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Feather isotope analysis discriminates age-classes of Western, Least, and Semipalmated sandpipers when plumage methods are unreliable

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ABSTRACT. Avian age-class discrimination is typically based on the completeness of the first prebasic molt. In several calidrid sandpiper species, juvenal flight feathers grown on Arctic breeding grounds are retained through the first three migrations. Thereafter, flight feathers are grown annually at temperate migratory stopover sites during the fall or on the subtropical wintering grounds. Standard methods for distinguishing age classes of sandpipers rely on a combination of traits, including body plumage, coloration of protected inner median covert edges, and extent of flight feather wear. We tested the ability of stable hydrogen isotope ratios in flight feathers (δD_f) to distinguish young birds in their first winter through second fall from older adults in three calidrid sandpiper species, Western (*Calidris mauri*), Least (*C. minutilla*), and Semipalmated (*C. pusilla*) sandpipers. We compared the apparent reliability of the isotope approach to that of plumage-based aging. The large expected differences in δD_f values of flight feathers grown at Arctic versus non-Arctic latitudes enabled use of this technique to discriminate between age-classes. We determined δD_f values of known Arctic-grown feathers from juveniles that grew their flight feathers on the breeding grounds. Flight feather δD_f values of southward-migrating adults showed bimodal distributions for all three species. Negative values overlapped with species-specific juvenile values, identifying putative second fall birds with high-latitude grown juvenal feathers retained from the previous year. The more positive values identified older adults who grew their feathers at mid- and low latitudes. Importantly, δD_f analysis successfully identified first-winter and second-fall birds not detected by plumage-based aging. Flight feather wear alone was a poor basis for age classification because scores overlapped extensively between putative second fall birds and older adults. Flight feather hydrogen isotope analysis enables more definitive assignment of age classes when standard plumage methods are unreliable.

RESUMEN. **El análisis de isótopos de plumas para la identificación de la edad en *Calidris mauri, C. minutilla* y *C. pusilla* cuando los métodos que usan el plumaje no son confiables**

La identificación de la edad en las aves es típicamente basada en el grado en la cual se completa la primera muda prebásica. En algunas especies del género *Calidris*, las plumas juveniles de vuelo que crecieron en las regiones Árticas donde nidifica la especie son retenidas durante las tres primeras migraciones. Después, las plumas de vuelo crecen anualmente en sitios de descanso durante la migración en zonas templadas durante el otoño o en sitios de invernación subtropicales. Los métodos estandarizados para distinguir las edades de este género dependen de una combinación de caracteres, incluyendo el plumaje corporal, la coloración de las franjas de las coberturas medias internas protegidas y el grado de desgaste de las plumas de vuelo. Probamos la capacidad de las proporciones de isótopos estables de hidrogeno en las plumas de vuelo (δD_f) de distinguir entre individuos jóvenes (en su primer invierno hasta su segundo otoño) y adultos mayores en tres especies, *Calidris mauri, C. minutilla* y *C. pusilla*. Comparamos la aparente fiabilidad de isótopos en comparación al método de usar el estado del plumaje para estimar la edad. Las grandes diferencias esperadas entre los valores δD_f en plumas de vuelo que crecieron en latitudes Árticos versus no-Árticos permitió el uso de esta técnica para distinguir las edades. Determinamos los valores δD_f de plumas que supimos que crecieron en el Ártico porque fueron de juveniles que crecieron las plumas de vuelo en los sitios de nidificación. Los valores δD_f de las plumas de vuelo de adultos que migraban hacia el sur demostraron distribuciones bimodales para las tres especies. Valores negativos se superpusieron con los valores de los juveniles específicos a cada especie, lo cual permitió la identificación de individuos supuestamente en su segundo otoño portando plumas

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juveniles cuales fueron crecidas en latitudes altas en el año anterior. Los valores mas positivos identificaron a los adultos mayores cuales portaban plumas que crecieron en latitudes medias y bajas. Importantemente, el análisis de δD_f exitosamente identificó a los individuos que estaban en su primer invierno o en su segundo otoño cuales no fueron detectados mediante la técnica de estimar la edad con el plumaje. El uso del desgaste de las plumas de vuelo como indicador de edad no fue confiable cuando fue el único método usado porque las medidas de desgaste de individuos supuestamente en su segundo otoño se superpusieron extensivamente con los de adultos mayores. El análisis de isótopos de hidrogeno en las plumas de vuelo permite una clasificación mas definitiva de la edad cuando los métodos que usan el plumaje no son confiables.

Key words: age-class discrimination, *Calidris mauri*, *Calidris minutilla*, *Calidris pusilla*, deuterium, hydrogen, molt, shorebird, stable isotope analysis

Information on the age structure of avian populations is critical for population studies because young and old birds may differ in habitat use, foraging behavior, predation avoidance, migration strategies, molt strategies, reproductive success, or survival (Cresswell 1994, Martin 1995, Holmes et al. 1996, Marra and Holmes 2001, Nebel et al. 2002, O'Hara 2003). Age-classes are typically assigned based on the completeness of the prebasic molt in juveniles versus adults (Humphrey and Parkes 1959). We define juveniles as individuals that have not yet completed the first prebasic molt, and adults, in this context, as individuals that have completed the first prebasic molt (Fig. 1). The ability of an observer to identify the age-class of a captured bird based on plumage characteristics depends on the species, its molt strategy, the time of year, and observer experience. Adult North American songbirds generally undergo prebasic molt immediately after the breeding season and before the southward migration. Individuals in their first year can be identified using wing molt limits until the second prebasic molt (Pyle 1997).

In contrast to most songbirds, Western (*Calidris mauri*), Least (*C. minutilla*), and Semipalmated (*C. pusilla*) sandpipers generally undergo prebasic molt either during southward migration or after arrival on the wintering grounds (Fig. 1). Juvenile shorebirds can be easily identified by distinctive juvenal body plumage until their first prebasic molt, after which distinguishing them from older birds is more challenging (Prater et al. 1977). We define adolescents as individuals that have completed the first, but not the second prebasic molt (Fig. 1). From late fall to early summer in the first year of life, the edge coloration of the protected inner median coverts can be used to distinguish adolescents (buffy-edged) from true adults (white-edged when replaced during the second prebasic molt; Prater et al. 1977, O'Hara 2003). However, by the time sandpipers make their second southward migration, worn covert edges and molting coverts preclude reliable identification of many adolescents. When aging by median coverts is difficult or impossible, excessive primary wear has also been used to identify adolescent birds on southward migration (Prater et al. 1977). Adolescents attempting breeding in their first summer retain juvenile arctic-grown flight feathers through the first three migrations (first southward, first northward, and second southward), whereas "true adults" (individuals that have completed the second prebasic molt; Fig. 1) only undergo two migrations on one set of flight feathers (northward and southward; Prater et al. 1977, Gratto-Trevor 1992, Cooper 1994, Wilson 1994, O'Hara 2003, O'Hara et al. 2005). Many adolescent Semipalmated Sandpipers and the occasional Western and Least sandpiper undergo a partial primary molt late in their first winter (Prater et al. 1977, Gratto-Trevor and Morrison 1981, Gratto-Trevor 1992, S. Franks, pers. observ.; Fig. 1), where an outer block of four to five primaries and an inner block of four to five secondaries are replaced just prior to northward migration. The contrast in feather wear between fresh outer and old inner primaries allows these individuals to be aged as adolescents until their second prebasic molt. Generally, however, complete flight feather molt in these and many other calidridine sandpipers begins with the innermost (first) primary and progresses outward to the tenth primary. Secondary molt begins when primary molt is about half-complete, starting with the outermost (first) secondary and progressing inward (Prater et al. 1977).

Stable hydrogen isotope analysis has been used extensively to infer the latitudinal movements of birds (Hobson 1999, Atkinson et al. 2005, Hobson et al. 2007, Yohannes et al. 2007,

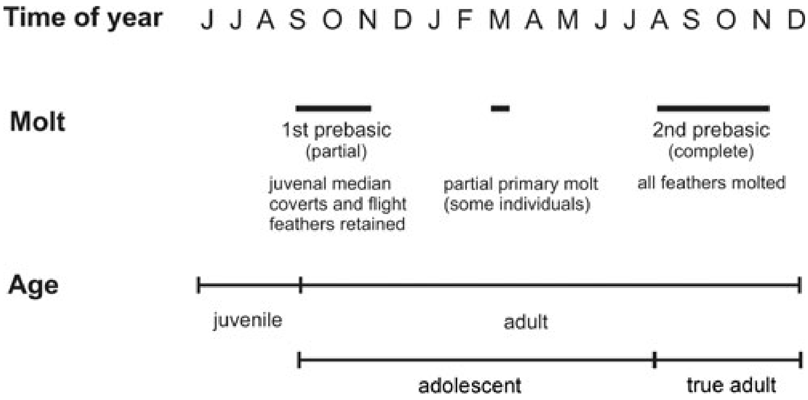

Fig. 1. Molt chronology and associated age classes of a typical small calidridine sandpiper. "juvenile" = individual that has not yet completed the first prebasic molt; "adult" = individual that has completed the first prebasic molt; "adolescent" = individual that has completed the first, but not the second prebasic molt; "true adult" = individual that has completed the second prebasic molt.

Hobson and Wassenaar 2008). The hydrogen isotopic composition of precipitation (δD_p) at a given location is assumed to be incorporated into the stable hydrogen isotope values of feathers (δD_f), providing information on the geographic location of feather growth. In the Americas, there is a large difference in δD_p values between arctic versus temperate and subtropical areas (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bowen et al. 2005). Adolescent sandpipers of many species retain arctic-grown juvenal flight feathers until their second fall or winter, whereas true adults undergo a complete molt every fall or winter at temperate stopover sites or on subtropical wintering grounds (Prater et al. 1977, Gratto-Trevor 1992, Cooper 1994, Naranjo et al. 1994, Wilson 1994, Watts 2001, Atkinson et al. 2005). We hypothesized that expected differences in δD_f values could be used to identify flight feathers grown at high versus lower latitudes and provide a technique for distinguishing young adults—adolescents—from older, true adults during fall migration and on the wintering grounds.

We used this technique to test the reliability of plumage-based methods used to identify adult age-classes of southbound migrants and wintering birds. Our specific objectives were to: (1) establish baseline δD_f values of known Arctic-grown feathers from juvenile Western, Least, and Semipalmated sandpipers captured on southward migration at a stopover site, (2) quantify the bimodality of migrant adult δD_f values to distinguish high versus lower latitude-grown feathers and, therefore, adolescents versus true adults, (3) apply bimodality scores to the distribution of δD_f values for wintering Western Sandpipers to identify undetected adolescents, (4) compare the age assignments produced using flight feather δD_f with those of plumage-based techniques, and (5) make predictions regarding the species and times of year where δD_f would be useful for discriminating age-classes.

METHODS

Western, Least, and Semipalmated sandpipers were captured during southward migration from July to September 2006 and 2007 at Quivira National Wildlife Refuge (38°10′N, 98°40′W) in central Kansas, USA (Fig. 2). Two Western Sandpipers captured at Bolivar Flats, Galveston, Texas (29°23′N, 94°43′W) in September 2006 were combined with the samples from Kansas. Sandpipers were captured in mist-nets and aged as either juvenile or adult by differences in plumage, with juveniles distinguished by a buff-colored upper chest, prominent white supercilium, and well-defined, fresh scapulars (Prater et al. 1977). Feather condition was scored on a scale of 1–5, where 1 = feathers that had heavily abraded and worn tips with large pieces missing, 2 = feathers that had numerous nicks and wear, 3 = one or two feathers with one or two shallow nicks, 4 = feathers that were minimally worn, and 5 = feathers that were freshly grown with no

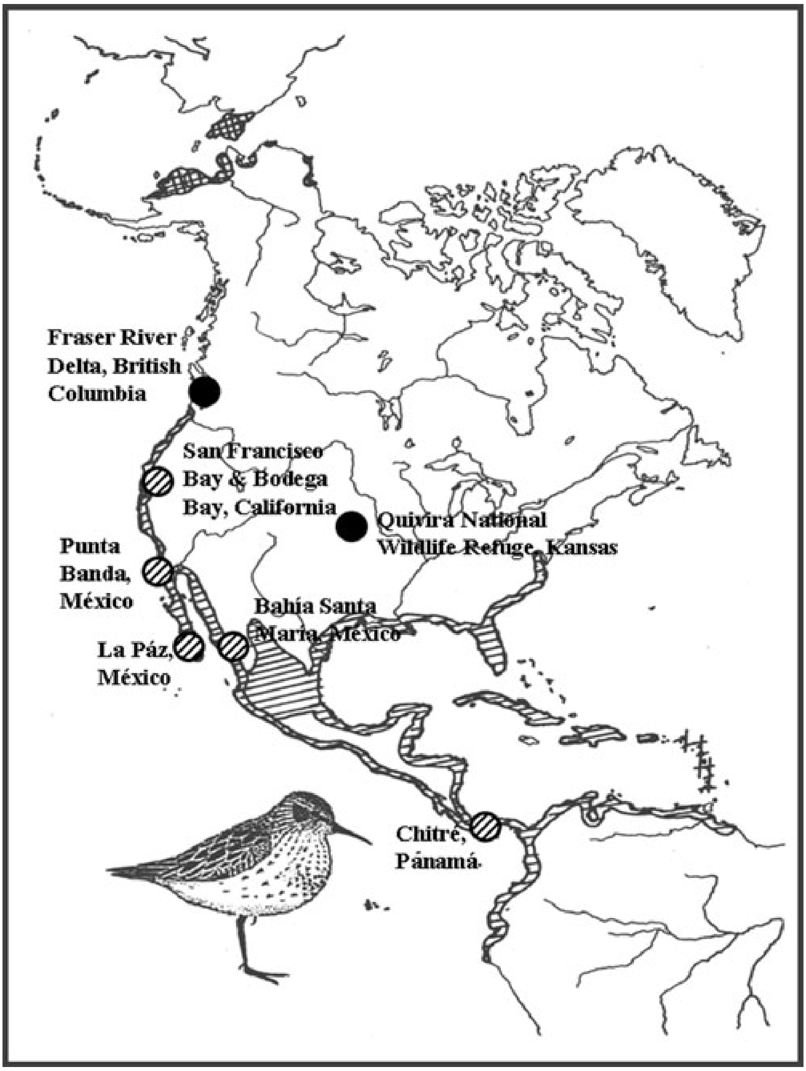

Fig. 2. Location of sampling sites. Southward migrants (solid dots) were captured in the Fraser River Delta and Kansas. Wintering birds (hatched dots) were captured in California, México, and Panamá.

wear (adapted from DeSante et al. 2008, Fig. 3). Flight feathers were collected from adults for isotope analysis. Where possible, the first primary was collected. However, for adults molting flight feathers, the next old feather to be molted was collected. To avoid removing a freshly grown primary from juveniles and creating an undue handicap, breast feathers were collected for δD_f. We assumed that because both breast and flight feathers from juveniles grow at the same time on the breeding grounds, they should have similar δD_f values.

Southward-migrating Western Sandpipers were also captured at Boundary Bay, a stopover site in the Fraser River Delta (FRD), British Columbia, Canada (49°06′N, 122°59′W) (Fig. 2). We collected first primaries from two juvenile birds and two adults captured on 10 and 13 August 1999 and ninth primaries from 55 adults captured from 11 to 13 July 2007. Birds captured in 2007 were aged in the field as adolescents if buffy edging was seen and as adults (includes both adolescents and true adults) if buffy edging was not seen (Prater

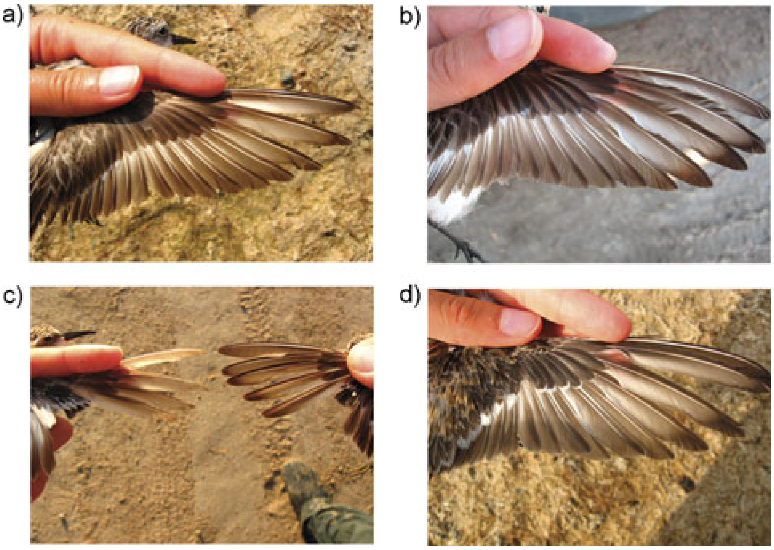

Fig. 3. Example flight feather condition (FF) scores on a scale of 1–5, where 1 is the most worn and 5 is freshly grown with no wear. (A) FF = 2; (B) FF = 3; (C) FF = 1 for bird on left, FF = 4 for bird on right; (D) FF = 5

et al. 1977). We scored feather condition as in Kansas.

Primary feathers from Western Sandpipers were collected from birds captured at five sites during the boreal winter (Fig. 2): (1) San Francisco Bay and Bodega Bay, USA (37°30′N, 122°20′W; 38°19′N, 123°02′W) on 15 and 16 November 2000, (2) Punta Banda, México (31°41′N, 116°35′W) from 27 January to 28 February 1998, (3) Bahía Santa María, México (25°02′N, 108°18′W) from 8 to 20 March 2001, (4) La Páz, México (24°06′N, 110°22′W) from 25 September to 10 November 2001, and (5) Chitré, Panamá (08°00′N, 80°50′W), 3 February to 13 March 1998. All birds were aged by plumage in the field as either adolescent or adult. First primaries were analyzed from Panamá birds, second primaries from California birds, and ninth primaries from the México sites.

Stable hydrogen isotope analysis was conducted at the Queen's Facility for Isotope Research (QFIR) in Kingston, Ontario, Canada. Feathers were washed using a 2:1 chloroform:methanol solution and then allowed to equilibrate with the local atmosphere for 72 h to ensure that all samples had an equal opportunity to exchange with the local atmosphere. Samples (0.10–0.15 mg) were then loaded into silver capsules and placed in an oven at 100°C for 24 h to remove surface water. Capsules were crushed and loaded into a reduction furnace (Finnigan TC/EA) at 1450°C and introduced online to an isotope ratio mass spectrometer (Finnigan MAT Delta Plus XL). All analyses of 2006/2007 samples were performed over a period of 2 mo in 2007. All wintering site samples were analyzed in 2005. Stable-hydrogen isotope ratios are reported in delta (δ) notation in per mil (‰) units, where $\delta = [({}^2H/{}^1H_{sample}/{}^2H/{}^1H_{standard}) - 1] \times 1000$ and ${}^2H/{}^1H_{standard}$ is the hydrogen isotope ratio of Vienna standard mean ocean water. Following QFIR procedures, for every 15 unknowns, we ran three in-house standards (mean ± SE): brucite (from the University of Michigan; –100 ± 0.9‰, $N = 28$), Georgia kaolinite clay (–62 ± 0.5‰, $N = 42$), and feather (–87 ± 0.4‰, $N = 28$). All standards closely matched values previously run in the laboratory. In addition to these standards, we ran duplicates (within the same run) of feathers from the same individual sandpipers ($N = 34$) that produced a mean difference of 4.3‰ (±0.5 SE).

Because analyzed feathers were not all taken from the same position on the wing, we compared two flight feathers from a subset of individuals to examine within individual variation. We compared first primaries to ninth primaries for 11 adult FRD Western Sandpipers, and tenth primaries to first primaries for six of the adult Panamá and two of the adult FRD Western Sandpipers. We used a paired *t*-tests to determine if δD_f values of outer (ninth or tenth) primaries differed from those of first primaries. Outer primaries (ninth and tenth) had a mean (±SE) value of –50 ± 4.1‰ compared to –40 ± 3.3‰ for first primaries ($N = 19$, $t = 2.8$, $P = 0.012$). This degree of bias was small relative to the range of δD_f values observed for feathers grown at Arctic versus non-Arctic latitudes and we did not correct statistically for feather position in subsequent analyses.

We established species-specific δD_f values of known Arctic-grown feathers from juvenile Western, Least, and Semipalmated sandpipers captured in Kansas and Western Sandpipers captured in the Fraser River Delta. We compared juvenile values with the distribution values of adult birds among southward migrants.

We used a maximum-likelihood procedure for cluster analysis to test for bimodality in δD_f values (Proc Modeclus, SAS Institute 2003). This procedure determines a bimodality coefficient (b) that is a composite function of skewness and kurtosis ($b > 0.555$ considered bimodal; SAS Institute 2003), determines numbers of component distributions (clusters) based on sets of a priori ranges of fixed-kernel ("R") δD_f values representing potential initial cluster widths, and provides relative fits of the data with log-likelihood and maximum probability values. If bimodality is supported, the procedure outputs probabilities that each observation belongs in each cluster. We classified observations into clusters based on >0.95 probability of belonging to one or the other cluster. Observations with a >0.05 probability of belonging to both component distributions fell in the area of cluster overlap. We determined a value of equal probability of membership in either component distribution (a "threshold value" defining component distributions). Where component distributions overlapped, we estimated the threshold value by linear interpolation of the values in the overlap area directly above and below the equal probability (0.5) mark. Where component distributions were completely separate or sample sizes were too small for a meaningful bimodality test, we estimated the threshold value by taking half the distance between the highest value of the lower distribution and the lowest value of the upper distribution. We applied the threshold value and overlap area produced to examine the distributions of δD_f values of wintering Western Sandpipers and to identify undetected adolescents. For Kansas and FRD southward migrants, we classified adolescents versus true adults based on 95% confidence assignment to the component distributions. We then compared feather condition scores to determine how well age-class could be distinguished by flight feather wear at that time of year.

RESULTS

δD_f values of migrants. δD_f values of juvenile Western, Least, and Semipalmated sandpipers captured during southward migration in Kansas showed unimodal distributions of values over a strongly negative range (Fig. 4A–C; Western: −114 to −84‰; Least: −152 to −115‰; Semipalmated: −132 to −82‰). In contrast, southward-migrating adult Western, Least, and Semipalmated sandpipers in Kansas and the Fraser River Delta showed bimodal distributions (Fig. 4A–C, 5). The most negative adult δD_f values fell within the species-specific juvenile δD_f distributions, indicating high latitude-grown juvenal feathers from the previous year. The more positive δD_f values correspond to feathers grown at temperate and subtropical latitudes. Cluster analysis produced quantitative descriptions of values that could be used to assign individuals to age-classes and potential boundary areas of cluster overlap (Table 1). No boundary values existed or sample sizes were too small for a meaningful bimodality test for Kansas Western and Semipalmated sandpipers or for FRD Western Sandpipers.

Identification of southward migrant and wintering adolescents by plumage versus δD_f. All FRD Western Sandpipers aged as adolescents based on buffy inner covert edges had high latitude (more negative) δD_f values (Fig. 5). However, more than half of the remaining individuals with high latitude δD_f values were not identified as adolescents because covert edges were too worn. Feather condition scores from southward migrants of all three species generally differed in the predicted direction between birds classified as adolescents versus true adults by δD_f (Fig. 6). Most adolescents had feathers classified in the more worn categories (scores ≤3). No putative adolescent Least or Semipalmated

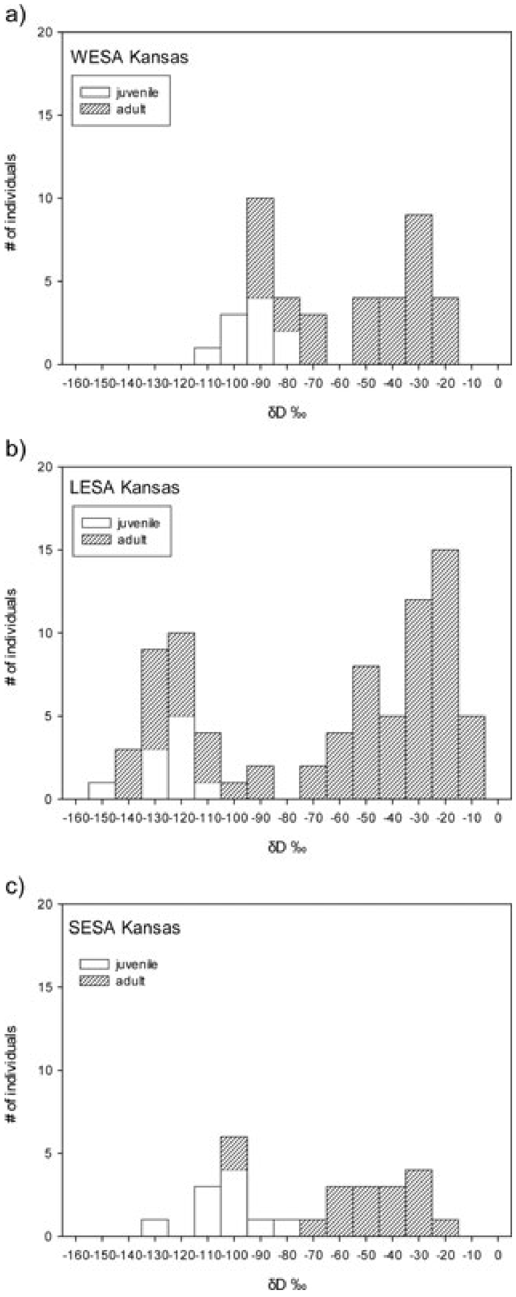

Fig. 4. δD_f distributions of adults (hatched bars) and juveniles (open bars) of three species from Kansas. Birds were aged as adult or juvenile by plumage methods. (A) WESA = Western Sandpiper, N = 8 (2006, N = 2 from Texas), N = 26 (2007); (B) LESA = Least Sandpiper, N = 72 (2007); (C) SESA = Semipalmated Sandpiper, N = 17 (2007).

sandpipers and few putative adolescent Westerns Sandpipers had scores of 4. However, due to extensive overlap among more worn categories (1–3) of birds classified as adolescents versus true adults by δD_f, feather wear alone would provide a poor basis for age classification on southward migration.

Western Sandpipers captured at wintering ground sites showed a range of δD_f values similar to migrants (Fig. 7). However, sample sizes for each site were too small for a bimodality test. The two Panamá birds identified as adolescent by plumage showed high latitude values. Throughout the winter, most adolescents should have been identifiable by their retained juvenal coverts. However, when we applied the modal boundary conditions determined from the migrant samples of Western Sandpipers to these data, it appeared that many adolescents were not identified as such on the wintering grounds.

DISCUSSION

Plumage coloration of the median coverts and feather wear are the most common methods used to assign age-classes to shorebirds (Prater et al. 1977). These techniques vary in their utility depending on season and species and often require expert training to be used effectively. We analyzed stable hydrogen isotope compositions of flight feathers from southward migrant Western, Least, and Semipalmated sandpipers captured at two temperate-zone stopover sites and from Western Sandpipers captured at several wintering sites. We found that the distributions of intraspecific δD_f values clearly distinguished high latitude-grown versus lower latitude-grown feathers. Thus, we were further able to classify adults as either adolescents (high latitude-grown retained juvenal flight feathers) or true adults (mid- or low latitude-grown flight feathers molted during the second prebasic molt at stopover or wintering sites).

By identifying adolescent birds that would otherwise have been aged less specifically as simply adult, δD_f improved upon age identification by plumage characteristics at times of year when using median covert edging color and feather wear is challenging. Our results suggest that during southward migration, covert-edging color can correctly identify adolescents, but can

Table 1. Bimodality test and cluster analysis results of δD_f (‰) by species, site, and age.

Species	Site	Age	*N*	*b*[a]	Threshold value[b]	Mean ± SD lower distribution (*N*)[c]	Mean ± SD upper distribution (*N*)[c]	Boundary range[d]	Number of boundary values[d]
Least Sandpiper	Kansas	adult	71	0.72	−87	−126 ± 15 (20)	−38 ± 17 (51)	−97 to −77	4
Least Sandpiper	Kansas	adult + juvenile pooled	81	0.72	−88	−128 ± 12 (29)	−39 ± 18 (52)	−104 to −79	4
Western Sandpiper	Fraser River Delta	adult	55	0.51	–	–	–	–	–
Western Sandpiper	Fraser River Delta + Kansas pooled	adult	87	0.56	−79	−98 ± 7 (28)	−50 ± 15 (59)	−87 to −78	1
Western Sandpiper	Fraser River Delta + Kansas pooled	adult + juvenile pooled	97	0.57	−76	−97 ± 8 (39)	−49 ± 14 (58)	−87 to −67	9
Semipalmated Sandpiper	Kansas	adult	17	0.50	–	–	–	–	–
Semipalmated Sandpiper	Kansas	adult + juvenile pooled	27	0.53	–	–	–	–	–

[a] Bimodality coefficient (b) values >0.555 are considered bimodal.

[b] Value (‰) of equal probability of membership in component distributions.

[c] Means (‰) calculated for values on either side of the threshold (*N* per cluster).

[d] Boundary values have >0.05 probability of being in either component distribution.

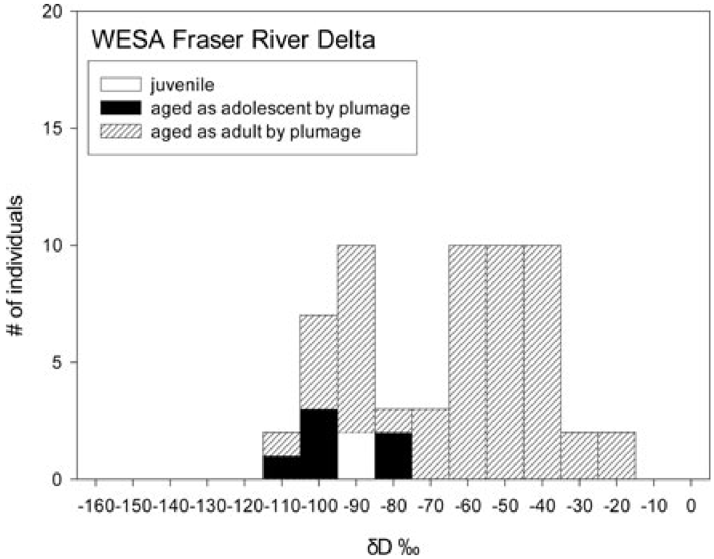

Fig. 5. δD_f distribution of Western Sandpipers captured in the Fraser River Delta and aged by plumage methods as adult (hatched bars), adolescent (black bars), and juvenile (open bars). $N = 55$ (2007), $N = 4$ (1999, 2 juvenile, 2 adult).

also fail to distinguish them if edges are worn or coverts are molting. Many adolescents were also undetected by plumage-based aging on the wintering grounds. Feather wear alone is an unreliable indicator of age-class at these times of year. The δD_f approach removes subjectivity and requires less expert knowledge and training.

Age-class discrimination was clearest for Least Sandpipers, presumably because the high-latitude values from this sample originate from an area with more negative δD_p values. In contrast, high-latitude values for Western Sandpipers appear to originate from an area with more positive δD_p values, whereas values for Semipalmated Sandpipers fell within a wider range between the values for Least and Western sandpipers. This corresponds with a priori knowledge about the range of δD_p in the far western Alaska breeding range of Western Sandpipers, and with what we believe to be the breeding ranges of Least and Semipalmated sandpipers migrating through Kansas that include eastern-Arctic areas with more negative δD_p values (Gratto-Trevor 1992, Cooper 1994, Wilson 1994, Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bowen et al. 2005).

Previous investigators have used stable isotope analysis to delineate molt patterns in a range of avian taxa (Norris et al. 2004, Perez and Hobson 2006, Greenberg et al. 2007, Knoche et al. 2007, Reudink et al. 2008, Yerkes et al. 2008). However, the utility of δD_f for age-class discrimination depends entirely on a priori knowledge about the expected magnitude of difference in δD_p between breeding grounds and molting sites, and the timing and duration of flight feather molt in the species of interest. The expected magnitude of difference in δD_p between breeding and molting sites of species whose breeding and wintering distributions are not widely disjunct may be small, and δD_f will be less useful for age-class discrimination than for species where breeding and wintering distributions are widely separated. For example, δD_f would be less useful for discriminating age-classes of Rock Sandpipers (*Calidris ptilocnemis*), Surfbirds (*Aphriza virgata*), and Black Turnstones (*Arenaria melanocephala*). Although adolescents of these species retain breeding ground-grown, juvenal flight feathers and true adults molt on the wintering grounds, the breeding and wintering ranges of these Pacific coast species are not widely disjunct and even overlap in some cases (Senner and McCaffery 1997, Handel and Gill 2001, Gill et al. 2002). When considering the isotope approach for coastal-dwelling species, an additional caveat is that δD_p values are less well resolved along the Pacific coast than

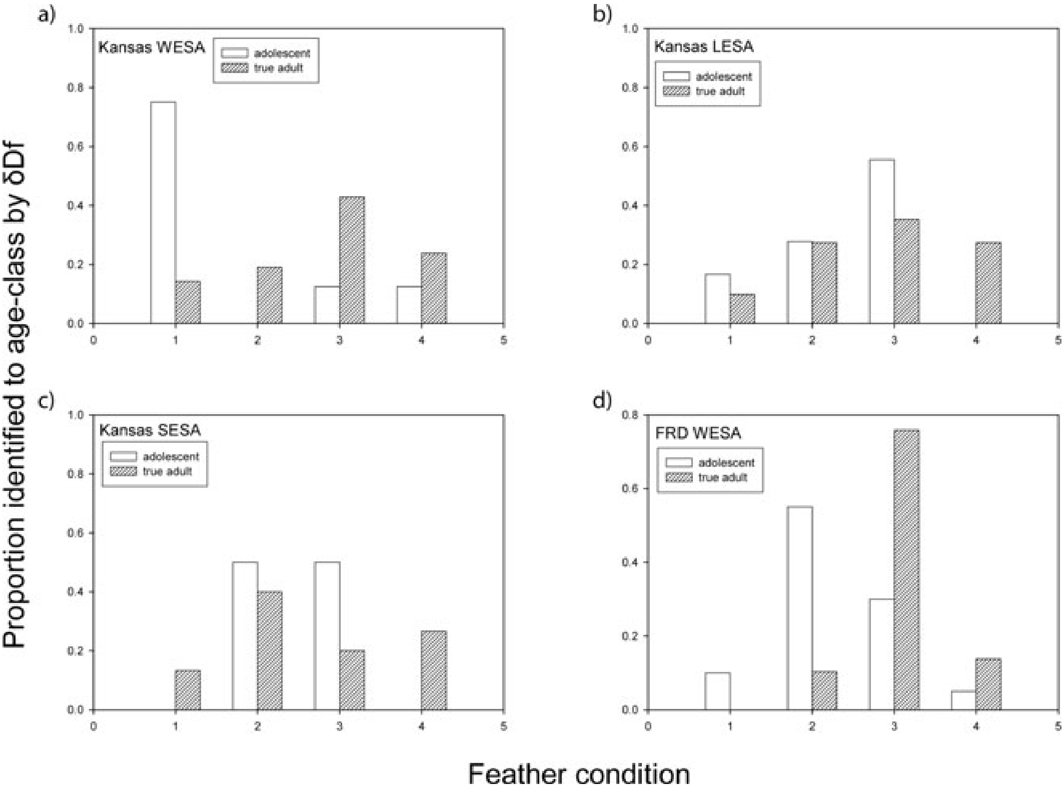

Fig. 6. Comparison of plumage-based (feather condition) versus isotope-based aging techniques for calidridine sandpipers. Feather condition scores indicate decreasing wear from left to right. Proportions of adolescents (open bars) versus true adults (hatched bars) based on age-class assignment criteria (see Table 1, age and site pooled results for Western and Least sandpipers, respectively). Semipalmated Sandpiper age-classes assigned by estimating the threshold value (−76‰) by taking half the distance between the highest value of the lower distribution and the lowest value of the upper distribution). (panel a) Kansas Western Sandpipers ($N = 8$ adolescents, 21 true adults); (panel b) Kansas Least Sandpipers ($N = 18$ adolescents, 51 true adults); (panel c) Kansas Semipalmated Sandpipers ($N = 2$ adolescents, 15 true adults); and (panel d) Fraser River Delta Western Sandpipers ($N = 20$ adolescents, 29 true adults).

values in the continental interior. This results in smaller expected magnitudes of difference in δD_p between coastal breeding and molting sites. For the δD_f isotope approach to be useful in such cases, a latitudinal difference between breeding and wintering sites great enough to produce a large expected difference δD_p is required, as in the case of Western Sandpipers that breed in western Alaska and winter as far south as Peru. A possible alternative to the δD_f approach for coastal species is using either δC or δN if the molt biology and the ecology of the species are appropriate, for example, if juvenal feathers are grown in terrestrial environments and adult feathers in estuarine environments.

δD_f for age-class discrimination will also not be useful for species where both juvenile and adult feathers are grown at the same latitude, such as in the three subspecies of North American Dunlin (*Calidris alpina pacifica, C. a. arcticola,* and *C. a. hudsonia*) where all individuals molt and grow flight feathers on the breeding grounds (Warnock and Gill 1996, Lank et al. 2003). Even for the species we considered, the existence of partial primary molt complicates the application of the technique. For adolescents with partial primary molt, analyzing the inner retained juvenal primaries would show Arctic values, whereas analyzing wintering-ground-grown outer primaries would

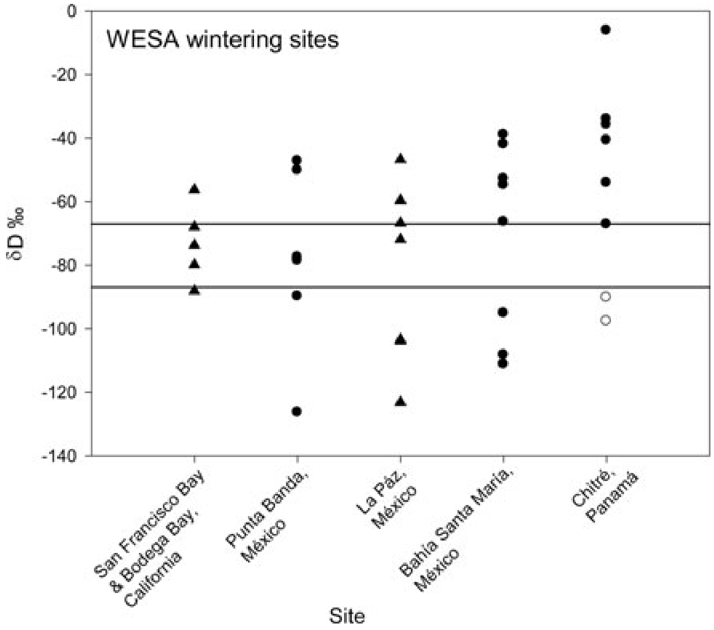

Fig. 7. δD_f values for Western Sandpipers sampled at five wintering sites, ordered left to right by decreasing latitude. Sandpipers were aged as either adult (filled symbols) or adolescents (open symbols), and were captured in either fall (triangles) or winter (circles). The area between the dashed lines (– 67 to −87‰) indicates δD_f values with > 0.05 probability of being in either component distribution (Table 1). Values ≤ -87‰ and ≥ -67‰ have a > 0.95 probability of falling into Arctic versus non-Arctic component distributions, respectively.

not, thus potentially incorrectly identifying age-class depending on the feather selected for analysis. Researchers interested in using δD_f to more accurately distinguish age-classes should first consider the expected range of δD_p for breeding and wintering ranges and the molt biology of their species. They should also consider that the mean δD_f values we present as identifying the two different adult age-classes for each species and site are relative rather than absolute. δD_f values may vary according to the population of the species sampled, the season or year of sampling or lab analysis, the location and hydrological regime of the sampling site, or the location of the lab analysis. Careful interpretation of results should be made within the appropriate framework. We emphasize that it is bimodality in adult δD_f values within a species- and site-specific framework that allows us to discriminate age-classes using this method.

Those interested in using either plumage-based methods or the isotope approach to determine age structure and population demographics should also be careful when extending apparent sample age structure to the population. Capture bias may result in the overrepresentation of a particular age-class, for example, if young birds are captured more easily than older birds. An age-class may also be underrepresented. Adolescent Western Sandpipers are latitudinally segregated by reproductive life-history strategy on the wintering grounds. Northern adolescents have a higher propensity to attempt breeding in their first summer, whereas southern adolescents tend to “oversummer” on the wintering grounds (Nebel et al. 2002, O’Hara et al. 2005). This increases the chance that adolescents may be underrepresented in a sample if birds are captured during migration or on the breeding grounds.

Time of year also affects the value of δD_f relative to traditional plumage methods. Juvenile sandpipers can be readily identified in their first fall up until the first prebasic molt, after which identification as an adolescent is more challenging. In late fall and early winter, covert edges are in good condition and adolescents can be distinguished by the presence of retained juvenal coverts with buffy edges. By late winter, however, buffy edges become harder to detect and distinguishing age-class using this criterion alone is more difficult. Feather wear may be helpful in assigning age-class in late winter and spring when comparing adolescent flight feathers grown on the breeding grounds to true adult flight feathers just grown on the wintering grounds, but has limited utility in the fall when it is an unreliable indicator of age-class. As spring and summer progress, covert edges become more worn and feather wear becomes more unreliable and, by the time a bird makes its second southward migration, plumage methods are unreliable for distinguishing age-class.

In summary, plumage methods are sufficient for discriminating adolescents from true adults in late fall through spring. However, plumage-based age-class discrimination becomes increasingly unreliable in later months, except in the case of partial primary molt with its strongly contrasting wear between outer and inner primaries. Although relatively more costly and time-consuming, δD_f enables more sensitive age determination in comparison to standard plumage methods, and in calidridine sandpipers, can distinguish adolescents at any time of year up until the second prebasic molt, except in the case of partial primary molt. Judicious combinations of plumage-based and δD_f methods may be useful in the future for determining age-classes of migratory birds.

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