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CORRELATION BETWEEN FEATHER ISOTOPES AND BODY CONDITION FOR SWAINSON'S HAWKS, AND IMPLICATIONS FOR MIGRATION STUDIES

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Abstract.—The study of individual movement patterns using stable hydrogen isotopes ($\delta\ ^{2}H$) as a natural marker has grown; however, recent studies have suggested that measurement of $\delta\ ^{2}H$ in feathers ($\delta\ ^{2}H_f$) may prove unreliable as a means for identifying region of origin of migrating or wintering birds, particularly raptors. In this study, we examine whether differences in body condition could explain some of the variability in $\delta\ ^{2}H$ in feathers. We analyzed growing feathers of 21 Swainson's Hawks breeding in northern CA for $\delta\ ^{2}H$, nitrogen ($\delta\ ^{15}N$), and carbon ($\delta\ ^{13}C$) stable isotopes in relation to body condition. We found that $\delta\ ^{2}H$ was variable (range = 40‰), and that variability was significantly associated with body condition. Raptors derive most or all of their moisture from prey. Therefore, we suggest that individuals in poor condition have an enriched pool of body water relative to individuals in good condition, due to fractionation of body water stores during respiratory water loss and metabolic processes. Body condition was also negatively correlated with $\delta\ ^{15}N_f$. However, $\delta\ ^{2}H_f$, $\delta\ ^{15}N_f$, and $\delta\ ^{13}C_f$ were not correlated, suggesting that the relationship between $\delta\ ^{2}H_f$ and body condition is a result of physiological processes rather than differences in dietary $\delta\ ^{2}H$. We used an isotopic basemap of $\delta\ ^{2}H_f$ values to assess individual origin as if they were encountered naively on the migration or wintering grounds, and all individuals fell within the 95% confidence interval of our study area. Conversely, the 95% confidence interval of $\delta\ ^{2}H_f$ values obtained encompassed almost the entire breeding range of this species, indicating little ability to differentiate origins of this species.

Key Words: *Swainson's Hawk*; Buteo swainsoni; *body condition*; *deuterium*; *nitrogen*; *stable isotopes.*

CORRELACIÓN ENTRE ISÓTOPOS DE LAS PLUMAS Y CONDICIÓN CORPORAL EN *BUTEO SWAINSONI* E IMPLICACIONES PARA ESTUDIOS DE MIGRACIÓN

Resumen.—El estudio de los patrones de movimiento individual utilizando isótopos estables de hidrógeno ($\delta\ ^{2}H$) como marcador natural ha aumentado; sin embargo, estudios recientes han sugerido que la medición de $\delta\ ^{2}H$ en plumas ($\delta\ ^{2}H_f$) puede ser poco fiable como medio para identificar la región de origen de aves migratorias o invernantes, particularmente en rapaces. En este estudio, examinamos si las diferencias en la condición corporal pueden explicar parte de la variabilidad de $\delta\ ^{2}H$ en las plumas. Analizamos los isótopos estables de $\delta\ ^{2}H$, nitrógeno ($\delta\ ^{15}N$) y carbono ($\delta\ ^{13}C$) en las plumas en crecimiento de 21 individuos de *B. swainsoni* reproductores que crían en el norte de California en relación a la condición corporal. Encontramos que el isótopo $\delta\ ^{2}H$ fue variable (rango = 40‰) y que dicha variabilidad estuvo significativamente asociada con la condición corporal. Las rapaces obtienen la mayor parte del agua que consumen a partir de sus presas. Por lo tanto, sugerimos que los individuos en malas condiciones presentan una reserva de agua corporal enriquecida en relación a los individuos en buenas condiciones,

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debido al fraccionamiento de las reservas de agua corporal durante la pérdida de agua por respiración y a los procesos metabólicos. La condición corporal también estuvo negativamente relacionada con el isótopo $\delta\ ^{15}N_f$. Sin embargo, $\delta\ ^{2}H_f$, $\delta\ ^{15}N_f$, y $\delta\ ^{13}C_f$ no estuvieron correlacionados, lo que sugiere que la relación entre $\delta\ ^{2}H_f$ y la condición corporal es el resultado de procesos fisiológicos más que de las diferencias en el $\delta\ ^{2}H$ proveniente de la dieta. Utilizamos un mapa base isotópico de valores de $\delta\ ^{2}H_f$ para evaluar el origen individual como si fueran encontrados espontáneamente durante la migración en las áreas de invernada y todos los individuos cayeron dentro del intervalo de confianza del 95% de nuestra área de estudio. Por el contrario, el intervalo de confianza del 95% de los valores de $\delta\ ^{2}H_f$ obtenidos incluyó la casi totalidad del área reproductiva de esta especie, indicando la escasa capacidad para diferenciar los orígenes de esta especie.

[Traducción del equipo editorial]

The use of naturally occurring stable isotopes within animal tissues as a tool to answer ecological questions has helped explain questions about diet, movements, and physiology of many bird species (Thompson et al. 2005, Fox and Bearhop 2008, Inger and Bearhop 2008, Kelly et al. 2008). The isotopes of carbon ($\delta\ ^{13}C$), nitrogen ($\delta\ ^{15}N$), and hydrogen ($\delta\ ^{2}H$) have been particularly useful in ecological studies (Thompson et al. 2005). In particular, $\delta\ ^{2}H$ is often used to assess movement patterns of individuals because $\delta\ ^{2}H$ varies consistently across the landscape due to variation in rainfall (Hobson and Wassenaar 1997). In fact, $\delta\ ^{2}H$ has been used to investigate a myriad of ecological questions associated with animal movement, such as migratory connectivity (Hobson 2005, Sarasola et al. 2008), migratory behavior (e.g., Cardador et al. 2015, Domenech and Pitz 2015) and natal dispersal (Hobson et al. 2004) in avian species. Birds provide an ideal study organism for such investigations because feathers provide researchers a source of isotopic material that is metabolically inert and retains the isotopic signature of the area in which it was grown (Hobson and Wassenaar 1997).

Despite increased interest and utilization of $\delta\ ^{2}H$ analyses, recent studies have suggested that stable isotope compositions may not be reliably measured within a population or even across an individual feather in some species (Smith et al. 2008, 2009, Wunder et al. 2009). These results indicate a lack of precision when trying to assess origin of tissues using $\delta\ ^{2}H$ or other isotopes. In spite of these questions, some studies advocate grouping observations into regions of origin, rather than providing precise estimates of geographic origin, to account for some of the variability between samples collected in the same location (Langin et al. 2007); however, the source of this interindividual variability is largely unknown. We hypothesize that some of this variation of feather-$\delta\ ^{2}H$ is the result of body condition-dependent processes, particularly for individuals that derive some or all of their water from food.

Other isotopes, such as $\delta\ ^{13}C$ and $\delta\ ^{15}N$, have been used to examine diet at the population and individual levels (reviewed in Inger and Bearhop 2008). Nitrogen is often used to reveal trophic positions of individuals because nitrogen becomes more enriched with increased trophic level due to fractionation (DeNiro and Epstein 1981, Hobson et al. 1993). However, in addition to trophic enrichment, several studies have demonstrated an enrichment of $\delta\ ^{15}N$ in nutritionally stressed individuals (Ambrose and DeNiro 1986, Hobson and Clark 1992, Hobson et al. 1993, Castillo and Hatch 2007). For example, Hobson et al. (1993) demonstrated that tissues from incubating Ross's Geese (*Chen rossii*) were enriched after the incubation period (i.e., post-fasting during egg-laying and incubation). The authors suggest that the enrichment is the result of catabolization of tissues that have already been enriched to meet energetic demands. Thus, catabolization causes enrichment of $\delta\ ^{15}N$ values above a baseline. However, not all studies have found $\delta\ ^{15}N$ enrichment correlated with measure(s) of body condition (Ben-David et al. 1999). Similarly, $\delta\ ^{13}C$ may vary by diet, as different photosynthetic pathways differ in their discrimination of the heavier isotope (Fry 2006) and may be depleted when food is restricted in some species (Robb et al. 2015).

For species that acquire most or all of their water from food resources, we predict that $\delta\ ^{2}H$ will also be isotopically enriched. In this study, we examined feathers collected from a population of breeding Swainson's Hawks (*Buteo swainsoni*) nesting in northern CA U.S.A. By only sampling feathers of nesting adults that were still in sheath, we ensured that all feather material was grown within a few km of the nest site (Woodbridge 1991). Therefore, all feathers should have similar isotopic signatures if the isotopic composition of precipitation ($\delta\ ^2H_p$) is the primary driver of the isotopic composition of feathers ($\delta\ ^2H_f$), as they were all grown within 30 km of each other with only 60 m of elevation change across the study area (Woodbridge 1991). The value of $\delta\ ^2H_f$ should be correlated with $\delta\ ^2H_p$, as $\delta\ ^2H$ from rainfall is incorporated into plants and subsequently prey. Fractionation can occur at all stages of the process, wherein lighter isotopes may be used preferentially in metabolic processes (e.g., evaporative water loss, respiration, etc.; Fry 2006). Therefore, individuals can become isotopically enriched relative to precipitation, but they should reflect $\delta\ ^2H_p$. In contrast, if other factors (e.g., body condition) play a role in controlling $\delta\ ^2H_f$, then we expect wide range of $\delta\ ^2H_f$ values, disrupting the correlation between $\delta\ ^2H_p$ and $\delta\ ^2H_f$. If such wide variability exists, $\delta\ ^2H_f$ would be a poor surrogate of molt location. Swainson's Hawks provide a good study species because they have relatively small home ranges (Woodbridge 1991) and generally do not drink standing water (Roest 1957, Cooper 1968). Like most birds of prey, they acquire most or all of their body moisture from their prey (Bartholomew and Cade 1957). Therefore, $\delta\ ^2H_f$ signatures of feathers grown on the breeding territory should reflect local prey, and should not vary substantially between individuals because there would not be differences in $\delta\ ^2H_p$ across territories.

METHODS

Study Site and Species. We monitored a population of breeding Swainson's Hawks in Butte Valley, CA U.S.A. (41°45.7′N, 121°48.37′W) from April through August, 2008–2010. We monitored territories annually and located nest sites by watching for nest-building, mating behavior, and territoriality (April–May). In the summer months, we found nests by watching for prey deliveries to the nest site. We trapped adults between June 29 and August 15 near the nest site using dho-gaza-style net with a Great Horned Owl lure (*Bubo virginianus*, Bloom et al. 1992) or a bal-chatri baited with mice (Berger and Mueller 1959). We color-marked adults using unique two-digit color bands and a U.S. Geological Survey (U.S.G.S.) aluminum band, and determined sex by presence/absence of a brood patch, by size measurements, and by observations of copulatory behavior.

We measured wing chord to the nearest mm and weight to the nearest 1 g. We also opportunistically collected a growing secondary covert (i.e., the feather was still in sheath) from either wing. However, growing secondary coverts were not in the same position on each individual; therefore, we could only collect these feathers if the individual was molting a secondary feather. We recorded whether each individual had any food present in its crop, which could bias our weight measurements. All procedures were approved by the University of Nevada, Reno, IACUC (protocol no. 000115).

Isotopic Analysis. We washed each feather to remove oils following the recommendations of Paritte and Kelly (2009). We collected all feather material from the distal portion of each feather approximately 50 mm from the tip of the feather and we avoided using the central rachis to avoid potential contamination with blood. We weighed out between 500–600 µg of feather material for $\delta\ ^2H$ analysis, and analyzed it following the technique of Hilkert et al. (1999), using $\delta\ ^2H$ standards obtained from L.I. Wassenaar (Environment Canada) to adjust for the exchangeable portion of hydrogen in keratin (Wassenaar and Hobson 2003). Results are reported in standard δ notation in units of ‰ versus VSMOW.

We weighed out an additional 500–600 µg of feather material for $\delta\ ^{13}C$ and $\delta\ ^{15}N$ analysis, and analyzed it following the technique of Werner et al. (1999). Results are reported in standard δ notation in units of ‰ versus VPDB and air, respectively. All samples were analyzed at the Nevada Stable Isotope Laboratory in Reno, Nevada U.S.A.

Statistical Analysis. We estimated an index of body condition by using a standard major axis (SMA) regression to predict body mass based on wing chord (Peig and Green 2009). We regressed the natural log of weight against the natural log of wing chord for all birds of one sex and obtained an index of condition for each individual by subtracting the mass predicted by the SMA regression from the observed weight. The difference between the actual weight of the individual and the predicted weight was considered the index of condition (i.e., a positive value indicates a heavier weight than would be expected for a given size of the individual). We calculated condition indices separately for males and females. We used Pearson correlations to examine potential relationships among $\delta\,^{2}$H, carbon ($\delta\,^{13}$C), and nitrogen ($\delta\,^{15}$N).

We used a linear mixed model to perform a series of three regressions examining $\delta\,^{2}H_{f}$, $\delta\,^{13}C_{f}$, and $\delta\,^{15}N_{f}$ and their relationships with (1) the residuals of the SMA regression (i.e., condition index), (2) capture date (Julian date), and (3) sex in R 3.3.1 (R Development Core Team 2009) and the nlme package (Pinheiro et al. 2016). Specifically, we regressed each of the isotopes against body condition and capture date as fixed effects and year was used as a random effect for all models to account for potential unmeasured annual differences. For all analyses, no individuals showed any signs of food in the crop. Due to low sample sizes, we did all regressions univariately to avoid overparameterization of the model. We set our significant threshold to $\alpha = 0.05$ for all models.

Geographic Assignment. We followed Hobson et al. (2009) to create a basemap of $\delta\,^{2}$H values for raptors of North America to determine where each individual would be naively located if it were encountered outside of the breeding range (e.g., Sarasola et al. 2008). Because there were too few Swainson's Hawks measured in the Lott and Smith (2006) study to create a basemap specific for Swainson's Hawks (Hobson et al. 2009), we created a basemap using all species measured in Lott and Smith (2006). Following Hobson et al. (2009) we used a reduced major axis regression to determine the average fractionation of $\delta\,^{2}H_{f}$ from $\delta\,^{2}H_{p}$, where $\delta\,^{2}H_{p}$ was calculated for the growing season (Meehan et al. 2004). We used the SD of the estimate from the SMA regression to create 1000 new estimates of $\delta\,^{2}H_{f.}$ We created percentiles (5th through 95th) based on those simulated results and used those estimates create a map of potential origins. We used these measures to assess the accuracy of using $\delta\,^{2}$H as a predictor in describing region of feather growth.

Table 1. Model results (estimates ± SE) from a linear mixed model of hydrogen ($\delta\,^{2}$H), nitrogen ($\delta\,^{15}$N), and carbon ($\delta\,^{13}$C) stable isotopes in breeding Swainson's Hawk feathers from Butte Valley, CA, from 2008–2010 against body condition, capture date, and sex.

ISOTOPE	CONDITION	CAPTURE DATE	SEX
δ 2H	−0.48 ± 0.11**	−0.33 ± 0.20	−2.92 ± 5.34
δ 13C	−0.02 ± 0.02	0.00 ± 0.03	0.37 ± 0.66
δ 15N	−0.04 ± 0.02*	0.04 ± 0.03	−0.32 ± 0.69

* Significance at $P < 0.05$.

** Significance at $P < 0.001$.

RESULTS

The estimated growing-season $\delta\,^{2}H_{p}$ within the study area was −102‰, and $\delta\,^{2}H_{f}$ values ranged from −71‰ to −114‰. There were no correlations among $\delta\,^{2}H_{f}$ and $\delta\,^{15}N_{f}$, or $\delta\,^{13}C_{f}$ isotopic compositions ($P >$ 0.24 for all comparisons). There was a significant relationship between $\delta\,^{2}H_{f}$ and body condition ($P <$ 0.001, $n = 21$) as well as $\delta\,^{15}$N and condition ($P <$

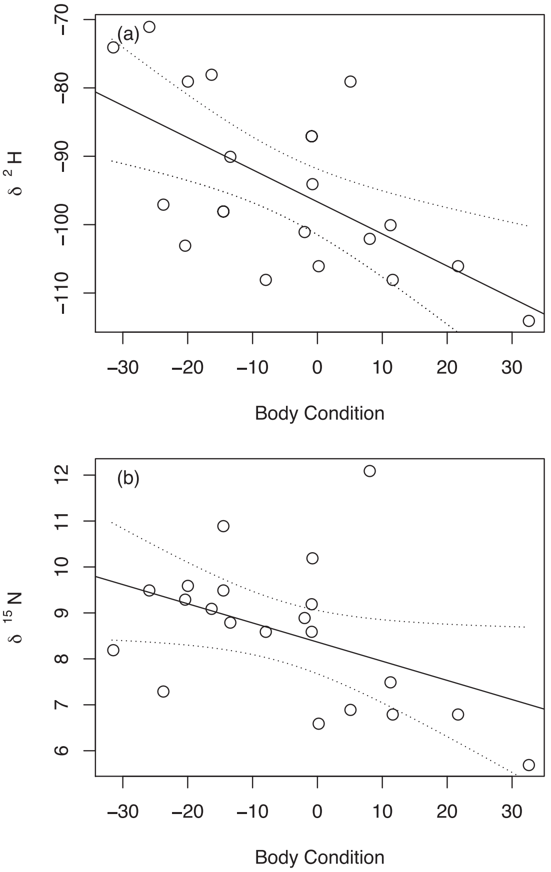

Figure 1. Isotopic compositions of hydrogen ($\delta\,^{2}$H; a) and nitrogen ($\delta\,^{15}$N; b) of growing feathers of breeding adult Swainson's Hawks in Butte Valley, CA U.S.A. Model estimates (solid lines) and 95% confidence intervals (dashed lines) of the relationship between isotope and body condition as measured by the residuals of an SMA regression.

0.05, $n = 21$; Table 1; Fig. 1). All other relationships were not significant ($P > 0.1$).

We calculated that the mean $\delta\,^{2}H_{f}$ value for our study area should be –106‰ ($n = 21$). The 95% CI for our error-propagated results for Butte Valley, CA was –147 to –64‰. Despite the variability in $\delta\,^{2}H_{f}$ composition, all individuals sampled fell within the 95% confidence interval based on the residuals from the SMA regression of $\delta\,^{2}H_{f}$, and the mean $\delta\,^{2}H_{f}$ observed from growing Swainson's Hawk feathers (–95 ± 3‰) were within the 50th percentile of predicted $\delta\,^{2}H_{f}$ values for our study area (Fig. 2).

DISCUSSION

We found isotopic enrichment of both $\delta\,^{2}H_{f}$ and $\delta\,^{15}N_{f}$ in Swainson's Hawks negatively related to body condition of breeding individuals. Isotopic enrichment of $\delta\,^{15}N$ in tissues has been described in several species (Ambrose and DeNiro 1986, Hobson and Clark 1992, Hobson et al. 1993, but see Ben-David et al. 1999). For example, Hobson et al. (1993) found that juvenile Japanese Quail (*Coturnix japonica*) that were food-deprived had more enriched $\delta\,^{15}N$ values compared to individuals fed ad lib. This relationship was also observed in Swainson's Hawks, with individuals in relatively poorer body condition having enriched feathers (Bearhop et al. 2002). The underlying cause of the relationship is still unknown; however, it is reasonable to suspect that the catabolization of tissues to meet energetic demands, and the subsequent fractionation as those tissues are used to fuel the individual, result in more enriched tissues. These enriched tissues are then incorporated into newly growing feathers, obscuring the relationship between $\delta\,^{2}H_{f}$ and $\delta\,^{2}H_{p}$.

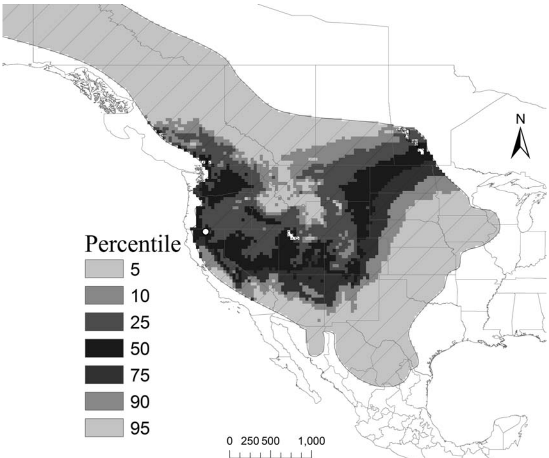

Figure 2. Isotopic basemap to naively estimate origins of Swainson's Hawks trapped in Butte Valley, CA, from 2008–2010. Estimates were based on feather $\delta\,^{2}H$ values following Hobson et al. (2009) from feathers collected from known-source raptors. All feathers used in the analysis were growing at the time of capture and should reflect values from within the study area (white circle). Diagonal barring indicates breeding range of the Swainson's Hawk (Bechard et al. 2010).

However, a similar relationship among body condition and isotopic enrichment has not been observed previously in $\delta\,^{2}H$ tissue values. Raptors derive most or all of their body water from prey, and are rarely observed to drink water (Bartholomew and Cade 1957). Individuals in poor condition (i.e., individuals that do not eat or do not eat enough to cover energetic costs) will therefore have a net water loss due to evaporative, respiratory, and metabolic water losses. Evaporative and respiratory water is expected to be isotopically light versus body water, due to the isotopic fractionation associated with the water liquid to water vapor phase change (Horita and Wesolowski 1994). Hence, without additional water input (in the form of prey intake), isotopic enrichment of remaining body water would occur, and this isotopically heavy signature would subsequently be recorded in the $\delta\,^{2}H_{f}$ composition. In fact, this is a mechanism proposed to potentially cause difference in $\delta\,^{2}H_{f}$ between nestling and adult American Kestrels (*Falco sparverius*; Greenwood and Dawson 2011) and Northern Saw-whet Owls (*Aegolius acadicus*; De Ruyck et al. 2013). The hypothesis of reduced intake of prey may also be consistent with the observed isotopic enrichment of $\delta\,^{15}N_{f}$ at low body condition, due to the nitrogen isotope fractionation associated with the deamination of amino acids (Macko et al. 1986), and depending upon the ratio of dietary nitrogen lost via excretion to dietary nitrogen uptake (Fry 2006).

It is possible that the relationship between body condition and $\delta\,^{2}H$ may explain some of the variation observed in raptor feathers in other studies (e.g., Smith et al. 2008, 2009). Variation in $\delta\,^{2}H$ within raptors has been observed in a number of species, and has been documented at >40‰ (e.g., Smith et al. 2008), which is similar to the variation among individuals observed in this population (43‰). Although such variation may be typical of raptors, it confounds our ability to accurately assess origins of feather growth in wintering or migratory species, even in regions where there is significant isotopic variation in precipitation. Although all samples fell within the 95% confidence interval for the study area, the 95% confidence interval also encompassed almost the entire breeding range of this species, indicating little ability to differentiate origins of this species. The only area excluded from our 95% confidence interval was the extreme northern part of this species' breeding range. Thus, the wide confidence intervals of the model, coupled with large intrapopulation variability, suggest that studies examining migratory connectivity of this species (e.g., Sarasola et al. 2008) may need more validation before definitive conclusions can be drawn, regardless of the mechanism underlying the intrapopulation differences in $\delta\ ^2H$.

There were no significant correlations among any of the isotopes we measured (i.e., $\delta\ ^2H_f$, $\delta\ ^{15}N_f$, and $\delta\ ^{13}C_f$). A lack of correlations among $\delta\ ^2H_f$ and $\delta\ ^{15}N_f$, and $\delta\ ^{13}C_f$ indicates that the correlation between $\delta\ ^2H_f$ and body condition may not be mediated by differences in prey base or trophic position of breeding individuals. Thus, the isotopic enrichment of $\delta\ ^2H_f$, and likely other tissues (Bearhop et al. 2002) in Swainson's Hawks, is more likely due to water loss without replacement if an individual does not eat, rather than isotopic differences or fractionation rates of differing prey items. Similarly, enrichment of $\delta\ ^{15}N_f$ may come from fractionation as tissues are catabolized.

Almost 90% of the diet of Swainson's Hawks in this area consists of small mammals, primarily Belding's ground squirrels (*Spermophilus beldingi*), Mazama pocket gophers (*Thomomys mazama*), and montane voles (*Microtus montanus*; Woodbridge 1991). Therefore, prey should also reflect the local $\delta\ ^2H$ values, as the species that are consumed in large numbers either are nonmigratory, or have not yet had time to migrate (i.e., young of the year or juveniles). However, because we did not sample prey, we could not explicitly rule out prey differences driving relationships among body condition and $\delta\ ^2H_f$ or $\delta\ ^{15}N_f$. Similarly, we could not exclude differential use of exogenous versus endogenous reserves within the individual (Oppel et al. 2010). In fact, Swainson's Hawks may refuel on their pre-breeding migration (Bechard et al. 2006, Kochert et al. 2011), which could provide outside $\delta\ ^2H$ or $\delta\ ^{15}N$ for fuel later in the season. Therefore, some variability in $\delta\ ^2H_f$ or $\delta\ ^{15}N_f$ values could reflect catabolization of body reserves collected months prior.

In addition, differences in diet and prolonged dietary restriction may reduce metabolic rate (Cherel et al. 1988), which can influence isotope fractionation factors and the observed $\delta\ ^2H$ values (Wassenaar and Hobson 2006). For example, individuals eating prey with higher fat content require more water per caloric unit (Kirkley and Gessaman 1990). Isotopic fractionation of body water for metabolic processes associated with processing high fat content could lead to enriched $\delta\ ^2H$ of available water stores within an individual. For populations that solely or primarily acquire water through their diet and whose location during molt is known, $\delta\ ^2H$ may provide a longer-term measure of body condition relative to mass adjusted for weight. This may be particularly beneficial in species whose ptilochronology cannot be assessed (Grubb 2006). However, more research is necessary on the underlying physiological mechanisms that cause increased $\delta\ ^2H$ compositions in individuals with low body weight relative to size (e.g., metabolic versus evaporative water loss and fractionation).

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