those involving a male and a female.

*Orientation and coordination.* Two Ratchet-pointing birds approach face to face, and repeatedly stare at one another, 0.2–3 body lengths apart. Alternately each bird looks away by Dip-shaking at 1–5-s intervals, and when eye contact again is established, the birds renew their ratchet-calling. As the display bout pro-

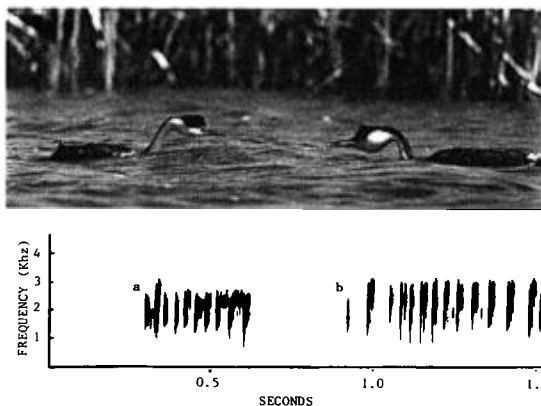


FIGURE 3. Ratchet-pointing by a male (right) and a female (left). Sonogram shows the "ratchet calls" of two different individuals.

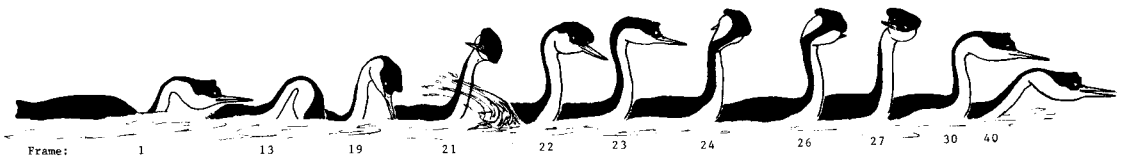
ceeds, one bird may inch slowly forward while the other retreats.

*Social contexts.* Ratchet-pointing is the most common display following initial eye contact and approach by two Advertising strangers. Displaying dyads may be two males (37%) or a male and female (63%), but almost never two females (sex ratio approximately 50:50). The display is loud and conspicuous and attracts the attention of other unpaired birds in the vicinity, which often skitter across the surface in their efforts to join or disrupt the pair. At other times, intruders quietly dive, using their bills to attack Ratchet-pointing birds from beneath the surface. Unpaired males were responsible for 77% of 98 attacks on Ratchet-pointing pairs. Most of their attacks were toward displaying males (90% of 61 directed attacks) rather than females, though often when a male and a female had been Ratchet-pointing, both birds frantically skittered away.

*Discussion.* Eye contact during Ratchet-pointing appears to be very important. The prolonged binocular stare and harsh vocalization appear to be intimidating, and display bouts involving two or more males frequently break out into frenzied chasing. As with Tick-pointing, the tempo usually mounts as the bout proceeds, especially if it reaches a climax with the Rush. At other times, bouts subside with no further display activity.

The threat posture used by paired birds at the nest provides a possible origin for the display. When approached by intruders, a bird defending its nest site holds its head low and crest forward, while emitting a "chucking" vocalization. This posture is at times virtually indistinguishable from Ratchet-pointing, and only the contextual and vocal differences provide a distinction between the two displays.

## DIP-SHAKING



## BOB-SHAKING

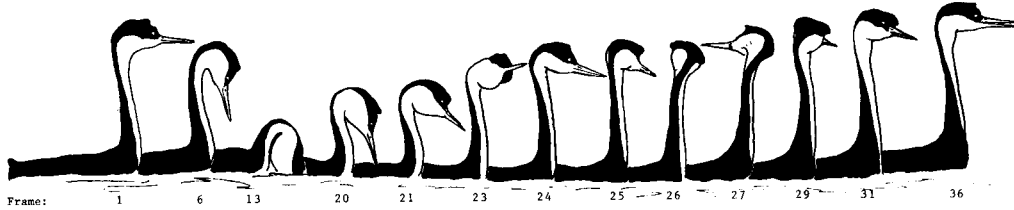


FIGURE 4. Comparison between Dip-shaking and Bob-shaking, traced from film exposed at 64 frames per s: Dip-shakes involve a low neck posture and conspicuous water splash, while Bob-shakes do not.

## DIP-SHAKING

*Typical performance.* From a head-low position, the bird dips the forepart of its head into the water and raises it again while rapidly wagging the bill from side to side (Fig. 4). With the first head movement, a conspicuous splash of water is thrown sideways. After the wagging, the grebe lowers its head again.

A bird usually Dip-shakes in discrete bouts of 3–15 displays, spaced 1–5 s apart. Total duration of a single display is 0.3–0.5 s. Each Dip-shake usually consists of three (in some birds two) lateral head movements. The direction of the first head movement (and hence water splash) can change even within a single display bout.

*Orientation and coordination.* Dip-shaking birds face one another at close range (0.2–3 body lengths) and usually Dip-shake alternately. Of 285 Dip-shakes performed during 38 interactions, only 16% were given by the same individual displaying twice in succession. Displaying birds appear to achieve this coordination by adjusting their own Dip-shaking rate to that of their partner. When one bird hesitates, the other often pauses also. Unlike the head-turning movements of Tick-pointing, the intervals between Dip-shakes often are quite variable.

*Social contexts.* Contexts are similar to those of Ratchet-pointing. Displaying birds may be two males, a female and a male, or several males and a female. Various outcomes of a Ratchet-pointing/Dip-shaking bout are possible. (1) If not interrupted, two unpaired birds nearly always follow it by mutual Rushing (96% of 302 bouts), though bouts sometimes subside (2%) or are followed by other displays (2%). (2) If an intruding male approaches, Dip-shaking birds either separate and skitter over the water surface, Rush prematurely (one or both

birds), or include the intruder in the bout. Such three-bird display bouts often become overt aggression or Barge-trilling by the two males, but also they may lead to Rushing. If an intruding male attacks from beneath the surface, the birds often Rush or skitter away upon seeing him dive. (3) If the two Dip-shaking birds are paired or familiar with one another, bouts are often brief and not accompanied by Ratchet-pointing. They also are followed by Bob-preening or Bob-shaking rather than Rushing. This “Greeting Ceremony” is discussed at length in a later section.

*Discussion.* As pointed out by Palmer (1962), Dip-shaking closely resembles bill-shaking movements used to remove water droplets or debris from the bill. During bill-shaking, however, the tail is not raised, the crest remains flattened, and since the bill is raised from the water before being shaken laterally, water is not thrown to the side. Also, Dip-shaking is organized into discrete bouts, while bill-shaking is not.

The functional significance of the water splash is unknown. Although Dip-shaking provides a prelude to Rushing and two birds facing off must determine somehow whether they will Rush to the right or left, film analysis shows no obvious correlation between the direction in which water is thrown and the direction of Rushing.

Neither Ratchet-pointing nor Dip-shaking appears to have a homologue in displays of other grebes.

RUSHING (WATER DANCE, RACE, RUN: Nero 1959; RACE: Palmer 1962)

*Typical performance.* With a sudden thrust from its legs, a bird whirls to one side, lunges forward out of the water, and runs rapidly across the surface side by side with one or more

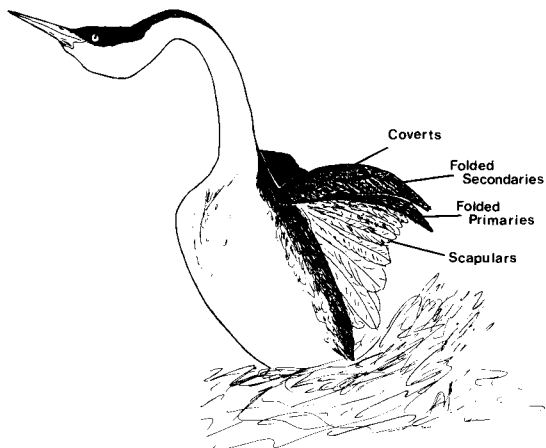


FIGURE 5. Wing position during Rushing. The wing is lifted but not opened and is held stiffly, not flapped.

other birds. The posture used during Rushing is unique, and wildlife artists have long puzzled over the exact positioning of the wings. Only a few of the best close-up movies show this well. The wings are lifted, but not extended, so that while the scapulars are spread, the secondaries and primaries remain folded beneath the elbow (Fig. 5). The wings are not flapped, but are held out stiffly to the side for the duration of the run. A Rushing bird maintains a nearly upright posture, holding its head forward with neck recurved. After Rushing perhaps 5–20 m, the bird lowers the wings and dives head first. No vocalizations are given, but the pattering of the feet on the surface at a rate of 16–20 steps per second is audible far away.

When starting a Rush, a bird may whirl either left or right. The duration of Rushing is highly variable, both among and within individuals (range = 0.1–7.6 s, median = 4.0 s,  $n = 157$ ). Sometimes the final dive is replaced by a long belly-glide or a skittering across the surface. This fleeing posture occurs especially when other birds either join in a Rushing performance or chase one of the participants.

*Orientation and coordination.* Two displaying birds usually Rush in a straight line, side

by side and 0.1–2 m apart. One bird begins Rushing; the other follows immediately (usually within 0.1–0.5 s). Two Rushing males often dive in close synchrony, whereas a Rushing male and female usually do not. If its partner fails to join in, a lone initiator usually turns in a tight semi-circle and dives almost immediately. When three birds Rush simultaneously, the female frequently drops out early, while the two males Rush farther. When more than three birds participate, coordination among the Rushing birds usually fails.

*Social contexts.* Before Rushing, birds nearly always engage in a bout of either Dip-shake/Ratchet-pointing or Tick-pointing. Groups involving only two Rushing birds are most common (Table 1) and may be either a male and a female (54%) or two males (46%). Groups of three or more birds nearly always consist of a single female and several males. Rushing by a single bird is rare and usually involves a male who has started prematurely because of attack by another male.

Rushing continues well into the breeding season (e.g., in late June), but individuals participating are nearly always unpaired birds. Rushes occurring within colonies usually involve transient courting birds, not nesting members of the colony. Pair formation and nest initiation can occur over a long period (April–July) in Western Grebes, and there is much overlap of these activities.

*Discussion.* During Rushing, the stiffly held wings may function as an air-foil, providing both lift and stability. A Rushing bird does not seem to be trying to out-run the other participant(s). Rather, one bird begins to Rush and the second bird, once it catches up, maintains a similar Rushing speed. This suggests that neither bird is Rushing as fast as it can. A similar conclusion can be drawn from films of three-bird Rushes in which intruding males getting a late start easily catch up to the Rushing pair.

Instances of males Rushing with other males probably are not mistakes in sex recognition. Instead males appear to engage in mutual Rushing to attract the attention of unpaired females in the area. The competitive nature of

TABLE 1. Composition of 897 Rushes according to size of the Rushing group and sex of the birds involved. Groups including birds of unknown sex were excluded from the analysis.

Size of Rushing group	Total frequency of group size (% frequency)	Sex of birds within groups (M = male, F = female)			Total number of birds rushing (%)	
1	30 (6.8)	M:	28	F:	2	30 (3.3)
2	359 (82.0)	MM:	168	MF:	193	718 (80.0)
3	47 (10.7)	MMM:	2	MMF:	45	141 (15.7)
4	2 (0.4)	MMMM:	0	MMMF:	2	8 (1.0)
	438			FFFF:	0	897



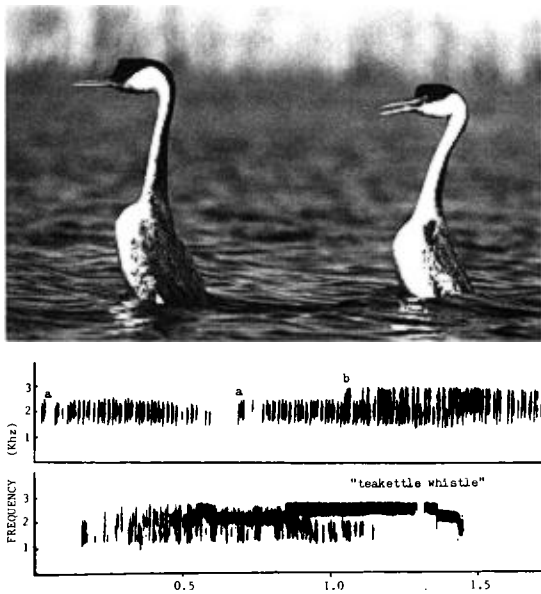


FIGURE 6. Barge-trilling by two males. Sonograms show (1) two trills by individual "a" overlapped in part by bird "b's" higher trill and (2) trill with a "teakettle whistle."

this and other displays occurring between males is evident in the interactions preceding and following Rushing, which frequently involve overt aggression. Attack is especially common when a female joins in the interaction or shows interest in one of the two displaying males. Lone males who are breaking up Rushing pairs direct most attacks at the male rather than the female.

Rushing appears unique to the Western Grebe, although several grebes are known to have displays involving raising the body nearly vertically in the water. The posture of the wings in this display is unique, but that of the head and neck is very similar to that used by several species of *Podiceps* while emerging from below the surface of the water in the Ghostly Penguin display (Storer 1969) and in precopulatory Rearing in most grebes.

**BARGE-TRILLING** (TREADING: Nero 1959, Palmer 1962; BARGING: Storer 1969)

*Typical performance.* With neck extended upward, crest raised, head horizontal, and wings folded, the bird vigorously paddles with its feet, causing the front half of its body to emerge nearly vertically from the water (Fig. 6). In this posture, the bird moves slowly forward, while emitting loud, repeated trills. Each trill lasts 0.5–2 s, with an interval of 0.2–2 s between trills. Throughout the display, the head is turned first to the side, then back again to the forward position. These slow and deliberate head-turns are highly stereotyped, and as in Tick-pointing, they are spaced regularly 2–

4 s apart. Total duration of a Barge-trilling performance ranges from 4–36 s (median: 10 s,  $n = 74$ ).

*Orientation and coordination.* Two birds usually Barge-trill side by side, in a parallel path 0.5–3 m apart. Although duration of Barge-trilling varies widely between performances, two birds displaying together generally subside at about the same time. In Head-turning the bill is directed towards the display partner. This results in brief bouts of binocular staring during which the birds give mutual trills.

Barge-trilling can sometimes be induced in a group of unpaired males by playing tape recordings of an Advertising, unpaired female (Nuechterlein 1981a). Usually the birds orient the display parallel to or directly toward the tape recorder and such playbacks can prolong Barge-trilling between two males or cause displaying males to turn abruptly toward the recorder. This experiment provides evidence that males may be orienting their display toward females in the vicinity.

*Social contexts.* Barge-trilling often occurs in female-choice situations and is unique in that, more than any other display, it primarily involves males. Unless approached by an additional male, male-female dyads very rarely Barge-trill. During such three-bird interactions the female is usually silent and her posture less exaggerated than that of the males. More frequently, males Barge-trill with each other when competing for the attention of a nearby female. Interested females join the displaying males and then choose one male for further courtship interactions such as Bob-preening (p. 361).

When Barging, a grebe expends a great deal of energy but makes only slow forward progress. Apparently the primary thrust of the legs is downward to maintain the bird's erect and highly visible body posture. Nero (*in* Palmer 1962) reported "a tea-kettle whistle (sound as of escaping steam)" heard during this display, but GLN recorded such "whistles" only infrequently, and they appeared to be correlated with bouts that included females. Possibly this is a female vocalization, but analysis of sound movies of Barge-trilling sequences involving females is needed to settle this question.

Barge-trilling has no certain counterpart in the behavior of other grebes, but displays involving male competition and extended parallel swimming are common among the colonial species of *Podiceps*. Silvery and Taczanowski's grebes have both an Arch-barging and a Barge-and-dive display, either of which may involve more than two birds. At least in Silvery Grebes, these barging displays are accompanied by mutual trills and usually involve competition between males. Hooded Grebes

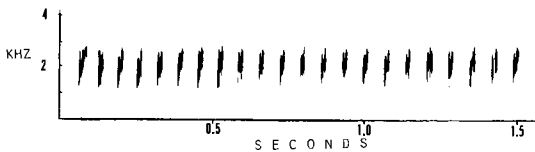


FIGURE 7. Neck-stretching by a male. Sonogram shows part of the trill given in the late stages of a Neck-stretching bout.

also have a mutual Barge-clucking display that involves extended parallel swimming by two or more birds, and Prinzing (1979) described a similar display ("Parallelschwimmen") for the Eared Grebe.

#### NECK-STRETCHING

*Typical performance.* This is an erect posture with crest raised, tail often cocked, and bill nearly horizontal (Fig. 7). Neck-stretching is variable in form and duration, and birds often dive or Bob-shake, then resume the posture. Late in a bout of Neck-stretching, a bird may emit a single, continuous 3–8-s trill reminiscent of that given during copulation.

*Orientation and coordination.* Two birds usually give this display face to face and establish prolonged eye contact while Neck-stretching 2–15 m apart. The stare is broken only at irregular intervals (5–30 s) and, as the bout proceeds, postural rigidity often increases until the birds eventually engage in simultaneous trilling.

*Social contexts.* When a bird surfaces after Rushing, it often Neck-stretches while attempting once again to establish eye contact with its partner. Males attempting to intervene, but arriving too late to break up a Rushing pair will often dive, then emerge simultaneously with them in a similar, Neck-stretched posture. This often appears to confuse the female, who then either chooses between the males or engages both in Barge-trilling. Birds

also use the display posture before and after Weed-dives (p. 360).

*Discussion.* Neck-stretching probably is a ritualized form of an alert posture. Only in courtship contexts, however, is the posture often accompanied by a trill. Mutual trilling usually occurs only towards the end of a bout, and usually it immediately precedes Weed-diving.

Neck-stretching possibly has a homologue in the upright postures and twanging calls used by the Great Crested Grebe before making a Weed-dive (Simmons 1975). Horned Grebes, and presumably Red-necked Grebes, have similar displays preceding Weed-dives. Alert, upright postures are also commonly assumed by grebes in other contexts.

#### BOB-SHAKING

*Typical performance.* From the Neck-stretching posture, the bill and fore-part of the head are suddenly dipped vertically into the water, then lifted out and shaken laterally two or three times (Fig. 4). The duration and number of shakes vary among individuals, and the initial shake may be directed either to the left or right. Unlike Dip-shaking, Bob-shaking does not involve a very conspicuous water-splash.

*Orientation and coordination.* Two birds usually face one another, 2–15 m apart, and perform Bob-shakes at irregular intervals of 3–15 s. Bouts usually include one to six Bob-shakes and birds tend to perform alternately.

*Social contexts.* Bob-shaking occurs in various contexts. Birds display most intensely during prolonged Neck-stretching sessions. Lone individuals also sometimes perform a single, less exaggerated form of Bob-shaking immediately before answering and approaching an Advertising bird. Paired birds also use the display in greeting and copulatory sequences.

*Discussion.* With neck fully erect, a grebe can both see and be seen for a considerable distance, and the postures of both Bob-shaking and Neck-stretching probably reflect their use as long-distance signals. They contrast with the low-neck positions used during Dip-shaking and Ratchet-pointing, which occur at close quarters. Like Dip-shaking, Bob-shaking may be derived from bill-shaking.

WEED-DIVING (WEED-TRICK: Huxley 1914, Palmer 1962, Storer 1969)

*Typical performance.* From the Neck-stretched posture, the grebe suddenly dives vertically, its head entering the water near the base of its neck. While submerged, it picks up organic material from beneath the surface and emerges in an erect posture (Fig. 8). Most Weed-dives

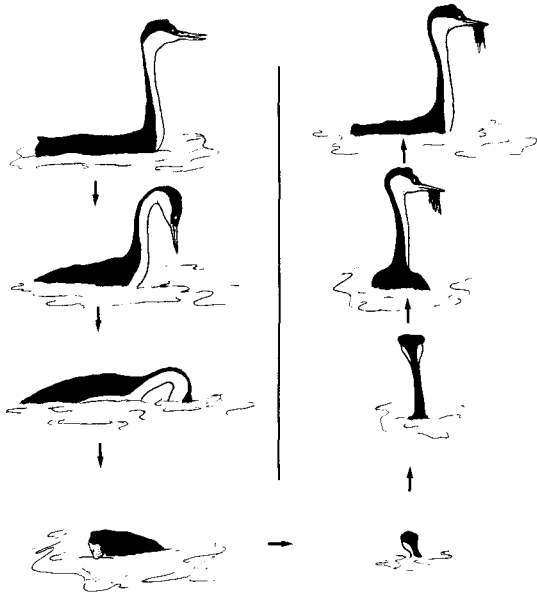


FIGURE 8. Weed-diving by a male. Most birds remain submerged less than 10 s.

are brief (3–15 s), and birds are often unsuccessful in bringing up weeds. In such cases they may dive repeatedly at intervals of 5–20 s until weeds are found. Emergents or weeds floating on the surface usually are not used and appear to be ignored.

*Orientation and coordination.* Two displaying birds are face to face, 5–15 m apart. Diving by one bird usually stimulates its partner to dive within 2–5 s. When only one individual finds weeds, the other immediately dives again. Meanwhile, the successful grebe remains on the surface with weeds held high or, if far away, approaches the other by diving again and resurfacing.

*Social contexts.* Weed-dives are performed by a male and a female, and usually follow Bob-shaking and Neck-stretching by both birds. Two males never engage in Weed-diving, although on occasion additional males will dive and approach with weeds. When this happens, both male and female usually drop their weeds and perform Barge-trilling with the intruder(s).

*Discussion.* Weed-dives tend to be much shorter than feeding dives (Table 2). This probably reflects the need for individuals to maintain close contact with their display partner. Rather than extending a dive indefinitely, an individual surfaces, looks for its partner, then dives again in search of weeds. Also, birds engaging in “unsuccessful” Weed-dives often may not be actually searching for weeds. If they were, unsuccessful dives should average longer than successful ones, but this is not the case

TABLE 2. Diving times for Weed-dives compared to feeding dives (level dives) by dark-phase Western Grebes on the Delta Marsh, Manitoba. All dives occurred in water less than 2 m deep.

Dive type	Successful		Unsuccessful	
	<i>n</i>	Duration (SD)	<i>n</i>	Duration (SD)
Feeding dive	14	26.0 (9.3)	50	34.6 (8.9)
Weed-dive	38	5.2 (2.1)	40	3.8 (1.7)

(Table 2). Moreover, females seem particularly prone to being “unsuccessful,” even in areas where weeds are known to be abundant. Diving without weed-gathering might be one means by which birds truncate a courting sequence. Less than 3% of Rushing male-female “pairs” eventually perform a mutual Weed-dance, and most sequences are broken off during Weed-diving, which occurs before the dance.

#### WEED-DANCING

*Typical performance.* With weeds in its bill, the bird rises to a nearly vertical position and churns vigorously with its feet, so that the anterior two-thirds of its body remain out of the water. During the Weed-dance, which lasts from 5 to 90 s (median = 17 s,  $n = 59$ ), the crest is flattened, the bill is raised 20–45° above the horizontal, and the wings remain folded (Fig. 9). Although the throat bulges, no vocalizations are heard.

*Orientation and coordination.* Weed-dances always involve close synchrony between the two participants. Both birds approach until less than a body-length apart, then rise up simultaneously, breast to breast. As they rise, they bring the weeds together above their heads, sometimes spiraling or moving slowly forward in the process. The performance ends when one bird withdraws slightly and then discards its weeds with a quick shake of the head. Its partner soon does likewise and both resume a horizontal body position.

*Social contexts.* Weed-dancing occurs only late in the pair-formation sequence and, in contrast to most earlier displays, it is limited to male-female dyads. Occasionally three birds approach one another with weeds but actual contact almost never occurs. More commonly, intervening males disturb Weed-dancing “pairs” either by underwater attacks or by direct surface attacks against the male.

*Discussion.* The Weed-dance is the only display that typically involves extended physical contact between two displaying birds. Weeds appear to be essential for the dance to take place. Only once in more than 90 observations was a bird without weeds seen performing a Weed-dance. In this instance, the male emerged



FIGURE 9. Mutual Weed-dancing by a pair. No vocalizations are given during the dance itself.

from an unsuccessful Weed-dive to find the female holding weeds immediately beside him. As he rose from the water, the male grasped the female's weeds and completed an abbreviated Weed-dance. The pair separated following a brief bout of Bob-preening.

Weed-dancing is probably derived from nest building, and it may be that the sight and mutual manipulation of weeds provide an iconic signal indicating willingness to proceed with pairing. The organic materials used during Weed-dancing are similar to those gathered from the bottom to build nests although, where these are not available, sticks or other substitutes sometimes are used for the Weed-dance. If the bottom has few weeds or if the water is deep, repeated Weed-dives may prove unsuccessful. In such cases, the pair usually omits Weed-dancing and continues with later displays of the pairing sequence.

#### BOB-PREENING (HABIT PREENING: Palmer 1962)

*Typical performance.* From the High-arch posture (described next), the bird suddenly reaches backwards, briskly runs its bill through the scapular feathers, then returns its head to the original position (Fig. 10). Each display lasts only 1–2 s, but it is often repeated many (5–60) times, 1–3 s apart, in bouts lasting several minutes. Postural intensity and preen frequency are both highly variable, and Bob-preening often merges almost imperceptibly into a bout of normal preening. Intense Bob-preens are easily distinguished from normal

preening by the lack of nibbling, the brevity of feather contact, and the height of the head between preens. Bob-preens are directed only at the scapular region, while normal preening involves many parts of the body.

*Orientation and coordination.* During intense Bob-preening, two birds are oriented side by side, 0.1–1 m apart. Either sex may be on the right or left. Intensely displaying birds usually turn their heads towards their display partner (86% of 452 Bob-preens filmed) and often synchronize their movements closely, thereby giving mutual performances a “mirror image” quality (Fig. 10). At other times members of a pair take turns, alternating regularly in their preening movements. As postural intensity drops, both types of temporal coordination also fall off and the pair eventually lapses into normal preening.

*Social contexts.* Intense mutual Bob-preening occurs only in male-female dyads. Although two males occasionally Bob-preen several times following Barge-trilling, such bouts are brief and not synchronized (Range = 1–10 preens/bout, median = 3, both males combined). Interactions among three or more birds similarly involve only sporadic Bob-preens. Within male-female dyads, Bob-preening is most intense following either mutual Rushing or extended Weed-dances. Well-formed pairs also Bob-preen in “greeting” (e.g., when meeting after a separation) and as a post-copulatory display.

*Discussion.* While Bob-preening side by side, a male and female are repeatedly turning towards one another, then averting their bills and engaging in preening movements. As with Dip-shaking and Bob-shaking bouts, eye contact is repeatedly broken, then re-established. During Bob-preening, however, the grebes are side by side rather than face to face, and mutual staring occurs only momentarily and with one eye. Possibly avoidance of extended eye contact explains both types of temporal coordination (i.e., synchrony and regular alternation), for both patterns lead to minimal staring.

Bob-preening is probably a ritualized version of a normal preening action. It possibly derives its signal value from the fact that preening usually occurs at times when an individual is in the company of familiar, non-threatening individuals. During the breeding season, for example, if two birds are seen preening side by side without others nearby they are usually members of a pair. Bob-preening appears to occur only between individuals that have engaged in previous courtship activities together and may be an important means by which they gain familiarity with one another.

Ritualized preening is included in the dis-

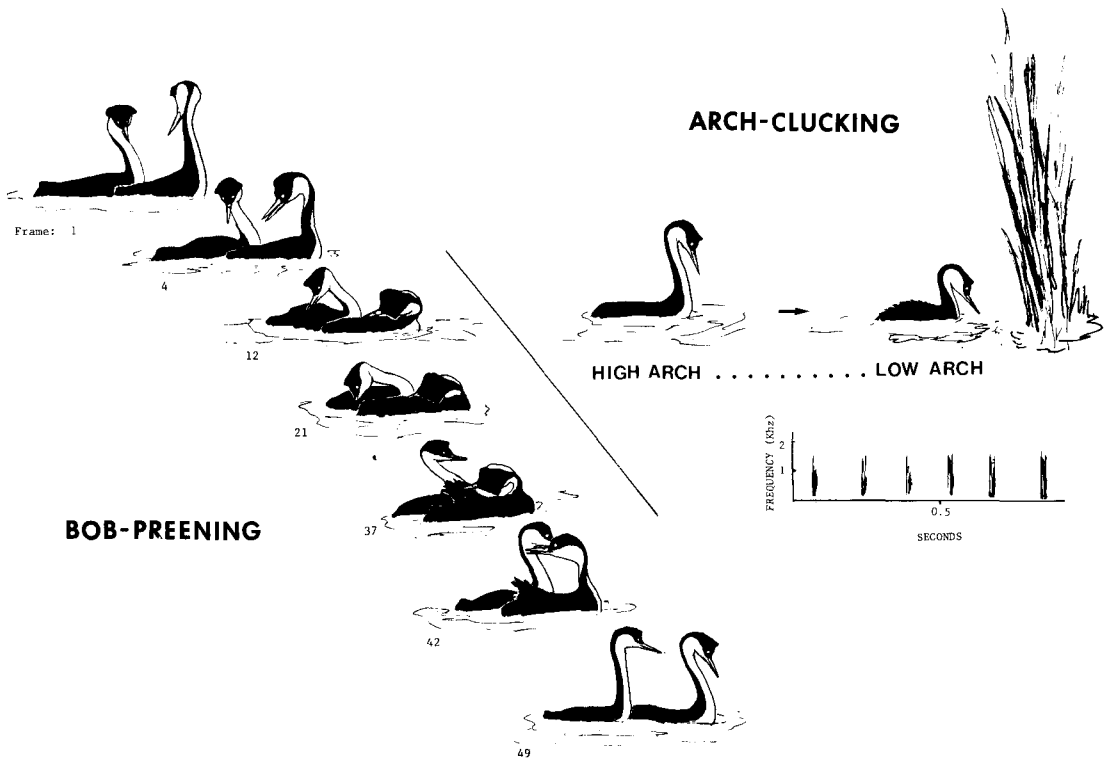


FIGURE 10. Mutual Bob-preening and Arch-clucking by a male and a female. Bob-preening partners often closely synchronize their preens. Arch-clucking often grades from High- to Low-arch (see text), but in both postures birds emit the same soft clucking vocalization.

play repertoires of several species of *Podiceps*: the Great Crested Grebe (Huxley 1914), the Eared Grebe (McAllister 1958), the Horned Grebe (Storer 1969), the Hooded Grebe (Storer 1982), and the Silvery and Taczanowski's grebes (Storer, pers. observ.). In at least three, the Great Crested, Horned, and Hooded grebes, it is included in the Discovery and Greeting ceremonies, much as Bob-preening is in the Rushing and Greeting ceremonies of the Western Grebe. Ritualized preening has not been described for two species of *Podiceps*, the Red-necked and Great grebes, or the other grebe genera, except *Aechmophorus*.

The term "Habit-preening" coined by Huxley (1914) is in general use for this display in *Podiceps*. We prefer to use a new term, "Bob-preening," for the corresponding display of the Western Grebe, which differs in starting and ending with the High-arch posture and a more exaggerated upward stretching of the neck.

#### ARCH-CLUCKING (BILL-WETTING, Palmer 1962)

*Typical performance.* Arch-clucking is a graded display with two extreme postures. At one end of the continuum is the High-arch, in which the neck is stretched to its full height while the bill points almost vertically downward. During this performance, the bird spreads its crest lat-

erally and clucks in short (0.1–0.3 s) bursts of 5–8 calls at intervals of 3–10 s (Fig. 10).

The High-arch posture may either be held for several minutes or it may grade into the Low-arch position. To assume a Low-arch, the bird lowers its head and brings it forward until the bill touches (or nearly touches) the water at a 10–30° angle. The bird's neck remains arched upward, but its head is held low. At high intensities the scapular feathers are conspicuously raised. As in the High-arch, short bursts of regularly spaced clucks are given.

*Orientation and coordination.* Mutually High-arching grebes are usually in close proximity (0.1–2 m), and either one leads the other or both swim side by side. High-arching need not be mutual, however, and performances can occur while mates are at greater distances. Low-arching, in contrast, is rarely mutual and usually it is performed while the birds are stationary and close together. The two postures are closely associated and are frequently seen whenever a pair swims in consort.

*Social contexts.* Arch-clucking is often the final display of a male-female ceremony. It is used by well-formed pairs as they swim from one part of the colony to another in search of a nest site. Although both sexes may use both extreme postures, High-arch is more frequent

in males, whereas Low-arch is more common in females. During nest-site selection, males assume the High-arch as they lead their female around, while females periodically stop and give a Low-arch at potential sites.

*Discussion.* Although clucking occurs during both Low- and High-arching, raising of the scapular feathers is associated only with Low-arching. Films of transitions from High-arch to Low-arch postures indicate that intermediate postures are usually transient. These observations suggest that divergence in the display may be occurring, and that High-arch and Low-arch may function as two separate but closely related signals. The gradient from High-arch to Low-arch does not appear to be correlated with the degree of display vigor, for as the posture becomes more rigid and the crest is raised, neck posture tends to drift towards either end of the continuum.

The Low-arch, including raising of the scapulars, is almost identical with the pre-copulatory posture used by birds soliciting from the nesting platform. During solicitation the bill usually does not touch the water, but this seems to result from the bird's elevated body position. Even the vocalizations are nearly identical in the two contexts and, although grebes cannot copulate on the open water (McAllister and Storer 1963), males make brief mounting movements toward females who are Low-arching intensely on the water beside them. Possibly, High-arching has been derived from Low-arching as a signal for use over greater distances. With its head lifted high, the displaying bird is both more conspicuous and better able to navigate.

Arch-clucking usually signifies that a liaison exists between two individuals and is most frequent during nest searching. When approached by lone courting birds, High-arching pairs frequently intensify their postures. This intensification suggests that the posture is used not only for intra-pair communication, but as a signal to others that a liaison exists and that they are unavailable for courting. Arch-clucking pairs rarely respond to Advertising calls of unpaired birds and are usually left unmolested by courting males. Birds defending nests, on the other hand, attack High-arching pairs vigorously.

## CEREMONIES

In the course of forming a pair-bond, a male and a female Western Grebe repeatedly perform the courtship displays in mutual, stereotyped sequences or "ceremonies." Such ritualized interactions characterize the display activities of most grebe species (Storer 1963b, 1969). Ordering of the displays comprising a

ceremony is quite stereotyped, but displays are frequently skipped, especially late in pair formation. Frequently, birds also are interrupted or they break off before completing the entire sequence. Complete sequences, as diagrammed in Figures 11–13, are therefore rare. Ceremonies, even more than displays, vary in form and duration.

### THE RUSHING CEREMONY

The Rushing Ceremony is the most frequent display sequence in spring courting groups. After answering one another's Advertising calls, two males or a male and a female approach one another, then face off menacingly, and begin a loud and often prolonged bout of Ratchet-pointing (Fig. 11). The intense staring and loud, raucous calls are interrupted at intervals as each bird gives repeated Dip-shakes. As the face-to-face display bout continues, the two birds inch closer together until suddenly both birds whirl and Rush noisily across the surface, side by side. After running perhaps 10–20 m, they fold their wings and silently dive. In a rare variant of the ceremony, mutual Tick-pointing replaces Ratchet-pointing as a preliminary to the Rush.

The Rushing Ceremony includes loud and conspicuous displays that frequently attract other unpaired males to the area. Hence three or more birds often participate simultaneously. Ceremonies involving two or more males are usually followed by competitive Barge-trilling, in contrast to those involving a male and a female, which often are followed by the more elaborate Weed Ceremony.

Like the Discovery Ceremony of the species of *Podiceps* sensu stricto (Huxley 1914, Simmons 1955, McAllister 1958, Wobus 1964, Storer 1969, Fjeldsø 1973), the Rushing Ceremony of Western Grebes appears to initiate pair formation. Both ceremonies are triggered by Advertising, and often lead to displays involving weeds in those grebe species that perform them.

However, the displays that occur between Advertising and weed ceremonies are completely different from these. Whereas all the displays in the Western Grebe are mutual, the roles in the Discovery Ceremonies differ, one bird giving the Cat Display while the other performs display dives and the Ghostly Penguin display. In the Great Grebe, the Nodding and Turning Ceremony, possibly preceded by diving, appears to be the pair-formation ceremony (Storer 1963a), but more observations are needed to verify this. Diving displays appear to be involved in pair formation in Rolland's Grebe (Storer 1967), the New Zealand Dabchick (Storer 1971), the Little Grebe

# THE RUSHING CEREMONY

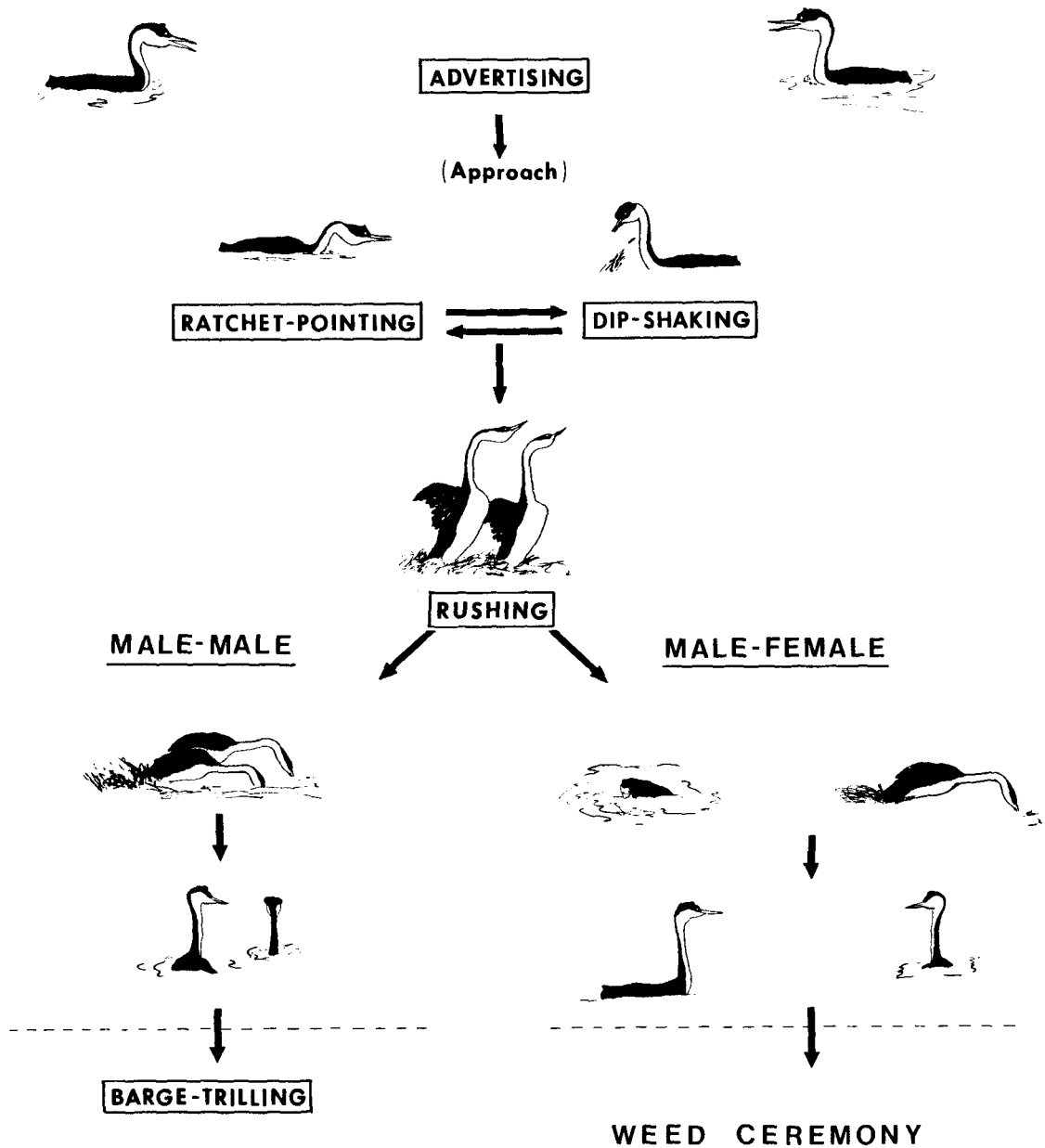


FIGURE 11. The Rushing Ceremony. The ceremony may be performed by two males, a male and a female, or several males and a female. When females are involved in the ceremonies, males usually Rush farther.

(Bandorf 1968; Simmons *in* Cramp and Simmons 1977), and presumably other related species.

## THE WEED CEREMONY

After Rushing, a female and a male may either separate, come together and Bob-preen, or

engage in a Weed Ceremony (Fig. 12). To initiate this Weed Ceremony, the participants emerge from the Rushing dive and swim toward each other in the Neck-stretching posture. As the two birds face one another, they begin Bob-shaking at irregular intervals until first one bird, then both together give pro-

# THE WEED CEREMONY

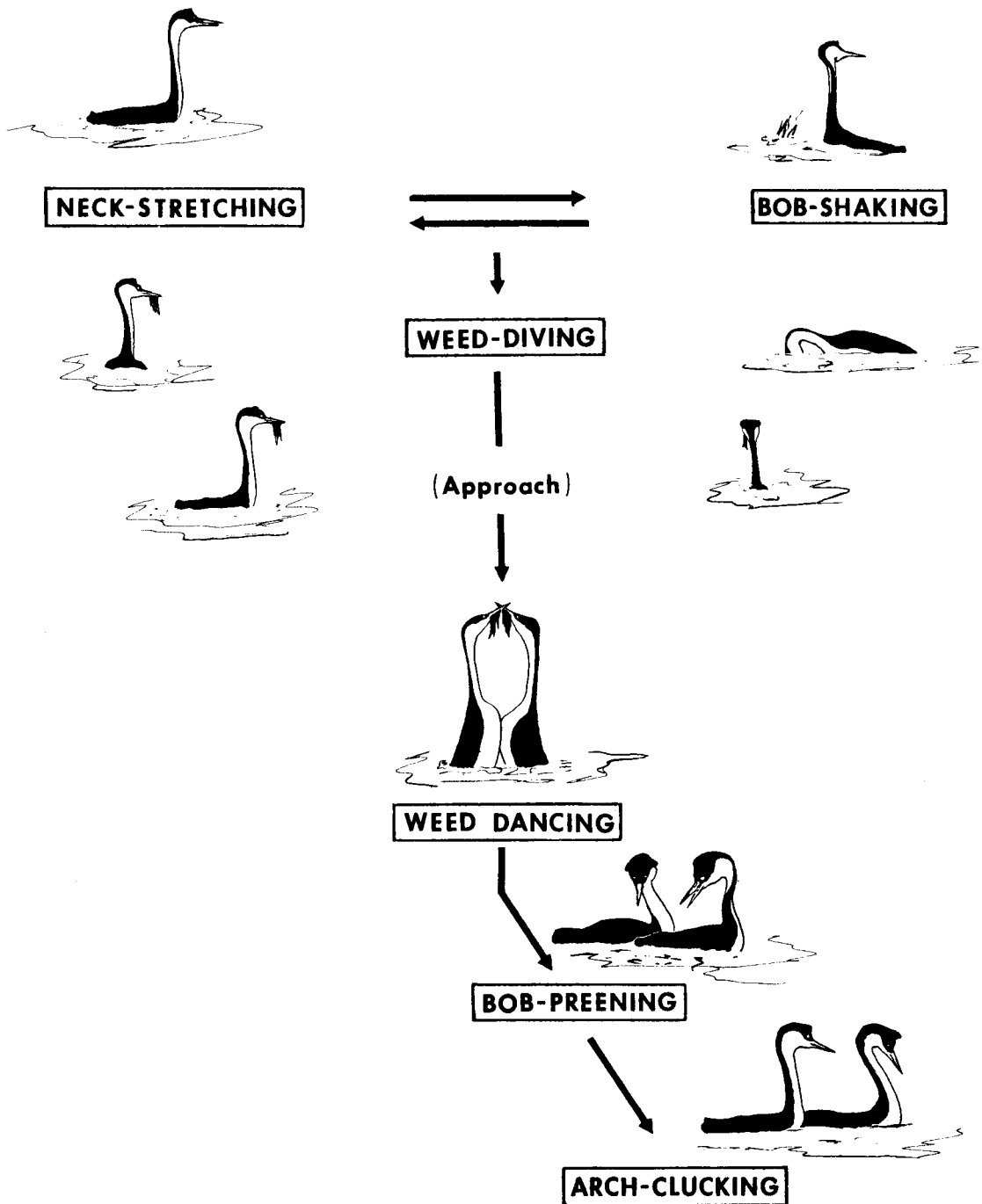


FIGURE 12. The Weed Ceremony, performed by a male and a female during pair formation.

longed Neck-stretching trills. Immediately following the duet, both birds Weed-dive repeatedly until they find suitable materials, and then they approach one another with the weeds in their bills. As they come into contact, the two

birds touch their bills and weeds together and paddle vigorously in a mutual, breast-to-breast Weed-dance. Pairs engaging in extended Weed-dances then drop their weeds and may begin repeatedly Bob-preening side by side. Even-



## THE GREETING CEREMONY

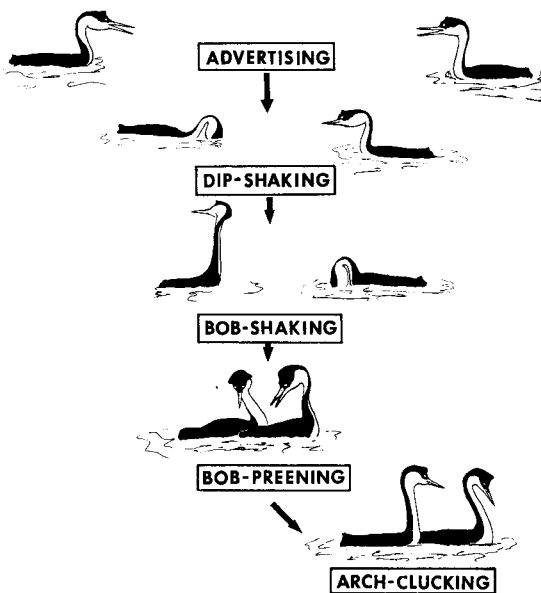


FIGURE 13. The Greeting Ceremony, performed by a pair after being temporarily separated.

tually these coordinated actions subside into normal preening, and the pair may begin Arch-clucking as they swim off together.

Weed Ceremonies usually involve a male and a female that have previously engaged in at least one Rushing Ceremony. They therefore occur more frequently in the later stages of pair formation. In contrast to the Rushing Ceremony, Weed Ceremonies always involve only two individuals and are quiet and inconspicuous. They often occur in or near emergent cover and, although common, are easily overlooked. Pairs often segregate themselves somewhat from other birds, and displays are obviously directed only toward the partner in the ceremony. Most displays are either silent or accompanied by soft clucks and trills in contrast to the harsh and far-reaching sounds of the Rushing Ceremony. Instead of face-to-face confrontation and conflict, displays of the Weed Ceremony involve close cooperation between the two participants.

Homologous weed ceremonies are also performed by three species of *Podiceps* sensu stricto: the Great Crested, Red-necked, and Horned grebes. In all three species, the ceremonies follow Discovery Ceremonies or modifications of them (i.e., greeting ceremonies), and include Neck-stretching and Weed-dives. Behavior following the Weed-dives differs among the species. Pairs of Great Crested

Grebes swim together rapidly, rising in a Ceremonial Rise-and-clash and perform a series of Weed-swings in an upright posture (Simmons 1975). Horned Grebes perform a series of Weed Rushes, alternately rushing side by side in an upright posture then moving apart, subsiding in the water, and turning before rushing again (Storer 1969, Fjeldså 1973). The Weed Ceremony of the Red-necked Grebe has not been adequately described (Simmons, *in* Cramp and Simmons 1977) but appears similar to that of the Great Crested Grebe except that the birds call loudly during the Weed-dance. Comparable weed ceremonies are not known in other grebes, although we have filmed less ritualized weed presentation ceremonies by both Silvery Grebes and Hooded Grebes.

## THE GREETING CEREMONY

As the bond between a male and a female grows, a less elaborate display sequence replaces the previous two ceremonies. In this Greeting Ceremony, the preliminary signals from both the Rushing Ceremony (Dip-shaking) and Weed Ceremony (Bob-shaking) are combined with the two final displays of the pairing sequence (Bob-preening and Arch-clucking). Therefore, it is an abbreviated version of the pair-formation sequence, from which the spectacular, energy-consuming core displays (Rushing, Weed-diving, Weed-dancing) are omitted (Fig. 13).

One consequence of this abbreviation is that the entire Greeting Ceremony may be completed in less than 10 s, and with little energetic cost. The movements and postures of displays remaining in the Greeting Ceremony are less stereotyped than those of the earlier courtship sequences. Dip-shaking bouts most often are not accompanied by Ratchet-pointing and consist of only one or two quick Dip-shakes per bird. The bouts of both Bob-shaking and Bob-preening are likewise abbreviated, and the Neck-stretched postures are more relaxed. Well-established pairs, in fact, may reduce the Greeting Ceremony further and rejoice with a simple Bob-shake or Bob-preen of recognition.

Greeting ceremonies have rarely been described in other grebe species but Simmons (1955, 1974) mentioned that bouts of low intensity Head-shaking often occur late in the season when disturbed pair members of Great Crested Grebes rejoin. Similarly, Horned Grebes may engage in a brief Head-shake plus Habit-preen bout as they come together late in the season (Storer, pers. observ.). Red-necked Grebes also use a low-intensity version of their earlier courtship duets in greeting (Wobus 1964; Storer, pers. observ.), and possibly this phenomenon is common in grebes.

The degree to which simplification occurs appears to vary directly with the strength of the pair bond and inversely with the strength of the stimulus for performing the ceremony. For example, two Horned Grebes with a well-established pair bond may merely give a single shake of the head when meeting, whereas earlier in the pairing stage, they might have stopped face to face, performed Head-shaking and Habit-preening, risen into a Penguin Dance, and ended with Weed-rushes. Aggressive encounters with neighboring pairs may result in bouts of Head-shaking after the members of the pair come together.

Thus, Greeting Ceremonies in both *Aechmophorus* and *Podiceps* sensu stricto are derived from and are simplifications of the pair-formation ceremonies, and are further alike in that the most energy-consuming elements are omitted first. Homologous ceremonies are likely to occur in other groups of grebes, but the pair-formation ceremonies are not yet known in sufficient detail.

## DISCUSSION

Pair-formation displays in grebes tend to involve ritualized attack behavior. Part of the Discovery Ceremony resembles an underwater attack, which is common in grebes, and the Rushing Ceremony most closely resembles a face-to-face confrontation followed by chasing. Although the two ceremonies appear to involve few displays that are structurally homologous, both may provide a step-by-step interaction procedure that allows the close contact necessary for mate assessment.

Nearly all species of grebes studied to date have a conspicuous "Advertising" display used to attract mates (Simmons 1968), but it is uncertain whether these are homologous. The upright Advertising postures used by all seven core species of the genus *Podiceps* (i.e., *cristatus*, *gallardoi*, *auritus*, *griseigena*, *nigricollis*, *occipitalis*, and *taczanowskii*) (Storer 1963b, 1982) are very much alike, except for variation in the degree to which the head plumes are raised (Storer 1969, pers. observ.). Vocal components of the display, however, differ widely even among closely related species; responses of birds to playbacks of Advertising suggest that the call may provide a vocal means of species, sex, and individual identification (e.g., Nuechterlein 1981a, b; unpubl. data for *P. auritus*, *P. nigricollis*, *P. occipitalis* and *P. gallardoi*).

Functionally and contextually, displays of the Rushing Ceremony in the Western Grebe appear to replace those of the Discovery Ceremony of most *Podiceps* species. Both ceremonies frequently occur when two Advertising

and approaching birds first see one another. Thus, they often involve strangers who are interacting for the first time. Although there are probably few, if any, homologous display components in the two ceremonies, both include displays apparently derived from aggressive behavior.

Weed Ceremonies are known to occur in at least three other grebe species—Great Crested Grebe (Simmons 1955, 1968), Red-necked Grebe (Wobus 1964), and Horned Grebe (Storer 1969)—and here the core displays of the four ceremonies may be homologous (Storer 1963b, 1969). Although the Weed-dance postures of the four species are similar, Horned Grebes rush back and forth side-by-side, whereas pairs of the other three tend to remain face-to-face, and Western Grebes point the bill upward 20–45°, rather than hold it horizontal. Weed-dances of both *Podiceps* species are preceded by Head-shakes, which resemble the Bob-shakes of Western Grebes, except that the bill is not dipped in the water. Finally, the weed ceremonies of all four species are associated with the later stages of pair formation (Wobus 1964, Simmons 1955, 1974, Storer 1969).

Two differing kinds of weed ceremonies are performed by species of *Podiceps*. *P. occipitalis*, *P. gallardoi*, *P. nigricollis*, and presumably *P. taczanowskii* have weed-presentation displays in which the members of a pair either dive for weeds or pick up floating bits of vegetation and alternately drop them near or on one another. These displays are far less ritualized than those of the Western Grebe and *P. cristatus*, *P. griseigena*, and *P. auritus*. Storer (1969) suggested a hypothetical evolutionary sequence from Weed-dance to Penguin Dance, and finally to incorporation of the Penguin Dance into the final stages of the Discovery Ceremony. If this scenario is correct, it suggests that the Western Grebe stock branched off early from a common *Aechmophorus-Podiceps* stock, and that, subsequently, ceremonies involving weeds became less stereotyped in the stock that gave rise to *P. nigricollis* and its South American relatives. Alternatively, the Western Grebe may have evolved from the line of *Podiceps* that perform stereotyped Weed-dances after that line branched from the *nigricollis* line. In the latter case, the Discovery Ceremony must have been replaced subsequently by the totally dissimilar Rushing Ceremony in the Western Grebe.

Fossil evidence indicating the time of this dichotomy is scant. The earliest record of *Aechmophorus* is of Upper Pliocene age (Murray 1967) and that of *Podiceps* (*P. oligocaenus* Shufeldt), Lower Miocene (John Day Forma-

tion; Brodkorb 1963). As *Aechmophorus* is the more derived genus morphologically, it is probable that a common ancestor with *Podiceps* would be more like the latter genus or even morphologically indistinguishable from it. Furthermore, *P. oligocaenus* is known from a single, fragmentary femur, and its assignment to the John Day Formation is questionable (Wetmore 1937). At this stage of our knowledge, we can say only that the two genera diverged before the Upper Pliocene.

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## RECENT PUBLICATIONS

**Songs of the Vireos & Their Allies/Family Vireonidae: Vireos, Peppershrikes, Shrike-Vireos, and Greenlets.**—Jon C. Barlow. 1981. Two 12-inch 33 $\frac{1}{3}$  rpm phonograph records, monaural. ARA-7, ARA Records. Source: ARA Records, 1615 N.W. 14th Ave., Gainesville, FL 32605. The primary songs of 39 of the 43 species of vireos and their allies are presented on these records, drawn from recordings by Barlow and several others. The album has been produced at high scientific and technical levels by J. W. Hardy. Coverage is intensive, using 68 entries to give examples from all the subspecies. Within each genus, the species and subspecies are arranged so as to illustrate increasing complexity of song and to reflect Barlow's views of the phylogenetic relationships. He spells out his observations and ideas in a long, pithy note on the album. Also given is a list of the entries, detailing the date, locality, and recordist for each. Except for the names of the birds, the same information is needlessly repeated in the announcements of the entries on the records themselves. While these records can, of course, be used as an aid in recognizing vireo songs, they will mean the most to specialists who are interested in the vocal habits and taxonomy of the family.

**Bird Songs in the Dominican Republic.**—Sound recordings by George B. Reynard. 1981. Two 12-inch 33 $\frac{1}{3}$  rpm phonograph records, monaural. Cornell Laboratory of Ornithology. \$10.00 (plus \$1.25 postage and handling). Source: Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850. These records offer the songs and calls of 100 species of birds that occur in the Dominican Republic. Produced from tape recordings most of which were made by Reynard over a span of 20 years, the acoustic quality is variable but generally high. Ambient sounds are often audible but some filtering and editing has been done, as explained in the liner notes. Entries vary in duration and are of generous length (including several cuts) for the more accomplished songbirds. Each species is announced by name only, without any narration. The species are not arranged in any discernible order although close relatives are mostly grouped within the same band, four bands per side. Thus, with the complete list of species given on the album, a desired entry can be found fairly easily. Dates and localities of the recordings are not given. Since the record is intended for the people of the D. R. as well as visitors, the announcements and the album notes are given in both Spanish and English. As a companion work, see Annabelle S. Dod's list of the birds of the D. R., offered in *The Bulletin Board*, this issue.

**Birds of Oak Hammock Marsh Wildlife Management Area.**—Kenneth A. Gardner. 1981. Manitoba Department

of Natural Resources. 172 p. \$10.50 Can. Source: Manitoba Museum of Man and Nature, Gift Shop, 190 Rupert Ave., Winnipeg, Manitoba, Canada R3B 0N2. This attractive little volume documents avifaunal changes resulting from the reestablishment of a managed wildlife marsh in an area drained for agricultural purposes in the last century. Located north of Winnipeg, between the lower ends of Lakes Manitoba and Winnipeg, the marsh (303 km<sup>2</sup>) was systematically surveyed just before, and just after reflooding. Fifty years of well-documented bird records add to the data base to provide visitors or local record-keepers with a comparison for their own observations. The report falls short of being an ecological comparison of conditions before and after reestablishment of the marsh largely due to lack of statistical data on vegetation or bird-life. Photographs, many in color; maps; literature cited.—J. Tate.

**Breeding Birds of Long Point, Lake Erie.**—Jon D. McCracken, Michael S. W. Bradstreet and Geoffrey L. Holroyd. 1981. *Canadian Wildlife Service. Report Series Number 44*. 74 p. Paper cover. \$11.75 Canada, \$14.00 other countries. Source: Printing and Publishing, Supply and Services Canada, Ottawa, Canada K1A 0S9. Long Point, Ontario extends about 35 km out into Lake Erie, some 125 km west of Buffalo. This booklet is an annotated checklist of its birds, with above-average content. Species accounts contain brief but thorough text, abundance and frequency estimates, nest data, egg dates, and a reference to breeding status on the adjacent mainland. In addition, about one-half of this paperback volume is devoted to a detailed examination of the vegetation communities of the study area, and breeding bird survey plots of major vegetation types. Statistical analysis of data on vegetation and birdlife appears thorough. Black-and-white photographs, figures and maps; frontispiece map in color; literature cited; appendix of plants mentioned.—J. Tate.

**Birds of Cattaraugus County, New York.**—Stephen W. Eaton. 1981. *Bulletin of the Buffalo Society of Natural Sciences*, Vol. 29, Buffalo, NY. 91 p. Paper cover. \$4.95. Written by the regional expert and heir apparent to the task, this is an annotated, historical record of a large (3,403 km<sup>2</sup>) western New York county. The introductory portions contain a correlation between bird life and glaciation, soils, forests, water bodies, and climate, which lead to an unusually detailed local history. As usual for books of this genre, the annotated list forms the heart of the book. The species accounts are filled with dates and names, but only limited attempts are made to reduce count data to summary statements. No raw data are presented. Frontispiece painting by W. C. Dilger reproduced in color; black-and-white maps; extensive literature cited.—J. Tate.