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CHERNOBYL AS A POPULATION SINK FOR BARN SWALLOWS: TRACKING DISPERSAL USING STABLE-ISOTOPE PROFILES

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Abstract. Stable-isotope profiles of feathers can reveal the location or habitat used by individual birds during the molting period. Heterogeneity in isotope profiles will reflect heterogeneity in molt locations, but also heterogeneity in breeding locations, because spatial heterogeneity in molt locations will be congruent with spatial heterogeneity in breeding locations in species with high connectivity between breeding and molting sites. We used information on the congruence of spatial heterogeneity in molt and breeding location to study population processes in Barn Swallows (*Hirundo rustica*) from a region near Chernobyl, Ukraine, that has been radioactively contaminated since 1986; from an uncontaminated control region near Kanev, Ukraine; and from a sample of pre-1986 museum specimens used to investigate patterns prior to the nuclear disaster at Chernobyl, from both regions. Previous studies have revealed severe reductions in Barn Swallow reproductive performance and adult survival in the Chernobyl region, implying that the population is a sink and unable to sustain itself. Female Barn Swallows are known to disperse farther from their natal site than males, implying that female stable-isotope profiles should tend to be more variable than profiles of males. However, if the Barn Swallows breeding at Chernobyl are not self-sustaining, we would expect males there also to originate from a larger area than males from the control region. We found evidence that the sample of adult Barn Swallows from the Chernobyl region was more isotopically heterogeneous than the control sample, as evidenced from a significant correlation between feather $\delta^{13}C$ and $\delta^{15}N$ values in the control region, but not in the Chernobyl region. Furthermore, we found a significant difference in feather $\delta^{15}N$ values between regions and periods (before and after 1986). When we compared the variances in $\delta^{13}C$ values of feathers, we found that variances in both sexes from post-1986 samples from Chernobyl were significantly larger than variances for feather samples from the control region, and than variances for historical samples from both regions. These findings suggest that stable-isotope measurements can provide information about population processes following environmental perturbations.

Key words: Barn Swallows; Chernobyl, Ukraine; correlation of stable-isotope profiles; Hirundo rustica; *sinks; sources; variance in stable-isotope profiles.*

INTRODUCTION

The mean and variance of the reproductive output of populations of free-living organisms vary considerably. Such variance is of considerable importance because populations that produce a larger and less variable number of recruits to future generations are considered less prone to extinction (Lande et al. 2003, Roff 2001). Two variance components are important contributors to such variability. Environmental variance similarly affects all individuals in a population due to variation in common environmental conditions, whereas demographic variance arises from individual variation in realization of survival and reproduction. Whether a population constitutes a net contributor to the maintenance of a globally viable population will depend on both environmental and demographic variances of each of the composite subpopulations. Pulliam (1988) originally suggested that populations with positive population growth, *r*, are source populations, while populations with negative *r* are sinks. Immigration may allow individuals to immigrate into sites where local recruitment would be insufficient for persistence of a population (Pulliam 1996). Source populations were subsequently defined as populations that have a positive intrinsic growth rate, while sink populations were defined as being unable to sustain not only their own populations, but also neighboring populations (Dias 1996, Hanski 1999). Successful identification of source and sink populations is therefore of considerable

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importance for conservation purposes, but also for ecological research. Many studies have found evidence consistent with predictions for source–sink metapopulations using a number of different ecological and genetic approaches (Dias 1996, Paradis 1995, Pulliam 1996, Pulliam and Danielson 1991, Stacey et al. 1997). Here we propose a novel approach to the identification and study of source and sink populations. This method is based on heterogeneity in stable-isotope profiles across individuals in the different parts of a metapopulation caused by different degrees of admixture in source and sink populations (Hobson 2005).

Here we argue that source and sink populations under certain assumptions can be identified using heterogeneity in stable-isotope profiles. The underlying assumptions are as follows: First, stable-isotope abundance recorded in the feathers or other tissues reflect the isotope contents of food, revealing information about the habitats and the geographical locations where the tissue was developed (reviews in Hobson 1999, 2004, Rubenstein and Hobson 2004). In the case of metabolically inactive tissues such as scales, feathers, and hair, isotope profiles provide a frozen snapshot of the environmental conditions experienced during development of the character. Individuals with specific characteristics will subsequently carry this signature until the next molt. As the feathers of birds wear out, they are replaced in a process of molt, normally at least once a year; in the Barn Swallow once a year. Second, the ratio of stable isotopes in the environment varies spatially, showing increasing heterogeneity with increasing area (e.g., Still et al. 2003, Urton and Hobson 2005). For example, previous studies of Palaearctic breeding birds that typically molt flight feathers on their wintering grounds have indicated that mixtures of wintering populations can be discerned based on variation in feather isotope profiles among individuals on the breeding grounds (e.g., Chamberlain et al. 2001, Møller and Hobson 2004). Third, population sinks are defined as requiring immigration of individuals to sustain populations, while sources do not (Pulliam 1988). This implies that individuals in population sinks have come from a larger area than those from population sources. Fourth, individuals from a single population will generally be found in the same region while the tissue is being grown (Berthold 2001), so that a population of individuals that have come from a larger area will tend, by necessity, to have a greater variance in isotope ratio. Fifth, spatial heterogeneity in a sample of individuals from the breeding grounds of birds also reflects spatial heterogeneity from the wintering grounds where the tissue has been grown. Sixth, sex differences in heterogeneity in samples from the breeding grounds are expected to reflect spatial heterogeneity from the wintering grounds because female Barn Swallows generally disperse considerably further than males. Seventh, in species with migration divides, where one population takes one migratory route and a second takes another migratory route (Berthold 2001), single breeding populations can consist of an admixture of birds from different wintering populations. R. Ambrosini, A. P. Møller, and N. Saino (*unpublished manuscript*) have analyzed spatial distribution patterns of over 1000 recoveries of Barn Swallows (*Hirundo rustica*) from the African winter quarters of birds breeding in the Western Palearctic. These analyses, based on Mantel tests, revealed a high degree of congruence in spatial patterns in the winter quarters and the breeding grounds. Thus, breeding birds from Western Europe winter in Western Africa, those from Eastern Europe winter in East Africa, those from Northern Europe winter in Southern Africa, and those from Southern Europe winter in Northern Africa. In other words, at large spatial scales, a heterogeneous sample of birds from the winter quarters, when considering the isotope composition of feathers caused by incorporation of stable isotopes during the annual molt in winter, also signifies a heterogeneous sample of birds in terms of previous breeding-ground origins. Barn Swallows breeding in Europe could be divided into western and eastern populations that differed in migration routes and wintering areas (R. Ambrosini, A. P. Møller, and N. Saino, *unpublished manuscript*), with birds from Finland, parts of Sweden, and eastern Europe migrating to eastern Africa along an eastern flyway, while birds from Norway, Denmark, and western Europe use a western flyway. Breeding populations in Denmark consist of an admixture of the two populations (Møller and Hobson 2004). Thus, our assumption that heterogeneity in stable-isotope profiles caused by heterogeneity in winter grounds also reflects heterogeneity in terms of breeding origin is supported by empirical evidence. These seven assumptions lead to the critical test that if we compare variances of isotope ratios of two or more samples, all things being equal, the sample with the greater variance is a sink to a greater extent than the one with the smaller variance.

However, there have, to the best of our knowledge, been no attempts to use stable-isotope techniques to investigate such admixture of populations to study population processes, including identification of sources and sinks. Several studies used stable isotopes to examine population demographics and population processes (Hershey et al. 1993, Marra et al. 1998, Kelly et al. 2002, Rubenstein et al. 2002, Sillett and Holmes 2002). Using isotopic variability in feathers among individuals to infer diversity of population origins will necessarily depend on the degree of variability in stable isotopes across potential contributing populations (Hobson et al. 2004, Hobson 2005). In general, we should expect breeding populations that constitute sinks to reveal greater variance in feather isotope profiles than populations that constitute source populations, as argued in the previous paragraphs. Males often differ from females in dispersal distance from site of birth to site of breeding, with female birds generally dispersing much further than males, while mammals commonly show the opposite pattern (e.g., Greenwood 1980, Clobert et al. 2001). Such sex differences, if well established in particular species, provide a unique opportunity to use one sex as a natural control group and the other sex as the "experimental" group when studying sources and sinks. Although it is often difficult to measure the range of isotopic variation in diet used by birds on their wintering grounds, where they molt feathers, in source–sink situations, we would expect individuals of the more-dispersing sex to show an increase in the variance in isotope profile due to admixture of individuals of different origins (potentially over hundreds or thousands of kilometers). In contrast, the more philopatric sex should show less variation. This prediction has a strong inference because individuals of the two sexes would be expected to otherwise be similar in many respects. Furthermore, if there are temporal controls in terms of tissue samples from before and after the creation of a sink population, strong inferences could be predicted with respect to temporal changes in variances in isotope profiles. Recently, Hobson et al. (2004) demonstrated that individual isotopic outliers among male Ovenbirds (*Seirus aurocapillus*) and American Redstarts (*Setophaga ruticilla*) in breeding populations in North America represented birds that had dispersed from other (unknown) areas. These authors suggested that isotopic variance within breeding populations could be used to establish minimum estimates of recruitment into populations of interest, provided that sufficient isotopic heterogeneity occurs among possible molting areas of source populations. We adopted a similar approach to examine the structure of Barn Swallows from two different regions in Ukraine that differ in sustainability.

The aims of this study were to investigate whether stable-isotope profiles could be used to identify a population sink in a wild population of Barn Swallows from Ukraine (see Møller and Mousseau [2001, 2003] for a description of this system). We can make three predictions. First, positive correlation between stable isotopes should break down when population admixture increases. For several elements, stable-isotope relative abundance in the food shows gradual clinal variation on continental scales (e.g., Still et al. 2003, Bowen et al. 2005). So, we should expect a sample of individuals from a population to be normally distributed in space because individuals from a given population winter and molt in a specific location, with both genetic and environmental factors contributing to heterogeneity in this spatial distribution. Such a normally distributed spatial distribution of individuals should cause stable-isotope ratios for C and N to be positively correlated. Such positive correlation has previously been found within samples (e.g., Møller and Hobson 2004), but has also been demonstrated for C and N stable-isotope ratios within food webs (Kelly 2000). However, if a sample from a specific region shows significant admixture of individuals from different breeding and, hence, wintering populations, positive covariance between stable-isotope ratios for C and N should no longer exist. The reason for this claim is that sampling sites should no longer show a normal distribution along the clinal gradients of the different stable isotopes in the environment. Second, males and females should differ in mean and variance of stable-isotope profiles due to sex differences in natal dispersal, again assuming that spatial heterogeneity in breeding sites is reflected in spatial heterogeneity in molting sites. Because female Barn Swallows disperse from their natal site to their future breeding site more than twice as far as males, with measured maximum dispersal distances reaching 700 km (Møller 1994, Glutz von Blotzheim and Bauer 1994), we would expect that females from the two areas in Ukraine would be more different in means and variances of isotope profiles than males. This prediction is based on the fact that females originate from a larger area than males, and that the variance in distances between the origins of females is greater than the variance in distances between the origins of males. Since long-distance dispersal is much more common in female Barn Swallows than in males (Møller 1994), we should expect the variance in stable-isotope profile to be greater in females than in males. Third, the variance in stable-isotope profile should be greater in population sinks than in population sources. Capture–mark–recapture analyses of Barn Swallows from the Chernobyl region has shown that adult survival is 60% lower than from the Kanev region, and estimates of reproductive success have shown that annual fecundity is 20% lower than from the Kanev region (Møller et al. 2005). Such large differences would suggest that Barn Swallows in the Chernobyl region are sustained by immigration from elsewhere. Such immigration should be particularly obvious in males, because males from the control region near Kanev were expected to be relatively homogeneous in isotope composition mainly due to local recruitment, while the males in the Chernobyl region should have a larger proportion of immigrants. We predicted that the patterns of stable isotopes in Kanev would be the same before 1986 and in 2000, but that the patterns would differ between these periods at Chernobyl. Explicitly, we would predict an increase in the stable isotopic variance at Chernobyl, particularly amongst males.

Materials and Methods

Study species

The Barn Swallow is a small (~20 g) passerine that feeds on insects, mainly Diptera and Hymenoptera caught on the wing. Barn Swallows arrive in Europe from the African winter quarters in April–June, and leave in August–October (Møller 1994). Males and females build nests inside buildings, where the female lays a clutch, usually 4–5 eggs. More than 50% lay a second clutch. Barn Swallows breed solitarily or in colonies that can exceed 120 pairs. Long-tailed males enjoy a mating advantage, as demonstrated by observations and experiments (Møller 1994). Male Barn Swallows in Chernobyl have dramatically increased asymmetry in their elongated outermost tail feathers and much paler throat coloration compared to males from a control region near Kanev and to males predating the Chernobyl accident (Møller 1993). Long-tailed males in particular are very pale compared to controls (Camplani et al. 1999). Genetic studies have reported increased mutation rates in Barn Swallows from the radioactively contaminated region around Chernobyl in Ukraine (Ellegren et al. 1997). Furthermore, the frequency of partial albinism is elevated compared to other populations, and such phenotypic deviants are associated with reduced fitness of Barn Swallows (Møller and Mousseau 2001). Of the phenotypic traits measured, those that differ the most between Chernobyl and an uncontaminated control region near Kanev, are also those that are most strongly associated with male mating success (Møller and Mousseau 2003). Barn Swallows from Ukraine winter in Southern Africa (Fig. 1), where they undergo a complete molt. Barn Swallows from Chernobyl and Kanev winter in the same areas (Fig. 1). There is no evidence suggesting that males and females winter in different areas (R. Ambrosini, A. P. Møller, and N. Saino, *unpublished manuscript*).

Study areas

We studied Barn Swallows in a region around Chernobyl, Ukraine (Shestopalov 1996), by visiting villages and checking collective farms for the presence of Barn Swallows (Fig. 2). Once such a farm had been located, we recorded radiation levels and captured adult Barn Swallows for measurements and subsequent banding. Capture was made with mist nets, providing a random sample of adults from the breeding farms. Our own field measurements of radiation at the ground level using a hand-held dosimeter (Inspector, SE International, Summertown, Tennessee, USA) revealed levels of radiation of 0.390 ± 0.317 mR/h (milliroentgens per hour; mean ± SE) at 14 farms in the Chernobyl region. As a control region, we used Kanev (~150 km southwest of Kiev), which has a relatively low level of contamination (Fig. 2). Mean levels of radiation were 0.025 ± 0.002 mR/h at five farms in this control region. We used the Chernobyl region for our study because radioactive contamination arising from the explosion of a nuclear reactor on 26 April 1986 released vast amounts of radioactive material into the environment. Most of the radioactive isotopes remain in the environment due to their long half-life, with serious detrimental effects on the reproductive success and adult survival of Barn Swallows (Møller et al. 2005). We studied Barn Swallows in the two study regions 6–12 June 2000 (A. P. Møller, T. A. Mousseau). The maximum distance between farms in the Chernobyl region was <20 km, and in the Kanev region it was <8 km. These distances are small compared to natal dispersal distances, and we considered it unlikely that this spatial scale would have any effect on variance is stable-isotope profiles. The wintering grounds of Ukrainian-breeding Barn Swallows, where the annual molt takes place, is shown in Fig. 1, based on recoveries of banded Barn Swallows from Ukraine (during the breeding season May–August) and South Africa (during winter December–February). Information on recoveries of banded birds was kindly provided by the Ukrainian Ringing Center, EURING (European Union for bird Ringing), and SAFRING (South African Bird Ringing Unit).

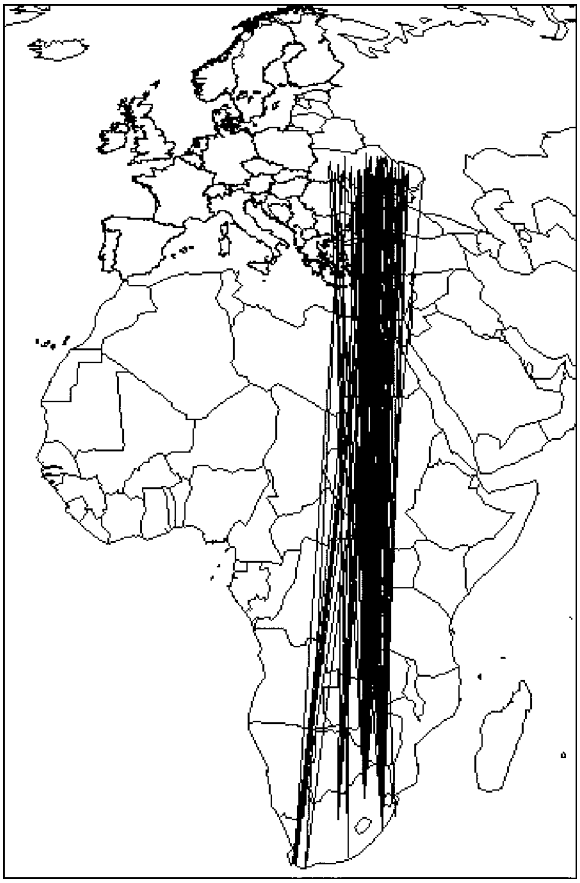

FIG. 1. The map shows connections between the banding sites of Barn Swallows breeding in Ukraine and winter locations in Africa.

As a second control sample from the Chernobyl region and the region around Kanev, we used samples of feathers from the Zoological Museum, Kiev, Ukraine. We only used adult birds collected during the breeding season (June–July) to avoid inclusion of specimens that might be migrants from more northern populations. Specimens attributed to the Chernobyl region derived from the same locations that are now within the contaminated areas (Fig. 2), while specimens from a similar area southeast of Kiev surrounding Kanev were considered to be controls. While long-term storage may affect samples from museum specimens, any changes

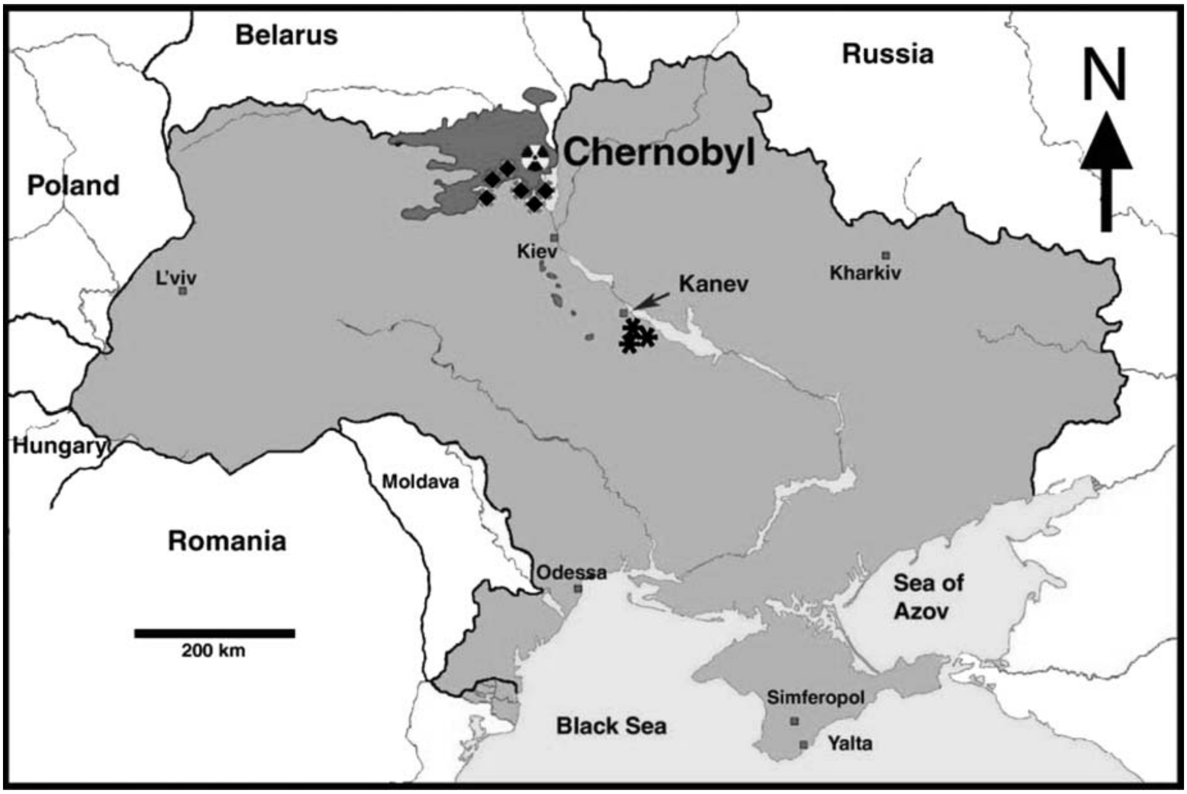

FIG. 2. Location of villages with study farms in 2000 and levels of radiation around Chernobyl and Kanev, Ukraine. The shaded region around Chernobyl demarks the area where >15 curies of ^{137}Cs per km^2 were deposited in 1986 (CIA 1986). The radiation levels in the contaminated areas were 0.390 ± 0.317 mR/h (mean ± SE) at 14 breeding farms in the Chernobyl region. In the control region near Kanev (~150 km southeast of Chernobyl) radiation levels were, on average, an order of magnitude lower (0.025 ± 0.002 mR/h). Approximate locations of villages with study farms are indicated either as black diamonds (in contaminated areas) or stars (relatively uncontaminated control areas).

should be uniform across samples and so should not influence our results in a heterogeneous way. The sample of museum specimens was collected by shotgun, whereas the recent samples of live birds were obtained by using mist nets. However, because the museum samples were collected with shotgun from breeding populations, we feel justified to assume that they also represent a random sample. Sample sizes for the two sexes, regions, and periods are reported in Table 1.

Collecting feathers

Upon capture, we collected the two outermost tail feathers from each adult. The feathers for each bird were stored at room temperature in a plastic bag in complete darkness until measurements were made. The tail feathers of adult Barn Swallows are molted in the African winter quarters (Cramp 1988; A. P. Møller, *unpublished data* from South Africa, Namibia, and Ghana), and so isotopic variability in feathers represents variability in the isotopic profile of the prey being related to the food web from which they come. The feathers from the museum specimens were the same as those for the field specimens.

Isotope analyses

Feathers were analyzed blindly with respect to information on origin and sex. Feathers were first cleaned of surface oils by rinsing several times in a 2:1 chloroform : methanol solution followed by air drying in a fume hood for several days. Feather vanes were then subsampled and 1 mg was weighed into small tin cups. These samples were then combusted in a Robo Prep elemental analyzer interfaced with a 20:20 isotope-ratio mass spectrometer (Europa Scientific, Manchester, UK). Resultant CO_2 and N_2 gases were measured for their stable-isotope ratios in δ notation relative to Pee Dee Belemnite (PDB) and atmospheric AIR standards, respectively, according to the formula presented in Hobson (1995). Based on thousands of measurements of internal laboratory standards (egg albumen and baleen keratin), we estimated measurement error to be 0.1‰ and 0.3‰ for δ^{13}C and δ^{15}N measurements, respectively.

Statistical analyses

We tested for correlation between feather δ^{13}C and δ^{15}N values using the different samples. Heterogeneity

TABLE 1. Results from tests for unequal variances with Barlett's test and for means with Welch's ANOVA for δ^{13}C and δ^{15}N from Barn Swallow feathers in relation to sex, region (Chernobyl and Kanev, Ukraine), and period (pre-1986, post-1986).

	Female			Male		
Sample, site, and period	*N*	SD	Mean absolute difference to the mean	*N*	SD	Mean absolute difference to the mean
δ ^{13}C						
Chernobyl						
Pre-1986	6	2.79	2.28	3	1.03	0.70
Post-1986	39	8.62	6.36	53	7.34	4.52
Kanev						
Pre-1986	8	1.73	1.44	21	2.37	1.68
Post-1986	29	2.29	1.80	25	2.47	1.83
δ ^{15}N						
Chernobyl						
Pre-1986	6	0.94	0.72	3	0.61	0.42
Post-1986	39	1.18	0.95	53	1.43	1.15
Kanev						
Pre-1986	8	1.10	0.75	21	1.04	0.84
Post-1986	29	1.30	1.13	25	1.06	0.78

Note: For δ ^{13}C, Bartlett's test, $F = 15.07$, df = 7, $P < 0.0001$; Welch's ANOVA, $F = 2.09$, df = 7, 26.5, $P = 0.08$. For δ ^{13}N, Bartlett's test, $F = 0.96$, df = 7, $P = 0.84$; Welch's ANOVA, $F = 4.18$, df = 7, 24.1, $P = 0.004$.

in Pearson correlation coefficients was tested using the procedure described in Sokal and Rohlf (1995). We did not transform data since they did not differ significantly from normal distributions according to the Shapiro-Wilk statistic. We tested for sex, region, and time effects on isotope profiles with Welch's ANOVA, which does not require equality of variances. Means for groups were compared using Fisher's protected least mean-squares test, adjusting means for unequal variances by weighting by the reciprocal of the sample variances of the group means. Variances in δ^{13}C and δ^{15}N values were compared among samples for different periods using Bartlett's test for homogeneity of variances (Sokal and Rohlf 1995). All statistical tests were made with JMP (SAS Institute 2000).

We used sequential Bonferroni correction to assess the tablewide Type I error rate by adjusting significance level to the number of tests (Holm 1979, Wright 1992). Strict application of this method severely reduces the power of tests (Wright 1992), but such sacrificial loss of power can be avoided by choosing an experiment-wise error rate higher than the accepted 5%. We used 10% as recommended by Wright (1992) and Chandler (1995).

RESULTS

Frequency distribution of stable-isotope values in feathers and correlation among stable isotopes

There were clearly unimodal distributions of δ^{13}C and δ^{15}N feather values with distributions not differing significantly from normality. When split among sex, region, and period categories, none of the distributions differed significantly from a normal distribution after sequential Bonferroni correction for eight statistical tests.

Correlations between δ^{13}C and δ^{15}N values for Barn Swallows from the recent field samples differed between regions. There was a nonsignificant relationship in Chernobyl ($F = 0.16$, df = 1, 90, $r^2 = 0.002$, $P = 0.69$; Fig. 3a), but a significant positive relationship in Kanev ($F = 17.48$, df = 1, 52; $r^2 = 0.25$, $P < 0.0001$, slope ± SE = 0.28 ± 0.07; Fig. 3b).

The correlations for the recent field samples were as follows: males from Chernobyl ($r = 0.009$, $t = 0.07$, df = 51, $P = 0.95$), females from Chernobyl ($r = -0.15$, $t = 0.92$, df = 37, $P = 0.37$); males from Kanev ($r = 0.35$, $t = 1.81$, d.f. = 23, $P = 0.08$), and females from Kanev ($r = 0.654$, $t = 4.49$, df = 27, $P = 0.0001$). The two correlation coefficients between δ^{13}C and δ^{15}N values for females were significantly different from each other ($t = 3.41$, $P < 0.001$), while the two coefficients for males were not significantly different ($t = 0.87$, $P = 0.39$).

Differences in means and variances in stable-isotope profiles between regions

Summary statistics for δ^{13}C and δ^{15}N values for the various sex, age, and region categories are reported in Table 1. Bartlett's test for unequal variances revealed a significant difference for δ^{13}C ($F = 15.07$, df = 7, $P < 0.0001$). However, a test for equal means for δ^{13}C did not reach significance (Welch's ANOVA, $F = 2.09$, df = 7, 26.48, $P = 0.081$).

In contrast to the results for δ^{13}C, there was no significant difference in variance for δ^{15}N (Table 1). A posteriori tests revealed a significant difference in means between regions, with a higher mean value in Chernobyl

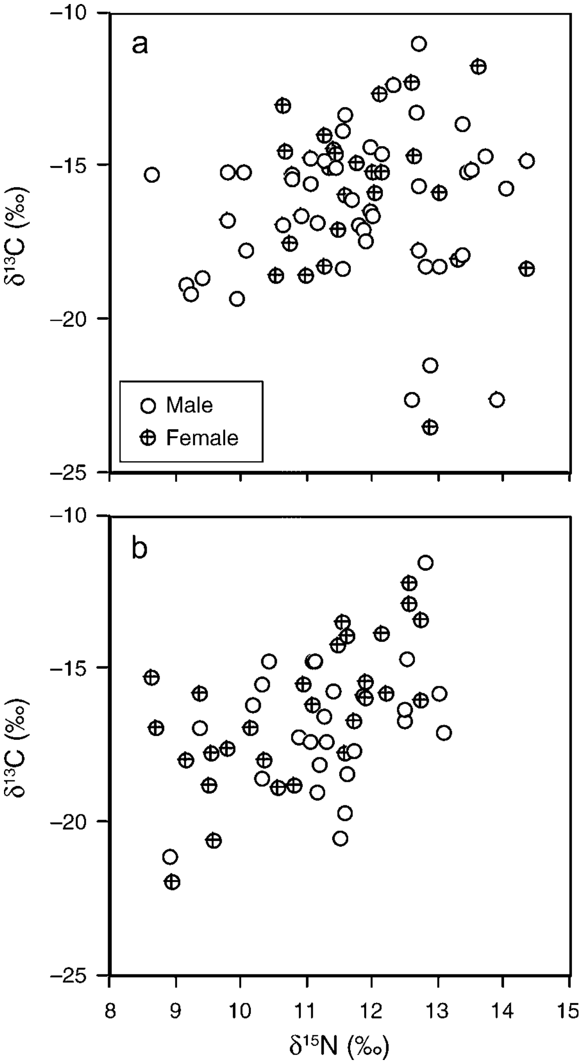

FIG. 3. Values of δ^{13}C in relation to δ^{15}N in feathers from adult male and female Barn Swallows trapped in 2000 from (a) Chernobyl and (b) Kanev.

than in Kanev (Fisher's protected least squares difference test weighted by the sample variances of the group means, $P < 0.001$). Likewise there was a significant difference in means between periods (Fisher's protected least squares difference test, $P < 0.001$), with lower values in the museum samples as compared to the recent samples. The difference between Chernobyl and Kanev differed between periods, with the difference being small in the museum samples, but considerable in the recent field samples (Fisher's protected least squares difference test, $P < 0.001$). In contrast, there was no significant sex difference (Fisher's protected least squares difference test, $P = 0.39$).

When we compared isotopic variances for the two isotopes for each sex between post-1986 samples from Chernobyl and from Kanev, and between post-1986 samples from Chernobyl and pre-1986 samples from both regions (Table 1), there were significantly larger variances in the recent samples from Chernobyl following sequential Bonferroni correction (variance ratio test, males: $F > 9.52$, $P < 0.01$; females: $F > 50.72$, $P < 0.001$). None of the sex differences were significant.

Discussion

The main findings of this study were that (1) correlations between the two isotopes differed significantly between regions for females, but not for males; (2) mean values for δ^{15}N differed between regions and periods; and (3) variances in stable-isotope profiles for δ^{13}C differed between periods for both sexes. These findings were consistent with our initial predictions for a population sink when individuals of the two sexes differ in natal dispersal distances, and this difference in dispersal depended on the recent environmental disaster in Chernobyl. We will briefly discuss each of these findings, and their limitations and implications.

Source–sink patterns of natural populations are a major finding in population biology, because they have important implications for theoretical and applied ecology (Pulliam 1988, Dias 1996, Hanski 1999). It is not straightforward identifying source and sink populations, and a number of different techniques have been proposed to achieve correct identification (Paradis 1995, Dias 1996, Pulliam 1996, Pulliam and Danielson 1991, Stacey et al. 1997). Here we proposed that stable-isotope profiles of feathers from migratory birds may provide information about heterogeneity in breeding populations, and such heterogeneity will reflect the net emigration and immigration rates of different populations. We found evidence consistent with this scenario based on (1) patterns of correlations between different isotopes, (2) temporal and spatial patterns of variation in isotope profiles, and (3) differences in variances in isotope profiles.

We found evidence of weak positive correlations between the two isotopes in three of four sex and region categories, and one of these correlations reached statistical significance. There were statistically significant differences in the strength of these correlations for females, but not for males, implying that the patterns of correlation between feather δ^{13}C and δ^{15}N values differed between Chernobyl and Kanev for females. The significantly stronger correlation among females from Kanev as compared to Chernobyl is consistent with the prediction that females from Kanev come from a smaller recruitment area than the females from Chernobyl, while there is no evidence of males from the two regions differing in the relationship between δ^{13}C and δ^{15}N. How does emigration and immigration and, hence, differences in migration and wintering areas among individuals, affect such correlations? If a sample of individuals with a greater dispersal distance molt their feathers in a larger wintering area (as observed in Palearctic Barn Swallow populations; R. Ambrosini, A. P. Møller, and N. Saino, *unpublished manuscript*), then stable-isotope variance will also be greater in that sample. If these birds then immigrate into a breeding population, we would predict that the isotopic variance of the breeding population would increase. Previous isotopic studies led to the expectation that $\delta^{13}C$ and $\delta^{15}N$ values within food webs are positively correlated (Kelly 2000). A previous study of adult Barn Swallows breeding in Northern Denmark did not reveal significant positive correlations between feather $\delta^{13}C$ and $\delta^{15}N$ values (males: $r = 0.10$, $t = 0.82$, df = 71, $P = 0.42$; females: $r = -0.05$, $t = 0.52$, df = 94, $P = 0.60$; Møller and Hobson 2004). However, this absence of a positive correlation depended on this Danish sample of breeding Barn Swallows having a highly heterogeneous isotope profile, presumably because at least two and likely three different populations with different winter quarters or winter habitats bred in the same area. When we reanalyzed this data set by excluding the small number of individuals with extreme isotope profiles, which caused bimodality in the distributions, we found a significant positive correlation for both sexes (males, $r = 0.36$, $t = 3.15$, df = 66, $P = 0.003$; females, $r = 0.22$, $t = 2.08$, df = 82, $P = 0.04$), as in the samples from Kanev in Ukraine. Therefore, weak positive correlations within "isotopic populations" seem to be common, with the exception of females from Chernobyl, which clearly differed from females from Kanev and from the homogeneous sample from Denmark. When extreme isotope profiles were included in the samples from Denmark, correlations also became weak and nonsignificant. This suggests that, when birds originating from other populations become admixed in a homogeneous sample of individuals, the positive correlation between $\delta^{13}C$ and $\delta^{15}N$ disappears. Such decoupling of the two isotopes has similarly been evoked as evidence for different ultimate sources of nutrition to omnivores (Hobson et al. 2000), but for an aerial insectivore like the Barn Swallow, such a mechanism is not expected.

We found differences in feather $\delta^{15}N$ values between regions and periods. Comparison of means from the different regions, periods, and sexes revealed a difference between Chernobyl and Kanev, between pre- and post-1986 samples, and a larger difference between Chernobyl and Kanev in post-1986 than in pre-1986 samples (Table 1). These findings are consistent with the prediction of a larger recruitment area for Barn Swallows breeding in the population sink in Chernobyl. They are also consistent with the expectation that no such effect should be visible prior to the nuclear disaster in 1986. That we did not see similar differences in mean $\delta^{13}C$ values is not necessarily surprising, because isotopic distributions across landscapes can be driven by different processes. For example, in addition to climatic factors, food web $\delta^{15}N$ values appear to be influenced more than $\delta^{13}C$ values by land-use practices (Rubenstein and Hobson 2004). Such difference between food web $\delta^{13}C$ and $\delta^{15}N$ values underlines the advantage of using more than one isotope in resolving structure within populations (e.g., Pain et al. 2004, Yohannes et al. 2005).

Variances in feather $\delta^{13}C$ values differed between regions, periods, and sexes. Both males and, in particular, females differed significantly between Chernobyl and Kanev in the post-1986 samples. Likewise, variances were larger in post-1986 samples from Chernobyl compared to pre-1986 samples from either region. Some of our samples of museum specimens were small, despite the Barn Swallows being one of the most common breeding bird species in Ukraine. Obviously, results based on such small samples should be interpreted with caution. Long-term studies of isotope profiles in swallow food webs have not been conducted at potential wintering sites in Africa. Such changes may be significant in areas of variable climate (Koch et al. 1995). In other areas, fish have shown constant carbon isotope contents over decades (Begg and Weidman 2001, Jamieson et al. 2004), and long-term stability in stable-isotope ratios has been demonstrated in tree-ring data spanning hundreds of years (see data and references in McCarroll and Loader 2004), showing that temporal change in isotope composition of food webs is not ubiquitous. There were no differences in variances for $\delta^{15}N$ values, which did show weak sex- and period-specific variation between the two regions, but no interaction effects. The findings for $\delta^{13}C$ values are consistent with our a priori predictions about differences in variances in isotope contents related to source–sink dynamics of the Barn Swallows in Ukraine. Variances may differ among samples for reasons other than a higher degree of admixture of individuals from different populations. For example, Pain et al. (2004) suggested that differences in variances in feather $\delta^{13}C$ values among populations of migratory birds wintering in Africa could be due to the degree of isotopic heterogeneity within molting areas, although they did not provide any empirical evidence to support this suggestion. More recently, E. Yohannes and K. A. Hobson (*unpublished manuscript*) determined low isotopic ($\delta^{13}C$, $\delta^{15}N$, δD) variance among years for nine species of Palearctic migrants molting at sites in sub-Saharan Africa. We find the explanation of isotopic heterogeneity proposed by Pain et al. (2004) unlikely for the Barn Swallow, given that such heterogeneity within different molting areas should match the spatial and temporal patterns of variation recorded. Without any evidence for this more complex explanation, application of Occam's razor would suggest that the more simple explanation based on the Chernobyl nuclear disaster is more likely to be the cause of heterogeneity.

Our studies of museum and field samples of isotopes from adult Barn Swallows from Chernobyl and a control region near Kanev in the Ukraine showed evidence consistent with the Barn Swallow sites around Chernobyl having become a sink following the disaster. What are the requirements for isotopes providing information that would allow identification of population sinks without providing false positives? Clearly, the relative abundance of stable isotopes must vary at a scale that allows identification of heterogeneous samples. If different populations of breeding birds were fully admixed during the period when feathers are molted and had identical foraging ecology, there would be little or no heterogeneity in isotope profiles among samples. Hence, it seems important that stable isotopes or other markers should show variation at a geographical scale similar to that at which population processes (such as local recruitment, emigration, and immigration) that affect local population size are acting (Hobson 2005). This is not trivial, since we found evidence consistent with source–sink dynamics for variances in Barn Swallow $\delta^{13}C$, but not for variances in $\delta^{15}N$ values. We suggest that this difference between $\delta^{13}C$ and $\delta^{15}N$ values may arise from differences in spatial distribution of stable-isotope ratios in the environment where feathers are grown.

In conclusion, we found evidence of isotope profiles and, in particular, variances in isotope profiles differing between areas and sexes in a way that is consistent with the Chernobyl region having become a sink following the nuclear disaster. In particular, we found evidence of sex differences in isotope profiles that are consistent with known sex differences in dispersal distances, but also with expected sex differences in dispersal between source and sink populations. These findings emphasize that stable-isotope profiles can provide powerful tools that can be helpful in analyzing population processes, when carefully considering temporal and spatial controls and the natural history of the study organism.

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