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Short Communication

Rapid assessment of the extent of feral introgression in British and Irish Rock Dove (*Columba livia*) populations

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Interbreeding of related forms following anthropogenic activity can lead to genomic homogenization, contributing to decreasing biodiversity. Assessing spatiotemporal variation in the extent of introgression is important for conservation but can be expensive and logistically complex. The Rock Dove *Columba livia* is threatened by interbreeding with its feral conspecific and it is difficult to identify wild birds when wild, feral and mixed populations exist. Here, using British and Irish populations, I assess whether the proportion of birds with wild type plumage corresponds to distinctive head morphotypes differing between Rock Doves and feral pigeons, and whether plumage can be used to identify Rock Dove flocks and infer the extent of hybridization. I also determine whether plumage proportions have changed since a prior study was carried out in the 1960s. I show that flocks in which > 75% of individuals have wild type plumage consist of Rock Doves, as determined by head morphotype. Plumage proportions vary geographically, corroborating known genomic assessments of Scottish and Irish Rock Doves. Finally, the number of birds with aberrant plumages has increased since the 1960s, even in regions where no such birds were identified previously. This highlights the value of the Rock Dove as a current case study with which to explore the process of extinction by hybridization.

Keywords: citizen science, extinction, feralization, hybridization, gene flow.

Hybridization can be both a diversifying and homogenizing force in evolution (Abbott *et al.* 2013, Quilodrán *et al.* 2020). Homogenization can cause extinction by hybridization, where introgression from an introduced population leads to the genomic replacement of a native form (Rhymer & Simberloff 1996). Extinction by hybridization is common where anthropogenic activity establishes contact between previously allopatric populations (Todesco *et al.* 2016). Despite this, our understanding of its spatiotemporal dynamics is limited and this reduces our ability to conserve at-risk populations (Smith *et al.* 2022a). Despite developments in genomic technologies that allow determination of hybrid ancestry with increasing precision, the challenges of data generation mean that it remains difficult to quantify hybridization, especially over large geographical scales (Senn *et al.* 2019). DNA sampling of many species in numbers, and across a wide area, can be logistically and financially challenging. An alternative option is to identify phenotypic traits that allow rapid assessment of patterns of introgression. This has the advantage of being fast, inexpensive and able to guide more tailored genomic sampling.

Extinction by hybridization is a particular threat to the undomesticated forms of domestic animals which have feral populations (Smith *et al.* 2022a). The wild–domestic interface is of significant economic importance given the frequent global use of domestic species (Zeder 1982, Bähr & Wolf 2012). Long-standing wild-feral hybridization has, in many cases, rendered the genetic status of the undomesticated form uncertain (Smith *et al.* 2022a). This represents the loss of a source of genetic diversity, as well as a loss of opportunity for scientific advancement by studying undomesticated populations in a natural setting to explore the evolution of model organisms (Taberlet *et al.* 2008, Bähr & Wolf 2012).

The persistence of the wild Rock Dove *Columba livia* across most of its native range is uncertain following hybridization with feral pigeons (Baldaccini 2020). Genomic analysis has revealed that Scotland and Ireland harbour relict Rock Dove populations that have experienced variable levels of gene flow from feral pigeons, with Outer Hebridean birds experiencing little introgression (Smith *et al.* 2022b). This corroborates the view of the range of the Rock Dove in the British Isles as encompassing northern Scotland and the western fringe of Ireland (Hewson 1967, Goodwin & Gillmor 1970). Further work to characterize the dynamics of introgression is required to inform conservation efforts focusing on this important reservoir of ancient genetic diversity.

A main hurdle to evaluating the status of the Rock Dove is the challenge of discriminating them from feral pigeons without genomic analysis (Blasco *et al.* 2014). One phenotypic difference suggested to differentiate them is head shape (Johnston *et al.* 1988, Michaelsen & Refvik 2003). A rounded head, thinner bill and smaller cere distinguish the Rock Dove from the feral pigeon

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(Fig. 1a). While single traits are not diagnostic, overall head morphotype is an effective multivariate trait reflecting genomic differences between Rock Doves and feral pigeons. This has been shown by plotting the first two principal components of craniofacial morphology, which has highlighted that the distribution of individuals according to their head shape corresponds to their genomic classification as a Rock Dove or feral pigeon (Smith *et al.* 2022b). Notably, birds sampled from actively hybridizing populations had intermediate head morphology. Those not familiar with feral pigeons and Rock Doves might find it hard to assess head morphotype from a distance, especially in currently hybridizing populations where intermediates predominate. It would therefore be useful to explore methods more compatible with a citizen science approach, which would be valuable in maximizing the geographical coverage of Rock Dove monitoring.

Rock Doves have a wild type plumage only, contrasting with feral pigeons that display plumage polymorphism, although many feral individuals have wild type plumage (Fig. 1b; Fr *et al.* 1949, Johnston & Janiga 1995). Wild type plumage consists of a blue-grey colour with (in the subspecies *livia*, the primary ancestor of the domestic pigeon, and the subspecies found in Europe) a large white rump patch and two black wing bars (Johnston & Janiga 1995). The variable plumage of feral and captive domestic pigeons results from selective breeding and introgression. For example, the common 'chequer' pattern was introduced from the Speckled Pigeon *Columba guinea* (Vickrey *et al.* 2018). Although plumage variation cannot be used to categorize individuals (some feral pigeons have wild type plumage, and Rock Doves with domestic introgression can have aberrant plumage features) it could be used at the level of a flock, on the basis that Rock Dove flocks will have a very high proportion of wild type individuals, whereas feral pigeon flocks will be dominated by plumage types originating under domestication, and mixed wild–feral flocks will have intermediate plumage proportions. For example, Hewson (1967) sought to categorize Rock Dove populations in Scotland; flocks composed of < 75% wild type individuals were designated as mixed or feral/domestic flocks, and those that surpassed this threshold were identified as flocks consisting of 'mainly Rock Doves'. This plumage threshold appears to have been determined fairly arbitrarily (another suggested threshold for identifying a Rock Dove flock was 80% wild type plumage) and the authors did not suggest a threshold to separate mixing flocks from unadmixed feral flocks. Plumage proportions could also allow us to infer the extent of feral introgression. Such an inference would be based on the premise that a flock of Rock Doves with solely wild type birds is likely to have experienced minimal gene flow from feral pigeons, and increasing numbers of birds with aberrant plumage indicates increasing levels of feral–wild admixture.

In this paper I combine head morphotype and flock-level plumage data to assess the validity of Hewson's 75% plumage threshold as a way of distinguishing Rock Doves and feral pigeons. I also infer the extent of feral hybridization among Rock Dove populations by using plumage variation as a proxy for domestic introgression, with the aim of providing a better description of the status of Rock Doves in the British Isles than has previously been possible. Finally, I compare records of plumage proportions collected by Hewson in the 1960s with those collected at the same locations as part of this study, in order to highlight the temporal progression of wild–feral hybridization in Rock Doves in Scotland.

METHODS

I examined flock plumage counts and head morphotype in birds from locations across the British Isles. Citizen scientist involvement in either counting birds of wild type and non-wild type plumage in a flock, or submitting a photograph for the author (W.J.S.) to count, was solicited through social media and local ornithological newsletters. Head morphotype was categorized by the author for birds in all 124 sites. Birds were categorized into the Rock Dove or feral pigeon head morphotype based on direct observations and photographic evidence. Photographs were supplied by citizen scientists, found on eBird and, in order to specifically target Rock Dove regions of interest, by searching for 'Rock Dove (s) + Scotland/Ireland (as well as individual island, region and location names) with Google, Facebook and Twitter. If head morphotypes varied within flocks, or individuals had a combination of traits of both forms, then they were categorized as 'intermediate/mixed' (Fig. 1a). To make the Rock Dove and feral pigeon morphotype classifications more objective, four traits were assessed (see also Fig. S1 for further comparisons of Rock Dove and feral pigeon head morphotypes).

A feral pigeon has:

- A swollen, fleshy cere, with the white part running up to, or past, the end of the nares.
- A flattened head shape with the top line of the forehead rising roughly in line with the top line of the bill.
- A thick, 'triangle-shaped', bill
- A pale/fleshy orbital ring surrounding the eye.

A Rock Dove has:

- A small cere, with the white part not running up to, or past, the end of the nares.
- A rounded head shape with the top line of the forehead rising well above the line of the top of the bill.
- A thin and long bill.

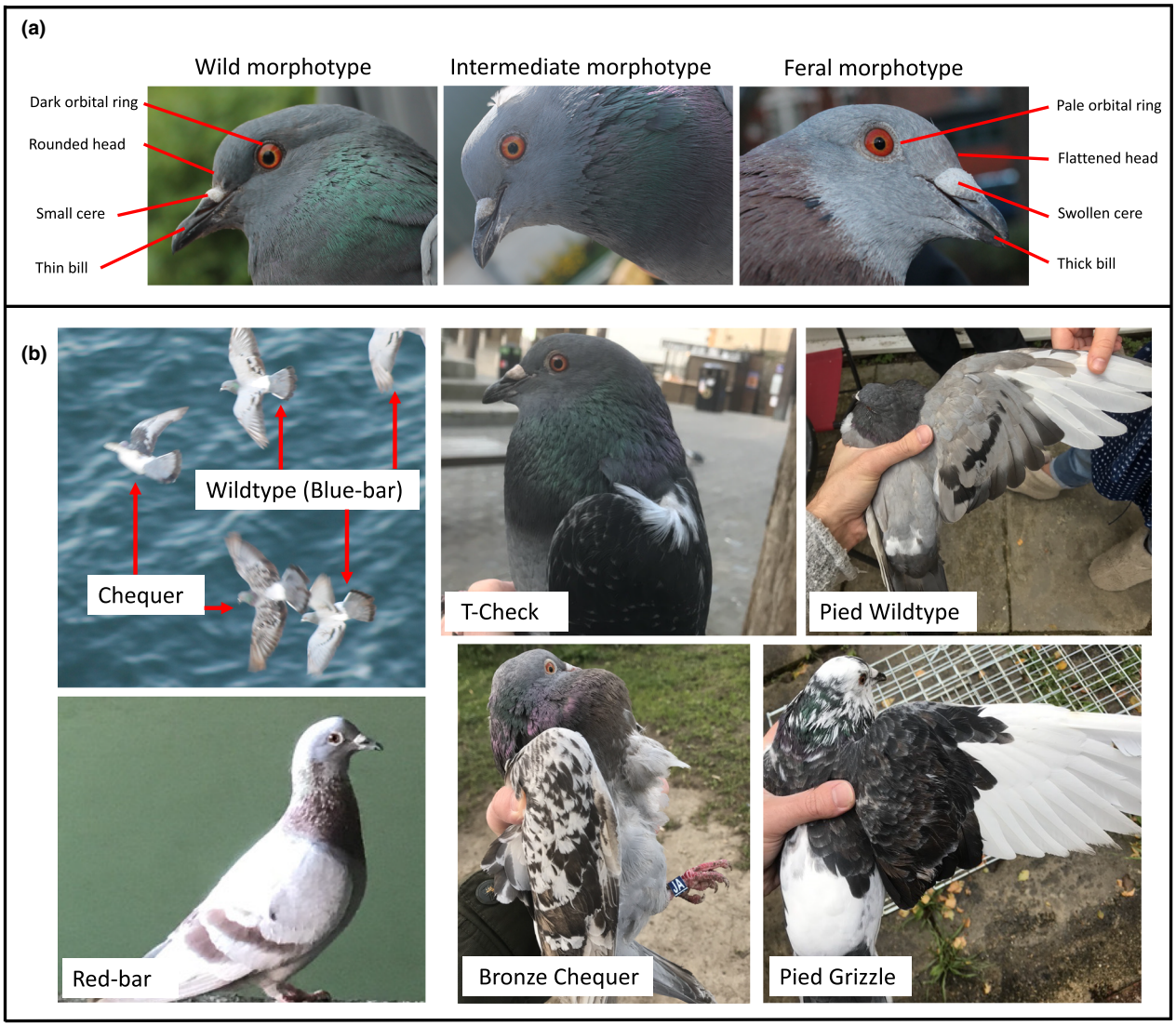

Figure 1. (a) Head morphology of *Columba livia* with key diagnostic features labelled. Wild bird is from Mull, Inner Hebrides, Scotland. Intermediate morphotype is from Mainland, Orkney, Scotland. Feral morphotype is from Leicester, England. (b) Common plumage morphs found in feral domestic pigeons, including those exhibiting the wild type plumage commonly found in wild Rock Dove populations. All photographs are from English feral pigeons. [Colour figure can be viewed at wileyonlinelibrary.com]

- A dark grey/thin orbital ring surrounding the eye.

For a bird to be categorized as belonging to the Rock Dove or feral pigeon morphotype, it must have all four traits. A minimum of three birds needed to be visible to determine head morphotype for a site. In practice, many more birds were usually visible and images or observations of as few as three birds' head morphotypes were only used when the overall count involved fewer than 10 individuals. Overall, site morphotype was based on assessing the head morphology of > 75% of individuals in 41% of flocks, 25–75% of individuals in 44% of flocks and < 25% of individuals in 15% of flocks.

At 100 of 124 sites (Figs 2 and 3), flocks of birds were observed to record plumage proportions. To prevent repeat counting of the same birds, multiple counts from the same site were not used. In cases where more than one flock was observed at the same site, the flock with the highest number of birds was used. To reduce the risk of counting the same birds at different sites (only a risk in the Outer Hebrides, Caithness and Orkney due to the higher density of counts in these

regions) I only used counts made within an hour of each other if the sites in question were > 10 km apart. The number of birds in each flock with wild type and non-wild type plumage ('flock plumage counts') was recorded (Fig. 1b). Flock plumage counts were collected by a combination of direct observations during fieldwork expeditions, photographs (collected as for head morphotype) and citizen scientist counts. Birds were surveyed at 124 locations (Fig. 2) between 2015 and 2020 (76 sites within and 48 outside the putative Rock Dove range), and flocks ranged from seven to 118 birds (mean flock count was 30 birds). Full location information and observation type are detailed in Table S1.

To determine the validity of Hewson's 75% plumage threshold, I assessed whether populations where the percentage of birds with wild type plumage was > 75% consisted of birds with the Rock Dove head morphotype rather than the feral pigeon or intermediate/mixed head morphotypes. I then mapped the presence of the Rock Dove head morphotype to depict the distribution of the Rock Dove. I also mapped plumage percentages to estimate variation in the level of feral introgression between different Rock Dove populations. Finally, I explored temporal change in plumage proportion to infer change in the level of introgression, by comparing the flock plumage proportions at sites where Hewson made a count in the 1960s with a repeat count made for this study between 2015 and 2020. These comparisons were made for either the same site or sites within 30 km of each other, given that 30 km is less than the normal diurnal movement between sites for this species (Baldaccini *et al.* 2000). For these historical comparisons, I excluded contemporary counts of feral pigeon populations in human settlements within the Rock Dove range (although such counts are included in the geographical assessment and the Hewson's threshold verification), as they were not noted by Hewson and so including them in temporal plumage proportion comparisons would have led to the inference of an exaggerated decline in the Rock Dove's genetic integrity. Using the raw counts, I used a two-proportion z-test with *prop.test* in R v4.0.2., and tested whether the proportion of birds with aberrant plumage types in the 1960s count for each site was less than the proportion of birds with aberrant plumage in the 2015–2020 count at the same site. I then plotted the percentages to visualize the changes.

RESULTS

Classifying flocks by Hewson's 75% threshold fully aligned with classifications based on head morphotype (Fig. 3). Where > 75% of birds in a flock had wild type plumage, individuals had the Rock Dove head morphotype (50 flocks). Below this threshold, populations were composed of individuals with only the feral head morphotype (43 flocks) or with an intermediate/mixed head morphotype (in seven flocks).

Within the Rock Dove range, there is considerable variation in the percentage of birds in flocks with wild type plumage (Fig. 2). In general, aberrant plumage morphs are less prevalent in populations further north and west, which are further from large feral pigeon populations. The only region where flocks of 100% wild type plumage were exclusively observed was the southern part of the Outer Hebrides (particularly in North Uist and South Uist). Outside the Rock Dove range, the only flock composed of > 50% wild type plumage was on Flamborough Head on the east coast of England, and this population was composed of birds with intermediate head morphology.

Of the 14 locations where a temporal comparison could be made between Hewson's and contemporary counts (2015–2020), nine had experienced an increase in the proportion of birds with non-wild type plumage. One region (Caithness) experienced a small (non-statistically significant) decrease from 17% to 13% non-wild type ($\chi^2 = 2.08$, $P = 0.07$, df = 1). Four regions, all islands with low feral pigeon presence, had no birds with aberrant plumage in either sample (Fig. 4). Only three of the nine sites where the proportion of birds with non-wild type plumage increased experienced a statistically significant change in the proportion of these birds present. These were North Ronaldsay (0–10%, $\chi^2 = 3.35$, $P = 0.03$, df = 1), Evie (7–16%, $\chi^2 = 2.90$, $P = 0.04$, df = 1) and north-west Sutherland (0–5%, $\chi^2 = 13.25$, $P = 0.0001$, df = 1). Despite this, at four of the nine sites, an increase from zero (in the 1960s) to a small handful of birds with aberrant plumage (in 2015–2020) is certainly biologically relevant.

DISCUSSION

In most species where extinction by hybridization has been studied, it is not possible to classify easily the different entities at a population level using phenotypic traits (Randi 2008, Senn *et al.* 2019). One reason for this is that the species are often not gregarious. Here, I show that it is possible to infer the presence of wild Rock Dove populations from field observations of flocks. This method does not require either the capture of birds or genomic analyses. It is amenable for citizen science and has the potential to be used over a wide area. I propose that it provides a useful tool to identify Rock Dove populations for more in-depth study, specifically where contemporary fronts of introgression occur.

Using flock assessments to infer geographical variation in the extent of introgression has allowed a more comprehensive and fine-scale coverage of the Rock Dove range than was possible in the recent genomic assessments. Genomic work shows that northern Scotland and

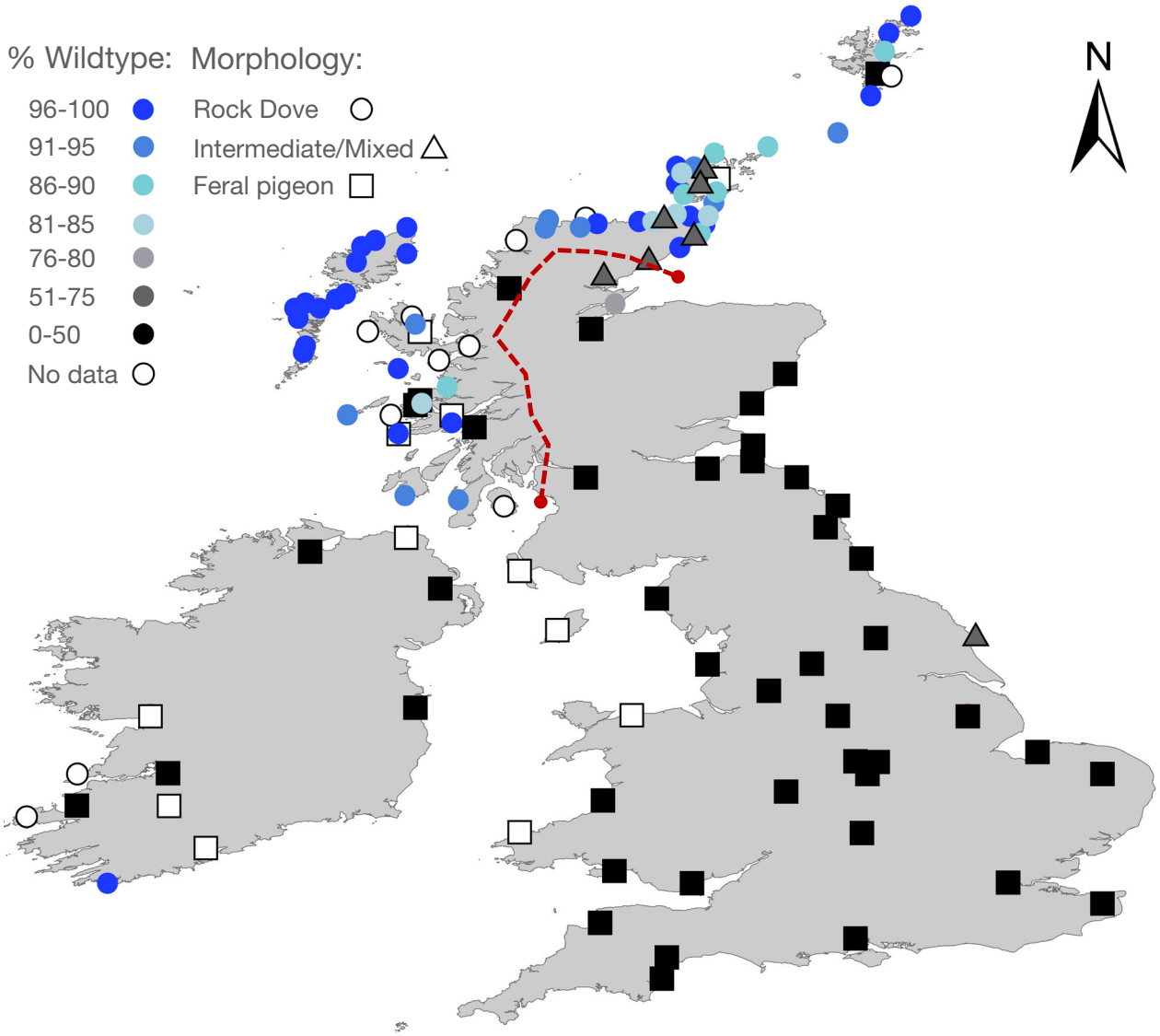

Figure 2. Locations of samples of Rock Dove and feral pigeon flocks that were assessed for this study, indicating both the percentage of birds with wild type plumage and head morphology. 'No data' indicates that the flock at that site was not large enough for the percentage of birds with wild type plumage to be useful. The putative limit of the Rock Dove's distribution in Scotland is indicated with a dashed line (Smith *et al.* 2022b). The putative range of the Rock Dove in Ireland is not well characterized but includes much of the western coastline. [Colour figure can be viewed at wileyonlinelibrary.com]

Orkney are home to hybrid swarms (Smith *et al.* 2022b). Our phenotypic assessments corroborate this, as there is variable morphology and wild type population plumage percentages in these regions. Within England, the count with the highest wild type percentage was from the feral pigeon colony at Flamborough Head – where Rock Doves are known to have persisted for longer than in the rest of the country (Johnston *et al.* 1988, Brown & Grice 2005). Populations of Rock Doves with low levels of feral introgression still predominate in the Inner Hebrides and Shetland. Significant populations with negligible signs of hybridization appear to be limited to the Outer Hebrides.

The assessment of flock plumage proportions could be used throughout the Rock Dove range to make a global appraisal of its hybridization status. This is important, as the species is currently classed as of Least Concern by the International Union for the Conservation of

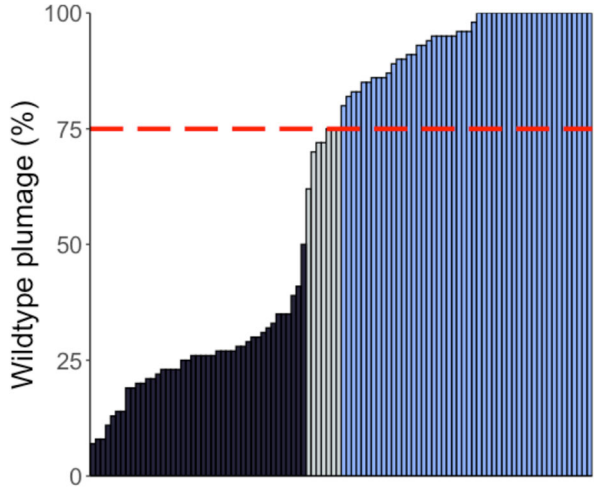

Figure 3. Percentage of birds with wild type plumage in individual flocks throughout the British Isles (n = 100). Each bar is an individual flock, colour-coded by head morphotype of birds within these flocks – from left to right: feral (black), intermediate/mixed (grey) and wild (blue). Hewson's 75% plumage threshold is indicated. [Colour figure can be viewed at wileyonlinelibrary.com]

Nature (IUCN). As a comparison, the European Rabbit *Oryctolagus cuniculus* is currently classed as Endangered as it is assessed based on its wild status, excluding its introduced populations. If the Rock Dove is shown to be as affected by introgression in North Africa, the Middle East and Asia as it is in Europe, then revision of its conservation status would be justified. To do this we would need to resolve the origins of different populations and to assess whether plumage proportions are valid for assessing provenance and inferring genetic integrity outside Europe (i.e. in subspecies other than the nominate *livia*). In some urban 'feral' populations, especially in the Middle East, there could be synanthropic Rock Doves (Baldaccini 2020). In contrast, many 'Rock Dove' populations could be domestic pigeons, as was the case with the previously claimed subspecies from Macaronesia and central Asia, now redesignated as feral pigeons (Vaurie 1961, Goodwin & Gillmor 1970). Resolving both issues would require genetic sampling, but mapping populations using flock percentages would be useful in identifying locations of interest.

At most of the revisited Hewson sites, there has been a decrease in the percentage of birds with wild type

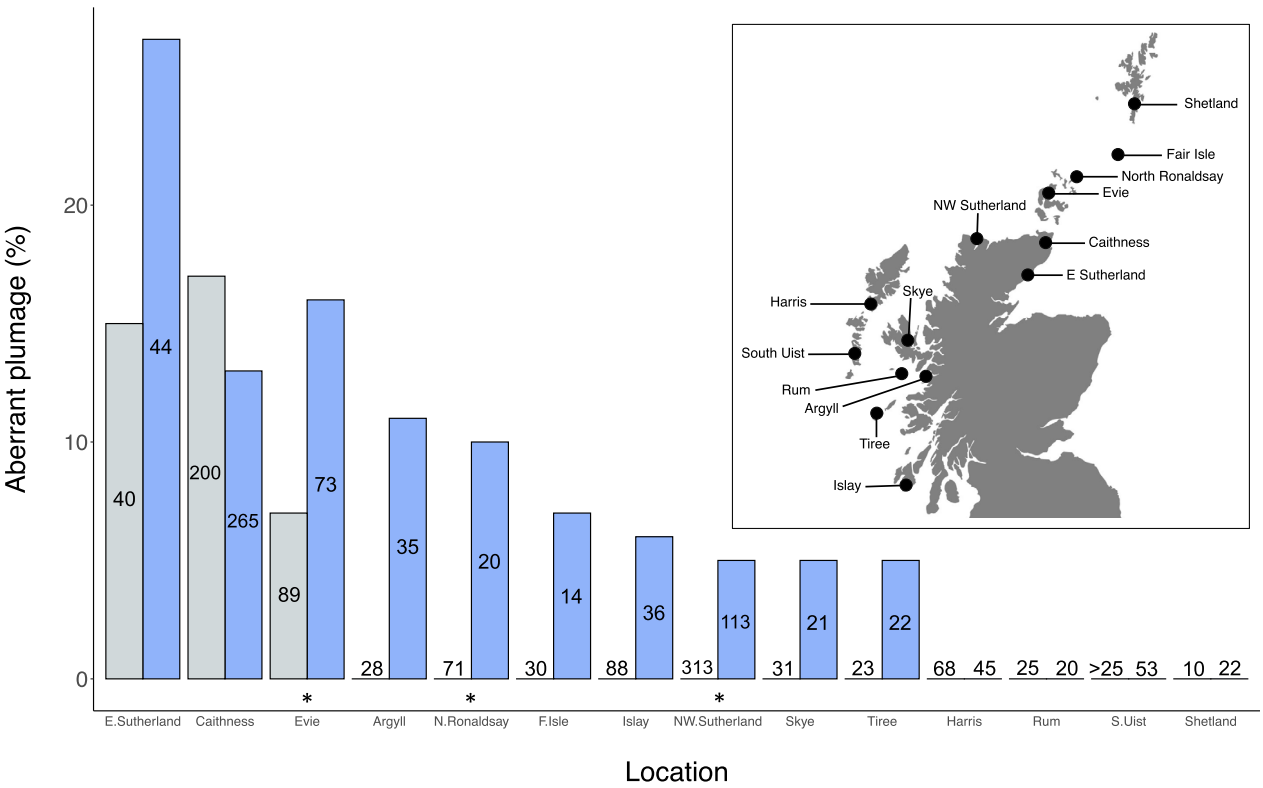

Figure 4. Change in the percentage of birds in flocks that exhibit aberrant (i.e. non-wild type) plumage. Grey bars represent Hewson's counts made in the 1960s. Blue bars represent counts in the present study, made between 2015 and 2020. The total number of birds used to estimate the percentage is recorded within the bars. The inset map shows the location of each region within Scotland, and an asterisk indicates statistical significance. [Colour figure can be viewed at wileyonlinelibrary.com]

plumage. This reflects high levels of domestic admixture, which will almost certainly, in the absence of conservation intervention, lead to the replacement of Rock Doves with birds of hybrid ancestry and eventually with feral populations, as predicted previously (Johnston *et al.* 1988) and observed in England, Wales (Brown & Grice 2010, Lovegrove *et al.* 2010) and, more recently, north-east Scotland and parts of Orkney (Smith *et al.* 2022b). The four individual sites where there was no evidence of introgression in either the 1960s or 2017–2020 are islands, but it is important to note that many islands, including Fair Isle, North Ronaldsay and Skye, held populations which showed evidence of admixture, indicating that although the relative isolation clearly delays contact, it is unlikely to prevent it in the long term.

CONCLUSIONS

Overall, I have shown that assessments of plumage are a valid method with which to identify Rock Dove populations and infer the level of domestic introgression that they have experienced. The Rock Dove in the British Isles experiences varying extents of genetic replacement, and in many locations, populations have been shown to have experienced declines in their genetic integrity. I have highlighted the generally unfavourable conservation status of these globally important populations. In making these assessments, I have highlighted the value of plumage polymorphism in making this system amenable to the study of extinction by hybridization.

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AUTHOR CONTRIBUTIONS

William J. Smith: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

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ETHICAL NOTE

None.

Data Availability Statement

All data are available in the Supporting Information for this article.

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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 Additional examples of Rock Dove/feral pigeon head morphotypes.

Table S1 Pigeon plumage data 2015–2020.