

*Aechmophorus
occidentalis*

FRENCH:
Le Grèbe de l'Ouest
SPANISH (NAHUATL):
Achichilique, Acitli

*Aechmophorus
clarkii*

FRENCH:
Le Grèbe de Clark
SPANISH (NAHUATL):
Achichilique, Acitli

Western Grebe

Clark's Grebe

The Western and Clark's grebes are conspicuous water birds of western North America from southern Canada to the Mexican Plateau. They are perhaps best known for their elaborate and energetic courtship rituals. These have been well-studied. Rushing, the most spectacular of these displays, has been shown on many nature films and is illustrated in the photograph of Western Grebes on the right. The courtship ceremonies in which these birds perform a series of displays in ritualized, apparently mechanical, sequences are among the most complex known in birds.

Perhaps even more remarkable is the fact that, with one exception, the rituals of these two species are identical. The exception is the number of notes, one or two, in the Advertising call; yet this,

plus differences in bill color and facial pattern, are enough for individuals to recognize birds of their own species and to choose them as mates. Discovery of this preferential mating led to several valuable studies of the degree of relationship between the two forms and to their recognition as distinct species

rather than color phases of the same species.

Western and Clark's grebes are unique among grebes in possessing a mechanism in the neck that permits them to thrust forward the head like a spear. Such a mechanism is well known in herons and anhingas, but its details remain to be worked out in these grebes.



Western Grebe



Clark's Grebe

The Birds of North America

Life Histories for the 21st Century

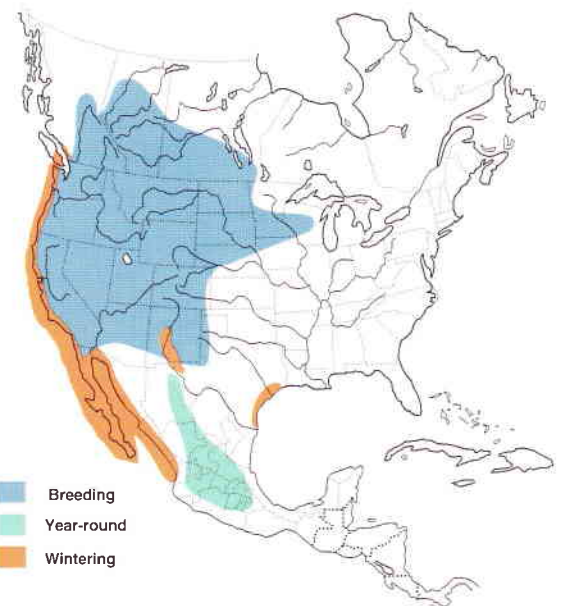


Figure 1.

Distribution of the Western and Clark's Grebe, whose ranges overlap. Breeding occurs in widely scattered suitable bodies of water within this area.

Because the Western and Clark's grebes were considered color phases of one species—the Western Grebe—from 1886 until 1985, the literature on them was combined under that name. Only rarely was mention made of the “phase” of the birds studied. Because of this, and because of the great similarity between the two species in morphology and behavior, this account treats both species. First, under Western Grebe, is given the information known to apply to that species alone, that common to both species, and that for which the “phase” was not mentioned. The companion account of Clark's Grebe (starting on p. 17) consists of information known to apply to that species and to known differences between the two.

Although the behavior of the northern subspecies of these birds has been well studied, little is known of their longevity and movements, owing to a paucity of banding recoveries. Parallel studies on the biology of the Mexican races of these species could greatly aid our understanding of the evolution of these species.

DISTINGUISHING CHARACTERISTICS

Western Grebe: large (55–75 cm long; 800–1,800 g), black, sooty, and white grebe with a narrow body, long neck, and long, sharply pointed bill. Distinguished from Clark's Grebe by the yellowish green bill and by the black of crown extending below bright red eyes. White in wing variable in extent, never in a well-defined patch. Crest triangular, black, raised and spread laterally in display. Tends to have less white in wing and on flanks than *A. clarkii*, but much overlap in these characters (Storer and Nuechterlein 1985). Sexes similar, but female smaller. Bill of female shorter, much thinner with a nearly straight culmen, which with the curvature of the mandible gives bill a somewhat upturned appearance. Sexes nearly 100% separable on bill size and shape.

DISTRIBUTION

AOU CHECK-LIST REGION

Breeding range. Occurrence within range (Fig. 1) depends on suitable lakes for breeding. Resident on some lakes from central California, south to n. Baja California and on the Mexican Plateau.

Winter range. Primarily on the Pacific coast from s. British Columbia to s. Baja California and Sinaloa. Also inland where there is open water from California east to s. Texas and, presumably, n. Mexico. Sparse and rare on the Texas coast.

Casual records west to Aleutians (Adak), north to s. Alaska and s. Yukon, east to New England coast, thence south to Florida and se. Texas. Not recorded outside AOU check-list region.

HISTORICAL CHANGES IN DISTRIBUTION

Western (and Clark's) grebes now nest in substantial numbers on Lake Havasu, AZ/CA. Prior to the late 1960s, there were no breeding records anywhere in this region—the lower Colorado River valley. All nesting there is in human-altered habitats, i.e., marshes that have grown up on large reservoirs (Rosenberg et al. 1991). Elsewhere within the range of these species, artificial reservoirs used for nesting and wintering have affected distribution on a local level, but to an extent not yet quantified.

FOSSIL HISTORY

Fossils of Western and/or Clark's grebes abundant in late Pleistocene deposits of Fossil Lake, OR. (Bones of the two species, as far as known, indistinguishable.) These referred to a separate, larger species, *A. lucasi* by Miller (1911) or, later, to a chronocline subspecies *A. occidentalis lucasi* by Howard (1946). Although averaging larger than bones of skeletons from s. California with which they were formerly compared, these fossils match in size bones of Western Grebes from northern part of species' range (Storer 1989). Pleistocene fossils reported from many parts of present range of species, including Mexico (Brodkorb 1963, RWS). A congener, *A. elasson*, described from late Pliocene deposits in Idaho (Murray 1967) and reported from Late Pliocene (Blancan) deposits in San Diego, CA (Chandler 1990).

SYSTEMATICS

Understanding the nomenclatural history of the Western and Clark's grebes is necessary for a correct interpretation of the literature on these species. Both described by Lawrence (1858), they later (Am. Ornithol. Union 1886) were considered color morphs of the same species (*A. occidentalis*). In 1963, Dickerman separated the small birds of both “color morphs” inhabiting the Mexican Plateau as a subspecies which he named *A. o. clarkii*, applying the name *A. o. occidentalis* to the larger, northern birds of both morphs. In 1985 (AOU 1985), the two former color phases were recognized as different species, *A. occidentalis* and *A. clarkii*. Finally, Dickerman (1986) proposed the names *A. o. ephemeralis* for the “dark phase”

Table 1. Linear measurements (mm) and mass (g) of Western Grebes (RWS original data).

| | <i>A. o. occidentalis</i> | | | | | <i>A. o. ephemeralis</i> | | | | |
|-------------------|---------------------------|-----|-----|------|------|--------------------------|-----|----|------|------|
| | Mean | s | n | Min | Max | Mean | s | n | Min | Max |
| MALES | | | | | | | | | | |
| Wing length (arc) | 203.9 | 4.7 | 109 | 192 | 216 | 185.1 | 3.7 | 9 | 179 | 192 |
| Tarsus length | 78.0 | 2.4 | 113 | 73.1 | 84.1 | 73.1 | 2.9 | 10 | 69.0 | 77.7 |
| Bill from nostril | 62.3 | 2.9 | 105 | 54.4 | 69.5 | 56.2 | 2.4 | 10 | 52.5 | 59.5 |
| Bill depth | 13.2 | 0.7 | 108 | 11.0 | 15.0 | 12.1 | 0.6 | 9 | 11.2 | 13.0 |
| Mass | 1429 | 163 | 41 | 1137 | 1826 | 1138 | 152 | 9 | 828 | 1338 |
| FEMALES | | | | | | | | | | |
| Wing length (arc) | 190.4 | 5.4 | 64 | 178 | 207 | 172.5 | 3.9 | 4 | 168 | 177 |
| Tarsus length | 71.3 | 2.3 | 67 | 66.5 | 76.3 | 67.5 | 2.3 | 4 | 65.0 | 70.5 |
| Bill from nostril | 53.1 | 2.5 | 61 | 47.7 | 59.4 | 47.0 | 0.6 | 4 | 46.2 | 47.5 |
| Bill depth | 10.2 | 0.7 | 62 | 8.7 | 12.4 | 0.3 | 3.8 | 4 | 9.0 | 9.8 |
| Mass | 1199 | 209 | 21 | 808 | 1753 | 857 | 38 | 4 | 823 | 912 |

Mexican birds and *A. o. transitionalis* for the "light phase" northern birds. Because the specific name *A. occidentalis* was applied to both species from 1886 until 1985, the literature of that period, unless specifying color phase, may apply to either or both species.

GEOGRAPHIC VARIATION

Resident birds of the Mexican Plateau smaller than those from the rest of the range (Table 1). Possibly a cline of increasing wing and bill length from south to north in the United States and Canada (Storer and Nuechterlein 1985), but samples contained both Western and Clark's grebes.

SUBSPECIES

Aechmophorus occidentalis occidentalis, breeding from Canada south through w. U.S. to n. Baja California, and *A. o. ephemeralis*, breeding on the Mexican Plateau.

RELATED SPECIES

Aechmophorus clarkii, widely sympatric with *A. occidentalis*.

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Nocturnal, probably in flocks. Many birds from northern populations move west to Pacific coast from early Sep to early Nov, peaking in Oct; move east to breeding grounds, primarily from late Apr to early May. Bent (1919) reported migration

northward along Pacific coast between early Apr and mid-May and southward from Sep to early Nov, but because Bent's records are not documented and Western Grebes winter along this coast, these dates, as well as extent of this migration, require verification. Some populations in sw. and w. U.S. are resident, as are (presumably) Mexican birds. Stragglers often reported in the U.S. east and southeast of the breeding range. 28 birds banded at Delta, Manitoba, recovered on Pacific coast from extreme s. British Columbia to s. California (San Diego); 2 birds banded in sw. Wyoming recovered in winter on Lakes Mead and Winnemucca, NV; 2 birds banded at Bear River marshes, UT, recovered in California (Monterey and Los Angeles areas). For a summary of banding data see B. A. Eichhorst (1992).

CONTROL AND PHYSIOLOGY OF MIGRATION

No information.

HABITAT

BREEDING RANGE

On fresh water lakes and marshes with extensive areas of open water bordered by emergent vegetation. Rarely on tidewater marshes (Weber and Ireland 1992). Breeding areas contain open water of at least several square kilometers, with largest colonies on most extensive lake systems.

SPRING AND FALL MIGRATION

Over land, usually stop on large bodies of water, occasionally on small, fishless ones.

WINTER RANGE

Majority on salt or brackish bays, estuaries, or sheltered sea coasts, less frequently on fresh water lakes, occasionally on rivers.

FOOD HABITS

FEEDING

Main foods taken. Fish.

Microhabitat for foraging. In open fresh or salt water of varying depths.

Food capture and consumption. Frequently peer into water with eyes below surface, presumably searching for prey or potential predators. Fish pursued under water. Crustaceans, polychaete worms, and bottom-dwelling fish in diet suggest birds may at times forage along bottom. Spearing mechanism for rapid extension of neck like that of herons (Ardeidae) and anhingas (Anhingidae), but structural details not worked out and action in life not recorded. Small, deep-bodied fish may be speared (Lawrence 1950), but many fish are taken by forceps-like action of mandibles. Small items often or usually swallowed under water. Large ones brought to surface and (especially stout-bodied, spiny catfish) pinched repeatedly in bill before being swallowed. Adaptive significance of sexual dimorphism in bill shape not understood.

Females fed large quantities of fish by mates during period of development of eggs (Nuechterlein and Storer 1989a). Mate feeding in winter also reported (James 1989).

DIET

Major food items. Wide variety of fishes taken (e.g., Palmer 1962) suggests that although Western Grebes are fish specialists, they are opportunists when it comes to species of fish taken. Other animals taken include a salamander (*Ambystoma*), crustaceans, polychaete worms, and insects (grasshoppers and variety of aquatic forms). Stomachs also contain many feathers, mostly from the bird's flanks and scapulars, tracts which are in almost constant molt. Feathers swallowed as they come out in the course of preening. Most feathers form ball in lumen of stomach, but some form plug at pyloric exit. Function not proven but thought to keep fish bones from injuring lining of stomach and reaching intestine or, as suggested by Piersma and Van Eerden (1989), to assist in the formation of pellets which can be ejected, eliminating indigestible material and a possible build-up of gastric parasites. Pyloric plug may reduce number of intestinal parasites, which are numerous (see Demography: mortality and disease).

Quantitative analysis. Fish reported to compose 81% (Lawrence 1950) to virtually 100% (Wetmore 1924) of diet.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLETT CASTING, AND DEFECATION

Drinks by taking beakful of water and raising head to swallow. Pellet casting not common, probably most frequently by birds feeding on invertebrates with chitinous exoskeletons. Pellets cast after bird makes several drinking movements (GLN and RWS orig. obs.). Defecates while swimming. Placing captive young in water induces defecation (Ratti 1977).

When being back-brooded, chicks defecate after parents wing-flap and dump them into water (GLN orig. obs.).

FOOD SELECTION AND STORAGE

No information.

SOUNDS

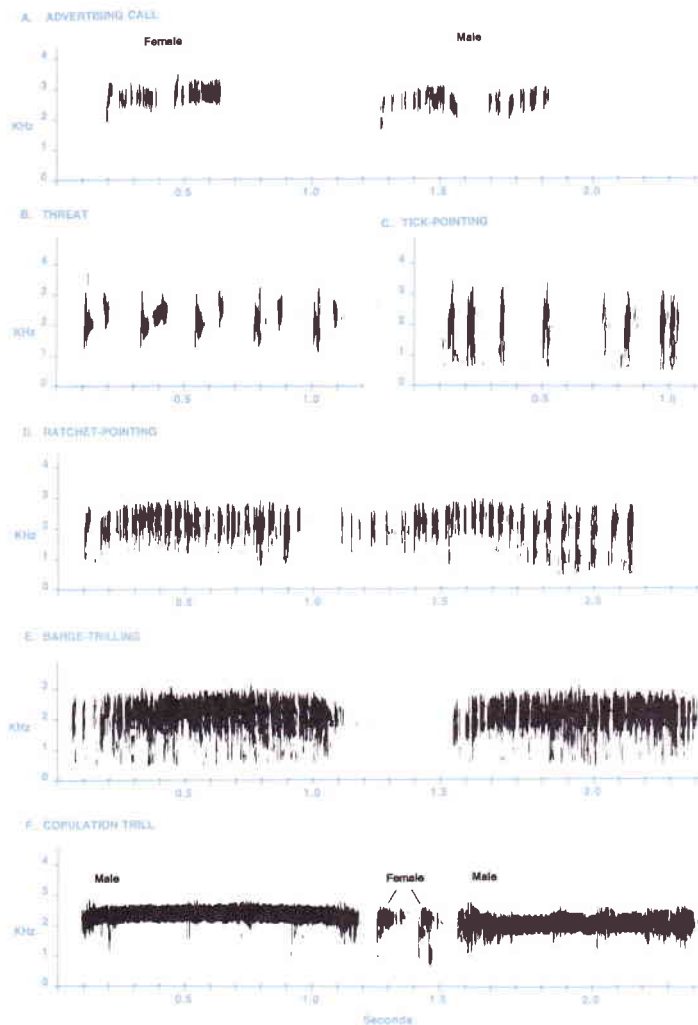
VOCALIZATIONS

Development. Young of the year not known to advertise before leaving breeding grounds.

Vocal array. Advertising call (Fig. 2A) a harsh, rolling *cree cree* individually variable and higher in pitch in females than in males. Given frequently by lone, courting birds either spontaneously or in answer to potential courting partners; also by paired birds separated from mate, by parents seeking young, and in other contexts in which one bird is temporarily separated from another. Number of calls/bout shifts from mostly 3 or more to 1 or 2 after pair bond formed. In nesting colonies, birds respond individually to mate's call (Nuechterlein 1981a). No geographic variation reported; advertising calls do not differ between birds from Manitoba and California (Nuechterlein 1981a).

Ratchet call (Fig. 2D) a loud, harsh trill given alternately with another bird while face to face in Ratchet-pointing display (Nuechterlein and Storer 1982).

Threat call (Fig. 2B) a repeated *tuk-tuk-tuk* given during nest defense, particularly during colony establishment. Also given when defending feeding areas when temporary concentrations of fish are available, such as near dams or spillways.



Begging a repeated, guttural *tuk-a* given by the female to elicit feeding by the male in mate-feeding bouts toward onset of egg-laying period. *Tuk* part of call similar to repeated *tuk* notes of Threat call (Nuechterlein and Storer 1989a).

Copulation Duet (Fig. 2F) a loud trill given by male with regular interspersed shorter call notes by female during copulation. Vocal roles reversed during reverse mounting.

Four other calls used in courtship displays; "Tick-pointing" (Fig. 2C), "Barge Trilling" (Fig. 2E), "Neck-stretch Trilling," and "Arch-clucking," discussed and figured in Nuechterlein and Storer (1982). Mutual grating call given during nest relief. Clucking food calls and ticking alarm calls given by parents to young (Nuechterlein 1988).

Phenology. Advertising calls given all year, but most frequently in breeding season, occasionally at night. Other calls associated with courtship

Figure 2. Some vocalizations of the Western Grebe. A. Advertising call, usually given in bouts of 1–6 similar notes. Males' calls are longer and lower in pitch than females'. B. Double-noted *tuk-tuk* Threat call. C. Irregularly spaced Ticking calls by several birds. D. Regularly alternated Ratchet calls by two birds. E. Regularly alternated Barge-trills by two males. F. Copulation duet.

mostly given early in the breeding season, but some fall courtship activities. Threat calls most frequently given in nesting season, but occasionally at other times of year.

Daily pattern of vocalizing. Advertising and other courtship vocalizations most common in early morning and late afternoon or early evening.

Places of vocalizing. Bird coming to colony Advertises and only mate on nest answers. Most vocalizing on water. Much threat behavior near nest. Begging by female while mate feeds her, away from colony at feeding grounds. Advertising and threat calls given on nest or water. Copulation duet given on nest platform.

NONVOCAL SOUNDS

During Rushing display, rapid foot movements make a loud, pattering noise that can be heard for several hundred yards on a calm day.

BEHAVIOR

LOCOMOTION

Terrestrial. Generally awkward on land. Foot-propelled pursuit divers with long, narrow body and feet at extreme posterior. Seldom come on land during normal course of life. When placed on ground, often move slowly forward on belly by kicking with feet, but can stand erect and have been reported to "run rapidly" after "momentarily spreading their wings as if for balance" (Nero et al. 1958).

Flight. Fast and direct with rapid wing beats, neck stretched with head slightly below level of body, feet stretched out behind. Migratory flights at night, rarely fly otherwise. Flight muscles atrophy shortly after birds arrive on breeding grounds (GLN, in Piersma 1988; RWS original data). Birds flightless until after simultaneous molt and regrowth of remiges.

Swimming and diving. On surface of water, swim with alternate strokes of feet; below surface, simultaneous foot strokes used. Occasionally, swim with one foot while other tucked under wing, especially while resting. Four types of dives described (Lawrence 1950: 3–4): "feeding dive" when surface is smooth, a "deliberate, forward and downward thrust of the head and a vigorous stroke of the feet, which propels the grebe beneath the surface in an effortless appearing dive;" a "springing dive," used especially on rough water, starts with "vigorous leap forward and downward," the fore part of the body springing clear of the water; an "alarm dive," the bird thrusting "its wings outward and virtually push[ing] the body

beneath the surface" followed by several beats of partially folded wings after submergence; and a "surface dive," a second type of escape dive in which bird dives from position with only head and neck above surface. Mean period below surface in feeding dives, 30.4 s ($n = 1,747$); mean interval between these dives, 21.3 s. One dive of 63 s reported (Lawrence 1950), but presumably birds can remain longer beneath surface. Springing dives more common while birds feed in deep water (Nuechterlein and Buitron 1989) and may be associated with deeper dives. For data on dive-pause ratios, see Ydenberg and Forbes (1988).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, etc. Preening in general like that of other water birds, with much use of large uropygial gland. Back of head often used as swab to spread oil. Comfort movements much like those described for the Anatidae (Storer 1969). Terminology follows that of McKinney (1965). Head-scratching under the wing. Stretching movements include both-wings stretch in which neck stretched forward with head pointed slightly upward and both wings spread and held over the water, at times for several seconds after head returned to normal position. Wing-and-leg stretch performed on water with one leg and wing of same side stretched backward and to the side. Jaw stretching frequent.

Shaking movements include rapid head shakes in bouts of preening or after dipping bill in water. Bob-shaking and Dip-shaking presumably ritualized developments of this. Swimming shakes, in which bird rises and shakes body beginning near the tail and ending with the head before subsiding in water. Presumably functions in arranging feathers. Common in preening bouts and often ends them. Foot shaking, a few rapid shakes of the foot used to remove water from foot before it is shipped under the wing and flank feathers. At times foot held up for several seconds before shipping.

Bathing with head held up and back while partially spread wings flapped, rapidly causing spray of water, often interspersed with dipping of body or shallow dives. This often preceded or followed by swimming shakes and/or preening. Do not sunbathe like small species of grebes (Storer et al. 1976). When not swimming actively often ship one or both feet under wing and flank feathers. This and tucking bill under neck presumably conserve heat.

Sleeping and resting. Like other grebes, with head pointed forward and bill under neck feathers. When one foot shipped, head usually kept on

same (high) side. Sleep on water, often in groups, or on nest.

Daily time budget. No information.

AGONISTIC BEHAVIOR

Physical interactions. During courtship period may attack conspecifics and others from under water, stabbing with bill. Also fight face-to-face while above water by grasping neck and jabbing with open bill. Physical contact rare in colonies.

Communicative interactions. Threats, in increasing degrees of intensity: bird may face another, crest spread forward, head held low and give Threat call (Fig. 2B), it may dash across the water after another, using wings or not, or it may dive toward another. Submissive bird may skitter across water, using wings or not, plumage compressed, head partially raised and held forward, or it may dive, especially if aggressor dives first.

SPACING

Individual distance. Roost in loose flocks on open water.

Territoriality. Territory confined to area around nest. When establishing territory, pair approaches previously established nests until owners give Threat call, then retreats to build nest platform nearby. Chase all species away from immediate vicinity of nest.

SEXUAL BEHAVIOR

Mating system and sex ratio. Monogamy. Unpaired males outnumber females in late-courting groups, suggesting a male-biased sex ratio.

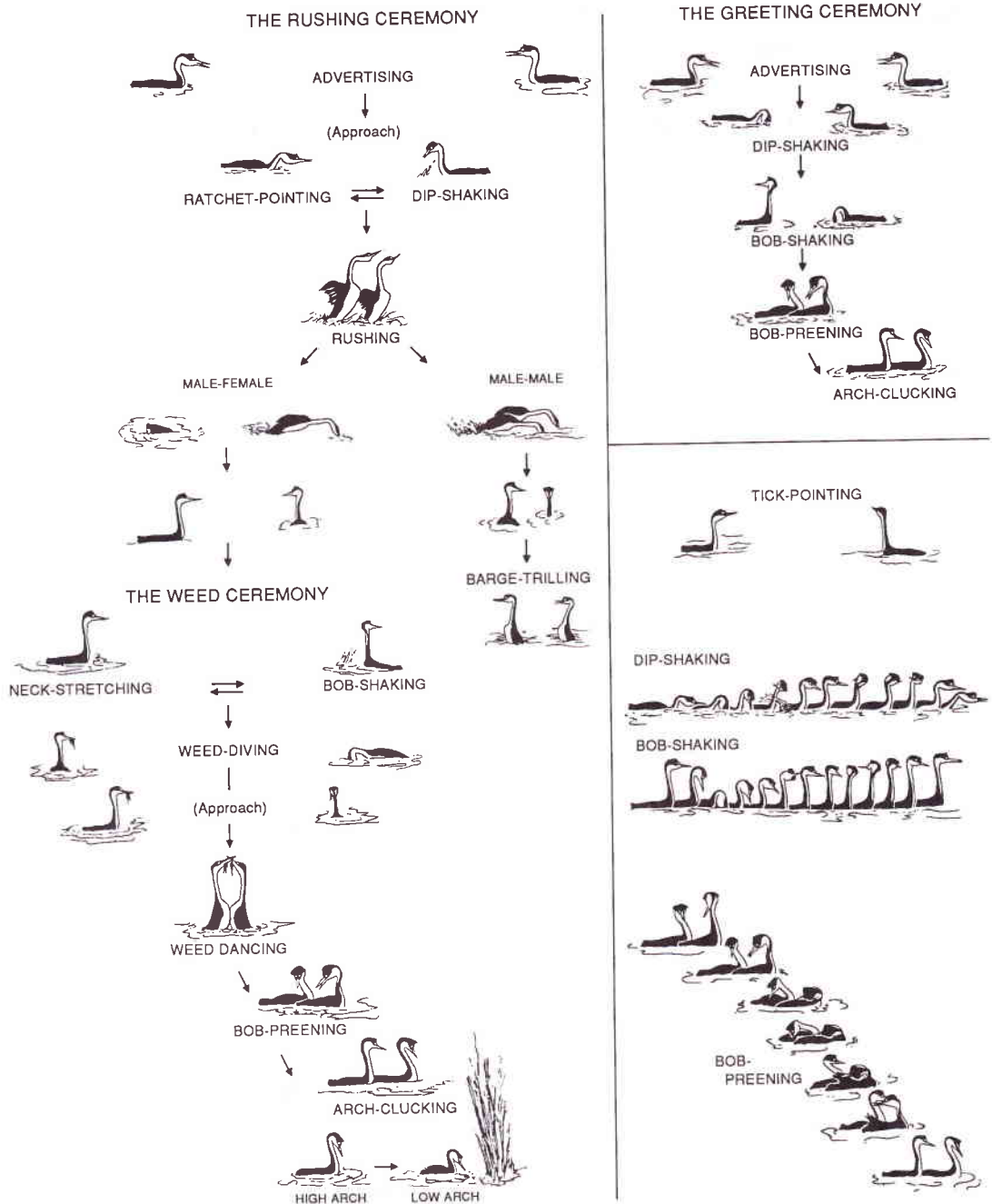
Pair bond. Maintained at least until chicks are several weeks old, at which time parents may split brood. Unknown if pairs reunite in subsequent years.

Two courtship ceremonies (Fig. 3). "Rushing Ceremony" includes Advertising, Ratchet-pointing, Dip-shaking, Rushing, and diving; "Weed Ceremony" includes Neck-stretching, Bob-shaking, Weed-diving, Weed-dancing, Bob-preening, and Arch-clucking (Nuechterlein and Storer 1982).

Advertising call (Fig. 2) given in bouts of 1-6 calls, crest raised but posture variable. Bouts longer in unpaired than in paired birds (means = 3.4 vs. 1.7 calls/bout). Ratchet pointing: harsh ratchetlike call given with head low, crest raised and held forward, throat bulging, bill pointed toward other bird; body low in water and tail cocked. Alternated with Dip-shaking in which bill and anterior part of head dipped into water, then

Figure 3.

The Rushing, Weed, and Greeting ceremonies of the Western Grebe. Displays occur in predictable order, but most sequences terminate early or omit some displays. When two males Rush together, Barge-trilling usually substituted for Weed Ceremony of pair. In rare cases, Tick-pointing is substituted for Ratchet-pointing and Dip-shaking of Rushing Ceremony.

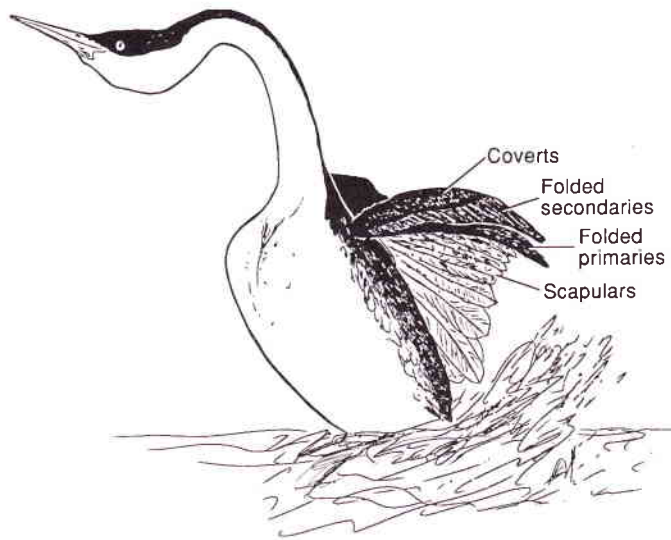


raised and waggled from side to side before head lowered again. Dip-shakes in bouts of 3 to 15, displays lasting 0.3 to 0.5 sec and spaced 1 to 5 sec apart; 2 to 3 lateral movements of the head/display. Rushing: two birds turn to one side, lunge forward body completely out of water, and run rapidly

across the surface side by side occasionally with one or more other birds. Posture unique, wings lifted, not extended, scapulars spread, but remiges folded (see Fig. 4). Unknown if wing in this position provides lift during Rushing. After Rushing 5 to 20 m, wings lowered and bird dives head first. No

Figure 4.

Posture during Rushing. By the author (GLN).



vocalization, but pattering of feet (16–20 steps/sec) audible at considerable distance. Male-male Rushing Ceremony (Fig. 3) includes Advertising, Ratchet-pointing, Dip-shaking, and Barging, in which birds move slowly forward in vertical posture with anterior two thirds of body out of water, bills turned at regular intervals toward partner and opened slightly while trills (Fig. 2E) emitted in long bouts. Appears to be used to attract females (Nuechterlein 1981d). Rarely, Tick-pointing with call (Fig. 2C) substituted for Dip-shaking/Ratchet-pointing early in Rushing Ceremony.

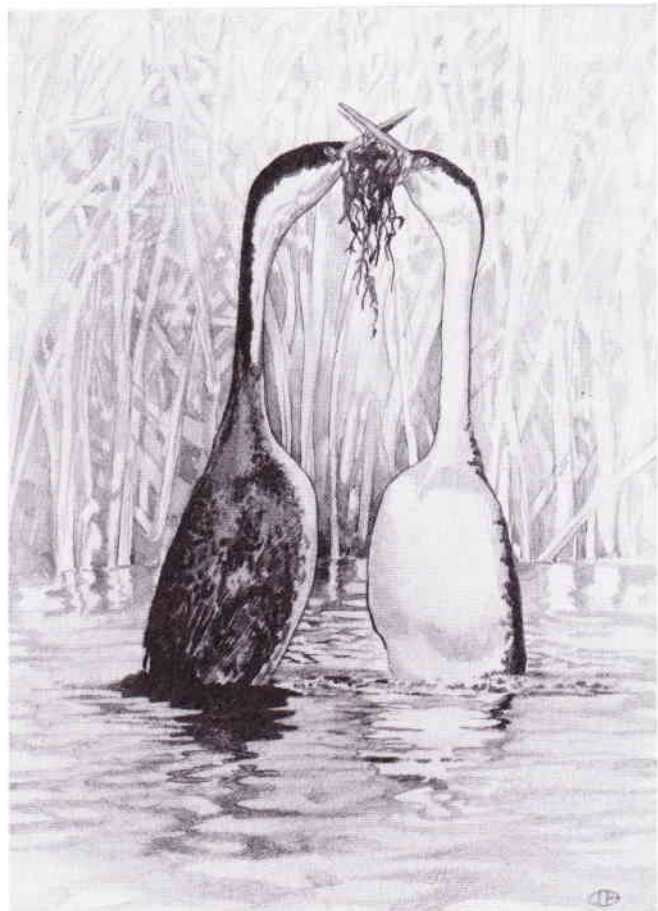
Weed Ceremony: Late in pair-formation, pairs may follow Rushing with Weed Ceremony, consisting of Neck-stretching. Birds usually face to face, 2 to 15 m apart, staring at one another in erect posture, crest raised, bill nearly horizontal, tail often cocked. As display proceeds, postural rigidity may increase until birds engage in simultaneous 3 to 8 sec trills resembling those given during copulation. **Bob-shaking:** from Neck-stretching posture, bill and forepart of head suddenly dipped vertically into water, raised, then shaken 2 to 3 times. Usually performed by two birds facing 2 to 15 m apart; displays in bouts of 1 to 6, 3 to 15 s apart, birds usually performing display alternately. **Weed-diving** follows, in which bird in neck-stretched posture suddenly dives vertically, head entering water near base of neck, bird brings organic material from below, surfacing in erect posture. When one bird dives, second usually does also. When both birds have weeds,

they approach, feet churning, and rise into vertical posture with most or all of body out of water, necks stretched upward, bills raised 20° to 80° above horizontal (Fig. 5); birds move slowly forward or spiral, heads may be rotated intermittently from side to side. Display ends when one bird discards weeds with quick head shakes and resumes horizontal body posture; other then follows suit. **Bob-preening** follows, birds swimming side by side in High Arch posture (see below), one suddenly reaches backward, runs bill through scapular feathers, and returns to original posture; display lasts 1 to 2 sec, but may be repeated 5 to 60 times. Postural intensity highly variable, display often merging with bout of normal preening.

The "Greeting Ceremony," an abbreviated form of Rushing Ceremony, given after well-formed pair has become temporarily separated. In most complete form, includes successively Advertising, Dip-shaking, Bob-shaking, Bob-preening, and Arch-clucking.

Figure 5.

Weed-dancing, part of the Weed Ceremony. By D. Otte.



Mate Guarding. Intense before and through egg-laying period. Includes long bouts of mate feeding (Nuechterlein and Storer 1989a) when female begs repeatedly while male is on surface. Begging most intense when male surfaces with fish and until he gives it to her. Begging stops when male dives.

Nest-selection displays. Male in High Arch posture leads female to potential site, then remains stationary in Low Arch before it. If site acceptable, both birds dive and bring up weeds, heaping them in a pile.

Copulatory displays, copulation, and post-copulatory displays. Female mounts nest and Invites by raising scapular feathers and holding head low, crest flattened, and giving repeated bouts of low clucking call similar to that used in High and Low Arch displays. Male mounts, and paddling alternately with feet, gives piercing copulation trill. Female also gives repeated calls (see Fig. 2F) and everts vent. Male tail-thrusts, ejaculates, and rapidly dismounts over head of female often continuing foot paddling briefly on water. Bob-shaking, Bob-preening and nest building common after copulations. Reverse mounting by female, during which roles are reversed and female gives copulation trill, frequent early in mating period (Nuechterlein and Storer 1989b).

Duration of pairbond. At least through nesting. Pair may split brood when young half-grown.

Extra-pair copulations. None recorded.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Highly gregarious at all seasons, but usually forage singly, or in pairs during period of mate-feeding just prior to egg-laying and in early brood rearing. Nesting colonies of up to several thousand birds reported but pairs may nest singly or in small groups.

Play. Not reported.

Interactions other than predation with members of other species. Males frequently engage in male-male Rushing Ceremonies with Clark's Grebes in mixed-species populations. Aggressive to other waterbirds. Probably stab other birds with bill from under water. Canvasback (*Aythya valisineria*) suddenly leaped from water and Western Grebe surfaced in its place. Mallard (*Anas platyrhynchos*) and Red-necked Grebe (*Podiceps grisegena*) found dead with stab wounds in abdomen (RWS orig. obs). Nest in colonies with Eared Grebes (*Podiceps nigricollis*), Black-crowned Night-Herons (*Nycticorax nycticorax*), Franklin's Gulls (*Larus pipixcan*) or Forster's Terns (*Sterna forsteri*). In colonies of the last, respond to terns'

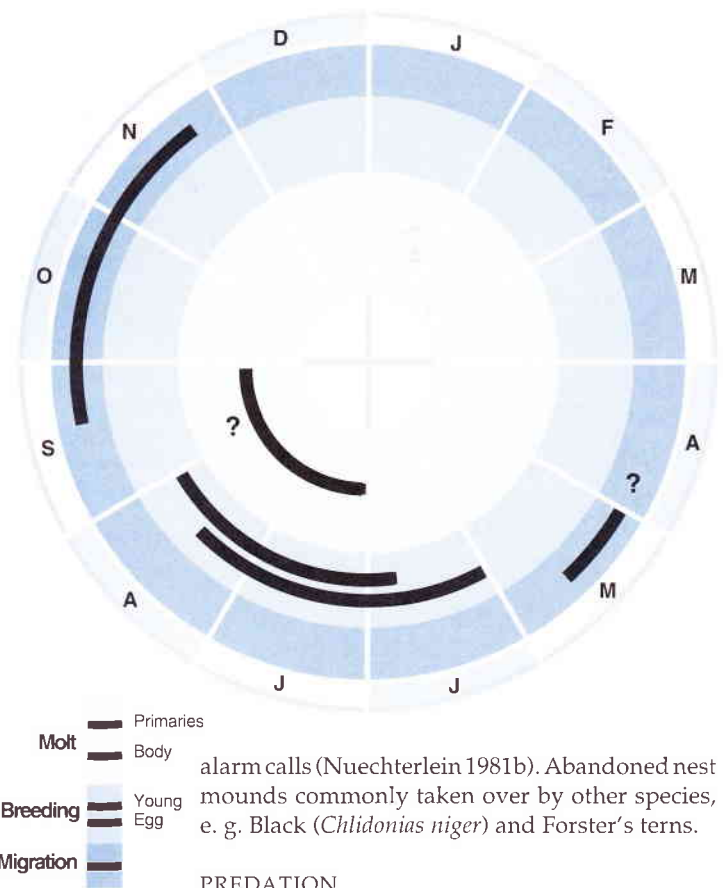


Figure 6. Annual cycle of migration, breeding, and molt of the Western Grebe, Manitoba.

alarm calls (Nuechterlein 1981b). Abandoned nest mounds commonly taken over by other species, e. g. Black (*Chlidonias niger*) and Forster's terns.

PREDATION

Kinds of predators/manner of predation. Mink (*Mustela vison*) important predators on nesting adults in some areas. Will return repeatedly to colony, taking birds off nests at night. Raccoons (*Procyon lotor*) also take adults and eggs. Remains of Western Grebes found beneath Bald Eagle (*Haliaeetus leucocephalus*) perches believed to have been of weak or emaciated individuals (Munro 1938).

Response to predators: Males and females defend nest from gulls and American Coots (*Fulica americana*) by jabbing with bill. Leave nest and often cover eggs with nest material when approached by mammalian predators, including humans. Not known to mob predators. Open bays rather than cover usually used as refuges by adults and broods.

BREEDING

PHENOLOGY

Extended nesting season (Fig. 6). Date dependent on location. At Delta, Manitoba, birds arrive about May 1, nest from late May through late Jul, depart in Oct.

Pair formation. Courtship during spring migration and shortly after arrival on breeding grounds.

Nest building. Starts after period of mate feeding, lasts 1 to 3 d.

First brood per season. Three to 6 d between laying first and last eggs of clutch. First chicks hatch in 22–24 d. Cessation of close parental care after 8 wk.

Second brood per season. Renesting common if nest lost, but usually only one brood per season.

NEST SITE

Selection. Colony localities somewhat traditional but vary widely with water conditions. Site selection highly social, with initial nests serving as epicenters from which colony grows outward.

Site characteristics. Site most often in flooded emergent vegetation. At Delta Marsh, Manitoba, bulrushes (*Scirpus* sp.) preferred to *Phragmites*, in turn preferred to cattails (*Typha*), but preference reflects water depth more than structure of vegetation; 99% of nests in water over 25 cm deep (Nuechterlein 1975). Beds of extremely thick submergent vegetation such as water milfoil (*Myriophyllum* spp.) and sago pondweed (*Potamogeton pectinatus*) also used. Occasionally nest in open, or rarely, on land. Most nests in colonies, up to hundreds or even thousands on one lake. Nests rarely < 2 m apart; 70% of 187 were 2.0 to 3.9 m apart (see Nuechterlein 1975, Lindvall and Low 1982 for details of nest placement).

NEST

Construction. Built by male and female of material brought from under water, the surface, or growths of emergent vegetation, usually near nest. Most building a mere piling up of materials, with birds alternating between bringing coarse emergent stems and algae or sodden material from the bottom which helps bind coarse material. Larger billed male brings more coarse material, female more sodden material. After nest provides sufficient support, either pair member may sit on it and arrange material while the other gathers additional material. Nest-building activity any time of day, but especially mornings. Nest sufficiently completed to hold eggs in 1 to 3 d, but added to continuously, especially in first week.

Structure and composition. A rather solid mound with shallow depression for the eggs. Built up from bottom or submerged snag or floating in up to 3 m of water and anchored to emergent or floating plants; rarely on land where built of small amounts of surrounding vegetation (Nero et al. 1958).

Table 2. Eggshell measurements (mm) and volumes (cc) of the Western Grebe (presumably including some Clark's Grebe sets) from the United States and Canada. (Data from Western Foundation of Vertebrate Zoology.)

| | Mean | s | CV | n | Min | Max |
|---------------------|-------|------|-----|-----|-------|-------|
| Diameter | 38.69 | 1.17 | 3.0 | 838 | 34.90 | 41.90 |
| Length | 58.33 | 2.31 | 4.0 | 838 | 53.30 | 65.70 |
| Volume ¹ | 45.60 | 3.47 | 7.6 | 838 | 36.16 | 56.65 |

¹Calculated by using the formula $\pi LD^2/6$.

Dimensions. Overall diameter highly variable: 67 nests at Bear River MBR (Ratti 1977) had mean of 53.8 cm (SD = 8.6); mean of 1.2 m for late nests of bulrush stalks in British Columbia (Munro 1941). Nests of coarse material have center of sodden material into which depression for eggs is made. Height above water, mean of 67 nests 9.4 (SD = 3.3) cm (Ratti 1977) to 15 cm (Palmer 1962).

Microhabitat. Wind velocity and wave action at nest sites often reduced by obstruction from emergent vegetation.

Microclimate. No information.

Maintenance or reuse of nests, alternate nests. New nests built at start of each breeding season and new materials added throughout incubation, especially during wind storms; may be used again if clutch is lost. Nests from which young have hatched frequently used by other late-nesting pairs.

Extra nests. Separate copulation platforms not built, in contrast to some non-colonial grebe species.

EGGS

Shape. Subelliptical to long elliptical, some tending toward oval. Radii of curvature of ends 12.84 ± 0.99 and 9.27 ± 0.88 ; elongation 1.53 ± 0.075 ; bicone to 0.115, asymmetry +0.143. (F. W. P[reston] in Palmer 1962.)

Size. Table 2. Means of Ratti's (1977) measurements of 174 eggs of *A. o. occidentalis* (no *clarkii* included) from Utah, length 57.6 mm (SD = 2.2), breadth 38.8 mm (SD = 1.1). Length of eggs decreases clinally from north to south in the U.S. and Canada; breadth varies more randomly. No eggs of Mexican race, *A. o. ephemeralis*, available, but presumably smaller. Mass of fresh egg not available. Assuming a specific gravity of 1 and using estimated mean volume in Table 2, average egg represents 3.8% of female's mass.

Eggshell thickness. Eggs collected 1893–1940, range 0.31–0.46 mm, mean 0.389 mm, sample size not given (Rudd and Herman 1972). 24 post-pesticide eggs from Clear Lake, CA, range 0.24–0.43, mean 0.33; 93 eggs from Bear River MBR, UT, where pesticides a less serious problem, mean of 0.38 (SD = 0.03) mm (Lindvall and Low 1980).

Color. Very pale bluish, unmarked when first laid, later white to buff, often stained brownish by sodden nest material.

Surface texture. Dull, sometimes with slight calcareous lumps.

Egg laying. Clutches often begun when nest only partially built. Eggs most often laid in mid-morning at 1–2 d intervals. Both members of pair usually at nest and defend it vigorously against intraspecific intruders of either sex. Male attends and guards female from mate-feeding period through egg-laying. Individual eggs not known to be replaced. Clutches replaced after an undetermined number of days. Additional eggs often laid in unattended or abandoned nests, and “dump” nests with more than usual number of eggs are common.

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation by male and female; begins between laying of first and second eggs.

Incubation patch. One large patch, in both female and male.

Incubation period. Mean 24 d for 14 clutches for which dates of laying and hatching of first egg known (Lindvall and Low 1982).

Parental behavior. Incubation nearly continuous, nests rarely left unguarded. If disturbed, adults may cover eggs with sodden nest material before leaving, but sun incubation unlikely. Male and female alternate in irregular, extended incubation bouts of several to many hours. Returning bird often dives and brings nest material. Mutual grating calls given, birds face to face with crests depressed and heads low.

Hardiness of eggs. Eggs abandoned in nest for more than 24 h sometimes capable of being hatched in incubator.

HATCHING

Preliminary events and vocalizations. Young peep loudly at irregular intervals, 1–2 d before pipping, and both parents may remain at nest, or may alternate at more frequent intervals. Aggressive, begging, and peeping calls given by brooded young.

Shellbreaking and emergence. Hatching rapid, accomplished in < 30 min after egg is first pipped, most frequent in late morning. Hatching asynchronous at 1 or rarely 2 d intervals.

Parental assistance and disposal of eggshells.

Young peep frequently, incubating parent intermittently stands or raises side as chick moves. Still wet, hatched chick emerges from under rear of adult and climbs beneath back feathers. As tail area is touched, parent raises folded wings slightly. Parents may push egg shells over side of nest or may grasp them and drop them in water several meters from nest.

YOUNG BIRDS

Condition at hatching. Mass: within 1 day of hatching, 21.7, 34.4, 36.0 g. Linear Measurements: wing length (wrist to tip), 11.6, 12.3 mm; tarsus length 16.2, 16.9 mm; bill length, 11.4, 11.5 mm. Amount and distribution of feathers: Head, except loreal area and patch on crown, with dense, velvety down, near blackish gray above (of Villalobos, *in* Palmer 1962), white below. A sharp line of demarcation along the sides, in some individuals continues across the lower part of the neck. Gray of crown overlaid by longer white down giving a silvery appearance from some angles. Broad eyering and lores white. Long down on trailing edge of wings pale gray. Sides of head with only a suggestion of striping like that of other grebes. (These patterns faint, almost damasklike, best seen in fluid-preserved specimens.) Color and pattern of down essentially unchanged until feathers of juvenal plumage appear. Color of bare parts: in hatchlings, bill black with white egg tooth near tip of maxilla and corresponding white spot on mandible. These retained until young reach weight of at least 156 grams, then appear to merge gradually with pale tip of bill rather than to drop off. Between ages of 40 and 80 d, bill color gradually lightens to nearly that of adult (Ratti 1977). Iris nearly black or dark gray, changing to pale gray and, not before 80 d, to adult color. Hatchlings to several weeks of age with bare straw yellow area on crown, changing to scarlet when young beg for food or become separated from parents (Nuechterlein 1985). Legs and feet, “nearly black” (Ratti) or “mostly slaty, the lobes somewhat greenish” (Palmer 1962).

Departure from nest. Leave on parent’s back at end of incubation period. Brief bouts of mutual Advertising often precede departure. Last egg sometimes abandoned, even though viable. Back-brooding pair may wander many kilometers away from nesting colony to wherever food most available, often to large open bays.

Growth and development. Mass increase: Growth curves for captive-reared young given by Ratti (1977). No differences found in growth rates of 4 Western and 3 Clark’s grebe young hatched and reared in captivity (White and Ratti 1977). Growth of body parts: early in development tarsus

grows more rapidly than wing; later the opposite holds (Fig. 7). Molt into mesoptile plumage: Primaries emerge at ca. 40 d and complete growth at ca. 70 d (Ratti 1977). Control of body temperature: newly hatched young very susceptible to cooling in water and spend only brief periods (1–5 min) off parent's back. Behavior and locomotion: young initially quite helpless in water, but by end of first wk make frequent short dives. Shortly after hatching, a hierarchy forms among brood members, with dominant chick receiving first food of feeding bout, subordinate chicks averting head (Nuechterlein 1981c). As chicks grow and parents' back space becomes too small to accommodate all, dominant chicks attain first access. Dependent on parents for 6 to 7 wk.

PARENTAL CARE

Brooding. Young climb onto parent's back within minutes of hatching. Back-brooding on nest while eggs in nest or in water until 2 to 4 wk of age. Brood does not return to nest after young are hatched. Both parents brood, male tends to carry newly-hatched young more frequently than female. At end of brooding bout parent rises up in water and flaps wings, young fall off and move to other parent. Adults may assist young in climbing back by holding one foot stiffly out on surface to rear, this used as foothold. Brooding adults may dive, but only when in imminent danger. Alarm tick call given and young held beneath compressed wings, but frequently fall off.

Feeding. Non-brooding parent brings food for young, who may be fed directly, or food may be passed to brooding parent who then feeds young. Parents feed their feathers to young from first day. Chapman (1908: 332) found 238 and 331 adult feathers in stomachs of downy young "not more than 3 days old." Young swallow food whole from first. Adults initially bring smaller prey items than they normally eat themselves, including a larger percentage of insect larvae. Parent approaches, giving clucking call. Young beg and emerge from other parent's back feathers, with bare patch on crown flushing from straw yellow to scarlet. Young fed by parents until 8 wk of age. When parent approaches with food, bare patch on young's crown becomes red (Nuechterlein 1985, 1988). One to several trips per minute with one food item brought per trip, carried in bill. Aggressive pecking between young common if more than one emerges. Dominance hierarchy governs food distribution.

Nest sanitation. Young defecate in water, the touch of which appears to stimulate this action. Adults carrying young flap wings and dump young into water at frequent intervals, this often stimulating immediate defecation, then young climb back on same or other parent.



Figure 7. Growth rates of tarsus and wing chord in a captive-hatched and reared Western Grebe chick. (GLN data).

Association with parents or other young. Newly hatched chicks totally dependent on parents, and pair remains together for at least several week, until back-brooding period is over. Thereafter, broods commonly split, with parents separating for long periods while foraging. Extent to which such pair members associate unknown, but roosting flocks of parents and their young gather nightly in central areas of large bays. By this time, young recognize parents' individual Advertising calls, which are used as long-distance food calls.

Ability to get around, feed, and care for self. As belly feathers begin growing (4 wk), young spend less time on parents' backs, but still ride occasionally when one half to two thirds grown. Young begin diving and feeding selves at several wk of age, gradually increasing independence until fledged. Flight feathers fully grown by approximately 70 d of age (Ratti 1977), by which time captive-reared birds able to make short flights (Ratti orig. obs.).

COOPERATIVE BREEDING

One known instance of third adult (male) feeding young (Forbes, 1985).

BROOD PARASITISM

Eggs of other species, e.g. "terns, ducks, and coots" (Bent 1919: 5) and Pied-billed Grebe (*Podilymbus podiceps*), Eared Grebe, American Coot, and Forster's Tern (GLN orig. obs.) occasionally found. Whether this a result of parasitism, egg dumping, or both unclear. Occasional broods with both Western and Clark's young (Ratti orig. obs.) may be result of dumping, parasitism, or hybridization. Responses of adults to foreign eggs unknown, but abnormally large clutches and eggs from other species frequently incubated. Eared

Grebes eggs hatched by Western Grebes (B. A. Eichhorst orig. obs.).

IMMATURE STAGE

Young often stay with parents until migration, associations thereafter unknown.

DEMOGRAPHY

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Birds probably can breed in first year, although instances of small groups of nonbreeding birds not uncommon. Normally one brood raised per year, but one case of adult with single, half-grown young resting beside nest while presumably new clutch being incubated (GLN orig. data). As far as known, birds breed annually.

Clutch size. Mean clutch size decreases through season (Table 3). Mean clutch size (*occidentalis* only) at Bear River MBR, 2.41 ($n = 160$), not corrected for season (Ratti 1977). Mean from museum collections (presumably including some *clarkii*) 4.06 ($n = 207$), may reflect collector bias, or may result from dump nests (Lindvall and Low 1982). Number of clutches per season normally one, but replacement clutches common.

Annual and lifetime reproductive success. Annual success variable and highly dependent on water conditions. In years of high water in Manitoba, colonies tend to be larger and farther into emergent vegetation where they are more immune to wind and wave destruction or disturbance by humans. Nesting success in Manitoba 46% to 84% ($n = 181$), ratio of young to adults in fall brood counts on breeding marsh 0.53 ($n = 267$) to 0.88 ($n = 429$). Lindvall and Low (1982) reported 21% of 221 nests in vegetation hatched at least one young—a low figure resulting at least in part from gull predation during human interference. Lifetime success unknown.

LIFE SPAN AND SURVIVORSHIP

One bird marked with nasal tag as adult sighted 14 yr later. The oldest banded Western Grebe was recovered 8 yr after being banded as an adult and hence was at least 9 yr old. Three others banded as adults were recovered at minimum ages of between 6.5 and 7 yr (Eichhorst 1992).

MORTALITY AND DISEASE

Causes of death. Weather. Major cause of nest and egg losses in this and other grebes is wave action during wind storms. Such washouts most extensive in low-water years, when thick emergent areas too shallow and inaccessible to grebes. May

Table 3. Seasonal changes in clutch size of Western Grebes at Delta Marsh. Clutches considered complete if nest held same number of eggs for > 48 h (GLN original data).

| Clutch | MAY | | JUNE | | JULY | |
|--------|--------|---------|--------|---------|--------|---------|
| | Number | Percent | Number | Percent | Number | Percent |
| 1 | 0 | 0 | 1 | 1 | 3 | 7 |
| 2 | 4 | 3 | 17 | 21 | 32 | 71 |
| 3 | 47 | 39 | 39 | 49 | 10 | 22 |
| 4 | 56 | 46 | 18 | 23 | 0 | 0 |
| 5 | 12 | 10 | 5 | 6 | 0 | 0 |
| 6 | 3 | 2 | 0 | 0 | 0 | 0 |
| Mean | 3.70 | | 3.11 | | 2.16 | |

include entire colonies and hundreds of nests. Large numbers of migrants have been frozen into a lake during a quick freeze-up (Nero 1960). Exposure. Adults awkward on land or nests, and newly hatched chicks frequently found dead and trampled in active, sodden nests, presumably due to exposure. Hundreds of young washed up on shores of Lake Manitoba after violent windstorms. Predation. Large gulls (*Larus* spp.) important predators on eggs and chicks if colonies disturbed by humans. Chicks vulnerable to predation by bass (*Micropterus* spp.) and pike (*Esox* spp.).

Human/research impacts. Small chicks frequently become separated from parents and die from exposure if adults crash-dive to avoid motor boats or other sources of sudden disturbance. If colony approached suddenly, fewer nests are covered before parents depart, which may cause overheating of eggs on hot, sunny days. Parents more likely to abandon late eggs of clutch if colony disturbed during period of asynchronous hatching. If large gulls present, predation on chicks and eggs likely during colony checks. Eggs are taken by crows (*Corvus* spp.), Common Ravens (*Corvus corax*), and gulls, or pecked and eaten by coots and Forster's Terns, usually after human interference.

Diseases and body parasites. No information on diseases of young. Adults support a variety of parasites, including the following (asterisks indicate grebe specialists): External: 2 mallophagans, *Aquanirmus occidentalis** (Edwards 1965) and *Pseudomenopon par* (Malcomson 1960). Mites on feathers and in nostrils unreported in this genus, but probably occur. Internal: Intestines of Western Grebes taken in Alberta yielded 3 trematodes, *Tylodelphys podicipina**, *Apatemon gracilis*, and *Petasiger nitidus**; 10 cestodes, *Schistocephalus solidus*, *Ligula intestinalis*, *Tetrabothrius immerinus*, *Tatria biremis**, *T. decacantha**

*Dubininolepis furcifera**, *D. podicipina**, *Wardium paraporale**, *Pararetinometra lateralacantha**, and *Diorchis** sp.; 1 acanthocephalan, *Polymorphus marilis*; and 2 nematodes, *Capillaria obsignata* and *Contraecaecum ovale* (Stock 1985). A nematode, *Ascaris* sp. taken from stomachs of Western Grebes from California (Lawrence 1950).

POPULATIONS

RANGE

Natal philopatry. Some birds marked with nasal tags returned to natal marshes but relative frequency unknown. Colony sites within marsh often vary widely between years and are highly dependent on water levels and emergent growth patterns.

Dispersal from breeding site or colony. Banded breeding birds from s. Lake Manitoba caught in gill nets on Lake Winnipegosis, n. Manitoba, suggesting post-breeding molt migration.

Home range. Adults and young rarely fly except during migration, and home range on breeding grounds largely determined by size of body of water on which breeding occurs. During incubation, adults may forage several kilometers from colony if water connections available. Adults within a marsh colony connected to Lake Manitoba made daily foraging trips out into open water. After hatching complete, pairs carried young out to lake, eventually spreading out over 50 km or more of shoreline.

POPULATION STATUS

Population numbers. No thorough survey available. Largest number of *Aechmophorus* reported on Audubon Christmas counts in last 12 yr, nearly 118,000 birds (including ca. 775 Clark's Grebes and 38,500 unidentified to species). This includes no counts of birds wintering or resident in Mexico (Anon. 1989). Total North American population presumably higher. A partial count of the resident birds of the Mexican Plateau was 740 to 840 (Williams 1982). This population may be declining.

POPULATION REGULATION

No information.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

From the early 1890s until approximately 1906, tens of thousands were shot for their "fur," the

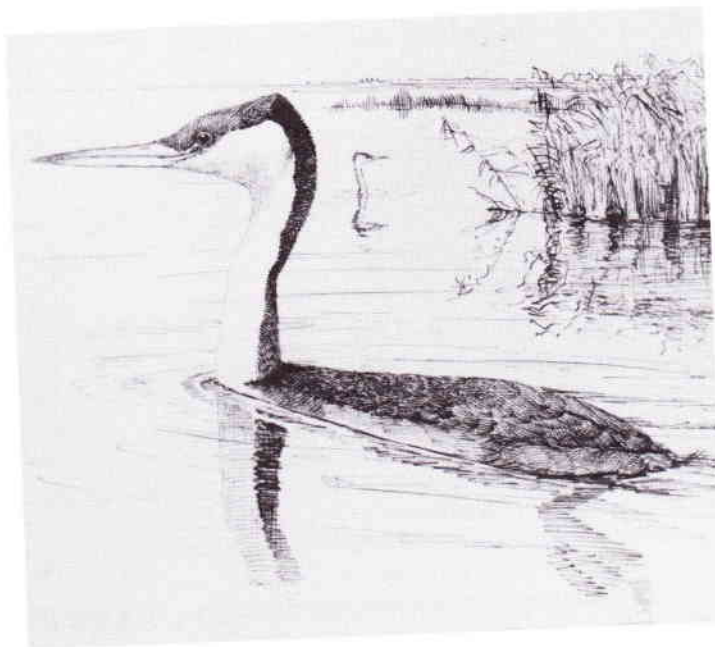


Figure 8.

Western Grebe in typical marsh habitat. Drawing by L. A. Fuertes; US Fish and Wildlife Service art collection, archives of the Academy of Natural Sciences (Stewart Library), Philadelphia.

silky, white, ventral plumage which was used to make capes, coats, and hats. Large colonies such as that at Lower Klamath Lake, OR, were virtually wiped out by market hunters (Finley 1907, Chapman 1908). Pesticides have drastically reduced some populations, notably at Clear Lake, CA (Herman et al. 1969) and drainage of lakes for agriculture has reduced nesting habitat (Cogswell 1977). Currently oil spills, and gill nets are major causes of mortality. Loss of waterproofing reported for birds landing on sewage lagoons (Nero 1968). Birds have been accidentally caught on fishing lures and have become entangled in discarded fishing line and rubber and plastic rings. When approached by humans all members of colony leave and nest contents become vulnerable to gulls and other predators. Repeated disturbances by curious boaters, especially in early stages of colony formation, lead to high incidence of nest abandonment. Areas with easy and frequent access, particularly to motorboat activities, unlikely to provide suitable nesting areas. In Mexico, cutting of tules has made large parts of lake areas shoreline unavailable for nesting (Williams 1982).

MANAGEMENT

As aquatic fish-eating specialists, with nests built over water (and because these birds almost never fly), except on migration, breeding waters must contain sufficient fish to sustain local populations. Winter kill of fish in shallow marshes often a problem. Colonies often conspicuous, may serve as prime attractants for human activity. Colony locations within large marsh of lake system only semi-traditional and may change from one

year to the next, particularly if water conditions change. Therefore, only population declines within entire marsh system, not colony site abandonment, cause for concern.

Management schemes should include water-control structures that allow manipulation of emergent growth patterns. Ideal nesting areas provide thick, but water-interspersed, clumps of emergents that block wave action. Large bulrush "islands" having inner open water areas and channels provide good colony sites, allowing accessibility to swimming or diving grebes during nest-site selection, yet protection from wave action. Such sites less conspicuous to boaters. Water depths within emergents at colonies 40 cm or greater for overwater nests. Fluctuating water levels important for maintaining these conditions, but water supply reservoirs with rapidly declining water levels during nesting season unsuitable.

Western Grebes feed and raise broods away from colony sites in open bays. Such bays need not be adjacent to colony, but must be connected by water to nesting areas with no dams, culverts, carp screens, or other obstructions blocking way.

Rearing Western Grebes in captivity very difficult; methods described by Ratti (1977). Loss of feather waterproofing a common problem, somewhat alleviated by replacing of water surface in pens by having an overflow spout and continuously flowing water. Feeding live fish highly desirable because it prevents fouling of water surface with fish oils. If dead fish are fed, they must be injected with liquid multivitamin supplements (Ratti pers. comm.).

APPEARANCE

MOLTS AND PLUMAGES

Sexes alike.

Juvenal plumage. Crown, back of neck, back, scapulars, upper wing coverts, and inner secondaries black. Feathers of lower neck, mantle, and scapular coverts edged with gray. Flanks vary individually from solid grayish black to white mottled with elongated blackish spots. Back feathers lax, without light edging. Primaries and all but inner secondaries sooty with varying amounts of white forming irregular wing patch extending from secondaries onto all or all but outer 1 or 2 primaries. Under wing coverts white to pale gray, lesser coverts white or edged with varying amounts of sooty. Distal half of greater under primary coverts grayish. Crown feathers somewhat elongated. These, scapular coverts, and lesser upper wing coverts often have white bases or centers. Sides of face to below eye sooty,

occasionally with black spots. Lores usually black, but occasionally white or pale gray. Underparts silky white. Prebasic I molt. Extent unknown, but at least juvenal flank feathers and scapulars replaced by harder adult feathers. (Because molt in these tracts occurs throughout the year, it may not be accurate to refer to this as a molt leading to a specific plumage.)

Basic I plumage. At least remiges retained from Juvenal plumage, scapulars and flank feathers replaced by adult type. Prealternate I molt. Evidently a partial molt including at least feathers of head and neck. Extent unknown.

Alternate I plumage. Similar to Basic I plumage, but crest longer and facial pattern more sharply defined (i.e., lores may become black and black spotting below eye lost). A molt of remiges at this time has been suggested (Storer and Nuechterlein 1985). Definitive Prebasic molt. Complete molt of body feathers accompanied by simultaneous molt of remiges in late summer. Not known if molt of birds in their second summer differs from that of older birds.

Definitive Basic plumage. As far as known, like Basic I plumage, although facial pattern may be like that of Alternate I. Definitive Prealternate molt. As far as known, similar to prealternate I molt.

Definitive Alternate plumage. As far as known, similar to Alternate I plumage. Extended molt of birds on Clear Lake, CA, reported by Storer and Nuechterlein (1985) probably a result of prolonged breeding season there. Molt schedule of birds nesting in northern parts of range probably more contracted. Molt schedule of birds aged by cloacal bursa size needed for definitive study of molts and plumages in this species. Adult similar to juvenal plumage, but crest feathers longer and lores black (Storer and Nuechterlein 1985).

BARE PARTS

Bill. Dull greenish yellow, blackish along culmen and lower part of rami of mandible.

Iris. Intense scarlet with narrow yellow ring around pupil.

Feet. Lower surface of tarsi and toes black, upper surface varies from olive green in juveniles and yearlings to yellow green or yellow orange in older birds.

MEASUREMENTS

Birds of Mexican Plateau (*ephemeralis*) significantly smaller in all measurements than those from the U.S. and Canada (n nominate *occidentalis*), Table 1.