SHORT COMMUNICATIONS

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VARIATION IN HYDROGEN STABLE-ISOTOPE RATIOS BETWEEN ADULT AND NESTLING COOPER'S HAWKS

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Abstract. Hydrogen stable-isotope analysis of feathers is an increasingly popular method for estimating the origins of migrating and wintering birds. Use of this method requires that investigators know which feathers are grown on breeding grounds and how the hydrogen stable-isotope ratios of feathers (δD_f) relate to those of local precipitation (δD_p). In this study, we measured δD_f of adult (primaries 1, 3, and 10) and nestling Cooper's Hawks (*Accipiter cooperii*) in Wisconsin, North Dakota, and British Columbia, Canada. As previously shown, δD_f of nestling feathers were related to δD_p. In contrast, the δD_f of adult feathers grown on the breeding grounds were substantially greater than those of their nestlings, and varied significantly across primary feathers and study areas. Our findings suggest that it is not possible to use hydrogen stable-isotope analysis of feathers to learn the origins of migrating adult Cooper's Hawks (or possibly adults of other large-bodied species with extended molting periods) until more is learned about the physiological or ecological mechanisms underlying these isotopic discrepancies.

Key words: Accipiter cooperii, *migration, molt, raptor*.

Variación en las Proporciones de Isótopos Estables de Hidrógeno entre Adultos y Polluelos de *Accipiter cooperii*

Resumen. El análisis de isótopos estables de hidrógeno en las plumas es un método cada vez más popular para determinar el origen de aves migratorias e invernantes. El uso de esta técnica requiere que el investigador conozca qué plumas crecen en los lugares de nidificación y cómo las proporciones de isótopos estables de hidrógeno de las plumas (δD_f) se relacionan con aquellas de la precipitación local (δD_p). En este estudio, medimos las δD_f en adultos (primarias 1, 3 y 10) y en polluelos de *Accipiter cooperii* en Wisconsin, North Dakota y British Columbia, Canadá. Como se ha mostrado previamente, las δD_f de plumas de polluelos se encontraban relacionadas con las δD_p. Por el contrario, las δD_f de plumas de adultos que crecieron en los lugares de nidificación fueron substancialmente mayores que aquellas de sus polluelos, y variaron significativamente entre plumas primarias y áreas de estudio. Nuestros resultados sugieren que no es posible utilizar el análisis de isótopos estables de hidrógeno de plumas para determinar el origen de adultos migratorios de *A. cooperii* (o de adultos de otras especies de aves con tamaños corporales grandes y con períodos de muda extendidos) hasta que los mecanismos ecológicos y fisiológicos que subyacen a estas discrepancias isotópicas sean mejor entendidos.

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Stable-isotope analysis of feathers is an increasingly popular method for tracking the movements of birds (Hobson 2002, Webster et al. 2002). In particular, hy-

drogen stable-isotope analysis has been used in several studies to learn the breeding or natal origin of migrating or wintering birds (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Meehan et al. 2001, Kelly et al. 2002; Rubenstein et al. 2002, Smith et al., in press). This method is based on the following principles: First, many adults and all nestling birds replace molted feathers or grow juvenal feathers near or at their breeding or natal area (Palmer 1988, Pyle and Howell 1997). Second, at a given locale, the growing-season hydrogen stable-isotope ratio of precipitation is incorporated into food webs and ultimately fixed in the keratin of growing feathers (Hobson and Wassenaar 1997). Third, once a feather is completely grown, the nonexchangeable portion of the hydrogen stable-isotope ratio, locked in feather keratin, is preserved throughout the life of the feather (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Finally, the growing-season hydrogen stable-isotope ratio of North American precipitation varies, somewhat predictably, with latitude (Hobson and Wassenaar 1997). Therefore, feather samples from birds captured during migration or on wintering grounds can be analyzed and the hydrogen stable-isotope ratios compared to precipitation maps (Hobson and Wassenaar 1997) to learn the approximate latitude of feather growth.

Several aspects of a species' biology should be understood before this technique is used. First, it should be established that feathers sampled during migration, or on wintering grounds, were grown on the breeding grounds. This premise requires a detailed understanding of a species' molt schedule (Hobson and Wassenaar 1997). Second, it should be established that feathers grown on the breeding grounds reflect the stable hydrogen isotope ratios of local precipitation in a predictable fashion. This linkage has been consistently demonstrated for insectivorous songbirds and diurnal raptors across North America (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Meehan et al. 2001, Lott et al. 2003). Third, the members of a migrating or wintering sample should not forage in marine ecosystems (Lott et al. 2003), because the hydrogen stable-isotope ratios of ocean water do not vary with latitude as do those of precipitation (Hoefs 1980). Stable isotopes of sulfur in feathers can be used to detect a migrating or wintering bird's incorporation of marine resources (Caccamise et al. 2000, Lott et al. 2003).

We wanted to use hydrogen stable-isotope analysis to estimate the breeding origins of migrating adult Cooper's Hawks (*Accipiter cooperii*). Therefore, we needed to (1) gather information on the timing and sequence of molt in adults and (2) verify that the hydrogen stable-isotope ratios of adult feathers grown on the breeding grounds were similar to those of their nestlings, which reflect those of growing-season precipitation on the breeding grounds (Meehan et al. 2001).

METHODS

STUDY AREAS AND FEATHER COLLECTION

We studied populations of breeding Cooper's Hawks in central Wisconsin (44°25′N, 89°30′W), northwestern North Dakota (48°37′N, 102°27′W), and Vancouver Island, British Columbia, Canada (48°27′N, 123°21′W) during the breeding seasons of 2001 and 2002. More information on study areas can be found in Rosenfield et al. (2002).

Molt of primaries in breeding adult Cooper's Hawks begins at or soon after the onset of incubation, proceeds sequentially from the innermost primary (P1) to the outermost primary (P10), and may take 4–6 months to complete (Meng 1951, Henny et al. 1985, Rosenfield and Bielefeldt 1993). Innermost primaries are entirely regrown during incubation or early to middle nestling stages at all three study areas (RNR, unpubl. data), while outermost primaries may be in molt or regrowth during autumn migration in birds captured in both eastern (D. Evans, Hawk Ridge Nature Reserve, pers. comm.) and western (J. Smith, HawkWatch International, unpubl. data) North America. Thus, we collected a newly grown adult P1 and P3 to represent feathers replaced on the breeding grounds during the breeding season and a worn P10 from the previous year to represent feathers replaced during the late breeding season or fall migration. When capturing adult Cooper's Hawks and collecting feathers, we also collected flight or body feathers from their nestlings that were, perforce, grown on the breeding grounds. Sample sizes across adult and nestling feather categories were unequal because in some cases P1, P10, and nestling feathers were collected, and in other cases P3 and nestling feathers were collected.

Before lab analyses, we randomly selected a male or a female adult per nest site for comparison with its nestling. We haphazardly selected a male or female nestling per nest site for analysis. We did not differentiate between nestling sexes because previous analyses have shown no biologically or statistically significant difference between the hydrogen stable-isotope content of male and female nestling feathers ($n = 40$, ANCOVA $P = 0.77$ for nestling sex and $P = 0.79$ for interaction between sex and precipitation isotope ratio; TDM and RNR, unpubl. data). Hereafter, the feathers from an adult and nestling at a given nest site are referred to as a "feather set."

STABLE ISOTOPE ANALYSES

We analyzed feather sets at the Stable Isotopes Laboratory at the University of New Mexico between December 2001 and August 2002. Before analyses, we washed feathers with a mixture of detergent and deionized water (Chamberlain et al. 1997), rinsed them, and allowed the exchangeable hydrogen in feathers to equilibrate with hydrogen in ambient moisture in the laboratory (Hobson and Wassenaar 1997). After two weeks of equilibration, we packed feather rachis clippings weighing 0.20 mg (range 0.18–0.22 mg) into silver capsules. Samples were pyrolyzed with a Finnigan MAT TC-EA elemental analyzer (Thermo Finnigan, Inc., San Jose, California) and measured for their stable hydrogen isotope ratios with a Finnigan Delta^{Plus}XL stable-isotope mass spectrometer in continuous flow mode (Sharp et al. 2001). Hydrogen stable-isotope ratios were converted into δD values using the following standard formula: $\delta D = [(\text{hydrogen isotope ratio of sample})/(\text{hydrogen isotope ratio of Vienna Standard Mean Ocean Water}) - 1] \times 1000$. δD values are reported in parts per thousand units (‰). The pre-

cision of our analyses was δ*D* ± 3‰ (SD), based on repeated measurements of internal laboratory standards.

Because feather samples were air equilibrated, the δ*D* values we report are for combined nonexchangeable (78–79%, Wassenaar and Hobson 2000a) and exchangeable hydrogen and should not be directly compared to feather δ*D* values derived from other laboratory methods (Wassenaar and Hobson 2000a). Keratin standards designed for standardizing δ*D* values across laboratories (Wassenaar and Hobson, in press) were not available during our analyses. Using δ*D* values composed of exchangeable and nonexchangeable hydrogen could have confounded our age comparisons if adult and nestling feathers had been analyzed during different times of the year because the δ*D* values of ambient moisture vary seasonally (Araguas-Araguas et al. 2000). We avoided this problem by analyzing all adult and nestling feathers from a given feather set consecutively, within 10 min of one another. While our comparison of adults and nestlings was not confounded by seasonal variation, the overall variation within age groups was probably increased due to our extending analyses over a nine-month period.

STATISTICAL ANALYSES

We plotted the δ*D* values of adult and nestling feathers per study site, adult primary feather, and adult sex for graphical comparison. We estimated expected δ*D* values for all feathers using a map from Wassenaar and Hobson (2001). This map was created by subtracting 25‰ from the isobars of their previously published map of δ*D* values of weighted-average growing-season precipitation (Hobson and Wassenaar 1997). The shift of −25‰ from precipitation to feathers was determined from an isotopic study of songbirds in Saskatchewan, Canada (Wassenaar and Hobson 2001). However, other isotopic studies of songbirds (Wassenaar and Hobson 2000b) and raptors (Meehan et al. 2001) have shown this simple shift to be a reasonable characterization of the relationship between the δ*D* values of precipitation and feathers. Next, within each feather set, we subtracted the δ*D* value of a nestling feather from each δ*D* value measured for adult P1, P3, and P10. These comparisons are hereafter referred to as "feather comparisons." We used three-way ANOVA to look at feather comparisons according to study area, adult primary number, and sex of adult. We used type III hypothesis tests because sample sizes were unequal across treatment combinations (Milliken and Johnson 1984). We report means ± SE except where indicated.

RESULTS

Figure 1 shows the δ*D* values of all feathers included in our study. Of these 117 feather values, 27, 18, 27, and 45 were from adult P1, P3, and P10, and nestling feathers, respectively. The dashed lines on Figure 1 indicate the expected δ*D* values for feathers per study area based on the typically reported relationship between feathers and precipitation (Wassenaar and Hobson 2001). Note that the δ*D* values of nestling feathers were generally as expected. In contrast, the δ*D* values of adult primary feathers were much greater than expected.

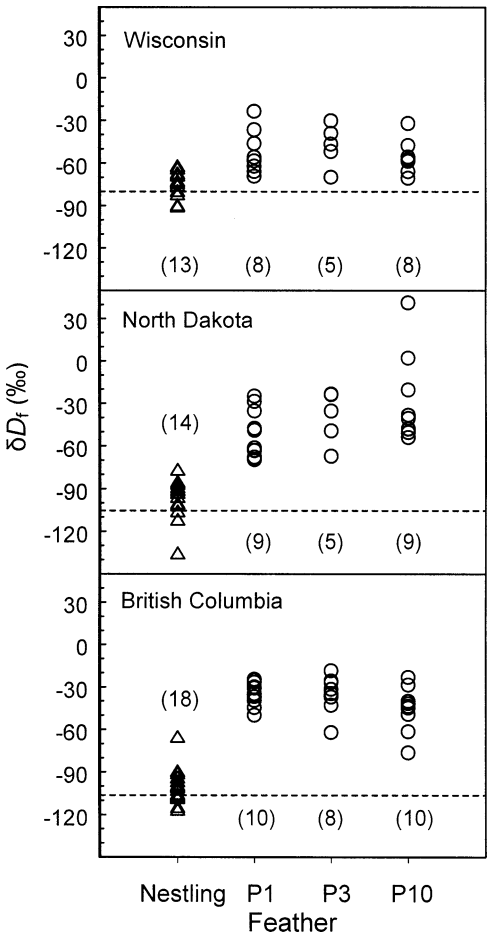

FIGURE 1. Stable-hydrogen-isotope (δ*D*) values of adult Cooper's Hawk primaries 1 (P1), 3 (P3), and 10 (P10) and nestling body and flight feathers from study sites in central Wisconsin, northwestern North Dakota, and Vancouver Island, British Columbia, Canada. Dashed lines are expected feather δ*D* values from Figure 1 of Wassenaar and Hobson (2001). Note that the δ*D* values of nestling feathers were as expected while those of adult feathers deviated substantially from expected. Numbers in parentheses are sample sizes.

When the 45 nestling values were regressed against predicted precipitation values from Hobson and Wassenaar's (1997) precipitation map, the resulting slope and intercept were 0.96 ± 0.15 and −21.90 ± 10.99‰, respectively, and the $r^2 = 0.50$. The average SD for δ*D* values of nestling feathers within each population was 11.64‰. This variation was slightly higher than usually reported in studies of bird feathers, and was a result of using measures of pooled exchangeable and nonexchangeable hydrogen and conducting our lab analyses over several months.

Three-way ANOVA indicated that feather comparisons varied significantly according to the study area

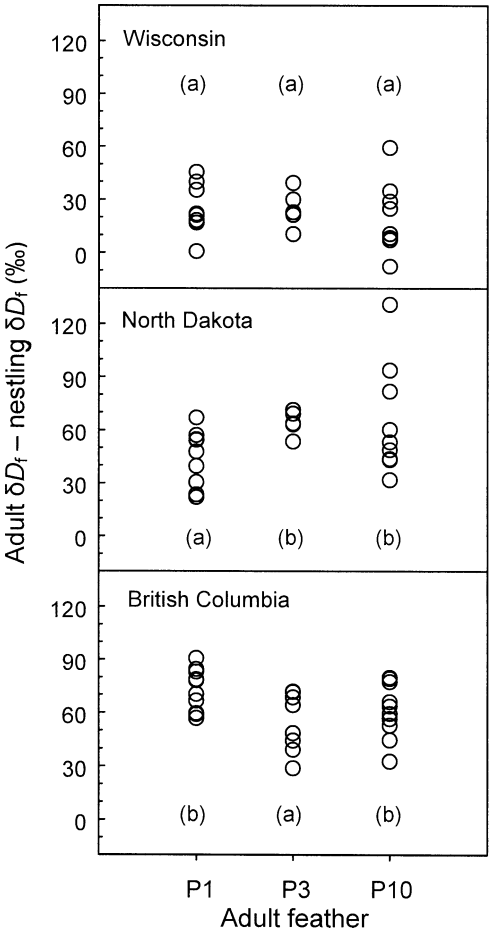

FIGURE 2. Differences between the δ*D* values of nestling feathers and adult primaries 1 (P1), 3 (P3), and 10 (P10) per territory from Cooper's Hawks at study sites in central Wisconsin, northwestern North Dakota, and Vancouver Island, British Columbia, Canada. Lowercase letters denote group membership from a Tukey's HSD multiple comparisons test. Adult feather sample sizes are the same as those in Figure 1.

($F_{2,55} = 27.2$, $P < 0.001$) and according to an interaction between the adult primary number and the study area ($F_{4,55} = 3.2$, $P = 0.02$; Fig. 2). A Tukey's HSD multiple comparisons test indicated that the difference between adult and nestling feathers was smaller for all adult primaries in Wisconsin, P1 in North Dakota, and P3 in British Columbia, and larger for all other primary × study area combinations (Fig. 2). The sex of a parent was not systematically related to the difference between the δ*D* values of adult and nestling feathers.

There was a possibility that if we had analyzed other inner and middle adult primaries, besides P1 and P3, we might have found an adult primary feather with a δ*D* value matching nestling feathers. During the non-

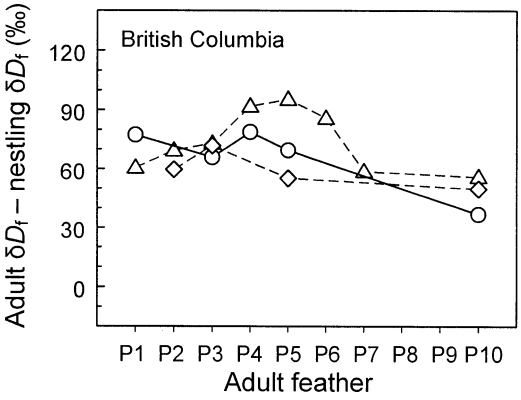

FIGURE 3. Differences between the δ*D* values of nestling feathers and adult primary feathers (P1 through P10) for three Cooper's Hawk nest sites on Vancouver Island, British Columbia, Canada. This limited sample suggested that analyzing other adult primaries, besides P1, P3, and P10, would have yielded feather δ*D* differences comparable to those in Figure 2.

breeding season in British Columbia, we found three radio-tracked adult Cooper's Hawks dead near their nesting sites. We sampled and analyzed several primaries from these birds and compared the δ*D* values to those of their known nestlings from the previous breeding season (Fig. 3). This limited comparison suggested that analyzing other primaries, besides P1 and P3, would yield similar differences between the δ*D* values of adult and nestling feathers.

DISCUSSION

We expected the δ*D* values of adult primaries 1 and 3 to be the same as those of nestling feathers because (1) these feathers are grown on the breeding grounds (RNR, unpubl. data) and (2) adults and nestlings eat the same prey (Rosenfield and Bielefeldt 1993). In contrast, we expected the δ*D* values of adult primary 10 to be greater than those of nestling feathers because adult Cooper's Hawks often molt and replace these feathers during fall migration, south of the breeding grounds, where the hydrogen stable-isotope ratios of their food are probably greater than those of their food on the breeding grounds. Contrary to our initial expectation, adult primaries 1 and 3 had considerably larger δ*D* values than nestling feathers. Though this pattern was apparent across North America, the degree to which primaries 1 and 3 deviated from nestling feathers varied significantly according to study area and sometimes according to which adult primary was being compared.

We have no ready explanation for the observed isotopic discrepancies between adults and nestlings. However, we do suggest some nonexclusive hypotheses for future testing. First, because adults grow inner primaries earlier in the breeding season, it is possible that they contain proteins derived from the muscle tissue of migrant avian prey. Because of the latitudinal pattern of δ*D* values of precipitation, the muscle tissue of northerly migrating prey may have greater δ*D* values

than local growing-season precipitation. This prey muscle tissue would remain relatively "heavy" (higher δD values) until it equilibrated with the local ecosystem.

A second possible mechanism causing heavy inner primaries is that Cooper's Hawks grow these feathers using reserves accumulated while wintering at lower latitudes (Hobson et al. 1997). Although this explanation is plausible for Cooper's Hawks from Wisconsin, where they are believed partially migratory (Bielefeldt et al. 1998) and North Dakota, where believed mostly migratory (R. K. Murphy, pers. comm.), it is not likely to be true for birds from British Columbia, where Cooper's Hawks are largely nonmigratory (ACS, unpubl. data).

A third possible explanation for heavy inner and middle primaries is related to fractionation of body water due to evaporative cooling from the upper respiratory tract by birds during the physiologically stressful breeding season. For example, while incubating and brooding, female Cooper's Hawks may absorb excess heat from their offspring and dissipate it through panting (evaporative cooling) in order to maintain a critical temperature range (Drent 1972). Also, during the egg-laying, incubation, and nestling periods, male Cooper's Hawks are especially active, providing food for the female and offspring (Rosenfield and Bielefeldt 1993). It is possible that this high level of activity also increases their rates of evaporative cooling. Evaporative cooling across the lung surface of birds may lead to enrichment of heavy hydrogen stable-isotopes in the body-water pool (Wolf and Martínez del Rio 2000, B. Wolf and A. McKechnie, unpubl. data). Since 26–32% of the nonexchangeable hydrogen in feather keratin is believed to come from body water (Hobson et al. 1999), substantial enrichment in body water could lead to heavy feathers. Detailed field studies of the δD values of Cooper's Hawk blood, feathers, and prey, throughout the breeding season, might help clarify which, if any, of the above hypotheses are correct.

If we had found a consistent difference between the δD values of adult primaries and nestling feathers, we could have calculated an empirical fractionation factor that could be applied to the feathers of adults captured during migration to aid in learning the latitude of feather growth. However, feather comparisons were not consistent across study areas or primary feathers. Therefore, our findings indicate that it is not possible to use hydrogen stable-isotope analysis of feathers to learn the breeding grounds of adult Cooper's Hawks until more is learned about the physiological or ecological mechanisms behind these isotopic discrepancies. Further, the discrepancies we observed in Cooper's Hawks may also be found in other species where molt is extended over several months and overlaps with reproduction.

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PREHISTORIC EXPLOITATION OF BIRDS ON THE PACIFIC COAST OF CHIAPAS, MEXICO

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Abstract. We report bones of 60 species of birds from the Paso de la Amada archaeological site (ca. 3600 to 3150 years old) in the Soconusco region of Chiapas, Mexico. Among 36 species of landbirds and 24 marine, estuarine, and aquatic species, four landbirds (*Harpia harpyja*, *Ortalis vetula*, *Cyrtonyx ocellatus*, and *Ara militaris*) have not been recorded previously from coastal Chiapas. Their nearest populations are characteristic of foothill or montane forest. The families of birds most commonly exploited at Paso de la Amada were Columbidae (pigeons, doves), Phasianidae (quail), Falconidae (caracaras), Ardeidae (herons), and Cracidae (chachalacas). Because of human interactions with birds and their habitats over the millennia, it is difficult or impossible to determine the

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