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Recovery of cirl bunting, *Emberiza cirlus*, song diversity after translocation

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Abstract

In order to improve conservation outcomes translocation or reintroduction of individuals may be necessary. When song learning birds are translocated, changes in the cultural diversity of song repertoires, or abnormal vocalizations, in the new population can be a problem. We monitored song production over 8 years in a reintroduced population of the cirl bunting (*Emberiza cirlus*). Chicks were removed from nests in Devon, UK, between 2006 and 2011, translocated at 6 days old to be hand-reared and released in Cornwall, UK. Recordings at the release site in 2011 showed a significantly reduced population repertoire and individuals sang abnormal song types compared to the source populations in Devon. However, recordings in 2019, showed population song repertoire had reached the level of source populations of similar size, and song types were species typical. Our study shows that species can recover from a cultural bottleneck and suggests that, for some song learning birds, if translocation of nestlings is necessary it may not lead to long-term problems for communication and thus population persistence. For future translocations of nestlings, we recommend that efforts are made to provide tutoring to enable song learning. This may be achieved by providing recordings, but may also include providing adult song tutors. In addition, playback of "normal" songs to translocated populations may aid in development of species typical song repertoires, although care must be taken that this is not disturbing the reintroduced birds.

KEYWORDS

abnormal song, conservation reintroduction, isolated population, song learning, song repertoire, songbirds

1 | INTRODUCTION

Conservation programmes often require translocation, or reintroduction, of wild individuals (Griffith et al., 1989; Seddon et al., 2014; review in Berger-Tal et al., 2019). In order to judge the success of these programmes, post release monitoring is essential to assess population growth, genetic diversity, behavioral diversity and overall

success of the conservation action (Sutherland et al., 2004; Williams et al., 2020). We will use the term translocation to indicate the movement of wild individuals to a new location, which may be done to either supplement an existing population or reintroduce a population to a previously occupied area (IUCN, 2013). Animal behavior issues are one of the most reported problems for translocations and are the main problem for those involving birds (review: Berger-Tal et al., 2019). The most common behavioral issue is dispersal away from the protected area to less safe areas, but the second is failure of animals to learn essential life skills (Berger-Tal et al., 2019). Life skills, such as following a migration route (e.g., northern bald ibis, *Geronticus eremita* Fritz et al., 2017), selecting suitable habitat (e.g., brown treecreeper, *Climacteris picumnus*, Bennett et al., 2012), developing foraging skills (e.g., bush stone curlew, *Burhinus grallarius*, Kemp & Roshier, 2016) or avoiding predators (e.g., little owls *Athene noctua*, Alonso et al., 2011) are needed in order for populations to persist after reintroduction. Another ability, producing appropriate vocalizations, is not always considered as potential issue. However, in the case of birds that socially learn vocalizations (a group of almost 5000 species, which includes Psittaciformes, Trocillidae and Oscines, Williams, 2008), a lack of opportunity to learn their song from conspecifics may be a significant issue for inter-individual communication (Laiolo, 2010; Laiolo et al., 2008; Valderrama et al., 2013), and result in negative consequences for population growth or persistence.

Most avian translocations have been conducted with species that do not need to learn their vocalizations (e.g., *takahē*, *Porphyrio hochstetteri*; red-cockaded woodpecker, *Picoides borealis*, see references in Williams et al., 2020). In these cases, species specific vocalizations will be produced regardless of whether there was opportunity to learn, unless there are genetic changes, for example, hybridization (Collins & Goldsmith, 1998; de Kort et al., 2002). However, when birds need to learn their song, the process of translocation may affect song diversity, production, or quality (Parker et al., 2012; Valderrama et al., 2013). The effect of translocation on song will depend to some extent on the species-specific learning process, but monitoring song changes within populations has been shown to be a useful method of predicting potential problems (reviewed in Lewis et al., 2021; Valderrama et al., 2013). Therefore, monitoring of song production, alongside breeding success etc., is something that should always be considered. As stated above around 5000 species of birds learn their song from conspecifics, some learn throughout their life (open-ended learners), others only during a critical period early in life (closed learners), from several weeks to a year (Catchpole & Slater, 2008, Slater, 1989). Both open-ended and closed learners generally require song models, or tutors (usually conspecific adults), to learn their songs from (Beecher & Burt, 2004), and translocation before the song learning period may disrupt that process. Song and element sharing can be essential for communication within populations (Beecher & Brenowitz, 2005; Bradley et al., 2012; Molles & Vehrencamp, 2001). Local song dialects, or population specific vocalizations, may be necessary for maintenance of territories (Slater, 1989, Slabbekoorn & Smith, 2002; Valderrama et al., 2013), mate attraction (Bradley et al., 2014; Rowe & Bell, 2007), and social interactions (Wright & Dahlin, 2018), all essential behaviors for individual survival and reproduction.

If adults are translocated, the founder population may be small and fragmented, which is also known to affect song characteristics (Baker, 1996; Hudson & Creanza, 2022; Laiolo & Tella, 2007; Laiolo & Jovani, 2007), and founders may have a reduced song diversity compared to the source population. If nestlings or chicks are reintroduced following hand rearing there will also be no mature adults present to learn from, for either closed or open-ended learners. Any disruption to the song learning process, or to overall song diversity in a population, may lead to problems (Collins, 2004; Grant & Grant, 1996; Slabbekoorn & Smith, 2002). As mentioned, species vary in the window during which song learning occurs, from a few weeks, a few years, or a lifetime (Catchpole & Slater, 2008; Marler, 1970, 1997). We do not know the sensitive phase for all species, but the common issue in song learners is that the number of tutors, and the songs that those tutors produce, is important for development of a full species-specific song (Beecher & Brenowitz, 2005). Therefore, anything which disrupts the number/type of tutors can have long term impacts on a population.

Much of what we know of effects of song learning disruption on population song characteristics comes from studies of isolated populations. Within isolated populations, which will share some issues with translocated populations, changes in birdsong are often pronounced (Parker, 2008; Paxton et al., 2019). Young birds have a reduced number of conspecifics to learn from (Baker & Jenkins, 1987) and may begin learning song from heterospecific sources (Laiolo, 2008). Laiolo et al. (2008) found the number of song types in a small, isolated population actually increased, through incorporating songs copied from heterospecific sources into their repertoire. This has also been found in species that have undergone translocation (Baker et al., 2003). However, usually song diversity is reduced in isolated and/or translocated populations (Paxton et al., 2019; Valderrama et al., 2013),

which could lead to problems in communication within populations, and between populations if they come into contact during population expansion after a successful conservation intervention.

Translocations offer unique opportunities for observing changes in population song diversity (Parker, 2008). Especially if the songs of founder individuals are known, and the song diversity in the population has been monitored over time (Parker et al., 2012). Translocation of songbirds usually only involves adult birds, in which case, song has already been learned (refs in Berger-Tal et al., 2019; Lewis et al., 2021). However, there is a paucity of data on how song is affected when chicks are translocated, especially when reintroduced before the song learning period (which typically starts around fledging). Translocation at the chick stage is often easier, and may be more likely to lead to population persistence (Parker et al., 2012; Sarrazin & Legendre, 2000), but translocated chicks may not be able to produce a normal song or repertoire (Catchpole & Slater, 2008; Marler, 1997; but see Slater & Ince, 1982). This may be a particular issue for closed learners who have a critical, and often brief, period in which to socially learn their song, and do not change their song after the initial crystallization period (Beecher & Brenowitz, 2005; Hultsch & Todt, 2004). In addition, releasing birds into the wild after having been rescued from the pet trade may be considered a special case of translocations. This kind of translocation may be more common in long lived species such as parrots as they are likely to survive a period in captivity. However, the origin of these rescued birds is often unknown making consideration of local dialects particularly relevant for the success of release (Martins et al., 2018). It is apparent that in a variety of conservation actions, the impact on song learning is relevant to a wide range of bird species.

Recently we had a unique opportunity to follow song changes in a reintroduced population, where chicks were translocated before the song learning period (Kreutzer, 1990). The cirl bunting (*Emberiza cirlus*) used to be widespread and locally common across southern England up until the 1930s (Stanbury et al., 2010; Jeffs et al., 2016), mainly in coastal areas (Holloway, 1996). However, the population crashed in the late 20th century within the UK (Evans, 1997a, 1997b; Gregory et al., 2004; Jeffs & Evans, 2004; Stanbury et al., 2010) due to decreased habitat and food availability (Gregory et al., 2004). There were just 118 pairs in 1989, found mainly within south Devon, UK (Evans, 1992). A species recovery plan resulted in over 697 pairs (Wotton et al., 2004). However, the range was still limited to a small area in South Devon. Therefore, the decision was made to begin a reintroduction programme (2006–2011), a collaboration between the Royal Society for the Protection of Birds (RSPB), Natural England, National Trust, Zoological Society of London and Paignton Zoo. Rear and release, where wild bred chicks are removed for hand rearing and then released at around 28 days old, was the chosen translocation method (Fountain et al., 2017). Moving adult birds, or first winter birds, was discounted because it was likely to result in too many losses (Fountain et al., 2017). Captive breeding was also discounted as cirl buntings do not do well in captivity. Chicks (47–72 per year, 376 in total) were released in a suitable site in Cornwall, UK, each year for 6 years, after being removed from nests from several sites in Devon at 6 days old (details in Jeffs et al., 2016). The reintroduced population went from nine pairs in 2007 up to 52 pairs in 2015 (Davies et al., 2011; Davies & Jeffs, 2016), intensive monitoring stopped in 2015, but the population reached 65 pairs in 2016 at the time of the last National cirl bunting survey (Jeffs et al., 2016).

Cirl buntings are closed end learners and birds isolated from 7 days old do not develop species typical songs, the syllables produced are simple and somewhat abnormal (Kreutzer, 1990). However, they do show typical cirl bunting elements (2–5 elements combined to make a syllable). Therefore, it was inferred that cirl buntings need a conspecific tutor to learn syllable formation from, although, the elements of song can be considered innate (Kreutzer, 1990). The translocated UK birds would not have had the opportunity to learn the correct syllable structure, as they were isolated from adult birds from 6 days old. The exact duration of the sensitive period of song learning for cirl buntings is unknown, but a similar species the yellowhammer (*Emberiza citronella)* learns during the first breeding season (Hansen, 1999), and in general birds start learning songs at fledging (Marler, 1970), well after 6 days old.

Our aim was to determine the effect of reintroduction of cirl bunting chicks on; (i) population song diversity, (ii) song sharing across populations, and (iii) to assess how long any song changes persisted, and finally, (iv) to make recommendations for future conservation actions involving the movement of chicks or nestlings in species that show vocal learning. We recorded cirl buntings in the reintroduced population in year six of the reintroduction period (2011—the last year birds were released), and again 8 years after the reintroduction ended (2019) and all birds were wild born. We also recorded eight populations across Devon that varied in size and isolation by distance from other populations, to determine whether any song differences found were due to the reintroduction process, or due to isolation by distance of the Cornwall population. For each population we measured population repertoire as the number of different song

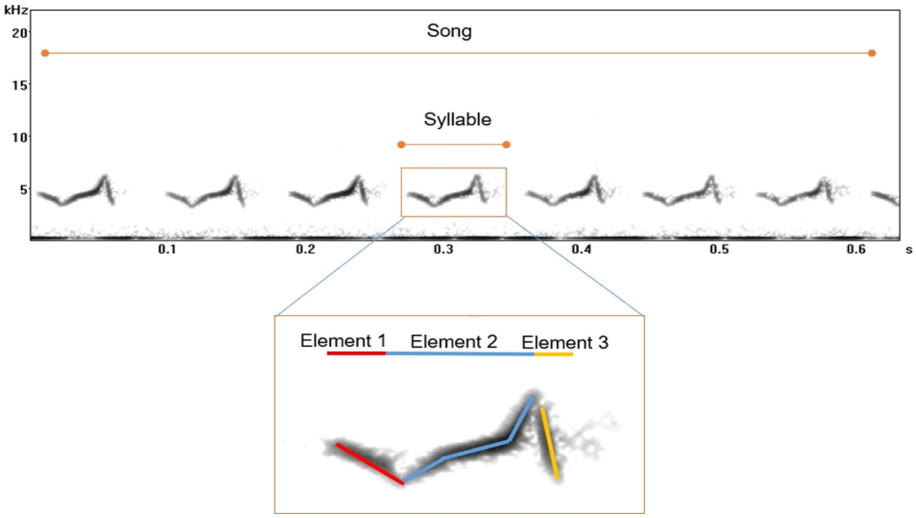

FIGURE 1 The structure of part of a typical cirl bunting *Emberiza cirlus* song, with below an expanded section showing a syllable consisting of three elements (FlatTop: FFT length 512, resolution 86 Hz; 93.75% overlap, resolution 0.7256 s). Song = continuous repeat of syllables, Syllable = repeated units that make up a song, Elements = species specific and apparently unlearned sounds combined to make a syllable.

types, and also calculated sharing indices across all pairs of populations to assess whether there were dialects (Catchpole & Slater, 2008; Osiejuk et al., 2003), and to what extent song types were shared across populations.

2 | METHODS

2.1 | Study species

The cirl bunting *Emberiza cirlus* is a small seed eating nonmigratory bird species, with very specialized habitat requirements (Evans et al., 1997; Evans & Smith, 1994). Cirl buntings can sing at any time of the day between April and August, from song perches on bushes and small trees around their breeding territory, which is usually quite small (diameter of area defended around the nest ~200 m^2, Stevens et al., 2002). The average song repertoire consists of three song types (range 1–6) (Kreutzer, 1979) and each song is made up of an average of 17 (±6) repeated, identical, syllables, with each syllable consisting of 1–5 elements (Figure 1).

2.2 | Study locations and song recordings

We recorded cirl buntings in 2011 and 2019 at eight locations in Devon (Source) and one in Cornwall (Reintroduced), all within the UK (see Figure 2a and Table 1). Each location is close to the South-West coast where the habitat is farmland with scrubby hedges, typically favored by cirl buntings (see Evans & Smith, 1994; Jeffs et al., 2016; Stevens et al., 2002; for habitat requirements). Each location was likely to be a different breeding population as cirl buntings tends to disperse no more than 2 km from their breeding sites (Evans, 1997a, 1997b).

2.3 | Song recordings

We recorded songs as WAV files with a sampling rate of 44.1 kHz using a Sennheiser ME66 directional microphone and Marantz Solid State Recorder PMD661 between 0730 and 1700 h throughout May–August in 2011, and June–July in 2019. Cirl buntings start singing around 0800 h and do not have a "dawn chorus" (personal observations).

We recorded several times at each location (mean 2.04 days per individual). In Devon (Source), we visited each population for 4–7 days depending on the number of males, and all males singing in the area were recorded at least twice, enough time to obtain a good estimate of the repertoire (Kreutzer, 1979). We identified individuals by following the males as they sang from song posts within their territory, allowing the territory boundaries of each to be determined, and making it possible to identify separate individuals.

The RSPB monitoring team made sound recordings of the reintroduced birds in the Cornwall location on the Roseland Peninsula in 2011 (Reintroduced 2011) over 10 days, during their usual monitoring process. Although this represents a longer recording effort than the locations in Devon (Source), the, recordings were more ad hoc due to the monitoring requirements. As a result of intensive monitoring territory locations and dimensions were known prior to sound recording. Of the 13 males recorded, five were un-ringed and resulted from breeding in the wild after reintroduction, while the remaining eight ringed males were hand reared. In 2019, we re-visited the reintroduced population over 5 days

TABLE 1 Number of male cirl buntings recorded, total number of recordings made, total number of songs, and population repertoire in each population. Cornwall populations are reintroduced, all others are Source populations.

Population (map ID)	Number of males	Recordings	Songs	Population repertoire
Berry Head (6)	5	39	329	7
Bolberry (3)	13	34	487	15
Broadsands (7)	5	28	323	4
West Charleton (5)	8	21	422	10
Cockington (8)	7	53	928	6
Salcombe (4)	8	65	454	11
East Prawle (2)	20	102	1154	17
Cornwall (1) 2011	13	63	467	6
Cornwall (1) 2019	16	38	292	17

(Reintroduced 2019) and all males encountered were recorded, RSPB monitoring had ended in 2015. Each male was only recorded once in 2019, but as males were no longer color ringed, we knew all males were wild born. Territory boundaries could not be determined; therefore, we assumed a male was a separate individual if they were recorded more than 500 m in a straight line from the previous male.

2.4 | Song measurements

We identified songs using spectrograms (FlatTop window; FFT 512, frequency resolution 86 Hz, 93.75% overlap—time resolution 0.72 s) in Avisoft SasLab Pro (Specht, 2002). A library of 54 unique syllable types was created, representing the song types of all individuals recorded.

Each individual song spectrogram was visually compared with the reference library of the 54 syllable spectrograms for classification (Figure 3 in the results shows a range of the different syllable types).

For each population we calculated the number of different song types (PopRep). We then calculated the Dice sharing index (Dice, 1945) between all possible pairs of populations using the following formula.

$$S = 2a/(b+c)$$

S = Dice sharing index, a = number of song types shared between two populations, b and c = the song repertoire sizes of the two populations.

In addition to the 36 (number of paired combinations with 9 populations) pairwise scores, we calculated an average song sharing score for each population, that is, the average of sharing with the eight other populations—SharedAll. We also looked at sharing just between the source populations (i.e., the original populations that had not been translocated)—SharedSource.

The total number of males (Males) recorded was used as a measure of population size. We also calculated distances between populations using Google maps (Distance). We measured distance between populations in a straight line (as the bird flies), adding bends around areas over water >2 km, as it was assumed the birds would not cross over larger areas of water, cirl buntings are thought only to move over suitable areas when moving sites (Evans, 1997a, 1997b). Median distance between locations was 22.7 km (2.8–32 km), excluding the Reintroduced population, which was 98–110 km from the Source populations in Devon.

Detailed measurements of individual songs for each male recorded, to allow calculation of within population sharing, syllable consistency within an individual, and similarity across individuals within/between populations will be addressed in a subsequent publication.

2.5 | Data analysis

All statistical analyses were conducted in RStudio (R Core Team, 2022).

We predicted that populations with more males would have larger population repertoires as has been found in other studies (Laiolo & Tella, 2007; Laiolo et al., 2008). A linear model *lm* was used to test the relationship between Males (number recorded) in a population and PopRep (population repertoire size, not significantly different from a normal distribution). As there was only one data point for the reintroduced population in 2011, and one in 2019, we could not analyze differences in population song repertoire size between Source and Reintroduced (2011 and 2019) populations statistically. Therefore, we used the outlier command, *car::outlierTest*

(Fox & Weisberg, 2019) to test for outliers in the linear model in order to determine whether the 2011 and/or 2019 Reintroduced populations were outliers in the model A Bonferroni correction, necessary for large samples, where some outliers are expected, was not used due to the small sample size (9 populations).

Differences between average song sharing across populations in Source, and Reintroduced (2011 and 2019) again could not be analyzed, as there is only one data point each for 2011 and 2019. However, we tested for outliers in: (a) SharedAll, and (b) SharedSource, using the Grubs test (Komsta, 2022).

The relationship of Distance between pairs of populations and degree of sharing (S value for each pair) was analyzed using a linear model (*lm*). We excluded the Reintroduced populations from this analysis; as those populations were translocated there is no expectation that song would relate to distance from the Source populations in Devon, leaving a sample size of 21 pairs.

All figures were produced in R using *ggplot2* (Wickham et al., 2016).

2.6 | Ethics

Sound recording in Source and Reintroduced populations, was performed with permission from the RSPB. Due to the endangered status of the cirl bunting in the UK it is a schedule 1 bird (Wildlife and Countryside Act 1981, UK), which means it is an offense to disturb the birds on or near the nest. Therefore, potential nest sites were avoided, and fieldwork was carried out under strict guidance that avoided any disturbance. The song recordings in the Reintroduced 2011 population were conducted by RSPB officers and followed strict protocols.

3 | RESULTS

3.1 | Population repertoire

There was a significant relationship between the number of males recorded and population repertoire size ($F_{1,7} = 12.96$, $p = .009$, $r^2 = .60$, Figure 3). However, the Reintroduced 2011 population had a smaller song repertoire size compared to the same population in 2019 and the Source populations and is a significant outlier in the model ($t = -3.26$, $p = .017$).

The Reintroduced 2011 population produced only six song types (Figure 3), one of which was found in Devon (Source), and one of which, in a hand-reared individual, was made up of a heterospecific syllable, possibly from a dunnock *Prunella modularis*. The same range of song types were produced by both hand-reared and wild born Reintroduced 2019 individuals.

Interestingly, the Reintroduced 2019 population still included the song type (designated O) that was originally found in nearly all the 2011 male repertoires, and not found in the Source populations.

3.2 | Song sharing

Both the Reintroduced 201**1** population and the Cockington population (Source) showed very low sharing

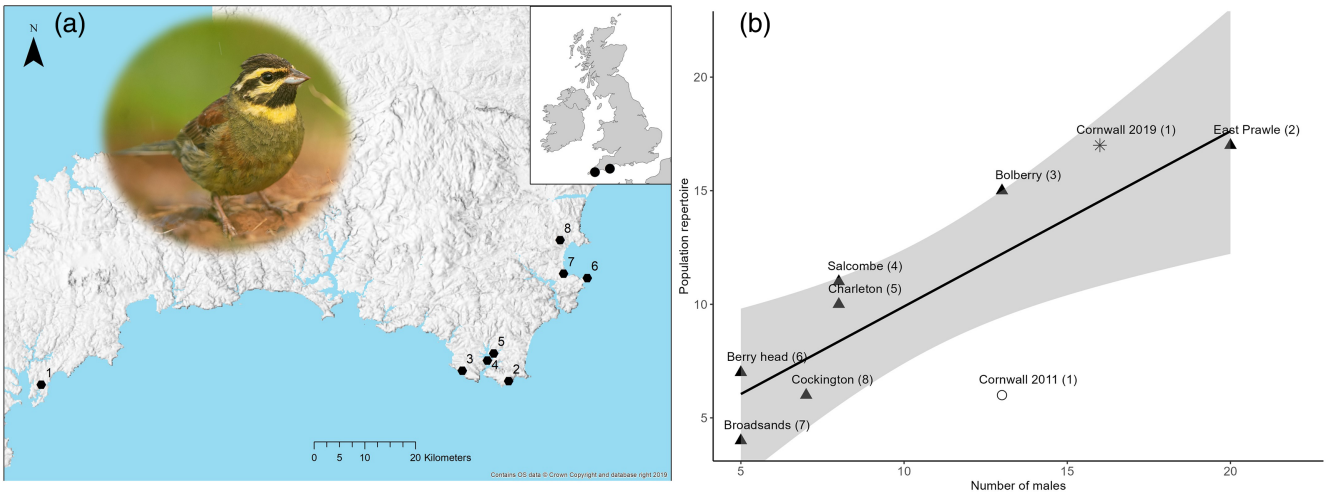

FIGURE 2 (a) Locations of cirl bunting populations sound recorded for this study, points reflect the center of the location. Location 1 is the reintroduced population in Cornwall. Locations 4 and 5 are near each other but are separated by water. Inset photo shows a cirl bunting (Ben Andrew rspb-images.com). (b) The relationship between the number of males recorded and the number of different song types in the population (location of population on map in label brackets). Confidence interval and fit line displayed. ▲ Source, ◯ Reintroduced 2011, * Reintroduced 2019.

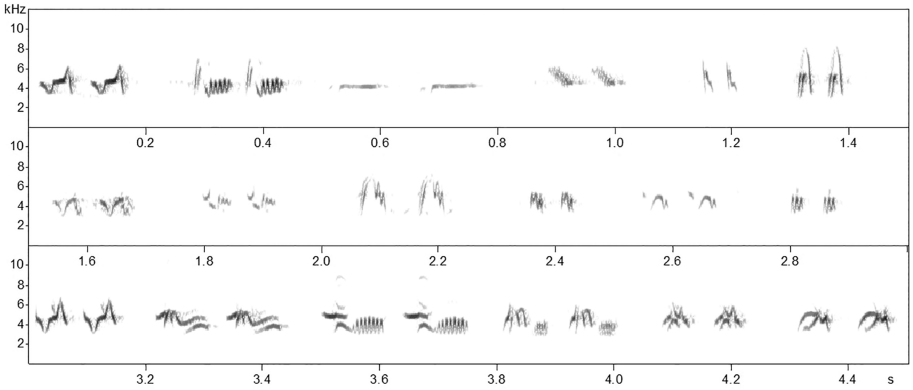

FIGURE 3 A range of syllable types from the reintroduced Cornwall population (Reintroduced) and the Devon (Source) populations. (a) All song types from Reintroduced 2011 including note type B (also found in Source), note H (heterospecific) and note O (never found anywhere else); (b) a range of the notes from Reintroduced 2019 and (c) a range of the common song types found in Source (sound file sampling rate 44.1 kHz. Window FlatTop: FFT 512 resolution 86 Hz; overlap 87.5% resolution 1.45 ms, frequency cut off 10 kHz).

with the other populations (see Table 2). Both are significant outliers in SharedSource (shared songs with just the Devon populations. Grubbs test: $U = 0.099$, $p = .007$). There were no significant outliers for SharedAll (sharing across both Devon and Reintroduced populations), although again Reintroduced 2011 had the lowest sharing.

3.3 | Distance and song sharing

There was no relationship with distance between pairs of populations across the Devon locations (Source) and the degree of song sharing ($F_{1,19} = 1.46$, $p = .24$, $R^2 = .021$).

TABLE 2 Average sharing index (S) for each population across all populations (including Cornwall 2011 and 2019—SharedAll), and only between the source populations (only sharing with Devon—SharedSource).

Population (map ID)	Average SharedAll	Average SharedSource
Berry Head (6)	0.11	0.15
Bolberry (3)	0.14	0.15
Broadsands (7)	0.16	0.20
West Charleton (5)	0.22	0.20
Cockington (8)	0.08	0.09
Salcombe (4)	0.15	0.18
East Prawle (2)	0.20	0.19
Cornwall 2011 (1)	0.04	0.03
Cornwall 2019 (1)	0.17	0.18

4 | DISCUSSION

We showed that a reintroduced population of a songbird initially had a significantly reduced song repertoire size compared to the source populations. The initial smaller repertoire size and abnormal, or unusual, syllables likely resulted from a lack of song learning opportunities during the species typical song learning period. The birds were collected for translocation as nestlings, and hand-reared in captivity before release and therefore did not have the opportunity to learn their song from adult conspecifics. This initially led to the concern that the reintroduced population would suffer reduced reproductive success through a lack of ability to communicate in a species typical manner. Defense of territories and attraction of mates are both likely to be disrupted when song is abnormal (Catchpole & Slater, 2008; Collins, 2004). However, 8 years after the reintroduction, the song repertoire had recovered, both to a typical size, and included typical cirl bunting song types, comparable to the Devon (Source) populations. The increase in song repertoire size in the reintroduced population was likely facilitated by social learning combined with genetically inherited components of the song (see below). In 2011, the reintroduced population shared only one of its song types with the source populations (as found for a translocated population by Parker et al., 2012), all other song types were unique. This contrasts with the source (Devon) populations which generally showed similar levels of sharing with each other. Interestingly, 8 years after translocation the reintroduced population still included a unique syllable first observed in 2011 and not present in the source populations.

Our results confirm that translocating chicks before the song learning period can disrupt song production in a

bird species with a critical song-learning period. As found before in isolated cirl buntings in a laboratory setting (Kreutzer, 1990), the initial overall song pattern shortly after reintroduction was similar to "normal" cirl bunting song, but the syllables making up the pattern were abnormal, including the incorporation of heterospecific sounds. In addition, nearly all males produced one of two song types. Kreutzer (1987) found that behavioral response to abnormal cirl bunting songs depended on individuals being exposed to that song type previously. This suggests that if the reintroduced (2011) birds had re-encountered the source population it would likely lead to significant communication issues in mate attraction and territory maintenance (Bradley et al., 2014; Slabbekoorn & Smith, 2002; Valderrama et al., 2013). However, this scenario was unlikely as there is little chance of the two populations mixing due to the distance between them. Nevertheless, the reintroduction is now a success, with the population established and considered self-sustaining (Davies & Jeffs, 2016; Jeffs et al., 2016). This success suggests that other important skills, such as habitat selection, foraging and predator avoidance, were acquired during the reintroduction process, likely due to the soft release protocol followed (Jeffs et al. (2016).

A possible explanation for the development of species typical song characteristics by 2019 in the reintroduced population, is that in buntings (Emberezids) there are species specific elements of song (which are combined to produce a full syllable) which appear to be innate (Kreutzer, 1990). What needs to be learned from conspecifics is how to combine these elements into the species typical syllables. In addition, as in many song-learning birds, during the sensorimotor phase of song learning (Marler, 1970), many different sounds are produced, called babbling. This phase is followed by song crystallization, when there is selection of song types from the "babble," resulting in the final adult song (Marler, 1970; Nelson & Marler, 1994; Nottebohm, 1970; Nottebohm, 1991). Given this process, new sounds could have been generated during the babbling phase of song learning in cirl buntings which were then incorporated into new, stable adult song types.

At present no other song learning bird species has been translocated at the chick stage (Williams et al., 2020), so we cannot be sure whether this process would be repeated. However, our work suggests that a typical population repertoire can develop over time in species where there are some innate components to song, and that show a babbling phase in song development. Even if abnormal songs are produced by the first few generations of translocated birds, recovery to a normal song repertoire size may be possible (but see Baker, 1996). In addition, as new syllables/songs develop during population expansion in a translocated songbird (Mundinger, 1980; Williams et al., 2022; Williams & Lachlan, 2022) species-typical sounds may be preferentially selected for during the babbling phase because they perform their function better, that is, attract a female or repel a rival (Nelson & Marler, 1994). Although we did not assess female song preferences in our study, it is important to remember that females also develop song preferences based on what they hear, often during a critical phase (see Nowicki & Searcy, 2004). The role of female song preference, and how that may drive the development of a species-typical population repertoire in a translocated population also needs to be considered in future studies.

When the cirl buntings were first released the population was very sparsely distributed around the reintroduction area, due to the low numbers of surviving birds (Jeffs et al., 2016). As in other low-density populations, we would expect fewer interactions between individuals (Lachlan & Slater, 2003) and plenty of space for territories and less competition for mate attraction. Therefore, there may have been a lower cost to having an abnormal song during the early stages of the reintroduction, due to reduced need to defend territories and sexual competition. As the population size and density increased, the ability to produce species-specific songs could have become more important, and there would also have been a higher rate of encounters between individuals. Both of these factors could have been important in the increase in population song repertoire size observed between 2011 and 2019 (Lachlan & Slater, 2003). It was noted that breeding success improved in the reintroduced population from around 2014, but whether this was due to improvements in ability to communicate, or to the fact there were more wild reared birds in the population is unknown (Jeffs et al., 2016). Many studies have shown wild born individuals are more successful after translocation/reintroduction (Berger-Tal et al., 2019).

We found no relationship with distance between the source populations and degree of sharing, as we might expect if the cirl bunting showed dialects, that is, closer populations share more. Kreutzer (1979) also found no indication that cirl buntings had dialects in France. In fact, in our study, two populations that were 2 km apart shared only three song types out of a population repertoire of 10 and 12 songs respectively. Cirl buntings, are unlike many other buntings, most of which do show song dialects (corn bunting, *Emberiza calandra*: McGregor, 1980; yellowhammer, *Emberiza citronella*, Rutkowska-Guz & Osiejuk, 2004; Ortolan bunting *Emberiza hortulana*, Osiejuk et al., 2007; overview—Catchpole & Slater, 2008), perhaps related to the fact they are remarkably sedentary (Evans, 1997a, 1997b).

Conducting playback studies to investigate source populations' response to abnormal song from reintroduced populations (as in Bradley et al., 2012) would be interesting as a test of likely communication difficulties that could be experienced by the original reintroduced population. However, our study showed that the initial loss of song repertoire size in the reintroduced birds recovered after 8 years. Therefore, we conclude that the cirl bunting reintroduction was a success both in terms of a viable population size and with the development of typical population song repertoire, several years post reintroduction. If contact should occur between reintroduced and sources populations there is no reason to predict any communication issues.

5 | CONCLUSIONS

To our knowledge, this is the first study to follow translocated songbird chicks over time to assess song development, paving the way for future chick translocation projects in other songbird species. It is possible that in this case the numbers of surviving birds facilitated the development of more song types, and high levels of survival may be essential for increases in song repertoire size, but this is still to be investigated. Nevertheless, despite the positive conservation story we present here, we advise that in the future the song learning development of a species is considered in translocation projects (sensu Spencer et al., 2007). If chicks are to be translocated then species-specific songs should be available for song learning while hand-rearing, by providing recordings (Houx & ten Cate, 1999; Marler, 1970; Marler & Peters, 1988) or conspecific live tutors (Adret, 1993; Payne, 1981, but see Nelson, 1998). Perhaps if isolated, or translocated, populations may encounter source populations in the future, songs from each population could be played back to the other. This has not previously been done as a tool to aid population song recognition but is likely to familiarize populations with previously unknown song types (Lewis et al., 2021; MacDougall-Shackleton et al., 2001). However, care must be taken as playbacks can also cause disturbance by simulating intruders, so a cautious and species-specific approach would be necessary. Playback of species typical songs to a reintroduced population alone may be the best option.

We can conclude from our study that translocation can have a negative impact upon song production in birds that need to learn their song. We would recommend that conservation actions need to take this into account, by not only providing learning opportunities for successful foraging, predator avoidance and migration, but also opportunities to learn population, or species, appropriate vocalizations. Although in our study the population recovered species-typical song characteristics, this may not always occur, likely leading to a reduction in breeding success. Indeed, if the population had not been so intensively monitored and managed, it is possible that the initial lack of species-typical song would have had a more negative effect in the cirl bunting.

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DATA AVAILABILITY STATEMENT

Data available at Dryad

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