



Social Learning of Migratory Performance

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continually along this feature before extensive ice sheet formation ~3.5 My B.P. (5).

In full glacial conditions [based on LGM (supplementary materials)], the flow of water is influenced by the ice overburden pressure, which forces water out of the canyon in parts of the upper Petermann catchment and along the direction of ice flow (Fig. 3B). Nonetheless, the canyon remains a conduit for the flow of basal water toward the coast even under LGM conditions, especially northward of ~79° N. For the present ice-sheet configuration, which is small and short-lived compared with its expanded full glacial state, steeper ice surface slopes (relative to LGM) force more water from the canyon to the west at certain locations (Fig. 3C and fig. S3A). In all cases, above ~76° N and within the entire length of the Petermann catchment, the canyon exerts a control on basal water flow. For ~200 km, it provides an uninterrupted hydraulic pathway (Fig. 3 and fig. S3A) that ends at the terminus of Petermann Gletscher. However, although extensive parts of northern Greenland have been identified as having a wet bed (fig. S4) (15), water currently may not be ubiquitous throughout its length. Under full glacial conditions, the ice sheet was larger and thicker than at present day (4), and therefore, a greater proportion of the bed was likely melting during the longer lasting LGM ice sheet configuration.

The lack of substantial subglacial lakes in the main Greenland ice sheet may be partly explained by generally steeper ice surface slopes as compared with those of Antarctica, but subglacial water must be evacuated by some means or it will pool. The subglacial canyon provides an efficient pathway for this water routing over an otherwise relatively flat bed (Fig. 3C). Given that water beneath former ice sheets in Greenland was likely to have been influenced by the canyon, it seems probable that conditions have never been well suited to substantial long-term basal water storage in this sector of Greenland.

The floating ice shelf in front of Petermann Gletscher has been found to possess sub-ice-

shelf channels 1 to 2 km wide and 200 to 400 m deep incised upward into the ice (16). These channels are associated with high basal melt rates, exceeding 30 m year⁻¹. Their existence has been attributed entirely to the action of the ocean (16). We believe the efficient routing of basal water via the canyon to the northern ice sheet margin is also important in explaining these features. Analysis of IPR echo-strength data has identified extensive regions of the northern half of the Greenland ice sheet that have water at the bed (15). Subglacial melt rates in the vicinity of the North Greenland Ice Core Project (NGRIP) drill site have been estimated to exceed 1 cm year⁻¹ (17) and are as high as 15 cm year⁻¹ near the onset of the Northeast Greenland Ice Stream (18). A study examining crustal thickness and geothermal heat flow in Greenland found a minimum in the former (and hence, a maximum in the latter) close to the northern limit of the canyon (Fig. 1) (9). Thus, substantial volumes of subglacial meltwater are generated at the bed, and additional surface meltwater may also penetrate to the bed near the coast (19). An effective means by which this basal water is routed to the ice-sheet margin must exist, else subglacial lakes would form. Basal water generated in the Petermann catchment is highly likely to be routed through the Canyon to the ice sheet terminus (Fig. 3C). Thus, basal water is likely to be delivered at a point source to the ice-shelf cavity, which is likely to influence the local subshelf water circulation (20). Similar sub-shelf channels have been identified underneath Pine Island glacier and elsewhere in Antarctica (21), and we suggest that well-organized subglacial meltwater flow is likely to play a similar role in the development of these features.

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Supplementary Materials

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Materials and Methods
Figs. S1 to S5
References (22–30)

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Social Learning of Migratory Performance

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Successful bird migration can depend on individual learning, social learning, and innate navigation programs. Using 8 years of data on migrating whooping cranes, we were able to partition genetic and socially learned aspects of migration. Specifically, we analyzed data from a reintroduced population wherein all birds were captive bred and artificially trained by ultralight aircraft on their first lifetime migration. For subsequent migrations, in which birds fly individually or in groups but without ultralight escort, we found evidence of long-term social learning, but no effect of genetic relatedness on migratory performance. Social learning from older birds reduced deviations from a straight-line path, with 7 years of experience yielding a 38% improvement in migratory accuracy.

Mechanisms underlying the complex phenomenon of animal migration have been particularly well studied in birds (1–5).

In some taxa, individuals may migrate alone, unaided by conspecifics and relying instead mostly on endogenous, genetically inherited navigation

programs (6). In other species, innate programs alone are not sufficient, and experiential learning is critical to successful navigation, as adult animals often have markedly better navigational capabilities than juveniles (7–9). Information transfer from more experienced individuals to inexperienced ones can be essential to navigational success,

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especially for species that travel in groups (8–10). Current hypotheses, richly supported by theoretical studies (11–13), posit that social learning, coupled with interindividual coordination of movements, is essential to successful migration and the maintenance of group structure. Despite these advances, disentangling the contributions of experience and social learning (mediated through cultural transmission of knowledge) versus innate navigation programs (inherited genetically) to migratory performance represents a key challenge in understanding animal behavior (2).

To address that challenge, we used databases emerging from long-term investment in the conservation of whooping cranes (*Grus americana*). Formerly widespread in North America, whooping cranes are now endangered and restricted to a relictual wild population, migrating between northwestern Canada and the Texas coast, and birds that originate from reintroduction efforts. The most successful reintroduction effort to date established the eastern migratory population (EMP). Most birds in the EMP migrate between a summering range centered on Necedah National Wildlife Refuge in Wisconsin and a wintering range in the area of Chassahowitzka National Wildlife Refuge in Florida (Fig. 1).

We used 2002–2009 relocation data for the EMP, which have two distinct features that allow us to partition genetic and socially learned aspects of migration. First, the EMP is wholly derived from a captive breeding program, and the pairwise genetic relatedness of all migrants is known from studbook pedigrees (14). Second, new captive-bred, naïve-to-migration birds were transferred each summer to Necedah National Wildlife Refuge and, during their first fall, were trained on their southbound migration route by human-piloted ultralight aircraft (15, 16). Thus, all birds were initially trained to follow the same migration route. Although another release method has been used in this population more recently, we included only ultralight-trained birds in our study. After this first training flight, the cranes migrate freely, flying in groups with other cranes but without ultralight aircraft on all subsequent north- and southbound migrations. Because of their endangered status, the stepwise progression of each bird's route on each migration is intensively monitored, yielding both detailed spatial information and comprehensive information on group composition on each trip.

The necessity for ultralight training suggests that successful migration in whooping cranes depends on both social learning and innate programs. As in storks (17), southward autumn migrations by naïve-to-migration, captive-reared juveniles flying in the absence of experienced individuals would be unlikely to lead to a successful journey, suggesting that cultural transmission of information is important (15). Innate programs influence initiation of migration in that ultralight-trained birds can initiate the northbound spring migration independently of experienced birds (or ultralight aircraft) (15).

To disentangle the effects of social learning and innate navigation programs on migratory performance, we extracted data on four predictor variables from the crane databases: (i) the age of all individuals on each flight (which we hypothesize as a measure of experiential learning), (ii) the age of the oldest individual(s) in a migrating group of cranes (which we hypothesize provides an upper limit on experiential learning within each group, as one or more individuals may be the oldest in a group), (iii) the group size as a measure for potential group navigation, and (iv) genetic relatedness (which captures interindividual nonindependence in the birds' innate navigation programs). We used deviations from a straight-line path between summer and winter ranges on the migratory route of individual birds as a proxy for migratory performance and built a hierarchical linear mixed model to examine how much of those deviations at each observed location on the migratory route could be explained by individual age, age of the oldest individual(s) in a migratory social group, group size, and genetic relatedness on both individual and group levels (18). In addition, our model included the effects of sex and season (18).

Social learning facilitated long-term increases in the accuracy of migration. The age of the oldest individual(s) in a group improved migratory performance by ~5.5% per year of age (Fig. 2), decreasing the average deviation from a straight-line path by ~4.2 km per year of age for each relocation event [posterior mode: -4.2 km, 95% highest posterior density interval (HPDI): -1.1 to -7.2 km]. Flight groups in which the oldest individual(s) had a migratory age of 1 year were predicted to deviate ~76.1 km from the straight-line path per relocation, whereas in groups in which the oldest individual(s) was 8 years old, the predicted deviation was only 46.8 km. Thus, 7 years of experience translated into a 38% improvement in migratory performance (Fig. 2). Overall, autumn locations were predicted to deviate 36.3 km more from the straight-line paths than did spring locations (95% HPDI: -21.0 to -54.3 km) (Fig. 2). We found no significant effects of sex (posterior mode: 2.4 km, 95% HPDI: -2.9 to 8.8 km), individual migratory age (as opposed to age of the oldest bird in a group) (posterior mode: -1.4 km, 95% HPDI: -3.8 to 1.2 km), or group size (posterior mode: -0.3 km, 95% HPDI: -4.8 to 5.8 km). The lack of an effect of group

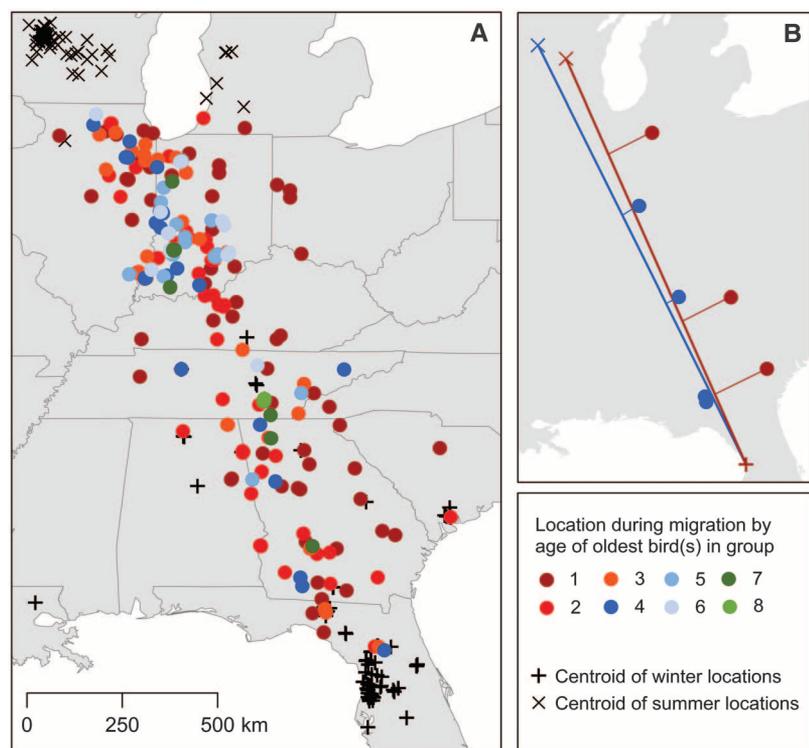


Fig. 1. Whooping crane location data. (A) Migration map for the EMP of whooping cranes (2002–2009). We identified each bird's summer and winter ranges in each year using the mean coordinates of all locations for that individual during summer and winter times when birds are not migratory. We then identified the straight-line path for each migration event linking consecutive summer and winter (or winter and summer) ranges for each bird. We calculated the deviation of each migratory relocation from the straight-line path and used this as a simple proxy for migratory performance. Variation in data availability over the 8 years of the study precluded application of more complex measures of deviation, such as those based on full trajectories that might take into account heterogeneity in wind strength and direction, topography, and the availability of suitable stopover sites. (B) Typical migratory pattern for two 1-year-old individuals migrating in spring 2005 traveling without (red) and with (blue) older birds.

size is interesting, as theory suggests that larger group sizes may aid navigation (13). In addition, a fixed effect for mean group genetic variance [i.e., the mean breeding value (19) potentially predicting better migratory accuracy] was indistinguishable from zero (standardized posterior mode: -0.03 km, 95% HPDI: -10.7 to 24.9 km) (Fig. 2). This finding implies that closely related birds did not migrate more similarly to each other (either increased or decreased accuracy) than did less related birds.

On average, 1 year olds that traveled with older birds deviated by 63.9 km from the straight-line paths, which was 34% less than for 1 year olds that traveled in same-age groups (mean deviation: 97.1 km) (Fig. 3). Accounting for other sources of variation, the modeled difference was 44.7 km (95% HDPI: 6.6 to 85.7 km). Groups of 1-year-old birds migrating without older birds were particularly prone to large deviations from the straight-line route. Fully 25% of locations of 1 year olds flying without older birds exceeded 150 km of deviation, the largest deviation observed for mixed-age groups (Fig. 3).

Previous research has contributed to overall understanding of the role of experience, social transmission of knowledge, and innate programs in navigation and route-learning of birds. How-

ever, results must be drawn piecemeal from across diverse studies. For example, translocation experiments involving several bird species have demonstrated individual learning (9), social learning (20), and innate programs (21) in isolation. The crane analyses reported here provide an integrated, multiyear portrait of these critical issues within a single species.

We show that learning of migration routes by whooping cranes takes place over many years and that social transmission of knowledge by experienced older birds yields progressive improvements in migratory performance of younger birds. In cranes, social learning may contribute to improved navigation through spatial memory of landscape features. Tracking studies on the relictual wild population of whooping cranes suggest that memory of landmarks across small scales and long-distance responses to large-scale topography may aid navigation (22, 23). Experience may also manifest as improved coping with weather patterns such as wind drift, as has been shown for raptors (24). More than 75% of our relocations were to the east of the straight-line migratory path, which accords with the predominantly westerly winds in the region (fig. S1). The absence of experienced adults may lead to failed or misdirected migration (8, 17). In our study, we found that

younger birds lack accuracy only when unaided by older birds (Fig. 3), suggesting the absence of intentional exploration. However, greater deviations in the fall migration may arise from explorations in search of alternative overwintering areas, because birds do not always return to the initially trained overwintering area (Fig. 1A).

In other bird species, the timing and direction of migration are strongly heritable (6). Even though we did not find a significant effect of genetic relatedness on migratory performance, other evidence indicates that innate programs must play a role in some aspects of crane migration. For example, the first independent northward migration can be initiated by flight groups that consist of only juvenile birds, demonstrating that some elements of migration knowledge need not be culturally transmitted in whooping cranes.

Beyond their contributions to understanding social learning of migration, our findings have important implications for conservation and reintroduction efforts of whooping cranes. If experience and learning accrue with time for crane reproduction, as demonstrated here for migration, additional experience may also improve successful reproduction in the wild, especially given the potential links between migratory performance and breeding performance (25). Because the average age of the whooping crane EMP is itself increasing, further improvements in migratory performance are expected. Previous studies have demonstrated that leadership plays an important role in bird homing navigation and that more experienced birds are more likely to become leaders (26); our results show that social learning enhances group navigation performance for long-distance migrants and that the benefits of experience accrue over many years.

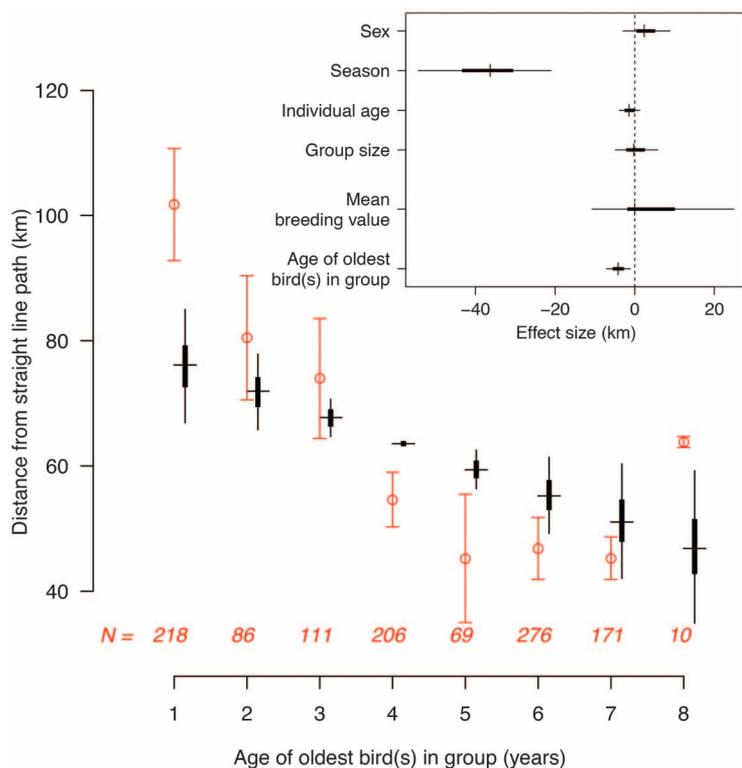


Fig. 2. Migratory performance of whooping cranes measured as deviation of locations from straight-line path versus age of oldest individual(s) in each flight group with more than one individual. Original data [red; means with 95% confidence intervals (CIs)] and model predictions (black; posterior modes, quartiles, and 95% HPDI) accounting for variation in several other factors, including migratory season, bird sex, and the birds' genetic relatedness, are shown. Sample sizes (N) are relocation events. (Inset) Posterior distributions of overall model terms. Mean additive genetic variance refers to the group effect of genetic variance [i.e., the mean breeding value (18)].

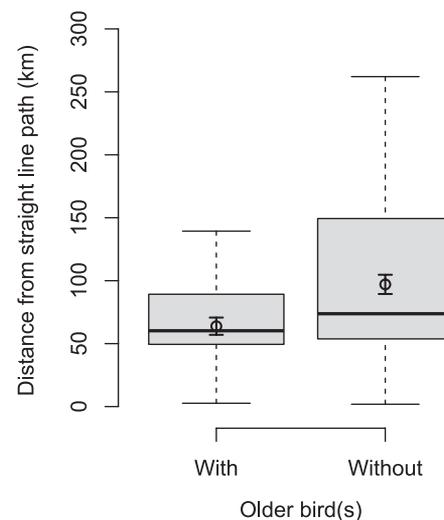


Fig. 3. Distance from straight-line path for locations of 1-year-old birds that migrated with older bird(s) compared with 1-year-old birds that migrated in groups without older bird(s). Box plots providing minimum, maximum, medians, and upper and lower quartiles are shown in gray. Means and 95% CIs are shown inside the box plots.

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Supplementary Materials

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Nuclear Wave1 Is Required for Reprogramming Transcription in Oocytes and for Normal Development

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Eggs and oocytes have a remarkable ability to induce transcription of sperm after normal fertilization and in somatic nuclei after somatic cell nuclear transfer. This ability of eggs and oocytes is essential for normal development. Nuclear actin and actin-binding proteins have been shown to contribute to transcription, although their mode of action is elusive. Here, we find that *Xenopus* Wave1, previously characterized as a protein involved in actin cytoskeleton organization, is present in the oocyte nucleus and is required for efficient transcriptional reprogramming. Moreover, Wave1 knockdown in embryos results in abnormal development and defective *hox* gene activation. Nuclear Wave1 binds by its WHD domain to active transcription components, and this binding contributes to the action of RNA polymerase II. We identify Wave1 as a maternal reprogramming factor that also has a necessary role in gene activation in development.

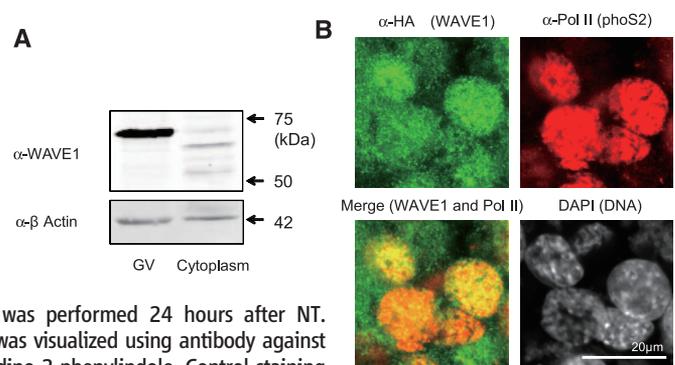
Eggs and oocytes efficiently reprogram transplanted somatic nuclei to an embryonic state (1, 2). This reprogramming ability of eggs and oocytes toward somatic nuclei is believed to relate to their natural activity to activate sperm nuclei at fertilization. Reprogramming factors are synthesized and accumulated during egg formation and are especially enriched in the amphibian oocyte nucleus, named the germinal vesicle (GV) (1). GVs also contain necessary factors for embryonic development (3, 4). It is unclear what

kinds of GV factors are required for reprogramming and for normal development, and how they contribute to these fundamental processes. To iden-

tify such a maternal factor, we have developed a nuclear transfer assay; hundreds of mammalian somatic cell nuclei are injected into the GV of *Xenopus* oocytes, and these nuclei undergo not only continuous transcription of active genes but also transcriptional reactivation of somatically silenced embryonic genes within 2 days (1). This system thus provides a unique opportunity to identify maternal factors responsible for reprogramming the transcription of somatic nuclei.

Previously, we found an important role of oocyte nuclear actin in transcriptional reprogramming (5). Actin dynamics are regulated by actin-binding proteins (ABPs) (6). Increasing evidence suggests that nuclear ABPs play crucial roles in transcriptional activation (7–9). Therefore, we tested the roles of nuclear ABPs in reprogramming and development. The effect of overexpressing ABPs in recipient *Xenopus* oocytes on transcriptional reprogramming of *Pou5f1* (*Oct4*) was examined by reverse transcription quantitative polymerase chain reaction (RT-QPCR) (fig. S1A) (10). Overexpression of two ABPs Tocal1 (5) and Rac1 significantly enhanced *Oct4* transcription from transplanted mouse C2C12 myoblast cell nuclei ($P < 0.01$) (fig.

Fig. 1. Wave1 is present in the *Xenopus* oocyte nuclei and transplanted mouse nuclei. (A) Western blot analysis revealed that Wave1 is accumulated in the GV of the *Xenopus* oocyte. (B) Mouse C2C12 nuclei were injected into the GV overexpressing HA-NLS-Wave1 (fig. S1A). Immunofluorescence analysis was performed 24 hours after NT. HA-NLS-Wave1 localization was visualized using antibody against HA (α HA). DAPI, 4',6'-diamidino-2-phenylindole. Control staining is shown in fig. S3.



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