# Releases of Asian Houbara must respect genetic & geographic origin to preserve inherited migration behaviour: evidence from a translocation experiment

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## Abstract

Maintaining appropriate migratory strategies is important in conservation; however, translocations of migratory animals may alter locally-evolved migration behaviours of recipient populations if these are different and heritable. We used satellite telemetry and experimental translocation to quantify differences and assess heritability in migration behaviours between three migratory Asian houbara (Chlamydotis macqueenii) breeding populations (640 km range across eastern, central and western Uzbekistan). Adults from the eastern population migrated twice as far (mean = 1,184 km ± 44 s.e.) as the western population (656 km ± 183 s.e.) and showed significantly less variation in migration distance than the central population (1,030 km ± 127 s.e.). The western and central populations wintered significantly further north (mean: +8.32°N ± 1.70 s.e. and +4.19°N ± 1.16 s.e., respectively) and the central population further west (-3.47°E ± 1.46 s.e.) than individuals from the eastern population.These differences could arise from differing innate drive, or through learnt facultative responses to topography, filtered by survival. Translocated birds from the eastern population (wild laid and captive-reared, n= 5) migrated further than adults from either western or central recipient populations, particularly in their second migration year. Translocated birds continued migrating south past suitable wintering grounds used by the recipient populations despite having to negotiate mountain obstacles. Together, this suggests a considerable conserved heritable migratory component with local adaptation at a fine geographic scale. Surviving translocated individuals returned to their release site, suggesting continued translocations would lead to introgression of the heritable component and risk altering recipient migration patterns. Conservation biologists considering translocation interventions for migratory populations should evaluate potential genetic components of migratory behaviour.

**Keywords:** bustard, migratory orientation, migratory strategy, population reinforcement, population reintroduction

## Introduction

Maintaining successful migratory strategies in the face of environmental change is a fundamental challenge facing conservation biology [1, 2]. Conservation translocations must ensure founders show appropriate physiological, behavioural and genetic characteristics (IUCN 2013); increasing use of translocations to reintroduce or reinforce migratory populations highlights the need to understand how translocated individuals establish their migratory behaviour [3]. In some vertebrates migration behaviours are culturally transmitted, allowing translocated individuals to learn traditional routes from conspecifics [4, 5] or humans [6]. But in many species, particularly where first migration occurs in the absence of experienced individuals, migratory traits are innate [3, 7] with a strong heritable component [8-10]. For such species, translocation for reinforcement using individuals from an allopatric source population may disrupt the recipient population's migration strategy, potentially altering fitness [11-13], while translocation for reintroduction of extirpated populations may not replicate historic migration strategies [14]. Even where phylogeographic analyses suggest large-scale population-genetic homogeneity this could mask finer-scale adaptation of behaviours under strong local selection. When developing a translocation program for migratory species, experimental investigation is therefore required to assess whether the interplay of facultative and heritable behaviour leads translocated individuals to establish appropriate migration routes.

Migratory species from all vertebrate groups are threatened [15, 16], with migrant birds more at risk than residents [17, 18], through phenological mismatches [19] and cumulative anthropogenic threats across breeding and wintering ranges and along migratory routes [20]. Diverse endangered migratory species are already subject to ex situ management and release [5, 6, 21], but success following release depends on the migratory pathways adopted [14, 22]. Novel migrations may facilitate responses to environmental change [23, 24], particularly when current routes are constrained, their disruption may assist adaptation to potentially suitable landscapes and climates lying beyond current pathways. However, if newly expressed migration routes achieve lower survival [25] or productivity (e.g. through carry-over effects [26]) relative to established strategies, this may reduce population viability [27] and potentially result in catastrophic population losses [28]. Conservation and welfare considerations combine to require that experimental evidence in an adaptive management approach is sought to avoid the potential negative consequences of translocations.

To explore the importance of genetic origin for reinforcement initiatives involving migratory species, we used the migratory Asian houbara (*Chlamydotis macqueenii*) as a model system, examining populations along a longitudinal gradient within the central Asian deserts. The species undertakes long-distance migrations and is subject to large-scale captive breeding and release programmes to reinforce threatened migratory populations throughout its range [29]. Observational studies suggest migration orientation and distance are heritable [30, 31] and differ across the range [30], with juveniles migrating independently of their mothers [31] and probably also of experienced adults, as they leave earlier than adults, and migrate more slowly flying fewer kilometres per day [31] spending longer on stop-overs [32]. Treating migratory Central Asian populations as a single unit for management therefore risks homogenising and potentially compromising population-specific migratory strategies [30].

To examine whether local migratory populations of Asian houbara retain distinct innate migration strategies, despite gene-flow and minimal population structure [33], we examined wild and translocated migration patterns in 3 breeding populations across 640 km (58.05°–63.90°E) of desert in Uzbekistan, a fine-grained scale relative to the full breeding span (4,460 km) of migratory Central Asian populations from Iran/Kazakhstan to China (51°–106°E). We experimentally translocated 'head-started' individuals (captive-reared from wild-laid eggs) of eastern origin into central and western populations. Using satellite telemetry we compared the migration routes of the source and recipient populations, and assessed the extent to which released birds replicated the migration patterns of recipient wild populations.

## Methods

### Study system

Within Uzbekistan we examined a west–east longitudinal range: from the 'western' population on the Ustyurt Plateau (43.87° N, 58.05° E) located towards the species' south-western range-limit; a 'central' population separated by the Aral Sea basin (Fig. 1) and lying ≈200 km east in the Aral Kum (42.88°N, 61.31°E); and an 'eastern' population in the Kyzylkum desert (40.40°N, 63.90°E), 640 km east of the Ustyurt and 450 km east of the Aral Kum. We considered these populations functionally disjunct: satellite-telemetry study of 170 adult-years (from 74 individuals) from the eastern population showed only one instance of short-term dispersal to the central population (an adult female from Bukhara moved west and re-nested, but subsequently returned to the eastern population), while no individuals moved to the western population. No individual moved from the central or western to the eastern population in 22 adult-years (12 individuals) of satellite-telemetry. Wild adults and juveniles from the eastern population primarily migrate along a south/south-westerly route [31] passing the Iran/Turkmenistan border between the Hindu Kush (maximum 7,690 m elevation) and the Kopet Dag mountains within the Turkmen-Khorasan range (maximum 3,190 m: forming a broad west–east topographic obstacle to the north–south migration), to winter in southern Iran and Pakistan (figure 1). Migration routes of central and western populations had not been characterized previously, but we a priori hypothesized that western individuals may follow a similar migration route to Asian Houbara breeding to the north-west (on the Turanian Plain in western Kazakhstan), which initially migrate south over the Ustyurt Plateau, then south-west to west crossing the Kopet Dag mountains which do not appear to act as a barrier to their migration [30, 32], to winter south-west of the Caspian Sea predominantly in southern Iran and Iraq.

### Migratory data acquisition

Wild breeding adults were captured during the breeding season and fitted with back-mounted solar-powered satellite transmitters (PTTs) programmed to record 5 (30 g PTT) or 12 (45 g PTT) GPS locations per day (accuracy within 18 m; further details in Supporting Information). Transmitters weighed <3% of bird body mass and are considered to have no detrimental effect on houbara [30]; and do not affect adult female breeding probability, clutch size, egg size or nest success [34]. All tracked wild adults had previously completed at least one return migration.

For head-starting and translocation, 11 wild clutches were collected from the eastern population (all from within a 30 km radius) in spring 2017, artificially incubated and hand-reared in captivity (electronic supplementary material, methods S1). Twelve individuals (eight males and four females sexed on size dimorphism) were randomly assigned to the central and western populations (six each): three mothers each contributed two chicks, of which one sibling was allocated to each treatment, remaining individuals were each from different mothers. Translocated birds were released at 6 months old in mid-September (as earlier release during hot August weather reduces survival [25]) and would have approximately one month of free-living to develop physiology, flight power and endurance before migration onset, if this occurred at the same time as their eastern (source) population (mean=21 October: [31]).

Migration strategy can be age-related in birds [35] and a comparison of translocated head-started birds with wild juveniles in the recipient populations would be the ideal. In this study we compared translocated juveniles to adults of unknown age, as it was not possible to trap wild juveniles in the two recipient areas. However, previous studies found no difference in migration distance or initial bearing, for larger samples of wild juvenile and adult Asian houbara [31, 32], while juveniles that survived their first winter returned to their first wintering sites in subsequent migrations [30, 31], consistent with the lack of population-scale age-dependent migration. Therefore, we consider it appropriate to compare migration of translocated juveniles to adults of the recipient population. However, one potential limitation in our experiment is that captive-rearing may affect first-winter migratory behaviour, as head-started juveniles previously migrated shorter distances than wild juveniles [31], probably owing to physiological limitation and the physical demands of flapping flight. We acknowledge this may curtail the migratory distance of captive-reared translocated juveniles relative to that of wild adults.

The animal research was approved by the UEA Animal Welfare and Ethical Review Body (AWERB), which is governed by UK Government Home Office (2014) guidance on the operation of the Animals Scientific Procedures Act (ASPA 1986; HMSO: London) and the European Commission (2010) Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes (Official Journal of the European Union L276:33-79). Details of trapping, collection, rearing and telemetry protocols are in electronic supplementary material, methods S1.

### Analysis

We focused analyses on migration traits considered likely to be under genetic control (and hence conserved): initial orientation during the first migration step (hereafter ‘first-step bearing’); departure date from the post-breeding grounds; bearing from post-breeding area to wintering site; wintering-site latitude and longitude; migratory distance (the straight-line displacement from post-breeding to wintering-site); wintering-site fidelity, and fidelity after return migration to breeding/release site [30, 31, 36]. We did not compare stop-over locations and timings, speed or migratory efficiency, as these are likely influenced by weather and certainly by age [31, 32]. Only tracks that could provide reliable estimates of each migratory parameter were included (sample sizes are shown in figure 2; details of telemetry data processing and criteria for identifying stop-over and wintering sites are in electronic supplementary material, methods S1).

Migration metrics were compared between the three populations using Generalized Linear Mixed Models (GLMMs), incorporating individual identity as a random effect. We considered the effect of population identity to be supported if incorporating that term reduced the AICc value (Aikaike's Information Criterion adjusted for small sample size) by ≥ 2 units relative to the null model [37], and subsequently tested pairwise differences between populations, controlling for experiment-wide error using a Tukey HSD test. All GLMMs had normal error structure, as bearings ranged between 120° and 280°; measures of site fidelity (breeding and wintering) were log-transformed. Model residuals were checked for normality and homoscedasticity.

The variance of each migration metric was compared between populations using pairwise *F* tests (after averaging each metric per individual to avoid pseudo-replication), controlling for experiment-wide error by Bonferroni procedure. In all tests $p<0.05$ was interpreted as a significant difference, and $p<0.1$ as marginally different (noting the small sample sizes of some wild groups). Translocated groups were qualitatively compared to data for wild groups owing to small sample sizes.

Analyses considered both males and females from the eastern population, but only males from the central and western populations as it was not possible to trap females in these areas. Previous analysis found no difference between male and female adult houbara for first-step bearing, departure date, migration distance, wintering latitude, or breeding-site fidelity [31, 32]. However, as a precaution we also examined analyses repeated while excluding females from the eastern population.

## Results

Model selection Tables and F-test results can be found in electronic supplementary information, appendix S2.

**Characterising wild strategies**

Adult migration strategies differed between the three populations (figure 1, figure 2, Supporting Information, Fig. S1), with western individuals wintering in Turkmenistan, central individuals wintering from Turkmenistan to southern Iran, and eastern individuals wintering mainly across Afghanistan, Iran and Pakistan and infrequently in Iraq and Turkmenistan. All populations had a similar migratory orientation (figure 2*a* and figure 2*b*), in terms of both first-step bearing (means ± s.e.: western 197.96° ± 13.34, central 205.73° ± 10.25, eastern 203.61° ± 3.33; ΔAICc=-3.86 on removal of the population term) and wintering-site bearing (mean ± s.e.: western 197.96° ± 10.95, central 201.62° ± 2.61, eastern 206.22° ± 7.46; ΔAICc=-3.74). Variance in first-step and wintering-site bearings was also similar between populations (all $F$ tests, $p=1$; Supporting Information, appendix S2). Departure day from the post-breeding areas did not differ between populations (mean ± s.e.: western 20 October ± 12, central 4 November ± 10, eastern 15 October ± 4; ΔAICc=-19.31 on removal of the population term, figure 2*c*) and variance in departure date was similar across populations (all $F$ tests, $p>0.44$, Supporting Information, appendix S2). However, populations differed in wintering latitude (ΔAICc=22.57 on removal of population term), with individuals from the eastern population wintering further south (mean latitude=30.17° ± 0.41 s.e.) than those from the central (34.36° ± 1.16 s.e., $z=3.61$, $p<0.001$) and western (38.49° ± 1.70, $z=4.90$, $p<0.001$) populations, and western individuals marginally ($z=2.09$, $p=0.087$) further north of those from the central population (figure 1 and figure 2*e*). Overall migration distance also differed between populations (figure 2*d*, ΔAICc=4.31 on removal of population term). Adults from the eastern population migrated nearly twice as far (mean = 1,184 km ± 44 s.e., figure 1 and figure 2d) as those from the western population (656 km ± 183 s.e., $z=2.88$, $p=0.001$), but had similar variance ($F_{49,2}=0.350$, $p=1$). Adults from the central population migrated an intermediate distance (1,030 km ± 127 s.e.), that did not differ significantly to either the western ($z=-1.75$, $p=0.18$) or eastern ($z=1.22$, $p=0.43$) populations, but with significantly greater variance than eastern individuals ($F_{49,6}=0.16$, $p< 0.001$; Supporting Information, appendix S2). Populations also differed in wintering longitude (figure 2*f*, ΔAICc=4.77 on removal of population term), with individuals from the central population (mean longitude=56.40° ± 1.42 s.e.) wintering significantly further west ($z=-2.453$, $p=0.035$) and the small sample of western birds (55.45° ± 2.08 s.e.) marginally further west ($z=-2.130$, $p=0.079$) than those from the eastern population (59.87° ± 0.50 s.e.). The variance in wintering latitude (figure 2*d*) of individuals from the central population was marginally greater than those from the eastern population ($F_{49,6}$=0.341, *p*=0.096), but other pairwise comparisons of wintering latitude variance did not differ (both *F* tests, *p*>0.169) and variance in wintering longitudes was similar across the populations (all *F* tests, *p*=1, electronic supplementary material, appendix S2). One male from the larger sample of eastern individuals undertook an anomalous migration, moving north-west to winter in Kazakhstan on the Caspian Sea (figure 1).

Wintering-site fidelity, the mean distance between successive annual wintering sites, was similar across individuals from all 3 populations (overall mean=44.7 km [28.6–70.0 95% CI]; ΔAICc=-3.87 on removal of population term; figure 2*e*, electronic supplementary material, appendix S2), and was fine-grained compared to both the scale of habitat extent within wintering ranges and the distances travelled during outward migration (overall mean=1,258 km ± 401 s.d.). Within-population variance in wintering-site fidelity (among individuals) was also similar between populations (all *F* tests *p* = 1, Supporting Information). Breeding-site fidelity was similar across populations (overall mean=10.2 km [8.9–13.0 95% CI]; ΔAICc=-2.25 on removal of population term, figure 2*f*). Across all 3 populations, the 20 wild adult males returned to their display areas, but two of the 33 eastern females changed breeding site between years by >200 km (figure 2*f*). Variance in breeding-site fidelity was similar across populations (all *F* tests, *p*>0.646, electronic supplementary material, appendix S2). Results were unchanged when the eastern sample was restricted to males.

Routes taken by the wild birds, with some exceptions, avoided crossing the Kopet Dag or Hindu Kush mountains; for the eastern population all except one track passed through the gap between these ranges, while individuals from the western population stopped before reaching the Kopet Dag rather than following the route of the Turanian plain breeding population that pass through or over this range. For the central population, four individuals flew over the Kopet Dag, one used the same gap as the eastern population, and two wintered in Turkmenistan to the north of the mountain range.

**Behaviour of released translocated birds**

Of 12 head-started birds translocated from the eastern population, three released into the western population and two released into the central population survived to initiate migration in autumn 2017 (comprising three females, two males, all from different mothers). Of the five individuals that initiated migration, four survived to reach a wintering location (according to criteria of stopover duration), and two (one from each recipient population) completed return-migration in spring 2018 and migrated again the following winter (figure 4: Western Bird 1 and Central Bird 2). Departure dates and first-step bearings of the five translocated individuals were similar to those of all three wild breeding populations (figure 2*a*), but subsequent movement steps during their first autumn migration appeared to be affected by the Kopet Dag mountains on the Turkmenistan–Iran border (figure 4).

Notably, all three eastern birds translocated into the western population that survived to migrate travelled *c* 330 km further south (mean difference=2.9° N ± 2.6 s.e.) than wild adults from the recipient population (figure 2*c*). Their first-winter outward routes showed an apparent mix of conserved orientation and facultative response to the Kopet Dag. One individual encountered the mountains, but did not cross and turned back north to remain and winter in Turkmenistan (figure 3: Western Bird 1), while two travelled south-east along the mountain range to its end at the Iran-Afghanistan border, and then persisted south (figure 3: Western Birds 2 + 3). Of these two, one survived 17 days after stopping migration movements and was considered to have reached its wintering site (at a latitude of 33.98°N), while the second died (latitude 35.56°N) 6 days after stopping migratory movements and may, therefore, not have fully reached its wintering site. Interestingly, the individual that encountered but did not cross the mountain range in its first winter initially followed a similar migration route in its second winter, but then flew over the Kopet Dag to Iran, thereby changing wintering site to a much lower latitude (710 km further south, first winter 39.24°N, second winter 33.53°N, figure 3: Western Bird 1, also see electronic supplementary material, figure S3).

Of the two eastern birds translocated into the central population that survived to migrate, one (Central Bird 1) wintered in Turkmenistan and survived to the following March. The second reached a site in Iran further south (29.72°N) than the central population mean (34.36°N), again showing an initial deflection by the mountains, but on its second autumn migration it followed a more direct route (similar to its previous return path) that avoided the

Kopet Dag and brought it to the southern coast of Iran (27.35°N, further south than all central individuals), before it turned north and died.

Both surviving translocated birds (Central Bird 2 and Western Bird 1) showed fidelity to their release areas, initially returning to within 11.9 km and 38.8 km respectively (figure 3); after its second migration Western Bird 1 (a female) subsequently survived a second migration, again returning to breed in the same location.

## Discussion

Three wild breeding populations across a longitudinal gradient spanning only 640 km (14% of the 4,460 km breeding range of migratory Asian houbara) had similar timing and orientation but differed in migratory distance and wintering latitude. Such differences in adult strategy could result from innate differences, learnt facultative responses to region-specific topography and environment along potential routes, or differential survival filters following sampling by first-year birds [38]. However, although based on limited sample size (n=5), migratory behaviour of experimentally translocated birds indicated a potentially considerable heritable component to the differing migration strategies. This would signify finer-scale adaptation than suggested for Asian houbara by neutral genetic markers [33] or broader-scale migration studies [30, 32].

Translocated birds showed a clear drive to continue migrating south similar to their source population and migrated further than individuals from their recipient populations, which is strongly indicative of an inherited and innate migration trait. The heritability of migration distance is also supported given that translocated birds continued to fly south despite (a) passing suitable wintering sites used by the recipient population, (b) the time and energy required to negotiate the Kopet Dag mountain barriers and (b) the expected weaker physical condition of captive-bred juveniles relative to wild adults [31]. Furthermore, though quasi-anecdotal, one translocated juvenile that failed to cross the mountain range in its first winter, subsequently migrated further south surmounting this mountain obstacle in it’s second winter, to winter further south than the recipient population. This is notable, as it runs counter to the explanation that experienced adult western birds winter north of the mountains because they have learnt this is favourable, and further emphasises the potential importance of a heritable drive to continue south that differed between translocated individuals and the recipient population.

The most probable mechanisms for innate control of migration distance are the duration of migratory activity and/or an innate latitudinal cue to settle [31]. It is not possible to rule out a contribution from social cues, but this appears unlikely given the slowness of the migration of the translocated birds and evidence suggesting they do not follow adults [30-32]. Ultimately — provided mountain ranges could be overcome or avoided — all southerly routes led to Iranian wintering grounds with suitable habitat and climate. Consequently, translocated individuals were able to survive the winter despite not following the migratory paths of their recipient population; but further research is needed to determine how survival rates and breeding productivity might differ between translocated birds and recipient populations. The migratory strategies of the central and eastern Uzbekistan populations have been maintained despite potential gene-flow (of subadult or late-returning males) from larger populations within the migratory flyway [30]. In contrast, western birds showed greater geographic isolation from this flyway and greater local adaptation in migration strategy. We predict that coarser-scale translocations across the migratory range and flyway, with individuals from Mongolia and China having an initial westerly trajectory before reaching Kazakhstan and turning south [30], would be even more disruptive than our fine-scale experiment. Releases into western Kazakhstan by the Sheikh Khalifa Houbara Breeding Centre in Kazakhstan (situated in eastern Kazahkstan), led to reports (R Sheldon pers. comm.) during winter 2019-20 of exhausted (and caught by hand) captive-bred Asian Houbara occurring in Lankaran province of Azerbaijan (darvic ring R491) and the Talesh (darvic ring T390) and Gilan (darvic ring C741) provinces of Iran, all situated on the western coast of the Caspian and highly anomalous for wild Houbara migration. The most likely explanation is that those birds crossed the Caspian on a bearing consistent with an innate south-south west migration bearing of houbara from east Kazakhstan and unlike those of birds from the Turanian Plain which would normally travel due south to avoid crossing the Caspian.

Translocated birds showed strong fidelity to release sites, allowing them to integrate with and reinforce the recipient population. Consequently, genotypes of translocated individuals are likely to introgress into recipient populations. Where released genotypes are even slightly less fit, supplementation can reduce population sizes and genetic diversity over the long term [27]. Large-scale releases of individuals of different geographical origins risk overwhelming locally adapted genotypes of recipient populations whatever the latter’s fitness advantage [39, 40].

Currently, there is no agreement in the Convention on Migratory Species or between range states on sustainable management and translocation strategies for this heavily-hunted migratory species, with multiple stakeholders releasing birds throughout its range [41]. There are 7 large-scale breeding centers distributed within Arabia and Central Asia (from at least 5 different organisations): those in Uzbekistan and Kazakhstan release captive-bred birds within their source populations [29, 42], but other centers in the Middle East have released more widely, including into Jordan, UAE, Kingdom of Saudi Arabia, Kuwait, Bahrain, Qatar, Pakistan, Kazakhstan and Uzbekistan [41, 42], involving thousands of translocated birds derived from breeding stock established from both resident (Afghanistan, Yemen, Iran) and migratory (Kazakhstan) Asian populations, with no information provided on the degree to which accessions are maintained as separate breeding lines, or the geographic match between released birds and recipient populations [43]. Our study suggests that the practices of interbreeding resident and migratory stocks and of releasing birds outside their geographic origin should immediately stop in order to preserve latent population structure potentially vital to the migratory capabilities of locally-adapted populations. Releasing birds sourced from the same geographic origin is a feasible and precautionary approach, as many populations within Central Asia have the potential to be managed sustainably with a reduced need for captive-bred supplementation, provided hunting pressure is reduced [29].

Where migratory behaviour is known or suspected to be heritable, translocations should respect fine-scale geographical structure of source and recipient populations. When this is not feasible (due for example to small population size), trial releases should be undertaken to assess both the potential differences between source and recipient populations and the effectiveness of further releases. The evidence presented here indicates the vital importance of experimental studies to evaluate the migratory behaviour of translocated individuals before scaling-up interventions to a conservation reinforcement.

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## References

[1] Berger, J. 2004 The last mile: How to sustain long-distance migration in mammals. *Conserv. Biol.* **18**, 320-331. (doi:10.1111/j.1523-1739.2004.00548.x).

[2] Wilcove, D.S. & Wikelski, M. 2008 Going, going, gone: Is animal migration disappearing? *PLoS Biol.* **6**, 1361-1364. (doi:10.1371/journal.pbio.0060188).

[3] Tenger-Trolander, A., Lu, W., Noyes, M. & Kronforst, M.R. 2019 Contemporary loss of migration in monarch butterflies. *PNAS* **116**, 14671. (doi:10.1073/pnas.1904690116).

[4] Mueller, T., O'Hara, R.B., Converse, S.J., Urbanek, R.P. & Fagan, W.F. 2013 Social learning of migratory performance. *Science* **341**, 999-1002. (doi:10.1126/science.1237139).

[5] Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L., et al. 2018 Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* **361**, 1023-1025. (doi:10.1126/science.aat0985).

[6] Fritz, J., Kramer, R., Hoffmann, W., Trobe, D. & Unsöld, M. 2017 Back into the wild: establishing a migratory Northern bald ibis Geronticus eremita population in Europe. *Int. Zoo. Yearb.* **51**, 107-123. (doi:10.1111/izy.12163).

[7] Willemoes, M., Strandberg, R., Klaassen, R.H.G., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M. & Alerstam, T. 2014 Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PLoS ONE* **9**. (doi:10.1371/journal.pone.0083515).

[8] Pulido, F., Berthold, P., Mohr, G. & Querner, U. 2001 Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. B* **268**, 953-959. (doi:10.1098/rspb.2001.1602).

[9] Lohmann, K.J., Putman, N.F. & Lohmann, C.M.F. 2012 The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342. (doi:https://doi.org/10.1016/j.conb.2011.11.005).

[10] Putman, Nathan F., Scanlan, Michelle M., Billman, Eric J., O'Neil, Joseph P., Couture, Ryan B., Quinn, Thomas P., Lohmann, Kenneth J. & Noakes, David L.G. 2014 An inherited magnetic map guides ocean navigation in juvenile pacific salmon. *Curr. Biol.* **24**, 446-450. (doi:https://doi.org/10.1016/j.cub.2014.01.017).

[11] Sanchez-Donoso, I., Rodríguez-Teijeiro, J.D., Quintanilla, I., Jiménez-Blasco, I., Sardà-Palomera, F., Nadal, J., Puigcerver, M. & Vilà, C. 2014 Influence of game restocking on the migratory behaviour of the common quail, Coturnix coturnix. *Evol. Ecol. Res.* **16**, 493-504.

[12] Söderquist, P., Elmberg, J., Gunnarsson, G., Thulin, C.G., Champagnon, J., Guillemain, M., Kreisinger, J., Prins, H.H.T., Crooijmans, R.P.M.A. & Kraus, R.H.S. 2017 Admixture between released and wild game birds: a changing genetic landscape in European mallards (*Anas platyrhynchos*). *Eur. J. Wildl. Res.* **63**. (doi:10.1007/s10344-017-1156-8).

[13] Blanco Gonzalez, E., Espeland, S.H., Jentoft, S., Hansen, M.M., Robalo, J.I., Stenseth, N.C. & Jorde, P.E. 2019 Interbreeding between local and translocated populations of a cleaner fish in an experimental mesocosm predicts risk of disrupted local adaptation. *Ecol. Evol.* **9**, 6665-6677. (doi:10.1002/ece3.5246).

[14] Villers, A., Millon, A., Jiguet, F., Lett, J.M., Attie, C., Morales, M.B. & Bretagnolle, V. 2010 Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: Releasing birds from Spain threatens attempts to conserve declining French populations. *Ibis* **152**, 254-261. (doi:10.1111/j.1474-919X.2009.01000.x).

[15] Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G.M. & Berger, J. 2009 Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* **7**, 55-76. (doi:10.3354/esr00173).

[16] Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V., et al. 2014 Migratory marine species: Their status, threats and conservation management needs. *Aquat. Conserv.* **24**, 111-127. (doi:10.1002/aqc.2512).

[17] Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. 2014 The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis* **156**, 1-22. (doi:10.1111/ibi.12118).

[18] Bairlein, F. 2016 Migratory birds under threat. *Science* **354**, 547-548. (doi:10.1126/science.aah6647).

[19] Zurell, D., Graham, C.H., Gallien, L., Thuiller, W. & Zimmermann, N.E. 2018 Long-distance migratory birds threatened by multiple independent risks from global change. *Nat. Clim. Change* **8**, 992-996. (doi:10.1038/s41558-018-0312-9).

[20] Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. & Foppen, R.P.B. 2010 Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. B* **277**, 1259-1266. (doi:10.1098/rspb.2009.1525).

[21] Caillouet Jr, C., Putman, N., Shaver, D., Valverde, R., Seney, E., Lohmann, K., Mansfield, K., Gallaway, B., Flanagan, J. & Godfrey, M. 2016 A call for evaluation of the contribution made by rescue, resuscitation, rehabilitation, and release translocations to Kemp's Ridley Sea Turtle (*Lepidochelys kempii*) population recovery. *Herpetol. Conserv. Bio.* **11**, 486-496.

[22] Lowrey, B., Proffitt, K.M., McWhirter, D.E., White, P.J., Courtemanch, A.B., Dewey, S.R., Miyasaki, H.M., Monteith, K.L., Mao, J.S., Grigg, J.L., et al. 2019 Characterizing population and individual migration patterns among native and restored bighorn sheep (*Ovis canadensis*). *Ecol. Evol.* **9**, 8829-8839. (doi:10.1002/ece3.5435).

[23] Sutherland, W.J. 1998 Evidence for flexibility and constraint in migration systems. *J. Avian Biol.* **29**, 441-446. (doi:10.2307/3677163).

[24] Newton, I. 2007 *Migration Ecology of Birds*. London, UK, Elsevier.

[25] Burnside, R.J., Collar, N.J., Scotland, K.M. & Dolman, P.M. 2016 Survival rates of captive-bred Asian Houbara *Chlamydotis macqueenii* in a hunted migratory population. *Ibis* **158**, 353-361. (doi:10.1111/ibi.12349).

[26] Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. 2011 Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**, 4-18. (doi:10.1111/j.1365-2656.2010.01740.x).

[27] Willoughby, J.R. & Christie, M.R. 2019 Long-term demographic and genetic effects of releasing captive-born individuals into the wild. *Conserv. Biol.* **33**, 377-388. (doi:10.1111/cobi.13217).

[28] Sawyer, H., LeBeau, C.W., McDonald, T.L., Xu, W. & Middleton, A.D. 2019 All routes are not created equal: An ungulate's choice of migration route can influence its survival. *J. App. Ecol.* **56**, 1860-1869. (doi:10.1111/1365-2664.13445).

[29] Dolman, P.M., Collar, N.J. & Burnside, R.J. 2018 Captive breeding cannot sustain migratory Asian houbara *Chlamydotis macqueenii* without hunting controls. *Biol. Cons.* **228**, 357–366. (doi:10.1016/j.biocon.2018.10.001).

[30] Combreau, O., Riou, S., Judas, J., Lawrence, M. & Launay, F. 2011 Migratory pathways and connectivity in asian houbara bustards: Evidence from 15 years of satellite tracking. *PLoS ONE* **6**, e20570.

[31] Burnside, R.J., Collar, N.J. & Dolman, P.M. 2017 Comparative migration strategies of wild and captive-bred Asian Houbara *Chlamydotis macqueenii*. *Ibis* **159**, 374-389. (doi:10.1111/ibi.12462).

[32] Madon, B., Le Nuz, E., Ferlat, C. & Hingrat, Y. 2015 Insights into the phenology of migration and survival of a long migrant land bird. *Insights into the phenology of migration and survival of a long migrant land bird*, 028597. (doi:10.1101/028597).

[33] Riou, S., Combreau, O., Judas, J., Lawrence, M., Al Baidani, M.S. & Pitra, C. 2012 Genetic differentiation among migrant and resident populations of the threatened asian houbara bustard. *J. Hered.* **103**, 64-70. (doi:10.1093/jhered/esr113).

[34] Burnside, R.J., Guilherme, J.L., Collar, N.J. & Dolman, P.M. in press Backpack harness solar powered PTTs do not affect reproductive traits in Asian Houbara *Chlamydotis macqueenii*. *Eur. J. Wildl. Res.*

[35] Meyburg, B.-U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I., Meyburg, C. & Vansteelant, W.M.G. 2017 Orientation of native versus translocated juvenile lesser spotted eagles (&lt;em&gt;Clanga pomarina&lt;/em&gt;) on the first autumn migration. *Orientation of native versus translocated juvenile lesser spotted eagles (&lt;em&gt;Clanga pomarina&lt;/em&gt;) on the first autumn migration* **220**, 2765. (doi:10.1242/jeb.148932).

[36] Liedvogel, M., Åkesson, S. & Bensch, S. 2011 The genetics of migration on the move. *The genetics of migration on the move* **26**, 561-569. (doi:https://doi.org/10.1016/j.tree.2011.07.009).

[37] Burnham, K. & Anderson, D. 2002 *Model selection and multi-model inference*. 2nd ed. New York, USA, Springer.

[38] Gill, J.A., Alves, J.A. & Gunnarsson, T.G. 2019 Mechanisms driving phenological and range change in migratory species. *Mechanisms driving phenological and range change in migratory species* **374**. (doi:10.1098/rstb.2018.0047).

[39] Storfer, A. 1999 Gene flow and endangered species translocations: a topic revisited. *Biol. Cons.* **87**, 173-180. (doi:https://doi.org/10.1016/S0006-3207(98)00066-4).

[40] Singer, F.J., Papouchis, C.M., Symonds, K.K. & Krausman, P.R. 2000 Translocations as a toll for restoring populations of bighorn sheep. *Restor. Ecol.* **8**, 6-13.

[41] Allinson, T. 2014 Review of the global conservation status of the Asian Houbara Bustard (*Chlamydotis macqueenii*). In *Convention of Migratory Species* (Quito, Ecuador, Convention on Migratory Species.

[42] IFHC. 2016 International Fund for Houbara Conservation Annual Report 2015-2016. (Abu Dhabi, UAE.

[43] IFHC. 2012 International Fund for Houbara Conservation Annual Report 2012. (Abu Dhabi, UAE.

## Figure Legends

**Figure 1.** Migration routes (Panel A) used by wild Asian Houbara adults from three different breeding populations in Uzbekistan (Bukhara: eastern, Aral Kum: central, Ustyurt: western). Starting points of tracks are indicated by solid dots, while the end of tracks are shown as larger dots with a white central dot; only one migration route is shown for each individual for clarity. Panel B shows topographic detail including obstacles (water bodies and mountains with darker shades representing higher elevations) to migration paths in Central Asia. Panel C shows the map in global position panel A.

**Figure 2.** Migration metrics for three wild populations (eastern, central and western) of Asian houbara in Uzbekistan and two groups of head-started birds originating from the eastern population and translocated to the western and central populations. Background dots show the data while the black points are model estimated means with standard error bars, tests between wild groups are indicated by horizontal bars and $p$ values. Translocated groups were not statistically tested. Boxes give the number of individuals and total number of migration tracks for each group.

**Figure 3.** Outward (autumn) and return (spring) migrations of head-started (wild-laid, captive-reared) Asian houbara translocated from their eastern source population into central (two individuals) and western (three individuals) Uzbekistan. One translocated individual from each release returned and subsequently completed a second migration [Central Bird 2, Western Bird 1]. Filled points indicate summer locations, hollow points indicate either wintering location [Western Bird 1, Central Birds 1 + 2] or the furthest stopping point reached on migration for individuals that died *en route* or after arrival [Western bird 3 and Western bird 2 respectively].

**Fig. 1**

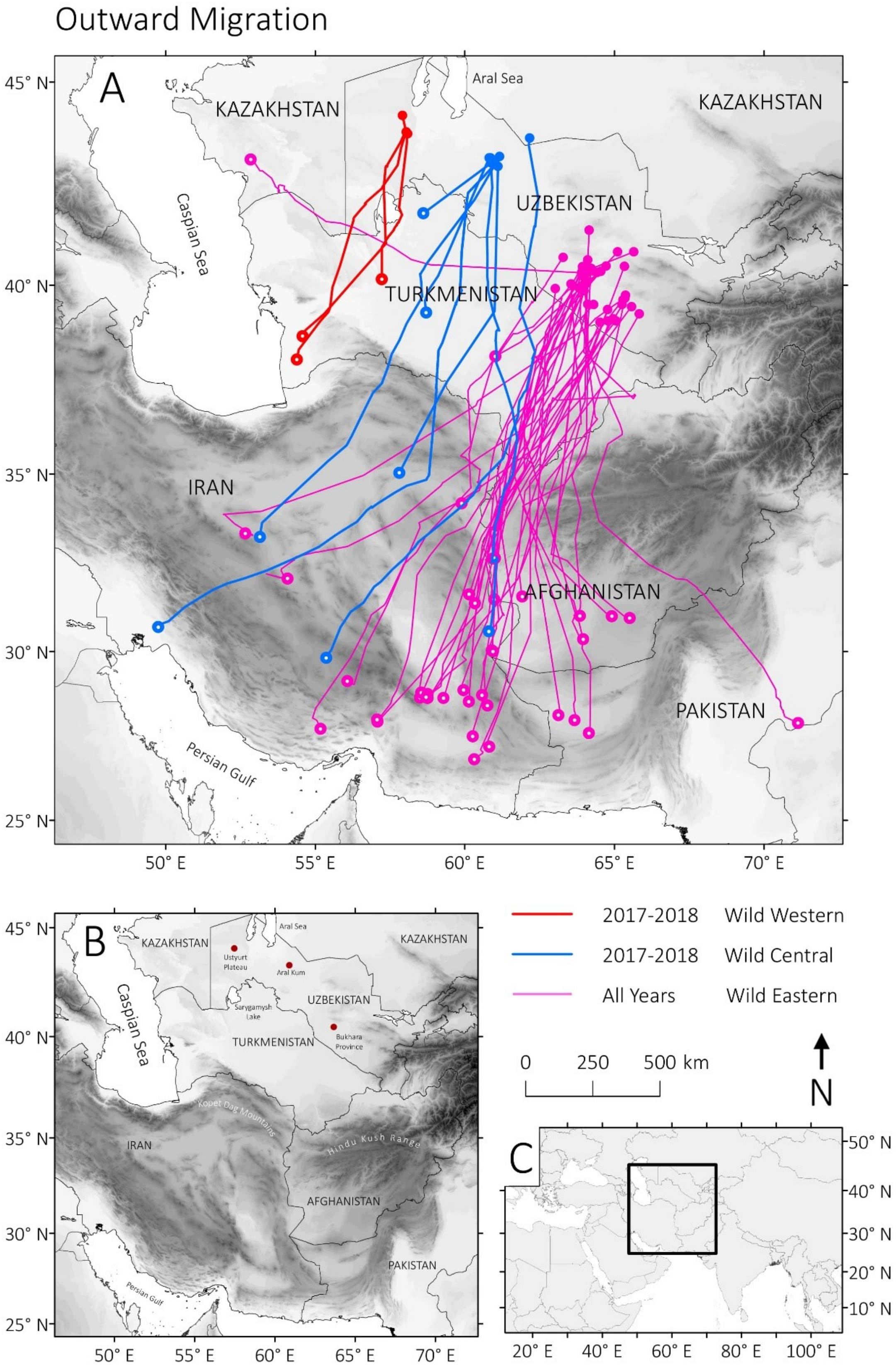

Outward Migration
A
Aral Sea
KAZAKHSTAN
KAZAKHSTAN
Caspian Sea
UZBEKISTAN
TURKMENISTAN
IRAN
AFGHANISTAN
PAKISTAN
Persian Gulf
45° N
40° N
35° N
30° N
25° N
50° E
55° E
60° E
65° E
70° E
B
KAZAKHSTAN
Aral Sea
KAZAKHSTAN
Ustyurt Plateau
Aral Kum
Caspian Sea
Sarygamysh Lake
UZBEKISTAN
Bukhara Province
TURKMENISTAN
Kopet Dag Mountains
Hindu Kush Range
IRAN
AFGHANISTAN
PAKISTAN
Persian Gulf
45° N
40° N
35° N
30° N
25° N
50° E
55° E
60° E
65° E
70° E
2017-2018 Wild Western
2017-2018 Wild Central
All Years Wild Eastern
0 250 500 km
N
C
50° N
40° N
30° N
20° N
10° N
20° E
40° E
60° E
80° E
100° E

**Fig. 2**

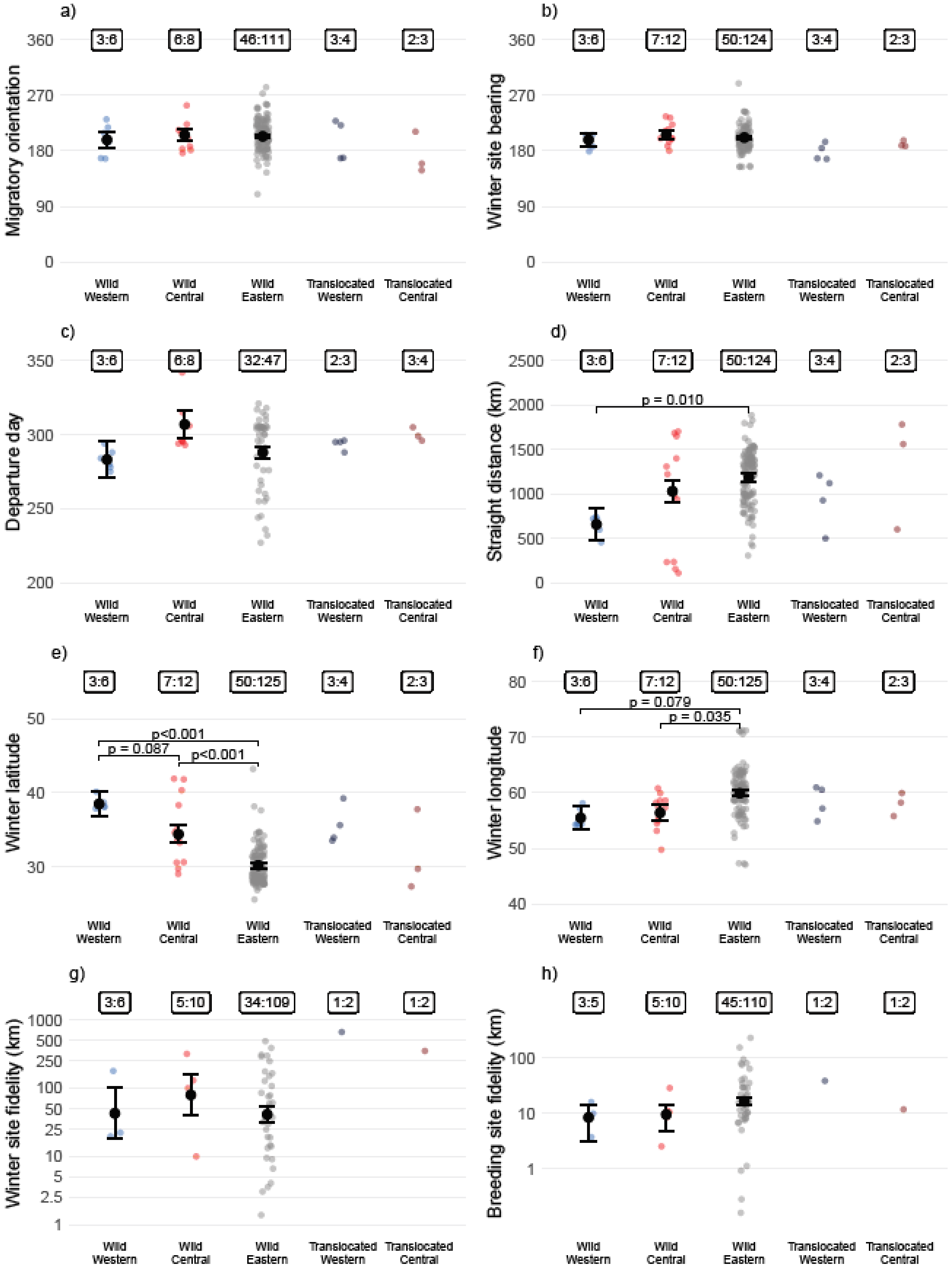
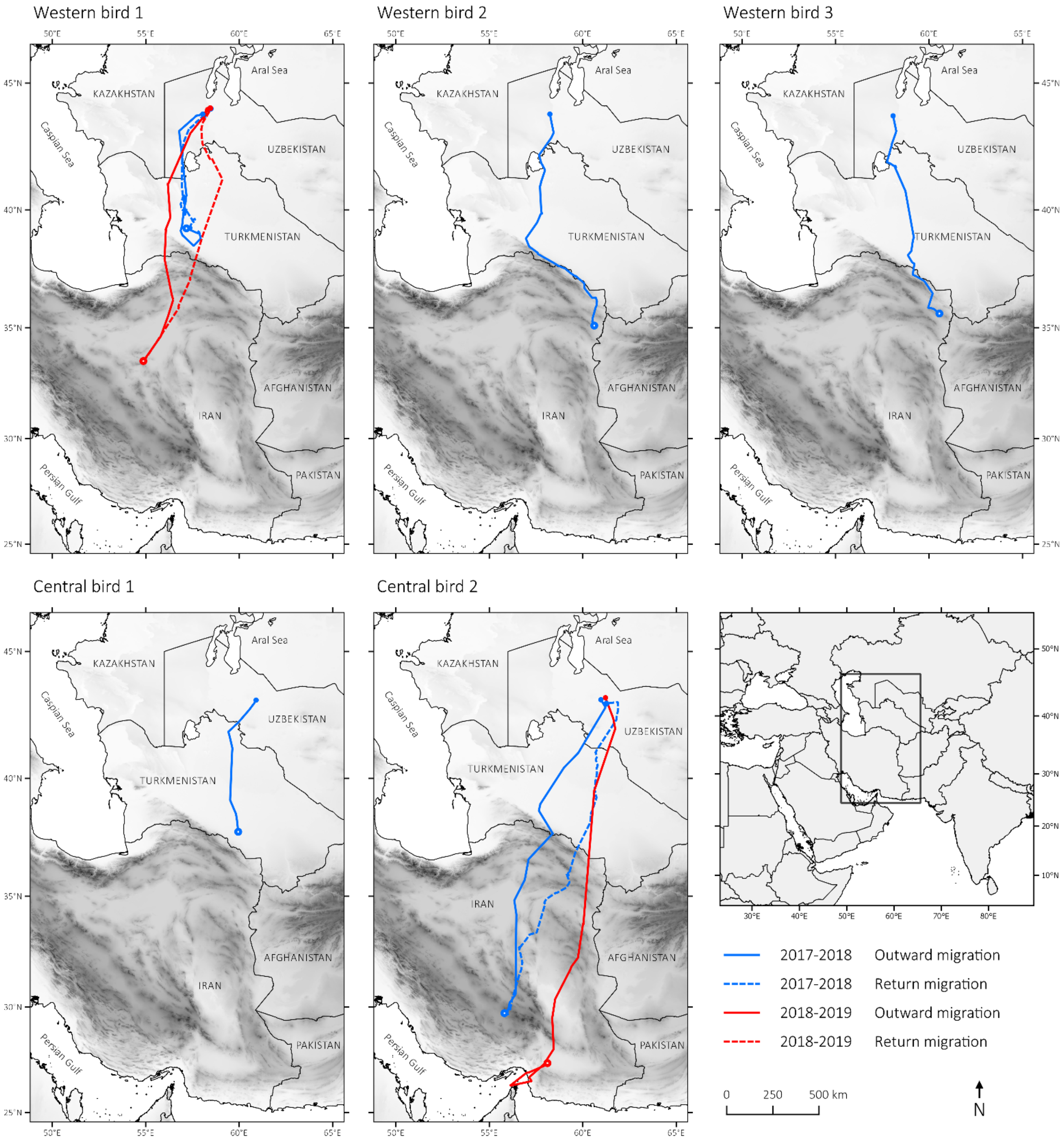

a)
3:6
6:8
46:111
3:4
2:3
Migratory orientation
360
270
180
90
0
b)
3:6
7:12
50:124
3:4
2:3
Winter site bearing
c)
3:6
6:8
32:47
2:3
3:4
Departure day
350
300
250
200
d)
3:6
7:12
50:124
3:4
2:3
p = 0.010
Straight distance (km)
2500
2000
1500
1000
500
e)
3:6
7:12
50:125
3:4
2:3
p<0.001
p = 0.087
p<0.001
Winter latitude
50
40
30
f)
3:6
7:12
50:125
3:4
2:3
p = 0.079
p = 0.035
Winter longitude
80
70
60
50
40
g)
3:6
5:10
34:109
1:2
1:2
Winter site fidelity (km)
1000
500
250
100
50
25
10
5
2.5
1
h)
3:5
5:10
45:110
1:2
1:2
Breeding site fidelity (km)
100
10
1
Wild Western
Wild Central
Wild Eastern
Translocated Western
Translocated Central

**Fig. 3**


Western bird 1
Western bird 2
Western bird 3
Central bird 1
Central bird 2
Aral Sea
KAZAKHSTAN
UZBEKISTAN
TURKMENISTAN
Caspian Sea
AFGHANISTAN
IRAN
PAKISTAN
Persian Gulf
50°E
55°E
60°E
65°E
45°N
40°N
35°N
30°N
25°N
30°E
40°E
50°E
60°E
70°E
80°E
50°N
40°N
30°N
20°N
10°N
2017-2018 Outward migration
2017-2018 Return migration
2018-2019 Outward migration
2018-2019 Return migration
0
250
500 km
N