COURTSHIP BEHAVIOR AND REPRODUCTIVE ISOLATION BETWEEN WESTERN GREBE COLOR MORPHS

GARY L. NUECHTERLEIN
Bell Museum of Natural History, 10 Church Street S.E., Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA

ABSTRACT.—In a study of behavioral isolating mechanisms existing between light- and dark-phase Western Grebes (*Aechmophorus occidentalis*) in two sympatric populations near the Oregon-California border, opposite-sexed birds nearly always chose to display with members of their own color phase. Males of opposite phase, however, frequently engaged in mutual display sequences to attract females. Film analysis revealed no color-phase divergences in form, duration, or sequential ordering of the many visual courtship displays. There were differences, however, in "Advertising," a call used to attract potential mates prior to the pair formation sequences. Dark-phase birds had calls with two notes ("cree-creet"), while light-phase birds had one-noted calls ("creeet"). In playback experiments, courting males of the two color phases readily distinguished the two call-types and only approached or answered female calls of their own phase. This response reversed when an artificial gap was spliced into the light-phase stimulus calls. Films of feeding dives by birds of each color phase also suggested differences that may relate to mean diving depth and hence ecological segregation of the two morphs. When the same playback experiments were repeated in a region of dark-phase allopatry (Manitoba), however, courting males showed very poor discrimination. This suggests that the high degree of segregation in sympatry possibly results from a learning process, whereby individuals rapidly sharpen their discriminative abilities by association. *Received 15 September 1980, accepted 19 December 1980.*

IN 1858, George N. Lawrence described two closely related species of the genus *Podiceps,* which he designated as *P. occidentalis* and *P. clarkii* (in Baird 1858: 894–895). Lawrence distinguished the two species by differences in bill coloration and by whether or not the black of the crown extended downward beyond the eye to the lores. Although Ridgway (1881) and Fannin (1891) accepted this classification, Coues (1874) and Henshaw (1881) believed that the two forms were varieties (i.e. color phases) of the same species. The first edition of the American Ornithologists' Union "Checklist of North American Birds" (1886) upheld the views of Coues and Henshaw, as have more recent editions of the checklist (1931, 1957) and Mayr and Cottrell's (1979) checklist. Presently, the Western Grebe (*Aechmophorus occidentalis*) is placed in its own monotypic genus, and Dickerman (1963, 1973) has distinguished *A. o. clarkii* as a smaller subspecies found on the Mexican Plateau and represented by members of both color phases. Mayr and Short (1970: 88) report the two color phases as a case of "scattered polymorphism."

The most detailed published description of the two color phases is that of Storer (1965). The most conspicuous difference, in the extent of black on the head, is especially striking in the field, where the brilliant eyes of the living bird draw attention to the facial region. The scarlet eyes of light-phase birds are surrounded by white feathers, in contrast to those of dark-phase birds, which are surrounded by a shroud of black facial feathers. The bills of light-phase birds are orange-yellow, those of dark-phase birds dull greenish-yellow.

Storer (1965) and Lindvall (1976) gave evidence of strong assortative mating within a sympatric population of the two color phases at Bear River Marsh, Utah, and a recent study by Ratti (1979) has confirmed that mixed pairs are rare (<3%) in Utah and California. Ratti (1979) also found spatial segregation within mixed flocks

The Auk 98: 335–349. April 1981

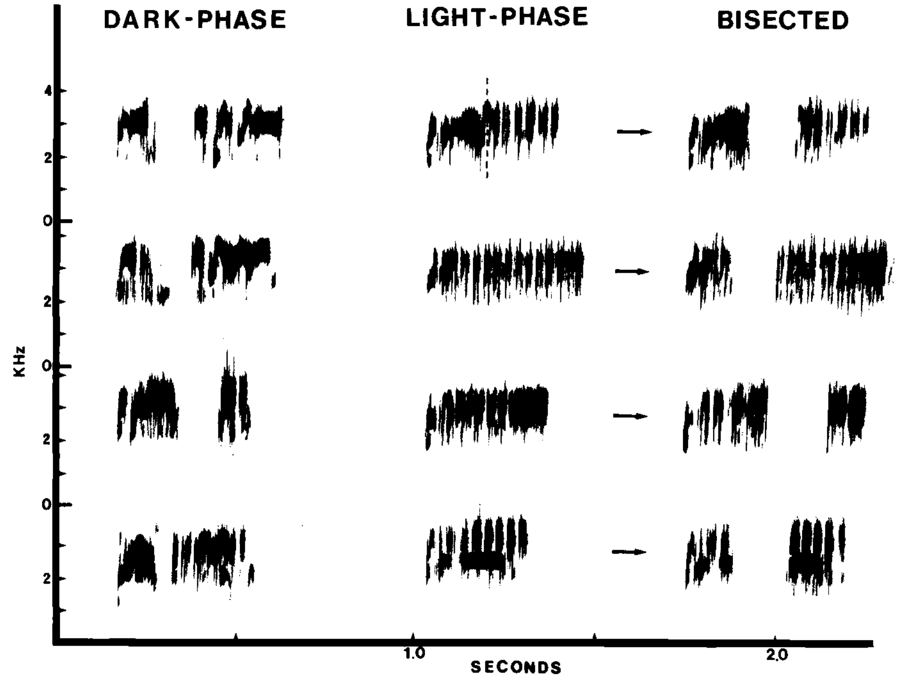

Fig. 1. Advertising calls of four dark- and light-phase Western Grebe females recorded at Tule Lake, California. Sonagrams are of the eight stimulus calls used in the reproductive isolation experiments. The importance of the call-gap to phase discrimination was tested by splicing a short segment of blank recording tape into each light-phase stimulus call and repeating the experiments.

of the two types at Utah and various locations in Nevada and California. My data confirm these observations for breeding populations in Manitoba (Marshy Point and the Delta Marshes of Lake Manitoba), Oregon (Upper Klamath Lake), and California (Tule Lake). Ratti (1979) recommends that the color phases be designated separate species and suggests "resurrection of *A. clarkii* as a separate species from *A. occidentalis,* as originally described."

To date, however, the specific reproductive isolating mechanisms important in segregating the two color phases have largely remained a matter of speculation. Storer (1965) suggested that imprinting on parental coloration could be involved, but Ratti (1977) was not able to confirm this with hand-reared chicks. Ratti's results were inconclusive, however, because his chicks apparently failed to imprint on any of the silent, stationary parental models used. I became interested in this problem during a study of variation in the Advertising call of Western Grebes. Recordings made during 1978 within several mixed-phase populations in Oregon, California, and Utah revealed a consistent and striking difference between calls of the two color morphs (Fig. 1). Advertising calls of dark-phase birds included two distinct notes ("cree-creet"), while those of light-phase birds consisted of a single, more drawn-out note ("creeet"). Advertising usually constitutes the first contact between two unpaired courting birds, and it seemed likely that this call difference might play a key role in reproductive isolation of the two color phases.

The basic objectives of the study were: (1) to analyze visual and vocal components of the courtship displays for differences between the color phases, (2) to determine the point in the extended pair-formation sequence at which isolation usually took place, and (3) to conduct playback experiments examining the extent to which differences in the Advertising call serve as a reproductive isolating mechanism. I also examined feeding-dive differences that may relate to ecological segregation between the two morphs. Display names used throughout this paper are those of Nuechterlein and Storer (in prep.).

METHODS

During April 1978 and April–May 1979, I watched courting Western Grebes in mixed-phase populations at the Klamath Basin National Wildlife Refuges (Tule Lake, Upper and Lower Klamath lakes), near the California-Oregon border. Display activity was particularly intense at Tule Lake Refuge, which is a major staging and breeding ground in this area. In 1979, grebe populations on Tule Lake peaked (estimated 2,000–3,000) during a stretch of windy, inclement weather in late March. On 5 April weather conditions became calm and sunny, initiating a period of very active courtship during which I recorded over 450 display sequences in a 7-day period. These sequences were dictated into a cassette recorder or recorded directly on data sheets.

For micro-analysis of display form, I obtained films and tape recordings of courtship sequences of both color phases. Films were made with a Beaulieu R16 16-mm movie camera and were examined frame by frame using a L-W Analyst Projector. A Uher 4000 Report-L tape recorder was used for all recording and playback of calls, and tapes were compared by use of a Spectral Dynamics real-time analyzer. Playback experiments were conducted during May 1979 at Upper Klamath Lake and were carried out from a small, camouflaged kayak on the edge of a channel frequented by courting males of both color phases. Tape loops used in the playbacks were spliced from tapes of Advertising calls of light- and dark-phase females recorded at Tule Lake, located 45 km away. This assured that males were reacting to phase-typical characteristics rather than individual features of calls of known females. The Advertising calls used for each experiment were chosen at random from tape loops of four females of each phase.

In all cases, the target bird was an actively courting, unpaired male that was swimming within 10–20 m of the tape recorder. Each male was tested three consecutive times with a single call variant. Positive responses were scored only if, within 5 s following the playback, he either (a) replied by giving the Advertising call ("Advertises") or (b) turned and approached the tape recorder ("Approaches").

RESULTS

DISPLAY DIFFERENCES BETWEEN THE COLOR PHASES

Although frame-by-frame film analysis of courtship sequences revealed many individual variants in courtship display movements and postures, none of these visual components of the displays was peculiar to either color phase. Sufficient films were obtained to analyze the form and mean duration of the four most frequent displays statistically, but no significant differences were found (Table 1). Comparisons of the postures and orientation of these and other displays similarly revealed no obvious differences. Finally, flow diagrams constructed from the 408 male-female courtship interactions observed at Tule Lake also showed no obvious differences between the two color phases in sequential ordering of the displays.

Vocal components of the following courtship displays were examined spectrographically: (1) Advertising, (2) Ratchet-pointing, (3) Tick-pointing, (4) Barge-trilling, (5) Neck-stretching, (6) Neck-arching, and (7) Copulation trilling. Although individual variations were common, there were consistent differences between members of the two color phases only in the Advertising call. Of 92 dark-phase birds observed Advertising at Upper Klamath Lake, 91 gave a distinctly two-noted call, while 76 of 77 light-phase birds gave one-noted Advertising calls ($\chi^2 = 161.0$, $P <$

TABLE 1. Mean duration of four courtship displays of light- and dark-phase Western Grebes filmed and analyzed frame by frame. Differences between the color phases were not significant for any of the displays.

Display name	Number of displays (individuals) analyzed		Mean duration[a] (S.D.) (s)		t-value
	Dark-phase	Light-phase	Dark-phase	Light-phase	
Dip-shaking	99 (19)	37 (24)	0.43 (0.04)	0.40 (0.05)	1.83
Rushing	12 (12)	20 (19)	3.41 (1.22)	3.96 (1.71)	1.04
Bob-shaking	16 (10)	12 (6)	0.50 (0.05)	0.48 (0.09)	0.53
Bob-preening	57 (12)	102 (12)	0.85 (0.16)	0.81 (0.19)	0.59

[a] These are the means of the mean values computed separately for each individual.

0.001). Repeated calls by the same bird were nearly identical, and no individual was heard to give calls of both types. This sharp distinction between the calls of dark- and light-phase birds was found in all other populations I examined. Because unpaired birds use the Advertising call to attract potential mates, these findings strongly suggest that differences in this call are partially responsible for the high degree of assortative mating observed in the field.

BEHAVIORAL ISOLATION OF THE COLOR PHASES

Male-female display sequences.—Observations of courtship interactions at Tule Lake from 1 to 22 April 1979 revealed almost total reproductive isolation between the color phases, even for preliminary displays of the pair formation sequence. Within this mixed population, comprised of approximately 22% light- and 78% dark-phase birds, 408 male-female courtship display sequences were recorded, of which only 13 (3%) involved members of both color phases. Frequency of inter-phase courtship varied from about 2–3% for early displays in the pair formation sequence (e.g. Dip-shake and Rush) to 0–1% for later displays of the sequence (Table 2).

The few sequences involving birds of both phases were usually aborted before or shortly following Rushing (8 of 12 cases). Of the remaining four sequences, two were unusual in that after Rushing, the pair reverted back to Dip-shaking, the first display of the pairing sequence. In only two instances did the sequence continue after Rushing, and in both the birds separated shortly after Bob-preening.

Male-male display sequences.—Unlike most other grebe species, two male Western Grebes frequently perform displays together, probably to attract the attention of females in the vicinity. Such male-male sequences frequently involved birds of opposite color phase. Of 94 interactions 16 (17%) involved males of opposite phase, a percentage that is significantly greater than that for male-female sequences ($\chi^2 = 22.4$, $P < 0.01$). In contrast to mixed-phase male-female sequences, those involving only males were not abbreviated, and in all respects they appeared to be similar to male sequences involving birds of the same phase. Frequency of inter-phase displaying varied from 17 to 20% (Table 2B).

The most common display was Barge-trilling, seen during 77 of 94 male-male interactions. Females in the vicinity of two displaying males frequently approached and then engaged in courtship with one of the males. In five such instances observed at Tule Lake, the females chose the male matching their own color phase. [These

TABLE 2. Chi-square analysis of assortative courtship displaying by dark- (D) and light-phase (L) Western Grebes on the Klamath Basin Wildlife Refuges. Displays are analyzed separately in their sequential order. (A) Male-female dyads, (B) Male-male dyads.

(A) MALE-FEMALE SEQUENCES

Courtship display	n	Number of dyads displaying D-D	L-L	D-L	L-D	χ^{2a}	Percentage mixed
Dip-shake	451	302	136	10	3	393.4	2.9
Rush	369	239	120	9	1	326.5	2.4
Bob-shake	248	165	82	1	0	243.5	0.4
Weed-dive	102	59	43	1	0	99.0	0.9
Weed-dance	27	17	10	0	0	27.0	0.0
Bob-preen	308	212	92	3	1	289.5	1.2
Arch-cluck	197	115	80	1	1	188.8	1.0

(B) MALE-MALE SEQUENCES

Courtship display	n	Number of dyads observed (expected) D-D	L-L	L-D	χ^{2b}	Percentage mixed
Dip-shake	50	31 (25.9)	9 (3.9)	10 (20.2)	12.8	20.0
Rush	54	35 (29.6)	9 (3.6)	10 (20.8)	14.7	18.5
Barge-trill	77	48 (38.6)	16 (6.5)	13 (31.8)	11.1	16.9

[a] For all values $P < 0.001$, df = 1.
[b] For all values $P < 0.01$, df = 2.

observations essentially constitute a natural female-choice experiment, $P = (½)^5 = 0.03$.]

Of 74 3-bird interactions observed on Tule Lake, 7 included birds of both phases. Such mixed-phase triads usually consisted of a female and one male of each color phase. Often their interactions appeared to be the result of confusion within dense courting groups, and in all cases, further displays were performed only between members of the same color phase.

PLAYBACK EXPERIMENTS WITH ADVERTISING CALLS

The field observations reported above showed that reproductive isolation occurs largely before birds reach the stage of close-range courtship interactions. Even Dip-shaking, the initial visual display of the pair-formation sequence, occurs only rarely between birds of different color phases. Evidence from continuously run, 30-min tapes recorded during April 1978 at Upper Klamath Lake suggested that Advertising may play a central role in isolating the two phases. Over a 7-day period I recorded 6.5 h of tape including 362 Advertising bouts, many of which consisted of two or more individuals engaging in short bursts of reciprocal calling. Because I could usually identify the color phase and sex of calling birds from the tapes, the tapes provided a valuable record of vocal interactions occurring within and between the color phases under natural conditions.

To provide an analytical framework for these data, I defined a "reply" as any Advertising bout occurring within 5 s of a preceding call bout. Each bout consisted of from 1 to 6 calls by the same individual, spaced 0.5–1.5 s apart. All recorded bouts were first divided into (1) those which received answers, and (2) those which did not. Answered bouts further consisted of (a) those answered by members of the same sex, and (b) those answered by members of the opposite sex. Calls too faint to distinguish from the tape with certainty were omitted from the analysis.

TABLE 3. Color phase composition of "replies" to (A) naturally occurring Advertising calls of each phase, and (B) playback calls broadcasted to a mixed population at Upper Klamath Lake, Oregon. Only heterosexual responses are tallied.

(A) NATURAL EXPERIMENT

	Advertising calls within 5 s[a]	
First call	Dark-phase	Light-phase
Dark-phase	36	6
Light-phase	4	61

(B) PLAYBACK EXPERIMENT

	Advertising calls within 5 s[b]	
Stimulus call	Dark-phase	Light-phase
Dark-phase	19	5
Light-phase	0	15

[a] $\chi^2 = 69.0$, $P < 0.001$, df = 1.

[b] $\chi^2 = 23.2$, $P < 0.001$, df = 1.

When summarized in this manner, these data essentially constitute a natural isolation experiment. If reproductive isolation by mating call type is occurring, heterosexual replies should come largely from individuals of the same color phase. Data from the analysis support this prediction. Of 137 recorded "replies," 107 followed a call by a member of the opposite sex. Of these 107 heterosexual replies, 91% followed individuals of the same phase type (Table 3A).

In early April 1979, I conducted a brief pilot experiment using playback calls. Female calls of each phase type were played to a mixed population of males at Upper Klamath Lake, and the phase of answering birds was recorded. Seventy-two trials were run, each 30 s apart, and a 5-s response period was allowed following each playback trial. Calls of each phase were alternated in 12-trial playback blocks. The results of this experiment suggest discrimination between morphs by Advertising call. Male "replies" to light-phase female playback trials were all from light-phase birds, while most replies to dark-phase female playbacks were from dark-phase males (Table 3B).

There were two difficulties with the interpretation of these results, however. Observations during the experiment indicated that some of the male "replies" were not given in response to the playback. Courting males often called spontaneously, apparently to attract the attention of nearby females. Active birds give such calls irregularly at 1–3 min intervals, and presumably some of these fall by chance within the 5-s playback response period. Also, nearby females (often of opposite color phase) sometimes happened to call simultaneously with the playback vocalization and elicited "inappropriate" male replies. But these sources of error were rare and presumably random with respect to the designated 5-s playback response periods, and both difficulties were largely eliminated in subsequent experiments by conducting several consecutive trials on individual males. When a male answered or approached within 5 s of two consecutive playbacks, I could be confident that the response was not spurious. When 3 consecutive playback calls were directed at each individual courting male, I scored a "positive" result only when the bird answered or approached after at least 2 of the 3 calls.

These three-trial playback experiments showed *complete* segregation of the color phases by Advertising (Table 4). Of 30 dark-phase and 26 light-phase males tested

TABLE 4. Reproductive isolation: number of (A) dark-phase and (B) light-phase males responding to playbacks of female Advertising calls of each color phase. Additional males were then tested with bisected, two-noted, light-phase calls having an artificial gap.

	Stimulus calls		
Playback response	Dark female	Light female	Light female (bisected)
(A) Dark males[a]			
Advertise/Approach	25	0	13
Negative response	8	30	4
(B) Light Males[b]			
Advertise/Approach	0	25	1
Negative response	26	4	11

[a] Significance tests for dark-phase males: (a) Dark versus light female calls, $\chi^2 = 37.7$ ($P < 0.001$); (b) Dark versus bisected light female calls, $\chi^2 = 0.003$ ($P > 0.75$).

[b] Significance tests for light-phase males: (a) Dark versus light female calls, $\chi^2 = 41.1$ ($P < 0.001$); (b) Dark versus bisected light female calls, $\chi^2 = 2.2$ ($P > 0.10$).

with calls of the opposite phase-type, none showed a positive response. In contrast, most dark males tested responded positively to playbacks of dark female calls, while light males tested responded positively to playbacks of light female calls (dark males: $\chi^2 = 37.7$, $P < 0.001$, light males: $\chi^2 = 41.1$, $P < 0.001$).

Mechanisms of call discrimination.—To examine the importance of the call gap to vocal segregation of the phases, a playback experiment with altered tapes was devised. Tapes of light-phase calls (copies of the same tapes used previously in the reproductive isolation experiments) were bisected with a scissors, and a short (1–2 cm) segment of blank recording tape was spliced into the middle of each call (Fig. 1). Both light- and dark-phase males showed complete reversal in responsiveness to the altered calls compared to the initial experiment (Table 4). Of 17 dark-phase males tested, 13 showed a positive response to the altered calls. Light-phase males, on the other hand, virtually ignored the calls with the exception of one male, which, for unknown reasons, responded vigorously to all three playback trials.

Geographical variation in discrimination responses.—A final playback discrimination experiment was conducted in Manitoba (Marshy Point) during May 1979, with somewhat surprising results. This experiment was a repetition of the color-phase discrimination playbacks initially performed at Upper Klamath. Procedures and tape loops were identical to those used in previous playbacks, except that only single-trial experiments were performed. Because light-phase birds are extremely rare (<0.5%) in this population, playbacks were limited to dark-phase males.

Table 5 compares the first-trial responses of Manitoba and Oregon males to the playback calls. Although Manitoba males did show some tendency to discriminate the two types of calls, segregation was not nearly as complete as it was for Oregon males. Chi-square statistical analysis suggests that this difference resulted largely from dark-phase Manitoba males showing more positive responses to light-phase female calls. In fact, nearly half of the 40 dark-phase males tested approached or Advertised. At the same time, males of the two populations showed little difference in responsiveness to dark-phase female calls.

OBSERVATIONS OF MIXED PAIRS AND PRESUMED HYBRIDS

Observations at Upper Klamath and Tule Lake confirmed Ratti's (1979) report of strong assortative mating within these mixed populations of the two color phases.

TABLE 5. Discrimination of dark- versus light-phase female Advertising calls by actively courting dark-phase males in areas of sympatry (Upper Klamath Lake, Oregon) versus allopatry (Marshy Point, Manitoba).

Stimulus call used	Response to call	Oregon males[a]	Manitoba males[b]
Dark-phase female[c]	Advertise and/or Approach	25	27
	No response	13	13
Light-phase female[d]	Advertise and/or Approach	1	19
	No Response	32	21

[a] Significance test for Oregon males: $\chi^2 = 30.0$, $P < 0.001$.
[b] For Manitoba males: $\chi^2 = 3.3$, $P = 0.07$ (N.S.).
[c] Significance test for differences in responsiveness to dark-phase calls: $\chi^2 = 0.03$, $P > 0.75$ (N.S.).
[d] For differences in responsiveness to light-phase calls: $\chi^2 = 18.0$, $P < 0.001$.

A pair count conducted on 2 April 1979 at Tule Lake yielded only one mixed pair out of a sample of 91 pairs (D-D: 71, L-L: 19, D-L: 1; $\chi^2 = 85.2$, $P < 0.001$). During my observations over a 2-week period at Tule Lake, I noted only two additional mixed pairs, which I differentiated by their individually distinct plumage patterns and Advertising calls (see Nuechterlein in press). While conducting playback experiments at Upper Klamath from 17 April to 10 May, I saw one additional mixed pair on several occasions. Observations of this dark-phase female interacting with her light-phase mate revealed that she had a *one-noted* Advertising call! This bird was the only dark-phase female I observed with such a call at Upper Klamath. Members of mixed pairs appeared to interact with their mates in a normal manner. The pair bonds seemed strong, and in one instance the male repeatedly defended his mate from intruders while engaging in mate-feeding. Eggs of the only mixed pair seen at Marshy Point, Manitoba were fertile and hatched successfully.

Birds with intermediate breeding plumage, probably progeny of such mixed matings, also were rare at both Upper Klamath and Tule lakes. Of a total of 18 individuals classified as "intermediates" (the black of the crown extending down to but not beyond the eye, Ratti 1979), 15 birds had orange bills (as in light-phased birds), while only 3 birds had dull greenish-yellow bills (as in dark-phased birds). Of 9 individuals with intermediate plumage observed Advertising, 6 gave one-noted calls and 3 gave two-noted calls. Repeated calls by a given individual were always of the same type. Thus, if these birds were indeed "hybrids," they were intermediate in facial coloration, but not call-type or bill coloration.

Six of the above intermediates were males observed while conducting playback experiments at Upper Klamath. Preliminary tests yielded positive responses from three of these birds, all responding to female playbacks of their own call-type. I was not able to perform the necessary control experiments on these individuals, however, so these data are only suggestive.

Observations of birds with intermediate plumage nesting within large colonies at Marshy Point, Manitoba, suggest that they are fertile, and eggs of one such female were observed hatching. Apparently, however, some intermediate birds, especially males, have difficulty obtaining a mate. Male-female courtship sequences at Tule Lake involving such males usually ended soon after Rushing (6 of 7 instances), though again male-male interactions involving intermediate birds (3 instances) were not so truncated. In two of these three instances, unpaired females approached and made a choice between the two displaying males; the nonhybrid individual was selected both times.

In Manitoba, birds with intermediate plumage appeared to be especially frequent in late-season courting groups of unmated birds. Such groups frequently contained individuals with obvious abnormalities, such as irregularities in their Advertising call. One late season courting male ("the voice-less male"), for example, had a hoarse, barely audible call, while another ("the clear-noted male") had a call consisting of very pure tones. A third bird, observed unpaired in July of two consecutive breeding seasons, had a three-noted call. Of the 18 intermediates observed at Upper Klamath and Tule Lake, only three were paired. One of these, an intermediate female with a one-noted call, was paired with a light male. The other two intermediates were paired with one another!

DIVING DIFFERENCES AND ECOLOGICAL SEGREGATION BETWEEN PHASES

Lawrence (1950) described four types of dives used by Western Grebes in different contexts. The "alarm dive" and "surface dive" were used in escape situations; the "feeding dive" and "springing dive" occurred during feeding. The latter differed in the extent to which the forepart of the body emerged from the water as the bird submerged. Although Lawrence did not attribute any special functional significance to the springing dive, he noted that it was more frequent in the ocean and in rough water.

Analysis of 49 dives filmed at Upper Klamath suggested that what I call "level dives" (="feeding dives" of Lawrence 1950) and "springing dives" probably represent extremes on a continuum of dive-forms used by Western Grebes while feeding. Level dives are the most common: the grebe sleeks its head and neck feathers, then propels itself smoothly forward beneath the water in a seemingly effortless, head-first motion. Neither the breast feathers nor the tarsi emerge from the water (Fig. 2A), and the bird submerges with scarcely a ripple. In springing dives, the grebe cocks its head backwards, after sleeking its feathers, then springs up out of the water while arching neck and body so as to enter the water more vertically. In its most exaggerated form, the entire body, including the feet and tarsi, emerge from the water as the head disappears under the surface (Fig. 2B).

I suspect that the bird goes deeper in springing dives than in level dives. Birds feeding far offshore at Upper Klamath during April 1978 frequently used springing dives, whereas those feeding close to shore used mostly level dives (Fig. 2B, $\chi^2 = 14.5$, $P < 0.01$). In a sample of 69 dives, dark-phase birds only once performed a full springing dive (breast and tarsus emerging from water), while light-phase birds did so frequently (Fig. 2A, $\chi^2 = 38.8$, $P < 0.01$). This probably was a result of spatial segregation of the two morphs during feeding. Light-phase birds generally tended to feed at a greater distance from shore than dark-phase birds. In shallow marshes such as Tule Lake, Bear River Marsh, and the Delta Marsh, I have only rarely observed springing dives, even by light-phase birds. Thus, I suspect that the critical factor determining the dive-type may be water depth rather than color phase *per se* and that light-phase birds may be more inclined to dive in deeper water when such areas are available. Ratti (pers. comm.) rarely observed light-phase birds in the shallow "borrow ditches" at Bear River Refuge that were commonly utilized by dark-phase birds. Further study of this topic is needed.

DISCUSSION

Ecological segregation.—Ratti (1979) suggests that morphologically and ecologically the two color phases are practically indistinguishable and that sympatric pop-

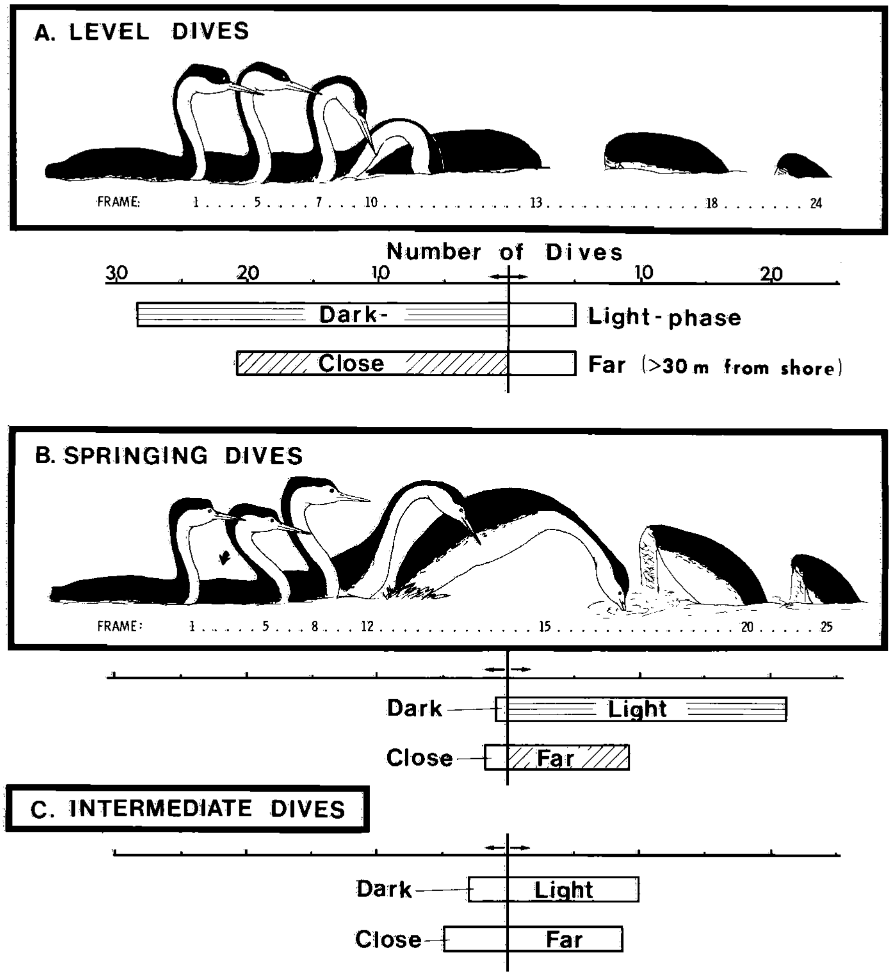

Fig. 2. Types of dives used by feeding dark- and light-phase Western Grebes at Upper Klamath Lake, Oregon. Dives were filmed at 25 frames/s; image size was used to determine relative distance from shore.

ulations may therefore represent one of the best avian examples of an exception to the competitive exclusion principle. My preliminary data on dive-types, however, suggest that the two color phases may be segregating behaviorally into two subtly different ecological forms specialized for feeding at different depths.

This is an important aspect of the speciation question in critical need of further study. Both Feerer (1977) and Ratti (1979) report that major differences exist in the proportion of light- and dark-phase birds comprising the breeding populations of neighboring lake systems within Oregon, California, and Mexico. For example, Ratti (1979) reports a large grebe population at Goose Lake, Oregon comprised of over 93% light-phase birds. This breeding population lies only 110 km east of Upper Klamath, Lower Klamath, and Tule Lake, all of which support predominantly dark-phase populations.

If the color phases are diverging ecologically with respect to mean diving depth, differences in the physiography of lake basins may be important in explaining many of the local irregularities that Feerer (1977) and Ratti (1979) report within the more basic north-south cline in color-phase frequencies described by Storer (1965).

Playback experiments.—For Western Grebes comprising sympatric populations of dark- and light-phase birds at Tule and Upper Klamath lakes, phase discrimination by call-type plays an important role in reproductive isolation. For most birds, call discrimination appears to be based largely on whether or not there exists a 20–200 ms gap dividing the Advertising call into two notes. There is no evidence of character displacement in gap length of calls recorded within mixed populations, but grebes in areas of sympatry do show increased discriminatory responses to the character difference.

Unfortunately, very little is known about the ontogeny of vocalizations or about the development of mating call preferences in Western Grebes. If these are both imprinting-like phenomena, results of the geographical variation experiment could suggest a sharpening or narrowing of the sexual imprinting process for birds within sympatric populations. Another explanation, however, is that individuals comprising sympatric populations discover through associative learning that birds having Advertising calls different from their own possess other traits making them less compatible as mating partners.

Most birds within the nearly allopatric populations of Manitoba may not have had ample opportunity to make the association. This is not true for all individuals, however. One marked dark-phase male, for example, responded positively to 16 of 20 dark-phase female calls played to him, but showed only one positive response to 20 playbacks of light-phase female calls.

Advertising songs and calls are probably important species recognition signals for many birds (Marler 1960). Among the songbirds (Passeriformes), for example, many closely related species-pairs have similar plumages but widely divergent Advertising songs, and Nottebohm (1972) suggests that song learning has played an important role in the group's rapid radiation. Although the importance of Advertising calls to reproductive isolation is well-established in other vocal species, such as the anurans (see reviews by Blair 1958, 1964; Littlejohn 1969) and orthopteran insects (Walker 1957, 1974; Perdeck 1958), the isolating role of birdsong has rarely been demonstrated (but see Szijj 1966, Payne 1973). This probably is because female songbirds usually fail to give easily quantified, overt playback responses in the field and, unlike anurans and orthopterans, are difficult to test in the laboratory. Unlike the grebes, most female songbirds have no Advertising calls of their own, and playback studies have largely been limited to male-male territorial responses.

In a series of extensive behavioral studies on hybridization and isolating mechanisms between Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, Gill and Lanyon (1964), Ficken and Ficken (1967; 1968a, b; 1969), and Gill and Murray (1972a, b) conducted reciprocal experiments, playing both types of Advertising song to territorial males of each species. Gill and Murray (1972b) summarize these data, which show song discrimination by both species. Further studies showed that, like Western Grebes, male Blue-winged Warblers in allopatric populations give weaker discrimination responses (Ficken and Ficken 1969, Gill and Murray 1972a). In contrast, Emlen et al. (1975) report that male Indigo Buntings (*Passerina cyanea*) and Lazuli Buntings (*P. amoena*), which defend interspecific territories, show more vigorous responses to calls of the other species within zones of sympatry. Authors of both studies suggest that these responses are learned by association. Gill and Murray (1972b) relate several instances of individually marked males eventually learning to discriminate song-types when their territories were bordered by members of both species.

This phenomenon of "response displacement" parallels character displacement in signal patterns but involves *individuals* of sympatric populations *learning* to alter their *responsiveness* to evolved signal differences, rather than *populations* genetically altering the *signals* themselves. Such learned discrimination responses to Advertising calls may have important bearing on the rate at which effective reproductive isolation takes place. Associative learning might explain, for example, the extremely rapid (within 10–20 yr) reduction in the frequency of cross-matings in Northern Oriole (*Icterus galbula*) subspecies reported by Corbin and Sibley (1977) and Corbin et al. (1979) in areas of recent sympatry.

Littlejohn and his associates have conducted numerous playback experiments showing the importance of male call differences to reproductive isolation of closely related anuran species (Littlejohn 1969, Blair 1974). In all cases where females showed better discriminative abilities between male calls recorded in areas of sympatry versus allopatry (Littlejohn 1960, 1965; Littlejohn and Loftus Hills 1968), these differences were associated with character displacement in temporal components of the male's mating calls. In birds, where learning plays a greater role in call discrimination, responses may be more flexible, and individuals sharpening their discrimination through associative learning should benefit, even in cases where there are only minor disadvantages to hybrid matings. Such initial disadvantages could relate to behavioral as well as genetic incompatibilities. (As a possible example, members of a mixed pair, while attempting to feed young, may experience difficulties in choosing a depth of water optimal for both birds.) In cases where there is no disadvantage to hybridization between individuals of two populations, "response convergence" to signal differences should occur and may result in rapid introgression. Where calls serve multiple functions (e.g. territorial advertisement and mate attraction), male and female need not show parallel changes in response. In cases of interspecific territoriality, for example, males may learn to react equally to both call-types, while females learn to discriminate the two calls. The meadowlarks provide a possible example (see Szijj 1966, Rowher 1972).

Reproductive isolation.—Observational data, film analysis, and playback experiments suggest that, in most cases, the later visual courtship displays of Western Grebes may have little to do with reproductive isolation, for species isolation is largely complete before they begin. Instead, such displays may be involved in mate evaluation at a more subtle level (Nuechterlein in prep.). Advertising is the only display commonly preceding such interactions between unmated birds. This provides strong circumstantial evidence of the central role of the Advertising call in isolating the two phases.

Within sympatric populations of the two color phases in California, Oregon, and Utah, reproductive isolation appears to be nearly complete, confirming reports by Storer (1965), Lindvall (1976), and Ratti (1979). Intermediates were frequent, however, within several Mexican populations examined by Feerer (1977). Although sample sizes are limited, he reports a frequency of 33% ($n = 54$) for birds with intermediate plumage counted at Laguna Tuxpan (population size: 105 individuals), and 30% ($n = 15$) for Laguna Cuitzeo (population size: 50 individuals). Plumage, but not bill color, intermediacy also appears to be more common in museum specimens (Robert W. Storer pers. comm.), and the possibility that there are seasonal plumage differences (Ratti 1979) should be investigated. Plumage differences between dark- and light-phase birds may be striking only for adult birds that are in full breeding plumage. This would mean that the plumage classification "intermediate" is a heterogeneous group comprised of hybrids, juveniles, and adults in winter plumage.

Within populations of breeding birds at Tule Lake and Upper Klamath, intermediates were very rare and showed no intermediacy in bill color or Advertising call characteristics. The hybrids of Blue-winged/Golden-winged Warbler crosses, "Brewster's" and "Lawrence's" warblers, similarly possess intermediate plumage, but not song (Gill and Murray 1972b). Ficken and Ficken (1968a, b) indicated that these hybrids also have difficulties in finding mates. Short (1963), Ficken and Ficken (1967), and Gill and Murray (1972a) all report rare instances of males having songs of the inappropriate species.

Systematic considerations.—Whether or not the two color phases should be recognized as separate species remains an open question. In a practical sense, Short (1969) recommends that populations capable of forming a zone of overlap and hybridization, where both parental and hybrid types coexist, be considered semispecies having separate binomial names. He warns that it is critical, however, to consider all reactions between two forms before undertaking a full taxonomic evaluation, for forms coexisting in one area of contact may interbreed in other areas (e.g. Sibley and West 1958), and "evidence of the stabilization of a single hybrid swarm warrants conspecific status for the parental forms" (Short 1969). In this regard, it seems important to investigate reproductive isolation and behavioral interactions within Western Grebe populations of Mexico.

If dark- and light-phase Western Grebes remain classified as morphs, they may represent a unique case, for "no other broadly sympatric avian polymorphic species is known to exhibit such a low incidence of interbreeding" (Ratti 1979: 584). If, however, they are classified as distinct species, they may still be unique, for I know of no other instance in which males of two separate species regularly engage in *mutual* display to attract females. This dilemma underscores the futility of attempting to impose static classifications on populations undergoing the continuous process of speciation via mechanisms still poorly understood.

Perhaps a more interesting and meaningfully phrased question is to ask instead whether isolating mechanisms are being diminished or strengthened, and whether the two morphs are genetically diverging or converging through time. Unfortunately, these are historical questions difficult to address except indirectly, for example through evidence of character displacement in areas of recent sympatry. The phenomenon of reproductive "response displacement" (i.e. the sharpening of discrimination responses to mating call or song differences within areas of sympatry), as found in this study, is similarly suggestive. It seems imperative that future studies examine more closely the actual mechanisms involved, the degree to which the phenomenon is general to birds, and the importance of such learned responses to the speciation process.

ACKNOWLEDGMENTS

This research was funded by the National Geographic Society, Chapman Memorial Fund, and by the Bell-Delta Fellowship of the Delta Waterfowl Research Station. I thank George Barrowclough, John T. Ratti, Carl D. Hopkins, Milton W. Weller, Harrison B. Tordoff, and James A. Cooper for reading the manuscript and providing helpful suggestions. My advisor, Frank McKinney, deserves special thanks for reading an early draft and providing important suggestions for its further development. Throughout the project Robert W. Storer gave freely of his insights on grebes. Finally, I thank all the many students and associates of the Delta Waterfowl Research Station for providing a most welcome atmosphere of criticism and encouragement.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1886. Checklist of North American birds, first ed. New York, Amer. Ornithol. Union.

———. 1931. Checklist of North American birds, fourth ed. Lancaster, Pennsylvania, Amer. Ornithol. Union.

———. 1957. Checklist of North American birds, fifth ed. Baltimore, Maryland, Amer. Ornithol. Union.

BAIRD, S. F. 1858. Birds. *In* Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean, vol. 9, part 2. Washington D.C., House of Representatives, 33rd Congress, 2nd Session. Ex. Doc. No. 91.

BLAIR, W. F. 1958. Mating calls in the speciation of anuran amphibians. Amer. Natur. 92: 27–51.

———. 1964. Evolution at populational and interpopulational levels: isolating mechanisms and interspecies interactions in anuran amphibians. Quart. Rev. Biol. 39: 333–344.

———. 1974. Character displacement in frogs. Amer. Zool. 14: 1119–1125.

CORBIN, K. W., & C. B. SIBLEY. 1977. Rapid evolution in orioles in the genus *Icterus*. Condor 79: 335–342.

———, ———, & A. FERGUSON. 1979. Genic changes associated with the establishment of sympatry in orioles of the genus *Icterus*. Evolution 33: 624–633.

COUES, E. 1874. Check List of North American birds. *In* Field ornithology. Boston, Massachusetts, Estes and Lauriat.

DICKERMAN, R. W. 1963. The grebe *Aechmophorus occidentalis clarkii* as a nesting bird of the Mexican plateau. Condor 65: 66–67.

———. 1973. Further notes on the Western Grebe in Mexico. Condor 75: 131–132.

EMLEN, S. T., J. D. RISING, & W. L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the great plains. Wilson Bull. 87: 145–179.

FANNIN, J. 1891. Checklist of British Columbia birds. Victoria, British Columbia, British Columbia Provincial Mus.

FEERER, J. L. 1977. Niche partitioning by Western Grebe polymorphs. Unpublished M.S. thesis. Arcata, California, Humbolt State Univ.

FICKEN, M. S., & R. W. FICKEN. 1967. Singing behavior of the Blue-winged and Golden-winged warblers and their hybrids. Behaviour 28: 149–181.

———. 1968a. Courtship of Blue-winged Warblers and their hybrids. Wilson Bull. 80: 161–172.

———. 1968b. Reproductive isolating mechanisms in the Blue-winged Warbler-Golden-winged Warbler complex. Evolution 22: 166–179.

———. 1969. Responses of Blue-winged and Golden-Winged warblers to their own and the other species' song. Wilson Bull. 81: 69–74.

GILL, F. B., & W. E. LANYON. 1964. Experiments on species discrimination in Blue-winged Warblers. Auk 81: 53–64.

———, & B. G. MURRAY, JR. 1972a. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. Evolution 26: 282–293.

———, & ———. 1972b. Song variation in sympatric Blue-winged and Golden-winged warblers. Auk 89: 625–643.

HENSHAW, H. W. 1881. On *Podiceps occidentalis* and *P. clarkii*. Bull. Nuttall Ornith. Club 6: 211–216.

LAWRENCE, G. E. 1950. The diving and feeding activity of the Western Grebe on the breeding grounds. Condor 52: 3–16.

LINDVALL, M. L. 1976. Breeding biology of pesticide—PCB contamination of Western Grebe at Bear River Migratory Bird Refuge. Unpublished M.S. thesis. Logan, Utah, Utah State Univ.

LITTLEJOHN, M. J. 1960. Call discrimination and potential reproductive isolation in *Pseudacris triseriata* females from Oklahoma. Copeia 1960: 370–371.

———. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). Evolution 19: 234–243.

———. 1969. The systematic significance of isolating mechanisms. Pp. 459–482 *in* Systematic biology. Washington D.C., Nat. Acad. Sci., Publication 1692.

———, & J. J. Loftus Hills. 1968. An experimental evaluation of premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). Evolution 22: 659–663.

MARLER, P. 1960. Bird songs and mate selection. Pp. 348–367 *in* Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, Eds.). Washington D.C., Amer. Inst. Biol. Sci.

MAYR, E., & L. L. SHORT. 1970. Species taxa of North American birds. Publ. Nuttall Ornithol. Club No. 9.

———, & G. W. COTTRELL. 1979. Checklist of birds of the world, vol. 1, second ed. Cambridge, Massachusetts, Mus. Comp. Zool.

NOTTEBOHM, F. 1972. The origins of vocal learning. Amer. Natur. 106: 116–140.

NUECHTERLEIN, G. L. In press. Variation and multiple functions of the Advertising display of Western Grebes. Behaviour.

PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. Ornithol. Monogr. 11: 1–333.

PERDECK, A. C. 1958. The isolating value of specific song patterns in two sibling species of grasshoppers (*Chorthippus brunneus* Thunb. and *C. biguttulus* L.). Behaviour 12: 1–75.

RATTI, J. T. 1977. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Unpublished Ph.D. dissertation. Logan, Utah, Utah State Univ.

———. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Auk 96: 573–586.

RIDGWAY, R. 1881. Nomenclature of North American birds contained in the U.S. National Museum. Bull. U.S. Natl. Mus. No. 21. Washington D.C., Smithsonian Inst.

ROWHER, S. 1972. A multivariate assessment of interbreeding between the meadowlarks, *Sturnella*. Syst. Zool. 21: 313–338.

SHORT, L. L. 1963. Hybridization in the wood warblers *Vermivora pinus* and *V. chrysoptera*. Proc. 13th Intern. Ornithol. Congr.: 147–160.

———. 1969. Taxonomic aspects of avian hybridization. Auk 86: 84–105.

SIBLEY, C. G., & D. A. WEST. 1958. Hybridization in the Red-eyed Towhees of Mexico: the eastern plateau populations. Condor 60: 85–104.

STORER, R. W. 1965. The color phases of the Western Grebe. Living Bird 4: 59–63.

SZIJJ, L. J. 1966. Hybridization and the nature of the isolating mechanism in sympatric populations of meadowlarks (*Sturnella*) in Ontario. Z. Tierpsychol. 23: 677–690.

WALKER, T. J. 1957. Specificity in the response of female tree crickets (Orthoptera, Grillidae, Oecanthinae) to calling songs of the males. Ann. Entomol. Soc. Amer. 50: 626–636.

———. 1974. Character displacement and acoustical insects. Amer. Zool. 14: 1137–1150.