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Comparative migration strategies of wild and captive-bred Asian Houbara *Chlamydotis macqueenii*

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For migratory species, the success of population reintroduction or reinforcement through captive-bred released individuals depends on survivors undertaking appropriate migrations. We assess whether captive-bred Asian Houbara *Chlamydotis macqueenii* from a breeding programme established with locally sourced individuals and released into suitable habitat during spring or summer undertake similar migrations to those of wild birds. Using satellite telemetry, we compare the migrations of 29 captive-bred juveniles, 10 wild juveniles and 39 wild adults (including three birds first tracked as juveniles), examining migratory propensity (proportion migrating), timing, direction, stopover duration and frequency, efficiency (route deviation), and wintering and breeding season locations. Captive-bred birds initiated autumn migration an average of 20.6 (±4.6 se) days later and wintered 470.8 km (±76.4) closer to the breeding grounds, mainly in Turkmenistan, northern Iran and Afghanistan, than wild birds, which migrated 1217.8 km (±76.4), predominantly wintering in southern Iran and Pakistan (juveniles and adults were similar). Wintering locations of four surviving captive-bred birds were similar in subsequent years (median distance to first wintering site = 70.8 km, range 6.56–221.6 km), suggesting that individual captive-bred birds (but not necessarily their progeny) remain faithful to their first wintering latitude. The migratory performance of captive-bred birds was otherwise similar to that of wild juveniles. Although the long-term fitness consequences for captive-bred birds establishing wintering sites at the northern edge of those occupied by wild birds remain to be quantified, it is clear that the pattern of wild migrations established by long-term selection is not replicated. If the shorter migration distance of young captive-bred birds has a physiological rather than a genetic basis, then their progeny may still exhibit wild-type migration. However, as there is a considerable genetic component to migration, captive breeding management must respect migratory population structure as well as natal and release-site fidelity.

Keywords: captive breeding, genetic control of migration, innate control of migration, reinforcement, reintroduction.

The release of captive-bred individuals to re-establish or supplement populations of threatened species is increasingly used in conservation management (Seddon *et al.* 2007, Armstrong & Seddon 2008) but has had mixed outcomes (Griffith *et al.* 1989, Snyder *et al.* 1996, Wolf *et al.* 1998, Ewen *et al.* 2014). Unintentional selection of traits that happen to be beneficial in captivity can increase the prevalence of alleles normally deleterious in the wild (Frankham 2008). Such domestication in captivity can be rapid (Araki *et al.* 2007), changing physiological responses (Tieleman *et al.* 2002), gut morphology (Moore & Battley 2006), organ morphology (Tieleman *et al.* 2002), physical abilities including flight (Hess *et al.* 2005) and responses to threat cues (Saunders *et al.* 2013), leading to lower survival (Brown *et al.* 2006) or

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lower reproduction (Rymešová *et al.* 2013) than in wild counterparts. The assumption that depleted wild populations benefit from the release of captive-bred animals therefore needs to be tested by comparing the performance of released animals with that of wild conspecifics (IUCN 2016) to inform refinements in practice. Establishing released animals in migratory populations may be particularly challenging, given both the mortality risks faced by all first-time long-distance migrants (Newton 2007, Sergio *et al.* 2014) and the potential erosion of migratory behaviour over multiple generations of captive breeding. Although in some species migratory behaviour may be culturally transmitted (Chernetsov *et al.* 2004, Palacín *et al.* 2011), more commonly it is genetically determined in interaction with physiology, condition and facultative fine-tuning (Newton 2007). Where it is genetically determined, translocated individuals from non-migratory populations may fail to migrate, as in the case of Iberian Little Bustards *Tetrax tetrax* released into a migratory French population (Villers *et al.* 2010). Conversely, migratory tendency may be undesirable, as seen with some Great Bustards *Otis tarda* of Russian origin released in the UK (Burnside 2013).

We investigated whether released captive-bred birds subsequently demonstrate wild migration behaviour in the Asian Houbara *Chlamydotis macqueenii*, a large-bodied bustard for which migration is probably genetically determined (Combreau *et al.* 2011). The Asian Houbara is classified by IUCN as Vulnerable, owing chiefly to widespread unregulated hunting and poaching (Combreau *et al.* 2001, Tourenq *et al.* 2005, Riou *et al.* 2011). The main conservation response has been intensive captive breeding and release (Saint Jalme *et al.* 1996, Allinson 2014), initially to support resident populations of the Asian Houbara in the Arabian Peninsula and African Houbara *Chlamydotis undulata* in Morocco. Later, as hunting activities have expanded into Central Asia, captive breeding and release has also been used to reinforce the Asian Houbara's migratory populations (Allinson 2014). However, if released captive-bred birds are to compensate for the loss of wild individuals by recruiting into the predominantly migratory free-living populations, they must be able to complete their annual return migration (Burnside *et al.* 2016). Therefore, the migratory performance of Houbara bred in captivity and released back to the wild needs to be assessed. First-winter Asian Houbara migrate independently of their mothers (the fathers playing no parental role), but may join small groups of conspecifics (PMD, NJC pers. obs.). So, whereas migratory restlessness and direction are expected to be genetically based, social information from experienced adults may influence choice of migration route and staging or wintering sites. Migratory performance, therefore, may depend on a combination of genetics, social cues and physiological condition.

We use data from 4 years of satellite tracking to compare the migration strategies of wild juveniles and wild adults with those of young captive-bred and released Asian Houbara (juveniles and yearlings) in their first autumn and spring migration movements following release. Parameters examined are described in Table 1. For any species, the observed migration strategies of wild adults represent the 'successful' subset of juvenile strategies that have been filtered by mortality and refined through the accumulated experience of multiple returns (Sergio *et al.* 2014). We therefore expect a degree of change in migratory performance with age, but are particularly concerned to determine the performance of young captive-bred birds compared with that of similarly naïve, wild migrants.

METHODS

Study system

We compared the migratory strategies of 29 captive-bred released Asian Houbara and 46 wild individuals (10 juveniles, three of which were monitored at both juvenile and adult life stages, and 36 additional adults). Sample sizes for most major contrasts were robust, particularly relative to typical sample sizes in satellite telemetry studies of avian migration, but were reduced by mortality prior to spring (return) migration. We are cautious in interpreting contrasts between sub-groups (wild adult male vs. female; captive-bred juvenile vs. yearling) that have smaller sample sizes and weaker statistical power.

Wild birds were sampled from a free-living breeding population (density 0.12–0.15 males/km^2; Koshkin *et al.* 2016a) in the southern Kyzylkum semi-desert, Bukhara province, Uzbekistan (40.40°N, 64.20°E). Substrates in the region consist of gypseous soils and consolidated or loose sands, and support heterogeneous, sparse, drought-resistant shrub communities grazed by sheep at

Table 1. Metrics characterizing migration movements of wild and captive-bred released Asian Houbara.

Migration metric	Description
Autumn departure date	Date (Julian day) of the final fix on the summer/post-breeding grounds when movement steps first transition from foraging movement speeds (< 2 km/h) to migration movement speeds (> 2 km/h)
Autumn departure direction	The absolute bearing (radians) of the above-defined movement, from the last fix on the summering/post-breeding area to the next fix
Arrival date on wintering site	Date (Julian day) of the final fix which marks transition from migration speeds to daily foraging speeds on the wintering site
Wintering site	Bird shows wintering behaviour comprising foraging, resting and local flights from arrival date until spring return migration in the subsequent year. For birds dying before the spring return migration, a criterion was used to classify the site as wintering rather than stopover site (see Methods)
Wintering latitude	The latitude of the fix defined in 'arrival date on wintering site' above to allow for unbiased comparison between birds that survived for variable amounts of time on wintering sites. Wintering latitude was correlated with distance from natal/breeding/release to wintering site
Wintering site fidelity	Distance (km) between consecutive wintering sites of the same individual tracked over consecutive winters. Winter site location taken as the centroid of wintering site fixes
Spring departure date	Date (Julian day) of the final wintering site fix before foraging movement speeds (< 2 km/h) change to migration movement speeds (> 2 km/h)
Spring arrival date	Date (Julian day) of the final fix which marks transition from migration step speeds to daily movement speeds on arrival on breeding season grounds (Uzbekistan, or the most northerly area reached)
Breeding season grounds	Bird shows either breeding behaviour (female nesting; adult male returning to previous display site; or, for yearlings, sedentary behaviour comprising foraging, resting and local flights, from spring arrival date until the end of the breeding period (mid-May))
Natal dispersal distance	Distance (km) between release site or nest-site for captive-bred and wild juveniles respectively to the centroid of fixes from the first 45 days after arrival to spring breeding grounds (spring centroid)
Distance travelled per stop (autumn & spring)	Mean distance travelled per stopover $= \text{Distance}_{\text{SLM}}/(\text{stopover}_n + 1)$, where $\text{Distance}_{\text{SLM}}$ is the straight line migration distance (km), i.e. the shortest distance on a great circle between the last fix prior to migration and the first fix indicating arrival on the wintering site, and stopover_n the number of stopovers made
Mean duration of stopovers (autumn & spring)	The mean duration (days) of all stopovers, square root-transformed for analysis, for an individual during a migration movement
Migratory efficiency (autumn & spring)	The deviation of $\text{Distance}_{\text{SAS}}$ (the sum of all step distances made during a migration movement, including stopovers and migration steps) from the straight line path (metres extra travelled per km of straight line distance, m/km): Migratory efficiency $= (\text{Distance}_{\text{SAS}}/\text{Distance}_{\text{SLM}}) - 1$
Rate of travel (autumn & spring)	Mean distance (km) travelled per day: Rate of travel $(\text{km/day}) = (\text{Distance}_{\text{SLM}}/\text{Total time})$, where Total time is the number of days between departure and arrival in a complete migration movement

relatively low densities. Extensive irrigated agriculture exists near permanent settlements to the south-east. The climate is continental with high summer (> 40 °C) and moderate winter temperatures, usually with intermittent winter snowfall. Descriptions of shrub communities and climate can be found in Koshkin *et al.* (2014, 2016a). Captive-bred birds were derived from a captive-breeding facility (involving first to third maternal generations) established by the Emirates Bird Breeding Center for Conservation (EBBCC) to counteract any effects of hunting in the southern Kyzylkum, with founders taken from the surrounding wild Bukhara population. All captive-bred birds carry metal rings (Koshkin *et al.* 2016b) and we are therefore certain that none of the sampled free-living adults, or the female parent of the free-living juveniles, was captive-bred. Moreover, free-living birds were unlikely to have been the progeny of surviving captive-bred releases (either second generation or sired by captive-bred males), for two reasons. First, although releases have occurred annually in Bukhara from 2011, numbers released per year have been relatively low, *c.* 7.5% of the wild population (Koshkin *et al.* 2016b), whereas high winter mortality (Burnside *et al.* 2016) limits recruitment to less than 1% per annum relative to wild numbers (Koshkin *et al.*

2016b). Second, an independent estimate (from captures and nest cameras) of the proportion of captive-bred birds within the free-living population is only 1.6% (95% CI 0.2–10.5%; Koshkin *et al.* 2016b). We are therefore confident that our sample of free-living birds represents the wild population and thus the wild migration strategy (Koshkin *et al.* 2016b); for simplicity we henceforth refer to these birds as wild adults and wild juveniles.

Wild adults were caught on their breeding sites during the spring using snares, following the methods of Seddon *et al.* (1999). All had completed at least one return migration: females were at least 1 year old, whereas males holding display territories were probably older than 3 years (Combreau *et al.* 2001). A further six overwintering individuals were caught in December using talon-baffled falcons. The sex of these birds was determined by bill, head and neck morphology and plumage, and age was determined by body mass (juvenile male 1.64 kg; four adult males 1.91–2.17 kg; adult female 1.48 kg); four of these returned to a different breeding population the following spring and were excluded from subsequent analysis. Wild juveniles (from broods of satellite-tracked wild females) were caught by hand at around 35 days old when still only capable of short flights, following the methods of Combreau *et al.* (2011). As all mothers of tracked wild juveniles were satellite-tagged, we were able to confirm that juveniles separated from their mothers at *c.* 50 days and were therefore no longer in a maternal family party at their first migration. They may have joined other conspecifics, including those from other breeding populations, as the Kyzylkum is used as a staging post by Asian Houbara migrating from Kazakhstan and China (Combreau *et al.* 2011).

Captive-bred birds were hand-reared by EBBCC and kept in cages containing around three individuals until released into suitable habitat within Bukhara under licence from the Uzbekistan government. Releases involved birds of two ages: fledged young of the year, released in late summer, so that when undertaking autumn migration, they were of similar age to wild juveniles; and yearlings released in spring after being overwintered in captivity, and therefore denied the opportunity to express migratory behaviour in their first calendar year (Burnside *et al.* 2016). For their first return migration, these are referred to, respectively, as captive-bred juveniles (10 individuals) and captive-bred yearlings (19 individuals), or collectively as captive-bred young. Thereafter, for any subsequent winters, they were reclassified as captive-bred adults. Released individuals that survived the winter within Bukhara to at least the end of the spring migration period (described below) were classified as non-migrants. The term ‘naïve birds’ refers inclusively to captive-bred young and wild juveniles.

Wild and captive-bred individuals were monitored using either 30 or 45 g GPS Microwave Telemetry Platform Terminal Transmitters (PTTs; 65 and four individuals, respectively), with six captive-bred individuals monitored with 35 g Argos-only units. All units were < 5% of bird body weight and are generally accepted to have minimal impact on Houbara (Combreau *et al.* 2011). PTTs were fitted using permanent Teflon backpack harnesses, but harnesses for wild juveniles incorporated elastic within the Teflon that could expand as the birds grew (Combreau *et al.* 2011). GPS-PTTs were mostly set to take five (usually diurnal) GPS locations per day, with an accuracy of ± 18 m (Microwave Telemetry 2011). For the few Argos-only PTTs, location data of classes 2 and 3 were used which have a one standard deviation accuracy of < 250 and 250–500 m, respectively, negligible relative to migration step-lengths of tens or hundreds of kilometres. Monitored captive-bred birds were selected at random from their release cohort and fitted with a standard harness at 3–5 months (juvenile) or as yearlings.

Data quality

A migration movement was defined as a journey commencing either from the post-breeding area in autumn or from the winter site in spring. A complete migration movement was considered to have occurred if the individual reached its wintering or breeding-season site. The median number of location fixes per day for each migration movement was 4.38 (interquartiles: 3.89–5), with only five (2.7%) migration movements averaging less than one fix per day. Where a migration metric (Table 1) could not be extracted confidently owing to gaps in the data, that individual was excluded from the relevant analyses. Only complete migration movements averaging at least three fixes per day were included when calculating migration efficiency and stopover metrics. Detailed sample sizes and exclusions are shown in Table S1.

Quantifying migration

Metrics that quantify various components of the migration movements were extracted as described in Table 1. To determine the start location and start date of migration we needed to define the transition from non-migratory behaviour, comprising foraging, resting and local flights, to migration characterized by substantially longer step lengths and higher speeds than in local movements. Typical speeds of 'steps' (the straight-line distance between two consecutive fixes/time elapsed between fixes) associated with foraging, resting or local flights were quantified during a post-breeding period (1–20 July) prior to any individual starting autumn migration. Subsequent steps were classified as migratory if the speed was greater than the 95% quantile observed during this period. For each individual, the onset of autumn migration was then defined by the departure date and origin of the first migratory step (Table 1). Migrating birds commonly pause to rest or refuel at stopover (i.e. 'staging') sites (Newton 2007). Stopovers were identified as a consecutive series of fixes linked by movement steps less than the migration speed threshold (thus representing resting/feeding), after which the individual resumed migration.

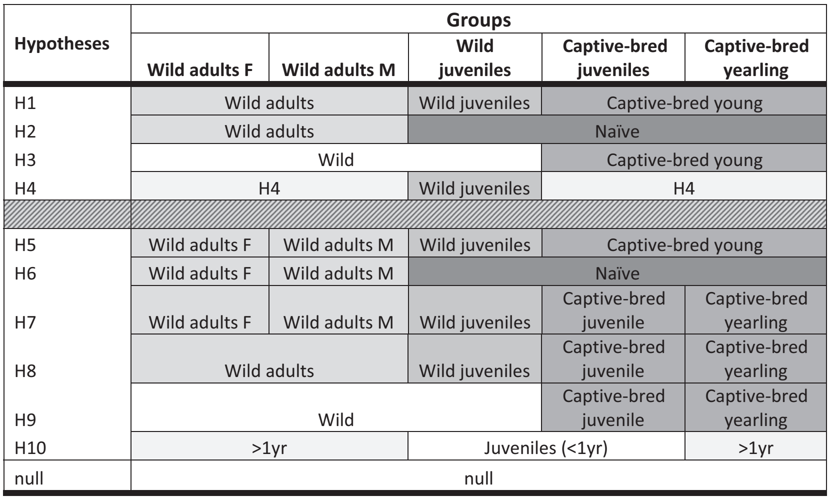
Distinguishing wintering sites from earlier stopovers was straightforward where birds survived to initiate spring return migration; for these individuals the wintering site was defined as the final fix of the autumn migration movement before steps changed to those characteristic of non-migratory behaviour. Spring migration was considered complete when birds became stationary through the spring (usually after reaching the breeding/natal region), and any non-migratory location prior to becoming stationary was classified as a stopover. Because Asian Houbara are generally faithful to their wintering sites (Tourenq *et al.* 2004, Judas *et al.* 2006), adults that did not survive the winter but had reached a previous year's wintering site were classified as having completed autumn migration. For first-time or previously untracked migrants that died during the autumn migration or wintering period we assessed whether an individual's last location represented a stopover or wintering site (and thus could be included in analyses of arrival dates and wintering location) by whether the time spent at that location was longer than the 97.5% quantile of observed stopover duration (14 days from 72 migration movements; Table S2). However, some birds that died more than 14 days after stopping might have been misclassified as having arrived on their wintering site, potentially introducing a bias to wintering latitude estimates; relevant tests were therefore repeated excluding all individuals that died during winter.

Fix locations were transformed into Asia north equidistant conic projection and successive step-length distances were calculated in metres using the adehabitatLT package in R (Calenge 2006). Speed was calculated using straight-line distance as kilometres per hour. Direction bearings were calculated in degrees using the geosphere package in R (Hijmans 2015) but converted to radians and analysed with Gaussian error structure rather than 'directional statistics', appropriate as no measurements approached the northerly limit. The shortest straight-line distance between summer and winter areas was calculated using the elliptical great circle measure from geosphere (Hijmans 2015) to account for the curvature of the earth.

Data analysis

Our main aim was to look for dissimilarities between the three primary cohorts: wild adults, wild juveniles and captive-bred young. Owing to low first-winter survival, only four captive-bred adults were tracked, too few for statistical analysis; these were therefore excluded from modelling but are shown in figures for reference and included in natal and winter-site fidelity estimates. For the remaining three groups we constructed models to test five comparisons for differences between group means (group structure shown in Table 2): H0 – null, all groups are similar; H1 – all groups are different; H2 – naïve birds are similar to each other (wild juveniles ≈ captive-bred young) but differ from wild adults; H3 – wild birds are similar to each other (wild juveniles ≈ wild adults) but differ from captive-bred young; and H4 – captive-bred young and wild adults are similar to each other but differ from wild juveniles. Additionally, to determine whether denial of first migration influenced captive-bred migration strategy, further models were constructed separating captive-bred young into sub-groups of captive-bred juveniles and captive-bred yearlings. Also, because sex can influence the timing and pattern of migration movements in sexually mature bustards (Palacín *et al.* 2009), we constructed models separating wild adults into sub-groups of wild adult females

Table 2. Model structures to test differences in group level means for 11 comparisons of migratory performance of wild and captive-bred released Asian Houbara.



Hypotheses	Groups				
	Wild adults F	Wild adults M	Wild juveniles	Captive-bred juveniles	Captive-bred yearling
H1	Wild adults		Wild juveniles	Captive-bred young	
H2	Wild adults		Naïve		
H3	Wild			Captive-bred young	
H4	H4		Wild juveniles	H4	
▨	▨	▨	▨	▨	▨
H5	Wild adults F	Wild adults M	Wild juveniles	Captive-bred young	
H6	Wild adults F	Wild adults M	Naïve		
H7	Wild adults F	Wild adults M	Wild juveniles	Captive-bred juvenile	Captive-bred yearling
H8	Wild adults		Wild juveniles	Captive-bred juvenile	Captive-bred yearling
H9	Wild			Captive-bred juvenile	Captive-bred yearling
H10	>1yr		Juveniles (<1yr)		>1yr
null	null				

Each row is a model differing in combinations of the five groups (see column headers) denoted by homogeneous shading of cell rows. F denotes female and M denotes male.

and wild adult males. All combinations of release group and sex with models H1–H4 resulted in a further five models, H5–H9 (Table 2). H10 primarily separates groups by age with juvenile birds (wild juveniles and captive-bred juveniles) being similar to each other but different from all older birds (wild adults and captive-bred yearlings, which are similar to each other), as sexual maturity could influence spring migrations. In all, 11 different models were compared to test the relative support for the different comparisons (Table 2).

Models were constructed using generalized linear mixed models (GLMMs) with random effects for individuals to account for repeat measures of experienced individuals, and year (categorical variable), as climatic variation can affect avian migration movements (Bauer *et al.* 2008). For each migration metric (i.e. dependent variable), the 11 competing models were constructed (Table 2) and ranked according to the Bayesian information criterion (BIC). BIC is better suited to less complex models than the corrected Akaike information criterion (AICc), which tends to retain more parameters, potentially leading to over-fitted models (Burnham & Anderson 2004); thus, our tests are conservative. Additionally, BIC is a stringent method for carrying out confirmatory hypothesis-testing and is therefore appropriate for testing the various comparisons listed in Table 2 (Aho *et al.* 2017). The best-supported model was identified as either (1) the top-ranked model with a BIC at least −2 below that of the second-ranked model (M_2) (Burnham & Anderson 2002), or (2) the most parsimonious of those models within 2 BIC units of the top-ranked model (Burnham & Anderson 2002), as inclusion of additional variables or sub-group levels did not result in a better-performing model.

All GLMMs were fitted by maximum likelihood using the lme4 package v. 1.1-10 (Bates *et al.* 2015), with Gaussian error structure. Mean duration of stopovers was square root-transformed, migration efficiency was logit-transformed for modelling, and estimates were back-transformed for results and figures. Models testing migration efficiency controlled for the mean number of GPS fixes per day (included as a covariate), as the efficiency parameter is derived from the cumulative step distance (Table 1) and was thus positively correlated with numbers of fixes. Wintering latitude was correlated with distance between site of origin and wintering site but wintering latitude was used in analyses with both metrics producing qualitatively similar results. Residual plots were inspected to confirm that assumptions of homoscedasticity and normality were met. All analyses and calculations were performed in R Gui (R Core Team 2013).

RESULTS

Migratory propensity

Four of the 75 individuals monitored overwintered in Bukhara, comprising one captive-bred young and three wild adults. Of the 34 wild adults captured during the breeding season, one overwintered in Bukhara (excluding two additional overwintering adults originally captured and fitted with PTTs in Bukhara during winter), compared with one of 29 captive-bred young, a similar ratio (Fisher exact test, $P = 1.00$), giving an overall migratory propensity of 96.8% (± 2.2% se). The remaining 71 migratory individuals (28 captive-bred young, 10 wild juveniles and 36 wild adults, of which three were initially monitored as juveniles) initiated a total of 183 migration movements between autumn 2011 and spring 2016 (Fig. 1).

Autumn migration

For departure date, model H3 (captive-bred young vs. wild birds) received the greatest support (H3 ΔBIC = −3.3 vs. M_2, Table 3). Captive-bred young birds departed post-breeding areas (mean 10 November, range 27 October to 13 December) an average of 20.6 days (± 4.6 se) later than wild birds (mean 21 October, range 22 August to 19 November, Fig. 2). Acknowledging modest sample sizes, being denied the first migration did not appear to affect the departure date of captive-bred yearlings, which was indistinguishable from that of captive-bred juveniles (H3 ΔBIC = −6.2 vs. H6, Appendix S1). Similarly, a sex difference in wild adults was unsupported (H3 ΔBIC = −5.7 vs. H5). In contrast to departure date, there was no support for a difference in direction of the first migration step (Table 1) between any groups, with the null model receiving greatest support (null ΔBIC = −3.4 vs. M_2, Table 3) and a mean estimated direction of 208° (± 2.8 se), a south-south-west bearing (Fig. 3).

Wintering site arrival dates, in contrast to departure dates, did not differ between wild juveniles and captive-bred young (H2 ΔBIC = −4.1 vs. H1; Appendix S1). The best-supported model (H2 ΔBIC = −4.1 vs. M_2, Table 3) revealed that naïve birds arrived later (29 November, range 7 November to 24 December, mean Δ = 23.6 days ± 5.44 se) than wild adults (mean arrival: 6 November, range 30 August to 12 December, Fig. 2). Again, acknowledging modest sample sizes, there was no support for a difference in arrival

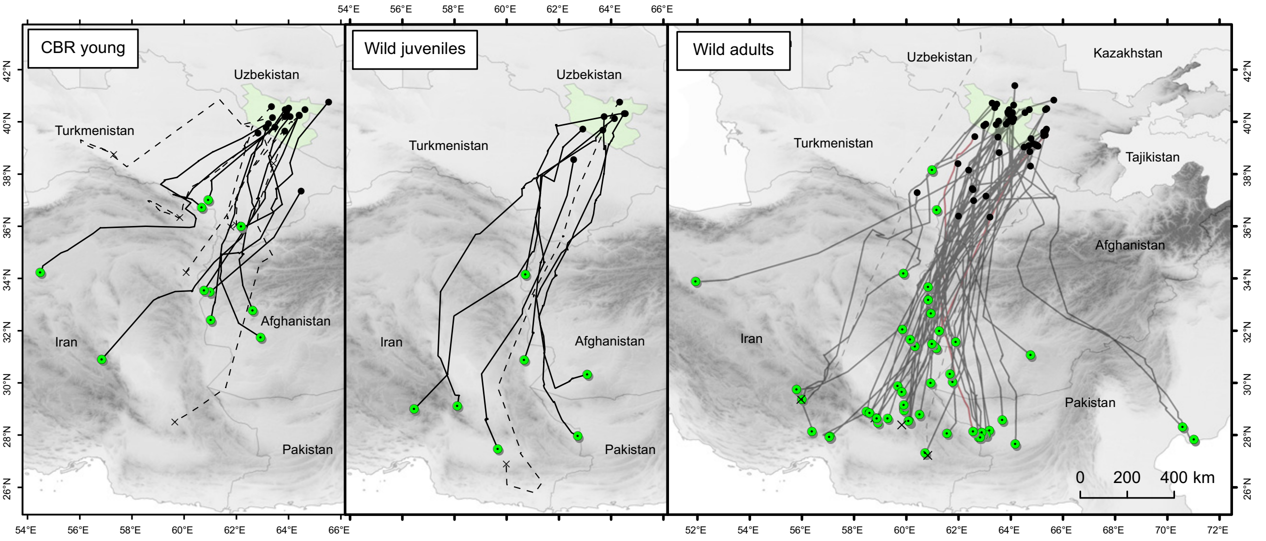


Figure 1. Autumn migration movements of Asian Houbara cohorts. Captive-bred young (CBR; left, $n = 18$), wild juveniles (centre, $n = 8$) and wild adults (right, n individuals = 33: n complete migration movements = 57) with start locations shown as black dots, wintering sites shown as larger open circles and solid lines, or as crosses and dashed lines for individuals that reached wintering sites but died during winter. Grey shading indicates elevation (darker = higher).

Table 3. Sample size and best-supported model for each *a priori* migration metric (Table 1) compared between wild adult, wild juvenile and captive-bred released (CBR) Asian Houbara, showing (in bold) model-estimated means and standard errors of each homogeneous group (major group, or sub-group depending on model support; cells with common shading).

				Group definitions (number of migratory individuals monitored)							
		Sample size		Wild adult (36)[b]		Wild juvenile (10)	Captive-bred young (28)				
Period	Migration metric	Obs.[a]	Inds: A (F,M); J; captive-bred (j,yr)	Wild adult F (27)	Wild adult M (9)	Wild juvenile (10)	Captive-bred juvenile (9)	Captive-bred yearling (19)	Best supported model	$\text{Model}_{\text{weight}}$	ΔBIC cf. M_2
Autumn	Departure date	96	33 (27,6); 10; 28 (9,19)	**21 October ± 4.6**			**10 November ± 4.0**		H3	0.63	−3.33
Autumn	Departure direction			**208° ± 2.8**					Null	0.59	−3.38
Autumn	Arrival date	83	33 (26,7); 8; 18 (8,10)	**6 November ± 5.3**		**29 November ± 4.6**			H2	0.81	−4.01
Autumn	Rate of travel			**165.6 km/day ± 29.3**		**74.4 km/day ± 28.7**			H2	0.61	−3.43
Autumn	Wintering latitude			**29.97°N ± 0.70**			**34.54°N ± 0.59**		H3	0.78	−4.04
Autumn	Distance travelled per stop[c]	75	31 (25,6); 8; 14 (6,8)	**228.1 km ± 22.7**		**137.1 km ± 20.9**			H2	0.73	−4.18
Autumn	Mean duration of stopovers[c]			**2.1 days ± 0.3**					Null	0.30	−1.27
Autumn	Migratory efficiency[c]			**31.5 m/km ± 13.3**		**134.5 m/km ± 65.4**			H2	0.72	−4.31
Spring	Departure date	70	32 (24,8); 7; 10 (6,4)	**1 March ± 5.4**	**20 February ± 6.0**	**27 March ± 6.7**	**13 April ± 6.9**	**20 March ± 7.8**	H7	0.72	−2.73
Spring	Arrival date	67	31 (24,7); 7; 10 (6,4)	**18 March ± 4.8**		**1 May ± 5.0**		**18 March ± 4.8**	H10	0.85	−4.65
Spring	Rate of travel			**169.5 km/day ± 29.9**					Null	0.37	−1.43
Spring	Distance travelled per stop[c]	64	31 (24,7); 7; 8 (5,3)	**253 km ± 13.86**		**171 km ± 34.6**			H2	0.72	−2.67
Spring	Mean duration of stopovers[c]			**2.63 days ± 2.2**					Null	0.48	−2.18
Spring	Migratory efficiency[c]			**47 m/km ± 20.2**	**11 m/km ± 7.0**	**110 m/km ± 61.4**			H6	0.68	−2.95

Sample size given as initial number of monitored individuals for each major group and sub-group and, for each dependent variable/model set, the total number of observations (Obs.) and number of individuals (reduced by mortality) for each major group and sub-group, denoted A – Wild adult (F – female, M – male); J – Wild juvenile; Captive-bred young (j – captive-bred juvenile, yr – captive-bred yearling). Detailed descriptions of sample sizes and exclusion of movements due to data gaps can be found in Table S1. [a]For wild juvenile and captive-bred young there is one observation per variable per individual, but for wild adults monitored across multiple years, total observations > number individuals. [b]Three of these were tracked as juveniles. [c]Excluding migration movements with mean < 3 fixes per day.

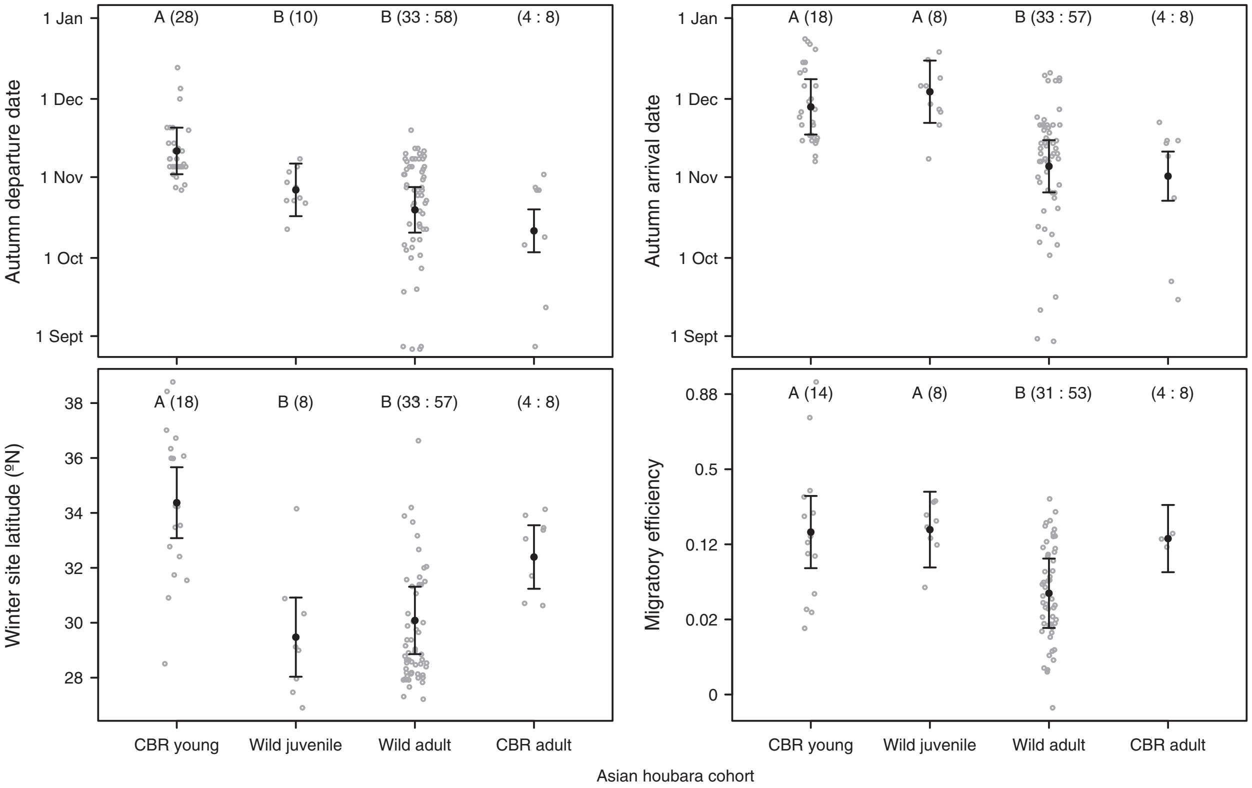


Figure 2. Metrics of migration movements from summer areas to wintering areas for wild and captive-bred (CBR) Asian Houbara. Grey dots represent data points (horizontal jitter added for clarity); black dots are the means estimated from the GLMMs with the standard error bars above and below. Letters at the top of each panel indicate homogeneous groups from the best-supported model (Table 3). Captive-bred (CBR) adults were not included in formal tests due to only four individuals being available. Numbers in parentheses are sample sizes of the individuals; for the wild adults and captive-bred adults, the numbers show the ratio number of individuals : number of migration movements, whereas for the naïve birds these are equal.

date between captive-bred young sub-groups (H2 ΔBIC = −8.4 vs. H8; Appendix S1), or between female and male wild adults (H2 ΔBIC = −1.9 vs. H6, Appendix S1). For naïve birds, winter arrival date was not related to autumn departure date (wild juveniles: $r = 0.42$, $t_6 = 1.16$, $P = 0.29$; and captive-bred young: $r = 0.15$, $t_{16} = 0.60$, $P = 0.56$). By contrast, wild adults that departed breeding grounds earlier, arrived earlier on their wintering site ($r = 0.66$, $t_{55} = 6.54$, $P < 0.001$).

The daily rate of travel differed between naïve birds and wild adults (H2 ΔBIC = −3.4 vs. M_2, Table 3), with the naïve birds travelling more slowly (74.4 km/day ± 28.7 se) than wild adults (165.6 km/day ± 29.3 se), but there was no support for a difference between wild juveniles and captive-bred young (H2 ΔBIC = −4.05 vs. H1, Appendix S1). There was no support for differences between captive-bred young sub-groups or male and female wild adults (Appendix S1). The results for daily rate of travel remained unchanged when repeated only with birds carrying 30-g PTTs to control for any effect of transmitter weight on flying ability.

Because captive-bred young departed later than other groups but travelled at a similar daily rate and stopped at a similar time to wild juveniles, they covered less distance, and consequently wintered on average 470.8 km (± 76.4 se) closer to the breeding grounds, in Turkmenistan, northern Iran and Afghanistan (mean latitude = 34.54°N ± 0.6 se; 746.9 km ± 76.4 se from release sites) than wild birds which predominantly wintered in southern Iran and Pakistan (mean latitude = 29.97°N ± 0.7 se; 1217.8 km ± 76.4 se from natal/breeding sites, Figs 1 and 2). Any bias from wintering site misclassification is unlikely, as this result (H3 ΔBIC = −4.0 vs. M_2, Table 3) was unchanged when excluding seven captive-bred young individuals that died during winter and were judged to have reached their wintering site based on the stopover duration criterion. Wild juvenile and wild adult wintering latitudes were similar (H3 ΔBIC = −4.0 vs. H1; Appendix S1).

Distance travelled between stopovers was much less for naïve birds, which made one stop for every 137.1 km ± 20.9 se, a shorter distance than for wild adults (228.1 km ± 22.7 se; H2 ΔBIC = −4.2 vs. M_2, Table 3), with no support for a difference between captive-bred young and wild juveniles (H2 ΔBIC = −4.2 vs. H1). For mean stopover duration, model selection was inconclusive, with two models (including the null model) within 2 BIC units of the top model (Appendix S1); from the null model the mean across all groups was 2.1 days (se ± 0.3; model on square root-transformed data, Table 3), although model uncertainty does not exclude some group differences. For the same subset of birds considered in stopover analysis, while controlling for the number of GPS fixes, wild adults were more efficient, covering only an extra 31.5 m ± 13.3 se per km of straight-line distance (Fig. 2) than naïve birds, which covered an extra 134.5 m ± 65.4 se per km (H2 ΔBIC = −4.3 vs. M_2, Table 3), with no support for a difference between captive-bred young and wild juveniles (H2 ΔBIC = −4.3 vs. H1, Appendix S1). Thus naïve birds made on average four times the deviation from the straight-line distance on their journey than did wild adults.

Captive-bred young that died before reaching a wintering site (n = 10) did not differ from those that arrived (n = 18) in either the variance or the mean of autumn departure date (variance ratio test: $F_{9,17}$ = 0.565, P = 0.298; group means, difference = 4.33 ± 4.36 se, t_{26} = 0.994, P = 0.330) or the mean of the first migration direction (group means difference = 2.66°, ± 10.7 se, t_{26} = 0.248, P = 0.806). However, those that failed to reach a wintering site showed a higher variance in their first direction (variance ratio test: $F_{9,17}$ = 0.318, P = 0.040), although we acknowledge small

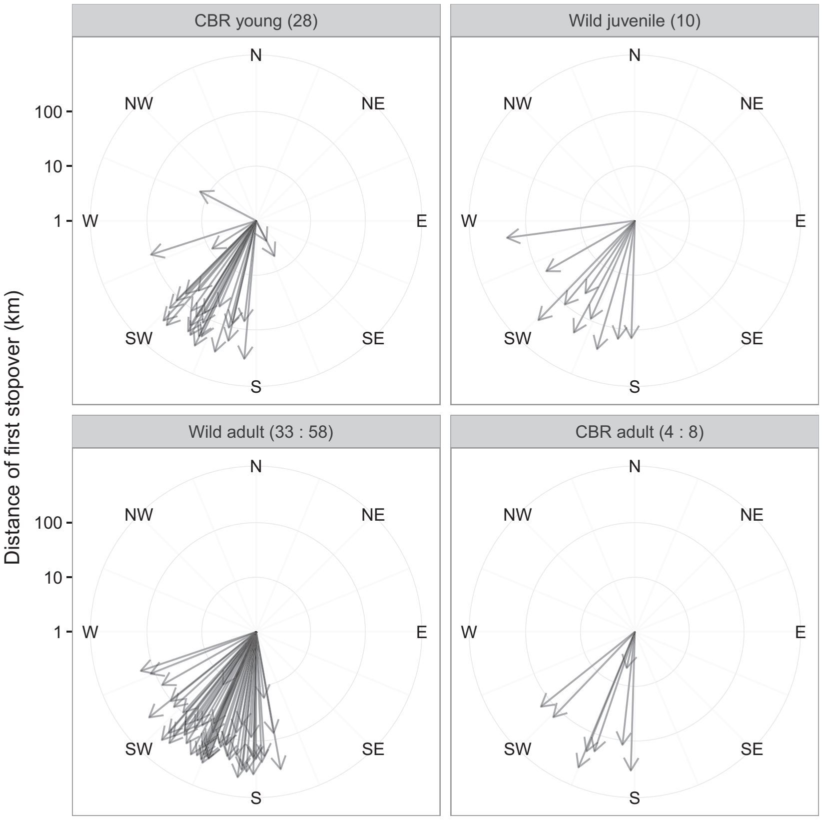


Figure 3. Direction and distance (km) of first autumn migration step to the first stopover area for four Asian Houbara groups. Numbers in parentheses are sample sizes of the individuals; for the wild adults and captive-bred released (CBR) adults, the numbers show the ratio number of individuals : number of migration movements, whereas for the naïve birds these are equal.

sample sizes. Wintering latitudes did not differ in mean or variance between those that arrived at a wintering site and subsequently survived to start spring migration, and those that arrived and died ($F_{9,7} = 0.364$, $P = 0.170$; group means difference = 1.56°N, ± 1.34 se, $t_{15} = 1.195$, $P = 0.251$).

Wintering site fidelity

Wild adults (13 individuals, providing 21 instances of subsequent winter-site selection) were generally faithful to their wintering sites, with a median interannual distance between consecutive wintering site centroids of 42.5 km (range 0.9–755.4 km). Only in two of 21 instances did a wild adult wintering site change by > 200 km. Four captive-bred adults tracked from their first migration showed similar fidelity to wintering sites, with median interannual distance of 70.8 km (range 6.56–221.6 km) between consecutive centroids, and only one female once moved her wintering site by > 100 km between years (Fig. 4). Of the three wild juveniles that survived to make a second autumn migration, two showed fidelity to their first wintering sites in their second winter (26.9 and 61.0 km), with one of these (a male) remaining faithful to the same winter area over three subsequent winters (mean 14.9 km, ± 6.7 se, Fig. 4). The third wild juvenile first wintered in southern Iran and then spent its second winter 964.6 km north in Turkmenistan (Fig. 4).

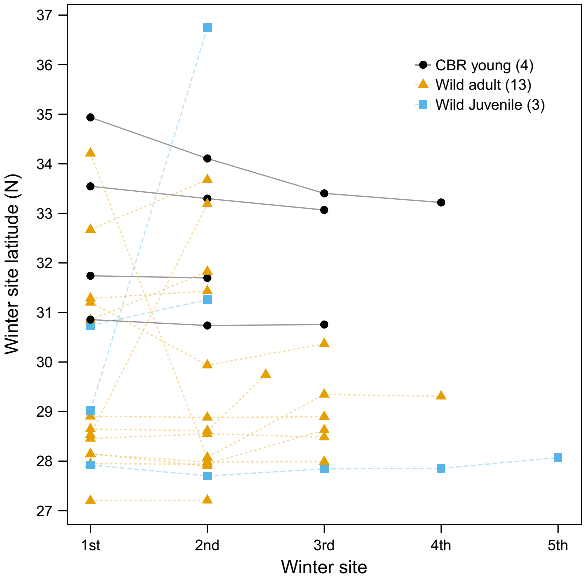


Figure 4. Consecutive wintering site latitudes for 17 Asian Houbara. For captive-bred released (CBR) and wild juveniles, '1st' represents the first wintering site, whereas for wild adults '1st' is the first year of tracking for that individual. Numbers in parentheses are the sample sizes of individuals.

Spring migration

Overwinter mortality reduced sample sizes available to examine spring departure date (Table 3). Nevertheless, the best-supported model indicated differences between the two captive-bred subgroups and between the adult sexes (H7 ΔBIC = −2.7 vs. M_2, Table 3). Captive-bred yearlings departed earlier (20 March, range 9–26 March) than captive-bred juveniles (13 April, range 27 March to 2 May), with wild juveniles departing between these dates (27 March, range 8 March to 10 April); and all naïve birds left later than the wild adults. Wild adult males left earlier (20 February, range 24 January to 3 March) than wild adult females (1 March, range 23 January to 21 March; Fig. 5).

All naïve birds that initiated spring migration completed their return journey, while two wild adult movements failed. Nine of the 10 captive-bred young returned to the Bukhara area (median distance from release site to spring centroid = 37 km, range 5–46 km), but one male spent the first spring in Turkmenistan 344 km to the south (but returned to Bukhara in subsequent years). Thereafter, all four surviving captive-bred adults showed release (natal) area philopatry, returning exclusively to Bukhara province (median distance from release site 29 km, range 18–61 km). Similarly, all but one wild juvenile returned to Bukhara province in the first year (median natal dispersal distance of 25 km, range 4–76 km from nest to spring centroid), with the exception, like the young captive-bred male, also spending the first spring and summer in Turkmenistan (356 km) before returning to Bukhara in subsequent years. Pooling the naïve birds gives a 12% chance (± 7.8 se estimated from binomial error distribution) of passing their first spring outside Bukhara province. Apart from two females which changed breeding location by > 160 km, all wild adults returned to Bukhara province during spring (median 21.6 km, range 0.12–132 km from previous year's breeding location).

For spring arrival dates the top-ranked model supported a difference between older and younger birds (H10 ΔBIC = −4.65 vs. M_2, Table 3). Wild

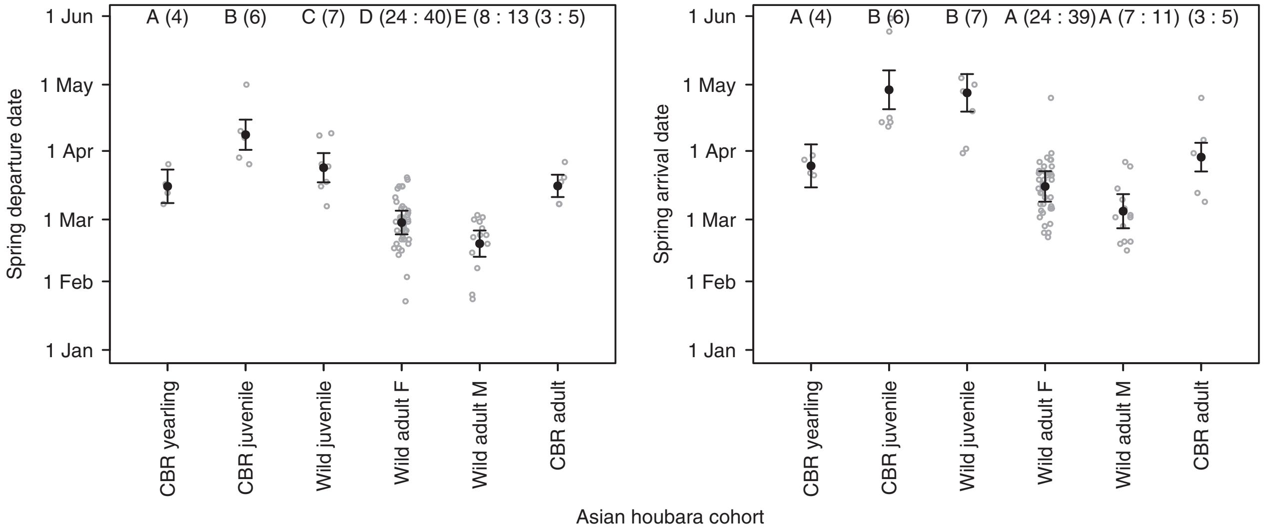


Figure 5. Return migration characteristics for Asian Houbara. Grey dots are individual journeys (horizontal jitter added for clarity); black dots (with standard error bars) are the means estimated from the GLMMs. Letters at the top of each panel indicate homogeneous groups from the best-supported model (Table 3). Captive-bred released (CBR) adults were not included in formal tests as only four individuals were available. Numbers in parentheses are sample sizes of the individuals; for the wild adults and captive-bred released adults the numbers show the ratio number of individuals : number of migration movements, whereas for the naïve birds these are equal.

adults and captive-bred yearlings arrived at a similar time (mean 18 March, range 19 February to 25 April) but earlier than captive-bred juveniles and wild juveniles (mean 1 May, range 31 March to 16 June; Fig. 5). There was no support for a difference between wild adult males and females (H10 ΔBIC = −4.65 vs. H7; Appendix S1). Daily rate of travel had three models within 2 ΔBIC of the top-ranked null model (Appendix S1); although the most parsimonious model was used for estimates, hypothesis tests are inconclusive for this metric (Table 3).

After removing movements with fewer than three fixes per day, there were too few captive-bred yearlings to compare the captive-bred subgroups (Table S1), so H7–H9 were not considered in the following three tests. As with outward migration, during spring the distance travelled between stopovers was much less for naïve birds (on average 171 km, ± 34.6 se), whereas wild adults stopped only every 253 km (± 13.9 se; H2 ΔBIC = −2.67 vs. M_2; Table 3). The mean stopover time, 2.6 days (± 2.2 se) did not differ between groups (null ΔBIC = −2.18 vs. M_2, Table 3). In terms of migratory efficiency, the best-supported model indicated that naïve birds (110 m ± 61.4 se further per km travelled) were again less efficient than wild adults (H6 ΔBIC = −2.95 vs. M_2; Table 3), but that wild adult males (mean 11 m ± 7.0 se extra per km travelled) were more efficient on their return than females (mean 47 m ± 20.2 se extra per km travelled).

DISCUSSION

The three main groups, wild adults, wild juveniles and captive-bred young, all showed different migration strategies. Notably, captive-bred young were similar to wild juveniles in all but two potentially crucial and probably related characteristics: later date of autumn departure and occupation of more northerly wintering sites. Captive-bred young initiated their autumn migration from the Kyzylkum desert around a mean of 10 November, travelling 20.6 days later and covering only two-thirds the distance of wild adults and wild juveniles (on average 470.8 km less). Given the wintering site fidelity of the species, these higher-latitude wintering sites appear likely to remain fixed for those captive-bred birds that survive to undertake further migrations; if so, the longer-term fitness consequences for these birds can only be speculated. Although the four captive-bred birds that survived to undertake further migrations showed similar departure and arrival dates to wild adults, their wintering sites remained in the more northerly distribution of the wild adults (Figs 1 and 2). First-time migration has a strong genetic component and although naïve birds may accompany conspecific groups, they do not complete their entire migratory journey with a single group of adults. Last, we found strong fidelity to the natal or release areas, which is important for reinforcing a migratory population.

Captive-bred young showed a similar migration propensity to wild birds, with only one individual from each group overwintering in the breeding area. The majority of captive-bred birds expressed migratory behaviour, with no differences in the first autumn migration between captive-bred juveniles and captive-bred yearlings. This indicates innately controlled behaviour, since culturally transmitted migratory behaviour can be rapidly eliminated by overwintering in captivity, as seen with reintroduced migratory White Storks *Ciconia ciconia* (Fiedler 2003). Whether orientation is wholly genetic or is also influenced by travelling with conspecifics is unknown. The south-southwest direction of wild autumn migrants was generally conserved in captive-bred birds, with three individuals that made movements outside the range established by wild birds quickly dying (Figs 1 and 3). This is supported by the reduction in variance but conserved mean direction for captive-bred birds that survived to reach wintering sites, indicating a filtering of potentially maladaptive traits.

Captive-bred young initiated autumn migration considerably later than wild birds, but the reasons for this can only be speculated. As houbara migrate by flapping, powered flight and are relatively heavy birds (1.2–2.2 kg), migration requires considerable energetic resources even when aided by strong tail-winds. It may therefore be that captive-bred young take longer to achieve migratory condition in terms of, for example, adapting physiologically and learning to forage in the environments into which they are released, accumulating the considerable fat reserves needed for migration (Moore & Battley 2006), and acquiring the physiological condition required for sustained flight (Hess *et al.* 2005). However, although captive-bred young did not ultimately travel as far, this seems to be a consequence of their later departure, as captive-bred young and wild juveniles were indistinguishable in efficiency, distance travelled between each stopover and rate of travel. Captive-bred young and wild juveniles then stopped at similar times, later than the wild adults, with arrival dates being independent of departure dates. This suggests an endogenous cue for stopping migration, such as day-length. Observations by hunters (J. Al-Khaili, pers. comm.) that Houbara often migrate and stop over in small groups opens the possibility of social transmission of migratory routes. However, given the slower migration of naïve birds (both wild juveniles and captive-bred young) compared with wild adults, with shorter flights and longer and more frequent stopovers, it appears unlikely that naïve birds travel from breeding to wintering grounds with a single adult group. This slower migration seems likely to be a consequence of lower reserves or physiological stamina rather than the additional weight of transmitters (30 g), as this is low (*c.* 2.5%) relative to the mean October body mass (> 1.2 kg) of naïve birds, which have a similar weight to wild females. The different stopover schedule of juveniles suggests that staging site selection may be facultative while resuming migration probably has a strong genetic component.

Whether the use of more northerly wintering areas by captive-bred young reduces winter survival chances or subsequent breeding fitness is not known. Migrants from Mongolia have wintered in the Turkmenistan–Uzbekistan border region (Judas *et al.* 2006, Combreau *et al.* 2011, Allinson 2014), four wild individuals tracked in this study overwintered in Bukhara and returned in spring to Kazakhstan, and three wild individuals from the local breeding population also overwintered in Bukhara. This might suggest that wintering in more northerly latitudes does not impose a high cost, but our study included some mild winters with no snow cover (2014 and 2015), so non-migrant individuals may have been responding facultatively or exhibiting a strategy that would be selected against in a cold year. The migratory behaviour of captive-bred young should be regarded as potentially maladaptive, as the selection pressures which cause wild juveniles to initiate migration at the same time and to the same latitudes as wild adults may disadvantage birds that do not conform to this regime. One cost could be in higher mortality, as eight of 18 captive-bred young died on their wintering sites even though their wintering latitudes were indistinguishable from those that survived. Indeed, survival through the entire winter period is known to be low (20%, 95% CI 0.07–0.33, $n = 35$) for captive-bred young (Burnside *et al.* 2016). Although no similarly robust estimates exist for wild juveniles, in this study seven of 10 survived the winter (70%, 95% CI 0.41–0.98), well above the upper confidence limit of the captive-bred estimate. This reinforces the suggestion that although captive-breeding programmes may usefully provide alternative quarry for hunting, they may contribute less to population recruitment (Burnside *et al.* 2016). Notably, all mortality of naïve birds during migration movements took place before January with none in the spring, and those surviving to midwinter maintained sufficient condition to return successfully.

Overall, naïve birds showed surprisingly strong natal site fidelity, with all but two individuals returning close to their natal or release site in the following spring, which is particularly important for captive-bred birds if they are to reinforce a local exploited population rather than diffusing into the flyway. Strong natal fidelity has been observed in the Great Bustard (Martín *et al.* 2008), while the tendency for juvenile males to undertake exploratory movements in their first year, as observed in this study, has also been reported in eastern Asian Houbara populations (Combreau *et al.* 2011) and Great Bustard (Martín *et al.* 2008). Generally, wild adults continued to return to the same breeding areas, but some females tended to move out of the study area into adjacent regions.

Notably none of the 43 wild birds tracked in this study showed any evidence of migration across the Straits of Hormuz. This strategy seems to have been eliminated by over-hunting on the Arabian Peninsula (Osborne *et al.* 1997, Launay *et al.* 1999, Combreau *et al.* 2011).

Implications for conservation and management

The results of this study raise two important considerations for the use of *ex situ* breeding and release to manage exploited wild migratory Asian Houbara populations. First, the captive-bred birds used in this study showed innate migratory ability, providing strong evidence for the genetic basis of this behaviour and indicating that one or two generations of captive breeding had not eliminated it. This, combined with release (natal) site fidelity, has serious implications for release programmes across the range of the species. Releases onto breeding grounds need to involve locally sourced birds with the appropriate population-specific migration strategy, not birds from other parts of the range. Mixing of populations with different migratory traits within a single breeding programme would incur substantial risks. Second, failure of released birds to replicate the departure date and wintering site distribution of wild birds is a potential constraint on the value of captive-bred birds for wild breeding population reinforcement. Given the current almost exclusive reliance of Asian Houbara conservation on captive breeding (Allinson 2014), diagnosis and understanding of any long-term consequences are paramount, as so little is actually known about the positive or negative impacts of the release of captive-bred birds on the species it is assumed to be supporting.

A further complication for the sustainable management of exploited populations is that wild birds from the Kyzylkum occupied wintering sites from Uzbekistan south to Pakistan, a minimum span of 1500 km, thereby overlapping with the winter ranges of many houbara breeding in eastern Kazakhstan, southern Mongolia and western China (Combreau *et al.* 2011). Such overlap in exploited wintering areas creates a problem for conservation authorities wishing to determine sustainable levels of offtake. Because the origins of the hunted birds are unknown, the impact of hunting on their populations cannot be predicted or modelled. Again, the appropriate scientific position is one of extreme precaution with wider investment needed into research into several aspects of Asian Houbara ecology and conservation. These include migrations, the efficacy of population supplementation from captive-bred stock, and the demography and trends of component breeding populations. These will support the development of more sophisticated models by which patterns of movement across the range of the species can be fully understood, and hunting eventually regulated to sustainable levels with or without the support of *ex situ* programmes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Detailed group and sub-group sample sizes for individuals and migration movements.

Table S2. Autumn migrant arrival at winter-site decision classification table for Asian Houbara that began migration but did not survive to the spring.

Appendix S1. BIC model selection tables for migration metrics classified in Table 1.