



RESEARCH ARTICLE

Wintering ecology of sympatric subspecies of Sandhill Crane: Correlations between body size, site fidelity, and movement patterns

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ABSTRACT

Body size is known to correlate with many aspects of life history in birds, and this knowledge can be used to manage and conserve bird species. However, few studies have compared the wintering ecology of sympatric subspecies that vary significantly in body size. We used radiotelemetry to examine the relationship between body size and site fidelity, movements, and home range in 2 subspecies of Sandhill Crane (*Grus canadensis*) wintering in the Sacramento–San Joaquin Delta of California, USA. Both subspecies showed high interannual return rates to the Delta study area, but Greater Sandhill Cranes (*G. c. tabida*) showed stronger within-winter fidelity to landscapes in our study region and to roost complexes within landscapes than did Lesser Sandhill Cranes (*G. c. canadensis*). Foraging flights from roost sites were shorter for *G. c. tabida* than for *G. c. canadensis* (1.9 ± 0.01 km vs. 4.5 ± 0.01 km, respectively) and, consequently, the mean size of 95% fixed-kernel winter home ranges was an order of magnitude smaller for *G. c. tabida* than for *G. c. canadensis* (1.9 ± 0.4 km² vs. 21.9 ± 1.9 km², respectively). Strong site fidelity indicates that conservation planning to manage for adequate food resources around traditional roost sites can be effective for meeting the habitat needs of these cranes, but the scale of conservation efforts should differ by subspecies. Analysis of movement patterns suggests that conservation planners and managers should consider all habitats within 5 km of a known *G. c. tabida* roost and within 10 km of a *G. c. canadensis* roost when planning for habitat management, mitigation, acquisition, and easements.

Keywords: California, conservation planning, *Grus canadensis*, home range, Sacramento–San Joaquin Delta, Sandhill Crane, scale, site fidelity, wintering ecology

Ecología de invernada de subspecies simpátricas de *Grus canadensis*: correlaciones entre tamaño corporal, fidelidad al sitio y patrones de movimiento

RESUMEN

Se sabe que el tamaño corporal se correlaciona con muchos aspectos de la historia de vida de las aves y este conocimiento puede ser usado para manejar y conservar las especies de aves; sin embargo, pocos estudios han comparado la ecología de invernada de subspecies simpátricas que varían significativamente en el tamaño corporal. Empleamos radio telemetría para examinar la relación entre el tamaño corporal y la fidelidad al sitio, los movimientos y el rango de hogar de 2 subspecies de *Grus canadensis* invernando en el Delta de Sacramento–San Joaquin de California. Ambas subspecies mostraron altas tasas de retorno inter anual al área de estudio del Delta, pero *G. c. tabida* mostró una mayor fidelidad intra-invernal a los paisajes en nuestra área de estudio y a los dormideros dentro de los paisajes que *G. c. canadensis*. Los vuelos de forrajeo desde los dormideros fueron más cortos para *G. c. tabida* que para *G. c. canadensis* (1.9 ± 0.01 km vs 4.5 ± 0.01 km, respectivamente) y, consecuentemente, el tamaño medio del rango de hogar invernal con un 95% de kernel fijo fue un orden de magnitud más chico para *G. c. tabida* que para *G. c. canadensis* (1.9 ± 0.4 km² vs. 21.9 ± 1.9 km², respectivamente). La alta fidelidad a los sitios indica que el manejo de los recursos alimenticios adecuados alrededor de los dormideros tradicionales puede ser efectivo para alcanzar las necesidades de hábitat de estas garzas, pero la escala de los esfuerzos de conservación debería diferir entre las subspecies. El análisis de los patrones de movimiento sugiere que los gestores de la conservación deberían considerar a todos los hábitats dentro de los 5 km de un dormidero conocido de *G. c. tabida* y dentro de los 10 km de un dormidero de *G. c. canadensis* cuando planifican el manejo, la mitigación, la adquisición y la servidumbre del hábitat.

Palabras clave: California, Delta de Sacramento–San Joaquin, ecología de invernada, escala, fidelidad al sitio, *Grus canadensis*, planificación de la conservación, rango de hogar

INTRODUCTION

Conservation planning for birds during winter requires estimates of key demographic parameters together with an understanding of habitat needs and movements (e.g., home-range size and site fidelity), which can help define the scale at which conservation and management should be focused (Guisan et al. 2006, Thornton and Fletcher 2014). More generally, scale is of fundamental importance for understanding species–environment associations (Levin 1992), in which scale is often a function of body size (Wiens 1989, Mech and Zollner 2002). Mechanistic explanations for this association are derived from findings that body size influences avian energetics (McNab 2001, 2003), social dominance (Bautista et al. 1995), and predation risk (Götmark and Post 1996). Such factors can influence access to resources and, subsequently, important life-history characteristics like home-range size (Schoener 1968, Haskell et al. 2002, Ottaviani et al. 2006), site fidelity (Mini 2013), and survival (Lindstedt and Calder 1976, Sæther 1989, Martin 1995). Knowledge of home-range size, site fidelity, and movement behavior can elucidate patterns of habitat connectivity and help identify the appropriate geographic scale for conservation planning.

Much of the comparative work related to body size and movement patterns has focused either on interspecific differences (Western and Ssemakula 1982, Olson et al. 2009, Morales-Castilla et al. 2012) or on intraspecific differences in species with considerable sexual size dimorphism (Székely et al. 2000, Krüger 2005). However, some species, such as Sandhill Cranes (*Grus canadensis*), exhibit large variation in body size among subspecies, which should be considered when investigating their ecology and conservation planning. Greater Sandhill Cranes (*G. c. tabida*) and Lesser Sandhill Cranes (*G. c. canadensis*) both breed and winter in western North America but show strong size dimorphism. Greater Sandhill Cranes (hereafter “*tabida*”) are large (mean male body size = 4.9 kg), relatively short-distance migrants (mean breeding latitude 45°N) compared with Lesser Sandhill Cranes (hereafter “*canadensis*”; mean male body size = 3.9 kg; mean breeding latitude 65°N) (Johnson and Stewart 1973). Such subspecific size variation is often associated with geographic segregation in winter, but these subspecies winter sympatrically in the Sacramento–San Joaquin River Delta region of California (hereafter “Delta”), USA, to the extent that birds share winter roost sites and may forage in the same fields. We predicted that the larger-bodied *tabida* would fly shorter distances to forage and therefore have smaller home-range sizes, and also that they would exhibit greater site fidelity, because of their higher energetic cost of flight.

From a conservation perspective, the Delta is an important wintering region for both subspecies (Pacific

Flyway Council 1983, 1997), and this region is under increasing pressure from habitat loss due to urbanization, changes in agricultural practices, and water supply limitations (Ivey 2014) that threaten to compromise its capacity to support cranes during fall and winter.

In the case of Sandhill Cranes, individual birds require a key habitat configuration on wintering areas: suitable night roost habitat surrounded by suitable foraging habitats (Tacha et al. 1994). In the context of refuging and central-place foraging theories (Hamilton and Watt 1970, Orians and Pearson 1979), cranes’ daily activity patterns can be viewed as ≥ 1 round-trip flight from a centrally located roost site to ≥ 1 foraging site. Therefore, conceptually, we can define an “ecosystem unit” for conservation and management of cranes to include a central roost surrounded by a foraging landscape extended to a certain radius.

Little is known about the wintering ecology of cranes that can be used to parameterize models like those described above or define the factors that contribute to variation in winter movement behavior. However, given that the subspecies differ in body size, we predicted that the scale of these important metrics would be smaller for *tabida*, which might lead to different conservation considerations for each subspecies. We used radiotelemetry to study movements of *tabida* and *canadensis* wintering in California to compare how body size was correlated with important life history traits. Specifically, our objectives were to (1) quantify site fidelity at the regional, landscape, and roosting wetland scales; and (2) estimate home-range size and commuting distance during winter. Resulting insights on how movement patterns are related to body size can be applied to conservation planning for cranes.

METHODS

Study Area

The vast majority of Pacific Flyway Sandhill Cranes winter in the Central Valley of California (Pacific Flyway Council 1983, 1997), which extends north to south from the city of Red Bluff to Bakersfield and west to east between the Coast Range and the Sierra Nevada Mountains. Their winter range in the valley is concentrated in 5 discrete regions: the Sacramento Valley, the Delta, the San Joaquin River National Wildlife Refuge (NWR) region, the Merced Grasslands, and the Pixley NWR region (Figure 1, inset). These regions support >95% of the crane use in the valley (G. L. Ivey personal observation). Most of our work was concentrated on the Delta region and was centered on several properties (Staten Island, Cosumnes River Preserve, Isenberg Crane Reserve, and Stone Lakes National Wildlife Refuge) that are managed to provide night roost sites for cranes and consequently support most of the

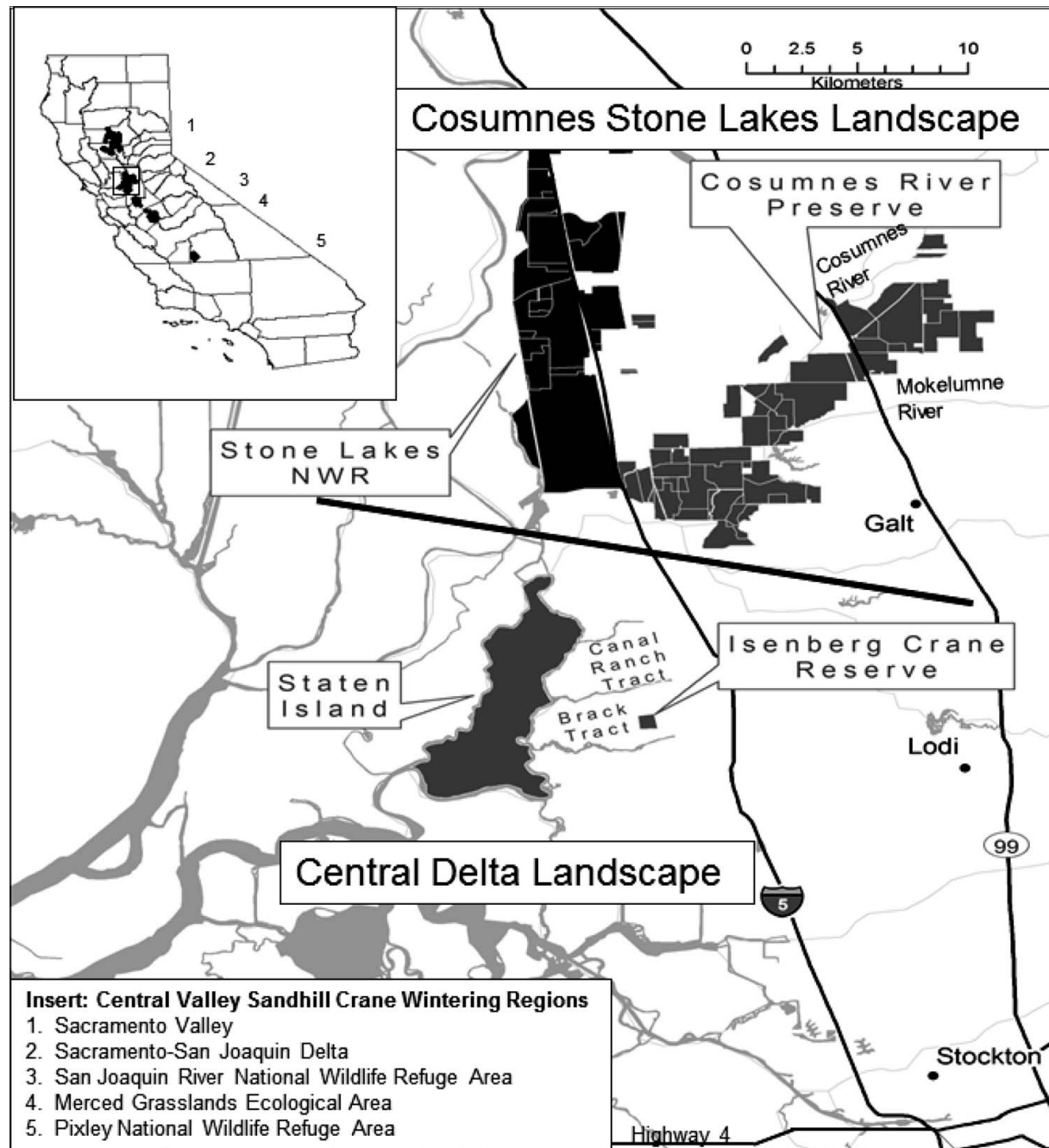


FIGURE 1. Map of the Sacramento–San Joaquin Delta region in California, USA, our primary study area for winter movements of Greater Sandhill Cranes (*Grus canadensis tabida*) and Lesser Sandhill Cranes (*G. c. canadensis*). The Delta region comprises 2 landscapes, which are delineated by the bold line. Key roost-site areas within each landscape are also shown. Inset map illustrates the 5 major wintering regions for cranes within the Central Valley of California; from north to south, these are the Sacramento Valley, Sacramento–San Joaquin Delta, San Joaquin River National Wildlife Refuge, Merced Grasslands, and Pixley National Wildlife Refuge.

cranes that winter in the Delta (Pogson and Lindstedt 1991, U.S. Fish and Wildlife Service 2007; Figure 1). The Delta region is primarily a rural agricultural landscape bordered by urban communities. Agricultural land uses included field and silage corn, fall-planted wheat, rice, alfalfa, irrigated pasture, dairies, vineyards, and orchards. The region also contains large tracts of oak savanna and floodplain wetlands along the Cosumnes and Mokelumne rivers.

We captured cranes primarily at Staten Island and Cosumnes River Preserve. Staten Island (3,725 ha) was a large corporate farm that was purchased by The Nature Conservancy (TNC) and is managed as an income-producing farm, but with a focus on providing habitat

for cranes and other wildlife. The Cosumnes River Preserve (9,915 ha within our study area) was established by TNC and is a conglomeration of lands owned or under conservation easements by TNC, Bureau of Land Management (BLM), Ducks Unlimited, California Department of Fish and Wildlife (CDFW), State Lands Commission, California Department of Water Resources, Sacramento County, and various private owners. This preserve provides habitats for cranes, including seasonal wetland roost sites, oak savannas, organic rice, and other crops. Isenberg Crane Reserve, located on Brack Tract, is owned and managed by CDFW and consists of 2 seasonal wetland roost sites (totaling 60 ha) that are surrounded by rice fields and other private agricultural lands.

We defined 2 landscapes within our Delta study region (Figure 1) that differed in the composition of habitat types available to wintering cranes (U.S. Fish and Wildlife Service 2007, Kleinschmidt Associates 2008). Previous work suggested that these landscapes were far enough apart to be viewed as distinct by *tabida* (G. L. Ivey personal observation). The Cosumnes–Stone Lakes landscape is located in the northern portion of the Delta, which includes the Cosumnes River, Mokelumne River, and Stone Lakes floodplains, and contains a diversity of crane habitats, including large areas of seasonal wetlands and native grasslands and oak savannas. The Central Delta landscape in the east-central portion of the Delta encompasses Staten Island, Isenberg Crane Reserve, and other islands north of Highway 4, which are composed primarily of croplands.

Capture, Radio-tagging, and Tracking

We captured and radio-tagged a total of 33 *tabida* and 44 *canadensis*. All were captured using rocket nets baited with corn (Urbanek et al. 1991) or noose-lines (Hereford et al. 2001). They were captured at Staten Island (6 *tabida* and 7 *canadensis*) and Cosumnes Preserve (27 *tabida* and 21 *canadensis*) between October 17, 2007, and February 27, 2008; on a spring migration staging site (Ladd Marsh Wildlife Management Area) near LaGrande, Oregon, USA, in April 2008 (6 *canadensis*); and on their breeding grounds near Homer, Alaska, USA, in August 2008 (10 *canadensis*). Our sample of *tabida* included 5 pairs, and our sample of *canadensis* included 3 pairs and 2 family groups of 2 adults and 1 first-year juvenile. One adult individual from each of these groups was selected randomly to be included in our analyses. Also, 1 *tabida* and 1 *canadensis* that died shortly after capture, and 4 of the *canadensis* marked in the Delta that were not located during the second season, were excluded from our analyses. These factors reduced our effective sample size ($n = 27$ *tabida* and $n = 32$ *canadensis* [17 from our study area]).

For each crane captured, we determined subspecies on the basis of morphological measurements (Johnson and Stewart 1973). We marked each individual with a U.S. Geological Survey aluminum leg band and a unique combination of color bands. For birds captured in California and Oregon, we attached a very high frequency (VHF) transmitter (model AVL6171; Sirtrack, Havelock North, New Zealand) that was mounted to a tarsal band (Krapu et al. 2011). Transmitters weighed ~ 30 g ($< 1\%$ of body mass), had a life expectancy of 730 days, and were equipped with a mortality sensor. The 10 *canadensis* captured in Alaska were marked with both a VHF transmitter (as described above) and a platform terminal (satellite) transmitter (PTT; model KiwiSat 202; Sirtrack), mounted to a tarsal band, which weighed 45 g and had a

life expectancy of 180 days. The PTTs were programmed to be on for 4 hr and off for 20 hr, repeatedly, during fall migration (60 days; mid-August through mid-October), then on for 4 hr and off for 116 hr during winter (60 days; mid-October through mid-December); then on for 4 hr and off for 20 hr during spring migration (120 days, mid-December through mid-April), repeating these cycles. All birds were processed and released at their capture site within 1 hr after capture.

We used handheld 3-element Yagi antennas and a truck-mounted null-peak antenna system (Balkenbush and Hallett 1988, Samuel and Fuller 1996) to aid us in visually locating VHF-equipped cranes in fields or at roost sites or to triangulate their location using Program Locate III (Nams 2005). We had ≥ 2 staff tracking cranes 7 days wk^{-1} (≥ 8 hr day^{-1}) from vehicles, searching throughout the study area during the entire study period. Searches were conducted beginning when the first cranes were marked during the first season (October 17, 2007) and continued for a few days after the last radio-tagged crane was encountered (March 7, 2008). During the second season, we began monitoring marked cranes on September 29, 2008 (first radio-tagged crane encountered October 4, 2008) and continued for 3 days after the last radio-tagged crane was located (through March 9, 2009). Our search for radio-tagged cranes was focused primarily on our Delta study area; however, to locate birds missing from our study area, we also conducted periodic searches of other crane wintering regions, which included 9 aerial searches (in 2007: November 6, December 2; in 2008: February 11, 26, October 28, November 4, 10, 18, December 5) and 7 ground searches (in 2007: December 23; in 2008: February 11, 19, December 11; in 2009: January 19, February 4, 6).

Statistical Analysis

Winter site fidelity. We used our sample of radio-tagged cranes to study winter movements and site fidelity at 3 spatial scales. We calculated the interannual return rate as the percentage of individual cranes radio-tagged during winter 2007–2008 in our Delta study area and known to be alive the following winter that returned to the Delta during winter 2008–2009. We defined “regions” as major crane roost complexes separated by ≥ 35 km from other such complexes. In this context, our Delta study area was 1 of 5 wintering regions in California’s Central Valley (Figure 1, inset). We also summarized the number of winter regions, landscapes (1 or 2; see above), and roost sites (defined as a set of associated roost sites within 5 km of each other) used by each radio-tagged crane during the second winter season. We used Fisher’s exact test (Sokal and Rohlf 1981:738) to compare interannual return rates and fidelity of the 2 subspecies at each scale; specifically, we compared the frequencies of individuals faithful to a single area with those using ≥ 2 areas within a season. In

cases where we had multiple members of 1 family unit radio-tagged (e.g., adults and young captured together and remaining together), we included only 1 member of each group in our analyses.

Commuting distance and home-range size. We quantified movements by calculating daily commuting distance and home-range size. On days when we located the same individual at its night roost and subsequent daytime feeding locations (a subset of our location data), we used a geographic information system to calculate commuting distance as the linear distance (km) between roost and feeding sites. We calculated winter home-range size (km²) from all our location data for each crane using the 95% fixed-kernel method (Worton 1989, 1995, Kernohan et al. 2001). We used the likelihood cross-validation (CVh) tool in Animal Space Use version 1.1 (Horne and Garton 2007) as the smoothing parameter (Rodgers et al. 2005) because it generally produces home-range estimates with better fit and less variability when home range is estimated from <50 locations per animal (Horne and Garton 2006).

We estimated home-range size for a subset of all cranes that were radio-tagged. We included only 1 individual from each family group to ensure independence. Additionally, home-range analyses can be sensitive to small sample size (Seaman et al. 1999). Consequently, we evaluated the effects of the number of locations on changes in home-range size and followed the recommendation of Odum and Kuenzler (1955) by including in our analysis only individuals whose home-range size stabilized as locations were added (change of <10% for 10 subsequent locations). Home-range size stabilized between 35 and 40 locations for most individuals (fewest was 26); however, home ranges of a few birds did not stabilize, even with >50 locations. Thus, from our sample of marked birds, we estimated home-range sizes for 27 *tabida* and 10 *canadensis* during the first season and for 23 *tabida* and 23 *canadensis* during the second season. We combined data from PTT locations and VHF locations for the 8 *canadensis* radio-tagged in Alaska that wintered in the Delta region to estimate their home-range sizes (45% of the locations were from PTTs). To assess whether the PTT locations introduced a bias in home-range estimates for this group, we used a 2-sample Student's *t*-test to compare home-range sizes of the non-PTT group with those of birds tagged with both types of transmitters.

We constructed a series of mixed-effects models (PROC MIXED, SAS/STAT release 9.2; SAS Institute, Cary, North Carolina, USA) with maximum-likelihood estimates to examine how commuting distance varied by subspecies, landscape, and date, which was included as a linear covariate and numbered sequentially within each season, beginning on October 1. Similarly, we used a set of mixed-effects models to test whether home-range size differed

between subspecies or by family status (pairs with first-year immature vs. unpaired cranes and pairs without young). We used a square-root transformation of the distance and area data to normalize distributions of residual errors. In both sets of models, we included individual bird (or family unit) as a random effect to account for repeated measures. We also included year as a random effect to account for temporal correlations in movements. We modeled the covariance structure of the data to control for this possible association and compared among unstructured, compound symmetry (random effects), variance components, and autoregressive covariance models and chose the covariance structure based on the lowest Akaike's Information Criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989). Once the appropriate covariance was chosen, we compared how the explanatory variables were associated with commuting distance. An increase in commuting distance with date can be an indication of food depletion (Krapu et al. 2004); thus, we investigated whether such a temporal pattern existed in our data for both subspecies.

For the analyses of commuting distance and home-range size, we constructed a set of a priori models (Tables 1 and 2) and compared model performance using an information-theoretic approach (Burnham and Anderson 2002). We evaluated models based on AIC_c and resulting model weights. Models with $\Delta\text{AIC}_c \leq 2$ in relation to the best model were considered competitive; we used model averaging across competitive models to estimate parameters and confidence limits and to evaluate the direction and size of the effect for explanatory variables. We did not include landscape in our home-range models because home ranges of some cranes overlapped both landscapes. All results are reported as model-averaged least-squares means \pm SE.

RESULTS

Winter Site Fidelity

The number of times that we relocated individuals within our study area was similar for the 2 subspecies, averaging once every 2.1 ± 0.1 days for both *tabida* ($n = 27$) and *canadensis* ($n = 31$; 6 of the *canadensis* captured outside of California did not use our study area).

For the sample of cranes radio-tagged in our study area in the first season, *tabida* and *canadensis* showed similar high interannual return rates to the Delta region the following season (Fisher's exact test, $P < 0.35$), as 93% of *tabida* (25 of 27) versus 88% of *canadensis* (15 of 17) returned to the Delta the second winter. Of the 2 *canadensis* that did not return to the Delta the second season, 1 was a yearling that wintered in the Merced region and the other was an adult that did not winter with its marked first-season mate and was found in the Sacra-

TABLE 1. Models to identify factors influencing commuting distance of Greater Sandhill Cranes (*Grus canadensis tabida*) and Lesser Sandhill Cranes (*G. c. canadensis*) wintering in the Sacramento–San Joaquin Delta, California, USA, 2007–2008 and 2008–2009. Models are ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). Number of parameters (k), change in AIC_c (ΔAIC_c), and AIC_c weights (w_i) are given for all models. Models with $\Delta AIC_c < 2$ were used in model averaging to calculate mean commuting distance.

Model structure ^a	k	ΔAIC_c ^b	w_i
S D	5	0	0.33
S D L S*L	7	1	0.20
S D L	6	1.3	0.17
S D S*D	6	2.5	0.09
S D L S*D	7	2.6	0.09
S D L D*L	7	3.1	0.07
S D L S*D S*L	8	4.1	0.04
S	4	12.5	0.01
S L	5	13.6	0.00
S L S*L	6	15.6	0.00
D	4	73.7	0.00
L	4	79.6	0.00
NULL	3	83.8	0.00

^aS = subspecies as *tabida* or *canadensis*; D = continuous date (October 15–February 28); L = Landscape (Cosumnes–Stone Lakes or Central Delta); NULL = no effects model.

^bLowest $AIC_c = 1,294.9$.

mento Valley. The 2 *tabida* that did not return to the Delta (a male and a female, both unpaired at the time of capture; likely subadults) wintered separately in the Sacramento Valley the second winter.

Within-winter fidelity to the Delta, to landscapes within the Delta, and to roost complexes did not differ during the 2008–2009 winter for *canadensis* radio-tagged in the Delta during the first winter ($n = 17$; 4 from this group were not located) versus *canadensis* radio-tagged in Alaska or Oregon ($n = 15$; 1 Alaskan crane apparently died during fall migration) that used our Delta study site during the second winter (Fisher's exact test, all $P > 0.28$); therefore, we combined the data from these 2 groups in our evaluation of fidelity. Our samples for within-season fidelity to region, landscapes, and roost sites included individuals' choices during the second winter season. Compared with *canadensis*, *tabida* showed stronger fidelity to the Delta region, to landscapes within the Delta, and to local roost sites (Fisher's exact tests for all 3 comparisons; $P < 0.001$). A greater percentage of *tabida* (100%; 27 of 27) used only 1 region, compared with 41% of *canadensis* (19 of 32; 12 used 2 regions, and 1 used 3 regions). Among *tabida*, 89% (24 of 27) used only 1 landscape, compared with 19% in *canadensis* (6 of 32). Finally, 84% of *tabida* used only 1 roost complex (24 of 27; the remaining 3 used 2), compared with 16% of *canadensis* (5 of 32; of the remaining 27, 17 used 2 roost complexes, 6 used 3, and 4 used 4).

TABLE 2. Models to identify factors influencing 95% fixed-kernel home-range sizes of Greater Sandhill Cranes (*Grus canadensis tabida*) and Lesser Sandhill Cranes (*G. c. canadensis*) wintering in the Sacramento–San Joaquin Delta, California, USA, 2007–2008 and 2008–2009. Models are ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). Number of parameters (k) and AIC_c weights (w_i) are given for all models. Models with $\Delta AIC_c < 2$ were used in model averaging to calculate mean home-range size.

Model structure ^a	k	ΔAIC_c ^b	w_i
S F	5	0	0.40
S F S*F	6	0.5	0.31
S	4	0.6	0.29
F	4	103.6	0.000
NULL	3	101.8	0.000

^aS = subspecies (*tabida* or *canadensis*); F = cranes with chicks vs. adults and subadults without chicks; NULL = no effects model.

^bLowest $AIC_c = 248.5$.

Commuting Distance and Home-range Size

The frequency distributions of commuting distances differed between the 2 subspecies (Figure 2). For *tabida*, 95% of the commuting flights ($n = 353$) were within 5 km of existing roost sites, compared with 64% of flights by *canadensis* ($n = 340$); 90% of flights by *canadensis* were within 10 km of the roost sites. For our analysis of commuting distance, models with a variance-components covariance structure had the lowest AIC_c , so we used this structure in our subsequent modeling to identify factors associated with commuting distance. Three models, which together received 70% of the model weight, were competitive (Table 1). The best-supported, most parsimonious model in the candidate set included subspecies and date. The other top 2 models also included an additive landscape effect and the interaction between subspecies and date. Model-averaged mean commuting distance was shorter for *tabida* (1.9 ± 0.01 km) than for *canadensis* (4.5 ± 0.01 km). Mean commuting-distance differences by landscape were small (0.35 ± 0.12 km and 0.12 ± 0.12 km longer in the Cosumnes–Stone Lakes than in the Central Delta landscape for *tabida* and *canadensis*, respectively). Also, the increase in mean commuting distance by date within season for all cranes was small (0.000096 ± 0.000004 km day⁻¹). Therefore, landscape and date effects did not appear to be biologically significant.

Our comparison of home-range sizes for *canadensis* with and without auxiliary PTT data revealed no difference between the means of these groups (no PTT: 4.7 ± 0.3 km²; PTT: 4.4 ± 0.5 km²; $t_{30} = 0.59$; $P = 0.56$); therefore, we combined the groups in our analysis. Models with the standard variance-components covariance structure had the lowest AIC_c , so we used that structure in our subsequent modeling of factors associated with home-range size. Three models were about equally competitive

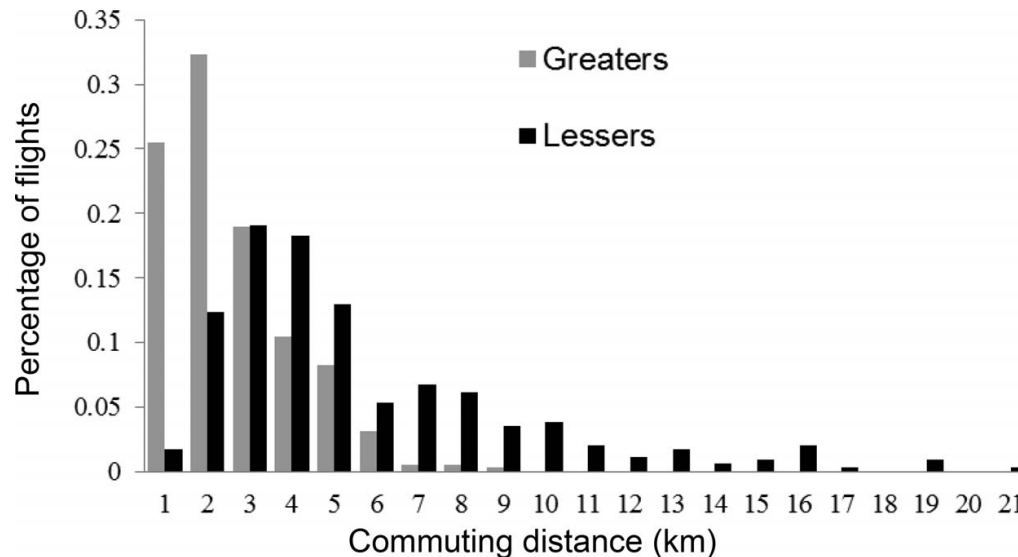


FIGURE 2. Frequency distribution of winter commuting flights (at 1-km intervals) between roost sites and foraging areas for Greater Sandhill Cranes (*Grus canadensis tabida*; $n = 354$) and Lesser Sandhill Cranes (*G. c. canadensis*; $n = 340$), during winters 2007–2008 and 2008–2009, in the Sacramento–San Joaquin Delta, California, USA.

and received 99.9% of the model weight: (1) the additive model with subspecies and family status ($w = 0.40$); (2) the interactive model between subspecies and family status ($w = 0.31$); and (3) the simple model including only subspecies ($w = 0.29$; Table 2). Both the null model and the model including only family status received virtually no support. Model-averaged mean home-range size was an order of magnitude smaller for *tabida* ($1.9 \pm 0.4 \text{ km}^2$) than for *canadensis* ($21.9 \pm 1.9 \text{ km}^2$). For *canadensis*, mean home ranges of pairs with young were smaller than those of pairs without young ($17.1 \pm 3.1 \text{ km}^2$ vs. $25.3 \pm 2.1 \text{ km}^2$, respectively). For *tabida*, however, there was no difference in home-range size between pairs with and without young.

DISCUSSION

Both subspecies showed very high interannual return rates to the Delta region. Our results confirmed our prediction that larger-bodied *tabida* would have greater site fidelity than *canadensis*, as they showed greater fidelity to wintering areas at all 3 geographic scales (region, landscape, roost site). Our prediction that *tabida* forage closer to roost sites, and therefore exhibit smaller winter home ranges than *canadensis*, was also confirmed.

Returning to the same wintering area may help cranes increase the likelihood of their own survival and the subsequent production or survival of offspring. Benefits of such site fidelity could include knowledge of the distribution of food resources, roost sites, and predators, advantages that have been reported for waterfowl (Raveling 1969, Nichols et al. 1983) and other avian species (Rappole and McDonald 1994, Sherry and Holmes 1996). Because most cranes remain paired for the entire year, they do not need to reunite, so fidelity to the wintering grounds must have some ecological advantage (e.g., familiarity with

good foraging areas or safe roosting sites; Raveling 1979). Returning to the same wintering area may also provide the advantage of allowing individuals to maintain social connections (Raveling 1969, Robertson and Cooke 1999).

High interannual return rates of both subspecies of Sandhill Crane to the Delta wintering area were similar to that recorded for *tabida* wintering in New Mexico, where repeated use of areas was thought to reflect habitat stability (Drewien et al. 1999). By comparison, a study of *tabida* wintering in Georgia reported a relatively low return rate (34%), which the authors speculated was caused by variable roost-site conditions (Bennett and Bennett 1989). Similarly, *tabida* in Florida moved between wintering areas in response to interannual changes in roost water levels and loss of foraging habitats (Wenner and Nesbitt 1987).

The patterns of high site fidelity that we observed in *tabida* may hold for much longer periods than our 2-yr study, given that periodic observations of marked *tabida* indicate that some individuals have wintered at local sites within the Delta for >12 yr (G. L. Ivey personal observation). Age and pair status likely contributed to the failure of some cranes to return to the Delta in year 2. A study in Georgia reported that age had a major influence on winter site fidelity of cranes: The return rate of adult cranes was 2.4 \times greater than that of subadults, and subadults that had been banded as juveniles exhibited the lowest return rate (Bennett and Bennett 1989).

Habitat stability might also affect within-season site fidelity. A previous study of *tabida* in the Central Valley of California reported much lower within-winter regional fidelity, with 22% of marked birds using 2 wintering regions, the Sacramento Valley and the Delta (Pogson and Lindstedt 1991), compared with none in the present study. Perhaps ideal roost-site conditions in the Sacramento

Valley during the 1980s were less reliable, because most roost sites were on private lands that were not managed to provide ideal conditions for cranes. These patterns suggest that *tabida* prefer to return to the same areas each winter but are capable of being opportunistic and shifting wintering regions when habitat becomes unsuitable. Thus, estimates of return rates and within-season site fidelity could provide an indication of habitat quality or management success. However, the cost of such shifts in winter sites in terms of survival and reproductive fitness is unknown and should be assessed to evaluate the effectiveness of habitat management.

In our study area, *canadensis* moved much longer distances, had larger home-range sizes, and exhibited lower within-season site fidelity than *tabida*, although our estimate of mean commuting distance for *canadensis* is within the range of estimates reported from other studies in Saskatchewan, Canada (Sugden et al. 1988), Texas, USA (Iverson et al. 1985), and Nebraska, USA (Sparling and Krapu 1994, Pearse et al. 2010). Several studies have reported estimates of home-range size for cranes, but methods of estimating home range vary considerably, making comparisons among studies difficult. A previous study in California estimated a much larger average home range for *canadensis* (342 km²; Petrula and Rothe 2005) than the 22 km² that we report; however, that study used a minimum convex polygon approach for calculating home range and included observations from multiple winter regions, such that polygons included large areas of unsuitable habitat (e.g., urban areas) not used by cranes.

The difference in scale at which the 2 subspecies moved during winter in our study has important implications for their habitat conservation and management in this region and perhaps elsewhere throughout their ranges. Differences in movement patterns between subspecies are likely partly attributable to a suite of factors that together influence the evolution of crane ecology during winter, including body size, dominance, social systems, and possibly diet, similar to findings in geese (Johnson and Raveling 1988, Durant et al. 2004, Jónsson and Afton 2009, Mini 2013). It is possible that *canadensis* need to store more energy for their longer migration and harsher conditions upon arrival in their more northerly breeding grounds, which may result in a need to rely on surplus fat (Krapu et al. 1985, Alerstam and Lindström 1990).

Larger-bodied *tabida* may meet their greater total energy needs by minimizing energy-intensive activities such as flight (Newton 2010) and may be able to stay in food patches longer because they can use their larger bills to access foods not available to *canadensis* (e.g., deeper in the soil). Because of their larger body size, *tabida* may be able to extract more energy from lower-quality foods than *canadensis* (Demment and Van Soest 1985), deplete body reserves more slowly, have greater fasting endurance (Afton

1979, Thompson and Raveling 1987), and take more time to reach starvation thresholds (Aldrich and Raveling 1983, Johnson and Raveling 1988). Physiological limitations related to the smaller body size of *canadensis* may translate to increased foraging time (Gloutney et al. 2001, Maccarone et al. 2008), having greater food densities remaining when giving up to move to other food patches (Charnov 1976), and selecting higher-quality feeding patches (Demment and Van Soest 1985, Durant et al. 2004). All of these behaviors would cause *canadensis* to move among habitat patches more often to seek higher-quality patches that may be more dispersed on the landscape.

In addition to energetic considerations, differences in behavior may play a role in the scale of movements of the 2 subspecies. Because of their smaller body size, *canadensis* are more likely to be displaced from feeding fields by the dominant *tabida* (Shelley et al. 2004, G. L. Ivey personal observation). Bautista et al. (1995) demonstrated that average food intake rate by Common Cranes (*G. grus*) in Spain was positively related to dominance. We observed *tabida* regularly feeding in small groups or as isolated pairs dispersed across the landscape near roost sites (G. L. Ivey personal observation); they may have been territorial, as Common Cranes are in winter (Alonso et al. 2004). By contrast, *canadensis* appeared to be more gregarious and were observed foraging in larger flocks. Such differences in behavior could contribute to differences in home ranges.

Diet preferences may also influence movement patterns of the 2 subspecies. Other studies have found that home-range size increases in animals at higher trophic levels (Schoener 1968, Harestad and Bunnell 1979). Although both subspecies of crane are generally omnivores, differences in the composition of their diet in the Delta have not been quantified. In California, *canadensis* have been found to prefer feeding in alfalfa fields, while *tabida* avoid them (Ivey 2015). Research elsewhere has documented a high invertebrate (high protein) component to the diet when cranes are feeding in alfalfa (Krapu et al. 1984, Reinecke and Krapu 1986), which suggests that *canadensis* may require larger home ranges than *tabida* to accommodate a more carnivorous diet.

During winter, Sandhill Cranes are central-place foragers, flying out from central night roost sites to forage nearby. Central-place foraging theory predicts that individuals concentrated within a central place will increase distance traveled over time as easily accessed food resources near the central place are depleted (Ashmole 1963, Elliott et al. 2009). On the major spring staging area along the Platte River in Nebraska, Sandhill Cranes' commuting distances increased as spring progressed (Pearse et al. 2010). Also in that region, commuting distances increased considerably during spring staging between the 1970s and 1990s, apparently because of declines in waste-corn availability due to increased

competition with waterfowl, improved harvest efficiency, and fewer acres planted to corn (Krapu et al. 2004, 2005, Pearse et al. 2010). By contrast, we found that commuting distance on wintering areas increased only slightly for *canadensis* as winter progressed, which suggests that food depletion was not pervasive throughout our study area. The fact that *tabida* remained sedentary also suggests that their food was not depleted, whereas *canadensis* may move among roost sites as a strategy for mitigating local food depletion.

Management Implications

The high winter site fidelity we observed suggests the current landscape composition and roost-site management for Sandhill Cranes in the Sacramento–San Joaquin Delta region of California is providing high-quality wintering habitat for both *canadensis* and *tabida*. Within the Delta, conservation planners should consider the combination of a roost complex and surrounding agricultural fields as the fundamental ecosystem unit for managing wintering Sandhill Cranes. The extremely strong fidelity of *tabida* to roost complexes within landscapes in the Delta indicates that conservation planning targeted at maintaining and managing for adequate food resources around traditional roost sites can be effective for meeting their habitat needs. Most *canadensis* relied on multiple suitable units (roost complex + fields) widely distributed in the Delta to meet their winter habitat needs.

Our data on commuting distances provide a useful measure of scale for habitat conservation planning around suitable roost sites. To maintain high use of traditional roosts by *tabida*, conservation planners and managers should consider all habitats within 5 km of a known crane roost when making zoning and land-use decisions. That radius encompassed 95% of the commuting flights made by *tabida* but only 64% of flights by the smaller subspecies. For *canadensis*, a conservation radius of 10 km would encompass 90% of the commuting flights. This radius may be more appropriate in the San Joaquin Valley regions, where flocks are dominated by *canadensis* (>97% of flocks; G. L. Ivey personal observation). Providing Sandhill Cranes with better foraging-habitat conditions within these radii should increase their ability to store endogenous fat reserves on the wintering grounds that are necessary for survival. Our findings indicate that management, mitigation, acquisition, easement, planning, farm-subsidy programs, and research would best benefit cranes when applied at these scales. Providing new roosts on the periphery of existing ecosystem units would also likely be effective in expanding ecosystem units for cranes because peripheral roosts should be readily discovered, even by the comparatively sedentary *tabida*. Additionally, in areas where hunting of cranes is authorized, managers could promote a relatively larger harvest of the more abundant

canadensis and reduce harvest of the less abundant *tabida* by restricting hunting to areas >5 km from roost sites.

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