The importance of early life experience and animal cultures in reintroductions

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Abstract
Even within a single population, individuals can display striking differences in behavior, with consequences for their survival and fitness. In reintroduced populations, managers often attempt to promote adaptive behaviors by controlling the early life experiences of individuals, but it remains largely unknown whether this early life training has lasting effects on behavior. We investigated the behavior of reintroduced whooping cranes (Grus americana) trained to migrate using two different methods to see whether their migration behavior remained different or converged over time. We found that the behavior of the two groups converged relatively rapidly, indicating that early life training may not produce lasting effects, especially in species that display lifelong learning and behavioral adaptation. In some cases, managers may consider continual behavioral interventions after release if desired behaviors are not present. Understanding the roles early life experience and animal cultures play in determining behavior is crucial for successful reintroduction programs.

KEYWORDS
captive rearing, Grus americana, migration, reintroduction, shortstopping, social learning, ultralight aircraft, whooping crane

1 | INTRODUCTION
Animal cultures, which are specific behaviors that exist across a social group and continue across generations (Claidière & Sperber, 2010), include crucial behaviors such as migration and foraging (Laland & Janik, 2006). One way in which cultures propagate through generations is by imitation, or social learning, where inexperienced individuals mimic the behavior of older, more experienced model individuals (Claidière & Sperber, 2010; Thornton & Clutton-Brock, 2011). However, declining populations of social animals risk the loss of adaptive culture if knowledgeable individuals are lost, much as small population sizes can lead to a loss of genetic adaptive potential by decreasing genetic diversity (Ellstrand & Elam, 1993). In population restoration efforts, one common way to promote conservation of animal culture is to introduce specific behaviors via early life training.

Understanding to what extent early life experiences determine adult behavior is critical for effective management of threatened species, particularly in reintroduction programs of long-lived species that rely on captive-reared individuals (Kleiman, 1989; Sutherland et al., 2010). In these programs, captive-rearing methods determine conditions during early development, but individuals’ behavior is unrestricted after release. A variety of captive-rearing techniques have successfully used early life training to increase survival of reintroduced individuals, for instance by promoting antipredator behavior or adaptive foraging strategies (Alonso, Orejas, Lopes, & Sanz, 2011; Homberger, Jenni, Duplain, Lanz, & Schauber, 2014; Whiteside, Sage,
& Madden, 2015). However, training is not always effective (Moseby, Cameron, & Crisp, 2012) and it is rare to track individuals for an extended period after release, meaning that it is largely unknown how long these trained behaviors persist or the conditions under which training has lasting effects, in other words whether and when early life experience effectively produces and maintains critical aspects of animal culture.

To fill this gap, we investigated whether experiences early in life have lasting effects on individual behavior in a long-lived species that exhibits lifelong learning. To do so, we measured the role of early-life migratory training in determining migration behavior in the reintroduced eastern migratory population of whooping cranes (Grus americana). Migratory behavior in whooping cranes is culturally inherited in the wild, where juvenile whooping cranes spend up to 11 months with their parents (Johns, Goossen, Kuyt, & Craig-Moore, 2005), but individuals continue to adapt their migration behavior into adulthood (Mueller, O’Hara, Converse, Urbanek, & Fagan, 2013; Teitelbaum et al., 2016). In the eastern migratory population, this adaptability has resulted in a dramatic northward shift in overwintering location in the 15 years since the beginning of its reintroduction; this shortstopping behavior has reduced the average migration distance of the population by about 50% (Teitelbaum et al., 2016; Urbanek, Szyszkoski, & Zimorski, 2014). Furthermore, within the reintroduced eastern migratory population, two different reintroduction methods have produced two distinct early migratory experiences: aircraft-trained birds were initially taught to migrate by following an ultralight aircraft to their wintering grounds, whereas conspecific-trained cranes follow other birds (usually other whooping cranes but occasionally sandhill cranes Antigone canadensis), rather than an airplane, on their first southward migration. All birds migrate without human assistance after this first autumn migration, meaning that the two groups differ only in their first migratory experience.

We examined the relationship between early life experience (aircraft training vs. conspecific training) and the shortstopping tendency of individuals over time. The differences between first migratory experiences could be important in determining shortstopping because aircraft-trained birds leave their breeding grounds on a date determined by managers and follow the aircraft to a predefined wintering location (~1,800 km from their summer grounds), whereas conspecific-trained birds could depart at any time and overwinter in any location and could even shortstop in their first year. We used intensive long-term tracking data of individuals to examine whether these two groups differed in their initial migration patterns, and how the behavior of each group changed over time.

2 | METHODS

2.1 | Dataset

We used data from the location database of the eastern migratory population of whooping cranes, which tracks individual birds throughout their lifetimes (Whooping Crane Eastern Partnership, unpublished data). The dataset is described in detail in Mueller et al. (2013) and Mueller, Teitelbaum, Fagan, and Converse (in press). The data are a combination of very high frequency (VHF) and global positioning system (GPS) data. Every bird in the population is identifiable for most of its lifetime via a unique colored leg band and VHF transmitter, allowing the entire population to be tracked by a combination of VHF telemetry and visual confirmation. In addition, 11 birds released in 2011 and 2012 were fitted with GPS transmitters that provided precise locations every 4 hours at night.

Training for the aircraft-guided migration consisted of imprinting of birds on costumed humans and ground-based training behind ultralight aircraft at a training facility from just after hatching to approximately 2–3 months of age, followed by training flights behind ultralights for several months on the breeding grounds. In the birds’ first autumn, the aircraft-led migrations themselves began on the breeding grounds in central Wisconsin. These aircraft-led migrations ended at Chassahowitzka National Wildlife Refuge on Florida’s peninsular Gulf Coast from 2001 to 2010; at St. Mark’s National Wildlife Refuge on the Gulf Coast of Florida’s panhandle from 2008 to 2010 and 2012 to 2015; and at Wheeler National Wildlife Refuge in northern Alabama in 2011. Birds remained at each of these wintering sites until they departed of their own accord in the following spring for the northward migration. All subsequent flights in both migratory directions were independent of the ultralights. Additional details about ultralight-led releases are provided in Urbanek et al. (2010). Beginning in 2005, 4 years after the initiation of ultralight-led releases, conspecific-trained birds were released directly on the same breeding grounds in central Wisconsin and were allowed to follow older whooping cranes or wild sandhill cranes to any overwintering location.

We used 117,223 locations of whooping cranes from October 2005 through March 2016 to identify overwintering sites. We used data only from cohorts of birds that included both aircraft- and conspecific-trained individuals, that is, 2005–2015 cohorts, omitting data from 2001 to 2004. We also imputed an additional 93 locations of juvenile birds on their wintering grounds (known from ultralight training), because the database does not track aircraft-trained birds in their first winter. Overwintering sites were defined as in Teitelbaum et al. (2016). Briefly, we considered an individual to be...
overwintering if it moved less than 10 km in a 15-day period during the winter months (November to April) (i.e., two observations at the same site at least 15 days apart and no observations >10 km away during that period). In the case that a single individual was classified as having multiple overwintering sites in a single year, we used the southernmost overwintering site to obtain a conservative estimate of shortstopping. We calculated the distance of each overwintering site from the centroid of the population’s summering grounds as a measure of the migration distance. In total, we based our analyses on 602 overwintering locations of 158 individuals over 11 winters.

### 2.2 Analysis

We compared the tendency of individual whooping cranes to shortstop over time, where we considered an individual to have shortstopped if it migrated less than 1,200 km in a given year (following Teitelbaum et al., 2016). We combined seven wild-hatched birds with the 58 captive-bred but conspecific-trained birds in one category (“conspecific-trained”) because both groups migrated independently of aircraft on their first migration. We then compared the probability of shortstopping of aircraft-trained and conspecific-trained birds using a generalized linear mixed-effects model with a logit link, where the response variable was a binary measure of whether an individual shortstopped. Fixed effects were release year, training method, and age, and the interaction between training method and age; the model also included a random intercept for each individual bird in order to account for repeated measures of individuals. In addition to this main model, we also considered an alternative model where we analyzed wild-hatched and captive-bred but conspecific-trained birds separately; our results were robust to this alternative assignment (Table S1). All analyses were performed in R (R Development Core Team, 2016) using the lme4 package (Bates & Sarkar, 2007).

### 3 RESULTS

Based on 602 overwintering events of 158 individual whooping cranes over 11 years (n = 93 aircraft-trained; n = 65 conspecific-trained, including 7 wild-hatched birds), we saw that all birds overwintered farther north with age (Figure 1). Overall, the probability of shortstopping increased with both age and release year, reflecting its emergence over time (Table 1). Moreover, the interaction between age and training method was an important predictor of shortstopping (i.e., the 95% confidence interval on the interaction term excluded 0). The model results overall indicated that conspecific-trained birds were initially more likely to shortstop than aircraft-trained birds, but this difference decreased with age (Table 1, Figure 1), reflecting a convergence of behavior of the two groups (Figure 2). Specifically, during their first winter, conspecific-trained birds overwintered 510 km farther north than aircraft-trained birds, but this difference decreased each year, until the two groups were indistinguishable by age 6 (when pooled by release year; Figure 1).

| Estimation from a linear mixed-effects model using year, age, and release method to predict shortstopping probability. The model also included a random intercept for individual birds |
|---|---|---|---|
| **Parameter** | **Estimate** | **SE** | **2.5%** | **97.5%** |
| Intercept | -3.709 | 1.416 | -6.749 | -0.949 |
| Training method (ultralight) | -5.790 | 1.083 | -8.401 | -3.988 |
| Age | 0.542 | 0.152 | 0.264 | 0.866 |
| Release year | 0.604 | 0.147 | 0.342 | 0.938 |
| Training method × Age | 1.313 | 0.291 | 0.8 | 1.974 |

### 4 DISCUSSION

In this population of reintroduced whooping cranes, birds trained to migrate by aircraft and those that learned by following conspecifics differed in their migration behavior for the first few years of life, but their behavior converged with both age and time. The convergence of behavior apparently resulted from aircraft-trained birds adopting the behavior of conspecific-trained birds; there was a dramatic change in migration distance with age among aircraft-trained birds, where 5-year-olds overwintered 713 km farther north than 1-year-olds (when averaged over release cohorts and individuals). In contrast, there was relatively little change in the migration distance of conspecific-trained birds, where these same age groups differed only 282 km in their migration distance (Figure 1). These results demonstrate that, although initial early life experiences are important and their effect can be traced over multiple years, a combination of cultural effects and individual behavioral adaptation to environmental conditions ultimately determine the migration distance of adults in this population.

In social species such as cranes, a combination of individual and social learning likely drives convergence in the behavior of groups with different early life experiences, as individuals adapt their behavior to their environment. Environmental changes over the last century, in the forms of climate and land-use change, have created suitable overwintering sites where they were not historically present, providing a basis for individuals to change their migratory behavior (Teitelbaum et al., 2016). Individual experience is important for initiating changes in migration behavior (Teitelbaum et al., 2016); here, we show that training method
**Figure 1** Overwintering locations of conspecific-trained and aircraft-trained birds converge with age. Conspecific-trained birds are shown in purple and aircraft-trained birds are shown in orange. Polygons are 90% minimum convex polygons of overwintering locations for all individuals in each group. Points show the centroid of overwintering location (mean latitude and longitude) for each group, pooled across years. The scatterplot shows mean overwintering latitude of each group over ages 0–6 years (purple and orange lines; left-hand axis) and the difference in overwintering latitude between groups (black line; right-hand axis).

**Figure 2** Model predictions for the effect of age, release year, and training method on probability of shortstopping. Lines show estimates from a generalized linear mixed-effects model predicting shortstopping from bird release year, training method, age, and the interaction between age and training method. The model also included a random intercept for each individual bird (not shown). Purple lines show predicted shortstopping probabilities for conspecific-trained birds and orange lines show probabilities for aircraft-trained birds released in 2005, 2009, and 2012. Shaded areas show 95% confidence intervals obtained via bootstrapping. In any year older birds are more likely to shortstop (i.e., shortstopping probability increases with age). Aircraft-trained birds are initially less likely to shortstop than are conspecific-trained birds, but this difference in behavior declines with age.
is a key component of individual experience that affects the use of shortstopping sites for overwintering. Further, our data show that social learning is important, as birds released when shortstopping had already begun to emerge in the population were much more likely to shortstop at younger ages than birds of the same age released in earlier years (e.g., predicted probability of shortstopping was 0.01 at age 1 for aircraft-trained birds released in 2005, compared to 0.40 at age 1 for aircraft-trained birds released in 2012) (Table 1, Figure 2). In other words, as the number of individuals with knowledge of suitable sites increased in the population, shortstopping tendency increased even in birds with little individual experience, highlighting the role of cultural transmission in driving shortstopping behavior.

Cultural transmission of behavior can maintain a wide range of population-level behaviors including breeding site selection, communication mechanisms, and tool use in animals as diverse as songbirds, primates, and cetaceans (Danchin, Giraldeau, Valone, & Wagner, 2004). In great bustards (Otis tarda), migration behavior is transmitted from mothers to female offspring, but males learn to migrate from unrelated adults in the population, resulting in sex-specific migration tendencies (Palacín, Alonso, Alonso, Magaña, & Martín, 2011). Because of the cultural transmission of bustard migration behavior, sex- and population-specific migration patterns remain consistent across years even though not all individuals migrate every year (Palacín et al., 2011). Similarly, whooping cranes are highly social and are known to adopt the migration behavior of conspecifics (Mueller et al., 2013; Teitelbaum et al., 2016). In this way, animal cultures maintain consistent behaviors within populations across time (Laland & Janik, 2006), even though individuals may experience different conditions in their lifetimes.

At the same time, animal cultures can shift rapidly, particularly in the face of changing environmental conditions (Helm, Piersma, & van der Jeugd, 2006). As has been shown for communication mechanisms in humpback whales, where novel song types spread from one population to the next each year (Garland et al., 2011), these rapid cultural changes arise from horizontal social transmission; this social learning can rapidly propagate a behavior even when not all individuals experience the same environmental stimulus. For migration in particular, individuals from diverse bird species are known to be flexible in the spatial elements of their migration behavior (Gill et al., 2014; Vardanis, Klaassen, Strandberg, & Alerstam, 2011), meaning that animals have the potential to modify their migration patterns depending on environmental and social contexts. In this population of whooping cranes, shortstopping did not appear until years after reintroduction began (Teitelbaum et al., 2016; Urbanek et al., 2014), but the behavior emerged shortly after release of the first conspecific-trained birds; it is unknown whether shortstopping would have emerged in aircraft-trained birds if conspecific-trained birds had never been released. Nevertheless, this rapid change in migration behavior illustrates the importance of animal cultures and social learning not only for maintaining behaviors across generations, but also for promoting rapid adaptation on the population level.

Previous studies of whooping cranes indicate that captive-rearing techniques can promote specific behaviors (e.g., aggression, foraging, sleep, vigilance) in individuals in captivity (Kreger, Estevez, Hatfield, & Gee, 2004), and to some extent after release (Kreger, Hatfield, Estevez, Gee, & Clugston, 2005). However, these techniques were monitored only on short time scales (weeks to months) and did not account for potential lifelong adaptation in these birds, which can live over 20 years in the wild (Binkley & Miller, 1988). In our long-term study (using 11 years of data), we show that these training techniques may not produce lifelong effects on behavior, at least for socially learned and adaptable behaviors like migration patterns. The degree to which early learning experiences affect long-term breeding behaviors remains a question of tremendous importance in the reintroduction biology of whooping cranes (Converse, Strobel, & Barzen, in press). Changes in behavior after release have also been observed in other reintroduced species (e.g., reintroduced European bison colonized unexpected habitats following reintroduction (Ziolkowska, Perzanowski, Bleyhl, O斯塔wowicz, & Kuemmerle, 2016). In addition to providing further evidence for the importance of behavioral change, our result emphasizes that it is difficult, if not impossible, to accurately predict an individual's behavior following initial training, adding yet another challenge for the management of long-lived species. Therefore, we highlight that managing long-lived social species may require adaptive interventions even after release (e.g., protection of newly colonized areas or continual behavioral interventions).

The success of a reintroduction depends on producing and maintaining behaviors that increase survival and fitness in reintroduced individuals after release. Because naïve animals often have the highest mortality in reintroduced populations (Banks, Norrdahl, & Korpimaki, 2002), training that successfully increases survival early in life may serve an important purpose, even if these behaviors eventually change. However, for these whooping cranes it is unclear if different migration behaviors ultimately produce fitness differences (i.e., if the trained migration or the adopted shortstopping is more adaptive). There is some evidence for higher survival of juvenile aircraft-trained birds in this population. However, aircraft-trained birds experience a “soft release,” where they are provided with food and protection during their first winter (Servany, Converse, & Bailey, 2014), suggesting that this higher survival may be unrelated to migration patterns. Preliminary evidence suggests that this difference may not continue after the first year (Converse, Servany, Moore, & Runge, in press), but this is uncertain, and continuing
to quantify long-term trends in survival and fecundity as migration patterns change will help identify whether migration distances themselves produce differences in fitness in this population. As it is impossible to predict exactly how behaviors will change over time, we hypothesize that, in species such as whooping cranes that exhibit social learning, an effective method of establishing adaptive behaviors will be to use a variety of reintroduction methods. By introducing multiple behaviors into a population, there will initially be greater behavioral variation on which cultural evolution and natural selection can act. Ideally, this will allow social learning and behavioral adaptation to lead to the most adaptive behaviors over time, resulting in successful reintroductions of self-sustaining populations.

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**SUPPORTING INFORMATION**

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