SHORT COMMUNICATIONS

Diving Differences between Western and Clark's Grebes

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In the sixth edition of the A.O.U. check-list (1985), Clark's Grebe (*Aechmophorus clarkii*) was designated a separate species from the Western Grebe (*A. occidentalis*). Once considered a light color phase of the Western Grebe, Clark's Grebe is generally more prevalent in breeding populations south of 44°N (Storer 1965, Feerer 1977). There is considerable local variation in the relative abundance of the two species, and they are sympatric throughout much of their range. In areas where both are common, they frequently form mixed feeding flocks, but their Advertising vocalizations are distinct, and interbreeding is rare (Ratti 1979, Nuechterlein 1981).

Western and Clark's grebes are foot-propelled, fish-eating surface divers. Fish typically are captured singly in the bill and may be swallowed either under the water or on the surface. Nuechterlein (1981) and Ratti (1985) showed that Clark's Grebes tended to feed farther from shore than Western Grebes at Upper Klamath Lake, Klamath County, Oregon. Nuechterlein (1981) found also that Clark's Grebes were more likely than Western Grebes to engage in *"springing dives"* (Lawrence 1950), in which the diving bird initially pulls its head back, then springs upward with the legs and leaps out of the water before submerging (see diagram, Fig. 1). Although no data on water depths were available in the preliminary study, Nuechterlein (1981) speculated that birds engaging in springing dives may attempt to dive more vertically and this form of dive was related to the depth an individual bird reached. This would result in ecological segregation between the two species.

The major purpose of our study was to document a possible relationship between the level and springing dives and the depth of water at which they occur in these two grebe species. We then examined whether these two variables were related to either the species or the sex of the bird or both.

Although artificial impoundments on many National Wildlife Refuges support large breeding populations of both species, such areas tend to be very shallow and have irregular depth contours, which may obscure relationships that normally occur between depth and distance from shore (Ratti 1985). The two study areas at Upper Klamath Lake provided a large population of each species that feed within a natural lake basin with water depths that vary from at least 0–8 m.

Prior to the observations, we located mixed feeding flocks of the two species during census counts. With binoculars and a 15–60× spotting scope, we classified birds to species from bill color (bright orange-yellow in Clark's Grebe and dull light-green in Western Grebes; Storer 1965, Storer and Nuechterlein 1985). We then compared the relative frequency of the two species along the east shoreline (Hank's Marsh) and west shoreline (Eagle Ridge Marsh) of Upper Klamath Lake. Each marsh supported a large, mixed-species nesting colony. Hybrid or intermediate birds were excluded from our sample.

We observed the diving behavior of Western and Clark's grebes on the east shore of Upper Klamath Lake, and at Lake Ewauna, a broadened section of the Klamath River, which flows into Upper Klamath Lake on the southeast end of the lake. To obtain information on diving behavior, we determined depths at both locations by plumb lines, and then placed styrofoam buoys in lines perpendicular to the shore to mark depth contours at 1-m depth intervals. This allowed us to record the water depth at which each observed dive occurred to the nearest meter.

We controlled for wave action by including only observations made under low-wave conditions. Dive types form a continuum, but were classified into three behavioral categories (see diagrams, Fig. 1): *springing dive* (entire body of the bird emerges from water prior to diving, breast and tarsus clearly visible), *intermediate dive* (breast of the diving bird emerges from the water, but not the entire tarsus), and *level dive* (neither breast nor tarsus emerges from the water).

In addition to water depth and dive type, we recorded dive times and the species and sex of birds that dived within the prescribed area. We distinguished sex visually by bill size, which in males of both species is longer and deeper (Storer and Nuechterlein 1985). Birds which could not be reliably sexed by this method were excluded. To avoid possible biases associated with repeated sampling of the same individual during extended dive bouts, observations were extended over several weeks, and we included only data from a maximum of 2 dives per individual observed on each occasion. We used one-way ANOVA tests and Newman-Keuls multiple-range tests to analyze dive times, and we used *G*-tests to compare the relative frequencies of different dive types.

A census conducted on Upper Klamath on 1 May 1984 showed highly significant differences in the distribution of feeding flocks of Western and Clark's grebes on Upper Klamath Lake. On the west shoreline of Upper Klamath Lake, Clark's Grebes were rare (7 of 103 birds), while on the east shoreline they comprised nearly 50% of the birds (152 of 305 birds, $G = 71.6$, $df = 1$, $P < 0.001$).

At both Upper Klamath and Lake Ewauna, Western

and Clark's grebes engaged in all three types of dives, but at both locations Clark's Grebes were significantly more likely to engage in springing dives (Fig. 1, G = 71.1, df = 2, $P < 0.001$ for Lake Ewauna; G = 53.1, df = 2, $P < 0.001$ for Upper Klamath Lake). At Lake Ewauna, 49% of the dives by Clark's Grebes (n = 79) were springing dives compared with only 7% for Western Grebes (n = 113); at Upper Klamath Lake the respective percentages were 47% (n = 78) and 6% (n = 175).

In both species there was a significant shift toward relatively more frequent level dives at the Upper Klamath Lake study area, which was shallower than Lake Ewauna (compare Fig. 1A vs. Fig. 1B; G = 7.7, df = 2, $P < 0.05$ for Western Grebes; G = 24.4, df = 2, $P < 0.001$ for Clark's Grebes).

Dive-type frequency was related significantly to water depth for both species at both locations (Fig. 2, significance levels in legend). In both species, springing dives were more frequent at greater water depths than level dives at that site. Clark's Grebes dived at the deepest water-depth zone available at a site, and were significantly more likely to use springing dives than were Western Grebes. (For Lake Ewauna at 6–7.9 m, Clark's Grebes used 62% springing dives vs. 6% for Western Grebes, G = 36.2, df = 2, $P < 0.001$; for Upper Klamath at 4–5.9 m, Clark's Grebes used 61% springing dives vs. 15% for Western Grebes, G = 35.4, df = 2, $P < 0.001$.)

At Lake Ewauna, neither species dived at depths of <2 m. Western Grebes most frequently fed at water depths of 4–5.9 m (50.4% of 113 dives; Fig. 2A), and they usually used level or intermediate dives. Clark's Grebes at Lake Ewauna were significantly more likely than Western Grebes to dive in deeper water (Fig. 2B; G-test on frequency totals for the water depths: G = 13.7, df = 2, $P < 0.01$).

At Upper Klamath Lake, water depths >6 m were not present, and Clark's Grebes were not significantly more likely to dive in deeper water than were Western Grebes (Fig. 2A; G-test on frequency totals for water depths, G = 5.6, $P > 0.05$). At depths <2 m, level dives predominated in both species and springing dives were absent entirely (Fig. 2, n = 13).

At both sites, the mean dive times for springing dives by Clark's Grebes were significantly longer than for level dives (Fig. 3). This relationship also held for Western Grebes at Upper Klamath, although sample sizes for timed springing dives were small (n = 9). At Lake Ewauna sample sizes for springing dives by Western Grebes were even smaller (n = 5), and differences were not significant.

Significant sex differences in dive type were found only in Clark's Grebes. Female Clark's Grebes used springing dives significantly more often than males (59% of 59 female dives vs. 42% of 98 male dives; Table 1). This was true despite the fact that water-depth distributions of dives by males vs. females were not significantly different for either species (G = 1.7, df = 3, $P > 0.05$, for Western Grebes; G = 5.3, df = 3, $P > 0.05$, for Clark's Grebes). Although female Western Grebes also used relatively more intermediate and springing dives than males, springing dives were rarely used by either sex in this species (7% of female dives, 5% of male dives), and overall sex differences were not significant (Table 1).

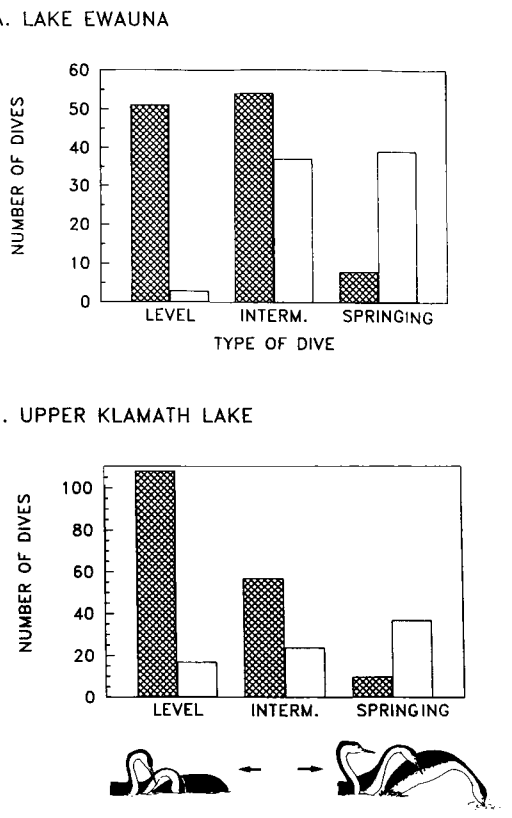

Fig. 1. Types of feeding dives of Western Grebes (hatched bars) and Clark's Grebes (open bars) at Lake Ewauna (A) and Upper Klamath Lake (B), Oregon. Springing dives (right illustration) differed from level dives (left) in the extent to which the body emerged from the water before submerging.

The most fundamental influence on dive type in our study was water depth. Our data are consistent with the hypothesis that birds that engage in springing dives attempt to dive deeper in the water column. Because shallow water makes it physically impossible for a bird to dive deeply, our observations over shallow water provide the most direct test of this hypothesis. Springing dives seldom were used by either species at depths <4 m (7% of 204 dives, species combined, Fig. 2) and were never seen at depths <2 m (n = 13). Springing dives also were almost never observed during 7 yr of studying the breeding ecology of Western Grebes on two shallow (2-m depth max-

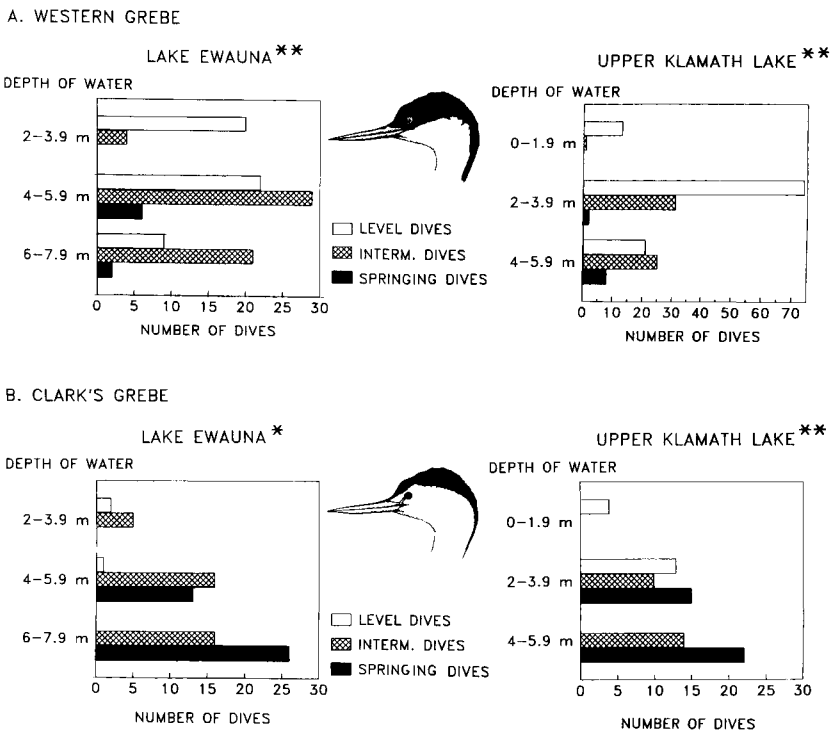

Fig. 2. Relationship between dive type and water depth in (A) Western Grebes and (B) Clark's Grebes at Lake Ewauna and Upper Klamath Lake. Levels of significance: ** = $P < 0.01$, *** = $P < 0.001$; for separate *G*-tests run at each location.

imum) wind-tide marshes in Manitoba (Nuechterlein unpubl. obs.).

Dives made in deep water are more difficult to interpret, because birds that feed on free-swimming fish may make either shallow or deep dives. Ratti (1985) did not report behavioral observations of dive types and thus did not address the possible relationship between dive type and depth. Birds that dive in deep water may feed at radically different depths, even with no spatial segregation on the surface. Feerer (1977) found that Clark's Grebe females' stomachs "contained significantly smaller fish ($P < 0.05$)" than those of Western Grebe females, but he found no significant differences between males of the two groups.

In ducks, loons, and grebes a positive relationship may exist between water depth and dive times (Dewar 1924, Dow 1964, Brodsky and Weatherhead 1985). This has been interpreted to mean that deeper dives may require greater submergence times. If true, the longer submergence times for springing dives in grebes (Fig. 3) provides independent evidence that birds may attempt to reach greater depths. By first thrusting its body out of the water and then diving vertically, a

TABLE 1. Sex differences in dive type (number and relative frequency) for males and females of Western and Clark's grebes. Relative frequency is in parentheses.

	Western Grebe[a]		Clark's Grebe[b]	
Dive type	Males	Females	Males	Females
Level	98 (0.60)	61 (0.50)	20 (0.20)	0 (0.00)
Intermediate	57 (0.35)	54 (0.43)	37 (0.38)	24 (0.41)
Springing	9 (0.05)	9 (0.07)	41 (0.42)	35 (0.59)
Total	164	124	98	59

[a] $G = 3.0$, df = 2, $P > 0.05$.
[b] $G = 23.3$, df = 2, $P < 0.001$.

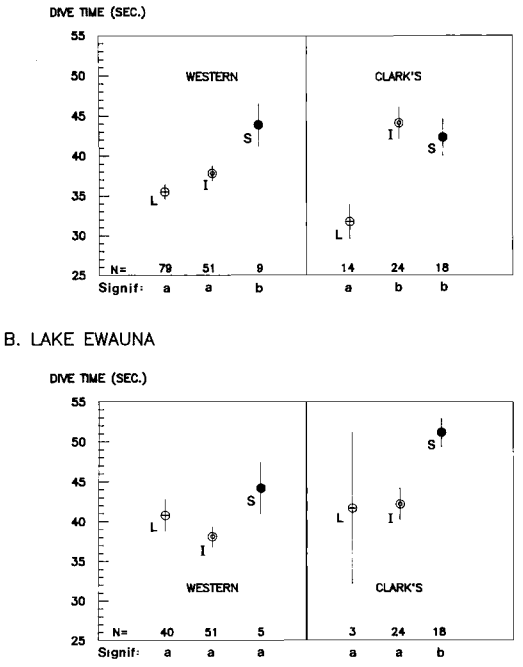

Fig. 3. Dive times ($\bar{x} \pm$ SE) for level (L), intermediate (I), and springing (S) dives of Western and Clark's grebes at (A) Upper Klamath Lake and (B) Lake Ewauna. Sample sizes are below each dive type. Significant differences among dive types are denoted by different lower case letters (Newman-Keuls multiple range test).

surface-diving bird is able to use the momentum of its body mass in air to provide a greater initial downward thrust to the dive, somewhat analogous to plunge-diving in other species.

Dive times for females were not significantly different than those of males in either species, and the biological significance of sex differences in the dive types of Clark's Grebes is unclear. However, female body weights may be 15–20% smaller than males in both species (Nuechterlein *in* Piersma 1988 and unpubl. data), which implies that female Clark's Grebes require a higher leap from the water to acquire a body momentum equal to that of males that dive to similar depths. Comparative observations are needed to test these hypotheses more directly.

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