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Research article

Translocation experiment of taiga bean geese *Anser fabalis* provides evidence for oblique social learning of moult migration

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While there is ample evidence supporting genetic control of migratory behaviour in short-lived passerines, long-lived social species have been assumed to rely solely on cultural inheritance of migratory routes. Evidence from experimental studies supporting this idea is scarce. We tested whether the moult migration in taiga bean geese *Anser fabalis* has an inherited component or whether the birds need oblique social learning (where knowledge on migration is transferred from any experienced individual to any naïve individual conspecific) to carry out this journey. In many waterfowl species, non-breeders and failed breeders migrate to remote places for wing moult while successful breeders stay at the breeding grounds and moult with their chicks. We translocated one-year-old taiga bean geese before their first moult migration to sites outside of the breeding range to examine whether they display innate moult migration behaviour without experienced conspecifics or not. The birds were equipped with GPS-transmitters and released in randomly assigned groups of two. Wild control one-year-old birds were released immediately after capture with other non-breeding geese, while a procedural control group consisting of older birds was held in captivity until being released at the same time with the translocated one-year-old birds but in the place where they were captured. Most translocated birds found conspecifics and either joined locally moulting breeders or followed experienced birds to moulting sites in Russia. Two of the translocated birds did not find other bean geese and settled to moult together in southwest Finland. The wild control birds moult-migrated as expected, while only one of the procedural control birds moult-migrated to Russia and the remaining three stayed with locally moulting breeders in Finland. Our results support the idea that moult migration in geese is culturally inherited, highlighting the importance of the non-relative, experienced adult individuals in maintaining population-specific behaviours.

Keywords: Anseriformes, biotracking, cultural inheritance, moult migration, oblique learning

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Introduction

It is well established that migratory behaviour in short-lived songbirds is under strong genetic control (Berthold 2003, Toews et al. 2019, Wynn et al. 2023). However, in long-lived, social birds, species migration routes are thought to be mainly culturally transmitted, i.e. experienced adult birds teach the naïve young birds (Sutherland 1998, Mueller et al. 2013) but the experimental evidence is limited (Chernetsov et al. 2004, Loonstra et al. 2023). Seasonal migration has been documented even in pre-avian dinosaurs (Suarez et al. 2017), therefore basic genetic components are possibly present in all living avian taxa including those thought to rely only on cultural inheritance.

The most common type of migration studied is the annual commute between clearly defined wintering and breeding grounds (Webster et al. 2002). On top of this, various waterfowl species undertake moult migration that entails movement from breeding grounds to remote areas where they undergo a complete change of their flight feathers and become flightless for a period of time (Salomonsen 1968). While the phenomenon of moult migration is generally well known, it is not known how this behaviour transmits between generations. Although the extent to which cultural transmission happens between any experienced individual and any naïve individual (i.e. oblique learning) or between parents and offspring (i.e. vertical learning; Whiten 2021), cultural transmission among geese is often thought to mainly occur between parents and their offspring instead of between non-related birds (Von Essen 1991, Kölzsch et al. 2019, 2020). However, moult migration cannot be learned from the parents as they are usually breeding at the time of the onset of the first moult migration of one-year-old birds (Salomonsen 1968, Piironen et al. 2021). Hence, one-year-old birds either learn the behaviour obliquely from other experienced birds (adults that have skipped breeding or 2–3 years old subadults that have not yet bred but have undertaken moult migration at least once) or they rely on genetically inherited instructions. Moult migration in geese follows as rigid a schedule as spring or autumn migration (Salomonsen 1968, Newton 2008, Piironen et al. 2021) suggesting that a genetic component could play at least some role. To our knowledge, which of the mechanisms the birds are using to reach the moulting sites has not been previously studied in the context of moult migration.

In Finland, the non-breeding one-year-old taiga bean geese *Anser fabalis*, together with older non-breeders and failed breeders, undertake moult migration to Novaya Zemlya in high Arctic Russia while successful breeders stay with their broods and moult in Finland (Piironen et al. 2021). In a field experiment, we translocated naïve one-year-old taiga bean geese from their breeding grounds ca 500 km south to areas in southern Finland where no other conspecifics occur, to find out if they can carry out moult migration to Russia without the guidance of experienced birds. The birds were equipped with GPS-transmitters that allowed us to accurately follow their movements after the translocation.

Since geese are a classic example of social migrants (Sutherland 1998) and capable of moving great distances, we followed the translocated geese in the field to verify if they have found other taiga bean geese. In case the translocated one-year-old geese did not meet other conspecifics, we expected them to display innate behaviour following one of the three alternative scenarios. 1) The moulting site location at Novaya Zemlya is genetically inherited and the translocated geese directly fly there from the release sites using 'goal-area navigation' (Rabøl 1978). 2) Moult migration follows 'clock and compass' inheritance and translocated birds deploy the same geocentric (Wehner 1998) route as their non-displaced conspecifics, ending up in moult sites shifted accordingly to the displacement (Perdeck 1958). 3) There is no genetic component to moult migration, but it has to be learned by following other birds, and the translocated one-year-old birds either remain close to the translocation site or move in random directions in search of conspecifics. In the case where the translocated birds find conspecifics, we expected them to carry out their moult in Finland with successful breeders or to join moult migrating failed breeders (Fig. 1).

Material and methods

Catching and tagging

We captured foraging groups of taiga bean geese using cannon nets at previously established feeding sites in Salla (66°50′N, 28°40′E) and Vaala (64°34′N, 26°23′E) in northern Finland from 26 May to 9 June 2023 (Fig. 1). The geese were aged based on the shape of the wing coverts and sexed by examination of cloaca (Mouronval et al. 2019, Supporting information). For each captured goose we recorded body mass, wing length and tarsus length (Supporting information). Birds were tagged with OrniTrack-44 solar-powered GPS-GSM neck collars (Ornitela UAB) weighing ~ 45 g. Transmitters weighed 1.2% (SD ± 0.14) of the body mass of a goose on average, which is well under the accepted 5% threshold (Portugal and White 2018). Transmitters were set to record a position every five minutes. Even though transmitters continuously recorded the positions, we programmed them to not attempt to transmit the data while in Russia due to the scarcity of GSM towers in the area. Because of this, we lost the on-line tracking possibility of the birds close to the Russian border and had to wait for the birds to complete moult and return to Europe to access the complete set of their positions. The transmitters also had a field-readable, three-digit code on the casing, which allowed individual identification of marked birds in the field (the code is also used for an individual identifier for each bird in the text). All captured geese were also ringed with a standard metal ring issued by the Finnish ringing centre.

Experiment

In total, we managed to capture 16 one-year-old taiga bean geese. Six were tagged and immediately released as a 'wild

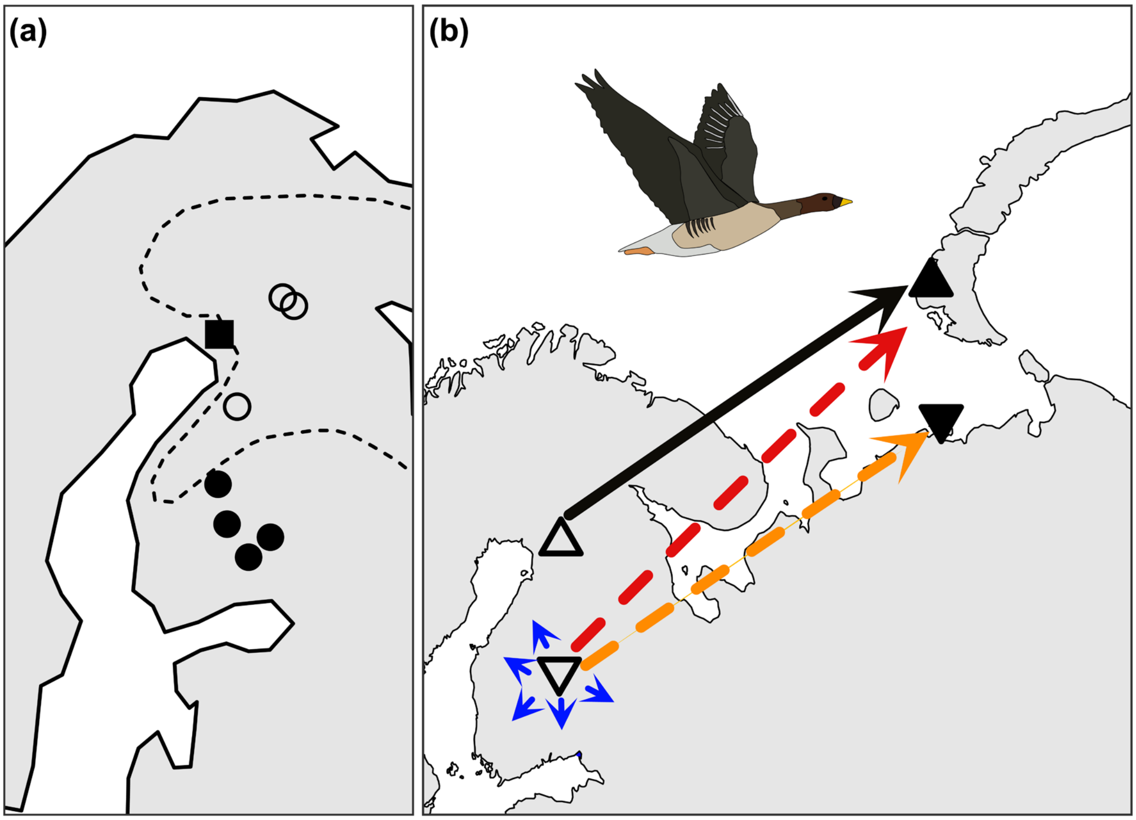

Figure 1. Locations of study sites. (a) The dotted line marks the approximate breeding range of the taiga bean goose in Finland. Hollow circles show the trapping sites and filled circles are the release sites. The solid square denotes the location of the aviary geese were kept in until release. (b) Schematic depiction of the experiment and hypothesized outcomes. The black line, connecting hollow (breeding area) and filled (moult site) triangles, shows an approximate normal moult migration route. A hollow inverted triangle shows an example of a displacement site. In outcome 1 (red dotted line), displaced one-year-old birds compensate for displacement and fly directly to the correct moulting grounds ('goal-area navigation'). In outcome 2 (orange dotted line), displaced birds migrate the same length and in the same direction as wild control birds and end up in a correspondingly shifted moulting area marked with a filled inverted triangle ('clock and compass navigation'). Outcome 3 (blue arrows), displaced birds fail to migrate and randomly disperse around the release site.

control' group, usually with other non-breeding, subadult birds. Importantly, they were free to associate with any birds right after capture, and represented the behaviour of non-manipulated birds. In addition to the wild control group, we used one of the one-year-old geese and three non-breeding adults as a procedural control group, which we also kept in the aviary along with the translocation group but released at the capture site (Fig. 1). The purpose of this group was to control the potential effects of captivity to the behaviour of the geese. We do not know whether any of the caught birds were related to each other. However, in general, one-year old taiga bean geese are not known to be associated with their siblings or other relatives in the spring. One of the wild control birds was predated possibly by a fox shortly after release (we found the remnants of the body and the transmitter a few kilometres from the tagging site), and one stopped transmitting data on the day of tagging, possibly due to transmitter failure. Thus, the final wild control group was four birds. The remaining 10 one-year-old birds were moved to an aviary with a 7 × 6 m outdoor area with soft mesh roofing and plenty of shaded spots. Birds at all times had access to 5 × 5 m indoor space. Water and food (water-soaked grain) were provided ad libitum. The aviary was located in Tervola (66°04′N, 24°49′E, Fig. 1). The distance from the aviary to the catching sites in Salla and Vaala was approximately 190 and 180 km, respectively. The transmitters were deployed to birds prior to moving them to the aviary, to give them a possibility to adjust themselves to the devices during the captivity period, thus minimizing the effects of tag deployment to their behaviour (Clausen et al. 2020, Schreven et al. 2024). Unfortunately, one bird died from an unknown reason while in captivity, leaving nine for the study. We continuously monitored the movements of the four 'wild control' birds and two days after the last one of them had initiated moult migration, we carried out the translocation experiment. Experimental birds tagged with GPS-neckbands were released within an eight-hour time window (from 16 June 22:00 to 17 June 07:00 h, UTC +3). We started by releasing the procedural control group (one one-year-old and three adults) at their capture site in Vaala, to see if the period of captivity had influenced their behaviour. These birds were allowed to associate with each other and other taiga bean geese. We assumed that the adults have the experience of at least one moult migration. Right after the release of the procedural control birds, we translocated the eight tagged one-year-old birds to southern Finland and released them in randomly assigned groups of two at four sites that lay outside of the taiga bean goose breeding range. The release sites were 340–520 km from the aviary, 180–610 km from the catching sites, and 50–300 km from known taiga bean goose breeding range borders (Fig. 1, Supporting information).

We selected translocation sites to be as suitable as we could (a small lake or pond close to fields suitable for foraging) and made sure these places were outside of the taiga bean goose breeding range, thus minimising the chance of them running into conspecifics. All released birds either flew directly or swam in the water at the release sites, giving no reason to think they had been injured during the transportation process.

Following the translocated geese

To be able to interpret the GPS tracks, we attempted to follow each goose and visually check if they were alone (or with a release pair), or if they had joined any other geese. We monitored the live positions of the geese using the Ornitrack online user interface provided by Ornitela UAB. Every time a goose moved and settled in a new place, if logistically possible we attempted to drive to the given location and see if it had joined conspecifics or other goose species. This was done carefully from a distance in order not to disturb the birds. In two cases where birds had settled in a wetland that was impossible to monitor from the ground, we deployed a remotely controlled drone with a thermal and video camera. Some of the birds that had settled at an even larger mire were checked by an observer from a helicopter (all observation records in the Supporting information).

Data analysis

We tested the effect of the time spent in captivity to the body mass loss of geese by fitting a linear regression model with body mass loss (in g) as response variable and time spent in captivity (in days) as explanatory variable. We further tested the effect of the body mass loss to moult migration using logistic regression with moult migration as binary response variable (moult migrated/did not moult migrate) and body mass loss was the explanatory variable. We also used a Welch two sample t-test to compare body mass of geese before and after the period of captivity. We tested whether initial movement direction of translocated birds was random or significantly oriented with Rayleigh test of uniformity. To estimate if birds moved from their release site to moult site directly or via lengthy detours, we calculated 'efficiency of travel' as a ratio of total distance travelled (km) / great circle distance (km) between the two locations. If the coefficient was close to one, the bird had used the shortest possible route to reach the moulting area. Coefficient value 1 means that the travel route was the shortest possible way to reach the destination, consequently the larger the coefficient value the less direct the route the bird took to reach the moulting site.

All the geographic position data were handled with a combination of Google Earth Pro and R ver. 4.1.1 (www.r-project.org). All graphs were created, and analysis was carried out with R 4.1.1. Great circle distances were calculated with standard equations (Gilg et al. 2013); and total travel distances were manually extracted with use of Google Earth Pro. Circular data were transformed and analysed with the R package 'circular' (ver. 0.4-93) with which we also extracted movement bearing on a 360-degree scale. To score initial movement direction we extracted the bearing from the release site to the point where birds had moved 5 km from the site. This distance was chosen after investigating initial movements of the translocated birds. At this distance, all of the translocated birds had set out on a determined longer flight away from the release site but had not yet reached the next longer staging site. We note that the result regarding the initial movement direction was not sensitive to chosen distance.

Results

Wild control

We successfully tracked four one-year-old geese of the wild control group on their first moult migration, all of which displayed the expected behaviour and moulted in Novaya Zemlya (Fig. 2a). The mean travelled distance from the capture sites and the moult site for these four birds was 1532 km (SD ± 210), which was very close to the great circle distance between the same two points (1311 km ± 185, Supporting information).

Procedural control

From the procedural control birds, one adult female (Y38) carried out normal moult migration to Novaya Zemlya by departing on 25 June and reaching the destination on 28 June (Fig. 2b). On 22 June Y38 was observed grazing together with five other taiga bean geese. Total travel distance for Y38 was 1789 km and the great circle distance between the capture/release site was 1598 km (Supporting information). The remaining three procedural control birds did not moult-migrate but instead moulted either exactly at the release site (Y33) or at locations ca 30 km away from the release site (Y29 and Y37). We confirmed with observations from a helicopter that Y33, Y39 and Y37 had joined groups of locally moulting breeding bean geese and their broods (Supporting information).

Translocated birds

All but one of the displaced pairs split up and went entirely separate ways shortly after the release. Initial movements of translocated birds when departing from the release sites were random (Rayleigh test of uniformity statistic = 0.34, p = 0.41, Supporting information).

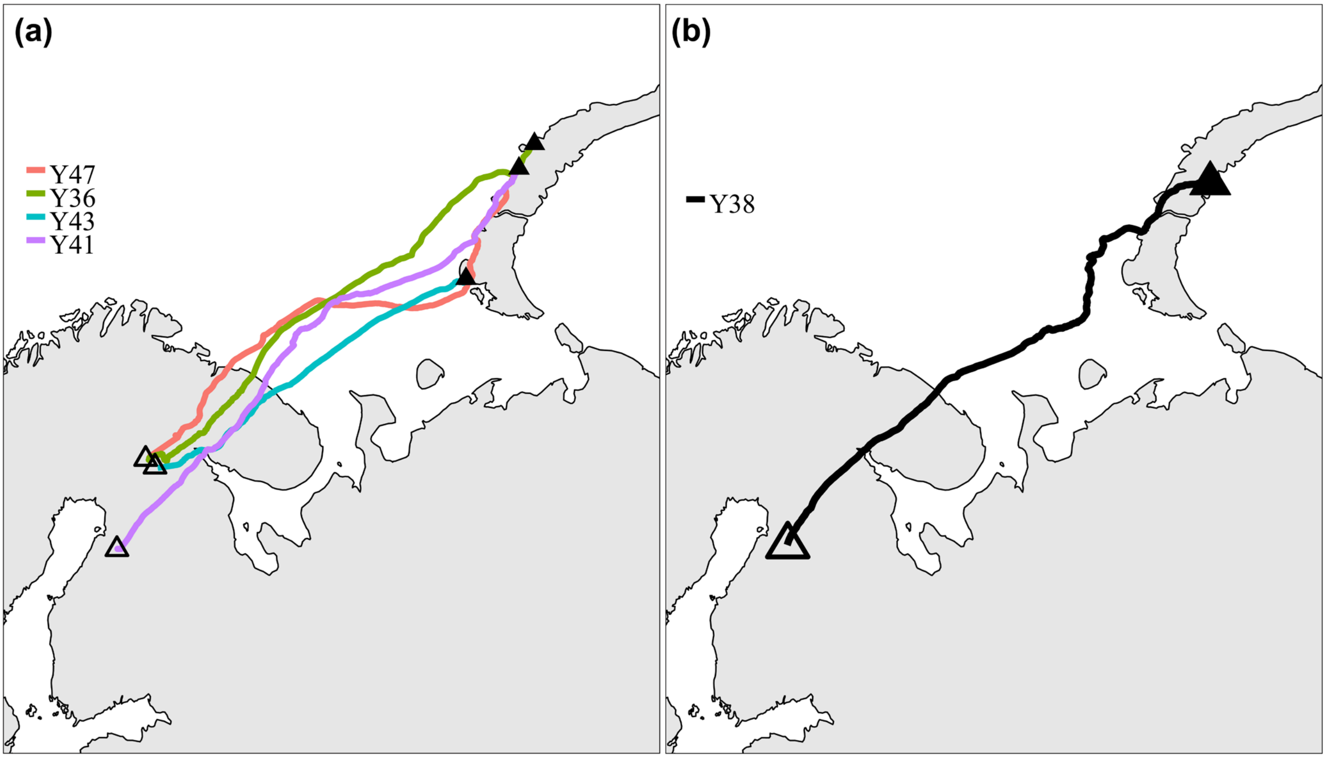

Figure 2. Tracks of control groups. (a) Moult migration route of the four wild control birds from trapping (hollow triangles) sites to moulting sites in Novaya Zemlya (filled triangles). (b) Track of the only procedural control bird that executed moult migration. Three procedural control birds (Y29, Y37, Y33) moulted at or near the release site and thus are not plotted on the map. The black line shows the moult migration route of Y38 from the release site (hollow triangle) to the moult site (filled triangle) in Novaya Zemlya.

The two birds that stayed together (X74 and Y34) did not find any conspecifics and, after travelling 1184 km over 19 days, they settled to moult together in southwest Finland at a site that was 283 km away from the release site along the great circle line (Fig. 3a, Supporting information).

Two birds (Y28 and Y32) after two and eight days, respectively, found groups of locally moulting adults with their chicks and settled there. Both birds travelled ca 150 km to their separate moult sites that were less than 50 km away from the release site. One individual (Y35) travelled 1022 km over 15 days to a moult site that was 329 km away from the release site (Supporting information). This bird settled at the site where the procedural control birds were moulting, often encountering the tagged procedural control birds (Fig. 3a, Supporting information).

Three of the translocated one-year-old birds (Y48, Y27 and Y26) carried out moult migration to Russia (Fig. 3b). Y48 was observed alone on 19 June, but had moved significantly more north by 3 July, from where it had begun a nearly nonstop flight to a moulting site on the Kanin peninsula (travel distance 1529 km). Y27 was observed with locally moulting broods on 22 June but was seen foraging on a field with six adult bean geese and no goslings on 2 July, strongly indicating that the group consisted of failed breeders or non-breeding birds. Two days later (4 July) Y27 left Finland and on 6 July it reached the moulting site in Novaya Zemlya (total travel distance 2577 km). The third bird, Y26, initiated a nonstop flight only a few hours after being translocated. The bird landed at the coast of the Kola peninsula where it spent seven days, after which it flew to the Kanin Peninsula and stayed there for three days, eventually reaching the moult site on Novaya Zemlya on 29 June (total travel distance 2973 km).

The average ratio of total travel distance/great circle distance for translocated birds was 2.9 (range 1.5–4.2), indicating that the translocated birds wandered notably before settling to moulting sites. The same ratio was 1.0 and 1.2 for procedural and wild control groups, respectively (Fig. 4, Supporting information), indicating that both control groups migrated to their moulting grounds using routes very close to the great circle (Supporting information).

Body mass loss in captivity

Seven of the experimental geese lost a considerable amount of mass (mean mass lost 554 g, range 160–940), four birds marginally increased in body mass (mean mass gained 140 g, range 40–220) and one did not change its body mass. Time spent in captivity was negatively associated with body mass loss (linear regression, $p = 0.024$), i.e. birds with shortest time in captivity had the greatest mass loss (Supporting information). The extent of the body mass change was not associated significantly with whether the birds moult migrated or not (binomial regression $p = 0.38$).

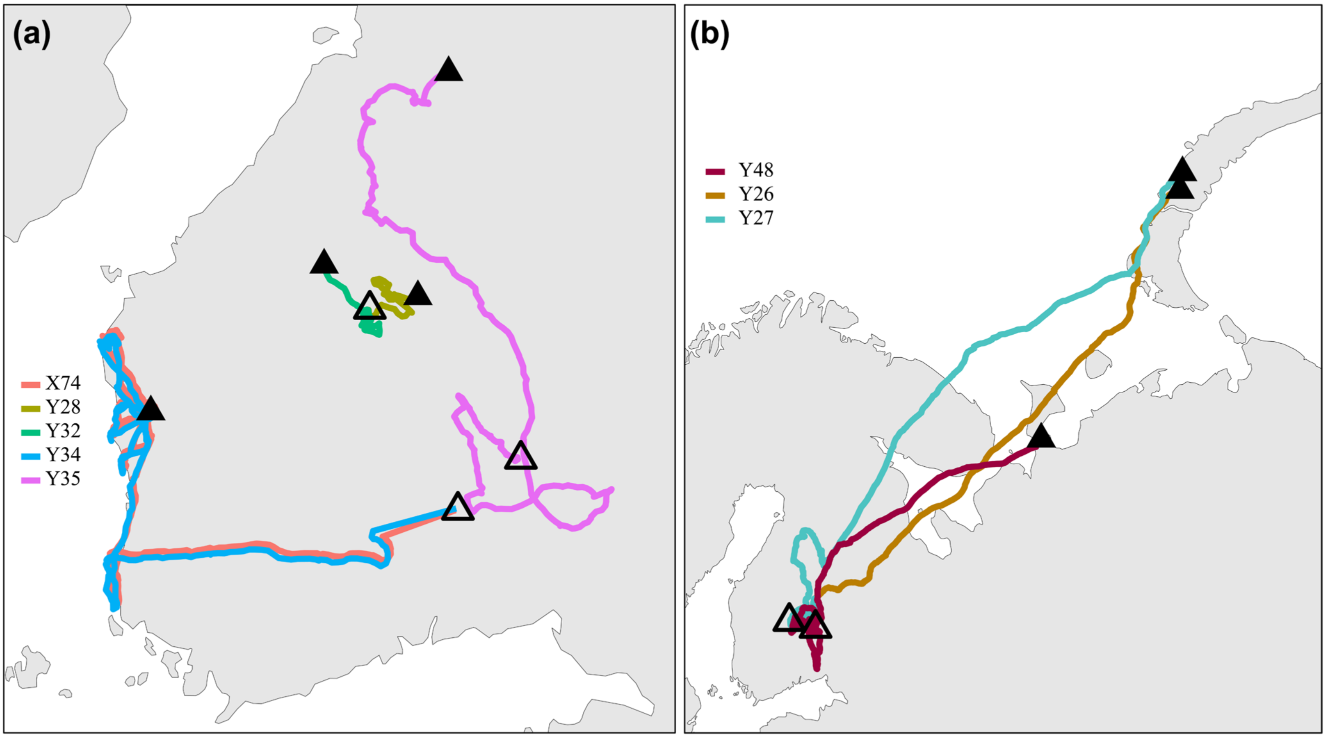

Figure 3. Tracks of translocated one-year-old taiga bean geese from their release sites to their moulting sites. (a) Tracks of birds that moulted in Finland. (b) Tracks of birds that moulted in Russia. Hollow triangles mark release sites and solid triangles the moulting sites.

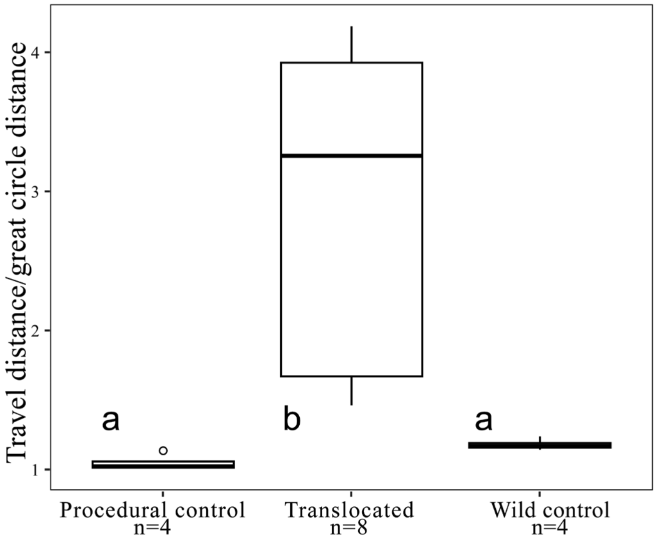

Figure 4. Efficiency of travel coefficient from the release site to the moulting site. The y-axis shows the ratio of the total travel distance (km) over the great circle distance (km) from the release site to the moulting site for three different treatment groups. Translocated birds reached moulting grounds through much less efficient routes than the other two groups ($F_2 = 8.82$, $p = 0.004$). Letters denote statistically different groups according to the post hoc HSD Tukey test (Alpha = 0.5).

Discussion

Our mixed results cannot exclude the role of genetics in moult migration behaviour of naïve one-year-old taiga bean geese. However, we think our study shows that learning from older, non-related conspecifics appears to be a crucial component for generational transfer of moult migration routes. Hence our results are consistent with oblique learning hypothesis, i.e. that knowledge related to the moult migration is socially learned, but not from the parents, but from other experienced conspecifics. From eight translocated one-year-old geese, we can be certain that only two did not find conspecifics, and these two birds moved together and moulted in a mire in southwest Finland. Three one-year-old birds found and joined groups of successful breeders in central Finland north from the release sites and moulted with them and their broods. The remaining three birds carried out moult migrations to Russia. One of these birds (Y27) found staging conspecifics and moult migrated to Novaya Zemlya. Another bird, Y48, most likely found other bean geese (we were not able to verify it visually), with whom it migrated to a less common but not unprecedented moulting site in the Kanin peninsula. Most peculiar is the behaviour of Y26 which, immediately after release, undertook a nearly nonstop flight to the Kola peninsula where it staged for a week before resuming its journey to Novaya Zemlya. We have no information on whether this bird found any conspecifics, but it is the most likely explanation when considering the behaviour of other birds. However, we cannot completely exclude the existence of some genetically inherited cues for moult migration of this bird.

The four wild control birds executed normal moult migration to Novaya Zemlya as expected. However, the behaviour of the procedural control group consisting of one one-year-old and three adults was unexpected. Only one bird (an adult) carried out moult migration to Novaya Zemlya, and the remaining three birds (two adults and the one-year-old bird) moulted at the release site with local breeders and their chicks. This suggests that these birds either were not in sufficient condition for undertaking the moult migration or had missed their individual time window for moult migration. The same could thus apply for the translocated one-year-old birds. However, it is worth noting that the translocated birds were clearly lost and reached the moulting sites in Finland after varying periods of seemingly random exploration, whereas both control groups deployed direct routes to their moulting sites.

We must address the fact that most of the birds lost a significant amount of mass while being held captive. This may have happened due to us not providing the correct food the birds would have otherwise foraged for in nature (Weber 2009), or some stress-related effect. Just like other avian taxa, geese before migration enter hyperphagia (i.e. a period of intensive foraging) to accumulate fat reserves necessary for the journey, which increases their body mass by up to one-third (McLandress and Raveling 1981, Ankney 1982, Prop et al. 2003, Gundersen et al. 2017). To our knowledge, migratory fuelling rates have only been studied in the context of spring and autumn migrations (Newton 2008). However, geese are known to increase their body mass prior to moult (Ankney 1979) and it is reasonable to assume that an increase in body mass must also take place before moult migration. Nevertheless, one of the procedural control birds and three of the translocated birds carried out normal moult migrations and the extent of the mass loss did not predict whether the bird will migrate or not.

We note that deployment of GPS neck-collars is known to have behavioural effects on geese, especially within a week after the deployment (Clausen et al. 2020), but effects on migration timing and breeding can also occur in the consecutive summer birds are marked in spring (Schreven et al. 2024). Hence, catching and marking most likely also had some effect on the behaviour of the geese in this study. However, deployment of similar GPS-transmitters on taiga bean geese in spring did not disturb the moult migration to Novaya Zemlya in earlier studies (Piironen et al. 2021, 2022). The translocated birds also had up to two weeks to habituate to the devices in captivity prior to their release; and, after the release, they flew distances comparable to the moult migration distance to Novaya Zemlya. Hence, we have no reason to believe that the main pattern observed regarding the learning of moult migration would be an artefact caused by catching and marking of birds.

Aside from our study, we are aware of two other translocation experiments on long-lived migratory social species, white storks *Ciconia ciconia* and bar-tailed godwits *Limnosa lapponica* (Chernetsov et al. 2004, Loonstra et al. 2023), both of which showed that autumn migration and in case of godwits also spring migration is entirely learned from experienced individuals. In the case of white storks, the results suggested that they may have inherited a general urge to move south but there were no additional details of the route or wintering quarters. In our study, the translocated birds dispersed randomly after the release (Fig. 3, Supporting information) and hence, we did not find any indication of an innate urge to move towards the presumed moulting grounds in Novaya Zemlya. Reintroduction efforts of sandhill cranes *Grus canadensis* and whooping cranes *G. americana* have shown that if captive-reared juveniles are released close to wild cranes near autumn staging sites they generally tend to follow the experienced birds (Urbanek et al. 2005, Mueller et al. 2013). In fact, the role of social learning aspect of inheriting autumn migration routes is so strong that it has already become a tool in applied conservation biology. Captively reared birds are being trained to follow manned aircrafts that teach them the desired migration routes (sandhill cranes: Urbanek et al. (2005), whooping cranes: Urbanek et al. (2010), glossy ibises *Plegadis falcinellus*: Fritz et al. (2017).

Geese are highly social throughout most of their life-cycle and recent findings indicate that pink-footed geese *Anser brachyrhynchus* might have learned a new migration route from another goose species (Madsen et al. 2023). In greater white-fronted geese *Anser albifrons* it has been shown that family groups migrate together in spring and are led by the parents (Kölzsch et al. 2020). Work on light-bellied brent geese *Branta bernicla hrota* strongly suggests that cultural inheritance of migratory behaviour is the main explanation for the existence of pronounced migratory connectivity (Harrison et al. 2010), and social learning is known to help geese to cope with the global change (Tombre et al. 2019). The results of our experiment are consistent with the conclusions from the above-mentioned studies and provide additional empirical support to the importance of social interactions in the life cycle of geese. This is supported by the fact that those translocated geese that found and joined locally moulting adult breeders decided to stay and moult with them, showing that if they are in the company of other geese, they are most likely to follow the behaviour of others. Moreover, the two translocated birds that did not manage to find other taiga bean geese settled for moult all by themselves, indicating that they may not have had the inherited knowledge on moult migration. All translocated geese that found and joined brood flocks in Finland, meaning that if there is any degree of innate urge to start moult migration, it is generally overruled by the overall behaviour of other, more experienced group members. However, given the relatively small sample size in our study and the fact that we do not know if one of the translocated birds (Y26) moult migrated by itself or not, the possibility of at least some genetic inheritance of migratory behaviour among geese should be studied further. Furthermore, it is also possible that these behaviours are, at least to some extent, learned from older siblings.

The social inheritance of migratory behaviour has most often been discussed in the context of parents teaching their offspring (vertical learning, Kölzsch et al. 2020, Méndez et al. 2021, Byholm et al. 2022). Our study presents a case where information of (moult) migration route is culturally transmitted from adults and older subadults to unrelated one-year-old birds (oblique learning). In addition to moult migration, several goose species have been observed to change their routes between breeding and wintering sites in ways that are difficult to explain only with vertical learning (Kölzsch et al. 2019, Madsen et al. 2023, Piironen and Laaksonen 2023). Although some of these changes are probably associated with pair formation (Kölzsch et al. 2019), learning from other conspecifics or even other species might play a role in shaping the traditional flyways between breeding and wintering areas (Madsen et al. 2023). Hence, the magnitude and importance of oblique versus vertical learning for the ecology and evolution of social migrant species provide fascinating topics for future research.

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Author contributions

Kristaps Sokolovskis: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Antti Piironen**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Validation (equal); Writing – review and editing (equal). **Toni Laaksonen**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (lead); Resources (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jav.03263.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjtbx (Sokolovskis et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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