The undomesticated Rock Dove in Britain and the Isle of Man

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Abstract The domestic pigeon *Columba livia* has a close relationship with humans, both in captivity and in a feral state, the Feral Pigeon. The domestic pigeon's ancestor, the wild Rock Dove, is, however, something of an enigma: following extensive hybridisation with Feral Pigeons across its range (with many populations of Rock Doves becoming extinct by hybridisation with Feral Pigeons), little is known of its contemporary distribution, nor of the genetic purity of the remaining populations. Putative populations of wild Rock Doves have long been known to inhabit coastal regions of Britain and the Isle of Man but they have been subject to little research. This paper outlines the existing knowledge regarding the distribution and genetic status of Rock Doves in Britain and the Isle of Man, and assesses the likely impact of ongoing hybridisation on the continued persistence of the Rock Dove.

Introduction

The Rock Dove *Columba livia* is native to the Old World, including Europe, northern Africa, the Middle East, India and Central Asia (del Hoyo *et al.* 1997), and was amongst the earliest animals to be domesticated. The domesticated form was transported worldwide and, following releases and escape from captivity, the feral form, Feral Pigeon, became established across the globe. Feral Pigeons can be extremely numerous, especially in areas around human settlement, and have now replaced wild Rock Doves across most of their former native range (Johnston & Janiga 1995). Although Feral Pigeons occur in a multitude of different colours (and some individuals can exhibit plumage features common in captive domestic pigeons, such as fanned tails or feathered legs), some birds can closely resemble wild, ancestral-type Rock Doves (hereafter simply 'Rock Doves'). Rock Doves have slimmer bills, smaller ceres, less exposed skin on the face, and rounder heads than Feral Pigeons (Smith *et al.* 2022). Rock Doves are associated with coastal cliffs and rocky mountainous regions, but genetic contamination from Feral Pigeons – which can occur in similar habitats, especially in areas close to urban or agricultural areas – is threatening Rock Doves with extinction by hybridisation.

The pre-domestication range and population size of the Rock Dove is uncertain. The situation is complicated, since Rock Doves were likely to have been associated with agriculture – and thus areas of human habitation – even before their domestication. It has therefore been suggested that the species may have spread to much of what we consider to be its native range in the wake of the expansion of agricultural activity (Murton & Westwood 1966; Goodwin & Gillmor 1970), much like the House Sparrow *Passer domesticus* (Ravinet *et al.* 2018). Despite this, excavations in Gibraltar suggest coexistence with *Homo neanderthalensis*, which did not practise agriculture (Blasco *et al.* 2014). It is nonetheless likely that anthropogenic activities led to an increase in the range and population of the Rock Dove to at least some degree, especially in more northern regions; for example, the species is reported

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to have become extinct on St Kilda, Outer Hebrides, following the evacuation of the human population (Hewson 1967).

Rock Doves have been categorised into various subspecies, which primarily occur in a contiguous range from western Europe and northwest Africa to southern Asia (Vaurie 1961). Variation is mostly clinal and future genetic studies may lead to redesignation and the loss of a number of the more tentative subspecies. The nominate subspecies, *C. l. livia,* found wild in Europe, North Africa and the Near East, has a white rump, while the easternmost subspecies, the 'Indian Rock Dove' *C. l. intermedia*, has darker plumage and a grey rump (Goodwin & Gillmor 1970). Most other subspecies are intermediate between these two subspecies, although the desert forms (notably *C. l. dakhlae*) are distinctly paler, and *gymnocycla* of western Africa is dark grey with a broader red orbital ring than the other subspecies (Vaurie 1961). Subspecies described from Macaronesia (*atlantis* and *canariensis*) and Mongolia (*nigricans*), which are from areas disjunct from the species' main distribution, are now considered to be Feral Pigeons (Vaurie 1961; Goodwin & Gillmor 1970; del Hoyo *et al.* 1997), although it seems possible that Rock Doves were once native to parts of Macaronesia at least.

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69. Rock Dove *Columba livia*, South Ronaldsay, Orkney, July 2019. This bird was shown to have a degree of Feral Pigeon ancestry and is part of a feral-wild mixed population.

Estimation of the current range of 'genetically pure' Rock Doves – i.e. those populations that have not experienced significant genomic admixture with Feral Pigeons – is difficult, and even European populations of apparent Rock Doves have an unclear conservation status given the uncertainty of hybridisation with Feral Pigeons (Johnston *et al.* 1988; Baldaccini 2020). In Scotland, Hewson (1967) characterised populations as Rock Doves rather than Feral Pigeons if more than 75% of birds showed a wild-type plumage (blue-grey with two black wingbars and no black chequering on the wing). Similar inferences, most of which have not been followed up by genomic analyses, have led to the generally accepted understanding that, in Europe, populations of Rock Doves are restricted to relictual populations in north and west Scotland, western Ireland, the Faroe Islands and the Mediterranean region (particularly populations on coastal cliffs in Crete, Sardinia, Cyprus and Croatia) (Fr *et al.* 1949; Johnston *et al.* 1988). Apparent Rock Doves in Scotland make up a significant proportion of the European population and, as a consequence, are of conservation interest. Further study is required in the rest of Europe, but Rock Doves are reported to persist along the western coast of Ireland, and these populations are likely also of conservation importance, although the presence of Feral Pigeons within these areas was noted by Hutchinson (2010).

In this paper, I outline the evidence to support the identification of such populations as 'true' wild pigeons, and discuss what is known regarding their historical and

contemporary distribution. I highlight variation in the level of hybridisation occurring throughout the Rock Dove's range in Britain and the Isle of Man, including through work with genetics, and outline its relevance from a conservation perspective.

The changing status of the Rock Dove in Britain and the Isle of Man

Historical confusion with Stock Doves *Columba oenas*, as well as the ongoing issue of confusion with Feral Pigeons displaying a wild-type plumage and poor recording of this 'uninteresting' species, makes it difficult to accurately map the former distribution of Rock Doves (or Feral Pigeons, for that matter) in Britain and Ireland (Brown and Grice 2005; see also Balmer *et al.* 2013). Despite this, it is likely that, before the widespread presence of Feral Pigeons, Rock Doves were present along all suitable coastlines, including the cliffs of southern England and eastern Ireland. The species' range may have been almost contiguous around the British coast, with gaps only in regions such as East Anglia, where there is a lack of suitable nesting habitat. It is also possible that Rock Doves bred away from the coast in rocky habitat, such as the mountainous regions of inland Scotland and Wales, as they are known to do in other parts of their global range (Baldaccini 2020).

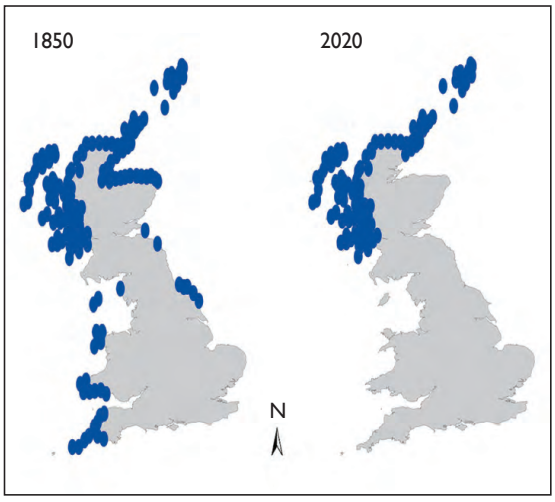


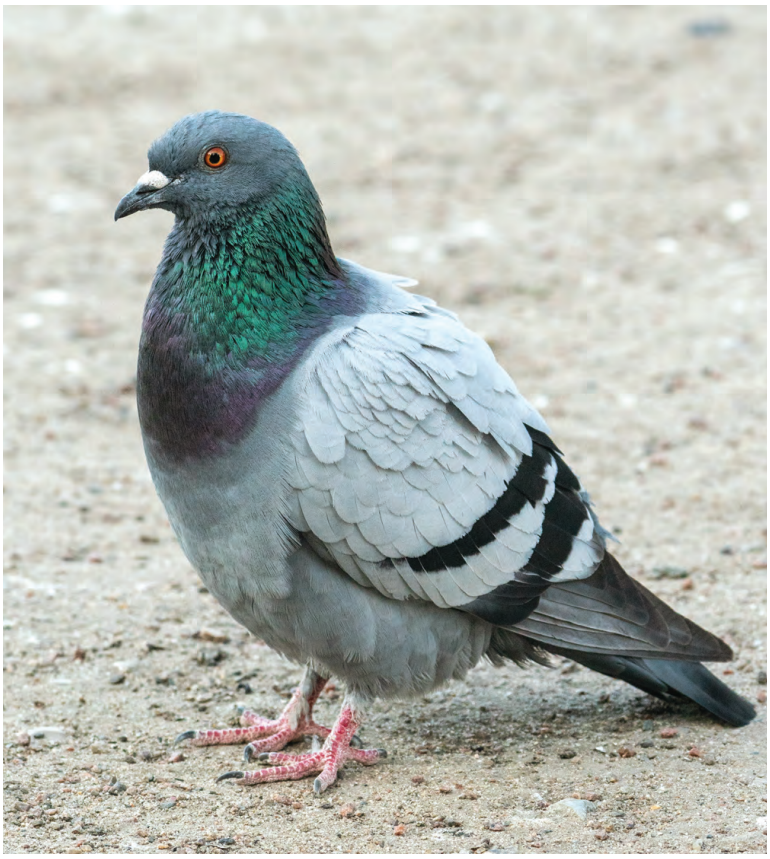
Fig. 1. The estimated range of the Rock Dove *Columba livia* in Britain and the Isle of Man in 1850 and in 2020. See text for discussion. Ireland's Rock Dove populations require further study in order to more accurately characterise the range of populations that now show signs of hybridisation with Feral Pigeons.

Despite some confusion over exactly which populations were wild and which were of domestic origin, Feral Pigeons were certainly well established in Europe by the early 1900s (Johnston & Janiga 1995) and Rock Doves had already been lost by hybridisation along vast tracts of European coastline, including in Britain and the Isle of Man (fig. 1). Saunders (1889) considered Rock Doves to be 'few and far between' in southern and eastern England and the Channel Islands, but present along the Welsh coastline, on the Isle of Man and at St Bees Head, Cumbria. The Rock Dove was also described as present at Flamborough Head/Bempton Cliffs, Yorkshire, which was historically likely to have been the largest colony in Britain, and in Northumberland, as well as at Bass Rock, Fife, and northwards, with the species reaching its highest densities in Scotland in Shetland, Orkney and the Outer Hebrides.

Populations in Devon and Cornwall persisted through the 1800s but were 'all but extinct' by the end of that century (Brown & Grice 2005). Despite extensive hybridisation with Feral Pigeons, the population at Flamborough/Bempton has retained many Rock Dove-like birds through the twentieth and into the twenty-first century. In Wales, the Rock Dove is described as having an unclear status during the late nineteenth century, with the last populations described as truly wild having been those on the cliffs of Pembrokeshire and Ramsey Island in the 1930s and 1940s (Lovegrove *et al.* 1994). Certainly, by the twenty-first century, the wild Rock Dove can be considered extinct in England and Wales following hybridisation with Feral Pigeons.

In Scotland, the range of the Rock Dove has undergone a significant reduction during the past 100 years, with extinction by hybridisation occurring along almost the entirety of Scotland's east coast, as far north as Caithness, where hybrid populations now predominate (Davey *et al.* 2015). However, Rock Doves are described as persisting on the islands of northern and western Scotland, as well as on the mainland from west of Caithness to Argyll (Thom 2010).

In the Isle of Man, Morris & Sharpe (2021) said that 'the "substitution" of this



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70. Feral Pigeon, Sweden, June 2021. A rather Rock Dove-like bird but which shows a swollen cere and feathered legs.

wild species [Rock Dove] by its domesticated form, Feral Pigeon, is one of the British Islands' overlooked ornithological tragedies', and Rock Dove appears to now be exinct from the island.

Ongoing hybridisation with Feral Pigeons

A genetic study by Stringham *et al.* (2012) showed that wild Rock Doves sit on their own branch of the species' phylogenetic tree, being genetically close to but distinct from domesticated forms and Feral Pigeons. The Rock Dove sampled in that study was from Skye, Highland; the study used just short fragments of genes (microsatellites) and did not look at possible hybridisation with Feral Pigeons.

In Smith *et al.* (2022), we examined genetic differences from across the full genome (rather than the short fragments of genes used in earlier work) of Rock Doves in Britain to determine which birds showed genetic influence from Feral Pigeons (i.e. clear signs of hybridisation) and which birds were pure Rock Doves (i.e. with little or no signs of hybridisation).

The results of this genetic study showed that a number of populations previously thought to consist of Rock Doves in fact consisted mostly of hybrids (individuals with mixed feral-wild ancestry, and not necessarily first-generation Rock Dove × Feral Pigeon hybrids): this was the case in Caithness and Orkney, where the populations appear to be 'hybrid swarms' – populations where hybridisation between the two parent forms is not necessarily ongoing but has resulted in a population consisting entirely of birds that have a mixture of Rock Dove and Feral Pigeon genes.

Despite this, some areas of Scotland still hold populations of Rock Doves that show little or no evidence of hybridisation with Feral Pigeons. The majority of birds in Shetland, Mull, Skye, Tiree and Islay showed only limited genetic evidence of hybridisation, despite a growing population of Feral Pigeons in, for example, Lerwick, Shetland. Birds sampled from the Outer Hebrides showed the least degree of hybridisation, with no individual sampled showing any significant evidence of past hybridisation with Feral Pigeons. This is reflected by visual observations: it is extremely rare to find any Rock Dove in the Outer Hebrides with plumage traits that deviate from the typical wild-type.

Given how little is known about the status and distribution of wild Rock Doves in Europe, and recent evidence of hybridisation in populations that were previously considered to be untainted by Feral Pigeons (e.g. Caithness and Orkney), the Outer Hebridean population is potentially of significant global importance for the conservation of the Rock Dove.

Factors affecting hybridisation

The complex pattern of geographic variation in the level of genetic admixture caused by hybridisation across Britain requires further study in order to understand its progression

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71. Rock Doves foraging on agricultural land, Berneray, Outer Hebrides, November 2021.

and predict its future dynamics. For example, gene flow can occur in two different contexts. In the first, lost racing or dovecote pigeons join wild Rock Dove flocks. This is observed across the entire range of the Rock Dove, including remote areas such as Shetland and occasionally the Outer Hebrides, although escaped birds typically do not persist in the population for long. In the second, range expansion by Feral Pigeons can bring their populations into contact with Rock Dove populations, as has happened in Caithness. It is unclear which mechanism is the most prevalent (although both will occur in tandem), and whether one is quicker at leading to feral-wild genetic admixing than the other. It is also unclear which factors might accelerate the rate of 'genetic replacement'.

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72. Rock Doves gathered on a ruined building, Vallay, Outer Hebrides, August 2020.

Disease transmission may also be a driving factor in the balance between Rock Doves and Feral Pigeons. *Trichomonas gallinae* is a disease that can be of great concern in endangered pigeons and doves globally (Bunbury *et al.* 2008; Marx *et al.* 2017). If infected Rock Doves experience a greater decline in their fitness than the potentially more genetically diverse, Feral Pigeon × Rock Dove hybrids, then this would give a selective advantage to the latter, which could facilitate the genetic replacement of Rock Doves with hybrids and Feral Pigeons.

Further study of the genomics and population dynamics of British and Irish Rock Doves will be necessary to resolve the complex progression of their gradual extinction by hybridisation. This should include research characterising the basic biology of the Rock Dove. For example, it is often written that Rock Doves are sedentary and rarely move. This is supported by BTO ringing recoveries, which have rarely been further than 10 km. However, extremely few Rock Doves are ringed every year (Robinson *et al.* 2022) and it's likely that many ringed birds are simply overlooked as likely being escapes from pigeon fanciers, which often also carry rings, although these are different in style from those used by the BTO ringing scheme. Consequently, we lack information on aspects such as juvenile dispersal and potential winter movements, though there is some anecdotal evidence for a degree of movement; for example, large flocks of Rock Doves have long been observed passing Fair Isle, perhaps moving between Shetland and either Orkney or Caithness (Lack 1986).

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73. Colour-ringed Rock Dove *Columba livia*, Vallay, Outer Hebrides, November 2021.

Future prospects

It seems inevitable that gene flow between Rock Doves and Feral Pigeons will continue. This, in turn, will cause further contraction of the range of 'true' Rock Dove populations. Already, Rock Doves in Caithness and much of Orkney can be considered to have gone extinct following hybridisation, as has previously happened in eastern Scotland, England, Wales, and many other areas of the Rock Dove's former native range. Attempting to reverse such trends would, given the significant populations of Feral Pigeons already in these areas, be exceptionally difficult. It is likely that efforts to reintroduce wild Rock Doves to locations where they have become extinct and could feasibly now sustain populations (e.g. the coasts of Pembrokeshire or Yorkshire) would be unsuccessful without continual removal of Feral Pigeons and continual monitoring to prevent new incursions. Any such populations would be completely conservation-dependent, which is not a desirable outcome. The only hope for expanding the British Rock Dove population would require a significant decline in the Feral Pigeon population.

Despite these challenges, it might be possible to conserve at least some of the existing Rock Dove populations. It is likely that in some regions, and particularly with respect to the large and relatively isolated population in the Outer Hebrides, monitoring for Feral Pigeon incursions and bans on keeping free-flying domestic pigeons would be sufficient to reduce gene flow and prevent extensive hybridisation. In regions where substantial Feral Pigeon populations are localised, such as Skye (in Portree), Mull (in Craignure and Tobermory) and Shetland (in Lerwick), complete removal of Feral Pigeons could be feasible. In Scotland, there is already a precedent for such conservation actions aimed at preventing

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74. Colour-ringed Rock Dove roosting in a ruined building, South Uist, Outer Hebrides, November 2021.

undesirable gene flow: Colonsay, Argyll, is designated as a protected area for a lineage of Honey Bee *Apis mellifera mellifera*, which is threatened by hybridisation with conspecifics in the rest of Britain (Muñoz *et al.* 2015). Likewise, various Hebridean islands act as designated 'refugia' for Red Deer *Cervus elaphus*, which are protected from gene flow with its introduced relative the Sika Deer *C. nippon* (Smith *et al.* 2018). Similar efforts could, relatively simply, maintain genetically diverse and self-sustaining populations of wild Rock Doves in Britain.

Acknowledgments

I would like to thank Michał Jezierksi, who read an early draft of this paper and provided useful comments.

References

Baldaccini, N. E. 2020. The synanthropic status of wild Rock Doves and their contribution to Feral Pigeon populations. *Rivista italiana di ornitologia* 90 (1). https://doi.org/10.4081/rio.2020.479

Balmer, D., Gillings, S., Caffrey, B. J., Swann, R. L., Downie, I. S., & Fuller, R. J. 2013. *Bird Atlas 2007–11: the breeding and wintering birds of Britain and Ireland*. BTO Books, Thetford.

Blasco, R., *et al*. 2014. The earliest pigeon fanciers. *Scientific Reports* 4: 5971.

Brown, A. F., & Grice, P.V. 2005. *Birds in England.* Poyser, London.

Bunbury, N., Jones, C. G., Greenwood, A. G., & Bell, D. J. 2008. Epidemiology and conservation implications of *Trichomonas gallinae* infection in the endangered Mauritian Pink Pigeon. *Biol. Conserv.* 141: 153–161.

Davey, P., Manson, S., Maughan, E., Omand, D., Smith, J., & Munro K. 2015. *Birds of Caithness*. Caithness SOC, Wick.

del Hoyo, J., Elliott, A., & Sargatal, J. (eds.). 1997. *Handbook of the Birds of the World*. Vol. 4. Sandgrouse to Cuckoos. Lynx Edicions, Barcelona.

Fr, N., Botni, P., & Williamson, K. 1949. Polymorphism and breeding of the Rock Dove in the Faroe Islands. *Ibis* 91: 17–23.

Goodwin, D. 1970. *Pigeons and Doves of the World*. 2nd edn. Trustees of the Brit. Mus. (Nat. Hist.), London.

Hewson, R. 1967. The Rock Dove in Scotland in 1965. *Scott. Birds* 4: 359–371.

Hutchinson, C. 2010. *Birds in Ireland.* A&C Black, London.

Johnston, R. F., Siegel-Causey, D., & Johnson, S. G. 1988. European populations of the Rock Dove *Columba livia* and genotypic extinction. *The American Midland Naturalist* 120: 1–10.

—, & Janiga, M. 1995. *Feral Pigeons*. OUP, Oxford.

Lack, P. 1986. *The Atlas of Wintering Birds in Britain and Ireland.* T. & A. D. Poyser, Calton.

Lovegrove, R., Williams, G., & Williams, I. 1994. *Birds in Wales*. Poyser, London.

Marx, M., *et al.* 2017. High prevalence of *Trichomonas gallinae* in wild columbids across western and southern Europe. *Parasites Vectors* 10: 242. https://doi.org/10.1186/s13071-017-21-70-0.

Morris, N. G., & Sharpe, C. M. 2021. Birds of Conservation Concern in the Isle of Man. *Brit. Birds* 114: 526–540.

Muñoz, I., Henriques, D., Johnston, J. S., Chávez-Galarza, J., Kryger, P., & Pinto, M. A. 2015. Reduced SNP panels for genetic identification and introgression analysis in the Dark Honey Bee (*Apis mellifera mellifera*). *PLOS ONE* 10 (4): e0124365.

Murton, R., & Westwood, N. J. 1966. The foods of the Rock Dove and Feral Pigeon. *Bird Study* 13: 130–146.

Ravinet, M., Elgvin, T. O., Trier, C., Aliabadian, M., Gavrilov, A., & Sætre, G-P. 2018. Signatures of human-commensalism in the House Sparrow genome. *Proc. R. Soc. B.* 285: 20181246.

Robinson, R. A., Leech, D. I., & Clark, J. A. 2022. The Online Demography Report: bird ringing and nest recording in Britain & Ireland in 2021. BTO, Thetford. www.bto.org/ringing-report

Saunders, H. 1889. *An Illustrated Manual of British Birds*. Gurney and Jackson, Bath.

Smith, S. L., Senn, H.V., Pérez-Espona, S., Wyman, M.T., Heap, E., & Pemberton, J. M. 2018. Introgression of exotic *Cervus* (*nippon* and *canadensis*) into Red Deer (*Cervus elaphus*) populations in Scotland and the English Lake District. *Ecol. & Evol.* 8: 2122–2134.

Smith, W. J., Quilodrán, C. S., Jezierski, M.T., Sendell-Price, A.T., & Clegg, S. M. 2022a. The wild ancestors of domestic animals as a neglected and threatened component of biodiversity. *Conserv. Biol.* 36: e13867.

—, *et al*. 2022b. Limited domestic introgression in a final refuge of the wild pigeon. *iScience* 25: 104620.

Stringham, S. A., *et al*. 2012. Divergence, convergence, and the ancestry of feral populations in the domestic Rock Pigeon. *Curr. Biol.* 22: 302–308.

Thom, V. M. 2010. *Birds in Scotland*. T. & A. D. Poyser, Calton.

Vaurie, C. 1961. *Systematic Notes on Palearctic Birds. No. 48, Columbidae, the genus* Columba. *American Museum novitates; no. 2043*. American Museum of Natural History, New York.

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