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RESEARCH ARTICLE

Trends in the body condition of Rocky Mountain Population sandhill cranes during spring and winter

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Abstract

Body condition during the spring and winter can have cross-seasonal effects on the reproduction and survival of migratory birds. The quality of resources on wintering and migratory stopover areas can impact nutrient reserves. During spring migration, greater sandhill cranes (*Antigone canadensis tabida*) in the Rocky Mountain Population rely on resources (e.g., grain, water) in the Middle Rio Grande Valley in New Mexico and the San Luis Valley in Colorado, USA. Our objective was to understand how sandhill crane body condition varies over time and in response to weather and resource availability. We collected sandhill cranes to determine an appropriate body condition index (BCI) for the species in this region and examine temporal trends in lipid and protein content during winter and spring. We then modeled within-year and across-year trends in the BCI of sandhill cranes in New Mexico harvested over a 20-year period (1999–2022) to determine the impact of weather (minimum temperature, drought severity) and habitat (surface water, vegetation, corn area) on BCI. Sandhill cranes increased lipid content throughout spring, with an average increase of 140 g for females and 146 g for males. The BCI that explained the most variation ($R^2 = 0.56$) in lipid content was body mass divided by the sum of tarsus length and wing chord. Of hunter-harvested sandhill cranes, BCI peaked in mid-November and again in early January; it increased by 22% between the lowest and highest observed values of normalized

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difference water index. In contrast, we observed a difference in BCI of only 2% between the lowest and highest observed minimum temperature values. We did not find a significant change in BCI over the 20-year study period, and no other covariates influenced BCI. While surface water and temperature influence body condition of sandhill cranes in this region, resource availability in the San Luis Valley and Middle Rio Grande Valley may be appropriate for meeting their energetic requirements.

KEYWORDS
Antigone canadensis tabida, harvest, lipid dynamics, migration, sandhill crane, wintering

Associations between body condition, or a measure of nutrient reserves (Labocha and Hayes 2012), and survival and reproduction have been found for several species of migrating birds (Alisauskas 2002, Devries et al. 2008, Gajdošová et al. 2023). Accumulation of lipids is important for migrating birds prior to and during migration, particularly during the non-breeding period, as lipids are the main energetic component for fueling migration (Jenni and Jenni-Eiermann 1998) and can improve survival probability during periods of low food availability (Haramis et al. 1986, Hepp et al. 1986). The influence of body condition can also be cross-seasonal (Devries et al. 2008, Sedinger and Alisauskas 2014, Fowler et al. 2020*a*). For example, poor body condition may delay departure from wintering or spring stopover areas (Lupi et al. 2016, Anderson et al. 2019, Vanausdall and Dinsmore 2021) and increase the overall duration of migration (Alerstam and Lindström 1990, Alerstam 2011). Delayed migration may result in a shorter timeframe for breeding or acquiring high-quality territory, which can ultimately affect reproductive success (Catry et al. 2013). Habitat quality and availability during the non-breeding period may directly influence body condition and could result in cross-seasonal effects on populations through reproduction or survival (Baker et al. 2004, Sedinger and Alisauskas 2014, Swift et al. 2020, Fowler et al. 2020*a*). Examining variation in body condition within seasons and over several years can inform the ability of a population to acquire adequate nutrient reserves and also provide insight into the quality of specific stopover and wintering areas for migrant birds (Baker et al. 2004, Fleskes et al. 2016).

Migratory birds may change in body condition over time owing to many endogenous and exogenous factors. Prior to and throughout spring migration, birds will accumulate lipids and may undergo significant internal changes to prepare for the migratory journey (Piersma and Jukema 1990, Mathot et al. 2020). Individuals may be low in condition at the start of autumn migration because of the challenges of breeding and brood-rearing, and the wintering period is an important time for species to acquire and maintain nutrient reserves (King and Fox 2012, Swift et al. 2020). Some species show a clear mid-winter decline in body condition (Miller 1986, Rhodes et al. 2006, Skalos et al. 2021), which may be stress-related and due to food shortage, harsh weather conditions, or the energetic requirements of pair bonding (Miller 1986, King and Fox 2012, Fox et al. 2013, Massey et al. 2020). There are also metabolic costs to greater lipid accumulation and increased risk of predation due to exposure when foraging (Witter and Cutthill 1993), so a decline in body condition may allow birds to balance energetic demands of the non-breeding period (King and Fox 2012, Fox et al. 2013). Habitat quality during the wintering period and at stopover areas is related to overwinter survival and can have other cross-seasonal effects during subsequent months (Raveling and Heitmeyer 1989, Sedinger and Alisauskas 2014, Swift et al. 2020). Measures of habitat quality linked to body condition include surface water availability for waterbirds (Veon et al. 2023), seasonal vegetation green-up (i.e., new vegetation growth) or insect availability (Drent et al. 2007, Kölzsch et al. 2016), and waste grain availability for waterfowl or sandhill cranes (*Antigone canadensis*; Anteau et al. 2011, Pearse et al. 2013). A common management strategy is to provide supplemental forage and adequate habitat for wintering or staging birds (Stafford et al. 2011, Hagy and Kaminski 2012, Boggie et al. 2023).

Weather and climate may affect body condition directly or through impacts on habitat (Baldassarre et al. 1986, Klimas et al. 2019). Some factors, such as temperature, may directly influence energetic regulation and maintenance of birds, including their ability to thermoregulate. Colder temperatures, for example, require an increase in respiration rate to maintain a stable body temperature (Peters 1986). At the other extreme, increasingly hotter temperatures or drought conditions have been associated with decreased body condition (Klimas et al. 2019, McLean et al. 2020), but other studies have found a positive trend between temperature and body condition (Baldassarre et al. 1986, McCloy and Grace 2023). Some research has identified a link between climate or habitat on nonbreeding grounds and population-level demographics later in the season (Bearhop et al. 2004, Sedinger and Alisauskas 2014, Saunders et al. 2021, Clements et al. 2022), while others have not (Horn et al. 2021). Examining the influence of weather and land use on body condition can inform management of resources for migrating birds under continued climate and landscape changes.

The status and population dynamics of sandhill cranes in the western United States are of particular interest for research and management because of their reliance on water for both roosting and foraging and their status as a game species throughout parts of their range. The Rocky Mountain Population (RMP) of greater sandhill cranes (*A. c. tabida*) primarily winters in the Middle Rio Grande Valley (MRGV) in New Mexico and breeds throughout Idaho, Montana, Wyoming, Utah, and western Colorado, USA (Drewien and Bizeau 1974, Kauffeld 1981). The San Luis Valley (SLV) in southcentral Colorado is a key stopover area, as >90% of the population is in the SLV at one time during spring and autumn migrations (Drewien and Bizeau 1974, Donnelly et al. 2021, Vanausdall et al. 2024). Cranes in this population primarily forage on waste grain (i.e., grain leftover in fields after harvest), especially barley and corn, during the migratory and wintering periods (Vanausdall et al. 2025). Grains and other foods high in carbohydrates allow for the rapid deposition of lipids (Krapu et al. 1985), which may be particularly important in the spring, allowing individuals to arrive on breeding areas in relatively good body condition. Most waste grain comes from private property, but state and federal agencies provide supplementary food in both the SLV and their wintering areas in New Mexico (Boggie et al. 2023). Sandhill cranes also roost and loaf in wetlands and riverine ecosystems on both public and private lands, generally within 5–10 km of foraging sites (Ivey et al. 2015, Collins et al. 2023).

Ongoing landscape changes from agricultural shifts, climate change, and increased pressure on water resources may affect habitat availability for sandhill cranes. The amount of harvested barley in the SLV, for example, has decreased by about 40% in the last 20 years (National Agricultural Statistics Service [NASS] 2023), in part because of changes in the economic demand for barley and increased pressure on depleting water resources in the region (Mix et al. 2010). Additionally, the SLV has lost nearly 50% of its wet area since 1984, and this threatens wetland and riverine habitat availability for sandhill cranes (Donnelly et al. 2019). Decreases in water availability throughout their range are due to reduced snowpack, overuse of water resources, and prolonged drought (Pederson et al. 2011, Llewellyn and Vaddey 2013, Dettinger et al. 2015). Water declines are projected to continue within the next century in Colorado and other parts of the Intermountain West (Ray et al. 2008, Llewellyn and Vaddey 2013). Severe drought is predicted to increase along their range (Dai 2011). Based on previous research, surface water is likely more limiting than forage availability (Donnelly et al. 2021), but a shift in either resource may influence the ability of RMP sandhill cranes to acquire and maintain adequate energy stores during the nonbreeding period. Changes in the juxtaposition of roosting and foraging habitats can influence the energetic requirements during migration and winter (Pearse et al. 2011).

Annual population indices for RMP sandhill cranes have increased gradually since 1997, and recruitment indices have been stable since 1972 (Seamans 2024). However, increased drought in the West has been attributed to reduced recruitment in RMP sandhill cranes (Drewien et al. 1995, Gerber et al. 2015), and other environmental conditions (e.g., grain availability, surface water availability, temperature) have been associated with movement and migration patterns (Donnelly et al. 2021, Bunting et al. 2022). A direct link between overwintering body condition and fitness the following season has not been documented for sandhill cranes, but documenting changes within and among years in body condition is still informative. If trends in the rate of lipid accumulation decline within the wintering or spring migration period, this could indicate limitations related to habitat quality or availability in either of these areas. A drop in body condition during a time of the year with lower energy requirements (i.e., winter) may be optimal and adaptive under reduced resource availability (Reinecke et al. 1982) or it could be maladaptive and lead to reduced survival probability or reproductive success (Alisauskas et al. 2002, Devries et al. 2008). If body condition declines across several years and is lower than average, this could suggest climate or habitat quality has changed or declined over that time frame.

In this study, we used a combination of scientifically collected and hunter-harvested sandhill cranes to examine variations in body condition during spring and winter and the impact of meteorological and habitat covariates on body condition. Specifically, we used scientifically collected sandhill crane specimens to examine the temporal trends of lipid accumulation in the SLV during 2 different projects separated by 20 years and to determine the best predictor of a body condition index for greater sandhill cranes. Body condition indices are proxies for nutrient reserves (usually lipids) and are often used in lieu of direct measures of nutrient accumulation in birds (Labocha and Hayes 2012). We then used the best approximating body condition index (BCI) to examine the within- and among-year trends in body condition for sandhill cranes harvested in New Mexico across 23 years. We used the hunter-harvested sandhill cranes to determine the influence of weather (i.e., minimum temperature, drought severity) and habitat availability (i.e., corn area, surface water, vegetation) on body condition. Given the importance of forage and roosting habitat to sandhill cranes (Donnelly et al. 2021), we expected the habitat model to be the most competitive and to see positive effects of corn area, water, and vegetation on BCI. We also expected weather covariates to be competitive, with a higher BCI under wetter conditions and with fewer nights with freezing temperatures. Lastly, we expected the weekly change in body condition to increase over time as sandhill cranes arrive on their wintering grounds and forage throughout the season.

STUDY AREA

Our study took place in the SLV in Colorado and the MGRV in New Mexico (Figure 1). The SLV is the northernmost portion of the Rio Grande Basin in the southwestern United States. The area of the SLV is approximately 8,200 km^2, and it is surrounded by the San Juan Mountains to the west and the Sangre de Cristo Mountains to the east. The mean elevation in the SLV is 2,100 m. The Rio Grande has its headwaters in the San Juan Mountains, and it runs through the SLV, down to New Mexico through the MRGV, and eventually to the Gulf of Mexico. The runoff of water from melting snow in the mountains is the primary source of water input in the SLV. The valley received about 200 mm or less of water in precipitation, while the mountains received 1,270 mm on average (Cooper et al. 2006). Two aquifers also contribute to the hydrology of the SLV in the form of water recharge and discharge. The average temperature in the SLV was 6°C, and winds were highly variable (Western Regional Climate Center 2013). The landscape of the SLV was largely characterized by alfalfa, barley, and potato production. Sandhill cranes primarily used private property in the SLV, but the Monte Vista National Wildlife Refuge (NWR) provides wetlands for a variety of waterbirds and grows supplemental grain for migrating sandhill cranes and waterfowl. State Wildlife Areas maintained by Colorado Parks and Wildlife also provide roosting and loafing opportunities. Vegetation such as cottonwood (*Populus deltoides*) and willows (*Salix* spp.) dominate riparian areas, while shrub-scrub makes up much of the non-wetland and non-agricultural areas on both private and public land.

The Rio Grande River runs south into the MRGV in New Mexico and is bounded by the Cochiti Reservoir to the north and the Elephant Butte Reservoir to the south (Dettinger et al. 2015). The MRGV is a narrow valley and approximately 746 km^2 in area with a mean elevation of 1,470 m. Precipitation averaged approximately 19 mm, and the mean temperature was 8°C. Similar to the SLV, the MRGV is dominated by agriculture, but urban and suburban

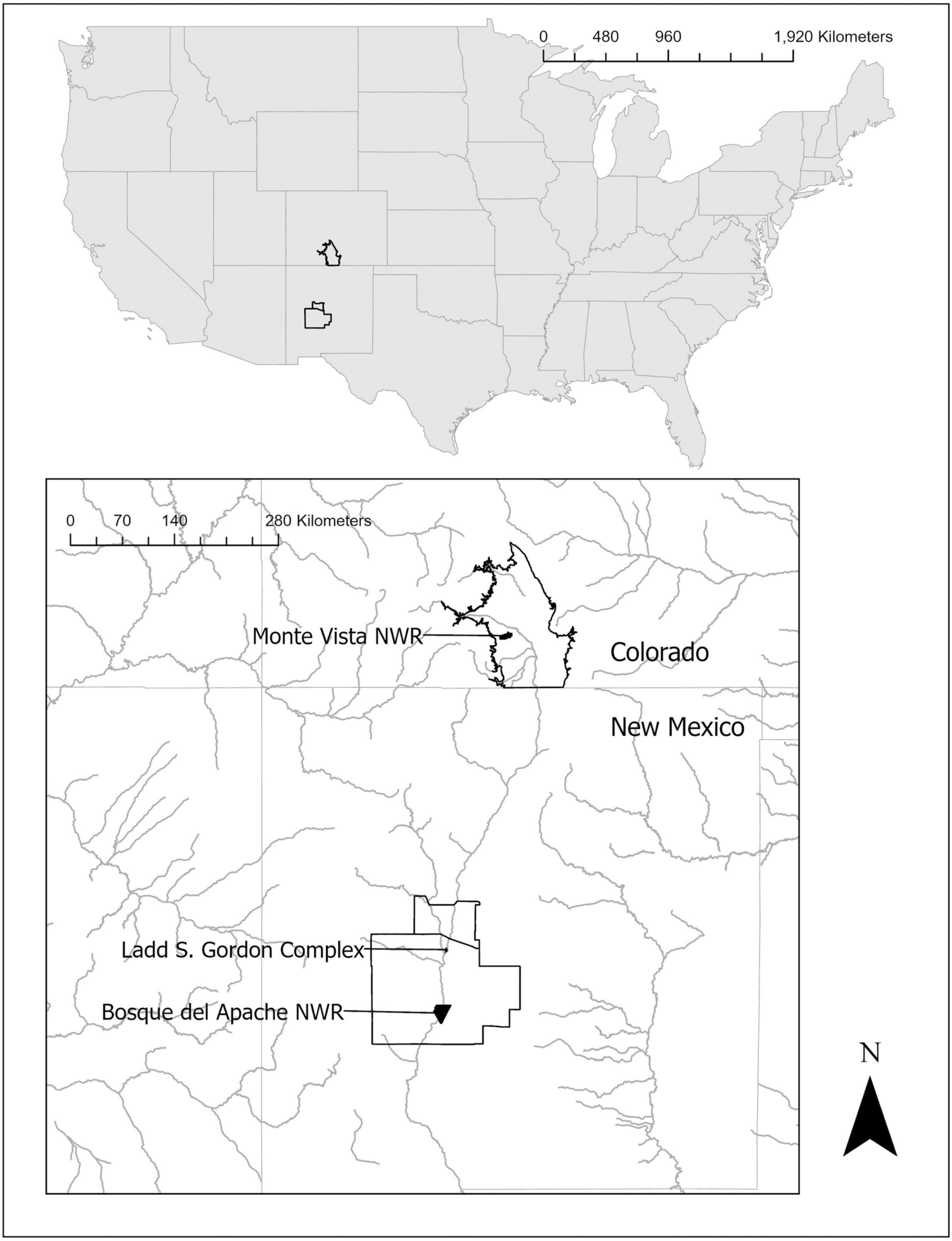

FIGURE 1 A map of the areas where Rocky Mountain Population sandhill cranes were collected or harvested in 1999–2022, which includes the San Luis Valley (SLV) in Colorado and Socorro and Valencia counties in New Mexico, USA. Two federal properties (Monte Vista National Wildlife Refuge [NWR], Bosque del Apache NWR) and one state property (Ladd S. Gordon Complex) are indicated.

areas are mixed throughout the region. Along with the Rio Grande and its tributaries, the diversion of water from the Colorado River via the San Juan-Chama project also provides water (Oad et al. 2009). Sandhill cranes intensely use both federal land, including Bosque del Apache NWR, and state land, specifically the Ladd S. Gordon Complex managed by the New Mexico Department of Game and Fish. Corn is planted to provide forage for wintering sandhill cranes each year, and the cranes roost in moist-soil managed wetlands and along the Rio Grande.

METHODS

Specimen collection and measurements

To examine temporal trends in lipid accumulation and determine the best-approximating body condition index, we collected greater sandhill cranes during 2 time periods. Initial collections occurred in spring (February–March) 1999–2001 in the SLV. The second period of collection took place during winter (December–January) 2020–2021 in New Mexico and spring (February–April) 2021 in the SLV. For both collection periods, we collected foraging sandhill cranes using rifles or shotguns. Because these studies were also a part of other projects examining the food contents of collected sandhill cranes, we observed individuals for approximately 20 minutes before collection to ensure the esophagus would contain forage. To get a more representative cross-section of the population, we tried to avoid taking mated pairs or pairs that had young with them. We distinguished adults from juveniles using plumage characteristics (Tacha 1988). We immediately froze the collected specimens.

After thawing individuals in the lab, we obtained a fresh carcass weight (g) and removed internal organs and ingesta. All individuals collected in both periods were weighed ±50 g. While we ensured that all specimens were not exposed to excess moisture prior to freezing, we recognize that thawing of frozen specimens could affect their mass because of evaporation or condensation. We measured the length (±1 mm) of the flattened wing chord, along with tarsus (i.e., the length between the intertarsal joint to the tibiotarsus), and culmen. We measured culmen length as the distance from the tip of the culmen to the post-nares for the 2020–2021 period, and as the entire culmen length in the 1999–2001 period. We plucked each sandhill crane and reweighed carcasses.

We sexed individuals by using observations from the field and examining internal organs in the lab. However, for the 37 individuals that could not be confidently sexed, we used genetics testing using methods defined in Lee et al. (2010). We isolated genomic DNA from 0.1 g of frozen muscle and amplified the *CHD* gene, located on the sex chromosome, using polymerase chain reaction (PCR) with the primers CHD1 R and CHD1°F (Lee et al. 2010). The PCR reactions to amplify *CHD* followed the standard HotStarTaq (Qiagen, Valencia, CA, USA) protocol. We then assessed sex by running the PCR product on a 1% agarose gel by gel electrophoresis. The presence of 2 bands in the gel at approximately 550 and 350 base pairs indicated the presence of both the Z and W chromosomes (i.e., female), whereas the presence of a single band at approximately 550 base pairs indicated the presence of only the Z chromosome (i.e., male; Lee et al. 2010).

Proximate analysis

We homogenized the ingesta-free carcasses and dried a 100–300-g sample of each carcass to a constant weight at 80°C. Based on the period of collection, we processed samples for lipid and protein using 2 separate but similar methods. For the 1999–2001 samples, we extracted lipids from the dried sample using petroleum ether in a modified Soxhlet apparatus (Dobush et al. 1985). We then placed the samples in a muffle furnace at 550°C to obtain protein. For the 2020–2021 samples, we used methods similar to Klimas et al. (2019) and Massey et al. (2020). We head-sealed a 1.0–2.0-g sample of the dried homogenate in an Ankom filter bag (Ankom Technology, Macedon, NY, USA), weighed the sample (±0.1 mg), and extracted lipids using an Ankom XT15 Lipid Extractor.

We reweighed the samples to obtain a lean dry sample mass. We extrapolated sample lipids and carcass lipids by multiplying the sample lipid amount by the inverse of the proportion of carcass mass represented by each homogenate, and we used the same method for protein content.

Hunter-harvested specimen collection

The harvest of sandhill cranes has been ongoing through much of their range since 1981, when the first modern-day hunt was initiated in Arizona (Seamans 2024). Currently, RMP sandhill cranes are legally hunted in 6 states and Mexico, and during 1999–2024, 522–1,670 individuals were harvested in the United States (Seamans 2024). Approximately 170–710 RMP sandhill cranes are harvested in New Mexico from October through January. Hunters must take collected sandhill cranes to check stations, where several measurements are taken by biologists, including body mass, wing chord, culmen length, and tarsus length, using the same methods described above. We used data from check stations in Socorro and Valencia counties, New Mexico, between 1999 and 2022 to examine trends in body mass and body condition. However, because of personnel changes from 2011 through 2015, we detected measurement errors in the body metrics. We excluded data from that timeframe (Figure 2).

Estimating body condition

The use of body condition indices is common when proximate analysis data are not available, but their use is still debated (Green 2001, Labocha and Hayes 2012). Body condition indices generally represent the amount of lipid or protein content of individual birds, with some indices showing a higher correlation with lipids or protein than others (Labocha and Hayes 2012). Many studies that use body condition indices often assume that a particular index of choice is correlated with actual lipid content without additional data (Fleskes et al. 2016, Vanausdall et al. 2022), but whenever possible this assumption should be validated (Fowler et al. 2018). We examined several commonly used

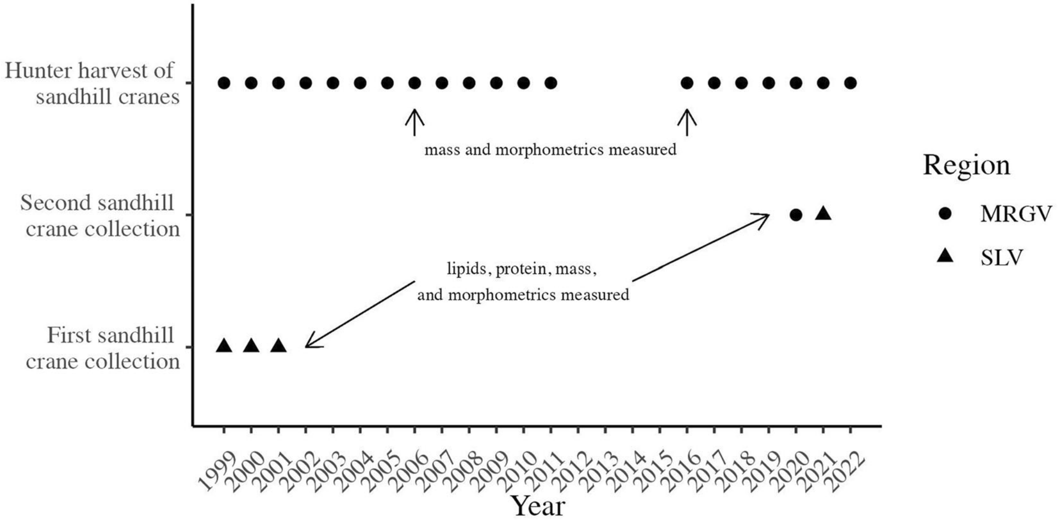

FIGURE 2 A graphical representation of the years during which Rocky Mountain Population sandhill cranes were collected or harvested in the Middle Rio Grande Valley (MRGV) in New Mexico and the San Luis Valley (SLV) in Colorado, USA.

body condition indices (Labocha and Hayes 2012) of the scientifically collected specimens and compared them to actual estimates of lipid content. We chose the following indices: 1) body mass, 2) body mass divided by wing chord, 3) body mass divided by tarsus length, 4) body mass divided by the sum of wing chord and tarsus length, 5) the residuals of a linear model with body mass by wing chord, 6) the residuals of a linear model with body mass by tarsus length, and 7) the scaled body mass index (Peig and Green 2009). While body mass alone can be a good indicator of nutrient reserves, this is not always the case (Labocha and Hayes 2012). Increases in the structural size of animals do not necessarily scale up in the same way as nutrient reserves, such as lipids, which means that heavier birds may not always be in better condition than lighter birds. The other indices attempt to account for increases in structural size as mass increases by, for example, dividing mass by a linear component of the bird's body (Labocha and Hayes 2012, Peig and Green 2009).

Weather and habitat covariates

We considered weather and habitat covariates that may influence the ability of sandhill cranes to acquire and maintain nutrient reserves during the wintering period in New Mexico. Minimum temperature can serve as a proxy for cold temperatures that may increase energetic demands (Peters 1986), but above-normal warming may also be costly to birds (Aubry et al. 2013, McLean et al. 2020). Additionally, drought can negatively affect the availability of water sources, including roosting habitat, used by sandhill cranes (Gerber et al. 2015). It may also indirectly affect forage availability if crops are stressed or of lower quality due to limited water for irrigation. We obtained gridded surface meteorological data (gridMET) using the package climateR in Program R (Johnson 2024). The gridded data are provided at a resolution of 4 km, and we used data for Socorro and Valencia counties in New Mexico for the study period. We obtained monthly average values for minimum temperature (TMin). The Palmer drought severity index (PDSI) is a commonly used method that measures drought severity using a water balance equation, which incorporates prior precipitation, runoff, evaporation, and moisture (Palmer 1965). The PDSI is autoregressive and is influenced by the previous month's score. It ranges between about −4 and 4, with lower values indicating more severe drought conditions and higher values indicating wetter conditions.

For habitat covariates, we used measurements that were likely to influence either roosting or forage availability for sandhill cranes. We estimated vegetation, a proxy for surface water, and corn availability throughout the MRGV. We obtained vegetation data using satellite imagery and the publicly available Google Earth Engine (Gorelick et al. 2017). We estimated monthly values of vegetation using the normalized difference vegetation index (NDVI) from Landsat 8 and 9 satellite imagery corrected for surface reflectance, which had a resolution of 30 × 30 m. Similarly, we used the normalized difference water index (NDWI) to estimate an index of monthly values of surface water. We obtained data on corn availability from the cropland data layer from the National Agricultural Statistics Service (NASS) for Socorro and Valencia counties. These data were yearly values of corn in hectares planted during the study period. We expected surface water, NDVI, and corn availability to indicate overall good roosting and foraging habitat conditions, so we predicted a positive effect of all covariates on body conditions.

Statistical analysis

To examine temporal trends in the body mass, lipid content, and protein content of scientifically collected specimens, we examined the 2 collection periods (1999–2001 and 2020–2021) both separately and together. We grouped dates of collection into 4 seasons: 1 December–5 February (winter), 15 February–28 February (early spring), 1 March–15 March (mid-spring), and 16 March–1 April (late spring). Specimens were not collected during 6–14 February. The seasonal bin cutoffs were primarily based on sample size constraints but also align with the expected movement patterns of sandhill cranes in the SLV. The probability of arrival increases throughout early spring, peaks in mid spring, and gradually declines in late spring (Vanausdall et al. 2024). Only the 2020–2021 cranes were collected during winter, so we first examined temporal dynamics in lipid, protein, and body mass of the more recently collected group. We used analysis of variance (ANOVA) with Type III sums of squares to determine if there was a difference in mean lipids, protein, and body mass among seasons. We did not have a large enough sample size to test for differences between the sexes. We then combined the 1999–2001 group and the 2020–2021 group to examine within-spring temporal trends in the SLV. We conducted an ANOVA with Type III sums of squares with season (excluding winter), sex, and collection period (i.e., group 1 = 1999–2001 cranes, group 2 = 2020–2021 cranes). The response variables (lipids, protein, and body mass) were scaled to have a mean of zero and a standard deviation of one. We determined covariates to be significant at $P < 0.05$. We used the Tukey-Kramer *post hoc* test to determine significant ($P < 0.05$ and 95% CIs did not overlap zero) differences among seasons, sex, and collection groups and also visualized modeled differences by plotting the estimated marginal means of response variables across observed covariates. We examined histograms of the 3 response variables (lipids, protein, and body mass) to ensure data were normally distributed and boxplots across season, sex, and collection groups to ensure homogenous variances. Finally, we plotted residuals of ANOVAs with the fitted values to assess model fit. We used the car package in Program R for the ANOVAs (Fox and Weisberg 2019, R Core Team 2024).

We combined cranes from both collection periods to determine the best predictive model for body condition. For each BCI, we used general linear models (GLM) in a Bayesian framework with lipids as the response variable and each BCI as an explanatory variable. We also included sex as a fixed effect (1 = female, 0 = male) to account for structural differences in specimens. We scaled and centered both the response variable (i.e., lipids) and each BCI. We assessed the performance of BCIs using 3 metrics. First, we compared models using the Watanabe-Akaike Information Criterion (WAIC), where the most competitive model had the lowest WAIC value (Spiegelhalter et al. 2002, Watanabe 2010). Compared to other information criteria, WAIC is fully Bayesian and appropriate for Bayesian hierarchical models (Gelman et al. 2014), which we use in the next set of analyses. Next, to assess the proportion of the variance explained by the GLM, we calculated R^2 values based on Gelman et al. (2019). Third, we examined the root mean squared error (RMSE) to assess the accuracy of each model, with a more accurate model having a lower RMSE. Once we determined the best predicting model for body condition, we used the resulting BCI to calculate body condition for hunter-harvested sandhill cranes and used the calculated BCI as the response variable in the next step.

In the second step, we examined the effects of age, sex, week, year, weather, and habitat covariates on the selected BCI of hunter-harvested sandhill cranes using a general linear mixed model (GLMM). Prior to model building, we assessed the collinearity of covariates by calculating the Pearson correlations and identified pairs of covariates that were highly correlated (i.e., $r > 0.70$), and we also examined variance inflation factors (VIF) in a simple linear regression. A VIF > 5 was considered to be evidence of multicollinearity. In this model, we used the top BCI from the first step as the response variable, while age, sex, week, year, and the environmental covariates were the explanatory variables. Specifically,

$$y_{i,g,t} \sim \text{Normal}(g(\alpha_g, \beta_p, x_p), \sigma^2)$$

$$g(\alpha_t, \boldsymbol{\beta_p}, \boldsymbol{x_{p,g,t}}) = \alpha_g + \boldsymbol{\beta_p x_{p,g,t}} + \varepsilon_t$$

$$\varepsilon_t \sim \text{Normal}\left(0, \sigma_\varepsilon^2\right),$$

where $y_{i,g,t}$ is the BCI for the ith harvested sandhill crane in week g and year t. The fixed intercept was allowed to vary by week g within each year. We grouped within-season times of harvest into 10 7-day periods, which we refer to as a week (Table 1), rather than using daily values, because the number of sandhill cranes harvested varied

TABLE 1 The date ranges for when Rocky Mountain Population sandhill cranes were harvested during the winters of 1999–2010 and 2016–2022 in the Middle Rio Grande Valley, New Mexico, USA.

Week number	Date range
1	23 October – 30 October
2	31 October – 6 November
3	7 November – 13 November
4	14 November – 20 November
5	21 November – 27 November
6	28 November – 4 December
7	5 December – 11 December
8	12 December – 18 December
9	2 January – 8 January
10	9 January – 16 January

each day. The vector of slope coefficients $\boldsymbol{\beta}_p$ represents the effect of each covariate p on BCI, with $\boldsymbol{x}_{p,g,t}$ representing the data collected for each covariate in week g and year t. We also included sex and age as fixed effects in all models and included an error term to account for unexplained temporal variation in each year t, which was distributed by a Normal distribution with a mean of zero and standard deviation of σ_{ε}^{2}. We scaled and centered response and explanatory variables. The weather covariates included TMin and PDSI, while the habitat covariates included NDWI, NDVI, and corn availability. The covariates TMin, PDSI, NDWI, and NDVI were average monthly values per year, while corn availability was only available for a year. We first determined the best within-season time (i.e., week) covariate that explained temporal variation in body condition. We hypothesized that accumulation of lipids would be nonlinear because of changing environmental conditions, so we examined 3 models, each with either a linear, quadratic, or cubic polynomial trend on week with all covariates as main effects and with only age and sex covariates. We used the pattern for week from the model with the lowest WAIC in all models for the next step. The weather model included week, a trend across seasons, and all weather covariates (i.e., TMin and PDSI). The habitat model included the same time covariates and the habitat covariates (i.e., corn area, NDWI, and NDVI).

We deemed a covariate to be influential if its 95% credible interval did not overlap zero. We calculated the weekly change in body condition across the entire study period (1999–2023) as derived posterior means. We examined the marginal effects of covariates across the observed values while holding other covariates constant at their mean. We assessed model fit for our global model and the more general model using posterior predictive checks (Kéry and Schaub 2012). We simulated a dataset using the estimated parameter values in the model and calculated the difference between the simulated dataset and the observed dataset. The Bayesian P value represents the proportion of time the simulated dataset is greater than the observed dataset. We would expect the Bayesian P value to equal 0.50 under a model that fits the data well, but values between 0.1 and 0.9 indicate an appropriate fit (Conn et al. 2018). We specified flat priors for intercept and slope parameters; we used Uniform(0, 50) for the standard deviation of the data (σ^2) and standard deviation for year-specific intercepts (${\sigma^2}_{\alpha}$) and used Normal(0,100) for slope coefficients for covariate p (β_p) and the mean year-specific intercepts (μ_{α}). We used a Markov chain Monte Carlo (MCMC) algorithm to sample the posterior distribution of parameters and used the rjags package (Plummer 2024) in Program R. We sampled posterior distributions using 3 chains that included 100,000 MCMC iterations with a burn-in of 40,000. We used trace plots and the Gelman-Rubin statistic with R-hat < 1.1 (Brooks and Gelman 1998) to assess convergence.

RESULTS

We collected 84 RMP sandhill cranes during the 1999–2001 period and 60 RMP sandhill cranes during the 2020–2021 period (Table 2). We excluded 7 RMP sandhill cranes from 2020–2021 because of measurement error. We did not find an effect of season on lipid content ($F_{3,49} = 2.050$, $P = 0.119$), protein content ($F_{3,49} = 1.064$, $P = 0.373$), or body mass ($F_{3,49} = 1.542$, $P = 0.215$) for the 2020–2021 collection group (Figure S1). Combining data for the 1999–2001 collection group and the 2020–2021 collection group in the SLV, we found an effect of season ($F_{2,103} = 11.236$, $P < 0.001$), sex ($F_{1,103} = 5.944$, $P = 0.0.16$), and collection period ($F_{1,103} = 11.828$, $P < 0.001$) on mean lipid content. Sandhill cranes increased lipid content by 116 g (95% CI = 38, 195 g; $P = 0.002$) between early spring and mid spring and by 155 g (95% CI = 68, 241 g; $P < 0.001$) between early spring and late spring (Table 2; Figure 3A). Males had a slightly higher lipid content than females (difference = 54 g, 95% CI = −1, 110 g; $P = 0.056$), but the difference in the estimated marginal means was nonsignificant and the 95% confidence interval overlapped zero. The 1999–2001 collection group showed a higher lipid content than the 2020–2021 collection group (difference = 111 g, 95% CI = 46, 177 g; $P < 0.001$). We found an effect of sex only for protein ($F_{1,103} = 9.349$, $P = 0.002$), with males having approximately 58 g (95% CI = 21, 95 g) more protein content than females (Table 2). Season ($F_{2,103} = 3.829$, $P = 0.025$), sex ($F_{1,103} = 24.593$, $P < 0.001$), and collection group ($F_{1,103} = 17.648$, $P < 0.001$) influenced body mass. Sandhill cranes weighed approximately 209 g (95% CI = −7, 425 g; $P = 0.058$) more in late spring compared to early spring, but the difference in the estimated marginal means was nonsignificant and the 95% confidence intervals overlapped zero. Males had a higher body mass than females and weighed approximately 306 g (95% CI = 167, 445 g; $P < 0.001$) more than females. The 1999–2001 group had a higher body mass than the 2020–2021 group (Figure 3C), with the 1999–2001 group weighing 334 g (95% CI = 170, 498 g; $P < 0.001$) more than the 2020–2021 group. The response variables met assumptions of normality (Figure S2) and homogeneity of variances across seasons (Figures S3A, S4A, S5A), sex (Figures S3B, S4B, S5B), and collection periods (Figures S3C, S4C, S5C). We did not find a discernible pattern in plots of the residuals and fitted values (Figure S6).

The best-performing BCI for RMP sandhill cranes was an index of body mass divided by the sum of tarsus length and wing chord, which had the highest R^2 value, lowest WAIC, and lowest RMSE (Table 3). All models converged (i.e., R-hat < 1.1) and had Bayesian P values at 0.50.

A total of 5,074 RMP sandhill cranes were harvested between 1999 and 2022, which did not include the winters of 2011–2015 (Table S1). Males were larger than females and adults were larger than juveniles on average (Table S1).

Average minimum temperature declined within a year (Figure S7A). The PDSI remained relatively stable (Figure S7B), average NDVI declined (Figure S7C), and average NDWI increased (Figure S7D) on average between October and January. Across years, TMin remained stable (Figure S8A), while average PDSI was highly variable (Figure S8B), and average NDWI declined (Figure S8C). Average NDVI showed a slight increase across the study timeframe (Figure S8D). The area of corn declined slightly throughout the study period (Figure S9).

A model for BCI of hunter-harvested sandhill cranes with a cubic polynomial time trend for time within seasons had the lowest WAIC, but a model with only a quadratic time trend was also competitive (i.e., ≤2 WAIC; Table 4). We decided to use the simpler competitive model, the quadratic time model, as the top time model for the next phase of model selection. After accounting for habitat and weather covariates, the top model included all covariates. No covariates were highly correlated (i.e., $r > 0.70$), and we did not find any covariates with a VIF > 5. Sex and age showed significant effects on BCI, with males having higher BCI than females and adults having higher BCI than hatch-year individuals (Figure 4, S10). The covariate NDWI (i.e., water) had a positive effect on body condition, but 95% credible intervals were wide (Figure 4). The effect of NDWI showed an increase of 22% in the sandhill crane BCI between the driest (−0.16) and wettest (−0.09) observed values of NDWI (Figure 5A). Average minimum temperature had a slightly negative effect on BCI, but the upper 95% credible interval was close to zero (Figure 4). The effect of TMin showed a decrease of 2% in BCI between the lowest (−8°C) and highest (7°C) observed values of TMin (Figure 5B). All other covariates (i.e., NDVI, corn availability) had credible intervals that overlapped zero. Parameters converged (i.e., R-hat < 1.1) and showed appropriate mixing in all models (Figure S11). Bayesian P values also indicated good model fit (i.e., P values = 0.50).

TABLE 2 The sample size (*n*), average ($\overline{x}$), and standard error (SE) of morphometrics, body mass, lipid content, and protein content of Rocky Mountain Population sandhill cranes collected in New Mexico and Colorado, USA, during the winter and spring of 2020–2021 and in Colorado during the springs of 1999–2001. The within-year seasons are winter (1 December–5 February), early spring (15 February–28 February), mid-spring (1 March–15 March), and late spring (16 March–1 April). Culmen length was measured as the tip of the culmen to post-nares in the 2020–2021 period, while it was measured as the entire culmen length in the 1999–2001 group. Tarsus measured the length of the tibiotarsus, and wing chord measured the length from the bend of the wing to the tip of the longest primary.

		Body mass (kg)		Total lipids (g)		Total protein (g)		Culmen (mm)		Tarsus (mm)		Wing chord (mm)	
	n	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE
2020–2021 group													
Winter													
Male	19	6.06	0.12	774.91	49.07	1,186.86	40.32	107.26	1.15	253.53	2.49	562.42	4.92
Female	10	5.58	0.11	666.15	53.86	1,070.73	27.37	100.40	2.09	237.10	3.36	542.40	7.32
Early spring													
Male	2	5.60	0.23	467.96	52.75	1,071.18	67.54	102.50	2.50	247.50	12.50	599.50	39.50
Female	2	5.28	0.09	505.68	104.88	1,083.66	68.99	93.05	2.05	242.50	2.50	539.00	9.00
Mid-spring													
Male	10	6.08	0.15	687.00	64.62	1,240.96	66.32	104.20	3.80	251.05	4.78	562.00	6.04
Female	1	5.47	0.00	630.96	0.00	1,066.98	0.00	101.00	0.00	220.00	0.00	539.00	0.00
Late spring													
Male	6	6.16	0.14	702.31	67.21	1,192.84	57.19	108.00	2.10	260.33	6.90	552.33	4.45
Female	3	5.64	0.22	660.30	129.69	1,163.54	57.26	103.00	4.36	244.00	10.69	520.00	11.55
1999–2001 group													
Early spring													
Male	15	6.23	0.07	692.25	25.74	1,176.76	13.02	134.75	1.91	237.40	2.88	548.93	5.56
Female	12	5.84	0.13	572.63	44.10	1,109.04	26.93	124.71	2.81	223.42	2.43	522.75	5.20

TABLE 2 (Continued)

		Body mass (kg)		Total lipids (g)		Total protein (g)		Culmen (mm)		Tarsus (mm)		Wing chord (mm)	
	n	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Mid-spring													
Male	17	6.37	0.08	762.58	30.38	1,201.46	23.11	133.92	1.54	236.76	1.51	553.41	5.59
Female	18	6.03	0.08	743.55	34.82	1,122.19	22.87	126.17	1.96	226.78	1.63	527.83	5.61
Late spring													
Male	15	6.33	0.09	845.80	39.20	1,168.07	27.55	132.91	1.23	237.47	2.55	554.40	4.89
Female	7	6.13	0.13	730.11	34.62	1,138.41	18.37	124.03	2.01	226.86	2.01	538.14	7.56

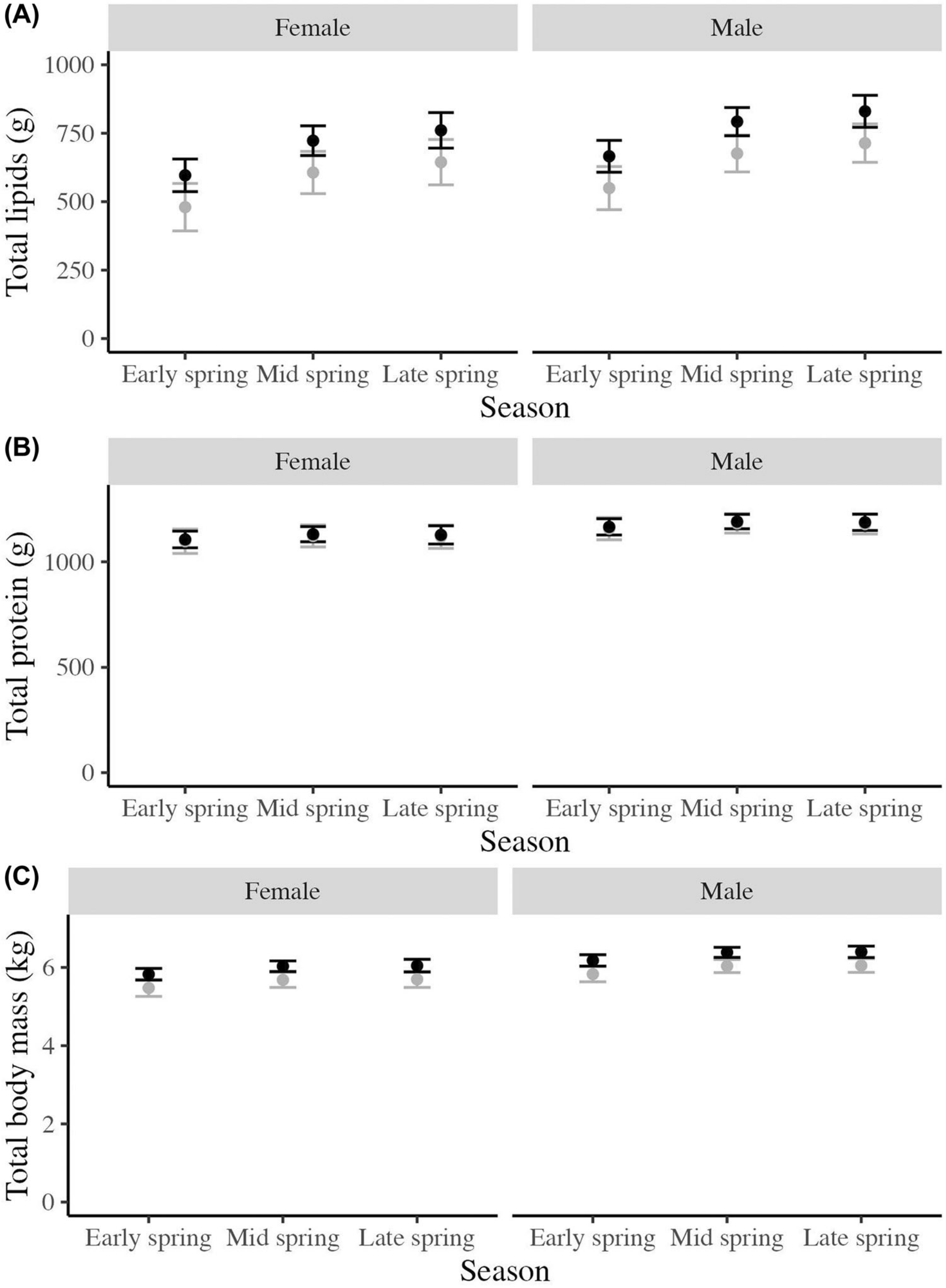

FIGURE 3 The estimated marginal means of (A) total fat (i.e., lipids), (B) total protein, and (C) total body mass from Rocky Mountain Population sandhill cranes collected during the springs of 1999–2001 (black circles) and 2021 (grey circles) in Colorado, USA. The vertical bars are 95% confidence intervals.

TABLE 3 Mean posterior values (and standard errors) of coefficient estimates (β_0, β_1, β_1) and predictive assessments from general linear models of lipid content regressed with body condition indices (BCI) for sandhill cranes in collected in New Mexico and Colorado, USA, during the winter and spring of 2020–2021 and in Colorado during the springs of 1999–2001. The predictive assessment included R^2 from Gelman et al. (2019), root-mean-squared-error (RMSE), and the Watanabe Akaike's Information Criterion (WAIC). Tarsus measured the length of the tibiotarsus, and wing chord measured the length from the bend of the wing to the tip of the longest primary.

Body condition index	β_0	$\beta_1(BCI)$	$\beta_2(sex)$	R^2	RMSE	WAIC
Body mass	−0.01 (0.09)	0.60 (0.08)	0.02 (0.16)	0.56 (0.04)	1.15 (0.07)	337
Body mass/wing chord	−0.08 (0.10)	0.62 (0.08)	0.21 (0.17)	0.55 (0.04)	1.17 (0.07)	340
Body mass/tarsus	−0.01 (0.09)	0.57 (0.08)	0.03 (0.16)	0.55 (0.04)	1.18 (0.07)	343
Body mass/(wing chord + tarsus)	−0.08 (0.10)	0.65 (0.08)	0.21 (0.16)	0.56 (0.04)	1.14 (0.07)	335
Residuals of wing chord × body mass	−0.06 (0.10)	7.13 (0.953)	0.14 (0.17)	0.55 (0.04)	1.17 (0.07)	342
Residuals of tarsus × body mass	−0.07 (0.10)	7.08 (0.91)	0.18 (0.16)	0.55 (0.04)	1.16 (0.07)	338
Scaled-body mass index	0.11 (0.10)	0.46 (0.08)	−0.27 (0.16)	0.54 (0.04)	1.24 (0.08)	355

TABLE 4 Model selection results for the effect of time, year, sex, age, weather covariates, environment covariates, and population estimates on the body condition of Rocky Mountain Population greater sandhill cranes in the Middle Rio Grande Valley in New Mexico, USA, 1999–2010 and 2016–2022.

Model[a]	WAIC	Bayesian *P* value
Week + week^2 + week^3 + year + sex + age + Tmin + PDSI + NDVI + water + grain	12,564	0.50
Week + week^2 + year + sex + age + Tmin + PDSI + NDVI + water + grain	12,566	0.50
Week + week^2 + year + sex + age + NDVI + water + grain (habitat only)	12,571	0.50
Week + week^2 + year + sex + age + Tmin + PDSI (weather only)	12,575	0.50
Week + week^2 + year + sex + age	12,576	0.63
Week + week^2 + week^3 + year + sex + age	12,589	0.50
Week + year + sex + age + Tmin + PDSI + NDVI + water + grain	12,590	0.50
Week + year + sex + age	12,630	0.61
Intercept only	14,136	0.65

[a] Covariates included minimum temperature (TMin), Palmer drought severity index (PDSI), normalized difference vegetation index (NDVI), normalized difference water index (water), and grain area.

DISCUSSION

Monitoring trends in the body condition of a migratory population provides insight into potential responses to environmental change. Hunter-harvested species coupled with body condition indices informed by collected individuals can provide a valuable source for understanding body condition dynamics (Labocha and Hayes 2012, Fowler et al. 2018). Our study documented the temporal pattern in the body condition of both scientifically collected and hunter-harvested RMP sandhill cranes at a spring stopover area and wintering area and identified covariates as influencing BCI. Spring-migrating sandhill cranes showed patterns in body condition consistent with trends whereby many migratory birds rapidly increase lipids prior to the breeding season (Krapu et al. 1985,

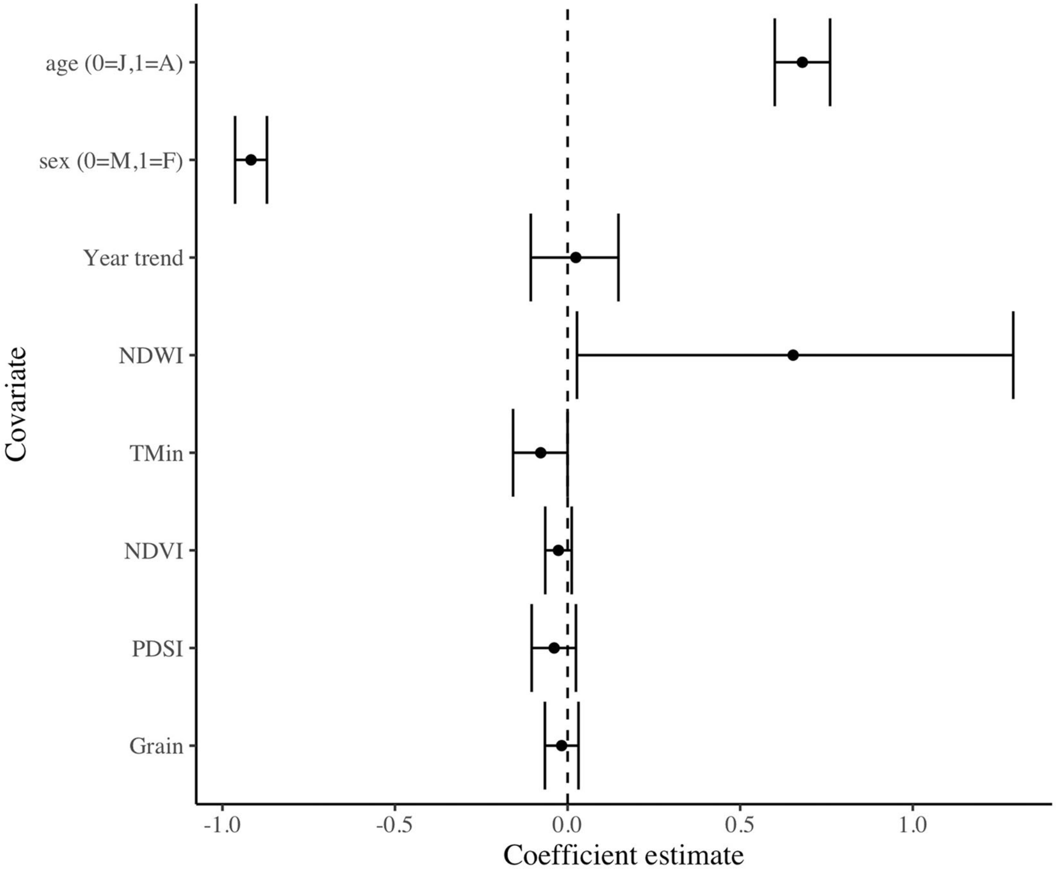

FIGURE 4 Coefficient estimates of variables in the best-supported model (time effects not shown) that evaluated the effects of age, sex, a year trend, normalized difference water index (NDWI), minimum temperature (TMin), normalized difference vegetation index (NDVI), Palmer drought severity index (PDSI), and grain area on the body condition (body mass divided by the sum of wing chord and tarsus length) of hunter-harvested Rocky Mountain Population sandhill cranes in the Middle Rio Grande Valley, New Mexico, USA, during the winters of 1999–2010 and 2016–2022.

Eichhorn 2005, Drent et al. 2007), while wintering sandhill cranes showed little temporal variation and more distinct differences among cohorts (i.e., males vs. females, adults vs. juveniles). We found that a habitat covariate (water index) and a weather covariate (minimum temperature) were associated with the BCI of hunter-harvested sandhill cranes, but the effect size of minimum temperature was small. Sex and age of sandhill cranes had much stronger effect sizes. While it is not yet known how body condition may relate to the population dynamics of the RMP, we provide evidence that environmental changes have the potential to impact sandhill crane energetics.

Sandhill cranes showed a change in the proportion of lipids and body mass and a slight change in protein during spring migration, but we only found this trend when combining both the 1999–2001 and 2020–2021 datasets. We acknowledge that the methods for extracting lipids were different for each dataset, and we attempted to account for this difference by including the collection period in models. The 2020–2021 collection group was also composed of a relatively small sample of specimens, which may explain the lack of a seasonal effect. However, the trend in lipid change over time was similar for the 2 collection groups. When combining both datasets, the increase in lipids in spring showed an average accumulation of approximately 140 g and 146 g for females and males, respectively, from early spring to late spring. Sandhill cranes in other populations and regions show a significant

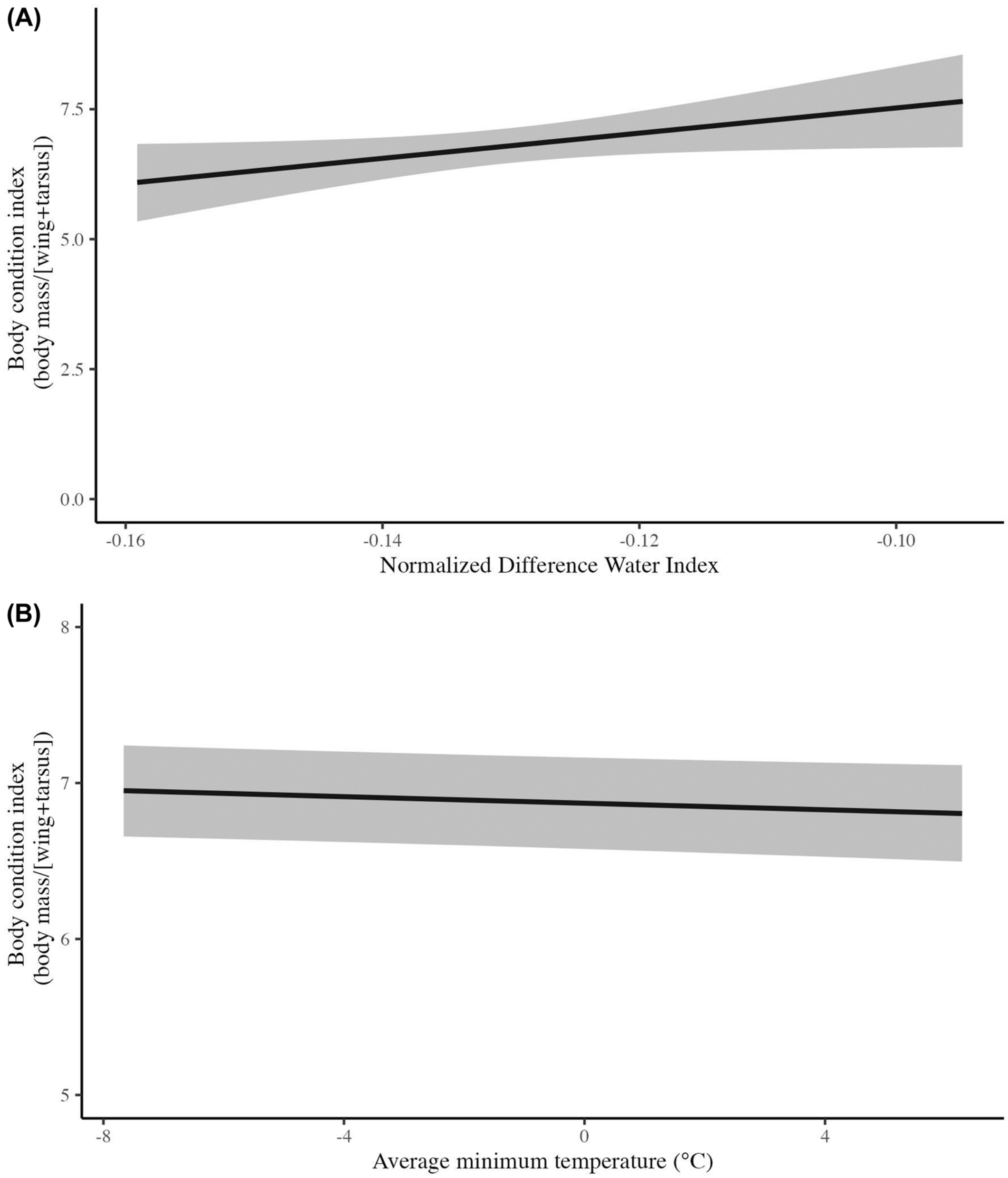

FIGURE 5 The effect of the (A) normalized difference water index (i.e., water availability) and (B) minimum temperature on the body condition (body mass divided by the sum of wing chord and tarsus length) of hunter-harvested Rocky Mountain Population sandhill cranes in the Middle Rio Grande Valley, New Mexico, USA, during the winters of 1999–2010 and 2016–2022.

increase in lipid content during spring migration (Krapu et al. 1985, 2014), and this pattern is also found in other migratory birds, including geese (Clausen et al. 2003, Pearse et al. 2011), shorebirds (Lyons and Haig 1995), and passerines (Goymann et al. 2010). While sandhill cranes are not complete capital breeders (Krapu et al. 1985), lipids and other nutrients play a role in egg formation and allow birds to complete migration (Alisauskas 2002, Eichhorn 2005), buffering against environmental variation at the breeding areas. Indeed, the decline and then increase in lipids and mass between winter and spring support the assertion that the SLV is important for sandhill cranes to replenish energy reserves before continuing migration to breeding areas. While we found a slight increase in protein levels during spring migration and a difference between males and females, the trend over time was not significant. This is in contrast to the findings of Krapu et al. (1985), who found a significant increase in protein levels among male sandhill cranes during spring. We cannot conclude if the lack of a change in protein levels is due to inadequate protein in the available forage, sandhill cranes in the RMP accruing more protein elsewhere during migration, or an inadequate sample size. Birds can use endogenous reserves of protein through catabolism of muscle, but for many species most protein for reproduction is acquired through the diet (Ankney and MacInnes 1978, Alisauskas and Ankney 1985, Ankney and Afton 1988). Compared to the Mid-Continent Population, RMP sandhill cranes travel much shorter distances between their spring stopover areas and breeding areas. Endogenous reserves may not play as critical a role in allowing RMP sandhill cranes to complete migration and arrive on breeding sites in good condition compared to the Mid-Continent Population, so it could be that protein used for reproduction by the RMP is mostly obtained from their breeding areas.

Several migrant birds experience a predictable change in overwintering body condition (English et al. 2018, Massey et al. 2020, Herzog et al. 2024), but we did not detect a distinct change in our estimate of body condition for RMP sandhill cranes in New Mexico during winter. Waterfowl, for example, may show a decline in mid-winter due to a limitation of habitat availability, the presence of harsh weather conditions, or endogenous drivers that may reduce energetic requirements during periods of lowered resource availability (Reinecke et al. 1982, Massey et al. 2020, Vanausdall et al. 2022). Harsh weather conditions could include freezing temperatures that limit water availability and require additional energy to maintain adequate body temperatures. However, we found that average minimum temperature had a slight (i.e., significant but close to zero) negative impact on body condition, which was contrary to our predictions. A decrease in body condition with increasing minimum temperature could be a strategy for optimizing energy use, as additional body stores may be energetically unnecessary when temperatures are warmer during roosting. We also found a slight increase in body condition over time, with adults having higher body condition than juveniles. Adults are likely more efficient foragers than juveniles, and adults with juveniles may not have access to the highest quality resources when avoiding social interactions, which could contribute to reduced body condition in young (Reinecke et al. 1982, Morton et al. 1989). We may not have detected a change in body condition because of the availability of supplemental forage on federal and state properties, which can be sufficient for overwintering sandhill cranes and waterfowl to meet their energetic requirements (Boggie et al. 2023).

The positive effect of NDWI, which served as an index for surface water, on body condition was consistent with our hypothesis. However, the 95% credible intervals were relatively wide so should be interpreted with caution. Several studies have identified winter habitat variables influencing body condition (Bearhop et al. 2004, Petrie et al. 2016, Fowler et al. 2020*b*), while others found little to no support (Horn et al. 2021). Surface water is important for sandhill cranes for roosting, as they prefer to roost in relatively shallow water with short vegetation, away from human disturbances, and close to foraging areas (Kauffeld 1981, Boggie et al. 2018*b*). Decreases in surface water may result in increased energy expenditure, as sandhill cranes may need to fly farther between roosting areas and foraging areas, which may lead to decreased body condition if individuals are unable to compensate. Surface water is also indicative of other foraging opportunities that may decline with reduced surface water. Boggie et al. (2018*a*), for example, found sandhill cranes regularly foraging in both wetlands and corn fields during winter. They found that alkali bulrush (*Scoenoplectus maritimus*) and yellow nutsedge (*Cyperus esculentus*), wetland plants found in the diet of wintering sandhill cranes, provide a lipid-rich source of food in New Mexico (Boggie et al. 2018*a*). Wetland plants and invertebrates can also provide additional nutrients that sandhill cranes may not obtain from grain alone (Krapu et al. 1984, Boggie et al. 2018*a*).

Additionally, negative NDWI values could be indicative of drought conditions. While we did not find a significant effect of our drought index, PDSI, the relationship with BCI was trending negative, indicating that wetter conditions resulted in greater BCI values. We linked drought to a decreased availability of roosting and loafing areas, reduced foraging opportunities (Petrie et al. 2016), and, as a result, reduced body condition. Other studies have linked drought conditions to reduced body condition due to forage limitations (Miller 1986). Indeed, Donnelly et al. (2021) identified flooded wetlands as being important in maintaining migratory connectivity for sandhill cranes in the West. However, in more agreement with our findings, Bunting et al. (2022) noted that sandhill crane presence in autumn pre-staging areas increased in drier conditions (i.e., negative values of PDSI), and they attributed this contrast to higher concentrations of sandhill cranes in areas with water, which is more limited in drier conditions. While drought severity may increase movement by sandhill cranes as they try to find water or the distance between roosts and forage areas increases, it is possible that wintering RMP sandhill cranes in New Mexico move less owing to limited water availability and focus on fewer areas with both forage and roosting opportunities. We may not have found a significant impact of PDSI on BCI because drought indices incorporate multiple factors related to soil moisture, temperature, and related factors (Heim 2002, Vicente-Serrano et al. 2010). There may be a particular aspect of PDSI masking the real impact of drought on BCI, which could warrant further investigation.

Contrary to our prediction, we found that the area of corn, which makes up a significant portion of the diet of migrating and wintering sandhill cranes (Krapu et al. 1984, Ballard and Thompson 2000, Boggie et al. 2018*a*), did not have a significant effect on BCI. We assumed that greater planted corn area would translate to greater grain availability for sandhill cranes, which would lead to better body condition. The lack of a relationship between corn area and body condition could be due to at least 2 reasons. First, the area of corn planted in the MRGV may not be a reliable indicator of the amount of corn or grain available to sandhill cranes, as it is not a measure of biomass available after harvest. Most grain fields are harvested in autumn, and the amount of seed spilled during harvest can be highly variable among individual fields. As a result, the addition of more corn fields in a year may not necessarily indicate an increase in grain availability. Harvest equipment has also become more efficient over the years and ultimately leaves less spilled grain than a few years ago (Krapu et al. 2004). Second, based on observations and tracking data, the majority of RMP sandhill cranes in New Mexico appear to primarily use publicly managed fields where corn is grown specifically for wintering sandhill cranes and waterfowl. These crops are rationed, with a majority not cut until the arrival of sandhill cranes in winter. A measure of corn area or biomass at publicly managed areas alone may show a different impact on body condition than when both public and private areas are combined.

There are limitations to our analysis that we recognize. First, inferences made from a sample of hunter-harvested sandhill cranes may not be completely representative of the population because of the potential for a condition bias in hunter-harvested individuals compared to those sampled randomly. Several studies on waterfowl have confirmed that birds in poorer body condition are more vulnerable to harvest, and individuals harvested over decoys may be in poorer condition than those collected at random through jump-shooting (Greenwood et al. 1986, McCracken et al. 2000, Szymanski et al. 2013, Fowler et al. 2020*a*; but see Grzegorczyk et al. 2022). While we found the BCI of harvested sandhill cranes obtained in December and January to be within the bounds of the 95% confidence intervals for individuals randomly collected during the same season, the latter group had a small sample size (n = 29) compared to the former (n = 2,008). We were not able to directly compare all harvested sandhill cranes with the randomly collected individuals collected in spring because of a difference in the timing of collection. Second, the correlation of the BCI with lipids of collected sandhill cranes was relatively low (r ~ 0.60), indicating that there is still variation in lipid content not being explained by the BCI measurements provided. Similar studies on waterfowl have used more than 3 external body measurements to account for body size and estimate condition indices (Afton and Ankney 1991, Ballard et al. 2006, Labocha and Hayes 2012). Furthermore, body condition indices that are highly correlated for one species may not be correlated with another species (Labocha and Hayes 2012). There could be a better indicator of structural size for sandhill cranes that is currently not being collected and that may better account for lipid content in hunter-harvested sandhill cranes.

MANAGEMENT IMPLICATIONS

Continued monitoring of sandhill crane body condition in winter provides a long-term dataset that can be used to examine potential responses of the RMP to environmental changes. This analysis identified a BCI (i.e., body mass divided by the sum of tarsus and wing chord) correlated with lipid levels in greater sandhill cranes that could be used to continue to monitor body condition over time in harvested specimens. Using this index, we found no significant changes in the body condition of sandhill cranes during the last 20 years. Supplemental forage provided for sandhill cranes and waterfowl on public areas on their wintering areas may ensure they continue to meet their energetic demands, while grain availability in the SLV seems to also be providing adequate forage for lipid accumulation. To further investigate the best-approximating body condition index and improve correlation between the index and lipid levels, additional morphological features and a larger sample size could be collected (Labocha and Hayes 2012). We also found that NDWI and TMin may affect crane bioenergetics, but these covariates did not explain as much variation in body condition as individual characteristics (i.e., sex and age). Other weather or environmental covariates may have a stronger effect on sandhill crane energetics, so continued investigation could be warranted.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our collection protocol was approved by Colorado Parks and Wildlife for both collection periods and the Colorado State University Institutional Animal Care and Use Committee for the 2020–2021 time period. The appropriate permits at the federal level (Permit #MB89291D-0) and for New Mexico (Authorization #3791) and Colorado (Permit #1849839645) were obtained.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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