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Short Communication

Genetic diversity and the implications of captive rearing for a small population of Black-tailed Godwits

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Black-tailed Godwit *Limosa limosa limosa* clutches have been collected for headstarting, a captive rearing intervention where eggs are taken from the wild and artificially incubated, and chicks are reared in captivity to fledging, before being released into the wild. This conservation measure has reduced local extinction risk for the UK population, but it may have impacts on genetic diversity and population viability, especially when wild-sourced eggs must be collected from a small population. Comparing the UK population of 42 pairs with the much larger breeding population in the Netherlands (~30 000 pairs), we found that levels of heterozygosity and inbreeding are not currently compromised, and allelic richness in the UK population was not significantly different from the Dutch population, but relatedness estimates suggest that 6.1% of the individuals in the UK are closely related, at the level of half-sibling and up, compared with 1.9% in the Dutch population. Increasing levels of relatedness could further deplete genetic variation, in the absence of immigration or the introduction of wild-sourced eggs from other populations.

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When attempting to recover small populations through translocations or captive rearing, basing management decisions on phenotypic and genetic variation is of crucial importance (Cavill *et al.* 2022). Black-tailed Godwits *Limosa limosa limosa* are on the red-list of Birds of Conservation Concern in the UK and are classed as endangered because of their rarity and range declines (IUCN risk of extinction for Great Britain; Stanbury *et al.* 2021). This species went extinct in the UK in the 1800s, due to widespread drainage of their wetland habitats, egg collecting and hunting (Cadbury & Kirby 1993), and recolonized the UK in the 1950s (Cottier & Lea 1969). Since then, the UK breeding population has probably never been larger than 100 pairs at four or five sites. In 2017, the population was known to be only 42 pairs, with 90% breeding in two locations in southeast England (Verhoeven *et al.* 2021). Given their rarity, declining status and risk of extinction, a 5-year conservation programme (Project Godwit: https://projectgodwit.org.uk/) was set up with the aim of securing the long-term future of this breeding species in the UK, by adopting conservation interventions that address the causes of decline.

Verhoeven *et al.* (2021) showed that the recent decline in the UK population was linked to a failure to produce enough fledglings because of high rates of nest and chick predation. A relatively novel conservation solution to reduce the impacts of predation is headstarting, where eggs from the wild are taken and artificially incubated, and chicks are raised in a predator-free captive environment before being released at fledging, to boost the reproductive success of the population (Laidlaw *et al.* 2021). However, past local extinction, current small population size and range, and an apparent lack of recent immigration from the larger but rapidly declining population in the Netherlands (−5% per year: Kentie *et al.* 2016) raised concerns that there may potentially be low genetic diversity in the UK population. This is especially important because headstarting could theoretically exacerbate low genetic diversity through collection of eggs from the wild. As the source population is small, and eggs are collected each year from the earliest clutches, the chance that eggs are repeatedly collected from the same females increases, because arrival on the breeding grounds and lay date are relatively consistent among individuals (Lourenço *et al.* 2011, Verhoeven *et al.* 2020) and, in this long-lived species, females may return to the nesting site for many years (Roodbergen *et al.* 2008, Fransson 2010). If genetic diversity is already low, repeatedly collecting eggs from the same females could further accelerate reductions in genetic diversity

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and potentially increase population consequences, through inbreeding, genetic drift and fitness defects.

Decreased genetic diversity has been associated with high juvenile mortality, diminished population growth, reduced immunity and, ultimately, higher extinction risk (Keller & Waller 2002, Kardos *et al.* 2021, Willi *et al.* 2022). Fitness effects associated with low genetic diversity have been observed in various wader species, for example southern Dunlin *Calidris alpina schinzii* (Blomqvist *et al.* 2010, Rönkä *et al.* 2021) and Snowy Plover *Charadrius nivosus* (Colwell & Pearson 2011). This means that it is important to consider conservation genetics when attempting to recover wader populations (Frankham *et al.* 2017, Kardos *et al.* 2021, Willi *et al.* 2022). Here, we explore whether levels of genetic diversity in the UK Black-tailed Godwit breeding population are low compared with the Netherlands, and consider whether headstarting might lead to increased relatedness and reduced genetic diversity. These results are discussed in the context of future conservation and management of small populations.

METHODS

Sampling and field methods, UK

Samples for genetic analysis of the small UK population of breeding Black-tailed Godwits (hereafter Godwits) were collected between 2017 and 2019. All samples originated from Godwits breeding at the Nene Washes in the Cambridgeshire Fens, southeast England (52.58771, −0.06012), a wetland nature reserve managed by the Royal Society for the Protection of Birds, where 83% of the UK population was breeding in 2017. All samples were collected as part of the monitoring of wild breeding attempts and the trial of headstarting as a conservation intervention. During the headstarting process, Godwit nests at the Nene Washes were located and whole clutches were removed and incubated in the captive rearing facility. The very earliest laid clutches were collected when they had been incubated in the wild for between 3 and 6 days, to increase the likelihood that those Godwit pairs would attempt a second breeding attempt in the wild. Once eggs hatched, each individual eggshell and its membrane were air-dried before labelling, and stored in individual envelopes. The resulting chicks were marked so that we knew which chick arose from which egg. In addition, in 2017, the remains of nine chicks from six families were recovered, having died or been predated in the wild. A leg from each chick was removed and stored in ethanol. This resulted in a total of 139 samples, from which DNA was successfully extracted from 74 (success rate: legs 82%; eggshell 54%). These samples arose from 13 Godwit pairs in each of three years (see Supporting information, Table S1). This level of sampling means that the genetic information presented here represents between 37 and 42% of the breeding pairs at the Nene Washes (Nene Washes Godwit pairs: 35 in 2017, 31 in 2018, 33 in 2019), which equates to an average of 30% of the UK population sampled in each year. The small population size and intensive monitoring of individually colour-marked Godwits meant that we were able to observe whether individuals arising from the genetically sampled eggs subsequently recruited into the breeding population up to and including 2022, 3 years after the last eggs were sampled.

Sampling, the Netherlands

We used published data from Trimbos *et al.* (2011), and especially 38 samples from a single breeding location in southwest Friesland, the Netherlands (hereafter Friesland). The Trimbos *et al.* (2011) study included 140 birds sampled at nine breeding locations from 2004 to 2008, genotyped at 12 loci using primers from Verkuil *et al.* (2009). This study incorporated only one individual per nest, to avoid pseudoreplication at the family level. The Dutch Godwits can be considered one population with free gene flow and no sign of inbreeding in any of the sampling sites (for further details see Trimbos *et al.* 2011). However, to avoid undetected genetic structure within the Netherlands confounding our comparison, we only used the largest sample from the single site in Friesland.

Molecular methods

DNA was extracted from samples using a salt extraction protocol modified from Richardson *et al.* (2001). A small piece of the sample (approximately 2 × 2 mm, for eggshell or leg) was added to 265 µl digesting solution (15 µl Proteinase K, 250 µl 20 mM EDTA, 120 mM NaCl, 50 mM Tris–HCl) and incubated at 55°C overnight. Then, 1.5 µl RNase A was added and left to stand for 3 min. Protein was precipitated using warm (~55°C) ammonium acetate and the sample was centrifuged at 13 000 rpm for 20 min. The supernatant was transferred to a clean Eppendorf tube, the DNA was precipitated with ice-cold 100% ethanol and the sample was centrifuged a 13 000 rpm for 20 min. The resulting DNA pellet was washed twice with room temperature 70% ethanol and dried at 55°C, before it was resuspended in solution (10 mM Tris–HCl, 0.1 mM EDTA) at an approximate concentration of 50 ng/ml.

Loci were amplified using a 2-µl polymerase chain reaction (PCR) technique (Kenta *et al.* 2008), using primers from Verkuil *et al.* (2009), tagged with FAM or HEX dyes and arranged into multiplex reactions (see Supporting information, Table S2). In each reaction,

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1 µl of genomic DNA solution was added to each PCR well and warmed at 55°C until dried. Then 1 µl of primer mix (which contained 0.2 µM of every forward and reverse primer for the multiplex reaction) was added to the dried DNA, along with 1 µl 2× Qiagen Multiplex PCR Mastermix. These were covered with mineral oil before thermocycling for PCR. The PCR schedule for all multiplexes began with a 5-min denaturing phase, at 94°C, followed by 36 cycles of 94°C for 30 s, 55.5°C for 30 s and 72°C for 30 s, finishing with a 5-min hold at 72°C.

The PCR product was diluted 125 times with sterile water, and then a further 10 times with formamide and ROX size standard, resulting in a 1250× dilution in total, which was genotyped on an ABI 3730 sequencer at the John Innes Centre in Norwich, UK. Allele sizes were determined using Gene Mapper version 3.7 (Applied Biosystems).

Analyses

All analyses were carried out using R version 4.0.2 (R Development Core Team 2020). For each locus in both datasets, allelic richness (N_a), rarefacted allelic richness (R_a), expected and observed heterozygosity (H_o and H_e), and the inbreeding coefficient (F_{is}) were calculated in Pegas 1.2 (Paradis 2010). To estimate R_a, equal sample size must be assumed; we set it to 32, the lowest sample size for any locus in both final datasets. Significant deviations from Hardy–Weinberg equilibrium were tested by comparing observed and expected heterozygosity estimates, using chi-squared tests (UK dataset) and GENEPOP (Raymond & Rousset 1995; Netherlands dataset, see Trimbos *et al.* 2011). In the UK dataset, one locus, LIM22, significantly deviated from Hardy–Weinberg equilibrium, possibly as a result of the presence of null alleles, so was excluded from population genetic analyses. Another locus, LIM26, was excluded because of amplification difficulties. To avoid pseudoreplication at the family level, the dataset was reduced to one chick per nest, randomly chosen after minimizing missing data.

Genetic bottleneck tests based on small numbers of microsatellite loci (Peery *et al.* 2012) are unreliable or would require sampling before and after the bottleneck (Luikart *et al.* 1998) so are not performed here. Pairwise relatedness between all individuals was estimated with the Ritland estimator (Ritland 1996) using the *related* package (version 1.0) in R (Pew *et al.* 2015). Statistical differences in genetic diversity and relatedness values between countries were assessed with Wilcoxon tests. To compare relatedness between pairs with zero, one or two individuals that recruited into the breeding population between 2019 and 2023, we used the Kruskal–Wallis test.

RESULTS

In the UK dataset, after filtering for individuals successfully typed at three or more loci, a total of 59 were genotyped at between three and nine loci (see Supporting information, Fig. S1). All loci were typed in most individuals and were retained for further analysis. In the Netherlands data, 38 samples were successfully genotyped at all nine loci.

Individual and locus-level genetic diversity

In both the UK and Netherlands samples, all loci were polymorphic, with 2–11 alleles per locus in the UK and 3–13 in the Netherlands (Table 1). To compare genetic diversity values in the UK population with those in the Netherlands population, the dataset was reduced to one chick per nest (UK, $n = 33$ and the Netherlands, $n = 38$). The UK sample showed a slight but non-significant reduction in all measures of diversity. The average number of alleles was 14% lower in the UK than in the Netherlands. After rarefacting to 32 individuals, allelic richness in the UK was 8.5% lower, which is not significantly different from the Netherlands ($V = 10$, $P = 0.16$). The average loss of heterozygosity in the UK amounted to just 5%, but was again not significantly different from the Netherlands ($V(H_e) = 15$, $P = 0.42$; $V(H_o) = 13$, $P = 0.30$). There was also no significant difference in levels of inbreeding ($V = 23$, $P > 0.99$).

Individual-level relatedness

In the UK, the relatedness distribution of all pairs of individuals was more positively skewed than in the Netherlands (Fig. 1). Within nests, never more than four alleles were present, which is consistent with chicks being full siblings (see Supporting information, Table S3).

Comparing relatedness values between the UK and the Netherlands using the between-nests data (UK, $n = 33$ and the Netherlands, $n = 38$), the median and 50% percentile of pairwise relatedness were very similar between the two countries (Fig. 1). However, the proportion estimates of $R_{Ritland} > 0.25$ in the UK population was 6.1%, and in the Netherlands was 1.9%. As expected, the headstarted UK breeding population has more closely related individuals (half-siblings and up) than the Dutch population.

Pairwise relatedness was similar in pairs where none, one or both individuals were known to have recruited into the population (recruited $n = 12$, not recruited $n = 16$; $\chi^2 = 1.03$, df = 2, $P = 0.599$; Fig. 2). This suggests that relatedness does not affect whether or not an individual recruits to the population.

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Table 1. Allelic richness and expected and observed heterozygosity for nine microsatellite loci from a UK Black-tailed Godwit *Limosa limosa limosa* population at the Nene Washes (one nestling per nest, $n = 33$), and the Dutch breeding population in southwest Friesland ($n = 38$, data from Trimbos *et al.* 2011). N_a, number of alleles; A_r, allelic richness (rarefaction at 32); H_e, expected heterozygosity; H_o, observed heterozygosity; F_{is}, inbreeding coefficient.

	Nene washes					Friesland				
	N_a	A_r (32)	H_e	H_o	F_{is}	N_a	A_r (32)	H_e	H_o	F_{is}
LIM10	7	5.87	0.71	0.69	0.033	9	7.48	0.82	0.82	0.003
LIM11	6	5.76	0.76	0.86	−0.121	7	6.77	0.79	0.79	0.001
LIM12a	11	9.70	0.84	0.76	0.104	10	8.31	0.85	0.87	−0.023
LIM25	2	2.00	0.23	0.27	−0.137	3	2.36	0.15	0.16	−0.060
LIM3	10	8.82	0.85	0.90	−0.059	13	10.42	0.86	0.74	0.141
LIM30	6	5.34	0.60	0.47	0.231	7	5.72	0.64	0.68	−0.075
LIM33	8	7.66	0.85	0.83	0.037	11	9.16	0.84	0.84	−0.006
LIM5	4	3.39	0.26	0.26	0.024	5	4.59	0.49	0.37	0.250
LIM8	8	7.11	0.79	0.69	0.132	7	6.03	0.78	0.79	−0.006
Average	6.9	6.18	0.66	0.64	0.027	8.0	6.76	0.69	0.67	0.025

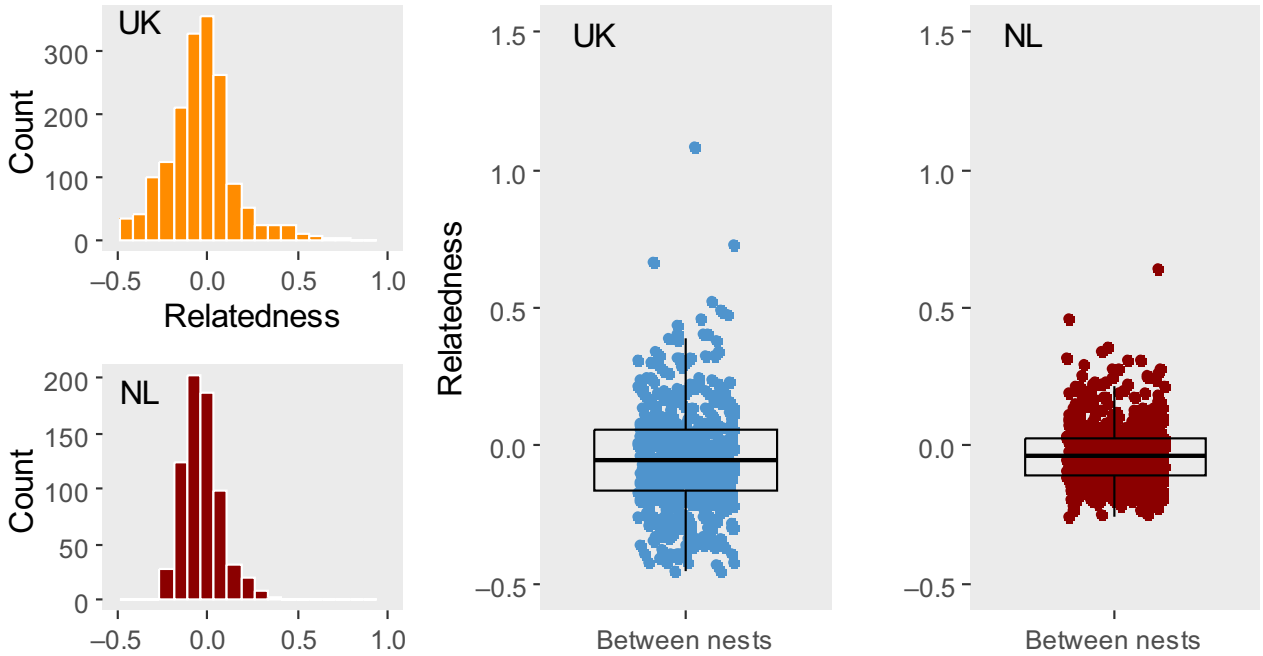

Figure 1. Relatedness distribution of all pairs of individual chicks sampled in the UK Black-tailed Godwit *Limosa limosa limosa* population in the Nene Washes (left top) and individual chicks and adults in the Dutch population in Friesland (left bottom). Relatedness distribution between nests in the UK population in the Nene Washes (centre) and between nests in the Dutch population in Friesland (right). Between nests were sampled from different nests, present in the same or different years.

DISCUSSION

This study found that the UK breeding population of Black-tailed Godwits showed a non-significant difference in genetic variation compared with the Netherlands but had slightly higher levels of relatedness. Loss of genetic variation might be expected in future, especially if the proportion of closely related individuals increases, due to the same (related) adults repeatedly contributing eggs to headstarting, which occurred during this study (Table 1). The UK population has slightly lower levels of genetic diversity compared with the Netherlands population genotyped by Trimbos *et al.* (2011) and Verkuil *et al.* (2009, not shown), but substantial levels of genetic diversity remain at the loci typed in this study. The results of this study are consistent with the observed small size of the UK breeding Godwit population. There was no evidence of a consistent reduction in observed compared with expected heterozygosity, which might be predicted if severe inbreeding were occurring.

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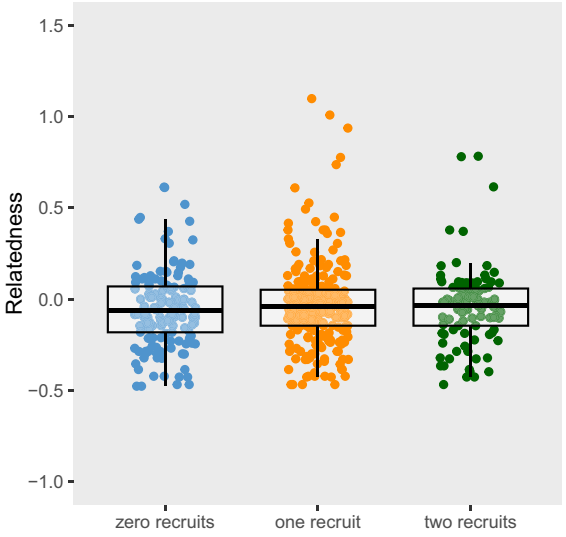

Figure 2. Relatedness within pairs of individual Black-tailed Godwit *Limosa limosa limosa* chicks from which none, one or two individuals are known to have recruited into the breeding population.

However, we cannot rule out mild levels of inbreeding resulting from the lower genetic diversity of the UK population.

Blomqvist *et al.* (2010) found that declines in a small population of Dunlin were associated with increased pairings between related individuals, affecting fitness at different stages, including reduced hatching success, increased embryo mortality and possibly also survival in the early days after hatching. Reductions in genetic diversity due to headstarting could compound low genetic diversity, especially if headstarted individuals become a significant component of the breeding population. In 2023, the number of pairs in this population was 47, and 60% of those pairs had at least one head-started Godwit (RSPB/WWT unpublished data).

We suggest that, currently, there is an apparent lack of immigration to the UK population from the Netherlands. Evidence for the lack of immigration comes from the absence of any colour-marked birds from the Netherlands being seen breeding in the UK, despite around 3% of that population being colour-marked (Jos Hooijmeijer pers. comm.). It may be that, although the UK population probably arose from Dutch immigrants in the 1950s (Bijlsma *et al.* 2001), the decline in the Netherlands since the 1960s means that there are fewer dispersing individuals and those that are dispersing can probably locate local territories. However, we cannot entirely rule out the possibility of a very low incidence of immigration, especially as we know that a small number of the UK headstarted individuals have recruited into other European breeding populations (Donaldson *et al.* 2024). This suggests that the tendency for long-distance natal dispersal remains present in the population, and a very low incidence of immigration (one bird in 10 years or each generation) might be enough to prevent low genetic diversity (Mills & Allendorf 1996).

Despite the increased relatedness of the UK population, there was no suggestion that relatedness between individuals had any influence on whether a headstarted individual recruited into the population or not. This either means that relatedness is not affecting the ability of these headstarted birds to survive or, if it is having an effect, it may be manifesting in earlier life stages. A more formal survival analysis might help to account for the likelihood of permanent emigration and detectability of individuals, but there are two reasons why we considered a formal survival analysis unnecessary. First, there is no suggestion from the analyses presented in Figure 2 that relatedness has any effect on recruitment. Secondly, this species is highly philopatric, so there would only ever be a small percentage of individuals that may permanently emigrate. We argue that it is extremely unlikely that those individuals would go undetected because (1) the small size of the UK population and the intensity with which it is studied mean that it is extremely unlikely that an individual could be alive and breeding in the UK without being seen, (2) of the individuals included in our analysis, most of the recruits joined the UK population but one individual recruited to a population in the Netherlands and (3) given the degree to which Black-tailed Godwits are studied intensively on their breeding grounds in Europe, Godwits from our study in the UK are very likely to be seen in other breeding populations if they occur. Indeed, six headstarted individuals are known to have been in locations outside the UK during the breeding season.

These results are important when making management decisions about such a small population and could allow for adaptive management informed by genetics, especially because translocations should not involve extensive use of donor stock from a single source (Sherwin *et al.* 2000). If headstarting is to continue in this population, are there alternative donor egg strategies that could prevent further loss of genetic variation or even enhance genetic diversity? Possible alternative strategies might be: (1) if there is a need to continue taking donor eggs from the southeast England population, avoid taking the earliest clutches in order to introduce eggs from different females with later timing of laying and therefore increase genetic variation among headstarted individuals; (2) avoid taking clutches from headstarted pairs, as that may further exacerbate relatedness; and (3) seek opportunities to introduce genetic variation by using donor eggs from a different population, for example from the other small populations in the UK or from the much larger populations in Continental Europe. Options 1 and 2 are only likely to prevent further loss of genetic variation, whereas option 3, especially

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taking from the Continent, could increase genetic variation. Given the perilously small size of the current breeding population, only a relatively small number of eggs may need to be introduced to boost the genetic variation reasonably rapidly and, from a conservation genetics perspective, it would seem a sensible precautionary approach that could have only positive consequences.

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AUTHOR CONTRIBUTIONS

Jennifer Smart: Conceptualization; funding acquisition; writing – original draft; writing – review and editing; project administration; data curation; investigation; methodology. **Yvonne I. Verkuil:** Writing – original draft; writing – review and editing; methodology; formal analysis; data curation; investigation. **Krijn B. Trimbos:** Data curation; investigation; methodology. **Nicola C. Dessi:** Investigation; conceptualization; methodology; data curation. **Rebecca Lewis:** Methodology; data curation; investigation.

CONFLICT OF INTEREST

No conflict of interest exists for any of the authors of this manuscript.

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ETHICAL NOTE

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at DOI:10.5061/dryad.nvx0k6f37.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Genotyping sample sizes for the UK Black-tailed Godwit population. (A) Counts of the number of individuals successfully genotyped at each locus, after excluding failed reactions. (B) The distribution of the number of loci typed across all individuals.

Table S1. Biological samples from nesting attempts from which DNA was successfully extracted across the 3 years in which samples were collected. The number of extractions from each nest, the identity, where known, of the parent birds and whether the sample came from nesting attempts that were wild or part of the headstarting programme (H-S).

Table S2. The 11 microsatellite loci from Verkuil *et al.* (2009) used in the present study.

Table S3. Allele call within nests.

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