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LOW FREQUENCY OF "DOUBLE MOLT" OF REMIGES IN RUDDY DUCKS REVEALED BY STABLE ISOTOPES: IMPLICATIONS FOR TRACKING MIGRATORY WATERFOWL

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ABSTRACT.—Ratios of the stable carbon ($\delta^{13}C$) and hydrogen (δD) isotopes in newly grown remiges of Ruddy Ducks (*Oxyura jamaicensis*) are influenced by the isotopic character of food types and ambient water. Systematic isotopic foodweb and water differences between coastal wintering grounds and prairie breeding grounds of Ruddy Ducks provide the basis for using isotopic analyses of feathers to trace the location and timing of molt. Anecdotal evidence, based largely on captive birds, suggests that Ruddy Ducks replace their remiges twice each year (once each on the breeding and wintering grounds), but a recent literature analysis indicates that this phenomenon is rare. Thus, we investigated the extent to which a biannual molt of the remiges occurs in the wild and at the population level. We analyzed the stable isotopes of carbon (n = 57 birds) and hydrogen (n = 50 birds) in flight feathers to estimate the prevalence of the so-called "double molt" of remiges in free-living Ruddy Ducks. Our data showed that natural populations of Ruddy Ducks express an overwhelming unimodal distribution of isotope ratios in their remiges, suggesting that they undergo a single molt at or near the breeding grounds. Only 3 to 6 of 50 birds from Manitoba showed isotopic evidence consistent with growing remiges on the wintering grounds. Feathers from Ruddy Ducks harvested during the fall in the Mississippi Flyway had isotopic profiles consistent with growth on northern freshwater breeding sites. Thus, our results confirm that the replacement of remiges twice each year by Ruddy Ducks is rare, and they suggest that this dual stable-isotope technique can be used to infer general molting origins of North American waterfowl. *Received 6 October 1998, accepted 26 May 1999.*

WATERFOWL REPRESENT 1 of 11 families in 8 avian orders that molt their flight feathers nearly simultaneously (King 1974), a process that produces a period of flightlessness. Only a few exceptions exist to the pattern of rapid replacement of remiges once per plumage cycle in the Anatidae, and these exceptions occur most often in the tribe Oxyurini, the stiff-tailed ducks. Nearly all of the eight species within this tribe are reported to have a double replacement of remiges that results in two flightless periods per year (Johnsgard and Carbonell 1996). However, these reports are documented primarily for birds in captivity, although Frith (1967) and Siegfried (1973) reported a biannual molt of remiges (hereafter, "double molt") in free-living Musk Ducks (*Biziura lobata*) and Ruddy Ducks (*Oxyura jamaicensis*), respectively.

The basis for double molt in North American Ruddy Ducks is anecdotal and largely unresolved, with the most conclusive evidence coming from the observations of Siegfried (1973). Based on the lack of primary wear in individuals captured during the breeding season, Siegfried concluded that Ruddy Ducks replace their remiges twice per year, with the first molt occurring in late winter or early spring. Siegfried (1973) also reported that two immature females were in the process of replacing their primaries, which must have been shed shortly

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after spring migration. Similar observations of remigial molt by Ruddy Ducks in late winter or early spring, all of which were immature birds, have been reported (Humphrey and Clark 1964, Palmer 1976, Joyner 1978, Hohman et al. 1992b, R. Brua pers. obs.).

The only attempt to assess double molt in free-living Ruddy Ducks was based on the qualitative observations of Siegfried (1973), and no other study has attempted such an investigation. However, Hohman (1996) used published and unpublished reports to conclude that the double molt in free-living Ruddy Ducks is rare. The qualitative determination of the wear of primary feathers of individuals caught in the spring on the breeding grounds could lead to erroneous conclusions about double molt in Ruddy Ducks. Thus, a more detailed and quantifiable examination of double molt in Ruddy Ducks is needed. A technique that promises to be very powerful in the analysis of avian life-history parameters, including molt strategies, is the measurement of naturally occurring stable isotopes in bird tissues.

For several chemical elements, naturally occurring stable-isotope ratios in diets are passed on to consumers (Peterson and Fry 1987, Tieszen and Boutton 1988). Isotopic ratios in feathers reflect diet during periods of feather growth (Mizutani et al. 1990, 1992; Hobson and Clark 1992), and measurements of stable-isotope signatures in feathers have been used to infer diet or locations of birds during that discrete period of feather growth (Hobson 1999). Stable hydrogen isotope ratios ($^{2}H/^{1}H$) in rainfall exhibit distinct patterns across North America (Sheppard et al. 1969, Taylor 1974, Cormie et al. 1994), and Hobson and Wassenaar (1997) and Chamberlain et al. (1997) recently showed that average deuterium isotope signatures in rainfall are correlated with those in bird feathers grown at the same locations. In general, stable hydrogen isotope patterns in feathers are expected to be more enriched (contain more of the heavier isotope of hydrogen) in the southern United States along the Gulf Coast and to become progressively more depleted (contain less of the heavier isotope of hydrogen) in a northwesterly direction toward Alaska (Hobson and Wassenaar 1997). Birds that consume food and water from a marine environment are also expected to show stable hydrogen isotope values in their tissues that are enriched compared with birds from terrestrial or freshwater foodwebs (Craig 1961, Craig and Gordon 1965, Taylor 1974). Similarly, marine foodwebs typically are more enriched in ^{13}C than terrestrial C-3 foodwebs (Fry and Sherr 1984), and the potential for segregation of feathers grown in marine versus terrestrial/freshwater foodwebs using $^{13}C/^{12}C$ ratios in feathers is also possible (Mizutani et al. 1990, Hobson and Wassenaar 1997). The feathers of birds that molt in the southern United States, either in terrestrial/freshwater or coastal marine biomes, should be substantially more enriched in deuterium (and possibly more enriched in ^{13}C) than the feathers of birds that molt at middle latitudes of the continent. We applied this hypothesis to evaluate evidence for double molt in Ruddy Ducks.

Ruddy Ducks winter along the Pacific, Atlantic, and Gulf coasts of North America, where they inhabit marshes and estuaries that vary in salinity; most of the birds use slightly brackish to brackish estuarine habitats (Stewart 1962, Johnsgard 1975, Bellrose 1976). Timing of remigial molt on the wintering grounds is highly variable but occurs mostly from January to April (Hohman 1996). During the breeding season, Ruddy Ducks use freshwater habitats in the prairie pothole region of North America, with the highest densities of birds in southwestern Manitoba (Bellrose 1976). Postbreeding Ruddy Ducks tend to molt their remiges during August (Hohman 1993, R. Brua pers. obs.) over a period of about three to four weeks (Hohman et al. 1992a). Ruddy Ducks are mostly carnivorous on the wintering grounds, eating primarily midges, brine flies, and small clams (Stewart 1962, Hohman et al. 1992b). During molt on the breeding grounds, they consume primarily invertebrates.

Because of seasonal differences in habitat use by Ruddy Ducks, we predicted that if birds replaced their remiges twice each year, then this should be reflected in different isotopic signatures of these feathers. We tested this hypothesis by isotopically analyzing the primaries of Ruddy Ducks captured on their breeding grounds and during fall migration, immediately following the prealternate molt.

METHODS

Feather collection.—Ruddy Duck primary feathers were derived from three sources. We obtained remiges from 31 males and 26 females captured on the

breeding grounds in southwestern Manitoba, Canada (50°10′N, 99°47′W), in June 1997. Age determination was based on wear of the rectrices (USFWS 1977). Molting remiges were noted and remigial wear was assessed following Siegfried (1973). Second, feathers from four hatching-year individuals that had completed their prebasic molt were salvaged from hunters in the fall of 1997 in southwestern Manitoba. Third, we obtained remiges from Ruddy Ducks harvested in fall and winter 1996–1997 in Mississippi and submitted to the "wing bee." Participants in the "wing bee" classified wings as adult or immature using qualitative characteristics (Carney 1992).

Stable-isotope analyses.—Feathers were cleaned of surface oils by rinsing two to three times in a 2:1 mixture of chloroform and methanol. Because a portion of the total hydrogen of feathers (mostly keratin) is available for isotopic exchange with ambient water vapor, it was necessary to quantify and eliminate the effect of this uncontrolled temperature-dependent variable. Unfortunately, complete elimination of exchangeable hydrogen by chemical techniques such as nitration is not possible for complex organic matter (Schimelmann 1991, Cormie et al. 1994, Chamberlain et al. 1997). Hydrogen-isotope exchange between feather and water vapor was first quantified by equilibrating samples with steam in a static chamber having a wide range of hydrogen isotopic values (−135 to +525‰) at constant temperature (130 ± SD of 0.1°C) and then measuring the total hydrogen δD values modeled after Schimelmann (1991). Hydrogen in feathers available for isotopic exchange at this temperature was determined to be 23 ± 0.7‰ (R^2 = 0.99, n = 30, $P < 0.001$).

We eliminated potential variability resulting from uncontrolled hydrogen-isotope exchange by controlled equilibration of all feather samples with steam (δD = −135‰) at 130 ± 0.1°C for 2 h. Sample reproducibility of repeated equilibrated samples was better than ± 2‰ for δD. Thus, total hydrogen isotopic results for equilibrated samples could be reliably compared among samples and sites. Following steam equilibration in Vycor breakseal tubes, all water vapor was cryogenically removed, samples were sealed under vacuum, combusted at 850°C in the presence of cupric oxide, and followed by cryogenic separation of CO_2 from H_2O. Waters of combustion were reduced to H_2 gas on hot zinc (Hobson and Wassenaar 1997). Stable-isotope analyses were performed on a Micromass Optima dual inlet isotope-ratio mass spectrometer. Stable carbon isotope analyses are reported in parts per thousand (‰) deviation from the Pee Dee Belemnite standard, with a sample reproducibility better than ± 0.1‰. Stable hydrogen isotope results are reported in parts per thousand deviation from Standard Mean Ocean Water (SMOW) standard, normalized on the VSMOW/SLAP scale, with a sample reproducibility of better than ± 2.0‰.

Results

Only one of 57 captured Ruddy Ducks (an after-hatching-year [AHY] male) had worn primaries, whereas all other captured individuals appeared to have primaries in good to excellent condition. Only one individual, a yearling male, based on notched tail feathers but in full breeding plumage, was replacing primaries when captured. One AHY female was replacing P10 on her right wing, and the rest of her primaries were developed fully.

Feathers of Ruddy Ducks caught on the breeding grounds in Manitoba had $\delta^{13}C$ values that were typical of a C-3 aquatic biome (Table 1). However, six individuals, all but one an AHY female, had $\delta^{13}C$ values more enriched than −20‰ (Fig. 1). Feather δD values from Manitoba also were distributed broadly. However, two groups were apparent, with most individuals averaging −125 ± SD of 18.3‰ (n = 44) and six outliers having feather δD values more positive than −80‰(Fig. 1). We found no significant difference between the sexes in feather $\delta^{13}C$ or δD values (carbon, t = 0.32, df = 55, P = 0.75; hydrogen, t = 1.6, df = 48, P = 0.11; Table 1).

Combining both $\delta^{13}C$ and δD data, we portrayed these individuals with feather isotope values relative to marine-freshwater/C-3 ($\delta^{13}C$) and latitude (δD) continua in North America (Fig. 1). We also plotted the mean isotopic position of feathers from two species of seabirds, Thick-billed Murre (*Uria lomvia*; n = 8) and Black-legged Kittiwake (*Rissa tridactyla*; n = 5), collected at Coburg Island, Northwest Territories, to illustrate the isotopic region where a marine-derived feather would be expected (combined sample; mean δD = −28 ± 11‰; mean $\delta^{13}C$ = −17.9 ± 0.6‰). The feathers of six Ruddy Ducks had isotope profiles that indicated they were grown in southern latitudes, and at least three (ellipse in Fig. 1) were enriched enough in both isotopes to suggest dependence on marine inputs during periods of feather growth.

Our sample of migrant Ruddy Ducks collected by hunters during the fall did not differ significantly in their isotopic distributions from the Manitoba breeders (Table 1, Fig. 1), al-

though there was a tendency for more enrichment in $\delta^{13}C$ values. Notably, the fall sample showed no individuals that were enriched sufficiently in both isotopes to suggest marine-derived elements in their feathers. Similarly, fall hatching-year birds shot at Raven Lake, Manitoba (50°20'N, 100°37'W), but from unknown breeding sites, showed a broad range of stable-isotope values; all were depleted compared with those expected for southern or marine areas (mean $\delta D = -131.4 \pm 13.5‰$; mean $\delta^{13}C = -28.0 \pm 1.9‰$, $n = 4$).

TABLE 1. Stable carbon ($\delta^{13}C$) and hydrogen (δD) isotope values of Ruddy Duck feathers examined in this study.

	$\delta^{13}C$ (‰)				δD (‰)			
	$\bar{x} \pm$ SD	n	Range	95% CI	$\bar{x} \pm$ SD	n	Range	95% CI
Breeding birds (Manitoba)								
Male	−26.9 ± 3.6	31	−33.0 to −16.0	−28.2 to −25.6	−124.0 ± 25	25	−176.5 to −58.7	−136.2 to −83.6
Female	−26.5 ± 6.0	26	−34.4 to −13.3	−28.9 to −24.1	−107.7 ± 33	25	−140.3 to −18.3	−121.4 to −94.0
Fall flyway migrants								
Sexes combined	−24.3 ± 3.5	32	−29.9 to −16.8	−25.6 to −23.1	−124.9 ± 24	32	−173.3 to −72.6	−133.5 to −116.4

DISCUSSION

We provide the first quantitative estimate of the proportion of North American Ruddy Ducks that undergoes double molt of their remiges. Isotopic evidence suggests that only about 6 to 12% of individuals molt their remiges in winter. Furthermore, if the prevalence of double molt differs for first year and older birds (immatures > adults) as suggested by Hohman (1996), and if decoy traps capture more immatures than adults, then this estimate may be biased high because adult status could not be verified for all birds captured on the breeding areas.

Based on examination of feather wear, our results indicate the possibility of double molt in Ruddy Ducks, similar to what Siegfried (1973) reported. However, our stable-isotope analyses are consistent with recent reports of wing molt in Ruddy Ducks. Hohman (1996) reviewed published and unpublished information of double molt in Ruddy Ducks and determined it to be less common than assumed previously. He proposed that only immature free-living Ruddy Ducks undergo a double molt, and he restricted this hypothesis to individuals that attain adult size and attempt to breed. Although we could not test this specific hypothesis (we captured only one yearling), our results support Hohman's (1996) more general hypothesis that double molt in Ruddy Ducks is rare.

Our isotopic model is based on the assumption that ducks would encounter foodwebs on their wintering grounds that were isotopically distinct from those on their breeding grounds, and that such isotopic differences would provide a natural marker for where feathers were grown. Although it is virtually impossible to conduct an exhaustive isotopic survey of all

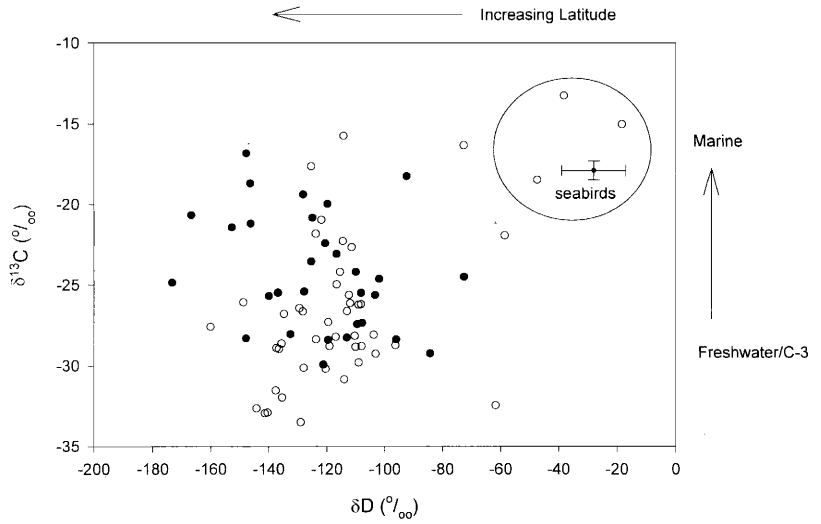

FIG. 1. Pattern of stable carbon and hydrogen isotope values for feathers of Ruddy Ducks sampled on the breeding grounds near Minnedosa, Manitoba, in 1997 (open circles), and for those sampled by hunters during in the Central Flyway in 1997 (filled circles). Positions of a sample of Thick-billed Murres and Black-legged Kittiwakes depict a typical marine endpoint. Ellipse indicates Ruddy Ducks that likely had grown some feathers on the wintering grounds.

foodwebs encountered by Ruddy Ducks, sufficient information exists on how foodweb isotopic signatures are expected to change with respect to biome or geographic gradient (see Hobson 1999). For carbon, enrichment in ^{13}C between marine and terrestrial freshwater or C-3 foodwebs is expected, but substantial overlap can occur among areas, especially in coastal regions or areas involving estuaries (e.g. Coffin et al. 1994). Isotopic variation in deuterium among foodwebs is less well documented owing to previous challenges in laboratory analysis and the need to correct organic samples for isotopic exchange. Nonetheless, strong continental gradients related to precipitation contours are now well documented (Cormie et al. 1994, Hobson and Wassenaar 1997, Chamberlain et al. 1997) and recent work (K. Hobson and L. Wassenaar unpubl. data) indicates that such continental gradients are also found in feathers of birds associated with shallow wetlands along a north-south gradient from Louisiana to Saskatchewan.

We also confirmed our general expectation that exclusively marine birds would show highly enriched $\delta^{13}C$ and δD values in feathers, which helped to provide an approximate endpoint with which to compare our Ruddy Duck sample. Although some variation in δD values among marine birds can be expected because of regional and trophic effects (Hobson 1999), the hydrogen isotope values in feathers of marine birds are expected to be relatively invariant because of ocean mixing. In fact, the international standard of comparison for hydrogen is the SMOW, because ocean water throughout the world is relatively constant and has arbitrarily been indexed as 0‰ (Craig 1961). Our seabird δD data indicate that isotopic fractionation between diet (including drinking water) and feathers was on the order of −28‰.

Interestingly, Ruddy Ducks sampled on the breeding grounds in Manitoba showed a trend of greater depletion in feather δD values in males than in females. This may be due to different metabolic demands on the sexes. However, like most waterfowl, male Ruddy Ducks appear to depart the breeding grounds to molt, leaving females on the breeding grounds to raise broods and to molt prior to fall migration. Although deuterium-precipitation isotopic gradients are known only approximately for North America, the relatively depleted δD values of males strongly suggest that males move northward from their breeding grounds to molt. A northward movement from the Minnedosa breeding area, corresponding to depletion in feather δD values of about 16‰, would

correspond to molting locations in the southern boreal forest (Hobson and Wassenaar 1997, Hobson 1999). Information on movements of postbreeding Ruddy Ducks is lacking throughout their range (Hohman et al. 1992a). However, anecdotal evidence (W. Hohman unpubl. data) suggests that some males in Manitoba move to Lake Winnipegosis, directly north of Minnedosa, to molt, an observation entirely consistent with our isotope results.

The mean deuterium isotope values of Ruddy Ducks taken during the fall harvest in the Mississippi Flyway were similar to those found for breeding males from Manitoba. Although we could not determine the sex of adults harvested in fall and winter, our isotope results suggest that, on average, these birds likely were males who had molted north of the breeding grounds in the southern boreal region. These results demonstrate how stable hydrogen isotope analysis may represent an exciting new tool to examine origins of fall-harvested waterfowl in North America. However, more studies are required to refine isotopic base maps for these and other species based on measurements derived from feathers grown at known locations (e.g. Hobson et al. 1999).

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