



Differential shortstopping behaviour in Whooping Cranes: Habitat or social learning?

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ABSTRACT

Many migratory bird species have begun shifting their wintering grounds closer to their breeding grounds, shortening their yearly migration distance through a behavior called shortstopping. While multiple studies have investigated possible drivers, it remains unclear why only some populations adopt this behavior.

We studied the differential occurrence of shortstopping in two populations of Whooping Cranes (*Grus americana*): a remnant population where juveniles migrate with their parents, and a reintroduced population consisting largely of captive-reared birds trained to migrate by unrelated conspecifics or by humans. Shortstopping is widespread in the reintroduced population, while the remnant population has not shown any appreciable northward movement of its overwintering sites. We examined potential drivers for this lack of shortstopping, including a lack of suitable habitat north of their current wintering area or social differences between populations.

Using characteristics of winter locations used by the reintroduced population, we found that 31.4% of the remnant migration corridor was predicted to be suitable for wintering, suggesting that insufficient habitat suitability is not limiting shortstopping behaviour. However, we found evidence for behavioural differences that might explain the absence of shortstopping in the remnant population: while all juveniles of the remnant population associate with their parents during overwintering, juveniles from the reintroduced population did not associate with older conspecifics in 12 out of 25 observed wintering events, suggesting that the social transmission of winter migration behaviours might be less effective in the reintroduced population. Although social learning is generally believed to increase flexibility in migratory strategies, a strong vertical transmission of behaviour might enforce adherence to established traditions and reduce the uptake of novel behaviours such as shortstopping. We suggest that, besides habitat availability, social factors may also play a role in explaining the absence of shortstopping behaviour in some migratory bird populations.

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1. Introduction

In recent decades, many migratory bird species have shifted their wintering areas closer to their breeding grounds, effectively shortening their yearly migration distances (La Sorte and Thompson, 2007; Visser et al., 2009; Potvin et al., 2016). These range shifts, identified as shortstopping (Elmberg et al., 2014), represent an important survival strategy in the face of climate change, potentially allowing migratory populations to adapt to changing vegetation phenology and earlier accessibility of breeding grounds (Sedinger et al., 2011; Barton and Sandercock, 2018; Polakowski et al., 2018). Shortstopping occurs across taxonomic groups (Paprocki et al., 2014; Guillemain et al., 2015; Potvin et al., 2016), but can vary widely, with differences in its magnitude or presence among populations of the same species and within the same region (Maclean et al., 2008; Visser et al., 2009; Goodrich et al., 2012; Flack et al., 2016; Potvin et al., 2016; Folliot et al., 2018). Understanding why shortstopping behaviour varies among populations and species is key to understanding and predicting the responses and resilience of migratory species to environmental change.

Shortstopping behaviour is driven partially by environmental factors. Novel foraging opportunities may arise through shifts in temperature and precipitation, as by-products of changing agricultural practices, or through supplementary feeding (La Sorte and Thompson, 2007; Lehikoinen et al., 2013; Jónsson and Afton, 2015; Teitelbaum et al., 2016). These environmental changes enable migratory birds to overwinter in areas that previously were unsuitable wintering habitat, thereby benefiting from decreased migration distances and associated decreases in energy expenditure (Alerstam et al., 2003) as well as increases in survival (Newton, 2006; Cheng et al., 2019).

Whether migrants respond to shifts in habitat availability may also depend on their migration strategies: Following changes in environmental cues, short distance migrants adjust their migration timing more readily than long-distance migrants (Usui et al., 2017; Powers et al., 2021); accordingly, decreases in migration distance have been observed primarily in short- and medium-distance migrants (Elmberg et al., 2014). Yet, there is evidence for shortstopping in species that perform extraordinarily long migrations (Takekawa et al., 2009; Bruner, 1994 as cited in Elmberg et al., 2014).

Migration strategies, including shortstopping, can be propagated socially through the transmission of knowledge between individuals (Galef and Laland, 2005; Hoppitt and Laland, 2013). While migration behaviours are genetically propagated in many bird species (Kramer, 1957; Gwinner, 1996; Åkesson et al., 2017), in some species – notably cranes and geese – a small number of particularly experienced or exploratory individuals are often responsible for establishing new migration strategies, including shortstopping, that are then transmitted to large parts of the populations via social learning (Teitelbaum et al., 2016; Clausen et al., 2018). Through social learning, new behaviours can spread more quickly than by genetic evolution alone, boosting the resilience of populations to environmental change (Sutherland, 1998). The social transmission of migration traditions can induce remarkable flexibility in migration strategies (Kondo et al., 2008; Ward et al., 2009; Jonker et al., 2012; Teitelbaum et al., 2016). On the other hand, the social transmission of behaviours can also act to conserve existing traditions in a population rather than promote the spread of new strategies, for example by facilitating behaviours that persist across generations (Galef, 2003; Keith and Bull, 2017). Because learning socially may represent a less costly alternative to asocial learning (Galef and Laland, 2005), the presence of socially transmitted information in a population may inhibit innovation through asocial learning, thereby reducing behavioural variation. In some cases, this lack of adaptability can decrease the resilience of a population to environmental change (Barrett et al., 2019). Thus, strong social bonds could either increase or decrease the probability that shortstopping emerges and spreads through a population.

Given that environmental factors, migration strategies, and learning mechanisms together are important drivers of shortstopping behaviour, the absence of shortstopping in a population could be related to any of these factors. To study the mechanisms underlying shortstopping behaviour, we leveraged a unique opportunity to compare two populations of Whooping Cranes (*Grus americana*), a social, migratory bird species. One of these populations is the product of a recent reintroduction effort and exhibits extensive shortstopping behaviour (Teitelbaum et al., 2016) while the other, a remnant wild population, rarely winters away from its traditional sites (Wright et al., 2014). This allowed us to investigate two competing hypotheses: (i) habitat differences between the two migration corridors produce the observed differences in shortstopping, or (ii) differences in the populations' social structure may be responsible.

The absence of shortstopping behaviour in the remnant population may be related to a lack of suitable wintering sites within its migration corridor, north of its current wintering range. To test this hypothesis, we built a habitat suitability model based on the wintering site selection of the shortstopping reintroduced population and subsequently predicted potential wintering habitat across the migration corridor of the remnant population. According to our hypothesis (i), we predicted that this corridor is largely unsuitable for wintering Whooping Cranes, i.e., the lack of suitable habitat is restricting shortstopping.

In the remnant population, juveniles presumably learn migration and wintering behaviours from their parents, with whom they are associated over the course of nearly an entire year (Stevenson and Griffith, 1946; Allen, 1952; Kuyt, 1992). Extended parental care throughout the winter is a common strategy in migratory cranes that has also been observed for Siberian cranes *Leucogeranus leucogeranus* and Hooded Cranes *Grus monacha* (Shao et al., 2014), Red-crowned Cranes *Grus japonensis* (Wang et al., 2011), Sandhill Cranes *Grus canadensis* (Hayes and Barzen, 2016) and Common Cranes *Grus grus* (Alonso et al., 1984). Here, social learning might act as a conservative force, constraining habitat preferences and exploratory behaviour, thereby impeding the development of novel behaviours such as shortstopping. In contrast, in the reintroduced population, juveniles were artificially trained to migrate by ultralight aircraft or unrelated conspecifics, with which they were associated for considerably less time (usually <6 months; Urbanek et al., 2014). This comparatively weaker regime of social transmission might allow for the development of novel behaviours through experiential learning, while still facilitating the spread of such innovations between individuals through the social bonds that remain.

We tested the strength of social ties between juveniles and potential adult tutors in the reintroduced population by calculating the distance between the wintering site of each juvenile and the wintering site of the nearest adult in that year. Juveniles with strong ties to

adult conspecifics should overwinter close to them, as is the case in the remnant population and populations of other migratory crane species, while juveniles with weak social ties should be more inclined to seek out a wintering site on their own, potentially farther away from other birds. Furthermore, we tested how migration distances differed between juveniles that wintered with and without adult conspecifics. According to our hypothesis (ii), we predicted that the average distance between wintering juveniles and adults in the reintroduced population is larger than the average winter territory diameter (a liberal estimate of juvenile-parent distances) of the remnant population, indicating weaker social ties. We did not expect weaker social ties to directly result in shortstopping during the first migration, because the development of this behaviour has been linked to the accumulation of experience over several years of migration (Teitelbaum et al., 2016).

2. Methods

2.1. Study system

The two extant migratory populations of Whooping Cranes are the Aransas Wood Buffalo Population (AWBP), which constitutes the last remnant Whooping Crane population after the species passed through a severe population bottleneck in the first half of the 20th century, and the Eastern Migratory Population (EMP), the product of an ongoing reintroduction effort (French et al., 2019).

The AWBP breeds in Wood Buffalo National Park in Alberta and the Northwest Territories, Canada, and overwinters in and around Aransas National Wildlife Refuge on the Texas coast, USA. Successful breeders migrate as family groups with their newly fledged offspring, and family groups virtually always stay together for the entire winter and portions of the subsequent spring migration (Stevenson and Griffith, 1946; Allen, 1952; Kuyt, 1992).

The EMP migrates between central Wisconsin in summer and as far south as the coast of Florida in winter (French et al., 2019). Beginning in 2001, human handlers trained captive-reared juveniles to follow ultralight aircraft on their first southward migration

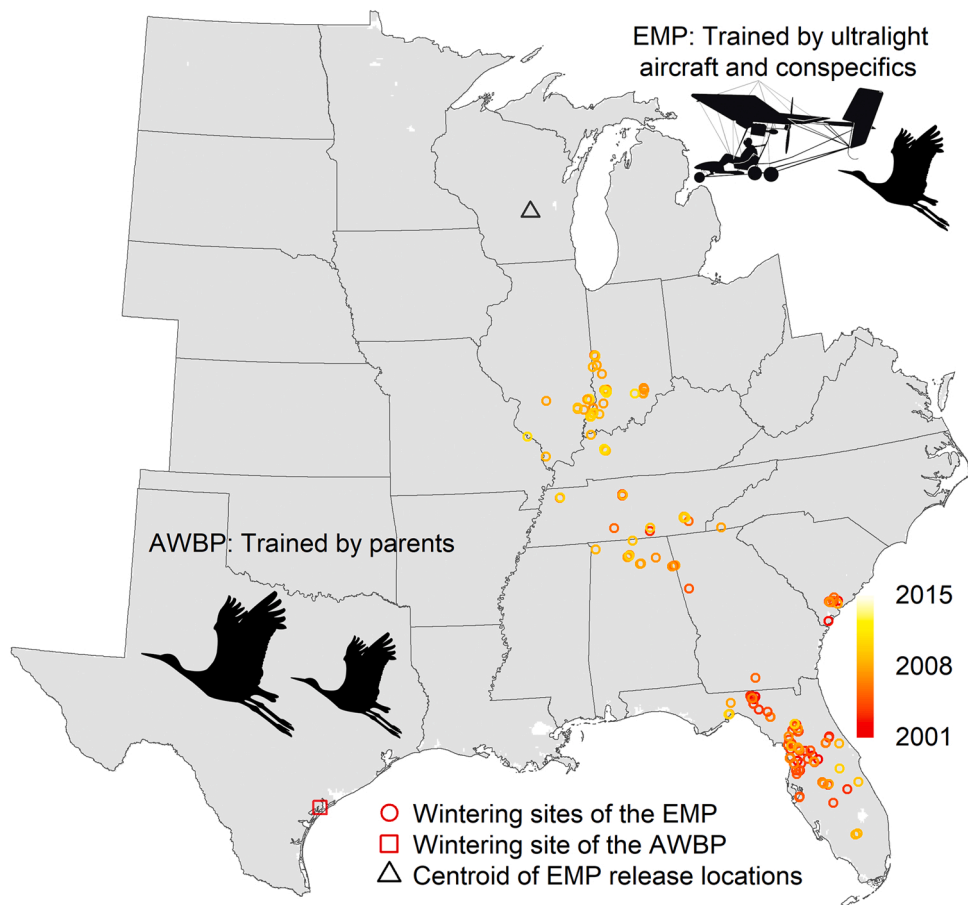


Fig. 1. : Traditional and novel wintering sites of the two migrating populations of Whooping Cranes. Every fall, the birds in the AWBP migrate in family groups from central Canada to Aransas NWR on the coast of Texas, while the birds in the EMP initially were artificially trained to migrate from Wisconsin to release sites in Florida (and Alabama in one year). The emergence of shortstopping behaviour has led to greatly reduced migration distances in the EMP as the cranes have discovered novel wintering sites far from the original release sites (Teitelbaum et al., 2016).

(French et al., 2019). The original reintroduction sites in coastal Florida featured extensive salt marshes and were chosen to resemble the wintering area of the AWBP (Urbanek et al., 2010; Urbanek et al., 2014). Individuals trained in this way migrated back to Wisconsin on their own, and continued to migrate twice a year without further human intervention (Urbanek et al., 2014); this method was discontinued in 2016. Beginning in 2005, managers implemented another method of migration training called direct autumn release (Urbanek et al., 2014), in which hand-reared cranes were released on the breeding grounds in autumn with the intention that they would follow migrating conspecifics. In 2013, a third release method was implemented, in which birds raised in captivity by Whooping Crane breeding pairs were similarly released on the breeding grounds (Converse et al., 2019). A relatively small number of wild-born juveniles have learned to migrate from their parents. Thus, since 2005, at least some of each new juvenile cohort has been released (or hatched) into areas where experienced conspecifics were present and undertook their first fall migration guided by knowledgeable conspecifics instead of ultralight aircraft.

Since the initial reintroduction, the wintering areas of the reintroduced EMP have shifted northward, effectively halving their annual migration distance (Teitelbaum et al., 2016). Past research has related this behaviour to warmer winter temperatures and availability of agricultural crops (Teitelbaum et al., 2016). For the AWBP, similar range shifts have not occurred (Fig. 1); it is rare for birds in this population to winter far from the coast of Texas (Wright et al., 2014), and the large majority of the population is present on or near Aransas NWR each winter (Butler and Harrell, 2017).

2.2. Tracking data

We accessed global positioning system (GPS) and very high frequency (VHF) location data, life history information, and migration training method for 327 birds in the EMP covering a total timespan of 16 years (2001–2016) from the Whooping Crane Eastern Partnership (WCEP) database housed at the International Crane Foundation. We performed all analyses using R (R Core Team, 2021) and GRASS GIS (GRASS Development Team, 2018).

2.3. Predicting potential wintering habitat of the AWBP

We identified individual wintering sites from the movement data of the EMP (for details see appendix A) and annotated the year, age-class (juvenile, subadult, or adult) and mode of migration training (ultralight, conspecific, or parent trained) of the respective individual to each site. Cranes in their first year of life were denoted as juveniles, while cranes in their third year of life and older were considered adults (Travsky and Beauvais, 2004). We then built generalized additive models with a Bernoulli response variable and a logit link function, contrasting the used wintering sites with a large number of potentially available sites (Manly et al., 2002; Guisan et al., 2017). Following Barbet-Massin et al. (2012), we generated 10,000 pseudo-absence points from the extent of available habitat, which we identified by calculating the minimum convex polygon around year-round EMP crane sightings after excluding the 1% of crane fixes that were located farthest from the population's migration corridor, i.e., outliers to the east and west of it (using the `adehabitatHR` package; Calenge, 2006). Wintering sites that were located outside of the MCP ($n = 4$) were not used in the habitat suitability model.

The environmental predictors in our habitat suitability model were selected based on published Whooping Crane habitat and feeding preferences and covered climatic, landscape, and anthropogenic factors that are either sought or avoided by wintering and migrating cranes (for details see appendix B). Our predictors included temperature of the coldest winter month (from MODIS; Wan et al., 2015), snow cover in the snowiest winter month (from MODIS; Hall and Riggs, 2015), land cover class (barren, developed, forest, perennial vegetation (from the U.S. Geological Survey National Land Cover Database; Homer and Fry, 2012), grain cover (National Agricultural Statistics Service Cropland Data Layer, 2017), or wetland (from the National Wetlands Inventory; Wilen and Bates, 1995; U.S. Fish and Wildlife Service, 2018)) and the Human Influence Index from the Last of the Wild Project (WCS and CIESIN, 2005). We recalculated all environmental raster layers so that a grid cell covered roughly 8 km^2 ($2800 \text{ m} \times 2800 \text{ m}$). In this way, the environmental variables sampled at any given point reflected the conditions of the surrounding landscape (Niemuth et al., 2018). Austin and Richert (2005) reported that the majority of distances between roosting and feeding sites of migrating Whooping Cranes in the AWBP were $< 1.6 \text{ km}$, which amounts to a circular area of roughly 8 km^2 . Because we searched for potential wintering territories in regions that are currently used for migration, we used this more liberal estimate for Whooping Crane space use instead of the smaller size of wintering territories located at Aransas NWR (Stehn and Prieto, 2010).

To avoid pseudoreplication, all wintering sites that fell into the same raster cell were grouped to one site. For each wintering site, we extracted the mean environmental conditions over all years in which it was in use, while for the availability points, we extracted the mean environmental conditions over the entire study period.

We assessed pairwise Pearson correlation coefficients between all predictor variables and examined instances of high collinearity ($|\rho| \geq 0.7$, Dormann et al., 2013). There was high collinearity between temperature and snow cover, therefore we built two separate sets of models, each containing one of the pair of correlated variables and all of the uncorrelated ones.

We tested for spatial autocorrelation in the model residuals using the test for Moran's I in the `ape` package (Paradis and Schliep, 2019), and subsampled the set of presence points until autocorrelation was no longer significant (for details see appendix C). Retaining only presence points that were at least 40 km apart resulted in non-significant ($p > 0.05$) autocorrelation while retaining a total of 47 sites ($\approx 27\%$ of all sites) as well as all pseudo-absence points.

To avoid overfitting, we used generalized additive model selection via the `gamsel` package (Chouldechova and Hastie, 2015) to determine the best subset of variables in the habitat suitability model (for details see appendix D).

Finally, we used the variables retained by each selection run to fit generalized additive models using the `mgcv` package (Wood,

2011). We chose the best among all created models by calculating the area under the receiver-operator-curve (AUC; Bradley, 1997), using the presenceabsence package (Freeman and Moisen, 2008b) via 100 iterations of 10-fold cross-validation to create training (using 90% of data) and testing (10%) data (Guisan et al., 2017), while keeping the prevalence constant over all folds (Randin et al., 2006).

Because our aim was to distinguish between “suitable” and “unsuitable” habitat, we converted the continuous predictions of the best model into a binary classification that was more readily interpretable than the estimated relative likelihood of occurrence. A map of the continuous predictions is supplied in appendix E. Following Freeman and Moisen, 2008a, we chose the threshold value to separate the predictions into binary categories by iterating over a range of values and finding the values that maximized the True Skill Statistic (TSS; Allouche et al., 2006) based on sensitivity and specificity of the binary predictions (using the ModelMetrics package; Hunt, 2020). Because the use of TSS to evaluate presence/pseudo-absence models has been criticized when the number of pseudo-absences is high and prevalence is low (Somodi et al., 2017), we also evaluated the binary model predictions using the Symmetric Extremal Dependence Index (SEDI, Ferro and Stephenson, 2011), an evaluation metric commonly used in meteorological studies that performs well in species distribution models based on presence/pseudo-absence data with low prevalence (Wunderlich et al., 2019).

We then used environmental data from the eastern and central US to predict suitable wintering habitat within the migration corridors of both Whooping Crane populations. We refrained from making predictions for grid cells that were located outside of the environmental range in which the model was initially trained, which we identified by computing multivariate environmental similarity surface (MESS, Elith et al., 2010) plots with the dismo package (Hijmans et al., 2017). To quantify the potential shortstopping area available to the AWBP, we overlaid the binary suitability map with the 95% core migration area of the AWBP as delineated by Pearse et al. (2018) and calculated the area of predicted shortstopping habitat within the migration corridor. Teitelbaum et al. (2016) considered a Whooping Crane in the EMP to be shortstopping if it wintered < 1300 km away from the EMP breeding grounds in

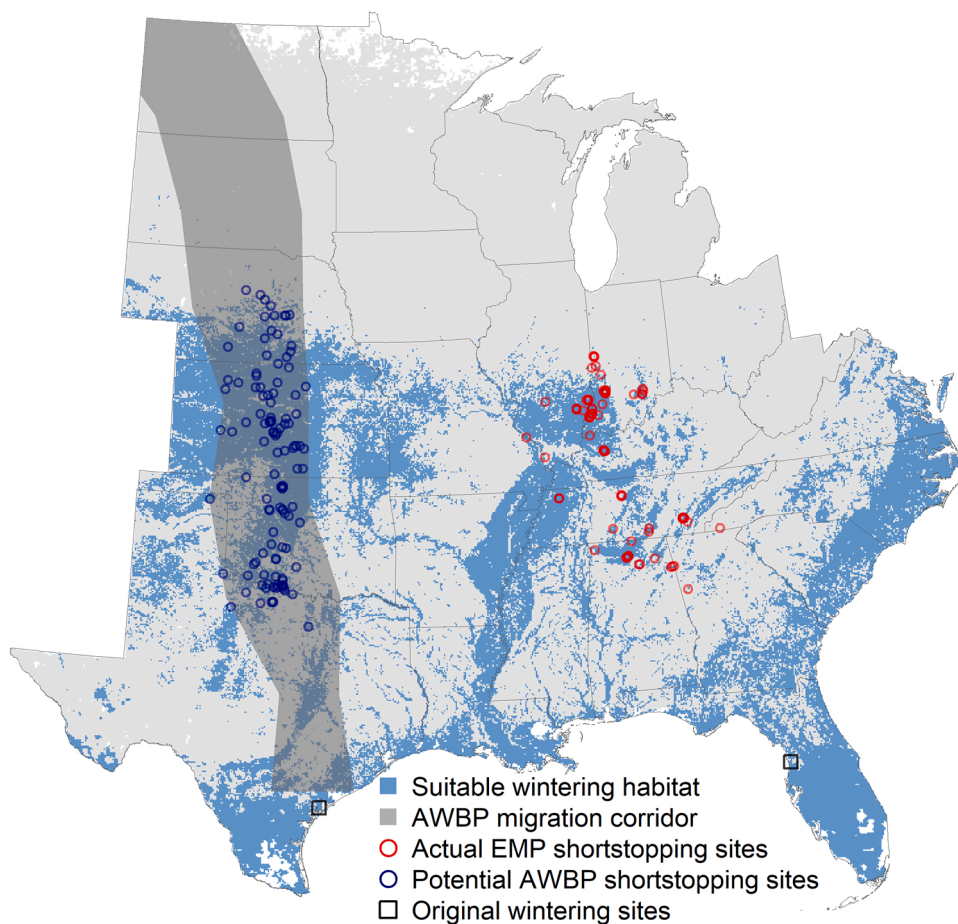


Fig. 2. : Prediction map of suitable Whooping Crane wintering habitat in the mid-eastern US. The migration corridor of the AWBP, as delineated by Pearse et al. (2018), overlaps with $\approx 213,000 \text{ km}^2$ of predicted wintering habitat in Texas, Oklahoma, Kansas, and southern Nebraska, USA. The depicted shortstopping sites are sites at least 500 km north of traditional wintering sites (Teitelbaum et al., 2016). For the EMP (red circles) these represent actual overwintering sites; for the AWBP, blue circles identify stopover sites during fall migration that overlapped with predicted winter habitat. We did not predict outside of the environmental range of the model. For continuous predictions of habitat suitability see appendix E.

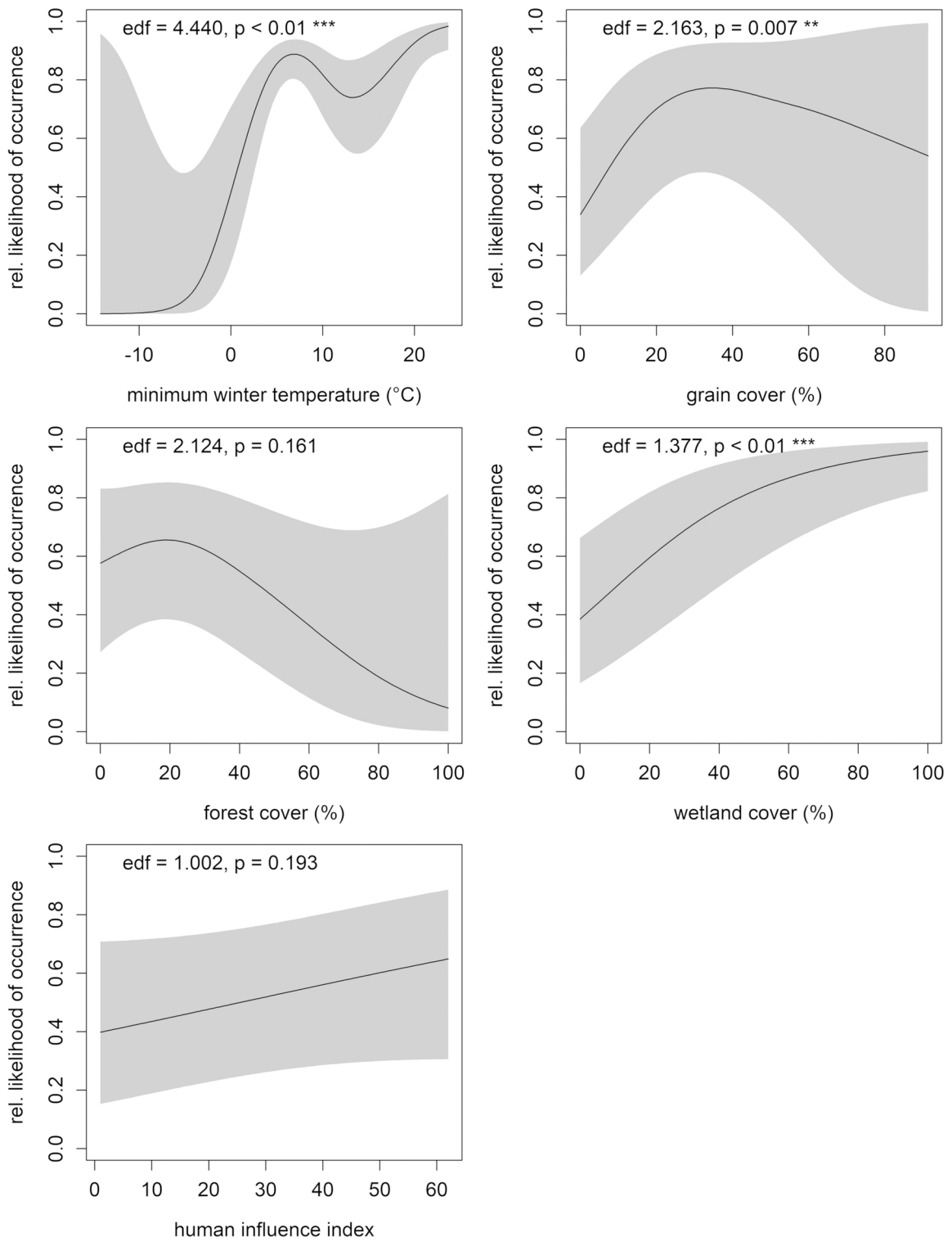


Fig. 3. : Response curves of the final model covariates, modelling the relative likelihood of Whooping Crane occurrence during winter. The grey shaded area represents the approximate 95% confidence interval.

Wisconsin, which represents a shortening of its migration by at least 500 km. We calculated both the total area of potential wintering habitat within the migration corridor and the area of potential shortstopping habitat at least 500 km north of Aransas NWR. To assess whether potentially suitable areas had actually been visited by individuals in the AWBP, we accessed daily GPS location data of 19

birds in the AWBP from [Pearse et al. \(2020\)](#) covering the 2010–2015 migration periods, and used it to identify AWBP stopover sites within the migration corridor and within the latitudinal range of the potentially suitable habitat. We then calculated the proportion of these stopover sites that were predicted to be suitable for wintering and shortstopping.

2.4. Evaluating the role of social factors

To analyse the strength of social ties between experienced (adult) and inexperienced (juvenile) birds in the EMP, we calculated the Euclidean distance between the wintering centroids of each conspecific-trained juvenile and the closest adult in the same wintering year. Ultralight-trained juveniles were not included in this analysis because their wintering location did not reflect their own choice. If multiple juveniles wintered within 10 km of each other, only one (randomly selected) juvenile was used in this analysis to avoid pseudoreplication.

We then used 10,000 bootstrap replicates to calculate the 95% confidence interval of the mean distance between juveniles and the nearest adult via the `boot` package ([Canty and Ripley, 2021](#)) using the bias-corrected accelerated method (as recommended by [Puth et al., 2015](#)) and assessed whether this confidence interval overlapped with the diameter of an average AWBP wintering territory (a liberal estimate of the juvenile-adult distance in the AWBP). [Stehn and Prieto \(2010\)](#) reported the average size of AWBP wintering territories to be 1.96 – 3.14 km² across years, which corresponds to territory diameters of up to 2 km (assuming a circular home range). It was not possible to directly calculate juvenile-adult distances for the AWBP because simultaneous GPS tracking data of wintering adults and their offspring are rare for this population. The most recent data release on GPS-tracked cranes of the AWBP contained only a single simultaneously tracked parent-juvenile pair during a single winter ([Pearse et al., 2020](#)).

For all conspecific-trained juveniles, we also calculated the distance between their respective wintering sites and the centroid of the EMP release locations in Wisconsin. We then computed a mean and 95% confidence interval of the difference in migration distances between juveniles with and without potential tutors (i.e., juveniles that wintered less than or greater than 2 km from the nearest adult conspecific, respectively) using bootstrapping as described above.

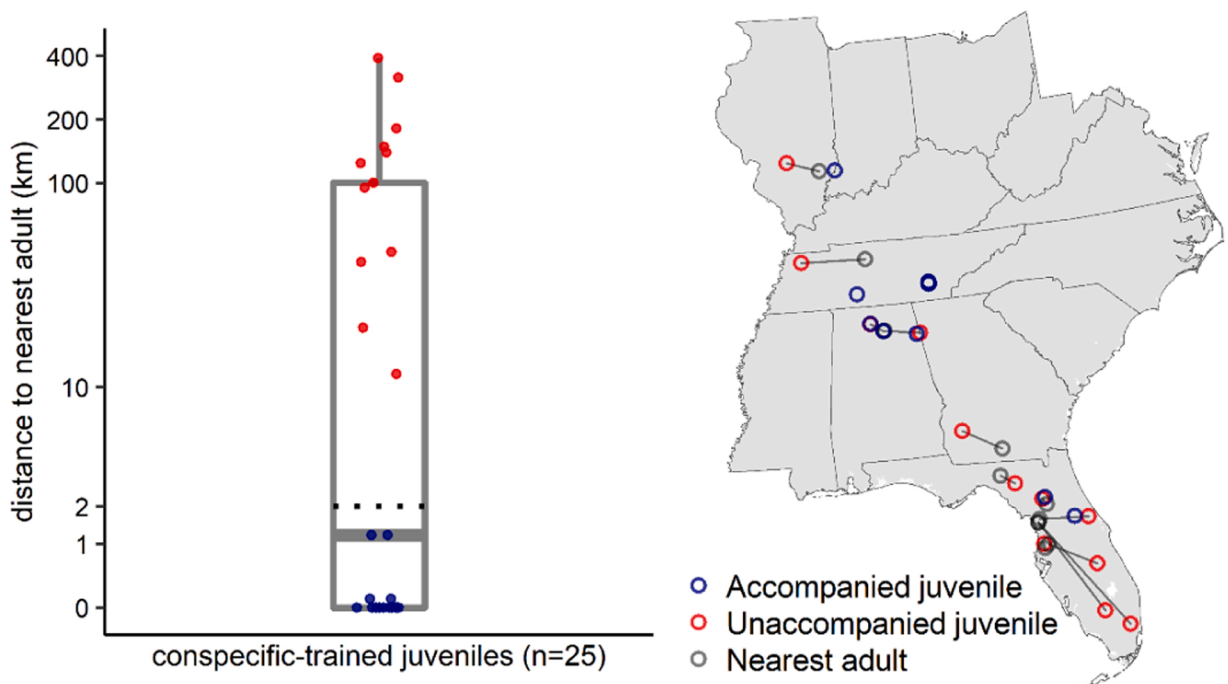


Fig. 4. : Distances between wintering sites of conspecific-trained juveniles and the nearest adult, depicted as a box-and-whiskers plot with a log₁₀-transformed y-axis (left panel) and geographically across the south-eastern United States (right panel). Left: Juveniles were observed wintering between 0 km and 392 km from the nearest potential tutor, with a mean distance of 64.9 km. Approximately half ($n = 13$, in blue) of the observed parent-juvenile distances were within the distance across a winter territory in the AWBP (2 km, see dotted line), while the other juveniles ($n = 12$, in red) wintered significantly farther away from an adult. Right: For each unaccompanied juvenile, the wintering site of the nearest adult in the same year is depicted in black, together with the straight-line distance to between them.

3. Results

3.1. Habitat availability

Our final habitat suitability model predicted that substantial areas of potential wintering habitat were present within the migration corridor of the AWBP (Fig. 2). We predicted that 31.4% ($\approx 213,000 \text{ km}^2$) of the AWBP migration corridor in the US was suitable for wintering. When discounting predicted wintering habitat within 500 km of Aransas NWR, 26.7% ($\approx 181,000 \text{ km}^2$) of the corridor comprised potential shortstopping habitat. Of 227 stopover sites that were visited by AWBP cranes during the fall migration within the latitudinal range of the potential wintering area, 63.4% (144 sites) were located on predicted winter habitat. Among stopovers > 500 km from Aransas NWR, 65.4% (121 of 185 sites) were predicted to be suitable for wintering.

Areas of predicted wintering habitat within the AWBP corridor ranged from eastern Texas to southern Nebraska, along with some isolated areas in South Dakota. No wintering habitat was predicted in North Dakota, and no predictions were made for the Canadian part of the migration corridor. The final model also predicted ample wintering habitat outside of the migration corridor of the AWBP, especially in Kansas, along the lower Mississippi Alluvial Valley, as well as throughout the US coastal regions from Texas to Virginia (Fig. 2). Wintering habitat also was predicted within the migratory flight path of the EMP: while most abundant in Florida, abundant wintering habitat was predicted to occur as far north as southern Illinois and Indiana (where EMP cranes have overwintered).

The final habitat suitability model achieved an AUC of 0.844 (95% Confidence Interval (CI) = [0.842; 0.846]), indicating good fit (Araújo et al., 2005). A relative likelihood value of 0.00431 constituted the optimal threshold to split model predictions into binary classes based on the True Skill Statistic. The binary classification of predicted wintering habitat achieved an overall sensitivity of 0.808 and a specificity of 0.728, showing that the model was capable of correctly identifying 81% of presence points and 73% of pseudo-absence points, resulting in a TSS of 0.536 [0.532; 0.54] and a SEDI of 0.700 [0.697; 0.704] (both on a scale from 0 (chance model) to 1 (perfect model)).

Of the nine initial variables, the final model included average winter temperature of the coldest month, edible grain cover, forest cover, human influence index, and wetland cover, all as spline terms (Fig. 3). The discarded variables included snow cover of the snowiest winter month, developed cover, barren cover, and perennial cover. Together, the fixed effects explained 20.2% of the residual deviance. See appendix F for the summary table of the final model.

3.2. Social comparison

Among the 830 bird-winters in our EMP dataset, we observed 42 winters for conspecific-trained juvenile cranes, 25 of which were far enough from other overwintering juveniles to be considered independent observations. On average, these juveniles wintered 64.9 km (SD = 20.2) from the nearest adult in the same year (Fig. 4). The bootstrapped 95% confidence interval of juvenile-adult distances in the EMP (33.5 km, 118.3 km) excluded our liberal estimate of average juvenile-adult distances in the AWBP (2 km). Thirteen EMP juveniles were observed wintering within 2 km of the nearest adult, while the other 12 wintered on average 134.9 km (SD = 31.8) away. Juveniles far from adults migrated on average 1517.3 km (SD = 509.4 km) compared to 1110 km (SD = 311.6 km) for juveniles that wintered within 2 km of an adult (Fig. 4). The average migration distance difference between juveniles that wintered close to versus far from an adult was 407.3 km (bootstrapped 95% confidence interval = 53.2 km, 710 km).

4. Discussion

The emergence of shortstopping behaviour in migratory birds varies among species and populations. We investigated two potential drivers affecting differential patterns of shortstopping behaviour in two populations of Whooping Cranes: the unavailability of suitable wintering habitat in the migration corridor of the AWBP, and differences in social structure between the non-shortstopping AWBP and the shortstopping EMP. We found large areas of potential shortstopping habitat within the AWBP migration corridor, suggesting that habitat suitability did not limit shortstopping behaviour in the AWBP. At the same time, juvenile cranes wintered farther away from the nearest adult in the EMP compared to the AWBP, indicating weaker associations between naive juveniles and knowledgeable tutors in the EMP. Compared to parent-reared and -trained juveniles of the AWBP, the mostly human-reared and conspecific-trained juveniles of the EMP may have weaker social bonds with potential tutors; as a result, the social transmission of migration behaviours may be less effective (Swaney et al., 2001; Gariépy et al., 2014; Guillette et al., 2016). While social learning has been shown to shape bird migration and facilitate innovation (Chernetsov, 2004; Mueller et al., 2013; Rotics et al., 2016; Teitelbaum et al., 2016; Meyburg et al., 2017), other studies have shown that such associations can inhibit innovation and that vertical transmission of behaviours can promote adherence to established traditions (Barrett et al., 2019; Galef, 2003; Keith and Bull, 2017). Our results highlight the possibility that the comparatively rapid uptake of shortstopping behaviour in the EMP may have been supported by the decreased vertical transmission of established behaviours in that population compared to the AWBP, where a strong adherence to socially learned migration traditions might have dampened the innovation and uptake of novel behaviours.

4.1. Environmental characteristics of crane overwintering sites

In many bird species, the development of shortstopping is linked to new wintering habitat becoming available closer to their breeding grounds, often caused by changes in winter climate or food availability (Vosslamber et al., 2010; Teitelbaum et al., 2016; Flack et al., 2016). In our habitat suitability model, the wintering preferences of the EMP were driven by selection for wetland habitats,

intermediate grain cover, and temperatures above freezing. Whooping Cranes use wetlands extensively during winter and migration for roosting and foraging for aquatic prey (Austin and Richert, 2005; Johns et al., 1997; Armbruster, 1990; Chavez-Ramirez, 1996). However, reintroduced Whooping Cranes have remarkable flexibility in their habitat choices (Fondow, 2013; Dinets, 2015; Teitelbaum et al., 2016), suggesting that while they may need wetlands for safe roosting, they are generalists in their food choices if other foraging opportunities exist in winter. Whooping cranes often rely on waste grain from harvested farmland as a food source during migration (Johns et al., 1997) and also feed on grain during winter, as they travel to farmlands adjacent to their wetland territories in times of drought (Shields and Benham, 1969; Chavez-Ramirez, 1996). Accordingly, the occurrence of agricultural grains has been linked to establishment of new wintering sites in the EMP (Teitelbaum et al., 2016). Generally, Whooping Cranes can tolerate a wide range of temperatures with their upper and lower critical temperatures predicted at 36 °C and – 13.5 °C, respectively (Chavez-Ramirez, 1996; Fitzpatrick et al., 2015). Cranes may avoid below-freezing temperatures because they rely on liquid water for feeding and safe roosting in wetlands (Westwood and Chavez-Ramirez, 2005), and have been shown to avoid areas of deep snow during migration (Abrahms et al., 2021). While Whooping Cranes commonly avoid forested areas (Armbruster, 1990; Niemuth et al., 2018) and react negatively to human disturbance (Johns et al., 1997; Lewis and Slack, 2008), we found no evidence of selection for or against these conditions in the reintroduced EMP. This too may indicate greater habitat flexibility compared to the remnant AWBP, as has also been observed in other reintroduced Whooping Crane populations (Fondow, 2013; Dinets, 2015).

While the AWBP has grown while relying on the Aransas region as its sole overwintering site (French et al., 2019), our results indicate that AWBP cranes could survive farther north, thus allowing them to take advantage of a shorter migratory route. A large number of stopovers were within predicted wintering habitat, indicating that AWBP cranes might have visited at least some of the potential wintering sites we identified. In the EMP, previous stopover sites were chosen as wintering sites in subsequent years (Teitelbaum et al., 2016). However, the amount of available shortstopping habitat might be overpredicted due to shortcomings of the habitat suitability model: Our habitat predictions for the migration corridor of the AWBP were based on average environmental conditions recorded over a 16-year period and did not consider interannual and multi-decadal environmental variability in winter conditions, which can be dramatic across the Great Plains (Doesken and McKee, 1991). Presumably, the amount of actually available shortstopping habitat across the AWBP migration corridor fluctuates between years. Additionally, the quality of wetlands as bird habitat is not only dependent on their extent, but also productivity and whether they are actually present in winter (Chastant and Gawlik, 2018; Baasch et al., 2019). In the absence of information on the productive output and ephemerality of wetlands, our habitat predictions could be imperfect. However, the habitat suitability model was able to adequately predict EMP wintering sites. While the amount of predicted suitable habitat depends on the specified threshold value used to bin the model predictions, we employed a robust approach to identify the best threshold.

4.2. Differences in social learning may inform differences in migration behaviour

Our findings suggest that drivers other than habitat availability may be determining uptake of shortstopping behaviour in the EMP. Specifically, we suggest the inhibition of novel behaviours due to strong social learning as a potential limiting factor in the AWBP, while weaker social bonds may facilitate novel behaviours and the adoption of shortstopping in the EMP. While social learning in bird migration often increases behavioural flexibility and facilitates adaptation to change (Sutherland, 1998; Whitehead, 2010), vertical transmission of behaviour can alternatively result in an adherence to established traditions even in the face of rapid environmental change (Keith and Bull, 2017). In a recent review, Barrett et al. (2019) emphasized that social learning can be maladaptive in the face of rapid environmental change, for instance by limiting the spread of adaptive behaviours. Social learning can act as either a progressive or conservative force in different populations, promoting the spread of innovative behaviours in some cases while conserving established behaviours, and thus inhibiting innovation, in others (Galef, 2003).

Our results suggest that the two migratory populations of Whooping Cranes differ in their capacity to socially transmit migratory behaviours, at least partially as a result of differences in the formation and strength of social bonds. Associations between inexperienced, hand-reared juveniles and unrelated but experienced adults were weak in the EMP, at least compared to the AWBP, where juveniles generally are reared by and migrate and overwinter with their parents (Stevenson and Griffith, 1946; Allen, 1952; Kuyt, 1992). Still, within the EMP, about half of the observed juveniles adopted the wintering preferences of older cranes, while the others did not. This difference suggests that while social learning is present within the EMP (Mueller et al., 2013; Teitelbaum et al., 2016), the vertical transmission of behaviour might not be as effective as in the AWBP (Swaney et al., 2001; Gariépy et al., 2014; Guillette et al., 2016). Consequently, the importance of experiential compared to social learning might have increased in the EMP (Galef and Laland, 2005). This may have resulted in increased exploratory behaviour in juveniles, which would explain both the reduced fidelity to the original wintering sites and the broader habitat preferences compared to the AWBP, two likely requirements for the development of shortstopping behaviour. Reduced association times between parents and juveniles may also affect social transmission of behaviours in geese, a taxon also known to rely on social transmission of migratory behaviours (Clausen et al., 2018), increasing the exploratory potential in juveniles and potentially causing them to break with the migratory traditions of their population (Jonker et al., 2012). An additional factor heightening the importance of experiential learning in the EMP might have been the initial lack of knowledgeable individuals and established behavioural traditions due to the reintroduction process. Whooping Cranes in two reintroduced non-migratory populations have also engaged in exploration and colonization of new habitat relative to the strict wetland preferences of the wild, migratory AWBP (Fondow, 2013; Dinets, 2015). Likewise, it seems possible that the social transmission of habitat preferences in the AWBP might have led to the conservation of Aransas as its only overwintering site after birds wintering there survived the near-extinction of their species (French et al., 2019).

While increased exploratory behaviour may be an important requirement for the development of shortstopping, we did not find

evidence that wintering far from knowledgeable conspecifics immediately resulted in decreased migration distances in the same year. On the contrary, we found evidence for shorter migration distances in juveniles that wintered close to adults, although this result may have been biased by two unaccompanied juveniles that wintered several hundred kilometres south of the southernmost reintroduction site (see Fig. 4). Overall, our findings are in accordance with earlier findings of Teitelbaum et al. (2016), who suggested that the manifestation of shortstopping behaviour likely occurs later in life, when individuals have greater experience of wintering conditions throughout their migration corridor. Still, juvenile Whooping Cranes might pick up shortstopping behaviour during their first migration by migrating with experienced conspecifics that already shortstop or by observing shortstopping conspecifics during migration (Aikens et al., 2022).

Our study did not assess how the strength of social bonds in ultralight-trained cranes might differ from conspecific-trained cranes. However, recent studies showed that ultralight-trained cranes were less successful in socially learning migration behaviours such as shortstopping and resource tracking than conspecific-trained cranes (Teitelbaum et al., 2019; Abrahms et al., 2021), suggesting they rely more on experiential learning. The initial innovation of shortstopping behaviour likely was due to older, ultralight-trained cranes (Teitelbaum et al., 2016). Therefore, we would expect that the inclusion of ultralight-trained cranes would only strengthen the pattern of weaker social bonds in the EMP as compared to the AWBP.

There remain other potential hypotheses for the differential occurrence of shortstopping behaviour in Whooping Cranes that we were not able to test. Habitat requirements may vary between EMP and AWBP due to differences in their migration routes: While EMP cranes apparently tolerate low temperatures and supplement parts of their diets with agricultural crops in order to shortstop (Teitelbaum et al., 2016), AWBP cranes may be much more restricted to consistently warm temperatures and a protein-rich diet of aquatic invertebrates in order to meet the energy demands of their decidedly longer migration. The predictably favourable conditions at the original wintering site may therefore outweigh the benefits gained by a comparatively small reduction in migration distance (Alerstam et al., 2003; Alves et al., 2012), especially given the low predictability of winter conditions at the potential shortstopping sites (Doesken and McKee, 1991). Correspondingly, shortstopping is most common in short- and medium-distance migrants (Elmberg et al., 2014), whereas long-distance migrants frequently display high site fidelity (e.g., Blackburn and Cresswell, 2016). However, the central Great Plains are being used for wintering by Sandhill Cranes *Grus canadensis* (Krapu et al., 2011; Pearse et al., 2016), which also appear to respond to annual fluctuations in habitat availability (Harner et al., 2015), indicating that shortstopping in these regions is possible for some wetland-dependent long-distance migrants.

Furthermore, it is possible that the reintroduction process affected the habitat preferences of the EMP in ways other than through breaking the established traditions of the AWBP, and thus contributed to the development of shortstopping. While the EMP was originally reintroduced to coastal wintering sites that featured salt marshes reminiscent of the AWBP wintering grounds (Urbanek et al., 2010), the prolonged exposure to human presence could have resulted in increased habituation to humans, allowing the EMP to colonize anthropogenic habitat such as agricultural fields. In cranes and geese, human-rearing has been reported to increase tameness or decrease vigilance and stress responses (Duff et al., 2001; Kreger et al., 2005; Hemetsberger et al., 2010). However, most released juveniles in the EMP were reported to avoid humans, while only a small number showed habituation (Urbanek et al., 2014). Additionally, the use of agricultural lands as supplementary feeding grounds has also been observed for the human-intolerant AWBP, if only during migration and times of food shortage (Johns et al., 1997; Shields and Benham, 1969).

It should not be overlooked that the differential quality of the original wintering sites of both populations could also have influenced the occurrence of more flexible habitat preferences, and thus shortstopping behaviour: Chassahowitzka NWR, one of the primary release sites of the artificial migration of the EMP, has been cited as potentially poor habitat, due to high water salinity, dense vegetation, and large tidal variations; however, cranes overwintered and returned there for years (Urbanek et al., 2010). Thus, even if the reintroduction process might not have introduced novel wintering habitat preferences in the EMP directly, it remains unclear how the suboptimal quality of the release site may have contributed to the development of broader habitat preferences, and ultimately shortstopping. Possibly, predation by bobcats (*Lynx rufus*) at the EMP wintering sites in Florida could also have contributed to Whooping Cranes moving to new overwintering sites (Cole et al., 2009). Conversely, while Aransas NWR has long been considered highly suitable wintering habitat for Whooping Cranes (Metzger et al., 2020), some individuals in the AWBP have been observed farther inland during an extremely dry winter (Wright et al., 2014). However, such behaviours were not repeated in the following years, and it remained unclear if those cranes were actually wintering, and whether or not they also visited the Aransas region during the same migration (Wright et al., 2014). Ultimately, an interplay of both environmental and social drivers might be necessary for shortstopping to arise, as a population might require a social structure that allows the innovation and propagation of new behaviours, combined with environmental factors that drive the population away from established wintering sites.

Although there may exist other potential drivers of differential shortstopping in Whooping Cranes that we were unable to evaluate, our study highlights the possibility that social learning might shape the adaptability of populations when facing changing environmental conditions. Our study provides indications that social learning might have the potential to impede the uptake of novel behaviours in birds, thereby decreasing the flexibility of populations when facing environmental change. We suggest that management actions inducing behavioural flexibility might be of interest to managers looking to mitigate negative effects of habitat loss due to rapid land use and climate changes. The AWBP, for instance, faces declines in winter habitat availability due to projected increases in sea levels at their traditional wintering site (Chavez-Ramirez and Wehtje, 2012), although future carrying capacity at these sites has been projected to meet recovery objectives (Metzger et al., 2020). Potential management actions could include introducing demonstrators of novel behaviours into populations (Shier, 2016) or artificially training migration following translocation (e.g. Urbanek et al., 2014). In populations with strong established traditions, the spread of newly introduced behaviours may be limited, so increasing social attraction at desirable sites (Buxton and Jones, 2012) or increasing the benefits of shortstopping through supplemental feeding (recognizing that supplemental feeding can have unintended consequences; Masatomi et al., 2007) may also be a potential tool for

managers. In these ways, management might facilitate range shifts in species otherwise imperilled by rapid environmental change. Ultimately, both habitat and social learning need to be considered in developing our understanding of species occurrence and range shifts in a rapidly changing world.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The movement and life history data of the EMP cranes used in this manuscript are stored by the Whooping Crane Eastern Partnership (WCEP), and data of the AWBP cranes were released as part of [Pearse et al., 2020](#). Derived data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02365](https://doi.org/10.1016/j.gecco.2022.e02365).

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