

A Test of Water Depth Niche Partitioning by Western Grebe Color Morphs

JOHN T. RATTI

Wildlife Biology, Washington State University, Pullman, Washington 99164-4220 USA

Dark- and light-phase Western Grebes (*Aechmophorus occidentalis*) have been described by Storer (1965) and Ratti (1981). Ratti (1979) and Nuechterlein (1981) reported on reproductive separation and isolating mechanisms between the color morphs. Data from Ratti (1979) indicate that "dark- and light-phase birds represent reproductively independent populations" and that the morphs are separate species. Ratti (1979) stated that "morphologically and ecologically, dark- and light-phase Western Grebes are practically indistinguishable" and may represent "one of the best avian examples of an exception to the competitive exclusion principle" (Grinnell 1904). However, Nuechterlein (1981) reported that light-phase birds tend to feed farther from shore than dark-phase birds. He also noted a preponderance of "level dives" by dark-phase birds and a preponderance of "springing dives" by light-phase birds. The light-phase diving posture is more perpendicular to the water surface and may facilitate diving to greater depths. These findings led to Nuechterlein's (1981) hypothesis that "the two color phases may be segregating behaviorally into two subtly different ecological forms specialized for feeding at different depths." The objective of this research was to test Nuechterlein's (1981) hypotheses.

Data were gathered at Goose Lake, Lower Klamath National Wildlife Refuge (NWR), and Tule Lake NWR, California; Upper Klamath Lake, Oregon; and Bear River NWR, Utah. Goose and Upper Klamath lakes are natural water basins; Lower Klamath, Tule Lake, and Bear River NWRs are artificial water impoundments. All surveys were initiated at sunrise,

when most birds were actively feeding, and usually terminated by midmorning. Survey routes were determined from previous field work (Ratti 1979). One survey was conducted at each study area and, thus, all data are statistically independent. Birds were classified as dark-phase or light-phase (Ratti 1981); rare intermediates were not recorded. Each bird observed was recorded into 1 of 3 categories, based on an ocular estimation of distance from shore; A = <25 m, B = 25-75 m, and C = >75 m. The location, number of birds, and color phase also were recorded on a map of the survey route. After completion of bird surveys, I returned to bird observation sites and conducted a minimum of 3 water-depth transects. Transect lines were 100 m apart, parallel, and generally perpendicular to the shoreline of the observation site. I traversed the transect lines from a canoe, and recorded water depth from ocular estimated distances of 15, 50, and 100 m from shore to correspond with the distance categories of bird observations. Throughout the study, distances were measured periodically from shore to verify my ocular estimations. Data from bird observations were tested using Chi-square analysis and mean depths were compared by *t*-test.

Between 15 June and 20 July 1981, I observed 1,132 dark-phase and 596 light-phase Western Grebes and measured water depth from 106 transects. Variation in the number of water-depth transects measured at each location was a function of the distribution of birds along the survey route.

Distance from shore.—Observations of the color morphs in categories of distance from shore were not random (Table 1). There was a clear tendency for

TABLE 1. Observations of dark- and light-phase Western Grebes in categories of distance from shore (A = <25 m, B = 25-75 m, C = >75 m) in 1981, and Chi-square test of pooled data.

Location	Color morph	A	B	C	χ^2_{a}
		n (%)	n (%)	n (%)	
Goose Lake	Dark	4 (8.7)	4 (8.7)	38 (82.6)	16.5**
	Light	1 (0.4)	41 (16.1)	213 (83.5)	
Bear River NWR	Dark	97 (38.0)	37 (14.5)	121 (47.5)	6.6*
	Light	22 (25.9)	9 (10.6)	54 (63.5)	
Tule Lake NWR	Dark	56 (14.0)	65 (16.3)	278 (69.7)	3.79
	Light	5 (8.2)	6 (9.8)	50 (82.0)	
Lower Klamath NWR	Dark	54 (34.0)	75 (47.2)	30 (18.9)	17.46**
	Light	11 (39.3)	3 (10.7)	14 (50.0)	
Upper Klamath Lake	Dark	67 (24.5)	146 (53.5)	60 (22.0)	13.25**
	Light	17 (10.2)	101 (60.5)	49 (29.3)	
All areas	Dark	23.8%	28.0%	48.1%	
	Light	16.8%	21.5%	61.7%	

* $P < 0.05$, ** $P < 0.01$.

TABLE 2. Mean water depth (cm) for categories of distance from shore (A = <25 m, B = 25–75 m, C = >75 m) measured at Western Grebe observation sites, 1981. Data from distance categories joined by a solid line were not different ($P > 0.05$); all other categories were significantly different ($P < 0.05$).

Location	Distance category			No. water-depth transects measured
	A	B	C	
Goose Lake ^a	13 (3.6)	32 (11.4)	82 (6.4)	11
Bear River NWR ^b	120 (110)	66 (31.2)	54 (38.8)	28
Tule Lake NWR ^b	102 (44.1)	111 (36.8)	117 (28.3)	20
Lower Klamath NWR ^b	113 (51.7)	65 (11.4)	69 (13.6)	38
Upper Klamath Lake ^a	205 (58.9)	364 (65.4)	290 (83.4)	9

^a Natural water basin.

^b Artificial water impoundment.

light-phase birds to occur farther from shore, with 62% of light-phase observations in category C vs. 48% for dark-phase. These data are consistent with, and provide a new aspect to previous reports of, "spatial segregation" between the color morphs (Ratti 1979). However, the data were not consistent among all study areas. At 3 of the 5 areas (Bear River, Lower Klamath, and Upper Klamath) the data revealed significantly greater use of category C by light morphs. At Tule Lake, use of each distance category showed no difference between color morphs. At Goose Lake, sample sizes were inadequate in categories A and B, and use of category C was nearly equal.

Water depth.—Water depths were not always directly related to distance from shore, especially at artificial water impoundment areas such as Bear River NWR (Table 2). Construction of dike roads often

created a "borrow ditch" parallel to roads, from dredging of fill material. The deepest water zone at several areas was immediately parallel to dike roads. Thus, distance categories were assigned to low-, medium-, and high-water categories according to mean depth (Table 3). Examination of Tables 1 and 3 allows comparison of some water-depth categories with distance categories (e.g. Goose Lake "C" = high-depth zone; Upper Klamath "C" = medium-depth zone). Some depth categories were not significantly different (Table 2) and were pooled for analysis (Table 3).

Chi-square tests were used to test for random use of water-depth categories by Western Grebe color morphs (Table 3). Only data from Upper Klamath Lake revealed greater use of high-water zones by light-morph Western Grebes. Although Goose Lake data were significant, most of the χ^2 value was gen-

TABLE 3. Chi-square analysis of water depth use by dark- and light-phase Western Grebes. Low, medium, and high water-depth categories were tested where mean depths were significantly different ($P < 0.05$).

Location	Color morph	Number observed (%) by water depth			χ^2
		Low	Medium	High	
Goose Lake ^b	Dark	4 (8.7)	4 (8.7)	38 (82.6)	16.7*
	Light	1 (0.4)	41 (16.1)	213 (83.5)	
Upper Klamath Lake ^b	Dark	67 (24.5)	60 (22.0)	146 (53.5)	14.4*
	Light	17 (10.2)	49 (29.3)	101 (60.5)	
	Dark	16.6%	15.4%	68.0%	
	Light	5.3%	22.7%	72.0%	
Lower Klamath NWR ^{c,d}	Dark	105 (66.0)	17 (60.7)	54 (34.0)	0.38
	light	11 (39.3)			
Bear River NWR ^{c,d}	Dark	158 (62.0)		97 (38.0)	4.2
	Light	63 (74.1)		22 (25.9)	
	Dark	64.0%		36.0%	
	Light	67.4%		32.6%	

* $P < 0.01$.

^b Natural water basin.

^c Artificial water impoundment.

^d No difference between low and medium depth zones; low and medium were pooled for χ^2 test.

erated from cells with inadequate sample sizes. No test was conducted on the Tule Lake NWR data because *t*-tests indicated the mean water-depth categories were not different. Bear River NWR and Lower Klamath NWR data sets revealed no difference in water-depth use by Western Grebe color morphs.

I also tested for differences in the proportion of each color morph at each water-depth zone (Miller 1981: 219). Of 15 cases tested, only 3 were significantly different: medium and high zones at Lower Klamath NWR and the low zone at Upper Klamath Lake.

The data support the hypothesis that light-phase Western Grebes feed farther from shore than dark-phase birds. However, the data are not totally consistent and, thus, this question warrants further study.

The data do not support the hypothesis that light-phase Western Grebes feed at greater water depth than dark-phase birds. However, the data must be viewed with caution due to several confounding factors: (1) water-depth categories were not directly related to distance categories; (2) 3 of 5 study areas were artificial water impoundments with relatively little change in water depth throughout the water basin (with the exception of "borrow ditches" adjacent to dike roads); and (3) the depth categories were only relative to other measurements on the same lake. Future research should concentrate on natural water basins to minimize these factors. Unfortunately, however, nearly all of the sympatric breeding populations in the U.S. are on artificial impoundments. One notable exception is Upper Klamath Lake.

A general hypothesis can be developed from these data. Most natural water basins have the shallowest water zones adjacent to shore, and water depth increases with approach to the approximate center of the basin. Light-phase birds may have evolved behavioral patterns closely associated with water depth. Use of a particular water-depth zone commonly may occur at a fairly consistent distance from shore. Thus, distance from shore may be an environmental "cue" regarding water depth and niche partitioning between the color morphs. Reduced niche overlap may

limit competition for food resources, i.e. a "coexistence mechanism" (Cody 1974: 7). An alternative hypothesis is that niche partitioning is accomplished by spatial separation of near shore vs. farther from shore, and water depth and the evolution of "springing dives" are secondary to spatial factors. In either case, at artificial water impoundment areas where mean water depth is relatively similar (compared to natural water impoundments), distance from shore may influence spatial behavior of birds more than water depth.

Travel support was provided by the Wildlife Biology Program, Washington State University. Dr. Tom McCabe assisted with field work and reviewed the manuscript. Duane Diefenbach assisted with data analysis. Sincere thanks to Drs. Rich Alldredge and Gary White for statistical consultation, and Drs. Fred Gilbert, Richard Johnson, John Kadlec, Gary Nuechterlein, Vince Schultz, John Thompson, and Kerry Reese for valuable comments on the manuscript.

LITERATURE CITED

- CODY, M. L. 1974. Competition and the structure of bird communities. Monographs in Population Biology No. 7. Princeton, New Jersey, Princeton Univ. Press.
- GRINNELL, J. 1904. The origin and distribution of the Chestnut-backed Chickadee. *Auk* 21: 364-382.
- MILLER, R. G. 1981. Simultaneous statistical inference, 2nd ed. New York, Springer-Verlag.
- NUECHTERLEIN, G. L. 1981. Courtship behavior and reproductive isolation between Western Grebe color morphs. *Auk* 98: 335-349.
- RATTI, J. T. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. *Auk* 96: 573-586.
- . 1981. Identification and distribution of Clark's Grebe. *Western Birds* 12: 41-46.
- STORER, R. W. 1965. The color phases of the Western Grebe. *Living Bird* 4: 59-63.

Received 18 June 1984, accepted 19 December 1984.

The Importance of Open Habitat to the Occurrence of Kleptoparasitism

DENNIS R. PAULSON

Burke Museum DB-10, University of Washington, Seattle, Washington 98195 USA

Direct competition among predatory birds for potential prey often is observed because of the large size of predator and prey, the often lengthy pursuit, and the open terrain in which many of these birds live. Such competition was brought to my attention vividly when I watched the interaction among four species of raptors over an open grassy prairie near Clewiston, Hendry County, Florida on 26 November

1961. A Merlin (*Falco columbarius*) flew rapidly over the prairie about 0.5 m above the ground and flushed two male Red-winged Blackbirds (*Agelaius phoeniceus*). It followed one blackbird closely until a male Northern Harrier (*Circus cyaneus*) rose from the prairie in front of them and struck at but missed the passing blackbird. The blackbird dropped to the ground and flew up again, and the Merlin forced it