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Assigning birds to wintering and breeding grounds using stable isotopes: lessons from two feather generations among three intercontinental migrants

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Abstract Geographic origins of populations and migration patterns of several vertebrate and invertebrate species have been inferred from geographically distinct isotopes in their tissues. To test the hypothesis that feathers grown on different continents would reflect continental differences of δD in precipitation and have significantly different stable isotope ratios, we analyzed stable isotopes in two generations of feathers from three bird species (American and Pacific golden-plovers, *Pluvialis dominica* and *P. fulva*, and northern wheatears *Oenanthe oenanthe*) that breed in North America and winter in South America, the South Pacific and Asia, and Africa. We found significant differences in stable isotope signatures between summer- and winter-grown feathers in the plovers, and our use of two generations of feathers provided similar variation to that reported in studies using larger sample sizes. In contrast to plovers, no differences were detected in isotope values between summer- and winter-grown feathers in wheatears. Discriminant analyses separated 80% of summer- and

winter-grown feathers for each plover species. Nonetheless, an “assignment with exclusion” method adapted from population genetics to impart a measure of confidence in assigning individuals to groups of origin resulted in an overall accuracy among plovers of only 41%, compared with a 63% assignment accuracy when the exclusion criterion was removed. Thus, we were unable to accurately assign feathers to origin of growth on the continental scale. Moreover, using δD expectations for North America, we were unable to assign summer-grown plover feathers to within better than several thousand kilometers of their true origins. We urge researchers to carefully consider the ecology and physiology of their study organisms, statistical methodology, and the interpretation of results when using stable isotopes to infer the geographic origins of feather growth.

Keywords Stable isotopes · Feathers · Migration · Molts

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Introduction

Understanding the ecology of migratory species requires knowledge of seasonal movements. These movements have historically been difficult to monitor in nongame species because of a general lack of population-level markers. Recent scientific advances have led to the development of intrinsic markers for tracking individuals and, in aggregate, populations. Geographically distinct stable isotopes have been used to infer breeding origins in birds sampled in Neotropical wintering areas (Hobson and Wassenaar 1997; Rubenstein et al. 2002), to delineate breeding and wintering bird and bat populations (Chamberlain et al. 1997; Hobson et al. 2001, 2004a, b; Meehan et al. 2001; Kelly et al. 2002; Rubenstein et al. 2002; Lott et al. 2003; Smith et al. 2003; Cryan et al. 2004), to investigate rearing habitats of

salmonids (Kennedy et al. 2005) and feeding locations of whales (Lee et al. 2005), and to infer migration patterns of late Pleistocene mammoths (Hoppe 2004). The development of these isotopic analyses has led to a proliferation of related studies (Hobson 1999; Kelly et al. 2002; Rubenstein et al. 2002). For example, Hobson et al. (2004a, b) suggested that they had discovered a previously unknown breeding population of Bicknell's thrush (*Catharus bicknelli*). Dugger et al. (2004) depicted a strong relationship between bird survival and rainfall on a species' wintering grounds. Other studies were successful in relating breeding locations of sharp-shinned hawks (*Accipiter striatus*) to the prevalence of avian hematozoa (Smith et al. 2004) and, in several species, feeding locations to the accumulation of contaminants (Fox et al. 2002; Buckman et al. 2004; Rocque and Winker 2004).

The potential for using stable isotopes as markers to study migratory animals relies on the assumption that geographically unique signatures of stable isotopes are incorporated into tissues from an animal's food and water. In keratin tissues, such as feathers and hair, isotopes are incorporated only during molt (Mizutani et al. 1990), and thus they provide a geographic signal of the location of growth of those tissues. In birds that molt distinguishable feathers on their breeding grounds and on their wintering grounds (i.e., different feathers are molted in different regions), geographic locations of molt (such as breeding and wintering areas) may be identified if feather isotope signatures are geographically distinct. Analyses of feathers in birds that carry two generations of feathers represent repeated measures of the same individuals and enable a statistical comparison among fewer individuals (Zar 1999) and may provide unique insights to seasonal changes in behavior of small populations of birds on breeding and wintering grounds.

Several stable isotopes show distinct geographic patterns, but hydrogen (δD) and carbon ($\delta^{13}C$) show considerable variation with respect to latitude, elevation, and climate (Dansgaard 1964; Korner et al. 1991; Hobson 1999; Graves et al. 2002; Rubenstein et al. 2002; Hobson et al. 2003). For example, in North America δD tends to become progressively depleted (more negative) away from the equator, with some of the most depleted values occurring in Alaska and northern Canada (Hobson and Wassenaar 1997; IAEA 2001; Bowen et al. 2005). Similarly, a latitudinal gradient in δD was reported for Europe (Hobson et al. 2004a, b), although such patterns may be less conspicuous in South America, Asia, and Africa (Bowen et al. 2005). The strong latitudinal gradient in δD and fine-scale correspondence between expected and observed values makes this isotopic marker a useful and popular tool for the study of bird migrations.

Recently, however, several bird migration studies described unexpected isotopic data. For example, Meehan et al. (2003) found high correspondence between precipitation δD_p and feather δD_f for nestling Cooper's hawks (*A. cooperii*) but no such correspondence with

adult feathers δD_f , although the adult and nestling feathers were collected from the same nests and the adults were molting at the time of collection. Similarly, Pain et al. (2004) found high variation and no discernable patterns in δD_f data from feathers grown in unknown wintering locations in the threatened aquatic warbler (*Acrocephalus paludicola*). These authors found that δD data from winter-grown feathers sampled from breeding birds was impossible to interpret. Finally, Wunder et al. (2005) found large variation in δD_f values from nestling mountain plovers (*Charadrius montanus*) in the Rocky Mountain region, and they concluded that assignment of individuals to their breeding grounds based on that marker alone was tenuous.

These studies suggest that stable isotope markers may not be applicable for all migration systems or bird species, especially on relatively small spatial scales. Nonetheless, recently developed precipitation maps that account for elevation and temperature (Bowen et al. 2005) suggest that isotopic markers would be of great value in tracking intercontinental migrants. In this study, we investigated the isotopic signals of three species of intercontinental avian migrants (American and Pacific golden-plovers, *Pluvialis dominica* and *P. fulva*, and northern wheatears *Oenanthe oenanthe*) that breed in Alaska and overwinter on three different continents: South America, the Pacific islands and Asia, and Africa, respectively. These species grow feathers on their breeding grounds in Alaska and then replace some of their feathers on specific body areas on their wintering grounds before returning to Alaska to breed. We sampled these two generations of feathers from each species to test the hypothesis that feathers grown on Alaska breeding areas would reflect high-latitude environmental signatures and would differ markedly from feathers grown the previous season on low-latitude wintering grounds on different continents. We expected that deuterium signatures in Alaska-grown feathers would be depleted (e.g., between -130 and -110‰) with low variation due to high-latitude sampling in a small geographic area with minimal topographic relief (Hobson and Wassenaar 1997). In contrast, based on annual average precipitation values for each overwintering region and based on interpolation of IAEA (2001) and Bowen et al. (2005), we hypothesized that winter-grown feathers would exhibit comparatively enriched values of δD (i.e., between -40 and -20‰ in South America; -60 and -10‰ in Asia, Hawaii, and the Pacific Islands; and between -20 and 20‰ in Africa). We expected that these values would differ from summer-grown feathers and that they would be characterized by relatively high variability in δD because winter-grown feathers were not actively sampled from birds growing these feathers in a small, known geographic region.

To ensure that changes in habitat (marine vs. terrestrial), elevation, or diet did not affect δD values, we also determined values of $\delta^{13}C$ and $\delta^{15}N$ for each feather. Numerous studies have documented localized and continental differences in values of $\delta^{13}C$ in bird species such

as hummingbirds in Ecuador (Hobson et al. 2003), aquatic warblers (Sylviidae) overwintering in sub-Saharan Africa (Pain et al. 2004), and black-throated blue warblers (Parulidae: *Dendroica caerulescens*) among 10 sites in North America (Bearhop et al. 2004). Others have used $\delta^{13}\text{C}$ with $\delta^{15}\text{N}$ to depict regional isotopic differences among shorebirds in Argentina (Farmer et al. 2003) and Canada geese (*Branta canadensis*) in North America (Caccamise et al. 2000). Although these differences are not necessarily predictable in a manner similar to changes in δD , they usually occur as a result of changes in elevation, plant communities, and diet between breeding and wintering areas (Kelly et al. 2002; Lott et al. 2003; Marra et al. 1998; Rubenstein et al. 2002). Furthermore, differences in values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, when analyzed together, can add to the discriminatory power of isotope analyses (e.g., Caccamise et al. 2000; Wassenaar and Hobson 2000a, b; Wunder et al. 2005). Thus, we hypothesized that similar to multiple genetic markers, in which differing allelic frequencies among populations can aid separation and diagnoses of member individuals (e.g., Cornuet et al. 1999), the use of multiple stable isotopes (e.g., δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$) would enable us to accurately assign individual feathers to known groups and to link birds of known breeding origin to wintering locations at the continental scale.

Materials and methods

Focal species

American and Pacific golden-plovers, *Pluvialis dominica* and *P. fulva*, are sibling species that breed sympatrically in western Alaska and occupy geographically distinct wintering areas (American Ornithologists' Union 1998). *P. dominica* migrates to wintering grounds in South America, and *P. fulva* winters in the South Pacific, most notably Hawaii, Asia, and Australia (Fig. 1). We chose these species based on our understanding of their molt schedule, which is summarized by Johnson and Connors (1996), and the ease with which feathers grown on breeding areas can be separated from those grown on wintering areas. Briefly, both species molt into dark breeding feathers ventrally (alternate plumage) on their wintering grounds, with some individuals completing this molt en route to breeding areas (Johnson and Connors 1996). Pale, summer-grown, ventral body feathers (basic plumage) begin replacing winter-grown plumage during incubation (Johnson and Connors 1996). We sampled both types of feathers from individuals collected in July 1998 and July 2000 on breeding territories on the Seward Peninsula, Alaska. Alternate, winter-grown breast feathers were considerably darker and easily distinguished from basic, summer-grown breast feathers that were newly grown and almost white. To further ensure that all basic feathers were grown on Alaskan breeding areas, only fresh (usually in sheath), unworn, pale feathers were sampled to represent basic

feathers in this study. We sampled feathers from adult birds collected on their breeding territories within a 100-km radius, where elevation changed from 0 to 100 m, to ensure minimal within- and between-species variation in isotopic signatures of samples from the breeding grounds. Feathers were expected to reflect average seasonal δD values in precipitation and, therefore, to differ significantly between summer-grown and winter-grown feathers in both species.

Wintering areas of both *Pluvialis* plovers are extensive but distinct between the two species in our study. In *P. fulva*, which occupy winter areas on over half the earth (Johnson and Connors 1996), evidence suggests a strong Alaska–Hawaii connection between breeding and wintering populations (Johnson et al. 2001a; b, 2004), although some Alaska-breeding birds likely winter on other South Pacific islands and in Japan (Johnson and Connors 1996). In contrast, American golden-plovers (*P. dominica*) winter in South America (AOU 1998).

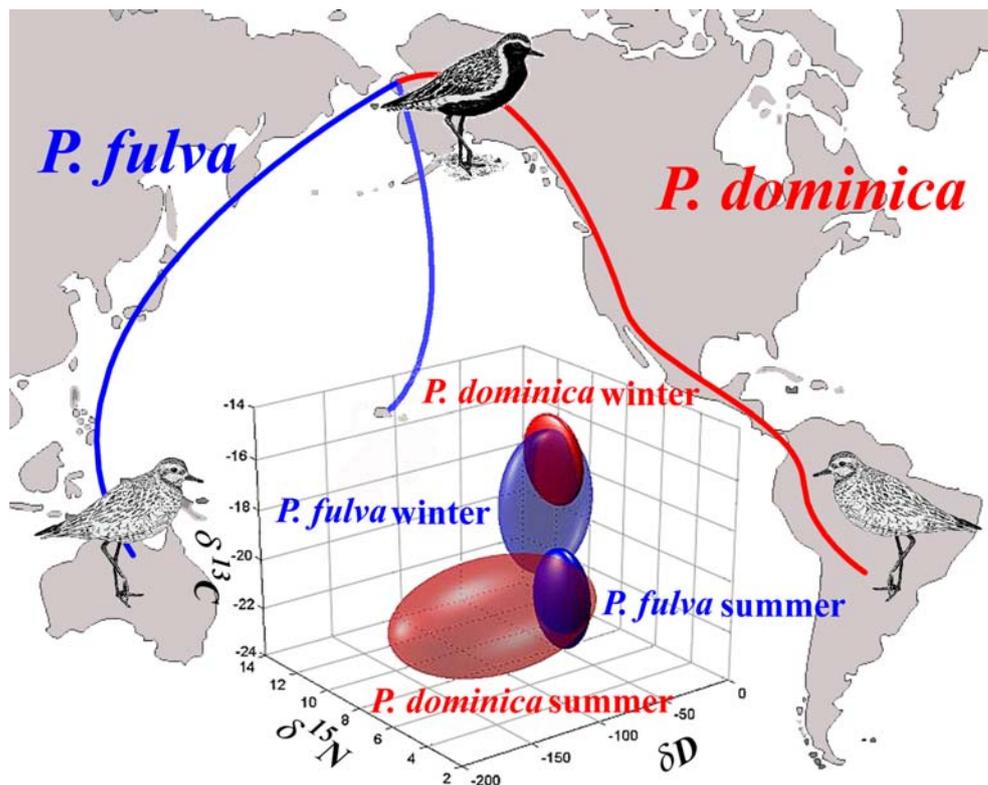
Adult northern wheatears of Alaska populations replace flight feathers on their breeding grounds during a complete molt into basic plumage prior to fall migration (Kren and Zoerb 2000). A partial alternate molt, which includes back feathers, occurs primarily on African wintering grounds (Kren and Zoerb 2000). We sampled both feather types from northern wheatears collected on breeding grounds in interior and western Alaska during the breeding seasons of 1997 and 1998. Flight feathers were secondaries and were sampled based on worn appearance. This criterion did not allow sampling of the same feather in all cases (i.e., secondary 1), because in a few instances feathers were missing or molting, but our sampling did ensure that each flight feather was grown on Alaskan breeding areas during the previous season. Care was taken to check for evenness of wear among secondaries to avoid the possibility of sampling a feather grown elsewhere through adventitious molt (unscheduled single-feather replacement).

We used interpolated maps of annual average δD values collected at stations across the wintering grounds of each of the three species to generate a priori predictions for changes in δD_f between breeding and wintering grounds (IAEA 2001; Bowen et al. 2005; Appendix). Because we had no information on the specific wintering location of each bird, we evaluated the expected range of δD feather values from these maps (Bowen et al. 2005). We used the annual averages of deuterium in the precipitation across wintering areas to predict feather δD values because wintering areas for all three of our focal species have year-long growing seasons.

Isotopic analysis

Body feathers were removed from study skins with scissors at the skin surface. Flight feathers were clipped between the vane and the calamus. Feathers were washed with a mild detergent and rinsed with deionized water to remove any dirt or surface oils and allowed to

Fig. 1 Breeding and wintering regions and migration routes of some populations of *Pluvialis dominica* (red) and *P. fulva* (blue) and the stable isotope ratios (95% confidence ellipses; sample sizes provided in Table 1) in summer-grown and winter-grown feathers of *P. fulva* and *P. dominica*. All plovers used in this study were from breeding grounds on the Seward Peninsula, Alaska.



dry. Samples were weighed (1–1.5 mg) into tin cups and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the mass-spectrometry facility, University of Alaska Fairbanks, using a Europa 20/20 continuous flow isotope ratio mass-spectrometer; δD was analyzed according to Wassenaar and Hobson (2000a) at the Stable Isotope Hydrology and Ecology Lab, National Water Research Institute, Environment Canada. Isotopic ratios are reported as per mil (‰) deviation from the standard as defined by $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where X is D, ^{13}C , or ^{15}N , and R is the ratio $\text{D}/^1\text{H}$, $^{13}\text{C}/^{12}\text{C}$, or $^{15}\text{N}/^{14}\text{N}$. Standards are Vienna standard mean ocean water (D), Peedee belemnite (C), and atmospheric N_2 (N). All δD values are reported as nonexchangeable H according to equations in Hobson et al. (2001).

Data analyses

Plover feathers represented four groups by species and season of growth (*P. dominica* summer, *P. dominica* winter, *P. fulva* summer, and *P. fulva* winter), and isotope values did not differ either by sex or year in any group for any isotope (Mann–Whitney, $P > 0.05$); subsequent analyses were performed on groups with year and sex combined. Transformations failed to normalize data that exhibited nonnormal distributions (Shapiro–Wilk) but were homoscedastic ($P > 0.05$, Bartlett’s test). Because general linear models are generally robust for homoscedastic, nonnormally distributed data (Sokal and Rohlf 1995), parametric tests were used in the

analyses. A repeated measures multivariate analysis of variance (MANOVA) design, with species and season as class variables and stable isotopes as response variables, was used to test for differences among species, season, and the interaction (species \times season). If differences were detected for the class variables in multivariate analyses, multiple univariate comparisons were performed with an ANOVA for that class with P -values of each comparison adjusted using a Bonferroni correction (Sokal and Rohlf 1995).

To assign individuals to group of origin, we used the principle of “assignment with exclusion,” a method adopted from population genetics that uses an exclusion criterion to reject unlikely sources (Cornuet et al. 1999; Wunder et al. 2005). We used the cross-validation procedure in discriminant analyses as an assignment method to classify feathers into known group of origin based on the three isotopic values. The limited number of sample sizes used in our analyses contributed to low power of some assignments, but power was increased by using three isotope values for each sample. Each feather’s posterior probability of membership for each group (*P. dominica* summer, *P. dominica* winter, *P. fulva* summer, and *P. fulva* winter) was calculated by determining the frequency distribution of all candidate groups with that feather removed from the dataset and then calculating the likelihood of that feather occurring in each group. The feather was assigned to the group with the highest probability of membership. In this method, feathers being assigned were given an equal prior probability of belonging in each population. We

placed an exclusion threshold of 80% or higher on the posterior probabilities for accepting group membership. Individuals with posterior probabilities lower than 80% were excluded as probable members of a group because of an unacceptably low confidence that this group was the true source. Because the true group of origin was known for all feathers, we were able to determine the accuracy of assignments to true group of origin based on multiple feather stable isotopes.

For northern wheatears we first regressed isotopic data against collection date and location to ensure that collection date and location did not contribute significantly to variation in isotope values. Northern wheatear feathers represented two groups (adult summer and adult winter) and were analyzed using parametric and nonparametric methods (Shapiro-Wilk; δD , $P > 0.05$; $\delta^{13}C$ and $\delta^{15}N$, $P < 0.05$). Isotope ratios in summer- and winter-grown feathers were compared using Wilcoxon signed ranks tests for $\delta^{13}C$ and $\delta^{15}N$. A t -test of paired samples was used to compare δD values. Lack of differences between feather types precluded further analyses in this species. All statistical analyses were performed with the Statistical Analysis System (1999 version 8e, Cary, NC, USA).

Results

Plovers

As expected given their sympatry in breeding, no differences were detected between *Pluvialis* species in Alaska-grown feathers for any isotope (δD , $\delta^{13}C$, and $\delta^{15}N$; Table 1). However, Alaska-grown plover feathers did not exhibit the low variation expected in δD from feathers grown in a small geographic area. This was especially true in *P. dominica*, where δD in summer-grown feathers ranged from -175 to -62 ‰. In *P. fulva*, deuterium values also drastically differed from the expected values between -130 and -110 ‰. Mean δD values in winter-grown feathers in *P. fulva* were consistent with the expected wintering range values of -60 to

-25 ‰ and exhibited the high variation that was expected in feathers grown over a large geographic area (Table 1). Winter-grown feathers in *P. dominica* were not consistent with expected wintering range δD values of -75 to -25 ‰, and the variation among these feathers was much lower than expected (Table 1). Despite the considerable variation in δD values for Alaska-grown *P. dominica* feathers and winter-grown *P. fulva* feathers, significant differences were detected in δD values among groups, separating the summer- and winter-grown feathers into two groups (Kruskal-Wallis $F_{3,23} = 12.88$, $P < 0.0001$; Table 1). No differences existed between any feather groups for $\delta^{13}C$ ($F_{3,28} = 2.83$, $P = 0.0567$; Table 1). Significant differences in $\delta^{15}N$ ratios were found in *P. dominica* between summer- and winter-grown feathers ($F_{3,28} = 7.92$, $P = 0.0006$; Table 1), but this difference was not present in *P. fulva*.

Multivariate analyses (with δD , $\delta^{13}C$, and $\delta^{15}N$ values combined) showed significant differences between season of feather growth ($F_{3,21} = 23.48$, $P < 0.0001$; Fig. 1), but no species or interaction effect between species and season ($F_{3,21} = 1.01$, $P = 0.4078$; MANOVA on ranks). As expected, there were significant differences between summer- and winter-grown feathers, but analyses did not detect significant differences between the winter-grown feathers of *P. fulva* and *P. dominica* (Table 1, Fig. 1).

Northern wheatears

No effects of collection date or location in Alaska on δD , $\delta^{13}C$, $\delta^{15}N$, or values were detected (Spearman's ρ , $P > 0.05$). Deuterium values for Alaska-grown feathers were very consistent with the expected value of approximately -130 ‰ and showed minimal variation (-131 ± 28 ‰; mean \pm SD). However, we were unable to detect differences in δD values between adult summer-grown flight feathers and winter-grown back feathers in wheatears ($T_{0.05(2), 14} = 0.74$, $P = 0.4736$; Table 1). The δD values of inter-grown feathers were drastically different from the expected values of -25 to $+15$ ‰ for

Table 1 Stable isotope values (‰) obtained from summer- and winter-grown ventral body feathers of *Pluvialis* plovers from the Seward Peninsula, Alaska (top), and summer- and winter-grown feathers of northern wheatears (*Oenanthe oenanthe*) from Alaska (bottom)

| Species | Feather | n | δD | | n | $\delta^{13}C$ | | n | $\delta^{15}N$ | |
|-----------------------------|---------|----|--------------|----|----|----------------|------|----|----------------|------|
| | | | Average/mean | SD | | Average/mean | SD | | Average/mean | SD |
| <i>Pluvialis dominica</i> * | Summer | 5 | -129^a | 69 | 7 | -20.51^c | 2.27 | 7 | 5.57^d | 2.62 |
| <i>P. dominica</i> * | Winter | 5 | -9^b | 6 | 7 | -17.00^c | 1.96 | 7 | 9.72^e | 1.76 |
| <i>P. fulva</i> * | Summer | 9 | -59^a | 19 | 9 | -20.93^c | 2.60 | 9 | 6.13^{de} | 1.90 |
| <i>P. fulva</i> * | Winter | 8 | -24^b | 48 | 9 | -18.40^c | 3.19 | 9 | 9.24^e | 1.24 |
| <i>Oenanthe oenanthe</i> ** | Summer | 6 | -132^f | 14 | 15 | -21.38^e | 2.86 | 15 | 4.18^h | 2.62 |
| <i>O. oenanthe</i> ** | Winter | 10 | -131^f | 28 | 16 | -20.64^e | 3.47 | 16 | 5.24^h | 2.71 |

Superscripts having at least one letter in common indicate no significant difference between samples. No comparisons were made between *Pluvialis* and *Oenanthe* feathers

*Tukey's multiple comparison test $P < 0.01$

** $P > 0.05$

feathers grown in equatorial Africa (IAEA 2001). Similarly, there were no differences in $\delta^{13}\text{C}$ ($T_{0.05(2),14} = 6.5$, $P = 0.7148$; Table 1) or $\delta^{15}\text{N}$ ($T_{0.05(2),14} = 25.5$, $P = 0.1189$; Table 1) between these flight and back feathers grown on different continents.

Assignment tests

Cross-validation in discriminant analyses was used to evaluate the ability to correctly classify plover feathers into their known group of origin based on the δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values of each feather. Pairwise analyses considered only two groups at any time in the assignment. Based on multiple feather isotope values, 82% of *P. fulva* and 80% of *P. dominica* winter- and summer-grown feathers were classified into the correct groups of origin, showing a good separation between summer- and winter-grown feathers for each species. However, this method correctly classified only 69% of the winter-grown feathers of the two species into their correct continental group. A three-way comparison to classify summer-grown feathers of both plover species and the two interspecific groups of winter-grown feathers correctly assigned only 63% of the samples.

When an 80% probability of membership exclusion threshold was applied to posterior probabilities, only 41% of *P. fulva* winter- and summer-grown feathers and 30% of *P. dominica* feathers were assigned to correct groups of origin. No winter-grown feathers could be assigned to their correct groups of origin under the 80% exclusion threshold; none had a posterior probability of correct assignment higher than 75%. The three-way comparison among the pooled summer-grown and the two groups of winter-grown feathers assigned 41% of feathers into correct groups at this exclusion threshold, reflecting a very low degree of confidence in correctly assigning individuals to groups of origin (known in this case) using multiple geographically variable stable isotopes.

Discussion

In American and Pacific golden-plovers from Alaska, δD signatures were distinct and, as expected, were significantly different between summer- and winter-grown feathers, despite the potentially vast region of growth for winter-grown feathers and the relatively small sample size. Among all three species, we expected the variation in isotopic signatures among winter-grown feathers to be relatively higher than among summer-grown feathers due to factors such as widespread geographic origins of growth (i.e., dispersed wintering among individuals) or an overlap of molt and migration (such as in plovers). This expectation was met in *P. fulva*, but it was not met in *P. dominica*. In the latter species, variability of isotopic values in winter-grown feathers was much lower than that observed in breeding-ground feathers (Fig. 1). This dif-

ference in variation may indicate a difference in habitat use or foraging behavior between the two species on their breeding and wintering grounds or differences in migration and molt patterns. The latter, however, are less likely because *Pluvialis* plovers are swift migrants, and most individuals arrive on breeding and Alaskan staging areas completely molted into alternate (dark) plumage (Johnson and Connors 1996). In addition, *P. fulva* that winter in Hawaii attain most of their dark, alternate body feathers before migrating (O. Johnson, personal communication).

The high variation in isotopic values in breeding-ground feathers of *P. dominica* suggests generalized diet and habitat use, whereas the low variation in isotopic values of the sympatric *P. fulva* likely indicates specialized diet and habitat use. The opposite appears to be the case for wintering grounds. Little information exists on habitat use, diet, and foraging behavior of *P. fulva* and *P. dominica*, especially in Alaska, but a study of *P. fulva* on the Malay Peninsula demonstrated differences in diet among individuals. While some individuals concentrated their feeding on ptychochetes, others specialized on mussels (Kato et al. 2000). Such individual variation may explain our observation of higher isotopic variation in winter-grown feathers of that species. Similarly, studies of related species demonstrated both high specialization as well as generalized foraging behavior on both breeding and wintering grounds. For example, European golden-plovers (*P. apricaria*) in the Southern Pennines showed specialized habitat selection related to the height of vegetation as well as highly specialized diet (mainly larval tipulids; Pearce-Higgins and Yalden 2003). In contrast, gray plovers (*P. squatarola*) in nine tropical and temperate sites showed high variation in foraging behavior in relation to the abundance of different prey types (Turpie and Hockey 1997), and semipalmated plovers (*Charadrius semipalmatus*) in Venezuela exhibited sex differences in foraging behavior (Smith and Nol 2000). Whether the sympatry and potential competition among such closely related species on the breeding grounds has influenced their tendencies for such hypothesized specialization is unclear and merits future investigation.

In the case of plovers, it is theoretically possible that shifts in habitat and diet to intertidal feeding might occur, due to breeding plovers' proximity to the coast. Such a shift to marine habitats might be responsible for the δD variation in summer-grown (and indeed among winter-grown) plover feathers and might explain some of the more positive δD values in our data. However, the correlation between enriched δD and enriched $\delta^{13}\text{C}$ values that is expected from marine inputs (Lott et al. 2003) was not exhibited in these feathers ($R = 0.26$, $P = 0.352$, Spearman's ρ). Johnson and Connors (1996) found little evidence of marine feeding in either breeding plover species and reported that the majority of their diets consisted of terrestrial invertebrates. Thus, although some seasonal dietary shifts may have occurred in plovers, as may be indicated by their $\delta^{15}\text{N}$ values, this shift was not likely associated with consumption of

marine-derived nutrients. Future research should include $\delta^{34}\text{S}$ in analyses when marine inputs may be a factor (Lott et al. 2003).

Feathers developed from nutrient stores from previously occupied habitats could also produce the unexpected isotopic ratios, although it is doubtful that nutrient stores from previous locations would persist throughout incubation and most of chick-rearing (the stage at which our samples were taken). Also, several studies have demonstrated that isotopic ratios in feathers reflect those in the diet at the time of growth (Mizutani et al. 1990; Hobson and Clark 1992; Ogden et al. 2004). Using $\delta^{13}\text{C}$, Klaassen et al. (2001) showed that 10 species of Arctic-breeding waders used local food sources for energetic requirements during the breeding season. Therefore, it is unlikely that the relatively enriched δD values we observed as well as the differences in variation in isotopic signatures of *Pluvialis* plovers can be explained by differential use of stored nutrients by these two species.

Alternatively, several other factors, such as element routing, metabolic rate, and diet-tissue fractionation of stable isotopes (Gannes et al. 1997; Pearson et al. 2003; McKechnie et al. 2004; Ogden et al. 2004), may have caused much of the variation we observed and compromised our ability to accurately assign summer- and winter-grown feathers to their geographic origins at an intercontinental scale. Poorly understood physiological processes, such as element routing (Gannes et al. 1997) and assimilation rates (Bearhop et al. 2002; Pearson et al. 2003; McKechnie et al. 2004) can introduce sources of variation that are often unaccounted for when attempting to assign individuals to geographic regions of origin. More enriched deuterium values associated with snow melt, evaporation in drinking water sources, and relative humidity may play a role in some of the variation we observed (Hobson et al. 1999a; Wassenaar and Hobson 2000b; McKechnie et al. 2004), but additional controlled studies are necessary to assess the impact of these factors on feather isotope ratios.

While our data may shed light on habitat use, diet, and potential competition between the two *Pluvialis* species on the breeding grounds, they did not exhibit sufficient differences to distinguish between the two species' winter-grown feathers, which come from different continents. In addition, Alaska-grown plover feathers did not have the δD signature expected among feathers grown within a 100-km radius with minimal elevational changes. Based on isotopic maps of North America (Hobson and Wassenaar 1997; Hobson 1999; Meehan et al. 2004; Bowen et al. 2005), isotopic ratios in these breeding-ground plover feathers are more concordant with a breeding latitude of between 55° to 45°N , rather than their true latitude of origin, approximately 65°N . Thus, we were unable to accurately assign individuals with confidence to their correct continent of origin or to assign breeding individuals to within better than several thousand kilometers of their true breeding origins using values of δD .

The case was more extreme for the northern wheatear feathers. These feathers exhibited a strong geographic signature with nominal variation in δD for the summer-grown, but not for the winter-grown, feathers. We found no relation between collection date (and thus the length of museum archiving) or location and isotopic ratios in wheatears. This indicates that the lack of difference between summer- and winter-grown feathers in the wheatear feathers was not caused by exchange of hydrogen-bearing molecules in those tissues while samples were stored (Wassenaar and Hobson 2000a). Despite differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in feathers from willow warblers (*Phylloscopus trochilus*) grown across wintering grounds in Africa (Chamberlain et al. 2000), these isotopes did not provide discriminatory power in separating summer- and winter-grown feathers for northern wheatears. Because northern wheatears were collected only on the Alaskan breeding grounds, we cannot disregard that their partial prealternate molt may not occur in Africa. However, Kren and Zoerb (2000) provided convincing evidence for such molt, and it is clear from molt patterns in Alaska (for example, changes of back color between seasons) that this prealternate molt occurs somewhere other than North America. Absent direct evidence to the contrary, we should assume that this molt follows the pattern of most long-distance migrant passerines and is completed before beginning spring migration.

Despite our success in distinguishing between summer- and winter-grown feathers in each plover species, our lack of success in confidently assigning individual feathers to known continents of origin is disturbing. Organismal biology, it seems, may not readily conform to expectations derived from abiotically measured isotopic characteristics at these scales. Also, unlike other studies, we did not stop at the assignment of individuals to groups (Caccamise et al. 2000; Wassenaar and Hobson 2000a, b; Wunder et al. 2005) but also evaluated the confidence in that assignment. Such confidence in an individual's assignment is critical to applying intrinsic markers in management and conservation (Cornuet et al. 1999). Although we were able to assign over 80% of feathers in each plover species to origin of growth, we discovered that when a liberal membership probability of 80% was applied to each assignment, acceptable numbers of correct assignments were dramatically decreased. In several of the analyses, feathers with a posterior probability of greater than 80% percent were misclassified. In a blind study attempting to assign feathers with similar variation to unknown origins, these erroneous assignments would go undetected. Although correlating isotope signatures along latitudinal gradients is useful in some species, the ability to track individuals or populations through their annual cycles based on tissue isotope ratios depends on clear understanding of the ecology and physiology of the study organism and the development and implementation of an assignment method with robust exclusion criteria. We believe that stable isotopes hold potential for tracking migratory birds across geographically distinct regions, but we urge

researchers to carefully consider statistical methodology and interpretation of results.

Zusammenfassung

Die Zuordnung von Vögeln zu Winterquartieren und Brutgebieten mit Hilfe von stabilen Isotopen: Untersuchungen von zwei Federgenerationen bei drei interkontinentalen Zugvogelarten

Für Untersuchungen der geografischen Herkunft von Populationen und von Zugmustern verschiedener Wirbeltiere und Nicht-Wirbeltiere wird in jüngster Zeit zunehmend mehr die Analyse von geografisch distinkten Mustern von bestimmten Isotopen im Gewebe genutzt. Zur Prüfung der Frage, ob Federn, die auf verschiedenen Kontinenten wachsen, Unterschiede im Deuteriumniederschlag widerspiegeln und ob diese Federn dann signifikant verschiedene Muster an stabilen Isotopen aufweisen, haben wir die stabilen Isotope in zwei Federgenerationen dreier Vogelarten untersucht (Amerikanischer und Pazifischer Goldregenpfeifer, *Phuvialis dominica*, *P. fulva*, und Nordischen Steinschmätzer, *Oenanthe oenanthe*), die alle in Nordamerika brüten und in Südamerika, im Südpazifik beziehungsweise in Afrika überwintern. Bei den Goldregenpfeifern fanden wir Unterschiede in den Signaturen an stabilen Isotopen zwischen Federn, die im Sommer bzw. im Winter gemauert wurden. Dabei entsprechen unsere Ergebnisse an zwei Federgenerationen früheren an einem größeren Datenmaterial. Im Gegensatz zu den Goldregenpfeifern konnten wir beim Steinschmätzer keine Unterschiede zwischen im Winter oder im Sommer vermauerten Federn finden. Diskriminanzanalysen separierten 80% der im Sommer bzw. Winter vermauerten Federn bei den Regenpfeifern. Allerdings ergab ein sog. Ausschlussverfahren, eine Methode aus der Populationsgenetik zur Zuordnung von Individuen zu bestimmten Gruppen, eine Zuordnungsgenauigkeit von nur 41%, verglichen zu 63%, wenn das Ausschlusskriterium weggelassen wurde. Daraus folgt, dass es uns nicht möglich war, Federn ihrem Entstehungsort auf kontinentaler Ebene akkurat zuzuordnen. Weiterhin zeigte sich, dass wir durch die Verwendung von Deuterium-Werten aus Nordamerika die Zuordnung von Federn zu ihrem Entstehungsort nicht genauer als einige tausend Kilometer angeben können. Wir schlagen deshalb vor, dass für die Interpretation von Ergebnissen aus der Analyse von stabilen Isotopen für die Herleitung geografischer Unterschiede im Mauerort die artspezifische Ökologie und Physiologie und die statistische Methode sorgfältig berücksichtigt werden sollten.

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Appendix

Choice of isotopes, a priori expectations of differences, and determination of expected values

Expected δD values in feathers were determined a priori using the North America isocline map (Hobson and Wassenaar 1997) and the isotope precipitation calculator developed by Bowen et al. (2005) and, for winter-grown feathers, precipitation values from the GNIP/ISOHIS database (IAEA 2001). We expected feathers grown on Alaskan breeding grounds to reflect the 40-year growing season averages in all three species (Hobson and Wassenaar 1997) and growing season precipitation isotopic estimates (Bowen et al. 2005). The expected δD values of approximately -130‰ in summer-grown feathers for all three species were based on nonexchangeable H and corrected for fractionation.

In winter-grown feathers, we calculated annual δD precipitation averages from precipitation stations located within each species' wintering range. Despite the large database, many stations were not continuously active, and some regions were not represented. Although derived from spatially and temporally discontinuous data, our expectations were based on the best available estimates over these broad geographic areas. For *P. dominica*, we used 20 stations in South America. Station names (number of samples), locations, and elevations were as follows: (1) Ciudad (76), $S34.38^\circ W58.28^\circ$, 0 m; (2) Corrientes (31), $S27.47^\circ W58.83^\circ$, 55 m; (3) La Suela (34), $S30.58^\circ W64.58^\circ$, 900 m; (4) Mendoza (21), $S32.88^\circ W68.85^\circ$, 827 m; (5) Nancunan (24), $S34.03^\circ W67.97^\circ$, 572 m; (6) Salta (18), $S24.78^\circ W65.40^\circ$, 1,187 m; (7) Santiago del Estero (3), $S27.78^\circ W64.27^\circ$, 187 m; (8) Asuncion (7), $S25.27^\circ W57.63^\circ$, 65 m; (9) Campinas (109), $S23.00^\circ W47.13^\circ$, 661 m; (10) Campo Grande (85), $S20.47^\circ W54.67^\circ$, unknown; (11) Cuiaba' (219), $S15.60^\circ W56.10^\circ$, 165 m; (12) Porto Alegre (175), $S30.08^\circ W51.18^\circ$, 7 m; (13) Sao Paulo (20), $S23.67^\circ W46.63^\circ$, unknown; (14) Santa Maria da Serra (97), $S22.66^\circ W48.06^\circ$, unknown; (15) Concepcion (13), $S36.46^\circ W73.03^\circ$, 11 m; (16) Juan Fernandez Island (36), $S33.62^\circ W78.83^\circ$, 6 m; (17) La Serena (13), $S29.55^\circ W71.12^\circ$, 146 m; (18) Puerto Montt (48), $S41.47^\circ W72.93^\circ$, 13 m; (19) Santiago (38), $S33.45^\circ W70.70^\circ$, 520 m; and (20) Temuco (26), $S38.46^\circ W72.38^\circ$, 114 m. Deuterium values in the precipitation from these sites averaged -27‰ ($\pm 28\text{‰}$ SD), and feather values grown from this region were expected to range from approximately -75 to -25‰ .

We used annual precipitation values collected at four stations across known wintering areas in the South

Pacific and 16 stations across Asia, Australia, and New Zealand to determine expected deuterium values in winter-grown *P. fulva* feathers. Station names (number of samples), locations, and elevations were as follows: (1) Hawaii (33), N19.72° W155.07°, 9 m; (2) Johnston Island (45), N16.73° W169.52°, 2 m; (3) Midway Island (227), N28.22° W177.37°, 13 m; and (4) Wake Island (88), N19.28° E166.65°, 3 m, for South Pacific locations. Deuterium values in the annual precipitation from these sites averaged -7‰ ($\pm 12\text{‰}$). Station names (number of samples), locations, and elevations from the other wintering areas of *P. fulva* were as follows: (1) Tokyo (18), N35.68° E139.77°, 4 m; (2) Balas-Balas (19), N09.29° E123.17°, 827 m; (3) Barrio Tongonan (15), N11.11° E124.65°, 420 m; (4) Bonga (22), N13.03° E123.92°, 600 m; (5) Botong (23), N13.05° E123.92°, 475 m; (6) Cagbulacao (15), N11.12° E124.62°, 200 m; (7) Diliman (12), N14.64° E121.04°, 42 m; (8) Guinlajon (22), N13.01° E123.96°, 220 m; (9) Inang Maharang (21), N13.07° E123.91°, 285 m; (10) Mahanagdong (12), N11.18° E124.66°, 800; (11) Palayang Bayan (23), N13.06° E123.93°, 520 m; (12) Ticala (19), N09.31° E123.20°, 350 m; (13) Upper Mahiao (13), N11.13° E124.66°, 850 m; (14) Brisbane (273), S27.43° E153.08°, 4 m; (15) Invercargill (152), S35.07° E173.28°, 76 m; (16) Kaitaia (216), S35.07° E173.28°, 76 m; and (17) Rarotonga (132), S21.20° E159.80°, 6 m. Deuterium values in the annual precipitation from these sites averaged -26‰ ($\pm 20\text{‰}$). The annual δD values from wintering areas of *P. fulva* averaged -16‰ ($\pm 16\text{‰}$), and feather values grown from this region were expected to range from approximately -60 to -25‰ .

We used annual precipitation values collected at eight stations across known African wintering areas to determine expected deuterium values in winter-grown northern wheatear feathers. Station names (number of samples), location, and elevation were: (1) Addis Ababa (191), N09.00° E38.73°, 2360 m; (2) Bamako (99), N12.32° W07.57°, 381 m; (3) La Entebbe (73), N00.05° E32.45°, 1155 m; (4) Geneina (36), N13.48° E22.45°, 805 m; (5) Khartoum (19), N15.60° E32.55°, 382 m; (6) N'Djamena (53), N12.13° E15.03°, 294 m; (7) Naimey (34), N13.52° E02.09°, 220 m; and (8) Sao Tome (59), N00.38° E06.72°, 8 m. Deuterium values in the precipitation from these sites averaged -3‰ ($\pm 23\text{‰}$), and values of feathers grown from this region were expected to range from approximately -40 to 0‰ .

Although carbon and, to a lesser extent, nitrogen have been used to discriminate among populations of migratory species (Chamberlain et al. 2000; Chérel et al. 2000; Wassenaar and Hobson 2000b), we did not generate any a priori expectations for these two isotopes. However, we included these isotopes in our analyses to provide additional discriminatory power and, in the case of $\delta^{13}\text{C}$, to provide potential isotopic evidence of marine feeding (Hobson 1987, 1990; Hobson et al. 1999b) and elevation influences (Korner et al. 1991; Hobson et al. 2003).

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