AN ANALYSIS OF PLUMAGE AND MORPHOLOGICAL CHARACTERS OF THE TWO COLOR FORMS OF THE WESTERN GREBE (*AECHMOPHORUS*)

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ABSTRACT.—The dark and light color forms of the Western Grebe (*Aechmophorus occidentalis*) are defined in this study by bill color. Considerable overlap between the phases was found in all plumage color characteristics except facial patterns. The feathers of the head are molted twice annually, and most facial intermediacy of juvenile and wintering birds disappears as the breeding season approaches. Most body feathers are molted once, except those of the flanks, scapular region, and base of the leg, which appear to be in a state of molt throughout the year. These feathers, especially those of the flanks, are believed to be those ingested regularly by the birds. Some birds molt the remiges with the annual (Prebasic) molt in late summer, but some, possibly birds in their first winter, molt them in midwinter. The measurement data indicate that the dark-phase birds on Clear Lake, California are larger and may be descendents of wintering birds from the north. *Received 3 April 1984, accepted 24 August 1984.*

THE two color forms or phases of the Western Grebe have been known since Lawrence (*in* Baird 1858) originally described them as two species, the dark-faced form as *Podiceps occidentalis* and the light-faced form as *P. clarkii* (Fig. 1). Until recently, they generally have been considered color phases of a single species, *occidentalis,* for which the genus *Aechmophorus* was erected by Coues (1862). Dickerman (1963) separated the small Mexican birds as a distinct subspecies, to which he applied the name *Aechmophorus occidentalis clarkii,* selecting one of Lawrence's cotypes as lectotype.

Storer (1965) reported assortative mating in these grebes, the birds usually selecting mates of their own color phase. Subsequently, Feerer (1977) presented comparative data on prey size and color patterns, plus an analysis of measurement data from a large series of Western Grebes from Clear Lake, Lake County, and Topaz Lake, Mono County, California collected in the late 1960's by Herman and Rudd for pesticide residues (Herman et al. 1969). Ratti (1979) presented further information on assortative mating, evidence for ecological segregation, color differences in the young, and possible isolating mechanisms. Nuechterlein (1981) demonstrated that the assortative mating resulted from differential responses to the phase-specific Advertising calls, which are single-noted in the light-phase birds and double-noted in the dark-phase birds.

Most of the birds Feerer (1977) reported on were kept frozen until August 1981, when Herman kindly gave them and other frozen California specimens to The University of Michigan Museum of Zoology (UMMZ). There they were prepared as specimens, and they form the primary basis for this report.

In the United States and Canada, Western Grebes show a clinal decrease in wing length from north to south. There is also an increase in the relative frequency of the light-phase birds in the south, from less than 1% of the population in Canada (Storer 1965) to 12–18% in Utah (Storer 1965, Ratti 1979) to more than 50% in Mexico (Dickerman 1973). Yet even within a local area, major differences exist in the proportion of light- and dark-phase birds from one lake to the next (Feerer 1977, Ratti 1979, Nuechterlein unpubl. data). It is evident that a large sample from a single, mixed population is needed for accurate analysis of the differences between the two forms. The Herman-Rudd sample of 111 birds from Clear Lake (39°N) and 47 from Topaz Lake (38°43'N) has provided such an opportunity.

In addition to describing geographic and intermorph differences in this complex, we have asked several questions: How much interme-

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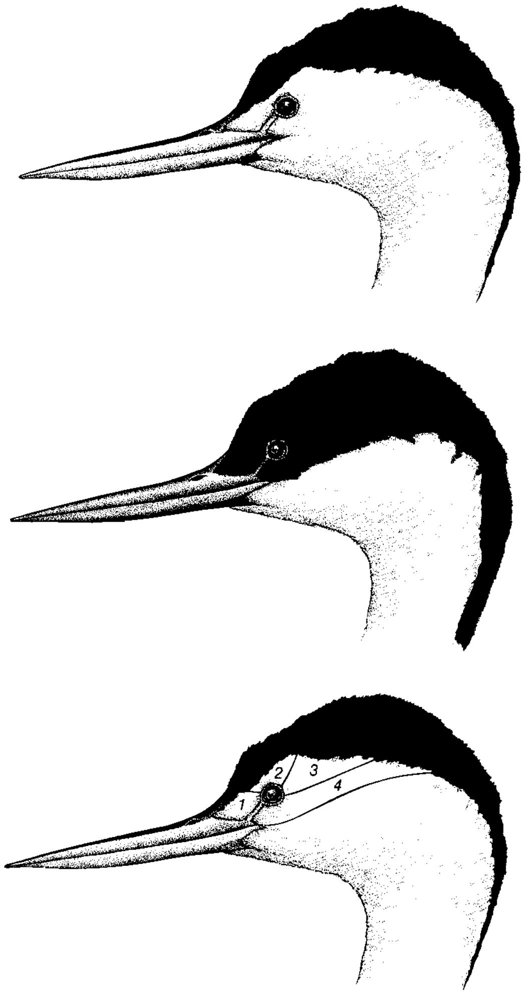


Fig. 1. Heads of light-phase (top) and dark-phase (middle) male Western Grebes. Bottom drawing shows areas into which the face was divided for analysis of pattern in the Clear Lake series (1 = lores, 2 = above eye, 3 = behind eye, 4 = below eye).

diacy is there between the forms, and how can this intermediacy be explained? Which color characters are consistent within each phase? What morphological characters might be associated with ecological differences in locomotion and foraging behavior between birds of the two phases?

Materials and Methods

The birds received from Herman were kept frozen until prepared. After thawing, each bird was measured by Storer as follows: wing length (arc) was measured on a mm rule, and tarsal length, bill length from the anterior edge of the nostril to the tip, and bill depth at the level of the posterior edge of the nostril were taken to the nearest 0.1 mm with dial calipers. The heads were then photographed in black and white. The birds were cut down the midventral line, skinned, the fat removed by scraping and soaking in Stoddard's solvent, and the pelt pinned out flat to dry. One wing of each bird had been removed before we received the birds, so the bones from the other wing were removed and saved with the rest of the skeleton, as were the bones of one foot. The pelts were used for the study of molt, age, and seasonal differences in plumage, as well as differences in the amount of dark and light in the plumage.

Data used for the study of geographic variation were taken by Storer on visits to approximately 100 collections in the United States, Canada, and England, where 540 specimens were examined and measured. Most of the specimens also were classed as light or dark phase on the basis of bill pattern and compared with a series of 6 sketches of various head patterns (Fig. 2). The measurements were the same as those taken on the Herman series. However, because the Herman birds were not dried when measured, their measurements were not combined with those of the museum skins for this analysis. For statistical analyses, we used Chi-square and two-tailed *t*-tests.

Aging.—The bursa of Fabricius (Bursa cloacalis, Baumel 1979), which is maintained but reduced in size through the first breeding season (Nuechterlein unpubl. data), is the best method available for aging Western Grebes. Because bursa data were not taken on the Herman series, we examined skeletons of the Herman series for characters that varied with age. The tarsometatarsus is the last major skeletal element to become completely ossified in grebes. The region near the fusion of the proximal epiphysis and the shaft is rough (pitted or grooved) until the birds are several months old (Storer pers. obs.). Virtually all of the 119 skeletons of Western Grebes that Nero (1960) found frozen in Lake Newell, Alberta, and deposited at UMMZ can be aged by this criterion. Assuming that most of these birds were hatched in mid-June, they were approximately five months of age when they died in mid-November.

The Pons supratendineus also was used in aging. This is a bridge on the anterior surface of the distal part of the tibiotarsus that lies across the tendon of M. extensor digitorum longus. It is cartilaginous in young birds and completely ossified in adults.

Molt.—The preparation of the Herman series as flat pelts permitted us to detect growing feathers from the underside of the skin. Each pelt was divided into ten areas: crest, face, throat, neck, back, flanks, belly, humeral tract, interscapular tract, and base of leg. For each area the stage of the molt was recorded as none (0), light (1), moderate (2), or heavy (3). As in other

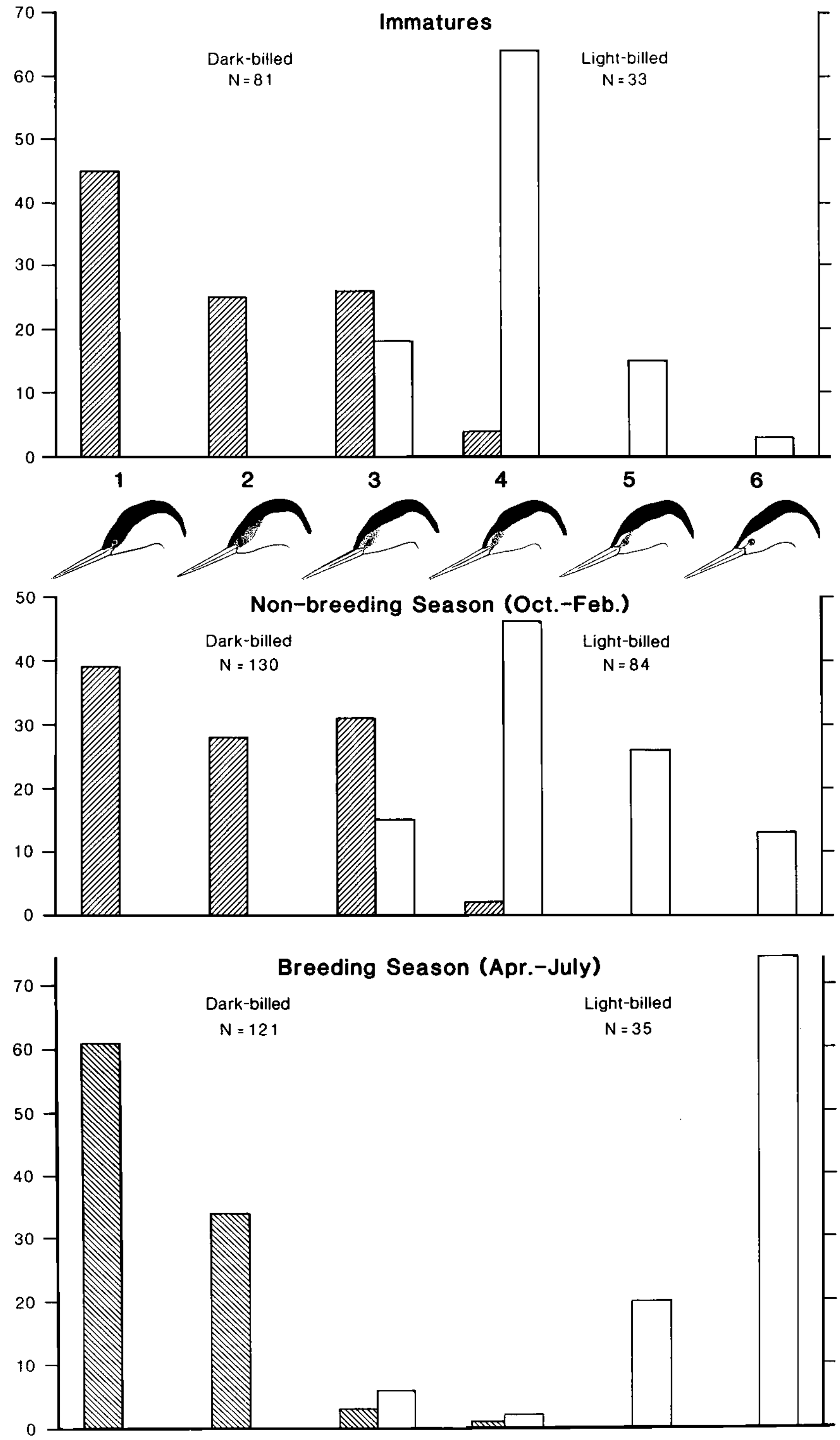


Fig. 2. Distribution of facial patterns by age, season, and color phase (data from museum skins).

TABLE 1. Geographical variation in Western Grebes.

	Mexico		Southern U.S.		Northern U.S.		Canada	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Males								
Wing length	18	186.7 (4.34)	18	196.9 (5.47)	39	201.5 (5.73)	32	205.8 (4.68)
Tarsal length	19	72.92 (3.01)	18	77.61 (2.97)	36	77.86 (2.75)	33	77.76 (2.48)
Bill from nostril	19	55.49 (2.76)	16	60.48 (2.82)	33	60.83 (2.83)	30	62.73 (3.33)
Bill depth	19	11.86 (0.50)	16	13.04 (0.65)	34	12.93 (0.71)	30	12.70 (0.62)
Females								
Wing length	14	174.1 (4.37)	13	184.4 (3.48)	21	190.5 (5.40)	26	192.4 (5.21)
Tarsal length	16	66.62 (1.91)	14	71.58 (1.70)	21	71.43 (2.51)	26	71.14 (3.31)
Bill from nostril	15	46.99 (2.58)	14	52.20 (2.20)	17	53.30 (2.65)	25	53.45 (2.69)
Bill depth	14	9.35 (0.48)	11	10.17 (0.69)	20	10.29 (0.74)	25	9.95 (0.73)

grebes, the remiges are molted simultaneously. The condition of these feathers was recorded as out (0), partially but less than half grown (1), more than half but not fully grown (2), or fully grown (3).

Skeletal measurements.—In addition to the measurements taken on the birds before preparation, the following measurements were made with dial calipers to the nearest 0.1 mm: the overall length of the ulna, femur, tibiotarsus, tarsometatarsus, and all but the ungual phalanges of the toes; the widths of the proximal and distal ends of the femur, tibiotarsus, and tarsometatarsus; the least width of the shaft of the last three elements; the length of the cnemial crest of the tibiotarsus; and the height and basal width of the patella. The lengths of the second, third, and fourth toes were estimated by adding the lengths of the phalanges (excluding the ungual ones). This gives a somewhat higher figure than the sum of these bones when articulated but is just as useful for the comparisons that we made.

Color characters.—For all plumage color characters analyzed except color over eye (which was either black or white), we selected a graded series of two to seven reference specimens. The specimens in each group were assigned consecutive numbers, beginning with 1 for the darkest state for the character. The characters, their states, and the UMMZ catalogue numbers of the reference specimens for each character are listed in the Appendix. The extent of plumage variation within and between the two color phases was determined by comparison of each pelt of the Herman series directly with those of each reference series, and we jointly assigned to it the number of the reference specimen it most closely matched. We did not analyze variation in the back feathers and their edgings (Storer 1965) because of seasonal changes due to wear and fading.

For the computer analyses we separated the specimens into the light and dark phases using bill color, which does not change with season. The bills of dark-phase birds have a layer of melanin that is diffused throughout the insides of both the upper and lower rhamphothecae. This gives the bill the dull yellowish-green appearance in life, rather than the bright orange-yellow of light-phase birds. The melanin of the bills of light-phase birds is largely confined to a narrow strip along the dorsal part of the upper rhamphotheca. From the outside, this dark strip contrasts sharply with the rest of the bill. Intermediates between these two types were rare and usually were immature birds. Long periods of freezing or drying may cause large irregular blotches of yellow to appear on the bills of dark-phase birds, presumably because the inside melanin layer separates from the rhamphotheca. For this determination, we therefore removed the rhamphothecae from the bills and viewed them from the inside.

RESULTS

GEOGRAPHIC VARIATION

Museum specimens taken in the breeding season were divided into four populations: Mexico exclusive of Baja California, Baja California and the United States south of 40°N, the United States north of 40°N, and Canada. (Further subdivisions were not made because of the paucity of breeding birds in the museum samples.) The sample sizes, means, and standard deviations for the four measurements for each population are shown in Table 1.

The Mexican birds were smaller than those of all the more northern populations in all measurements (two-tailed *t*-tests, $P < 0.001$). In the three northern populations there is a cline of increasing wing length from south to north. The differences between males in adjacent populations were significant at the 0.01 level, as were those between females of the southern and northern United States populations. Although the difference between the northern

TABLE 2. Size (mm) vs. color phase in the Mexican population.

	Dark phase		Light phase		Significance level (*t*-test)
	n	Mean (SD)	*n*	Mean (SD)	
Males					
Wing length	5	185.0 (2.45)	11	188.1 (4.46)	0.17
Tarsal length	6	72.08 (2.45)	11	73.54 (3.50)	0.38
Bill from nostril	5	55.56 (2.04)	12	55.02 (3.01)	0.72
Bill depth	5	11.98 (0.53)	12	11.73 (0.45)	0.33
Females					
Wing length	6	174.3 (4.18)	8	174.0 (4.78)	0.89
Tarsal length	6	67.22 (1.88)	10	66.26 (1.93)	0.35
Bill from nostril	6	47.20 (1.11)	9	46.86 (3.29)	0.81
Bill depth	6	9.55 (0.59)	8	9.20 (0.34)	0.19

United States population and that of Canada was in the same direction, it was not statistically significant.

Neither of the two northernmost samples contained enough light-phase birds to test for differences between the phases. Therefore, only the Mexican and Clear Lake samples were used. In the small Mexican sample, there were no significant differences between the phases (Table 2). In the Clear Lake sample, the dark birds averaged larger than the light birds in all four dimensions. Differences in tarsal length in both sexes and in bill depth in females were not significant (Table 3). In most measurements, the dark-phase birds were more like the birds from the northern United States or Canada, and light-phase birds like those from the southern United States. This suggested that many of the dark-phase birds collected on Clear Lake may have been wintering birds from northern populations. However, dark-phase birds taken in the breeding season (May–October) showed similar results.

AGING

The breeding season for Western Grebes on Clear Lake is much longer than in Canada. This was reflected in our finding birds in the Herman sample with incompletely ossified tarsometatarsi from 14 August to 27 March. In one bird taken 28 December at Clear Lake, the proximal epiphysis was not yet fused to the shaft of the bone. The length of the breeding season and consequently the occurrence in winter and spring of young birds differing as much as six months in age complicated the analysis of molt in the Clear Lake sample.

In 168 of 180 birds, the ossification of the Pons supratendineus was in agreement with the ossification of the tarsus. Of these, 146 were "adults" and 22 immatures. In 5 of the remaining 12, the tarsometatarsus showed the adult condition, and the bridges on one or both sides were incompletely ossified. This indicated that ossification of the supratendineal bridge may be completed later than that of the tarsometatarsus. The condition of the remaining seven birds was not clear, but of these, only one appeared not to follow the general pattern. It was a bird with a possibly unfused tarsometatarsus and a probably ossified bridge. Oddly, asymmetry was apparent in the amount of ossification of the bridge in five birds: either the bridge on the right or left tibiotarsus was noticeably more ossified than its mate.

MOLT

The molts and plumages of the Western Grebe have not been well described. What has been known was summarized by Palmer (1962: 95). The Definitive Alternate (adult nuptial) plumage is "acquired by [a] Prealternate molt in spring, involving (so far as is known) mainly [the] head and neck." The Definitive Basic (adult winter) plumage is "acquired by [a] complete Prebasic molt in fall, the flight feathers shed simultaneously (a flightless period). A bird flightless in midwinter, owing to molting of rectrices [sic], was examined by J. Munro (W. E. Godfrey) .... In spring, a partial molt [in first-year birds] produces the black crown .... 'In this first nuptial plumage adults and young are practically indistinguishable.'" Subsequently, Sibley (1970: 373) found Western

TABLE 3. Size (mm) vs. color phase in the Clear Lake population.

	Dark phase		Light phase		Significance level (*t*-test)
	n	Mean (SD)	*n*	Mean (SD)	
Males					
Wing length	34	203.4 (3.81)	15	198.6 (3.56)	0.001
Tarsal length	41	78.14 (2.49)	18	77.44 (2.41)	0.32
Bill from nostril	35	62.61 (2.58)	17	60.25 (2.48)	0.003
Bill depth	39	13.59 (0.60)	18	12.97 (0.49)	0.001
Females					
Wing length	22	190.0 (5.34)	13	183.9 (3.33)	0.001
Tarsal length	25	71.70 (1.96)	14	71.35 (1.36)	0.56
Bill from nostril	22	53.16 (2.59)	14	50.41 (2.21)	0.003
Bill depth	22	10.47 (0.42)	14	10.21 (0.43)	0.081

Grebes with molted or growing primaries in late January and early February in southern California.

Remiges.—Specimens of grebes taken in the period of molt and regrowth of the remiges are rare (Stresemann and Stresemann 1966), and the timing of the molt of the remiges in grebes is not well established. The California sample obtained from Herman is remarkable in containing 21 birds in various stages of the molt and regrowth of the remiges. Adult males with freshly molted remiges were taken 24 July (1), 31 August (2), 21 September (2), and 18 October (1) and with growing remiges 31 July (1), 14 (1) and 21 (2) August, and 5 (1), 21 (2), and 23 (1) September. Adult females with freshly molted remiges were taken 24 July (1) and 31 August (2) and with growing remiges 21 August (2) and 5 September (2). In addition, a female from Santa Barbara with partially grown remiges was taken 1 February 1969. It is thus evident that the remiges are molted by some birds in midwinter and by others in late summer. The age of birds molting in midwinter is unknown.

Thirteen birds with adult skeletal characteristics had worn primaries in the period from 21 June to 23 September, and one had fresh primaries by September. Two probable adults had worn primaries on 17 July and one, fresh primaries on 21 September. Six possible one-year-olds had fresh primaries in the period from 17 July to 15 September. Thus adults go into the breeding season with worn primaries, presumably grown the preceding summer, whereas at least some yearlings begin the breeding season with fresh primaries. These may be birds that have had a midwinter molt of the remiges. It is unclear whether these birds again molt their remiges in summer, six months or so after the midwinter molt. Two birds from the Herman sample (UMMZ numbers 204,564 and 204,567) taken 5 September and 21 August were growing their remiges, but the evidence for their being yearlings was not entirely convincing.

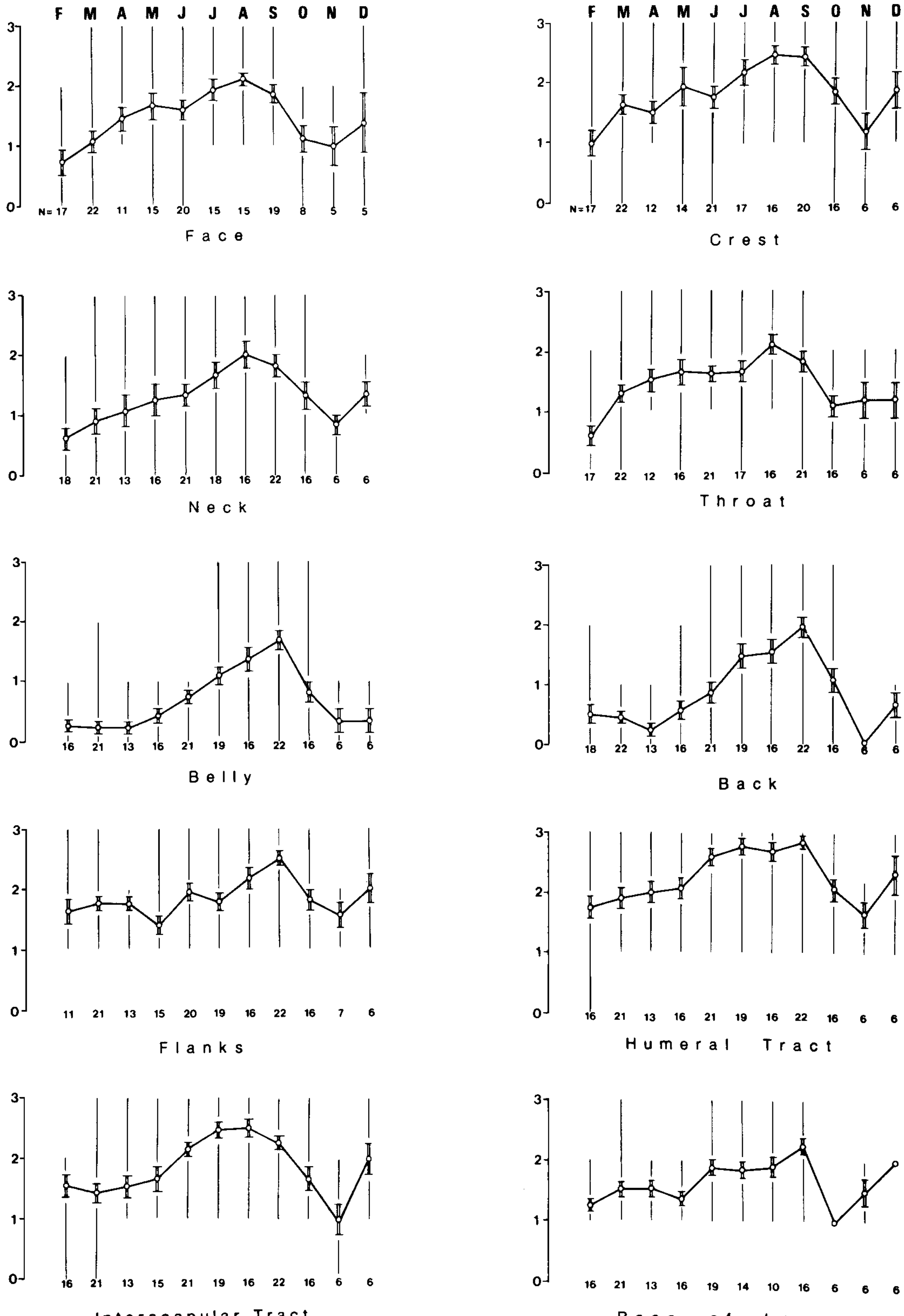
Crest.—Birds with the crest in the process of molt were found throughout the year, and only 6% of the sample showed no molt in this area. The peak of the molt occurred during the period of the annual molt, June through October, but there was also considerable molt of the crest from March through May, the latter presumably the prenuptial (Prealternate) molt suggested by Palmer (1962: 95). (For mean monthly scores for molt of this and other areas, see Fig. 3.)

Face.—The molt pattern of the face was similar to that of the crest, although the rankings were somewhat lower. This is also consistent with the occurrence of a prenuptial molt.

Throat.—The molt pattern of this area was hardly distinguishable from that of the face.

Neck.—Some birds were growing neck feathers each month, but the peak of the molt coincided with the annual molt, being greatest from July through September.

Belly.—The molt of the belly feathers was rarely more than light, except at the time of the annual molt (July through September). These feathers evidently are molted once a year and, compared with other tracts, in relatively small numbers at any time. These are the feathers that are constantly in contact with the water and presumably are of vital importance in keeping water from penetrating to the skin. For this reason, selection can be expected to have favored a molt of few feathers at a time rather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Humeral Tract
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Interscapular Tract
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Base of Leg

than an extensive molt that might radically reduce waterproofing. In this connection, it should be noted that the belly feathers also are the first to develop in young grebes.

Back.—The seasonal molt pattern of the back was similar to that of the belly, but there were relatively more birds in the heavier molt categories. This shift may reflect less rigorous selection for a gradual molt like that in the molt of the belly feathers.

Flanks.—Some flank feathers were growing in all birds in the series, moderate molt being the most frequent category. In only one month (May) was light molt (1) more frequently found, and in one (September) heavy molt (3) was the most frequent. Virtually every grebe of all species that Storer has examined (unpubl. data) has had growing flank feathers. These feathers are presumably a major source of those swallowed by the birds and retained either in the lumen of the stomach or as the separate pyloric plug (Storer 1969: 185).

Humeral tract.—Like the flanks, this area (with one exception) was always in molt, and it was the only area in which heavy molt (3) was the most frequent category. Heavy molt was found in every month except November. [The small sample for that month (6) probably accounts for this discrepancy.] Also, like the flanks, this tract probably is a major source of feathers for the stomach.

Interscapular tract.—This tract also appeared to undergo molt almost constantly. Only 4 of 171 birds (2.3% of the sample) showed no molt in this area. Light molt predominated in most months, but the peak of the molt coincided with the annual molt, occurring from June through September.

Base of leg.—The area around the distal end of the tibiotarsus was constantly in molt. The light molt category (1) was the most frequent, except during the period of the annual molt (June through September).

Color Characters—Herman Series

Facial characters (Figs. 1, 4).—The border separating the black and white feathers on the face frequently intersected the eye on nonbreeding adults. Such intermediacy in facial plumage (character state 2) was especially common for light-phase birds, for which it was the most frequent character state (Fig. 4). However, adults taken in the breeding season (here defined as from late April–October) showed little intermediacy and no overlap.

In all 87 dark-phase birds, the black of the top of the head either intersected or came below the eye. Only 1 of 20 adult light-phase birds in the breeding season had this character state, but outside the breeding season 15 of 31 adults and 10 of 12 immatures of the light phase were similar to the dark-phase birds in this state.

Breeding birds showed no overlap in the color pattern behind the eye. All dark-phase birds were rated 1, 2, or 3, whereas all light-phase birds were rated 5. Outside the breeding season 2 of 35 dark adults, 1 of 10 dark immatures, 14 of 30 light adults, and 11 of 13 light immatures were ranked 4, indicating a moderate degree of overlap.

Breeding adults showed no overlap in the color below the eye. All dark birds were rated 1, 2, 3, or 4, whereas all light adults were rated 6. In the nonbreeding season there was a shift of light-phase birds toward the dark phase: 11 of 31 adults and 9 of 12 immatures were ranked 5. The only overlap was a light-phase immature that was rated 4, as were 11 dark-phase birds, 6 adults and 5 immatures.

Breeding adults showed a complete segregation by color phase in the color of the lores. Dark-phase birds all had dark or light gray lores, whereas light-phase birds all had white lores. This segregation also held for the nonbreeding season, with the single exception of a light-phase juvenile with light gray lores taken 28 November.

Mottling of the lores was uncommon. In the breeding season, only two (both dark phase) of the 62 adults had this character state. The sample from the rest of the year had a higher proportion of birds with mottled lores: 1 of 34 dark adults, 1 of 11 dark immatures, 2 of 30 light adults, and 5 of 13 light immatures. The differ-

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Fig. 3. Mean monthly molt scores for various parts of the body (phases combined). Bars show standard error and ranges. Ordinal scores ranged from 0 (no molt) to 3 (heavy molt). No birds were collected in January.

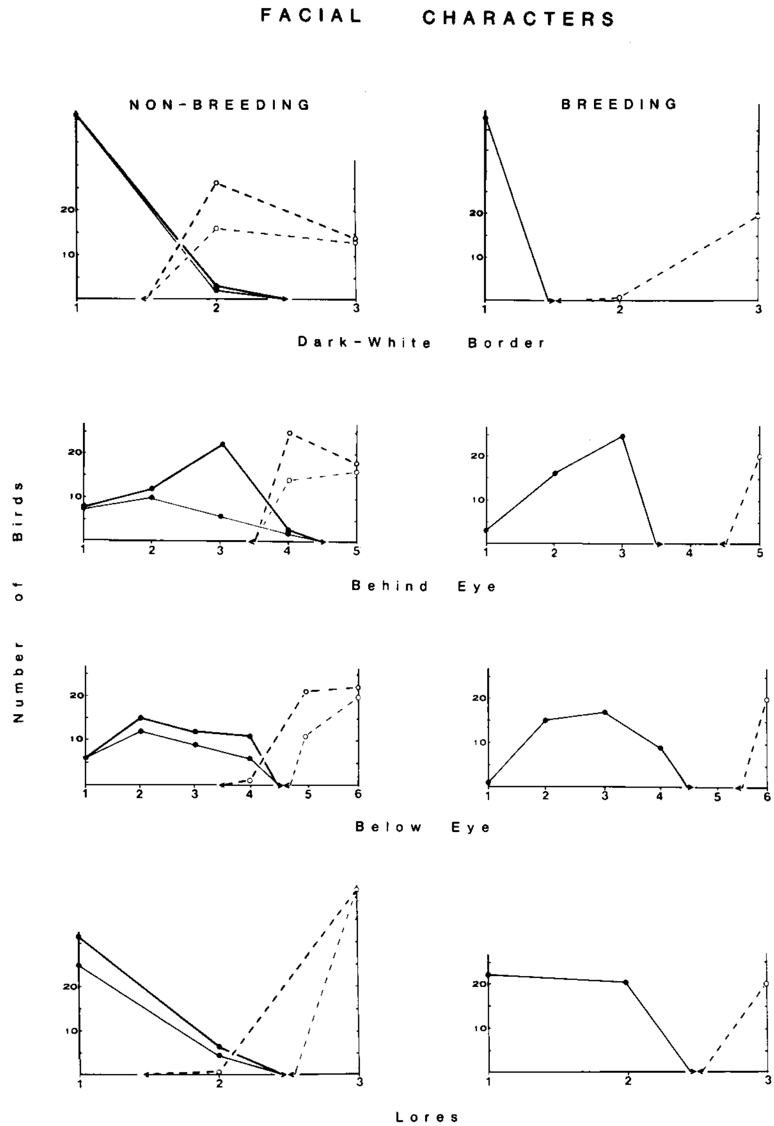

Fig. 4. Distribution of four facial color characters by color phase and season. Solid lines represent dark-phase (dark-billed) birds; dashed lines, light-phase birds. Heavier lines and dashes on graphs of nonbreeding birds represent total sample, lighter lines and dashes total adults. Arrows indicate that no birds were assigned to remaining color states. Numbers on abscissa represent states of color characters (darkest state of each is on the left; see Appendix for description of states).

ences between light adults and immatures were significant ($\chi^2 = 7.6$, $P < 0.05$), but mottling occurred in both age groups of both phases.

Other characters (Figs. 5, 6).—There was complete overlap between the phases in the amount of gray or white at the base of the crest, although the dark birds tended to have darker bases (85 of 90 birds in the two darkest classes). These trends apparently were not related to season or age, although light juveniles had a relatively higher proportion in the lightest category (4) and a lower proportion in category 3 than adults.

The amount of white at the base of the scapulars tended to sort out by phase, with considerable overlap. About 23% of the dark birds and

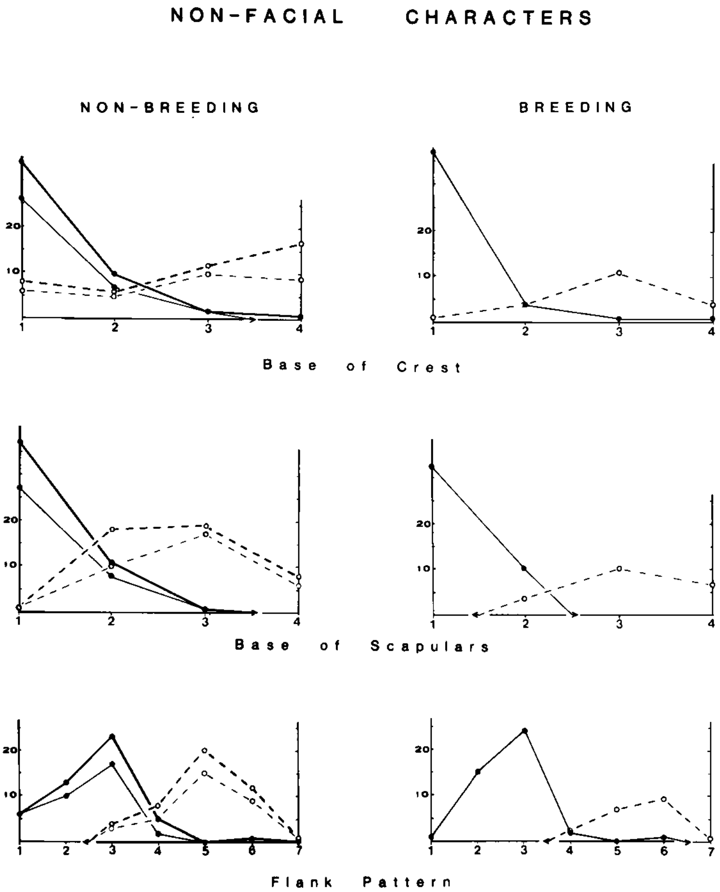

Fig. 5. Distribution of three nonfacial body characters by color phase and season. For explanation of symbols and lines, see legend to Fig. 4.

38% of the light birds were in category 2 (of 4). No conspicuous seasonal differences were apparent.

The flank pattern varied greatly, but few birds had either the dark or light extremes of the 7 categories. Again there was considerable overlap, but there were concentrations of dark birds in the dark categories (72 of 81 in categories 1–3) and of light in the light categories (50 of 65 in categories 5–7). There were no conspicuous age or seasonal differences. In addition to the variation from dark to light, there was much individual variation in the pattern of the dark spots. Such individual variation may be used by birds as individual identification marks.

The amount of white in the lesser upper wing coverts showed a large overlap between the phases (Fig. 6). Although 60% of the dark birds were in category 1 (of 4) and 50% of the light birds were in category 3, 36% of the birds in each phase were in category 2.

The lesser underwing coverts also showed complete overlap, some birds of each phase being in each category. The majority (53%) of the dark birds and 25% of the light birds were in the intermediate category, whereas the majority of the light birds (72%) was in the lightest category (3) with 12% of the dark birds.

The greater underwing coverts were unique among the characters studied in that the greatest number of birds in both phases was found in the lightest category (3). There was still a tendency, however, for more dark birds to be in the darker categories. There appeared to be no consistent age or seasonal differences in the distribution of any wing-covert character by color phase.

The wing pattern (Figs. 6 and 7) also varied

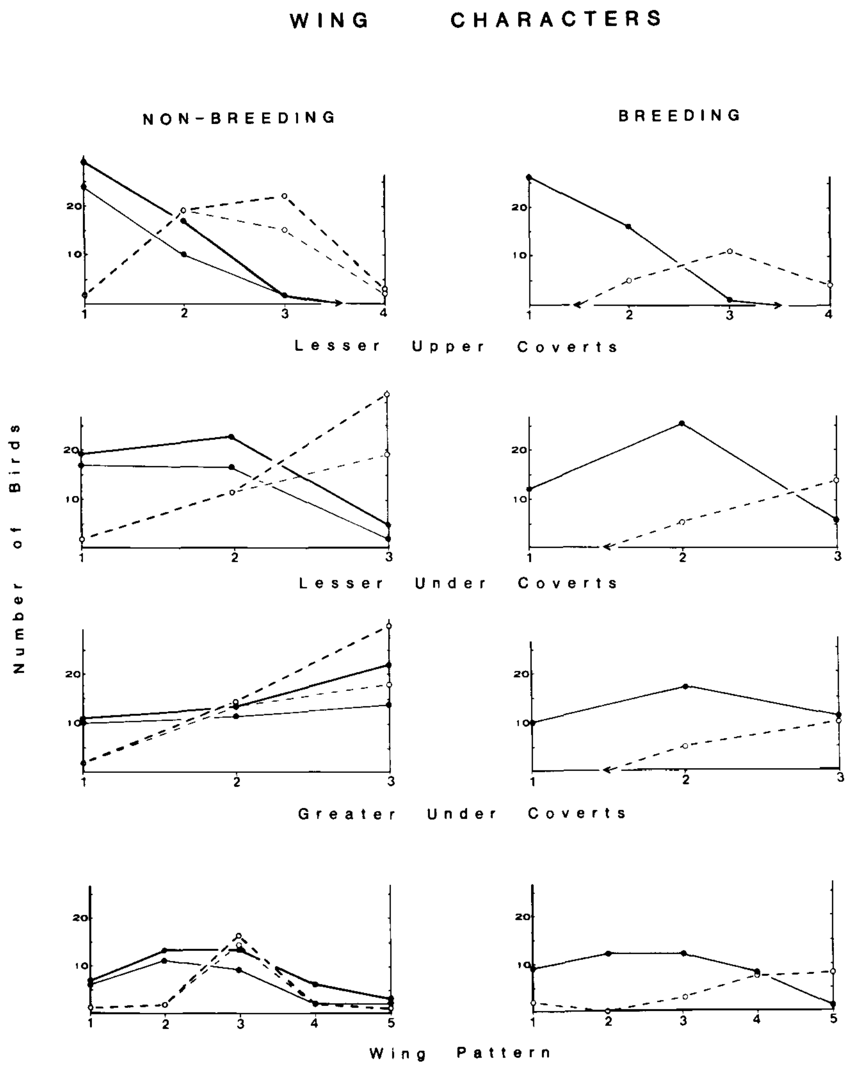

Fig. 6. Distribution of wing characters by color phase and season. For explanation of symbols and lines, see legend to Fig. 4.

greatly and there was complete overlap between the phases, birds of both phases being found in each category. While there was a tendency for dark birds to have less and light birds more white in the wing, the median category (3) contained 31% of the dark birds and 30% of the light ones.

Skeletal Measurements—Herman Series

Comparison of the measurements of the leg bones and phalanges showed no significant differences between birds of the two color phases (Table 4). In addition, the ratios of the lengths of the toes to that of the tarsometatarsus did not differ significantly between the sexes.

The differences in ulna length between birds of the two phases was highly significant (t-test, $P < 0.01$) in both sexes. This confirms the difference in wing measurements made from freshly thawed birds (Table 3).

On the other hand, the length of the maxilla from the anterior edge of the nostril measured on the skull did not differ as significantly as did the bill-from-nostril measurement on freshly thawed birds (Table 3). Because of the

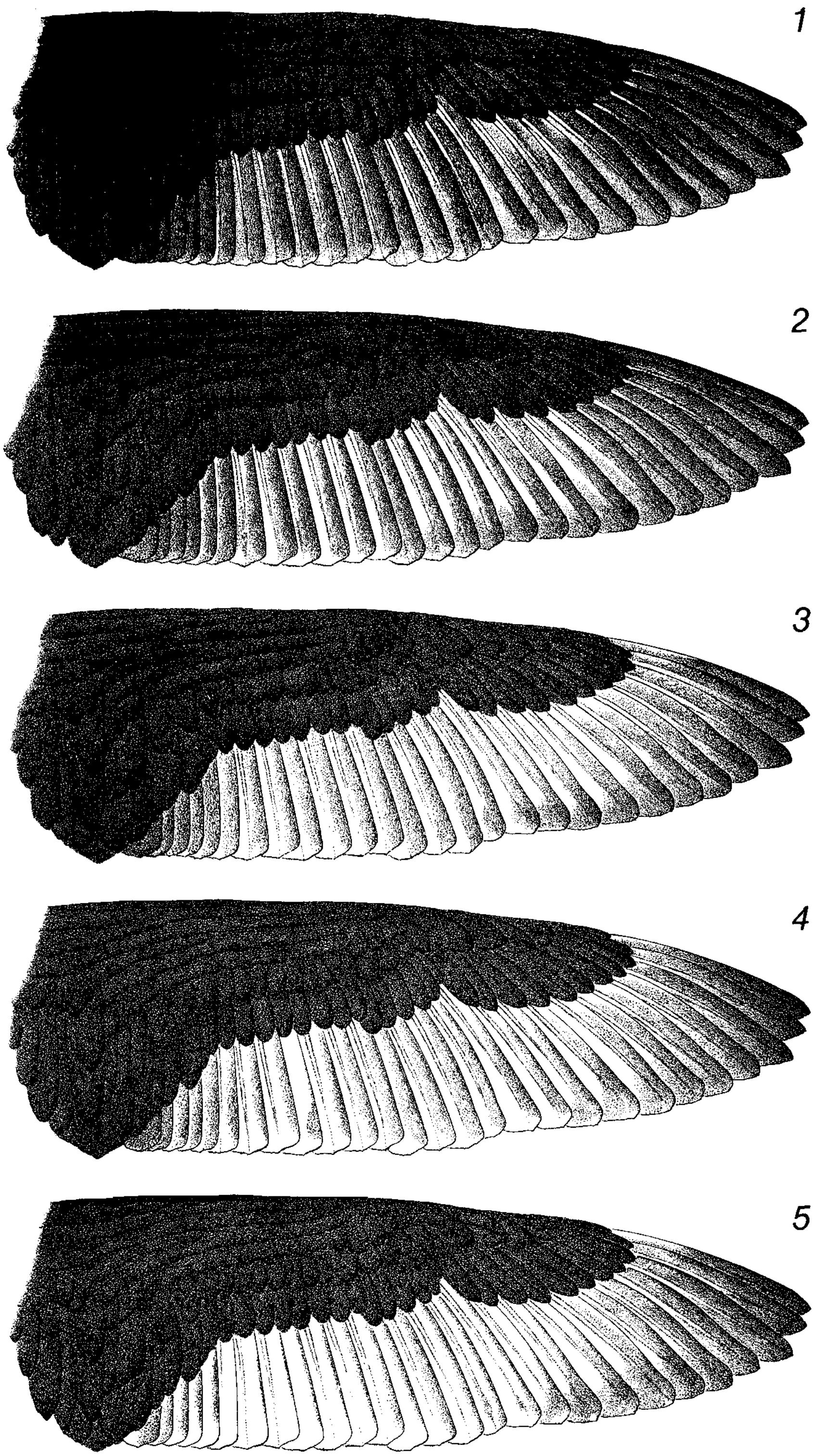

Fig. 7. Wing patterns of reference series of Western Grebes.

continual growth and wear of the rhamphotheca, the former measurement is probably the more precise.

Other Museum Specimens

Data on color patterns collected by Storer from study skins in various museums and from wings saved with the skeletons from Lake Newell, Alberta were also analyzed and compared with the Clear Lake results. The data from museum study skins agreed with those from the Herman series in showing a lesser degree of intermediacy in facial characters between the phases in breeding adults than in immature and winter birds (Fig. 2).

The color phase of the Lake Newell birds was not determined, but because the Canadian populations consist of approximately 99% dark-phase birds, we compared the Lake Newell birds only with the dark birds from Clear Lake. In the wing pattern and all three characters of the coverts, the Lake Newell birds showed more white on the average than the Clear Lake birds. We attribute much of this difference to the fact that immature birds tend to have more white in these areas than adults (Table 5). The Lake Newell sample is strongly biased in favor of immatures (94 to 23), whereas the opposite is true for the Clear Lake birds (12 to 79). In both samples there are relatively more immatures in the lighter categories than in the darker ones.

Nearly one fourth (22%) of the Lake Newell sample had a white patch on or near the leading edge of the wing. This was the result of white on the outer web of one or more of the outer primaries. This extended from the base of the feather well beyond the tips of the primary coverts and was separated from the white of the inner primaries and secondaries by the black of the primaries between. The white patch involved one (12 birds), two (6), three (7), or four (1) primaries, beginning with either the outer or next primary.

Discussion and Conclusions

The picture of the molt cycle shown by the Herman sample is somewhat blurred by the extended breeding season on Clear Lake. Even so, the general pattern presented by Palmer (1962: 95) appears to be correct in that there is an obvious concentration of the molt of all areas from July through September and a second molt, largely confined to the head, from March to May. The face patterns of light- and dark-phase birds show virtually no overlap in the breeding season, but there is a tendency for intermediacy or overlap in these characters in winter and in immature birds. This is consistent with the evidence for a partial prenuptial molt.

Given that preferential mating occurs within phases, selection would be expected to favor individuals having a breeding plumage pattern that is nonambiguous with respect to color-phase type. Of the differences in plumage color that we studied in birds of the two color phases, only the facial characters and flank pattern are readily apparent in the living bird. The importance of eye contact in courtship displays (Nuechterlein and Storer 1982) indicates that facial differences might be the most effective visual characters for this purpose. These characters show virtually no overlap during the breeding season.

In contrast to facial characters, there is considerable overlap between the phases in all other characters. Of these, only the flank pattern is ordinarily visible and therefore subject to selective pressure for divergence. The variation in the flank pattern, while showing overlap in overall darkness or lightness, is subject to great individual variation in the pattern of spots, which may result from selection favoring differences that permit individual recognition by the birds.

The feathers of the flanks, humeral tracts, interscapular tracts, and base of the legs appear to undergo molt almost continuously. At least in the case of the flanks, this situation appears to be the rule in grebes. This continuous molt makes possible the ingestion of feathers throughout the year. We have seen no behavior indicating that feathers are actually plucked by the grebes; instead, the feathers swallowed appear to be those that are lost naturally during preening. Frequent preening of this area and subsequent feather loss may possibly stimulate molt. In any case, the constant molt and regrowth of feathers for use in the stomach is probably unique to grebes.

The wide variation in the wing patterns of Western Grebes contrasts with the relatively fixed wing patterns found in many water birds. Selection for a fixed, species-specific pattern probably is not strong in Western Grebes because these birds migrate at night, rarely fly at

TABLE 4. Skeletal measurements (mm) from Clear Lake birds by sex and color phase.

	Dark females		Light females		Dark males		Light males	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Femur								
Length	11	43.16 (1.45)	10	42.70 (1.82)	16	47.16 (1.63)	15	46.27 (1.76)
Prox. width	12	13.23 (0.48)	11	13.46 (0.70)	16	14.69 (0.66)	17	14.41 (0.47)
Shaft width	12	5.20 (0.20)	11	5.20 (0.31)	16	5.69 (0.28)	15	5.54 (0.18)
Dist. width	11	14.05 (0.40)	11	14.08 (0.62)	16	15.36 (0.50)	17	15.19 (0.54)
Patella								
Length	12	20.10 (1.28)	11	19.53 (1.69)	16	21.46 (1.28)	17	21.55 (1.20)
Width	12	8.97 (0.37)	11	8.80 (0.67)	16	9.60 (0.58)	16	9.44 (0.52)
Tibiotarsus								
Length	12	133.27 (2.78)	9	133.87 (5.55)	16	143.84 (5.45)	13	142.75 (3.91)
l to artic.	12	113.67 (2.61)	9	114.04 (3.95)	16	123.36 (4.52)	15	122.05 (3.43)
l crest	11	19.59 (0.74)	11	19.76 (1.59)	12	20.79 (1.88)	15	20.81 (0.90)
Prox. width	12	9.97 (0.30)	11	10.03 (0.41)	16	10.90 (0.29)	17	10.78 (0.37)
Shaft width	12	5.53 (0.30)	11	5.70 (0.31)	16	6.17 (0.24)	17	6.05 (0.22)
Dist. width	12	10.11 (0.38)	11	10.18 (0.61)	16	11.15 (0.30)	17	11.09 (0.41)
Tarsometatarsus								
Length	12	71.68 (1.94)	11	72.11 (2.20)	16	77.21 (2.73)	17	77.43 (2.56)
Prox. width	12	12.13 (0.38)	11	12.31 (0.74)	16	13.40 (0.30)	17	13.38 (0.45)
Shaft width	12	3.38 (0.18)	11	3.25 (0.39)	16	3.67 (0.26)	17	3.59 (0.15)
Dist. width	12	8.08 (0.32)	11	8.11 (0.48)	16	8.91 (0.34)	17	8.86 (0.23)
Digit I	7	11.86 (0.74)	11	12.32 (0.56)	15	12.38 (0.92)	14	12.59 (0.67)
Digit II								
Phalanx 1	12	25.23 (0.92)	11	25.42 (0.95)	16	26.73 (1.14)	17	26.54 (0.87)
Phalanx 2	12	23.80 (0.96)	11	24.53 (1.29)	16	26.08 (0.97)	17	25.98 (0.66)
Digit III								
Phalanx 1	12	24.28 (0.92)	11	24.68 (1.08)	16	25.94 (1.15)	17	25.91 (0.76)
Phalanx 2	12	18.01 (0.61)	11	17.92 (0.76)	16	18.83 (0.69)	17	18.92 (0.65)
Phalanx 3	12	17.41 (0.62)	11	17.67 (0.95)	16	18.82 (0.82)	17	18.88 (0.71)
Digit IV								
Phalanx 1	12	27.94 (1.22)	11	28.36 (1.23)	16	29.88 (1.57)	17	30.05 (1.00)
Phalanx 2	12	13.51 (0.51)	11	13.44 (0.67)	15	14.03 (0.49)	17	14.29 (0.51)
Phalanx 3	12	12.91 (0.76)	11	13.00 (0.51)	15	13.55 (0.67)	17	13.30 (0.57)
Phalanx 4	11	14.73 (0.77)	11	14.82 (0.85)	16	15.74 (0.78)	17	15.82 (0.50)
Digit II								
Total length	12	49.03 (1.80)	11	49.95 (2.12)	16	52.80 (2.04)	17	52.52 (1.44)
Digit III								
Total length	12	59.70 (1.96)	11	60.27 (2.66)	16	63.58 (2.47)	17	63.71 (1.74)
Digit IV								
Total length	11	69.08 (2.90)	11	69.61 (2.91)	15	73.02 (2.97)	17	73.46 (2.03)
Digit I/TTL[a]	12	0.76 (0.002)	9	0.76 (0.004)	16	0.77 (0.003)	13	0.77 (0.003)
Digit II/TTL	12	0.38 (0.007)	9	0.38 (0.012)	16	0.37 (0.011)	13	0.37 (0.006)
Digit III/TTL	12	0.45 (0.010)	9	0.45 (0.015)	16	0.44 (0.013)	13	0.45 (0.012)
Digit IV/TTL	11	0.52 (0.018)	9	0.52 (0.018)	15	0.51 (0.015)	13	0.52 (0.013)
Ulna								
Length	23	101.37 (3.27)	13	98.39 (1.86)	38	109.45 (3.36)	18	106.19 (3.37)
Bill (skeleton)	20	40.74 (2.08)	12	39.60 (2.89)	41	48.73 (2.89)	18	46.40 (2.92)

[a] TTL = length of tibiotarsus.

other times, and otherwise show the wing pattern only during wing stretching, a comfort movement with no known social function. The winter sample shows more intermediacy than the sample taken in the breeding season. Dark juveniles tend to have more and light juveniles less white in the wings than adults. Whether juveniles acquire different wing patterns after their first wing molt or whether this apparent difference results from the small sample size

TABLE 5. Wing characters of Clear Lake and Lake Newell birds by age.

		Clear Lake		Lake Newell	
Character	State	Adult (%)	Immature (%)	Adult (%)	Immature (%)
Lesser upper coverts	1	50 (63)	5 (42)	6 (26)	39 (42)
	2	26 (33)	7 (58)	12 (52)	50 (54)
	3	3 (30)	0 (0)	5 (22)	4 (9)
	Total	79	12	23	93
Lesser under coverts	1	29 (37)	2 (18)	3 (14)	3 (3)
	2	41 (53)	6 (55)	19 (86)	60 (67)
	3	8 (10)	3 (37)	0 (0)	26 (26)
	Total	78	11	22	89
Greater under coverts	1	20 (26)	1 (9)	2 (9)	1 (1)
	2	28 (36)	2 (18)	10 (43)	6 (6)
	3	30 (38)	8 (73)	11 (48)	86 (93)
	Total	78	11	23	93
Wing pattern	1	15 (21)	1 (8)	5 (22)	3 (3)
	2	23 (32)	2 (17)	13 (57)	16 (17)
	3	21 (20)	4 (33)	3 (13)	37 (40)
	4	10 (14)	4 (33)	2 (9)	32 (34)
	5	3 (4)	1 (8)	0 (0)	5 (5)
	Total	72	12	23	93

remains to be determined. Some birds of unknown age molt their remiges in midwinter.

The morphological differences between light- and dark-phase birds on Clear Lake, California correspond closely to those between the birds of the southern United States and the more northern populations, respectively. The clinal increase in wing length without a parallel change in tarsal length indicates a relatively longer wing in the north, which presumably is related to the extensive migrations undertaken by the northern birds. The differences in the birds of the two color phases on Clear Lake may be the result of colonization of this lake by dark-phase northern birds. If the dark-phase birds of the Clear Lake population colonized the lake from the north, the morphological differences between birds of the two phases may not be representative of the species as a whole.

In a sample of 40 birds from the Bear River marshes, Utah that was evenly divided between males and females and between dark- and light-phase birds, Ratti et al. (1983) found the length of bill from nostril was significantly greater in dark-phase birds of both sexes. Wings were longer, but not significantly so, in dark-phase birds of both sexes. Total culmen length and bill depth were significantly greater in females of the dark phase. Even at Bear River, the birds nest in an artificially maintained habitat, and therefore the population may not be suitable for analyzing possible differences between the phases in a population where the two have been coexisting for a long period.

Lawrence (1950: 11) found that centrarchid fishes comprised the major part of the diet of Western Grebes on Clear Lake, but he did not analyze his data on food habits by sex or color phase. Feerer (1977: 84–87) examined stomach contents of the Herman sample from Clear and Topaz lakes and found centrarchids in 25 of the 31 stomachs containing identifiable prey, cyprinid fishes in 8, and crayfish in 2. The male grebes in this sample had ingested "significantly larger fish ($P < 0.01$) than female Western Grebes." This difference between the sexes in food habits is to be expected because of the sexual dimorphism, especially in the size of the bill. Feerer also found that stomachs from light-phase females contained "significantly smaller fish ($P < 0.05$)" than dark-phase females, although he found no significant differences between males of the two groups.

Nuechterlein (1981: 343–344) pointed out that light-phase birds tend to use "springing dives" (Lawrence 1950) more frequently than "level dives" and suspected that this was a result of their going deeper, which in turn resulted from "spatial segregation of the morphs during feeding." Light-phase birds generally tended to feed further from shore than dark-phase birds. These observations suggested possible adaptations for foraging at different depths, but analysis of measurements of the leg and toe bones (Table 4) indicates that there are no significant differences in size or proportion of the hind limb between birds of the two color phases. Thus no osteological differences have evolved in the leg to accompany this apparent behavioral difference.

A thorough study of the comparative ecology of birds of the two color phases of the Western Grebe has yet to be undertaken on a body of water that has not been considerably altered by man. The levels of Clear and Topaz lakes and of the Bear River marshes are artificially controlled. The widespread use of pesticides containing chlorinated hydrocarbons caused a disastrous decline in the Western Grebe population on Clear Lake and, presumably, other serious changes in the ecology of the lake. Most of the centrarchids taken by Western Grebes on Clear Lake [bluegills (*Lepomis macrochirus*), crappies (*Pomoxis* spp.), and largemouth bass (*Micropterus salmoides*)] are introduced, as is the carp (*Cyprinus carpio*), the most frequent prey of the grebe at the Bear River marshes (Lindvall 1976: 50). Introduction of exotic aquatic plants and destruction of plants by introduced fishes can radically alter habitats by increasing the turbidity of the water and altering the kinds, sizes, and shapes of available prey. Such factors could affect, and probably have affected, the balance between birds of the two color phases in the areas where they have been studied most intensively. For this reason, conclusions as to the comparative ecology of these birds must be regarded as tentative.

Intermediates in the facial pattern between the phases apparently are rare among breeding birds collected north of Mexico. Intermediacy is expressed almost entirely in the winter plumage. Ratti (1979: 575) suggests that "whitish lores on dark-phase birds are associated with winter plumage and the lores may darken in breeding plumage." Our evidence from the Herman series and from museum skins supports this idea and indicates that many of these "intermediates" are first-year birds. Feerer (1977: 83) listed nine birds "intermediate" between the two phases in plumage. He determined four of these to be immatures on the basis of the presence of down in the plumage. We received four of the remaining five, all of which had incompletely fused tarsometatarsi and hence were young birds. The fifth bird, collected 2 May 1968 on Clear Lake, had testes measuring 13 × 8 mm and 11 × 7 mm, considerably smaller than those of other males collected on that date. Thus, it is likely that this bird was hatched late in 1967 and had not attained full nuptial plumage by the time it was collected.

Feerer (1977) suggests that "significant clinal distributions in latitude and mean air temperature indicate that Western Grebe forms have a different climatic preference." Yet there are important exceptions to this clinal distribution hypothesis (Feerer 1977, Ratti 1979), and the possible selective factors favoring the different patterns of dark and light in the plumage have not been studied. The longer retention of white down by light-phase young as compared to their dark-phase counterparts (Ratti 1979) may be related to the prevention of heat stress through reflection of solar radiation. A similar argument might be made for the more extensive light edging of the back feathers of adult light-phase birds. Finally, differences in the amount of light and dark in the flanks might possibly be related to differences in the optimal pattern of countershading while diving at different water depths. These speculations might merit investigation.

The Western Grebe (*sensu lato*) represents a seldom documented stage in the speciation process. Both color phases occur sympatrically throughout the range of the species, and geographic variation in size occurs independently of phases. This parallel variation in size indicates that if the phases evolved as allopatric populations, their ranges merged completely before the behavioral isolating mechanisms developed or became effective. There is some evidence that males with an intermediate facial pattern experience difficulty in finding mates (Nuechterlein 1981), but this needs further documentation. The preponderance of dark-phase birds in the northern part of the species range and the longer wings of the northern birds are evidence that dark-phase birds may have arisen in the north when the species was divided [perhaps, as Feerer (1977: 62–66) suggested, during a period of arid climate when habitats at intermediate latitudes were absent] and that it subsequently merged with the smaller, light-phase birds to the south. [Feerer's (1977: 66) citing of "evidence of non-overlap of morphological characters of light-form and dark-form Western Grebes in Mexico

(Dickerman 1973) stemmed from a misinterpretation of Dickerman's table, in which Dickerman used *clarkii* for the whole Mexican population and *occidentalis* for those in the United States and Canada, rather than for the color phases.]

Before the merging of the populations, the Advertising call differences (Nuechterlein 1981) may have arisen in the two populations but with incompletely specific response to each. Thus, early in the merging process, differences in size presumably became fixed, and color characters not involving the face became mixed (if there was segregation of these characters in the period of isolation) within the various populations through extensive interbreeding between birds of the two phases. At present, reproductive isolation between the phases may be increasing, and with it the completion of the speciation process. Regardless of whether or not the forms arose in allopatry, it appears that the later stages of the process are occurring in sympatry. With speciation accomplished, selection can be expected to favor ecological differences, such as those Feerer and Nuechterlein have suggested, to become accentuated, and with them, morphological differences.

Taxonomic considerations.—From the recent studies of Feerer (1977), Ratti (1979), and Nuechterlein (1981), it is evident that in the Western Grebe populations in Utah and California a high degree of assortative mating occurs and that this is largely based on behavioral isolating mechanisms. Yet mixed pairs and birds of intermediate facial plumage are known to produce viable young (Nuechterlein unpubl. data), and males of the two phases frequently join in mutual courtship displays (Nuechterlein 1981). One important isolating mechanism is a difference in the number of notes in the Advertising call, which is used to attract mates. Were such assortative mating the rule throughout the range of the Western Grebe, the two phases could be said to have reached the level of species. However, in the northern part of the range, where the light-phase birds are rare, the phase-specific response to Advertising calls is lowered (Nuechterlein 1981), and in Mexico there appear to be many intermediates. Because breeding in Mexico often is nonseasonal, it is not clear whether these are young, birds in winter plumage, or hybrids. If the last is the case, we think the two forms may better be treated as color morphs.

A further complicating factor is that all birds of the Mexican population are distinctly smaller than those of the rest of the species' range. Thus, if the two phases are considered species, the dark-phase Mexican birds and the light-phase northern birds will require subspecific names. We prefer the conservative treatment, that is, to recognize the two phases as species if and when the color phases in the Mexican population are shown to be reproductively isolated from each other. In either case, it is the situation, not the nomenclature (or the potential length of life lists), that is of prime biological interest. We know of no other similar situation.

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APPENDIX. Western Grebe color character states and reference specimens from The University of Michigan Museum of Zoology (UMMZ).

Character	State	UMMZ number
Position of dark-white border	1—Below eye	No reference specimens
	2—Intersects eye	
	3—Above eye	
Color over eye	1—Black	No reference specimens
	2—White	
Extent of color behind eye	1—All dark	204,475
	2	204,574
	3	204,478
	4	204,530
	5—All white	204,476
Extent of color below eye	1—Much	204,475
	2	204,574
	3	204,478
	4	204,477
	5	204,459
	6—None	204,476
Color of lores	1—Dark gray	204,475
	2—Light gray	204,477
	3—White	204,468
Mottling of lores	1—Unmottled	None
	2—Mottled	204,459
Base of crest	1—Dark gray	204,475
	2—Light gray	204,477
	3—Mottled	204,476
	4—White	204,468
White bases to scapular coverts	1—None	204,558
	2—Little	204,550
	3—Moderate	204,473
	4—Much	204,485
Flank pattern	1—Solid dark	204,553
	2	204,551
	3	204,552
	4	204,469
	5	204,476
	6	204,468
	7—Small dark spots	204,485
White bases to lesser upper wing coverts	1—No white	204,554
	2—Small centers	204,552
	3—Medium centers	204,473
	4—Large centers	204,469
Lesser under wing coverts	1—Heavy dark edges	204,554
	2—Thin dark edges	204,551
	3—All white	204,485
Greater under wing coverts	1—Gray	204,558
	2—Speckled	204,553
	3—White	204,485
Wing pattern	1—Darkest	204,558
	2	204,554
	3	204,551
	4	204,548
	5—Lightest	204,485