



Original Article

Utility of Vocal Formant Spacing for Monitoring Sandhill Crane Subspecies

MATTHEW R. JONES,¹ *Museum of Southwestern Biology, Department of Biology, University of New Mexico, MSC03 2020, Albuquerque, NM 87131*

CHRISTOPHER C. WITT,² *Museum of Southwestern Biology, Department of Biology, University of New Mexico, MSC03 2020, Albuquerque, NM 87131*

ABSTRACT Three migratory subspecies of sandhill crane (*Grus canadensis*) occur in North America: greater (*G. c. tabida*), Canadian (*G. c. rowani*), and lesser (*G. c. canadensis*). These subspecies vary clinally in size from the large *tabida* to the small *canadensis*. All 3 subspecies co-occur during the nonbreeding season, but field identification is challenging and census efforts typically do not even attempt to distinguish them. We developed a novel method to determine the subspecies composition of nonbreeding sandhill crane populations using formant spacing in vocalizations. Each note in a crane vocalization is comprised of several formants, or energy peaks in the frequency spectrum. Formant spacing is inversely proportional to the length of the sound-emitting tube, or trachea. Analysis of formant-spacing distributions for *tabida* and *canadensis* revealed that *tabida* has reduced formant spacing, as predicted based on its larger body size and correspondingly larger trachea. Comparisons of these subspecies-specific formant-spacing distributions to formant-spacing distributions from calls recorded at 2 crane wintering areas in New Mexico, USA, showed that the wintering crane populations of the Middle Rio Grande Valley and the Lower Rio Grande Valley contain strikingly different proportions of the globally rare *tabida* (75.5% and 5.6%, respectively). These findings are concordant with crane subspecies composition estimates derived from hunter check stations in New Mexico. Formant-spacing provides an indirect, noninvasive method of estimating body-size distributions that has several practical advantages. We expect it to be most useful when body-size classes have limited overlap, as is the case with New Mexico sandhill crane populations. © 2012 The Wildlife Society.

KEY WORDS formant spacing, *Grus canadensis*, monitoring, New Mexico, population, sandhill crane, sonogram, subspecies, vocalization.

Animal vocalizations potentially contain a variety of valuable information including the sex, age, size, and subspecific identity of the vocalizer (Fitch 1997, 1999; Riede and Fitch 1999). Vocal analysis has been suggested for population monitoring in a wide variety of taxa, including canids (Darden et al. 2003, Hartwig 2005), birds (Policht et al. 2009), and bats (Fukui et al. 2004). Recent research on vocal identification of animals has focused on a vocal characteristic called formant spacing, or formant dispersion, because it has been shown to correlate with body size (Fitch 1997, 1999; Riede and Fitch 1999).

In birds, as a column of air passes through the trachea it vibrates at certain frequencies. The frequencies at which the air vibrates are the formant frequencies or peaks of acoustic energy in the frequency spectrum (Fant 1960). Formants appear as bright horizontal bands on a sonogram (Fig. 1) and formant spacing is the average distance measured in

hertz between adjacent formants (Fitch 1997). Formant spacing is primarily determined by the length of the sound-emitting tube (the trachea in birds) and is predicted by the equation

$$D_{\text{pred}} = \frac{c}{2L} \quad (1)$$

where c is the speed of sound (337.5 m/sec at 10° C) and L is the length of the sound-emitting tube in meters (Fitch 1997, 1999). This equation shows a simple inverse relationship between trachea length and formant spacing—as trachea length increases, formants are more closely spaced. Formant spacing can predict the body size of the vocalizer because of the scaling relationship between body size and trachea length (Fitch 1999, Riede and Fitch 1999). Migratory sandhill crane (*Grus canadensis*) subspecies vary greatly in body size and are of high management priority, making them ideal candidates for testing the conservation utility of formant spacing.

Sandhill Crane Subspecies and Management

Sandhill cranes comprise 6 recognized subspecies in North America and Cuba (Tacha et al. 1992, Rhymer et al. 2001), 3 of which are migratory (greater, *G. c. tabida*; Canadian, *G. c. rowani*; and lesser, *G. c. canadensis*; hereafter, *tabida*, *rowani*, and *canadensis*, respectively). Migratory sandhill cranes that

Received: 19 April 2011; Accepted: 29 November 2011;
Published: 10 February 2012

¹Present address: Berry Biodiversity Conservation Center, Department of Zoology and Physiology, University of Wyoming, 1000 E University Avenue, Department 4304, Laramie, WY 82071, USA.

²E-mail: cwitt@unm.edu

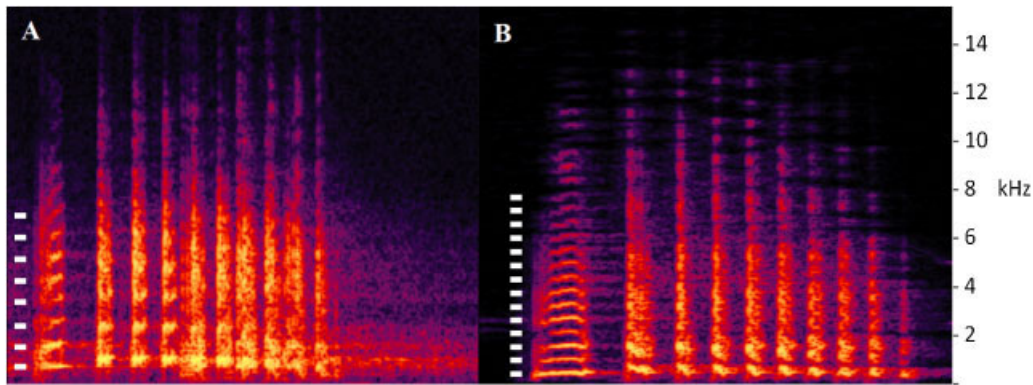


Figure 1. Sonograms of guard calls of (A) *Grus canadensis canadensis* (Macaulay Library Catalog no. 138201) and (B) *G. c. tabida* (Macaulay Library Catalog no. 105207). White horizontal bars on left side of each note indicate positions of formants.

occur in New Mexico, USA, are derived from 2 geographically distinct breeding populations: the Mid-Continent Population (MCP), the largest (estimated 378,420 cranes in 2006, Sharp et al. 2007) consisting of *tabida*, *rowani*, and *canadensis*, and the Rocky Mountain Population (RMP), consisting of approximately 20,321 *tabida* in 2008 (Drewien et al. 2009). New Mexico hosts only *canadensis* and *rowani* from the MCP that winter mainly in the Pecos Valley and Lower Rio Grande Valley (LRGV) in Doña Ana and Sierra counties. Smaller numbers of MCP cranes winter in the Middle Rio Grande Valley (MRGV) in Socorro and Valencia counties, where they mix with the majority of RMP *tabida* (Drewien and Bizeau 1974). Small numbers of RMP cranes also winter in the Pecos and Lower Rio Grande Valleys (Schmitt and Hale 1997, Mitchusson 2003).

Sandhill cranes have been the subject of substantial research and conservation effort and, in particular, the RMP *tabida* are of concern because of their small global population size (Drewien et al. 1995, 2009; Benning et al. 1997; Sharp et al. 2007). A combination of habitat destruction and overhunting in times past is thought to have led to the precipitous decline in crane populations in the late 19th and early 20th centuries (Bailey 1928, Walkinshaw 1949). Intrinsic factors such as recruitment rate contribute to the vulnerability of the species. Sandhill cranes have the lowest recruitment rate (typically 8–10% juv during autumn) of any hunted bird species in North America and recruitment rates of RMP cranes have been known to drop as low as 2% during drought conditions (Drewien et al. 1995). If drought frequency and severity increase as predicted (Seager et al. 2007, Woodhouse et al. 2010), RMP *tabida* may not be able to sustain current harvest levels and management agencies may be justified in managing hunts by subspecies as the New Mexico Department of Game and Fish (NMDGF) has done since 1961, when the first crane hunts in eastern New Mexico were authorized only for cranes from the MCP (Sharp and Vogel 1992). Opening the RMP cranes to hunting in 1981 increased the potential stress on this population. Rocky Mountain Population *tabida* harvest in 2009–2010 reached a record high of 1,392 cranes, 86% higher than the mean from the previous 10 years (Kruse et al. 2010). Given predictions of increased drought in the western United

States, high harvest rates may not be sustainable (Seager et al. 2007, Woodhouse et al. 2010). The high risk of population decline in RMP *tabida* and the extensive subspecies mixing in nonbreeding populations underscores the importance of effective subspecies monitoring and conservation plans (Johnson and Stewart 1973, Tacha et al. 1985).

Subspecies composition typically is determined by visual counts or by hunter harvest data, but neither method is ideal. First, visual identification of sandhill cranes to subspecies (especially when distant or flying) is extremely difficult and requires skilled, seasoned observers. Yet, even with skilled observers, identification errors may occur due to the difficulty of estimating size and relative proportions in the field (Drewien and Bizeau 1974, Drewien et al. 1995). Second, hunter harvest data is only collected on a few weekends during late autumn and early winter and is, thus, unable to distinguish shifts in phenology from population trends. Furthermore, the continued collection of hunter harvest data is contingent on the long-term sustainability of moderate harvest levels.

We developed a subspecies monitoring method that identifies sandhill crane subspecies using the vocal characteristic of formant spacing. Because formant spacing is inversely proportional to length of the sound-producing tube, we hypothesized that *tabida*, the significantly larger subspecies (ad F: \bar{x} = 4.933 kg, n = 1,669, ad M: \bar{x} = 5.600 kg, n = 1,904, New Mexico Department of Game and Fish hunter data, T. Mitchusson unpublished data), would have a longer trachea and, therefore, reduced formant spacing relative to the smaller *canadensis* (ad F: \bar{x} = 3.064 kg, n = 634, ad M: \bar{x} = 3.494 kg, n = 707, New Mexico Department of Game and Fish hunter data, T. Mitchusson, unpublished data). In this paper, we 1) establish distributions of formant spacing for *tabida* and *canadensis*, 2) predict the formant-spacing distribution for *rowani*, and 3) examine the feasibility of using formant spacing as a monitoring tool for sandhill cranes by assessing subspecies composition at the MRGV and LRGV in New Mexico.

STUDY AREA

The MRGV was the wintering area for the majority of RMP cranes. The valley stretched approximately 120 km from

Albuquerque (Bernalillo County) south to Bosque del Apache National Wildlife Refuge (Socorro County), was 1.5–8.0 km wide, and had an average elevation of 1,430 m (Drewien et al. 1995, Mitchusson 2003). In 1986, sandhill crane hunts opened in the MRGV (Schmitt and Hale 1997). The LRGV of New Mexico was located between Caballo Reservoir and Hatch Valley in Sierra and Doña Ana counties and served as a major wintering location for *canadensis* from the MCP; it also supported smaller numbers of RMP cranes (Schmitt and Hale 1997). Sandhill crane hunts began in the LRGV in 1982 (Schmitt and Hale 1997). Agricultural fields comprised the predominant crane habitat in both of these areas.

METHODS

Formant-Spacing Distributions

We obtained vocal recordings of sandhill crane subspecies from the Macaulay Library of Sound (macaulaylibrary.org) and Xeno-Canto (xeno-canto.org). We included recordings in the analysis if they were made at a locality and date at which only one subspecies is likely to occur, and we attributed the recordings to the corresponding subspecies. We obtained no recordings that we could confidently identify as *rowani* because its geographical range substantially overlaps with those of the other subspecies (Walkinshaw 1965). Thus, we established estimated formant-spacing distributions for *tabida* and *canadensis* and a predicted distribution for *rowani* based on body size, as described below. Conveniently, *rowani* comprised a very small percentage of wintering sandhill cranes in New Mexico (Schmitt and Hale 1997, Mitchusson 2003). In addition, its status as a distinct subspecies has been a subject of debate. Several genetic studies demonstrate that *rowani* is not diagnosable at effectively neutral mitochondrial DNA or nuclear microsatellite loci (Rhymer et al. 2001, Glenn et al. 2002, Petersen et al. 2003, Jones et al. 2005). These genetic data indicate that *rowani* does not have a deep history of allopatric isolation and may be the product of introgression between *canadensis* and *tabida* along a latitudinal gradient (Jones et al. 2005). Regardless of whether *rowani* is a transient hybrid population or a recently evolved and locally adapted taxon, it represents a morphologically diagnosable size class (Johnson and Stewart 1973) with well-defined breeding and wintering distributions and it, therefore, warrants management consideration.

We recorded sandhill crane vocalizations from the MRGV and LRGV between October 2010 and January 2011. In the LRGV wintering area, we made recordings at Arrey (32°49.588'N, 107°18.175'W), Derry (32°42.574'N, 107°14.409'W), and Hatch on 24 October 2010, 12 December 2010, and 3–4 January 2011. At the MRGV wintering area, we recorded at Bosque del Apache National Wildlife Refuge (33°51.569'N, 106°52.601'W), San Antonio (33°55.752'N, 106°51.297'W), and Bernardo on 10 November 2010, 19 December 2010, and 4 January 2010. We made recordings using a Sony PCM-D50 Audio Recorder (Tokyo, Japan) and a Sennheiser ME66/K6

Super-Cardioid Short Shotgun Condenser Microphone (Hanover, Germany). A representative subset of these recordings is available at the Macaulay Library of Sound (ML Catalog no. 139423–139433).

We recorded cranes along roads and trails in different-sized groups (ranging from single individuals to thousands), engaged in different behaviors (e.g., foraging, ascending on thermals, morning flights, roosting), and in different habitats (e.g., rivers, agricultural fields, marshes). Although sampling exclusively in highly accessible areas such as roads and trails, termed “convenience sampling,” is often associated with unrepresentative data (Anderson 2001, 2003), this approach is reasonable for wintering sandhill cranes because they congregate in highly visible areas such as agricultural fields. In addition, wintering crane subspecies roost and forage in the same habitats and are frequently observed together (Mitchusson 2003; MRJ, personal observation). We are unaware of any differences in flock size or rates of vocalization among subspecies or between sexes, either of which could affect our results.

We attempted to analyze vocalizations for as many individuals as possible per recording, while taking strict precautions against including the same individuals more than once. Individual cranes were generally easy to distinguish due to simultaneous or overlapping calling, calls that occurred out of synchronization with an established caller’s rhythm, and calls with significantly different tone. When it was difficult to distinguish between individuals in a recording, we did not measure multiple calls from the same group unless they were specifically observed to have come from different individual cranes. As a result, our sample size per recording was positively correlated with flock size, but individuals in smaller flocks were almost certainly overrepresented in our data set. Each recording was annotated by voice with information on the location, flock size, and context.

We analyzed sonograms of recordings using Adobe Soundbooth. We determined formant spacing (D_f) using the formula proposed by Fitch (1997):

$$D_f = \frac{\sum_{i=1}^{N-1} F_{i+1} - F_i}{N - 1} \quad (2)$$

where D_f is the formant spacing in hertz, N is the total number of formants measured, and F_i is the frequency of the i th formant in hertz.

Cranes have a large repertoire of calls (Walkinshaw 1949, Nesbitt and Bradley 1997). During initial analyses, some calls showed variation in formant spacing within individuals; therefore, we took great precaution choosing the type of call to use for our analysis. Guard calls are loud rattles consisting of several closely spaced notes, the first of which is usually slightly longer (Nesbitt and Bradley 1997; Fig. 1). We chose to measure the first, long note of guard calls because they were consistent for formant spacing within individuals and were simple to measure.

We established a predicted formant-spacing distribution for *rowani* by estimating formant spacing as a log-linear function of body mass. We used the median body mass

and median formant-spacing values for *canadensis* and *tabida*, respectively, to estimate the function. We then predicted the formant spacing for each value of body mass for the 395 *rowani* individuals weighed at hunter check stations in New Mexico since 1983 (New Mexico Department of Game and Fish hunter data, T. Mitchusson, unpublished data).

Subspecies Composition

To determine subspecies structure in the 2 New Mexico wintering areas we compared formant-spacing distributions from the LRGV and MRGV to the formant-spacing distributions for *tabida* and *canadensis*. We considered formant-spacing values that overlapped between presumed *tabida* and *canadensis* individuals to represent unknown subspecies. We used the range of formant-spacing values that was unique to *tabida* to classify individual calls from the LRGV and MRGV as *tabida*. Similarly, we used the range of values that was unique to *canadensis* to classify calls as *canadensis*.

New Mexico Department of Game and Fish compiled sandhill crane hunter harvest data. Age, sex, subspecies, and morphological measurements were determined at check stations by C. Gregory Schmitt from 1983 to 1994 (Schmitt and Hale 1997) and by Tim Mitchusson from 1995 to 2009. We obtained the combined data set (1983–2009) from NMDGF and, when possible, used the measurement data to assign unknown individuals to subspecies based on the criteria of Schmitt and Hale (1997). Because we could not discount the possibility that we analyzed vocal recordings of immature cranes, our analyses included immature individuals that CGS and TM confidently identified to subspecies. We have no reason to believe that trachea lengths and formant spacing are different in immature and adult birds. We determined subspecies composition for the entire time interval (1983–2009), by season, and by site. We also determined subspecies composition for 1993–2009 in the MRGV, which we deemed a reasonable estimation of present subspecies composition based on markedly different subspecies composition prior to 1993, and from 2000 to 2009 in the LRGV, which was more thoroughly sampled than prior years. We used years to refer to the year at the beginning of each season (e.g., 1983 refers to autumn 1983 to winter 1984 season). We considered all cranes killed in Socorro and Valencia counties to winter in the MRGV and all cranes killed in Sierra and Doña Ana counties to winter in the LRGV. No crane hunts were held in the LRGV for the 1985–1987, 1989, or 1997 seasons (Mitchusson 2003). No hunt data exist for the 1994 season in either the MRGV or LRGV.

RESULTS

Formant-Spacing Distributions

We analyzed 49 calls recorded along the MRGV. The mean formant spacing was 603.1 Hz/formant (± 131.3 Hz/formant) and values ranged from 450 Hz/formant to 1,200 Hz/formant (Fig. 2B). Fifty-four calls from the LRGV showed a mean formant spacing of 875.9 Hz/formant (± 148.8 Hz/formant) and ranged from 500 Hz/formant to 1,375 Hz/formant (Fig. 2D).

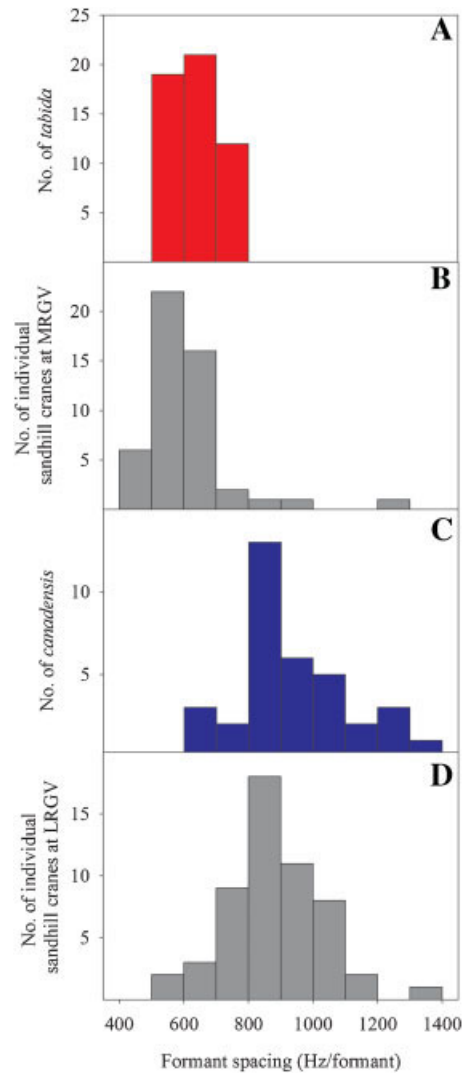


Figure 2. The distribution of formant spacing (Hz/formant) for (A) greater sandhill cranes (*Grus canadensis tabida*), (B) sandhill cranes recorded in the Middle Rio Grande Valley (MRGV), New Mexico, USA, (C) lesser sandhill cranes (*G. c. canadensis*), and (D) sandhill cranes recorded at the Lower Rio Grande Valley (LRGV), New Mexico.

Presumed *tabida* and *canadensis* guard calls overlapped in formant spacing from 642.9 Hz/formant to 733.3 Hz/formant (Table 1). We classified all calls in this formant-spacing range as unknown, all calls <642.9 Hz/formant as *tabida*, and all calls >733.3 Hz/formant as *canadensis*. By these criteria, cranes recorded in the LRGV were 5.6% *tabida* ($n = 3$), 87.0% *canadensis* ($n = 47$), and 7.4% unknown ($n = 4$; Fig. 3A). Cranes recorded in the MRGV comprised 75.5% *tabida* ($n = 37$), 10.2% *canadensis* ($n = 5$), and 14.3% unknown ($n = 7$; Fig. 3B).

The log-linear function of body mass and formant spacing as determined by the median body mass and formant-spacing values for *canadensis* (3,220.5 g, 875 Hz/formant, respectively) and *tabida* (5,227.5g, 610 Hz/formant, respectively) was defined as $\log_{10}(\text{formant spacing}) = 5.555 - [0.745 \times \log_{10}(\text{body mass})]$. From this equation, we predicted *rowani* has a formant-spacing range of 532.7–866.5 Hz/formant (Table 1).

Table 1. Formant spacing (D_f) summary statistics for *Grus canadensis canadensis* and *G. c. tabida* based on recordings. Summary statistics for *G. c. rowani* were based on a log-linear function of body mass and formant spacing. Body mass data were collected from hunter-shot specimens in New Mexico, USA, from 1983 to 2009.

Subspecies	<i>n</i>	Median D_f , Hz/formant	Mean D_f , Hz/formant	±SD, Hz/formant	D_f range, Hz/formant
<i>canadensis</i>	35	875.0	924.5	±172.2	642.9–1,340.0
<i>tabida</i>	52	610.0	600.9	±65.1	500.0–733.3
<i>rowani</i>	395	630.6	633.5	±53.3	532.7–866.5

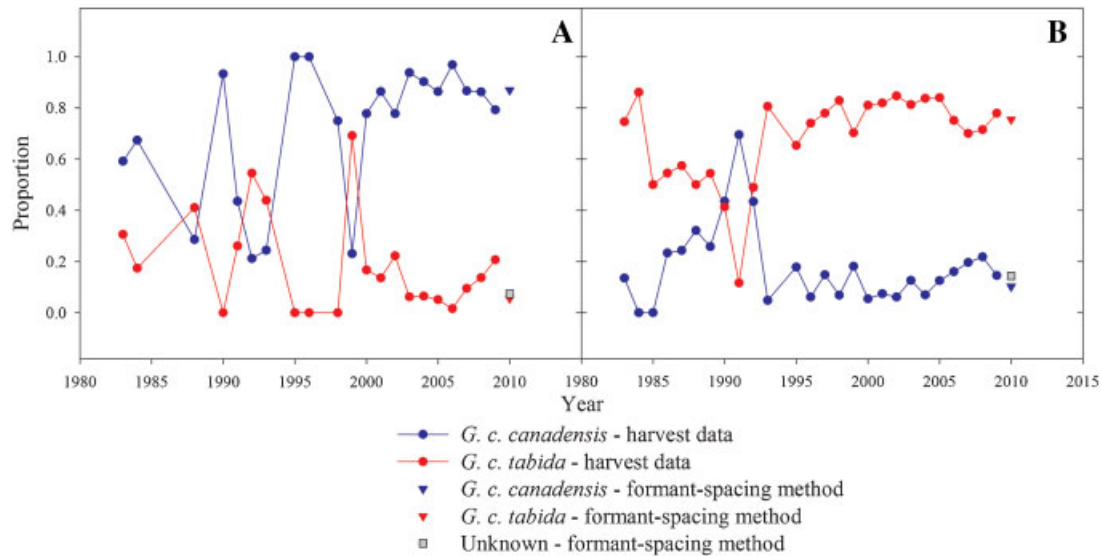


Figure 3. Proportions of *G. c. canadensis* and *G. c. tabida* over time in (A) the Lower Rio Grande Valley and (B) the Middle Rio Grande Valley (NM, USA). Estimates are based on hunter harvest data from 1983 to 2010 (circles with lines) and our formant-spacing method (triangles and squares).

Harvest Data

Hunter harvest data from the MRGV over 1983–2009 exhibited a consistent subspecies composition, averaging 72.0% *tabida* ($n = 4,258$), 16.4% *canadensis* ($n = 967$), 6.4% *rowani* ($n = 376$), and 5.2% unknown ($n = 308$). The LRGV hunter harvest averaged 18.7% *tabida* ($n = 153$), 72.5% *canadensis* ($n = 592$), 5.4% *rowani* ($n = 44$), and 3.4% unknowns ($n = 28$) over the same period.

Prior to 1993, the MRGV saw substantially lower proportions of *tabida* (Fig. 3B). Subspecies composition in the MRGV from 1985 to 1992 averaged 48.9% *tabida* ($n = 533$), 32.9% *canadensis* ($n = 359$), 4.9% *rowani* ($n = 54$), and 13.3% unknown ($n = 145$). From 1993 to 2009, subspecies composition was constant and *tabida* in the MRGV averaged 77.3% ($n = 3,642$) with 12.7% *canadensis* ($n = 600$), 6.7% *rowani* ($n = 318$), and 3.3% unknown ($n = 154$). Prior to 2000, the LRGV showed erratic year-to-year variation in subspecies composition due to small sample sizes (Fig. 3A). From 1983 to 1999, the LRGV averaged 32.3% *tabida* ($n = 97$), 47.7% *canadensis* ($n = 143$), 12.7% *rowani* ($n = 38$), and 7.3% unknown ($n = 22$). After 2000, sample sizes increased and the average proportion of *tabida* decreased to 10.8% ($n = 56$) with 86.8% *canadensis* ($n = 449$), 1.2% *rowani* ($n = 6$), and 1.2% unknown ($n = 6$).

DISCUSSION

Formant spacing previously has been shown to vary with body size within and among species (Fitch 1997, 1999; Riede and Fitch 1999) but the range of potential uses for this physical acoustic correlation has not yet been realized. This study demonstrates a potential management application of formant spacing as a tool for monitoring of RMP sandhill cranes. Importantly, the hunter harvest data gathered over 27 seasons show overall agreement in subspecies composition with data from our technique based on vocalizations. Both data sets show that the MRGV has a much higher concentration of *tabida* than other subspecies (75.5% by formant-spacing method, 72.0% by all harvest data, and 77.3% by harvest data 1993–2009). In the LRGV, on the other hand, *canadensis* predominates (87.0% by formant-spacing method, 72.5% by all harvest data, and 86.8% by harvest data 2000–2009). The estimates of subspecies composition based on formant spacing were remarkably concordant with the subspecies composition at hunter check stations from 1993 to 2009 in the MRGV, when subspecies composition remained relatively static to the present day, and 2000–2009 in the LRGV, when sample sizes increased. Although the high level of concurrence between data sets could suggest that both methods are tracking real patterns, this concurrence does not necessarily attest to the accuracy

of the formant-spacing method due to inherent biases in hunter data.

The harvest data indicate a large shift in subspecies composition in the MRGV and LRGV around the mid-1990s to 2000 toward larger proportions of *tabida* and *canadensis*, respectively. Whereas the high variability in population estimates in the LRGV may be an artifact of small sample size (prior to 2000, 5 seasons were based on fewer than 20 cranes), the shift in subspecies composition in the MRGV around the mid-1990s is well-supported by the data, suggesting a level of inter-seasonal dynamicism in nonbreeding crane populations that would justify systematic monitoring.

Utility and Limits of Formant-Spacing Method

Although mitochondrial DNA haplotypes of *rowani* fall into the *tabida* clade (Rhymer et al. 2001, Glenn et al. 2002, Jones et al. 2005), *rowani* is morphologically diagnosable (Johnson and Stewart 1973), occupies a distinct intermediate (albeit overlapping) latitudinal breeding range, and does not completely overlap with either subspecies in its wintering range (Walkinshaw 1973). As a result, it merits recognition by managers. Discrimination of subspecies composition by vocalizations is far more powerful in the absence of a substantial proportion of *rowani*, but it would still have utility when *rowani* is present in large numbers. Our predicted formant-spacing distribution for *rowani* indicates that some *canadensis* and *tabida* individuals can still be identified in the presence of a high proportion of *rowani*. In such areas, formant-spacing values of 866.5–1,340 Hz/formant can be assigned to *canadensis* whereas values of 500–532.7 Hz/formant correspond to *tabida*. Furthermore, qualitative assessment of formant-spacing distributions in comparison with the distributions presented here (Fig. 2) will provide an overall portrait of the body size distribution of nonbreeding sandhill crane populations even when many *rowani* are present. When *tabida* and *canadensis* are the dominant components of the population, such a distribution would be bimodal and would provide an estimate of relative proportions of these 2 subspecies. In contrast, when all 3 subspecies are present in equal proportions the distribution would resemble a broad plateau. We classified 14.3% of cranes in the MRGV and 7.4% of cranes in the LRGV as unidentified because their formant-spacing values were in the range of overlap between *canadensis* and *tabida*. Based on our formant-spacing distributions of *canadensis* and *tabida*, we would expect 10.8% of values to fall into the unidentified range by chance if sampling from an area with equal proportions of *tabida* and *canadensis*. With equal proportions of *canadensis*, *tabida*, and *rowani*, we expect 39.7% of individuals to fall into the unidentified range. The individual crane calls that could not be identified likely include some female and small-bodied male *tabida* and male and larger bodied female *canadensis*, as well as the rarer *rowani*. Furthermore, an unknown proportion of *rowani* may have been classified incorrectly with *canadensis* or *tabida*.

Although the formant-spacing method has limited power in classifying intermediate-sized cranes, several aspects of this technique make it appropriate for use in the field. First,

gathering data for vocal analysis is rapid, inexpensive, and not labor-intensive. A single series of recordings of the morning flight of cranes from roosting to feeding sites could yield recordings of hundreds of individuals, and analysis should only take a few hours. The potential exists for achieving higher resolution using the formant-spacing method by examining the range of values within flocks. Males and females of the same subspecies differ in body size and are correspondingly expected to vary in formant spacing. Sandhill crane flocks consist of family groups that nearly always contain both sexes. Therefore, it should be possible to restrict the analysis to extreme formant-spacing values in each flock to provide more discriminatory power by explicitly testing for the presence of male *tabida* and female *canadensis*, each of which should be less subject to overlap among subspecies.

A key advantage of the formant-spacing method over hunter data is the ability to space sampling through the season and correspondingly evaluate potential shifts in phenology separately from population trends for each subspecies. This highlights a potential weakness in our data because some of our recordings are from late October at the LRGV, prior to substantial migratory arrival from either the RMP or MCP. Additionally, and perhaps most importantly, the formant-spacing method is noninvasive, ensuring its long-term viability for populations that may not be able to sustain current harvest rates, as is the case with the RMP.

Future refinements of this method may come from new data on the relationships among trachea length, formant spacing, and body size in sandhill cranes. In particular, the scaling of trachea length with body size should be investigated with respect to subspecies and sex. Whooping cranes (*G. americana*) have been shown to perceive formant spacing in species-specific calls (Fitch 2000), suggesting that this vocal characteristic may have previously unappreciated biological significance for sandhill cranes beyond its potential use in monitoring.

MANAGEMENT IMPLICATIONS

This study highlights the importance of implementing sensible and cautious conservation policies in the MRGV where nonbreeding crane populations are comprised primarily of *tabida* from the RMP. The formant-spacing method presented here could aid in monitoring *tabida* from the RMP or other low-latitude populations of concern in areas where they overlap with the globally abundant *canadensis* during the nonbreeding season. The intermediate size class (*rowani*) presents the most challenging problem for visual and vocal identification, but we recommend qualitative analysis of formant-spacing distribution in light of estimated and predicted distributions presented here. Further research is needed to clarify the diagnosability of sandhill crane subspecies using the formant-spacing method. However, our data suggest that the formant-spacing method may be implemented by management agencies to determine the subspecies composition of sandhill crane populations. In addition, the method could potentially be extended to other species in which populations that vary in size occur together, such as

Canada goose (*Branta canadensis*) and white geese of the genus *Cben*. This method, in conjunction with standard census methods, may provide a monitoring tool with sufficient resolution to detect distribution shifts or declines in RMP sandhill cranes, a discrete population that is esthetically and economically important.

ACKNOWLEDGMENTS

We thank the Macaulay Library of Sound for donating sandhill crane recordings and for archiving our recordings. We thank G. C. Schmitt for supplying hunter harvest data from 1983 to 1994 and T. Mitchusson of NMDGF for providing hunter harvest data from 1995 to 2010 and for specimen subspecies identification criteria. We thank E. J. Beckman, P. M. Benham, S. G. DuBay, M. O. Hilchey, A. B. Johnson, C. J. Schmitt, A. Smiley, R. VanBuskirk, and N. A. Wright for assistance in the field with vocal recordings at the MRGV and LRGV. We thank S. Maliakal-Witt, L. Smith, and G. Crane for assistance with logistics, permissions, equipment, and analyses. This project was facilitated by funding from the Sunzia Southwest Transmission Project. Finally, we thank 2 anonymous reviewers whose comments and suggestions greatly improved this manuscript.

LITERATURE CITED

- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29:1294–1297.
- Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Society Bulletin* 31:288–291.
- Bailey, F. M. 1928. *Birds of New Mexico*. Judd & Detweiler, Washington, D.C., USA.
- Benning, D. S., R. C. Drewien, D. H. Johnson, W. M. Brown, and E. L. Boeker. 1997. Spring population estimates of Rocky Mountain greater sandhill crane in Colorado. *Proceedings of the North American Crane Workshop* 7:165–172.
- Darden, S. K., T. Dabelsteen, and S. B. Pedersen. 2003. A potential tool for swift fox (*Vulpes velox*) conservation: individuality of long-range barking sequences. *Journal of Mammalogy* 84:1417–1427.
- Drewien, R. C., and E. G. Bizeau. 1974. Status and distribution of greater sandhill cranes in the Rocky Mountains. *Journal of Wildlife Management* 38:720–742.
- Drewien, R. C., W. M. Brown, and W. L. Kendall. 1995. Recruitment in Rocky-Mountain greater sandhill cranes and comparison with other crane populations. *Journal of Wildlife Management* 59:339–356.
- Drewien, R. C., P. P. Thorpe, and D. S. Benning. 2009. September 2008 count of the Rocky Mountain Population of greater sandhill cranes. Special report in the files of the Central Flyway Representative, Denver, Colorado, USA.
- Fant, G. 1960. The acoustic theory of speech production. Mouton, The Hague, The Netherlands.
- Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* 102:1213–1222.
- Fitch, W. T. 1999. Acoustic exaggeration of size in birds via tracheal elongation: comparative and theoretical analyses. *Journal of Zoology* 248:31–48.
- Fitch, W. T. 2000. Perception of vocal tract resonances by whooping cranes (*Grus americana*). *Ethology* 106:559–574.
- Fukui, D., N. Agetsuma, and D. A. Hill. 2004. Acoustic identification of eight species of bat (Mammalia: Chiroptera) inhabiting forests of southern Hokkaido, Japan: potential for conservation monitoring. *Zoological Science* 21:947–955.
- Glenn, T. C., J. E. Thompson, B. M. Ballard, J. A. Roberson, and J. O. French. 2002. Mitochondrial DNA variation among wintering Mid-Continent gulf coast sandhill cranes. *Journal of Wildlife Management* 66:339–348.
- Hartwig, S. 2005. Individual acoustic identification as a non-invasive conservation tool: an approach to the conservation of the African wild dog *Lycaon pictus* (Temminck, 1820). *Bioacoustics* 15:35–50.
- Johnson, D. H., and R. E. Stewart. 1973. Racial composition of migrant populations of sandhill cranes in the northern plain states. *Wilson Bulletin* 85:148–162.
- Jones, K. L., G. L. Krapu, D. A. Brandt, and M. V. Ashley. 2005. Population genetic structure in migratory sandhill cranes and the role of Pleistocene glaciations. *Molecular Ecology* 14:2645–2657.
- Kruse, K. L., D. E. Sharp, and J. A. Dubovsky. 2010. Status and harvests of sandhill cranes: Mid-Continent, Rocky Mountain and Lower Colorado River Valley Populations. U.S. Fish and Wildlife Service, Denver, Colorado, USA.
- Mitchusson, T. E. 2003. Long-range plan for the management of sandhill cranes in New Mexico. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.
- Nesbitt, S. A., and R. A. Bradley. 1997. Vocalizations of sandhill cranes. *Proceedings of the North American Crane Workshop* 7:29–35.
- Petersen, J. L., R. Bischof, G. L. Krapu, and A. L. Szalanski. 2003. Genetic variation in the Mid-Continental Population of sandhill cranes, *Grus canadensis*. *Biochemical Genetics* 41:1–12.
- Policht, R., M. Petru, L. Lastimoza, and L. Suarez. 2009. Potential for the use of vocal individuality as a conservation research tool in two threatened Philippine hornbill species, the Visayan hornbill and the rufous-headed hornbill. *Bird Conservation International* 19:83–97.
- Rhymer, J. M., M. G. Fain, J. E. Austin, D. H. Johnson, and C. Krajewski. 2001. Mitochondrial phylogeography, subspecific taxonomy, and conservation genetics of sandhill cranes (*Grus canadensis*; Aves: Gruidae). *Conservation Genetics* 2:203–218.
- Riede, T., and T. Fitch. 1999. Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). *Journal of Experimental Biology* 202:2859–2867.
- Schmitt, G. C., and B. Hale. 1997. Sandhill crane hunts in the Rio Grande Valley and southwest New Mexico. *Proceedings of the North American Crane Workshop* 7:219–231.
- Seager, R., M. F. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. P. Huang, N. Harnik, A. Leetmaa, N. C. Lau, C. H. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181–1184.
- Sharp, D. E., and W. O. Vogel. 1992. Population status, hunting regulations, hunting activity and harvests of the Mid-Continent Population of sandhill cranes. *Proceedings of the North American Crane Workshop* 6:24–32.
- Sharp, D. E., K. L. Kruse, and J. A. Dubovsky. 2007. Status and harvests of sandhill cranes: Mid-continent and Rocky Mountain Populations. U.S. Fish and Wildlife Service, Denver, Colorado, USA.
- Tacha, T. C., P. A. Vohs, and W. D. Warde. 1985. Morphometric variation of sandhill cranes from Mid-Continental North America. *Journal of Wildlife Management* 49:246–250.
- Tacha, T. C., S. A. Nesbitt, and P. A. Vohs. 1992. Sandhill crane (*Grus canadensis*). No. 31 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA. <<http://bna.birds.cornell.edu/bna/species/031>>. Accessed 24 Jan 2011.
- Walkinshaw, L. H. 1949. The sandhill crane. Volume 29. *Cranbook* Institute of Science, Bloomfield Hills, Michigan, USA.
- Walkinshaw, L. H. 1965. A new sandhill crane from central Canada. *The Canadian Field Naturalist* 79:181–184.
- Walkinshaw, L. H. 1973. *Cranes of the world*. Winchester Press, New York, New York, USA.
- Woodhouse, C. A., D. M. Meko, G. M. MacDonald, D. W. Stahle, and E. R. Cooke. 2010. A 1,200-year perspective of 21st century drought in southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America* 107:21283–21288.

Associate Editor: Peterson.