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Where do winter crows go? Characterizing partial migration of American Crows with satellite telemetry, stable isotopes, and molecular markers

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RESEARCH ARTICLE

Where do winter crows go? Characterizing partial migration of American Crows with satellite telemetry, stable isotopes, and molecular markers

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ABSTRACT

Partial migration—a strategy in which some individuals are resident and others are migratory within the same population—is widespread among avian species and could play an important transitional role in the evolution of migratory behavior. Nevertheless, detailed movement data are unavailable for most partial migrant species. We examined migration strategies of the American Crow (*Corvus brachyrhynchos*), a partially migratory species that overwinters in large communal roosts, from which some birds migrate north to breed. We used a combination of satellite telemetry, isotopic signatures (δ^2H), and molecular markers (33 microsatellites) to describe and characterize the migratory movements of individuals from overwintering roosts on the east coast (Utica, New York) and west coast (Davis, California) of the United States. We collected 11,951 data points from 18 satellite-tagged individuals between 2014 and 2018, among which 14 (77.8%) were migratory (8 of 11 and 6 of 7 birds on the west and east coasts, respectively). Migration distances were 280–1,095 km and 177–793 km on the west and east coasts, respectively. Individual birds were consistent in their migratory behavior across years, and breeding-site fidelity was high: both migratory and resident birds returned to the same location in the breeding season of each year. Both isotopic signatures and molecular markers could generally differentiate residents from long-distance migrants (i.e. those breeding at latitudes >3.5°N of the resident populations), but they did not consistently differentiate residents from migrants with shorter migration distances. Overall, these data on the migratory movements of American Crows and the proportion of migrants in their roosts can serve as a baseline against which to test predictions about how partial migrants will respond to environmental alterations such as climate change and urbanization.

Keywords: Corvus brachyrhynchos, deuterium, isoscapes, microsatellites, mixed migration strategies, urbanization

¿A dónde van los cuervos en invierno? Caracterizando la migración parcial de *Corvus brachyrhynchos* con telemetría satelital, isótopos estables y marcadores moleculares

RESUMEN

La migración parcial—una estrategia en la cual algunos individuos son residentes y otros son migratorios adentro de la misma población—está ampliamente difundida entre las especies de aves y podría jugar un rol transicional importante en la evolución del comportamiento migratorio. Sin embargo, no se cuenta con datos detallados del movimiento de la mayoría de las especies que son migrantes parciales. Aquí, examinamos las estrategias de migración de *Corvus brachyrhynchos*, una especie migratoria parcial que pasa el invierno en grandes dormideros comunitarios, desde los cuales algunas aves migran hacia el norte para reproducirse. Usamos una combinación de telemetría satelital, firmas isotópicas (δ^2H) y marcadores moleculares (33 micro-satélites) para describir y caracterizar los movimientos migratorios de los cuervos desde los dormideros de invierno en la costa este (Utica, Nueva York) y la costa oeste (Davis, California) de los Estados Unidos. Colectamos 11,951 puntos de datos a partir de 18 cuervos seguidos por satélite entre 2014 y 2018, entre los cuales 14 (77.8%) fueron migratorios (8/11 y 6/7 aves en las costas este y oeste, respectivamente). Las distancias de migración fluctuaron entre 280 y 1095 km y entre 177 y 793 km en las costas oeste y este, respectivamente. Las aves individuales fueron consistentes en su comportamiento migratorio a lo largo de los años y la fidelidad al sitio reproductivo fue alta: las aves tanto migratorias como residentes regresaron a la misma ubicación en la estación reproductiva de cada año. Tanto las firmas isotópicas como los marcadores moleculares pudieron por lo general diferenciar a los residentes de los migrantes de larga distancia (i.e., aquellos criando a latitudes >3.5° al norte de las poblaciones residentes), pero no diferenciaron de modo consistente a los residentes de los migrantes con distancias migratorias más cortas. En general, estos datos de los movimientos migratorios de *C. brachyrhynchos* y la proporción de migrantes en sus dormideros pueden servir como línea de base contra la cual evaluar las predicciones sobre cómo los migrantes parciales responderán a las alteraciones ambientales, como el cambio climático y la urbanización.

INTRODUCTION

Despite decades of research, the evolution of migration is still largely a mystery. Partial migration—a strategy in which some individuals are resident and others are migratory within the same population—is a central precursor in many of the hypotheses that have been set forth to explain its origin (Berthold 1999, Griswold et al. 2010, Zink 2011), potentially acting as a transitional stage in the evolution of complete migratoriness (Berthold 2001). Although partial migration is widespread across taxa, occurring in fish, mammals, insects, and birds (Shaw 2016), the phenomenon of partial migration is itself understudied and poorly understood (Chapman et al. 2011). Fundamental uncertainties remain, for example, about the extent to which it is a conditional strategy or a fixed trait with a genetic basis (Pulido et al. 1996, Gillis et al. 2008, Velez-Espino et al. 2013) and how environmental change might alter its expression (Nilsson et al. 2006, Chapman et al. 2011). Likewise, little is known about how partial migration might enable species to adapt to novel environments (Pulido 2011, Gilroy et al. 2016) or about the role of partial migration in disease transport (Daszak et al. 2001, Reed et al. 2003, Takekawa et al. 2010, Muzaffar et al. 2012, Bengtsson et al. 2016). Acquisition of movement data (e.g., routes, consistency, distance traveled) from partially migratory species, preferably from multiple populations (Chapman et al. 2011), is essential to understanding the evolution and implications of partial migration. We still lack detailed information about individual movements in many partial migrant species, however, despite rapid advances in tracking technology (Runge et al. 2014, Gilroy et al. 2016).

Here, we describe the migratory movements of the American Crow (*Corvus brachyrhynchos*; hereafter "crow"), a partial migrant that overwinters in populations comprising both year-round residents and migratory individuals that depart in spring to breed (Verbeek and Caffrey 2002, Ward and Raim 2011). In winter, crows aggregate in large nocturnal roosts (sometimes >10,000 birds; Hinton et al. 2015), often in areas of high human density and activity (Gorenzel and Salmon 1995, Hinton et al. 2015, Taff et al. 2016). Crows are of particular concern with respect to disease transmission because they are common urban and suburban birds in North America (McGowan 2001) that can harbor numerous pathogens important to humans, domestic animals, and wildlife, including West Nile virus (Wheeler et al. 2014, Hinton et al. 2015), *Campylobacter jejuni* (Weis et al. 2016, Taff and Townsend 2017), and other pathogens (Miller et al. 2010, Halová et al. 2014,

Freund et al. 2016, Jamborova et al. 2017, Townsend et al. 2018).

Despite their conspicuous abundance in North America, their striking migration patterns and winter social behavior, and their potential relevance as disease vectors, published data on the migratory behavior of crows are limited. Spring and fall migratory movements have been reported in many parts of the range of both of the recognized northern subspecies (*C. b. brachyrhynchos* to the east and *C. b. herperis* to the west), and migration routes have been inferred in some locations through banding data (reviewed in Verbeek and Caffrey 2002). A single previous tracking study (using radio telemetry) described the spring migration of 6 migratory crows from Illinois (*C. b. brachyrhynchos*) to their breeding grounds in Michigan (Ward and Raim 2011). Nothing had been reported, however, about the extent to which migration is a fixed or flexible strategy or about the proportion of migratory birds within their overwinter roosts.

Our study had 2 objectives. First, we described the migratory movements of crows from 2 overwintering populations, one on the east coast (Utica, New York) and the other on the west coast (Davis, California) of the United States. We used satellite telemetry to track migratory routes of individuals, fidelity to breeding and wintering sites, and the extent to which individual birds were consistent in their migratory behavior across years. Second, we compared the efficacy of 2 intrinsic markers (molecular and stable isotope data) as tools to assess the breeding origin of overwintering crows in these large urban roosts. We then used these intrinsic and extrinsic markers to estimate the proportion of migrants at each roost. These data can serve as a baseline against which to test predictions about the responses of partial migrants to environmental change.

METHODS

Satellite Telemetry

We captured crows roosting in large (>7,500 birds) overwintering flocks on the west coast (Davis; 38.53°N, 121.75°W; *C. b. herperis*) and east coast (Utica; 43.09°N, 75.22°W; *C. b. brachyrhynchos*) of the United States. Crows were captured during the winter roosting period (January–March) using a net-launcher or baited drop-in trap. On the west coast, we captured 49 crows in 2014 and 2015; on the east coast, we captured 15 crows in 2016. Captured crows were marked with both a numbered USGS band and a unique color band. We determined age (i.e. second-year or after-second-year) by plumage character-

istics (Pyle 1997). Blood samples ($\sim$75 µL) were preserved in lysis buffer for genetic analysis, and 1 or 2 tail feathers were collected from each bird for isotopic analysis. We applied satellite tags to 11 of these birds in Davis (3 on March 8, 2014; 8 in January–February 2015) and to 7 of the birds in Utica (in February 2016). Satellite tags (12 g Solar PTT-100; Microwave Telemetry, Columbia, MD, USA) were secured by backpack harnesses made from 1.5 mm nylon cord following Taff et al. (2016). The weight of the tags was <3.5% of each bird's body weight (range: 353–470 g). After harnesses were attached, crows were released into an aviary for ≥1 hr to ensure that the harnesses did not impede movement. Crows were released after this holding period. Movements were monitored using the Argos satellite tracking system from time of release until April 23, 2018. Movement data were stored in the online database Movebank (Wikelski and Kays 2017) and analyzed in R 3.3.1 (R Core Team 2016).

Isotopic Analysis

In principle, stable hydrogen isotopes can be used to infer migratory origin because δ^2H in feathers is derived from δ^2H in food and water in the location where the feather was grown (Hobson 1999). In North America, δ^2H in precipitation (δ^2H_p) is generally lower at higher latitudes and elevations (Bowen et al. 2005). Crows undergo their annual postbreeding molt prior to autumn migration (Verbeek and Caffrey 2002, Townsend et al. 2009); therefore, deuterium in feathers (δ^2H_f) collected on the wintering ground reflects δ^2H_p at the breeding location. To assess the proportion of migratory birds in winter roosts, we collected and analyzed δ^2H_f from feathers that we found beneath overwinter roosts from November through February ($n = 93$ and 45 individuals in California and New York, respectively). Feathers were cleaned twice (first with detergent and then with 2:1 chloroform:methanol; Paritte and Kelly 2009), weighed (California: 1.2 ± 0.01 mg; New York: 0.4 ± 0.01 mg), and submitted to the stable isotope facilities of the University of California at Davis (for the west coast feathers) or Cornell University (for the east coast feathers) for isotopic analyses using established keratin standards. Hydrogen isotope values (δ^2H) were reported as the corrected delta value measured against a reference scale (Vienna Standard Mean Ocean Water).

We used δ^2H_f in feathers collected from known-origin birds to validate our origin assignments. Known-origin samples included feathers from satellite-tagged birds with known breeding grounds (including both "known residents" and "known migrants"), passively molted feathers collected in the summer months (June–August) from adult resident crows on their breeding territories ("known residents"), as well as passively molted adult crow feathers collected in summer months at higher latitudes, presumably originating from local breeders in those locations. On

the west coast, known-origin samples included 79 samples collected from "known resident" crows in Davis (38.53°N) in the summers of 2012–2014, and 20 samples from latitudes north of Davis, spanning a latitudinal range of 38.53–48.25°N. These northern samples included 8 satellite-tagged migratory birds with known breeding grounds and 12 passively molted feathers collected in the summer of 2014 along this latitudinal band. On the east coast, known-origin samples included 4 feathers collected from resident crows in Utica (43.09°N) and 5 feathers from our satellite-tagged migratory birds with breeding grounds ranging from 45.8°N to 48.3°N.

We developed a model to predict and analyze δ^2H_p across the range of the crow on the east and west coasts in IsoMAP (http://isomap.org). We selected precipitation isotope ratios from April, May, June, July, and August (the months encompassing the annual crow molt) from 1960 to 2010. We predicted δ^2H_p as a function of elevation, latitude squared, and longitude squared (measured at each isotope monitoring station) with maps spanning known crow migration routes, based on satellite telemetry data. The δ^2H_p isoscapes created for this study are available in Supplemental Material Figure S1 and at http://isomap.org (west coast: longitudinal range −123.3°W to −117.5°W, latitudinal range 38.5°N to 49.5°N, IsoMAP jobkey 66075; east coast: longitudinal range −82.3°W to −66.5°W, latitudinal range 41.4°N to 49.5°N, IsoMAP jobkey 66078).

Isoscapes generated by IsoMAP are based on precipitation isotope ratios, which can scale differently from δ^2H_f. Therefore, we developed sample transfer functions on each coast to rescale δ^2H_f to δ^2H_p (Bowen et al. 2014). Transfer functions were made from a regression of known-origin δ^2H_f values against δ^2H_p values at those origins (estimated in IsoMAP), which we used to rescale the δ^2H_f values for IsoMAP calculations. The west and east coast transfer functions were $\delta^2H_{p(west)} = 31.95 + 0.73*\delta^2H_{f(west)} - 0.03*(\delta^2H_{f(west)} + 83.19)^2$ and $\delta^2H_{p(east)} = -13.55 + 0.39*\delta^2H_{f(east)}$, respectively. We then generated a geographic likelihood assignment surface for each feather in IsoMAP using the "individual assignment" function. Standard deviations for individual assignments were derived from the residuals from the water/feather transfer functions (west coast: 6.3‰; east coast: 3.3‰).

Genetic Analysis

We genotyped birds at a panel of 33 microsatellite loci developed for the American Crow (Tarr and Fleischer 1998, Stenzler and Fitzpatrick 2002, Schoenle et al. 2007, Ernest et al. 2008, Verdugo et al. 2012). Locus characteristics (e.g., alleles per locus, null allele frequencies, and tests of Hardy-Weinberg equilibrium) and polymerase chain reaction conditions are given in Supplemental Material Tables S1 and S2. Mean allelic diversity was 9.8

± 1.2 alleles locus^{-1} (range: 2–39 alleles locus^{-1}), and frequencies of inferred null alleles were <0.1 at all loci (mean null allele frequency: 0.03 ± 0.01). Six of 33 loci deviated significantly from Hardy-Weinberg equilibrium (i.e. homozygosity excess); such departures were consistent with the regular occurrence of inbreeding in these crows (Townsend et al. 2010, A. K. Townsend personal observation). We scored all birds at a minimum of 30 loci; most were scored at the complete panel of 33 loci (mean proportion of loci scored >0.99). We confirmed that all feathers were derived from unique individuals by comparing genotypes and removing duplicates.

We visualized genetic structuring between the resident and migratory populations using STRUCTURE 2.3 (Pritchard et al. 2000). We limited our sample to birds for which we had other lines of evidence indicating resident or migratory status. We specified individuals as probable residents (west coast: $n = 496$ residents; east coast: $n = 40$ residents) when they were sampled during the breeding season or from late-summer roosts (May–August) or when satellite telemetry or resight data indicated year-round residency. We specified individuals as probable migrants (west coast: $n = 38$ migrants; east coast: $n = 33$ migrants) when satellite telemetry data indicated migratory behavior or if their isotopic signatures were ≥10‰ smaller than values observed among probable residents. On the west coast, δ^2H of probable residents ranged from −68.9‰ to −95.5‰ (mean ± SE = −81.5 ± 0.9‰; $n = 65$ residents with corresponding isotopic and genetic data); on the east coast, it ranged from −84.5‰ to −95.2‰ (−89.8 ± 2.6 ‰; $n = 4$ residents with corresponding isotopic and genetic data). We therefore specified individuals as probable migrants when δ^2H values were less than −105‰ (range of values among probable migrants: −107.4‰ to −147.2‰ on the west coast, −105.4‰ to −122.0‰ on the east coast). Additionally, the east coast "probable migrant" sample included 20 passively molted feathers collected from crows in summer months at higher latitudes along their migration route in 2017.

On each coast, we specified probable residents as belonging to "sampling population 1" and probable migrants as belonging to "sampling population 2." We specified a LOCPRIOR model (burn-in = 10,000; MCMC repetitions =100,000; correlated allele frequencies; $K = 2$) using "sampling population" as an informative prior. This modeling framework assists in clustering when genetic structuring is weak: LOCPRIOR models place more prior weight on clustering outcomes that are correlated with these metadata yet do not tend to find structure when it is absent (Hubisz et al. 2009). Data were plotted in the program DISTRUCT (Rosenberg 2004). To facilitate comparisons with other studies, we estimated genetic differentiation (F_{ST}) between residents and probable migrants on each coast using GENEPOP 4.2. We did not attempt to determine the number of source populations using STRUCTURE because it estimates population number based on deviations from Hardy-Weinberg equilibrium (HWE) among populations. In this system, deviations from HWE occur within populations (Supplemental Material Table S1), violating the assumptions of that analysis.

We characterized winter crows as migrants or residents using the program ONCOR (Anderson et al. 2008), which performs assignment tests and leave-one-out cross-validation analysis. To evaluate the performance of assignment tests, we first limited our baseline sample to the same putative migrants and residents from STRUCTURE analyses, specifying probable population of origin (resident or migratory) for each individual. We then ran the leave-one-out test, which removes each individual sequentially from the baseline population, estimates its origin, and records the fraction of correct classifications. To estimate the proportion of migratory birds at the winter roosts, we then performed assignment tests on all individuals sampled in winter. Assignment tests classify individuals to the baseline population (resident or migratory) that would have the highest probability of producing that genotype. The baseline file, again, was limited to birds of known origin.

RESULTS

Satellite Telemetry
We collected a total of 11,951 data points from 18 tagged crows (6,968 and 4,983 points from the west and east coasts, respectively). Tag transmission duration ranged from 54 to 1,305 days (mean = 388.8 ± 78.7 days [SE]). In total, 14 of the 18 satellite-tagged birds (77.8%) were migratory (8 of 11 and 6 of 7 birds on the west and east coasts, respectively). All resident birds remained within 25 km of the center of their breeding-season territory in all months of the year (Figure 1). Among the migratory birds, migration distance ranged from 280 to 1,095 km (mean = 589.3 ± 101.8 km) on the west coast and from 177 to 793 km (mean = 461.7 ± 81.3 km) on the east coast, corresponding to breeding latitudes ranging from 40.4°N to 48.3°N (mean = 43.6 ± 0.9°N) on the west coast and from 44.4°N to 48.4°N (mean = 46.3 ± 0.5°N) on the east coast. First recorded fall migratory movements of 13 of the 14 migrants are shown in Figure 2. After arrival at their breeding grounds (during March 26–April 8), all migrants remained within 25 km of the center of their territory for the entire breeding season (i.e. until at least September of that year).

Multiple breeding seasons (April–August) were tracked for 7 birds (2 breeding seasons for 4 birds; 3 breeding
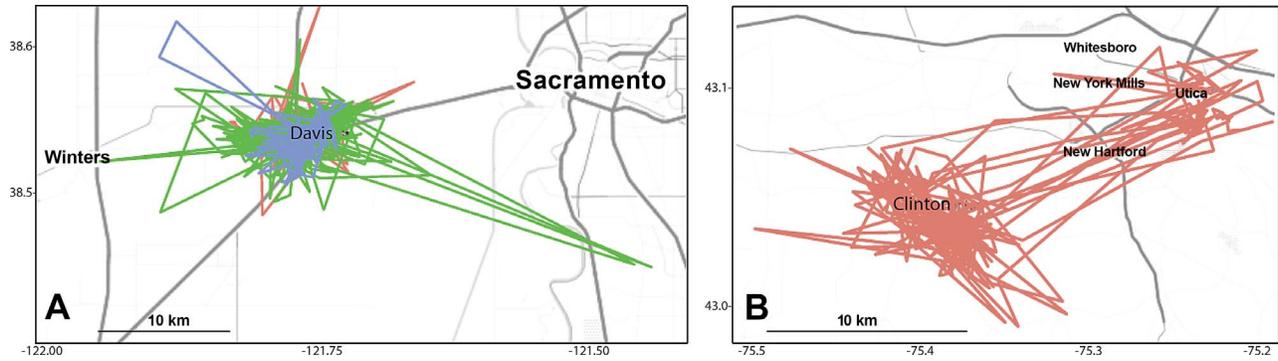
FIGURE 1. All recorded movements of (**A**) 3 satellite-tagged resident American Crows in Davis, California, and (**B**) 1 resident in Utica, New York, USA, over the duration of the study. Colors indicate different individuals. Data were recorded for each bird over a 12–42 mo period.

seasons for 2 birds; and 4 breeding seasons for a single bird). Two of these birds were residents and 5 were migratory. Breeding-site fidelity was high: migrants and residents returned to the same locations in the breeding season across years. In 2016, however, one migrant, a second-year pre-breeder, wandered for 78 days during its northward migration before settling down at one site for the remainder of the breeding season. In 2017, it returned to the same breeding site via a much more direct route (Supplemental Material Figure S2).

Data from multiple winter seasons (November–February) were collected from 5 birds (2 winters from 4 migrants; 4 winters from 1 resident). The resident bird remained in the same geographic area (within 25 km of the center of its breeding-season territory) in all months of the year for 4 breeding and overwintering seasons. Data transmission for migratory birds was very low during the second winter ($n = 3, 6, 21,$ and 36 transmissions). These transmissions showed that 2 of the 4 birds moved from site to site (some sites >300 km apart) during winter, and that 3 of the 4 birds spent at least part of the winter within 0–60 km and at the same latitudinal band (43.03–43.09°N) as their initial trapping site. For one bird, all winter transmissions ($n = 36$ transmissions) indicated that it did not return to its winter capture site in Utica but overwintered 260 km north in an entirely different location in the second winter (Ottawa, Ontario, Canada; 45.42°N, 75.69°W).
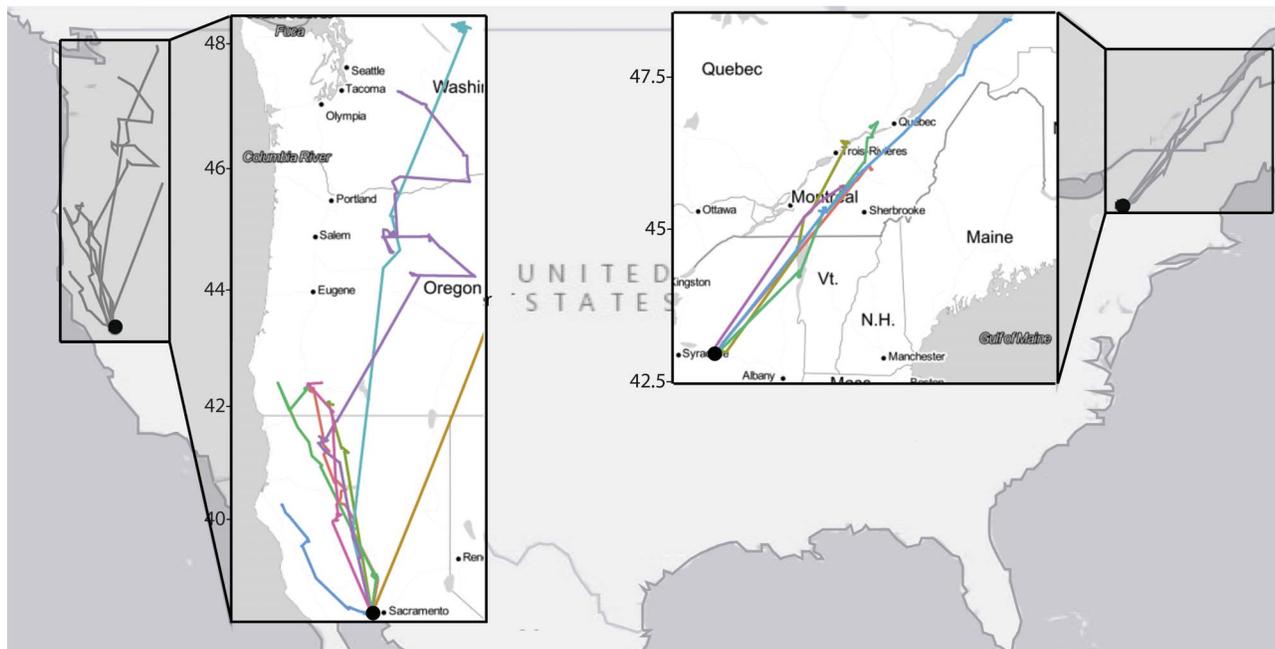
FIGURE 2. First recorded fall migratory movements of 8 satellite-tagged American Crows on the west coast and 5 on the east coast of North America. Colors indicate different individuals.
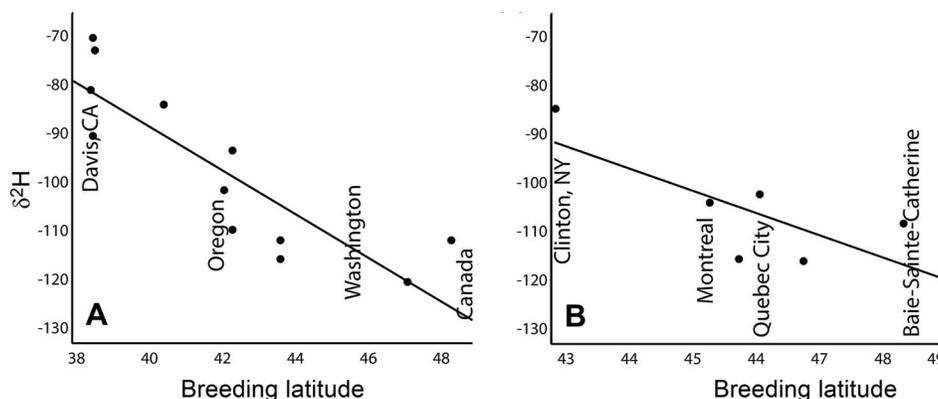
FIGURE 3. Feather deuterium levels were negatively correlated with breeding latitude among known-origin, satellite-tagged American Crows on the (**A**) west coast ($\delta^2H_f = -4.47 *$ latitude $+ 91.1$; $t_{10} = -5.4$; $P = 0.0003$; $r^2 = 0.47$) and (**B**) east coast ($\delta^2H_f = -4.69 *$ latitude $+ 110.5$; $t_7 = -3.8$; $P = 0.007$; $r^2 = 0.67$) of North America.

Isotopic Analysis

Feather isotope ratios (δ^2H_f) were negatively correlated with latitude on both coasts (Figure 3). On the west coast, IsoMAP indicated a strong isotopic difference in δ^2H_p between the Sacramento Valley (which encompassed the resident population of Davis) and areas north of the valley; however, no clear gradient in δ^2H_p with latitude was otherwise apparent (Figure S1A). We therefore simply classified birds as "possible residents" when their likely origin included the Sacramento Valley (including Davis), or as "probable migrants" when their likely origin did not include Sacramento Valley. We quantified assignments for each individual by comparing their average likelihood surface within the Sacramento Valley at the latitude of Davis (38.53°N; longitude −121°W to −122°W) to the distribution of all likelihood values on the range map. If the assignment likelihood of an individual to Davis was greater than the mean likelihood value for all regions on the range map, that individual was considered a "possible resident."

This classification method discriminated residents from most migrants with relatively long migration distances. When we limited the sample to birds of known origin, all resident birds ($n = 79$; 38.53°N latitude) and all birds with breeding origins <2.5°N of the resident population ($n = 13$; 39°N to 40.94°N) were classified as "possible residents." Among known migrants breeding at higher latitudes (42.39°N to 48.25°N), 5 of 6 (83.3%) were classified as "probable migrants."

On the east coast, IsoMAP indicated that δ^2H_p levels generally decreased with increasing latitude within the range of satellite-tagged crows; moreover, δ^2H_p values in the Mohawk Valley (including the resident Utica population) were distinctly elevated in comparison with most northern latitudes (Figure S1B). We therefore classified birds as "possible residents" when their likely origin included Utica and as "probable migrants" when their likely origin did not include Utica. We quantified assignments for each individual by comparing their average likelihood surface within the Mohawk Valley at the latitude of Utica (latitude 43.09°N, longitude −75.1°W to −76.1°W) to the distribution of all likelihood values on the range map. As before, an individual was considered a "possible resident" if the assignment likelihood of an individual to Utica was greater than its mean likelihood value for all points on the range map. When we limited the sample to birds of known origin, all resident birds ($n = 4$; 43.09°N latitude) were classified correctly. Four of 5 known migrants originating from higher latitudes (45.80°N to 48.38°N) were classified as a "probable migrant" and the other one (breeding latitude 46.13°N) was misclassified as a "possible resident."

Winter birds for which δ^2H_f values were available included 93 and 45 individuals sampled near the winter roosts on the west and east coast, respectively. On the west coast, likelihood surfaces within IsoMAP indicated that ≥26 of 93 winter birds (28.0%) were probable migrants; on the east coast, ≥12 of 45 winter birds (26.7%) were probable migrants.

Genetic Analysis

Overall genetic differentiation between residents and putative migrants was low. Pairwise F_{ST} values between putative residents and migrants were 0.026 and 0.012 on the west and east coasts, respectively. Despite low differentiation, clear genetic distinctions between migrants and residents (Figure 4) were apparent in the program STRUCTURE using the LOCPRIOR modeling framework. On the west coast, leave-one-out cross-validation analysis in ONCOR indicated that the likelihood of assignment of known-origin birds to the correct population (resident or migrant population), based solely on molecular markers, was very high: 99% of putative residents were correctly assigned to the "resident" cluster, and 95% of putative migrants were correctly assigned to the migrant cluster.
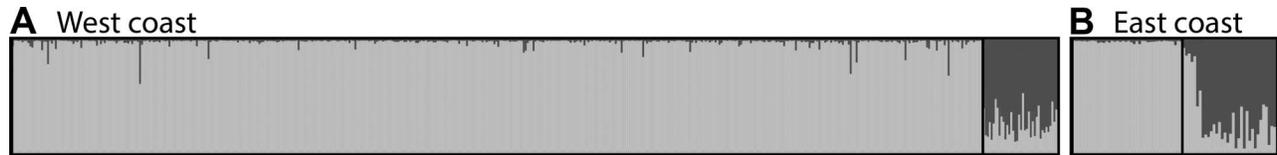
FIGURE 4. Membership coefficients ($\hat{Q}$) of each individual American Crow to a given cluster (left cluster: known residents; right cluster: probable migrants). (**A**) On the west coast, 484 of 496 (97.6%) putative residents had a high probability ($\hat{Q} > 0.9$) of membership in the "resident" cluster, and none of the 38 probable migrants were assigned to the resident cluster with probability >0.53 (mean $\hat{Q}$ of putative migrants to the resident cluster = 0.25 ± 0.01). (**B**) On the east coast, all putative residents had a high probability of membership in the "resident" cluster ($\hat{Q} \geq 0.94$), and only 1 of 34 putative migrants was assigned to the resident cluster with probability ≥0.9 ($\hat{Q} \geq 0.925$).

On the east coast, likelihood of correct assignment was lower, but still fairly high: 84% of putative residents were correctly assigned to the "resident" cluster, and 76% of putative migrants were correctly assigned to the "migrant" cluster. East coast resolution improved when we restricted our sample to residents vs. relatively long-distance migrants. After removing 4 birds that bred within 2°N of the resident population, 92% of putative residents were correctly assigned to the "resident" cluster, and 81% of putative migrants were correctly assigned to the migrant cluster.

We then ran assignment tests in ONCOR to estimate the proportion of winter birds that were migratory. These samples included 89 and 53 individuals sampled near the winter roosts of the west and east coast, respectively. On the west coast, ONCOR assigned 51.7% (46 of 89) of birds to the "resident" category with probability >0.96 (mean probability of membership in resident group = 0.99 ± 0.00; $n = 46$ birds); the other 48.3% of birds were classified to the migrant group with probabilities ranging from 0.2 to 1.0 (mean probability of membership in migrant group = 0.91 ± 0.04; $n = 43$ birds). On the east coast, ONCOR assigned 33.9% (18 of 53) of winter birds to the "resident" category with probability >0.91 (mean probability of membership in resident group = 0.98 ± 0.01; $n = 18$ birds); the other 66.0% of birds were classified in the migrant group with probabilities ranging from 0.2 to 1.0 (mean probability of membership in migrant group = 0.87 ± 0.05; $n = 35$ birds).

Comparison of Methods

The percentages of birds classified as migratory by each method are summarized in Table 1. More than one type of data (telemetry, molecular, or isotopic) was available for different subsets of winter-caught birds. On the west coast, both molecular and isotopic data were available from 89 winter birds; 11 of these were satellite-tagged. Overall congruence between classifications by molecular and isotopic data was 80.1% (72 of 89 samples). Almost all birds classified as residents in ONCOR (46 of 47 birds) were also classified as residents in IsoMAP, a result consistent with available telemetry data ($n = 3$ confirmed residents).

Twenty-five birds were identified as migrants by both ONCOR and IsoMAP, again consistent with telemetry data ($n = 5$ confirmed migrants; all breeding at latitudes 3.84–9.7°N of the resident population). Seventeen birds were classified as migratory in ONCOR but resident in IsoMAP. The telemetry data in this subset ($n = 3$ confirmed migrants) indicated that this group included migrants with short or intermediate migration distances (breeding 1.9–3.9°N of the resident population). On the east coast, both molecular and isotopic data were available from 42 winter birds; 6 of these were satellite-tagged. Here, congruence between classifications by molecular and isotopic data was 64.3% (27 of 42 samples). Again, almost all birds classified as residents in ONCOR (16 of 17 putative residents) were also classified as residents in IsoMAP, a result consistent with available telemetry data ($n = 1$ confirmed resident). Eleven birds were identified as migrant by both ONCOR and IsoMAP, again consistent with telemetry data ($n = 4$ confirmed migrants; all breeding at latitudes 2.8–5.3°N of the resident population). Fourteen birds were classified as migratory in ONCOR but resident in IsoMAP. Telemetry data in this subset ($n = 1$ bird) indicated that this group included a migrant with an intermediate migration distance (breeding 3.1°N of the resident population).

Considered in concert, these data suggest that both intrinsic markers usually were successful at discerning long-distance migrants (i.e. those breeding at latitudes >3.5°N of the resident populations) from residents but did not always distinguish residents from relatively short-distance migrants. Isotopic signatures were more likely than molecular markers to misclassify short-distance migrants as residents on both coasts.

TABLE 1. Percentages of American Crows in overwintering roosts classified as migratory by satellite telemetry, microsatellite markers, and stable isotopes (deuterium). Proportions are shown in parentheses. West coast = roost in Davis, California, USA; east coast = roost in Utica, New York, USA.

Coast	Telemetry	Microsatellites	Isotopes
West	72.7% (8/11)	48.3% (43/89)	28.0% (26/93)
East	85.7% (6/7)	66.0% (35/53)	26.7% (12/45)

DISCUSSION

We used satellite telemetry to track the partial migratory behavior of birds from 2 overwinter roosts of the northern subspecies of the American Crow. We then compared tracking data with characterizations based on molecular markers and isotopic signatures and estimated the proportion of migratory birds in the overwinter roosts. Tracking data indicated that 73% of tagged crows (8 of 11) in our western population (*C. b. herperis*) and 86% of tagged crows (6 of 7) in our eastern population (*C. b. brachyrhynchos*) migrated north for the breeding season (Figures 1 and 2), with mean migration distances of 589 km (range: 280–1,095 km) and 462 km (range: 177–793 km) on the west and east coasts, respectively. These data were consistent with published band recovery data, showing that some crows in these subspecies move between the southern provinces of Canada and the contiguous United States (longest recorded migration distance >2,800 km; Brewer et al. 2000) or make shorter migratory movements within the contiguous United States (reviewed in Verbeek and Caffrey 2002). The short-distance migratory distances that we observed were similar to those reported in a single previous tracking study of crows (based on radio telemetry data), documenting spring migratory movements of 6 migratory crows (*C. b. brachyrhynchos*), during which birds traveled an average of 571 km (range: 382–725 km) from Illinois to Michigan (Ward and Raim 2011). Our study was the first, however, to estimate the proportion of migratory birds in overwintering roosts, to track breeding- and winter-site fidelity of migrants, and to examine consistency in migratory behavior of individuals across years.

Partial migration may play an important role in the evolution of complete migration (Berthold 1999, Griswold et al. 2010, Zink 2011), the local persistence and long-distance spread of disease (Reed et al. 2003, Takekawa et al. 2010, Muzaffar et al. 2012), and population responses to environmental change (Gilroy et al. 2016), yet fundamental questions remain about the extent to which it is a plastic or fixed trait (Pulido et al. 1996, Gillis et al. 2008, Velez-Espino et al. 2013). We found no evidence that migration in crows was a facultative strategy. All satellite-tagged birds for which we had multiple years of data were consistent in their migratory behavior (migratory or resident) from year to year, and all were faithful to their breeding territories across years. We note, however, that the sample size of birds for which we had multiple years of data was small (5 migrants, 3 residents), limiting the scope of the inferences that we can draw.

Better understanding the degree to which birds can conditionally adjust their migratory behavior is particularly urgent as we seek to predict the responses of partial migrants to climate change. Recent work suggests that partial migration might buffer some species against a warming climate, although taxon-specific data on the effects of climate change on partial migration are scarce and the mechanisms underlying this pattern are unclear (Gilroy et al. 2016). It is possible, for example, that the proportion of sedentary birds in some partially migratory populations will increase as milder winters permit them to remain on their breeding grounds year-round (Berthold 1999), although empirical data are scarce and do not provide strong support for this prediction (Nilsson et al. 2006, Meller et al. 2016). Another possibility is that they may have the ability to shorten their migration distances by overwintering at higher latitudes in warmer years. Our tracking data—although sparse across winters—indicated that migratory crows were flexible with respect to their overwintering sites, moving among sites across and within winter seasons. Therefore, even if individual crows do not completely switch between migratory and sedentary behavior, they might be able to conditionally adjust the distance that they travel to their overwinter roosts in response to temperature.

Urbanization is another environmental alteration that could influence the behavior of partial migrants. Crows are a particularly valuable system for urban ecology studies because they often exploit urban areas for their overwinter roosts (Gorenzel and Salmon 1995, Hinton et al. 2015, Taff et al. 2016) and breeding territories (McGowan 2001). Some studies have found that urbanization is associated with increased sedentariness among partially migratory species (Adriaensen and Dhondt 1990, Partecke and Gwinner 2007, Evans et al. 2012), an effect that may be due, in part, to the milder winters of the urban "heat island" (Partecke and Gwinner 2007, Evans et al. 2012). If these patterns hold true for crows, we might expect them to exhibit increasing sedentariness in urban areas, or to shorten their southward migration distances and exploit urban overwinter sites at higher latitudes, in tempo with increasing temperatures.

The second major aim of this study was to evaluate the efficacy of intrinsic markers (isotopic and molecular signatures) as tools to characterize migratory propensity. In contrast with satellite tags, which are costly and are too heavy for many passerine species (Wikelski et al. 2007), intrinsic markers are relatively cost-effective, noninvasive, and easy to collect but can have coarse spatial resolution (Bowen et al. 2005, Ruegg et al. 2017). Using subsets of these markers in combination can improve the efficacy and resolution of origin assignment (Van Wilgenburg and Hobson 2011, Vander Zanden et al. 2015, Ruegg et al. 2017). In the present study, molecular markers indicated that ≥48% of birds on the west coast and ≥66% of birds on the east coast were migratory, whereas isotopic signatures identified only 28% of western birds and 27% of eastern birds as migrants. Comparison of these characterizations with actual origins of known-origin birds indicated that

both isotopic and molecular signatures were generally successful in distinguishing residents from migrants with relatively long migration distances (i.e. those breeding at latitudes >3.5°N of the resident populations) but sometimes failed to distinguish residents from migrants with shorter migration distances. This limitation was more pronounced for characterization based solely on isotopic signatures. Considered in concert, our results indicate that—when telemetry data are not feasible to collect—genetic tools are a better option than isotopic signatures to identify long-distance migrants in crows. However, extreme isotopic values (as observed among long-distance migrants) would be useful to strengthen the certainty of assignment and could be used as priors in analyses of population structure. Similar conclusions were drawn in a study using genetic and isotopic markers to characterize migration in Wilson's Warblers (*Cardellina pusilla*; Ruegg et al. 2017).

Here, we compared migratory characterization results based on separate analyses of each data type (tracking, molecular, and isotopic data). Collection and comparison of more than one data type is become increasing common in migration studies (Cunjak et al. 2005, Boulet et al. 2006, Procházka et al. 2017), and some of these studies have begun to integrate 2 or more data types into a single analysis (e.g., band recovery and isotopic data [Van Wilgenburg and Hobson 2011]; band recovery, geolocator data, and other covariates [Procházka et al. 2017]; mark–resight and tracking data [Korner-Nievergelt et al. 2017]; isotopic, environmental, and molecular data [Ruegg et al. 2017]). Although, in some systems, specific data types (e.g., molecular markers) can perform nearly as well as integrated data types in population assignment (Ruegg et al. 2017), an integrated approach could reduce potential bias inherent in the collection of the individual data types and add detail and precision to migrant–resident characterizations (Robinson et al. 2010, Van Wilgenburg and Hobson 2011, Korner-Nievergelt et al. 2017, Ruegg et al. 2017). Ultimately, the development of a modeling framework that integrates the data types used in our study (satellite telemetry, microsatellites, and isotopes) would be a valuable tool for the migratory characterization of crows and other species for which this combination of data is available.

In summary, the data presented here on the migratory movements of American Crows in 2 of their northern subspecies, and the characterization of the proportion of migrants in 2 overwinter roosts, can serve as a baseline against which to test predictions about changes in migratory behavior with climate and urbanization. Observing the extent to which the expression of partial migration in crows matches theoretical expectations will allow us to better predict how environmental changes might affect other species of partially migratory passerines, the majority of which are, at present, too small to permit satellite tracking (Bridge et al. 2011) and for which migratory movements have not yet been elucidated (Runge et al. 2014, Gilroy et al. 2016).

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