ORNIS SCANDINAVICA 16: 253–260. Copenhagen 1985

Moult patterns and moult migration in the Black-necked Grebe Podiceps nigricollis

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Storer, R. W. and Jehl, J. R., Jr. 1985. Moult patterns and moult migration in the Black-necked Grebe *Podiceps nigricollis*. – Ornis Scand. 16: 253–260.

In late summer, hundreds of thousands of Black-necked (Eared) Grebes *Podiceps nigricollis* assemble on Mono Lake, California, where they undergo their annual (Prebasic) moult. Here, both adults and subadults have a complete moult in contrast to the juveniles which replace all but the remiges. This compressed, intense moult is believed to be an adaptation for exploiting the superabundant food source (brine shrimp, *Artemia* sp.) that is available in summer and autumn. No other grebe species is known to have so impressive a moult migration. Compared with moult migrations of anatids, this migration is unusual in that members of both sexes and all age groups are involved, and large, hypersaline/alkaline lakes are used.

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1. Introduction

Mono Lake, a large, hypersaline and alkaline lake at the eastern base of the Sierra Nevada in central California, is the terminus of a moult migration for several hundred thousand Black-necked (Eared) Grebes *Podiceps nigricollis californicus*. The birds begin to arrive immediately after the breeding season in late July. The population builds to a peak of some 750 000 adults and juveniles by late October (Fig. 1) and remains on the lake until the brine shrimp *Artemia* sp. population crashes in late autumn (Jehl and Bond 1983, Cooper et al. 1984).

The moults of this grebe have been outlined by Palmer (1962), Gauckler and Kraus (1968), and Cramp and Simmons (1977). In the course of ecological studies at Mono Lake, Jehl was able to assemble sufficient material for us to attempt to work out the moult sequence more thoroughly and to compare it with that of the Western Grebe *Aechmophorus occidentalis*, the only other grebe for which comparable data are available (Storer and Nuechterlein 1985). The analysis has been made difficult by the small amount of early spring material, the protracted nature of some moults, and variation within the several age and sex classes, which depends, in part, on a bird's breeding status. Because the autumn population is likely to be derived from a broad geographic area (Jehl unpubl.), regional differences in breeding schedules may impose further variability in the timing of the moult within any age class. On the positive side, the availablity of a large series as flat pelts on which growing feathers can be seen readily, and the recognition of plumage and bursa criteria allowing the recognition of several age classes, have facilitated the analysis.

2. Methods

Data from more than 200 grebes collected or salvaged at Mono Lake by Jehl form the basis of this study. This material was obtained year-round from March 1981 through May 1984. Additional material was salvaged on the wintering grounds in southern California. Some additional data were taken from museum skins by Storer, and a few pelts of the nominate race of the Black-necked Grebe obtained by S. M. Goodman from the

Accepted 14 February 1985

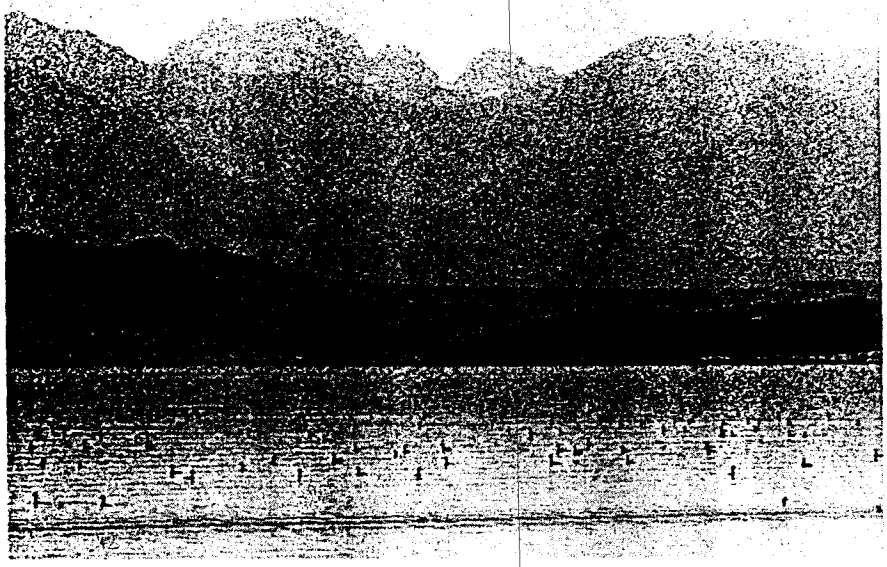

Fig. 1. Black-necked Grebes on Mono Lake, California.

bird markets at Port Said and collected in the general Lake Manzala area, Egypt, were compared with the California samples. (Lake Manzala is also a saline lake.) Material from both localities was prepared as flat pelts, and in many cases also as nearly complete skeletons. The pelts were degreased and pinned out to dry. The material has been catalogued as part of the bird collections of The University of Michigan Museum of Zoology (UMMZ).

Standard measurements were taken on the specimens in the flesh by Jehl: exposed culmen and tarsus length to the nearest 0.1 mm, wing length (arc) and length of the cloacal bursa to the nearest mm, and weight to the nearest g. Soft-part coloration was determined on a large number of fresh birds in the field by Jehl.

Feathers serve several functions in grebes. In addition to their roles of protection and thermoregulation, they promote species recognition, keep the skin of the underparts dry, absorb solar radiation, and, when consumed, aid digestion. Because the feathers serving each of these functions are concentrated on specific areas of the body, the timing, extent, and intensity of moult in each area may reflect selection for different functions.

We established a set of reference specimens (Tab. 1) and ranked each of the following areas on each bird from States 0 (no moult) to 3 (heavy moult): head, neck, back, scapulars, flanks, and belly. The remiges, which are moulted simultaneously, were ranked 0 (recently shed), 1 (partly, but less than half-grown), 2 (more than half-grown, but not fully grown), and 3 (fully grown). To make this study as similar as possible to that of the Western Grebe, the ranking was done by Storer. Moult scores of the six areas (exclusive of the remiges) were summed to give an estimate of the intensity of the moult.

Tab. 1. Black-necked Grebe reference specimens (UMMZ catalogue numbers). Moult states: 0 = no moult, 1 = little moult, 2 = moderate moult, and 3 = heavy moult.

Moult state	Throat	Back	Belly	Scapulars	Flanks
0	204847	204847	204847	none	none
1	204844	204814	204814	204811	204844
2	204814	204815	204842	204848	204843
3	204846	204846	204815	204815	204846

UMMZ no. 204811: Humeral tract 1; UMMZ no. 204814: Throat 2, back 1, belly 1; UMMZ no. 204815: Back 2, belly 3, humeral tract 3; UMMZ no. 204842: Belly 2; UMMZ no. 204843: Flanks 2; UMMZ no. 204844: Throat 1, flanks 1; UMMZ no. 204846: Throat 3, back 3, flanks 3; UMMZ no. 204847: Throat 0, back 0, belly 0; UMMZ no. 204848: Humeral tract 2.
Extent of rufous on upper wing coverts: UMMZ no. 204817: Little; UMMZ no. 205625: Moderate; UMMZ no. 204812: Much.

The amount of white on the tips of the inner primaries and the amount of rufous on the lesser and median upper wing coverts were also scored by comparison with reference specimens (Fig. 2, Tab. 1).

3. Results

3.1. Age determination

Plumage characters, soft-part coloration, the presence and size of the cloacal bursa, and moult pattern make it

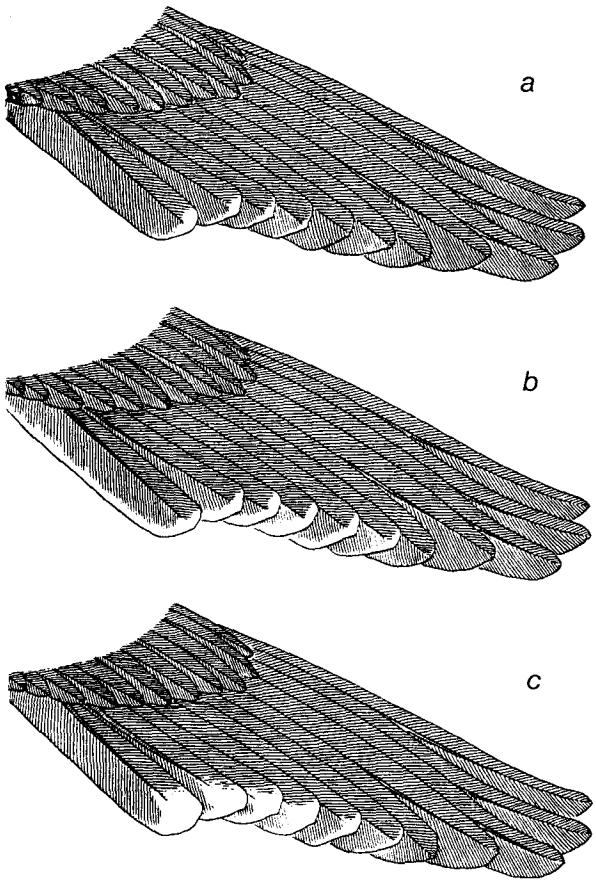

Fig. 2. Variation in the extent of white tipping on the inner primaries of Black-necked Grebes *Podiceps nigricollis californicus*. a: little (UMMZ no. 206 451), b: moderate (UMMZ no. 204 811), c: much (UMMZ no. 204 871).

possible to categorize nearly all autumn-taken specimens as juveniles (birds hatched in the immediately previous summer), subadults (birds older than one year and presumed to be 13–16 months of age), and adults. In spring, we could not consistently distinguish juveniles from older non-breeders, and we have lumped these as subadults. Determination of sex was based on examination of gonads.

3.1.1. Plumage

Plumage characters of juveniles and adults of the nominate race in autumn have been described by Cramp and Simmons (1977). Juveniles have a brownish tinge on the head and neck and can usually be recognized in the field by their coloration and unworn plumage, white chin, and iris colour (see below). Variability in the extent and timing of moult among older birds precludes the separation of adults from subadults in the field at this season.

In spring, adults are recognizable by their bright breeding plumage, which includes a black neck, bright golden ear tufts, and rufous flanks (brighter in males than in females). Sub-adults are duller, often mottled with brown and black; their flanks are brownish, and their ear tufts tend to be pale, often straw coloured. Many undergo no more than a partial moult, so that the spring plumage contains a mixture of feather generations. Worn and bleached feathers may be conspicuous.

Considerable rufous is found on the lesser and median upper wing coverts of some birds in spring. This seems to be characteristic of the African race, *gurneyi*, but is not mentioned in standard descriptions of *californicus*. It is both more frequent and more extensive in subadults than in adults (sexes combined, $\chi^2 = 8.24$, df $=1$, $P < 0.005$), and in males than in females (age groups combined, $\chi^2 = 9.22$, df $=1$, $P < 0.005$). Within age or sex groups, however, it is significantly greater only in subadult vs. adult males ($\chi^2 = 4.94$, df $= 1$, $P < 0.05$). Thus, these differences provide clues to age and sex, but not proof.

Old World races of the Black-necked Grebe (*nigricollis, gurneyi*) are characterized by having the inner four or five primaries largely white. In the North American population white in these feathers is confined to a narrow margin (occasionally a spot) on the tips. These markings vary with age, occurring in 93% of the juveniles, in which they form a narrow but conspicuous band 2–4 mm wide at the tips of primaries one to five (Fig. 2). The extent and frequency of the patterning are reduced in older birds (Fig. 3); white tips were found in 34% of subadults and 30% of adults and in these groups were most commonly expressed as narrow fringes (up to 1 mm wide) on the inner two or three primaries. These differences are sufficiently pronounced to be useful in distinguishing juveniles from older birds. We found no sexual differences in wing patterning in any class.

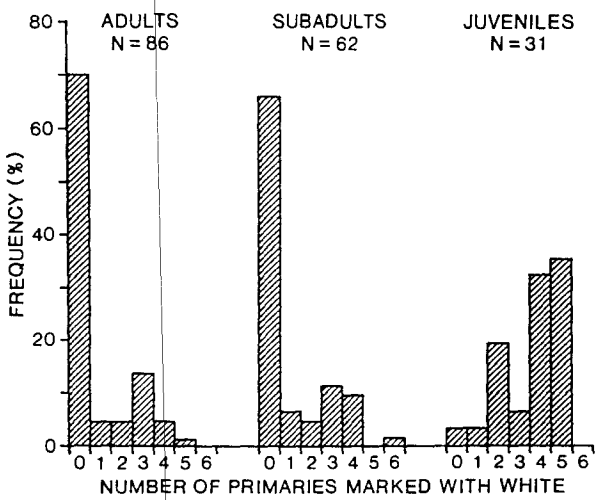

Fig. 3. Age variation in the number of inner primaries with white tips in *Podiceps nigricollis californicus*.

3.1.2. Soft-part coloration

Juveniles. Iris tan with orange tint that brightens in late fall. Lateral surface of legs and feet olive-green, medial surface greenish-yellow in early autumn. As autumn progresses these colours darken, the lateral surface becoming greenish with black tones and the medial surface pale green with yellow tones, the latter being most evident on the margins of the toes and tarsometatarsus.

Sub-adults. Iris usually orange to orange-red, rarely bright red as in adults. Lateral surface of legs and feet blackish-green to greenish-black; medial surface grey-green or bluish-grey with yellowish tones.

Adults. Iris usually bright red, sometimes paler red-orange or, rarely, orange. Lateral surface of legs and feet blackish, sometimes with blue, green, or even yellow tones; medial surface usually bluish with black markings, but sometimes with blue-green, blue-grey, or greenish-yellow markings. Light areas on the margins of the toes are usually lacking.

3.1.3. Cloacal bursa (Bursa of Fabricius)

The cloacal bursa is a dorsal diverticulum from the cloaca. Prominent in most newly-hatched and young birds, it usually reaches maximum size within two or three months of hatching, then regresses and disappears by the time sexual maturity is reached. However, in Western (G. Neuchterlein pers. comm.), Slavonian (Horned) *P. auritus* (Storer pers. obs.) and Black-necked Grebes, it is prominent through the first 1–1.5 yr or more of the bird's life. In Black-necked Grebes, the bursa of juveniles averages 15–21 mm long in autumn. It regresses very slowly and may be nearly as large the following autumn (Fig. 4) or later. Most regression appears to take place late in the second winter, as shown by the high variability of the large January sample (which includes birds that were not precisely aged), and by some small (<10 mm) bursas among the spring samples, which we presume represent birds nearly two years old. Three post-breeding females collected on 14 August (two) and 6 September 1984 (one) on Mono Lake had bursas measuring 12 × 6, 7 × 5, and 10× 7 mm. The first had three ruptured ovarian follicles and a greatly enlarged oviduct; the other two had also laid and each had an enlarged oviduct. Thus the presence of a bursa does not preclude breeding. A male captured in January 1983, which succumbed in May 1984 at a minimum age of 23 months, had a bursa measuring 7 × 4 mm. Hence, the bursa is probably retained for more than two years in some birds.

We found no sexual differences in the timing of bursal regression that might provide clues to the age of first breeding.

Because the bursa plays a major role in the avian immune system (Glick 1983), the adaptive significance of its prolonged retention in grebes is worth further study.

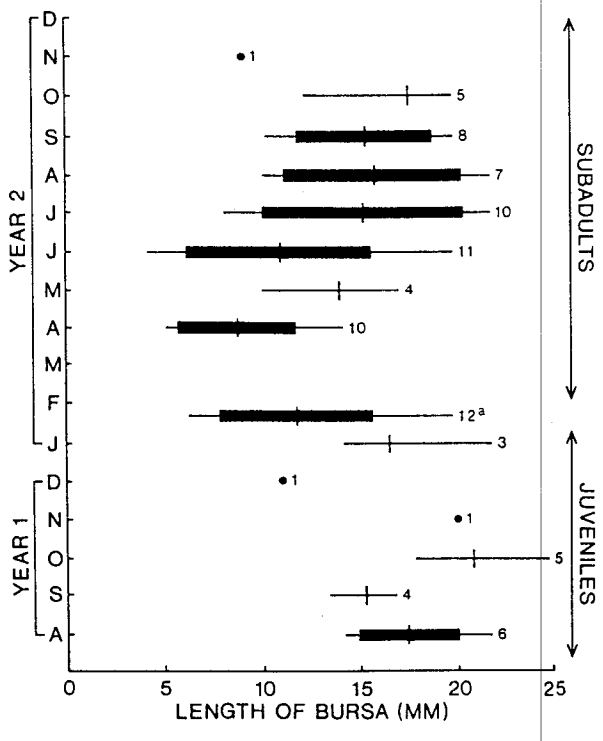

Fig. 4. Seasonal variation in the length of the cloacal bursa. Juveniles (Year 1, August–January) are birds known to have hatched in the previous summer. Subadults (Year 2) from June–December are at least one year old. The precise age of birds taken from January–May (subadults) cannot be known and the category includes birds hatched in the previous two summers. Vertical bar indicates mean, dark bar ± 1 S.D.

3.2. Moults

3.2.1. Prebasic I (Post-juvenal)

This moult begins on the breeding grounds, and probably involves all or most of the body plumage but not the remiges. Wing coverts are not usually moulted at this time, but the presence of rufous upper wing coverts in one January specimen indicates that some juveniles replace these feathers too. The earliest juveniles at Mono Lake (6 August 1982) showed body moult in all tracts (State 1 on head and neck, and belly; State 2 elsewhere), which continued at low intensity through the autumn. Three juveniles taken on 11 November were moulting fairly heavily (total body scores of 9–10; heaviest on flanks (3), none on belly), but most seem to have completed body moult by late November or early December. Thus, the duration of this moult approximates 4+ months. Birds taken on the wintering grounds in early January show very little, if any, moult (total score 0 to 1).

3.2.2. Prealternate I (Pre-breeding)

Body moult resumes by late February or early March, concurrent with the start of migration. Two males taken on 3 March had light or moderate moult on the head

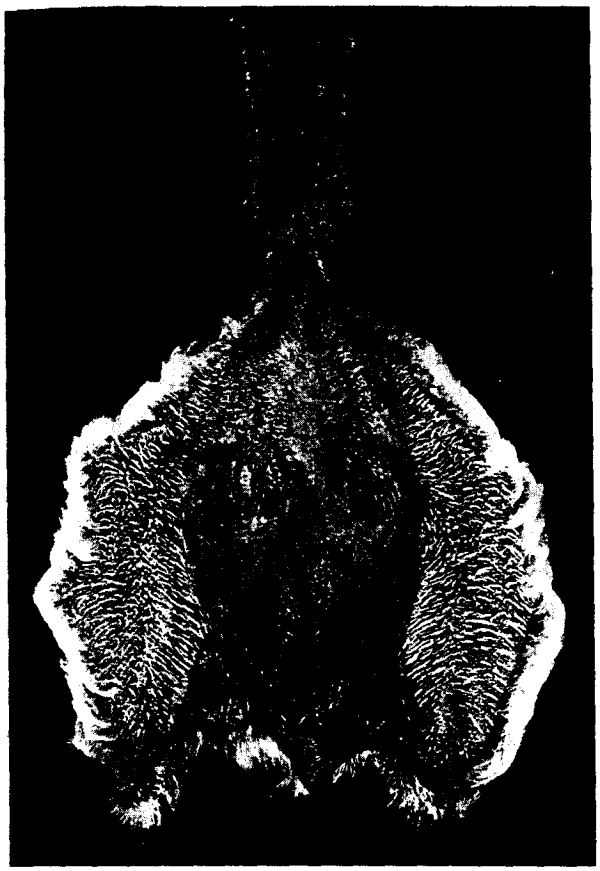

Fig. 5. Photograph of the under side of a pelt of the Black-necked Grebe, showing extensive moult.

and neck and one showed light moult on the rest of the body. By April moult occurs over the entire body (scores 7, 8, 9; N = 3). No bird showed any sign of mid-winter or spring moult of the flight feathers, but wing coverts (some or all) are replaced. Often these have a strong rufous tint, brighter in males than in females (p. 255). This moult is protracted and highly variable, and we are not clear when it is completed. The presence of birds in winter aspect in early June suggests that some birds miss it entirely. Those that moult, however, do not attain the bright breeding plumage of the adults. They may have blackish markings on the head and neck, but the facial plumes are poorly developed or drab, and the flanks are brownish rather than rufous.

3.2.3. Prebasic II (Post-breeding)

This is a complete moult and, like subsequent prebasic moults, is far more intensive than the prealternate moult. Often 50% or more of the feathers in any tract are growing at once (Fig. 5). Evidently birds that do not undergo much moult in early spring begin in mid to late May, and by mid-June many summering birds are moulting heavily on the body; others, however, show little moult except on the humeral tract and flanks.

Summering subadult males outnumber females by about 2:1 (Jehl unpubl.) and probably begin the prebasic moult much earlier than females on average, adding further complexity to the situation.

Some non-breeders begin wing moult in late spring. Dawson (1923) reported one that had moulted its remiges on 28 May; Jehl collected one on 16 June whose wing was nearly full grown (length 129 mm) and that must have moulted in early May (see Fig. 6). Summering subadults usually moult flight feathers in July or August. Perhaps the male on 1 September that had just moulted remiges, and another on 24 October (wing 119) that was a week or so short of finishing, had bred. The start of body moult seems to precede the loss of remiges, but we have too few data to determine the usual condition. The bird collected on 16 June (above) had only light body moult (score 6), even though its primaries were regrown.

Although there is more variation in timing than we can document, subadults evidently lose the bursa by the end of their second summer and thus become indistinguishable from older birds. We cannot be certain when they finish moulting. For this group as a whole, moult extends from May to November, but it is so intense that we think most individuals replace the majority of their feathers in two months or so.

3.2.4. Prealternate II (Pre-breeding)

We infer that most birds attain breeding age by their second spring. At this time the body plumage and some or all of the wing coverts are renewed. The new upper wing coverts are usually blackish; rufous areas, if present, average smaller and duller than in younger birds. Only six of 18 adults taken from March to May were moulting on the venter, so it is not clear if that entire tract is replaced.

Approximately 20 adults examined by Jehl after a wreck in January 1983 (Jehl and Bond 1983) showed no

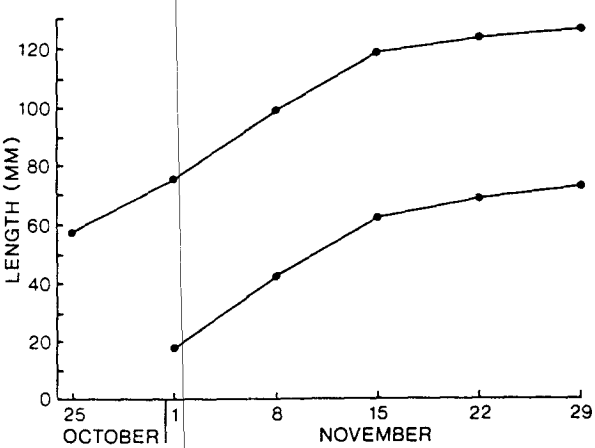

Fig. 6. Regrowth of the flight feathers as indicated by the length of the wing (above) and the 10th (outer) primary (below) of a captive Black-necked Grebe.

signs of body moult. Evidently, moult begins in mid-February and may be slightly advanced in males. Feathers on the head and neck are the first to be replaced, and some adults have prominent head markings by mid to late March.

Although many grebes appear to be in full breeding plumage in mid-April, examination of pelts shows that moult is continuing; some birds are still moulting well into May. Interpreting this moult is difficult. Because replacement is continuous on the flanks, we are uncertain when body moult ends. A non-breeding male was replacing a few feathers on neck, flanks, and belly on 16 June 1982; this may have represented the start of the prebasic rather than the end of the prealternate moult. It appears that moult is protracted in individual birds in spring. Yet, because most migrants seem to have passed through the Mono Lake region by mid-May, and because some adults complete body moult by late April, we suspect that our sample is biased by the inclusion of data from late migrants that may not breed and whose moult is delayed.

3.2.5. Prebasic III (Post-breeding)

This complete moult begins on the breeding grounds. When post-breeding males reappear in mid-July they show moderate to heavy moult on the body. A similar degree of replacement in females is not realized until they appear at staging areas, several weeks later. (In *Podiceps auritus* females begin this moult about a month earlier than males [Fjeldså 1973]).

Moult begins virtually simultaneously in all body tracts. The wing is usually moulted as a unit, almost immediately after the birds' arrival. Field estimates that it takes approximately 30 d for remiges to be replaced were verified by observations on a captive, maintained at the Sea World Park in San Diego, which required 35 d (Fig. 5). The captive moulted its primaries, secondaries, tertials, upperwing coverts on the manus, and entire underwing at one time. Upper secondary coverts were retained an additional 10 d or so, then were lost irregularly, some by rows and some scattered.

Because Mono Lake is often windy, debris blows ashore quickly. Therefore, the presence of floating feathers can be used to index the duration of the moult period. Remiges are found commonly from early August to mid-September (when windrows appear on lee shores), are less common in late September, and are not seen in October. Thus, even the latest birds will regain flying ability by early November, before dwindling food supplies require them to migrate. The absence of body feathers on the water in October indicates that birds of all ages have largely finished ecdysis; examination of pelts, however, shows that feather growth occurs into November in most birds. Because the intensity of this moult is so great, we judge that individual birds can replace the entire body and wing plumage in about 6 wk. By January, except for persistent moult of the flanks, body moult is quiescent.

3.3. Moult patterns

3.3.1. Remiges

Remiges are large feathers and they must be functional before birds can leave the staging area for the wintering grounds. Thus, they are moulted very early. Adults replace them in late summer or early autumn, almost immediately after arriving at Mono Lake. With the exception of a non-breeding female taken in June with the primaries half grown, all of our adults in the process of wing moult were taken in August (seven males, one female) or September (five males, three females). Summering non-breeders, especially males, may shed remiges as early as May. Moulting subadult males were taken in June (three), July (three), August (one), September (two), and October (three, all with remiges more than half grown); and sudadult females in July (four), August (one), and September (two).

We have no evidence of a regular winter (February) moult as reported by Stresemann and Stresemann (1966). Such a moult may occur in some segment of the population, as also may be the case in the Western Grebe (Sibley 1970, Storer and Nuechterlein 1985), but it seems more likely to us that birds moulting the remiges in winter have missed the autumn moult.

One of the birds mentioned by the Stresemanns (Field Mus. Nat. Hist. no. 254 503), a female taken in the Faiyum, Egypt, on 21 February 1939, shows a partial wing moult. The secondaries are fresh and fully grown, the primaries on the right wing are ca. 45 mm long, whereas on the left wing the three outer primaries are ca. 25 mm long, but the next two had not been shed and are extremely faded and worn. This condition contrasts sharply with the pattern at Mono Lake, where remiges are shed and grown simultaneously. A subadult male with a bursa 12 × 8 mm (UMMZ no. 206 539), taken on 1 January 1984 in the Lake Manzala area of Egypt, is replacing faded, worn plumage on the head, neck, and back, had faded, worn wings and appears to be a candidate for a February moult of the remiges. Six other birds from the same area taken on 30 December 1983 to 3 January 1984, lacking bursas and presumably adult, are in normal winter plumage (although one has very faded wing tips), as is a subadult with a bursa 8 × 6 mm. A second subadult (bursa 14 × 6 mm) has considerable fading on the wing tips and on some of the scapulars and inner secondaries. Although their presence makes feathers less subject to wear, melanins are alkali-soluble and hence long stays on alkaline lakes, such as Mono Lake (pH ≈ 10) may result in fading and wear.

The second bird mentioned by Stresemann and Stresemann (1966), Field Mus. Nat. Hist. no. 23 315, a male taken on 22 February 1906 on Lake Atitlan, Guatemala, is in winter plumage and nearing the end of what appears to be a normal wing moult. The presence of rufous on the lesser wing coverts is evidence that this bird is probably a subadult. A male lacking a bursa found dead on Mono Lake on 14 February 1983 (UMMZ no.

206 086) had primaries that were no more than fringed shafts, and it would have had to undergo a late winter or spring moult of the remiges to reach the breeding grounds.

Not all Black-necked Grebes of the North American populations take part in moult migrations; some in the southern parts of the range appear to moult the remiges on the breeding grounds. An adult male (UCLA no. K311) taken on 18 June 1922, on Buena Vista Lake, Kern County, California, had a wing ca. 90 mm long, was growing remiges, and was in alternate plumage. Two of three Black-necked Grebes collected by Robert W. Dickerman on 23 May 1962 at Laguna Santa Maria del Oro, Nayarit, Mexico, are in the process of wing moult: a male (Univ. Minn. no. 23 477) had recently shed his remiges and was early in the prebasic moult, and a female (Univ. Minn. no. 23 479) had new remiges ca. 10 mm long and was largely in basic plumage. The latter is evidently the "immature" reported by Dickerman (1969). A third specimen, an adult female with ovary 16 × 8 mm, had begun the prebasic moult.

3.3.2. Head and neck

Feather replacement on the head and neck results in the greatest seasonal change in the grebes' appearance. These are the first areas to be moulted in spring, insuring that species-specific recognition marks will be fully developed early. The prebasic moult of these areas is intense in adults from August through October. It starts earlier and is more protracted in subadults as a group (especially males), but this is the result of samples that include summering birds as well as non-breeders that return early. In juveniles the prebasic moult of the head and neck seems even more prolonged but is far less intense.

3.3.3. Flanks

Like those of the head and neck, the feathers of the flanks differ in colour seasonally, being deep rufous in the breeding season and dark grey the rest of the year. The semiannual moults producing these colour changes are superimposed on the nearly continual moult of the flank feathers which, as in most or all grebes, probably provide the major portion of those swallowed and retained either in the lumen of the gizzard or as the pyloric plug (Storer 1969, Storer and Nuechterlein 1985). Black-necked Grebes may be unusual in that little or no moult of the flank feathers occurs in midwinter. Perhaps correspondingly, the ball of feathers in the gizzard is small at this season (Jehl MS). We have not made a thorough study of the pyloric plug, but the only two specimens in which we failed to observe it were collected in mid-April. Both had few feathers in the gizzard.

3.3.4. Other feather tracts

Feathers of the interscapular and humeral tracts are in moult for much of the year and presumably make up an appreciable part of the feathers swallowed by the birds; the same is true of the Western Grebe (Storer and Nuechterlein 1985). In both tracts, as is the case with the flank feathers, there appears to be a slowing or stopping of the moult in midwinter.

The moult of the belly feathers peaks with the prebasic moult in late summer. We found no evidence of moult from December through February and few birds were moulting this tract from March through May (one of six birds in March, four of nine in April, and three of nine in May). All of those moulting had scores of 1 (little moult) for this tract, except one bird with a score of 2.

At least some of the back feathers are replaced in the prealternate moult. All six birds taken in March, seven of nine April, and all nine in May showed little or moderate moult. The prebasic moult is more intense and includes the dark-based feathers lying over the heavily pigmented skin of the back, both of which presumably are involved in heat absorption in sun bathing (Storer et al. 1976). As the prealternate moult occurs in late winter and early spring, when air and water temperatures are low, a gradual moult is probably advantageous, because a larger number of fully grown feathers are maintained to function in insulation and heating.

4. Discussion

In his review of moult migrations, Salomonsen (1968) says "apparently grebes *Podicipedes* sometimes have a moult migration, but only to a slight degree and not yet demonstrated with certainty." Recently, however, Vlug (1983) has reported up to 40 000 Great Crested Grebes *Podiceps cristatus* moulting in IJsselmeer, Netherlands. Black-necked Grebes almost certainly moult at Great Salt Lake, Utah, as well, where numbers even larger than at Mono Lake are present in autumn. In addition, J. Fjeldså (pers. comm.) has seen moulting assemblages of several hundred Silver *Podiceps occipitalis,* Hoary-headed *Poliocephalus poliocephalus* and, perhaps, Hooded *Podiceps gallardoi* grebes. The moult migration of Black-necked Grebes to Mono Lake, however, is far larger and much more spectacular than that of any other grebe, or even of the anatids reviewed by Salomonsen. Such migrations should be looked for in populations of *nigricollis* in the Old World, and may be suggested by large concentrations in winter at Lake Burdur, Turkey, on the southern Caspian Sea (Cramp and Simmons 1977) or on saline lakes in the Rift Valley of Africa.

The moult migration of the Black-necked Grebe in North America differs from that of most anatids in that members of both sexes and all age groups are involved. It is also unusual in that hypersaline and alkaline lakes are used. The timing, duration, and extent of the moult can be seen as adaptations to exploit these areas when food is superabundant. Thus, the birds moult their remiges in late summer and compress an intense body

moult into a relatively short time in the autumn. Joining a large aggregation at this time of relatively great vulnerability is presumably an advantage to the individual through a lowered risk of predation.

Although comparisons are made difficult by the very long breeding season of the the Western Grebe on Clear Lake, California, the moult pattern of the Black-necked Grebe generally resembles that of the Western (Storer and Nuechterlein 1985). The principal differences are the shorter, more intense prebasic moult of the Black-necked Grebe mentioned above, and the cessation of moult on the flanks and in the humeral and lateral interscapular tracts of the Black-necked Grebe in winter.

As Stresemann and Stresemann (1966) mentioned, specimens of grebes taken during the wing moult are rare. Furthermore, documentation of the length and timing of the breeding season in the tropics is generally poor so that the relationship between moult and breeding is difficult or impossible to determine. In southern Texas, the timing of the wing moult of the Least Grebe *Tachybaptus dominicus* varies considerably: three moulting specimens were taken between late August and late September, two in late January, and eight between 12 March and 21 May. Although these birds have been found nesting in Texas in all months, the peak of the breeding season occurs between 15 April and 30 August (Palmer 1962). It is thus likely that some birds shed their remiges soon after the breeding season, like most grebes, but that the majority moult them shortly before the breeding season. In the United States and Canada, Pied-billed Grebes *Podilymbus podiceps* moult their remiges between July and October (12 specimen records), but at least in Mexico some may moult during the breeding season. A female taken on 13 October in Veracruz had growing remiges ca. 70 mm long, had recently laid two eggs and had two large follicles in the ovary; and a "breeding" male taken on 8 April in southern Baja California had a wing measuring 75 mm with growing remiges.

We have no explanation for the adaptive significance, if any, of the rufous wing coverts found in some Black-necked Grebes, especially because these rufous feathers are more frequent in first-year birds than in adults. Although the wings are spread in some courtship displays (Cat Display, Retreat Ceremony), the rufous areas are not conspicuous and the white of the secondaries forms a far more conspicuous signal than would rufous in the coverts. We know of no displays in which young birds signal their status to adults. Rufous coverts, however, are sometimes found in the Horned Grebe and in *P. n. gurneyi*.

Acknowledgments – This research was supported, in part, by the Los Angeles Department of Water and Power under a joint agreement with the U.S. Fish and Wildlife Service. Additional support was received from Hubbs Marine Research Institute, Mercury Outboard Motors, Kawasaki Motors of America, and Sevylor Boats. Completion of this paper would not have been possible without the assistance of Suzanne I. Bond, who prepared most of the specimens and typed the manuscript. S. M. Goodman, K. C. Parkes and J. Fjeldså commented on the manuscript.

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