

On the Origin and Spread of Feral Pigeons

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The rock pigeon *Columba livia* Gmelin, 1789 is presumed native to the Mediterranean, Saharo-Arabian and Eastern Oriental regions, and is believed to have been domesticated in the Middle East in the early Neolithic. At some point during the domestication process, the first feral pigeons arose, whose populations subsequently undertook a remarkable expansion that has resulted in them being found today across almost the entire global urban landscapes. Indeed the spread of these feral birds has been so prolific, that it raises questions about whether any true wild rock pigeon colonies still exist, or whether they have been admixed with, or even fully replaced, by feral birds? While several studies have investigated the complex evolutionary history of pigeon breeds, none have yet addressed the question of pigeon feralisation, and how this evolutionary process might be jeopardizing the species' status as a wild entity. In this study, we generated and analysed a genomic dataset produced using the Genotyping-by-Sequencing (GBS) method of 450 feral pigeons sampled across 41 worldwide localities. Our analyses reveal that the global feral pigeon population can be divided into four major groups, each exhibiting different levels of genetic diversity and contamination with domesticated genotypes. We also find signs of strong population structure, including very divergent clades of what seems to be relatively wild populations. Lastly, we find evidence of human-mediated dispersal through past colonial links.

Archaeological evidence suggests that the rock pigeon (*Columba livia* Gmelin, 1789), and in particular the (*C. l. livia*) subspecies, was first domesticated during the Neolithic period in the Middle East, probably via a commensal pathway². While it was initially exploited as a source of food and fertiliser, later on, the extent of its service to humankind spanned a wider variety of roles, including incorporation into religious rituals, a tool for communication, a source of medicine, and even as a navigation aid³. Furthermore, in addition to its practical functional roles, and in parallel with many other domestic animals such as dogs, chickens and cats, the eighteenth century witnessed an explosion of interest in the development of so-called fancy breeds. Such interest led to the establishment of numerous pigeon breeds, of which over 230 are currently recognised by the *American National Pigeon Association* (NPA; www.npaula.com). Artificial selection in modern breeds resulted in a truly fabulous amount of phenotypic diversity, which has long attracted the attention of scholars, and even formed a cornerstone of Darwin's nascent thoughts on his famous theory concerning the evolutionary processes [1].

The history of the pigeon domestication has also been tightly coupled with a correlative evolutionary process—feralisation. The process of feralisation is thought to have begun through domestic pigeons escaping from captive

stocks (kept within Europe, North Africa and Western Asia). As to the ecological niche of their wild ancestors, feral pigeons tend to utilise hardscape habitats as urban analogues of rocks/cliffs (Lundholm and Richardson, 2010) and become a synurbic species (Francis and Chadwick, 2012). As with other feralised domesticates, the species experienced an extreme ecological range expansion much later in time, when during the modern colonial period they were transmitted to, and subsequent release across, almost all continents of the world, successfully populating extensive urban areas. Therefore, at present, the feral pigeon is ubiquitous across the world's urban landscapes, where it is often considered a pest species requiring active management. Furthermore, given that both domestic and feral pigeons can almost certainly still interbreed with their wild ancestor, it has been proposed that in regions of co-occurrence, the wild rock pigeon gene pools (and thus their integrity as a natural species) might be to some extent contaminated with domestic genotypes as has been demonstrated for other domestic species^{5,6}.

Although studies aiming to shed light on the genomic relationships among pigeon breeds have been conducted^{7–9}, fundamental questions concerning today's feral pigeon populations have yet to be addressed in depth. These include i) which breeds principally contributed to the formation of the feral pigeon populations, and ii) which are the genomic

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relationships among these populations. Additionally, in light of the global expansion of both domestic stocks and feral populations during the past few centuries, and a third key question is iii) whether the wild rock pigeon has undergone a process of genomic extinction as seen with the wild ancestors of other domesticates^{6,10}.

In this study, we employed the Genotyping-by-Sequencing (GBS) method to generate a genomic dataset for 450 free-living pigeons from 41 localities covering a world-wide distribution, as well as XXX pigeons representing other subspecies/species^{??}. We use this dataset to reconstruct the phylogenetic relationships among these populations, as well as to investigate their patterns of both genetic structure and

diversity revealed by analyses of MDS, Admixture and population genetics statistics.

We hypothesize that populations inhabiting remote localities within the believed natural range will show the lowest levels of contamination with domestic genotypes, while those populations inhabiting urban localities within the believed natural range will have moderate signals of admixture with domesticates. Besides, those populations outside the natural range will show the highest levels of influence by domestic genotypes, and, given that these populations were formed through human-mediated dispersals, we also expect that there will be a signal linking former colonies-colonizers relationships (e.g. London and Johannesburg).

Results

Sampling effort. To investigate the genomic patterns of current pigeon populations of different evolutionary histories, we intentionally targeted our sampling to cover four distinct categories (Figure 1). Furthermore, to help root the evolutionary relationships between these groups, we also included a small number of individuals representing the *Columba livia intermedia* (Strickland, 1844) subspecies. Specifically in this regard, we sampled five populations from Sri Lanka, where two of them were from urban localities (Colombo and Trincomalee), one was from a Conservation National Park (Pigeon Island) and two others were captive populations maintained by local breeders (Wattala and Wellawatte) (Supplementary Fig. 1). To check for data reproducibility, we sequenced two of the samples twice (Tehran_16-GBS and Perth_02-GBS) to serve as replicates. Finally, to serve as external outgroups,

we also generated data from five samples of (*Columba palumbus Linnaeus*, 1758) captured in Copenhagen (Denmark), one captive sample of (*Streptopelia risoria Linnaeus*, 1758), and additionally incorporated previously published whole genome resequence data from a *Columba rupestris*⁸. (we also included the WGS library to serve as another replicate) (Supplementary Spreadsheet).

Sequencing data and filtering.

Population genetics statistics.

Phylogenetic relationships among feral pigeon populations.

Population structure among pigeon populations.

Contribution of pigeon breeds to current non-domesticated populations.

Discussion

Methods

Sequencing data generation and processing.

Data analysis.

Population genetics statistics.

Phylogenetic reconstruction.

Inference of Population Structure.

Contribution of pigeon breeds to current non-domesticated populations.

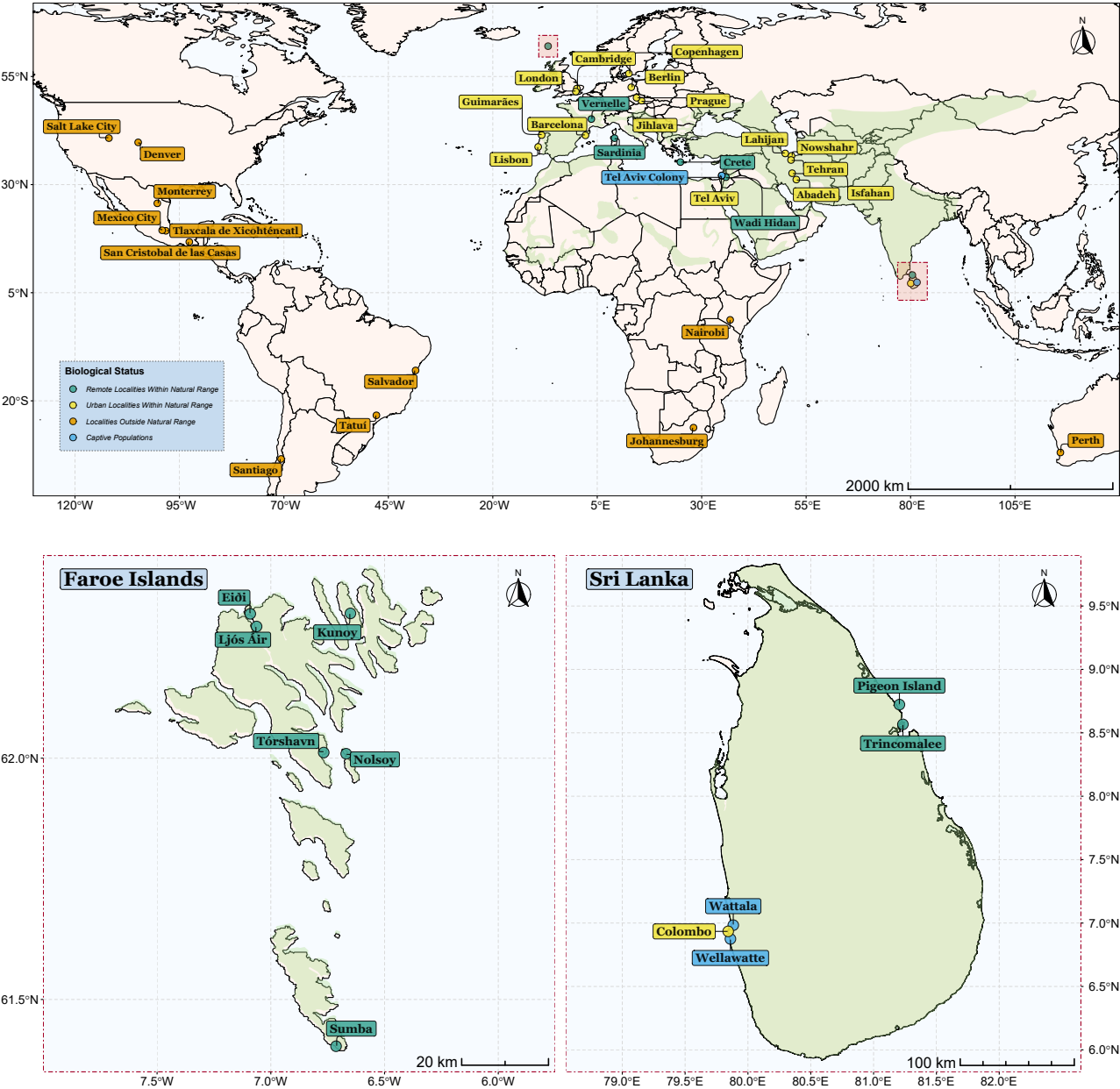


Fig. 1 Map of sampling effort. This is a trial attempt.

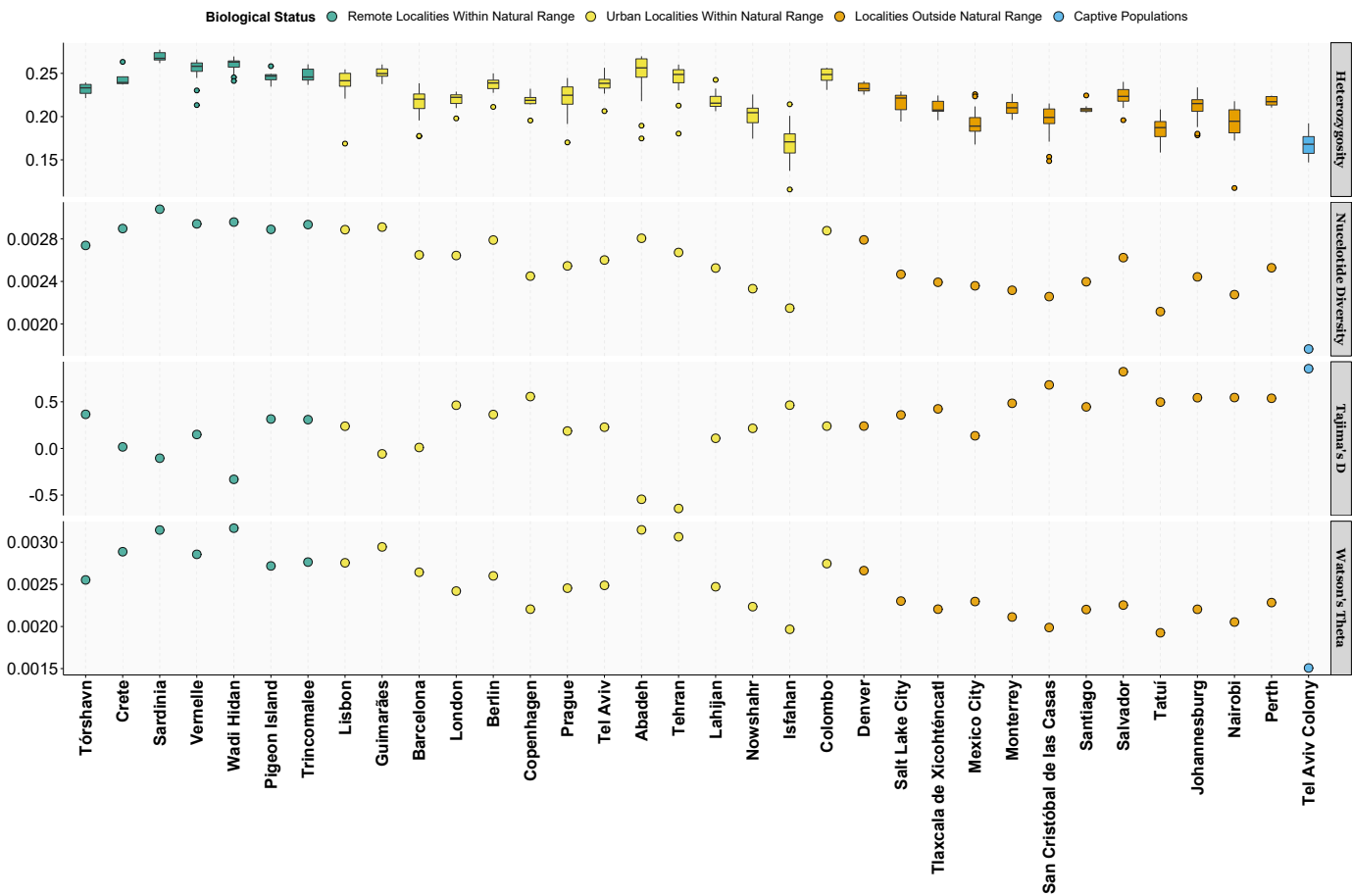


Fig. 2 Map of sampling effort. This is a trial attempt.

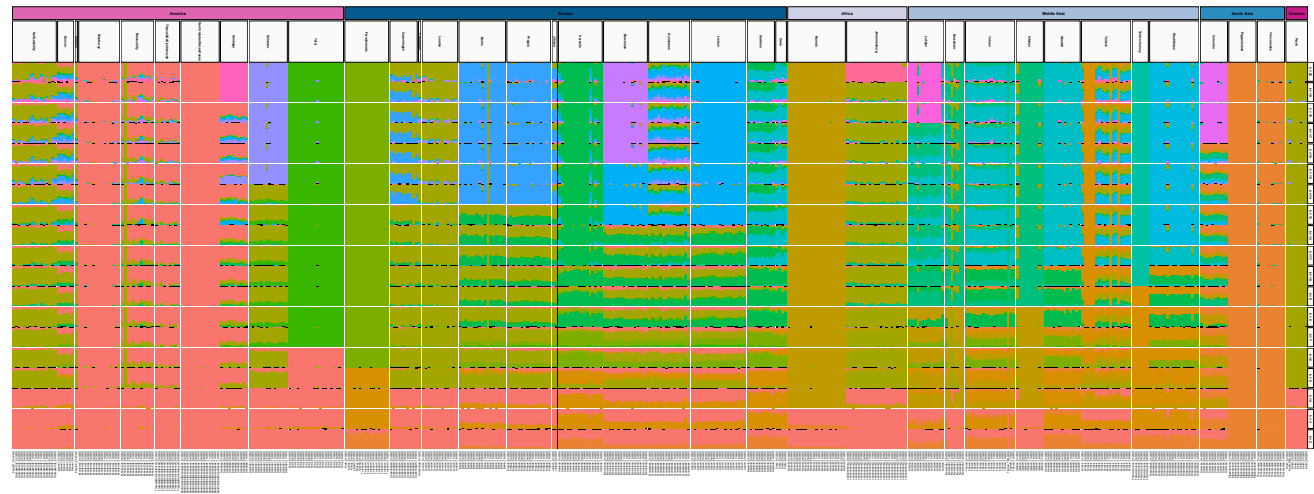


Fig. 3 Map of sampling effort. This is a trial attempt.

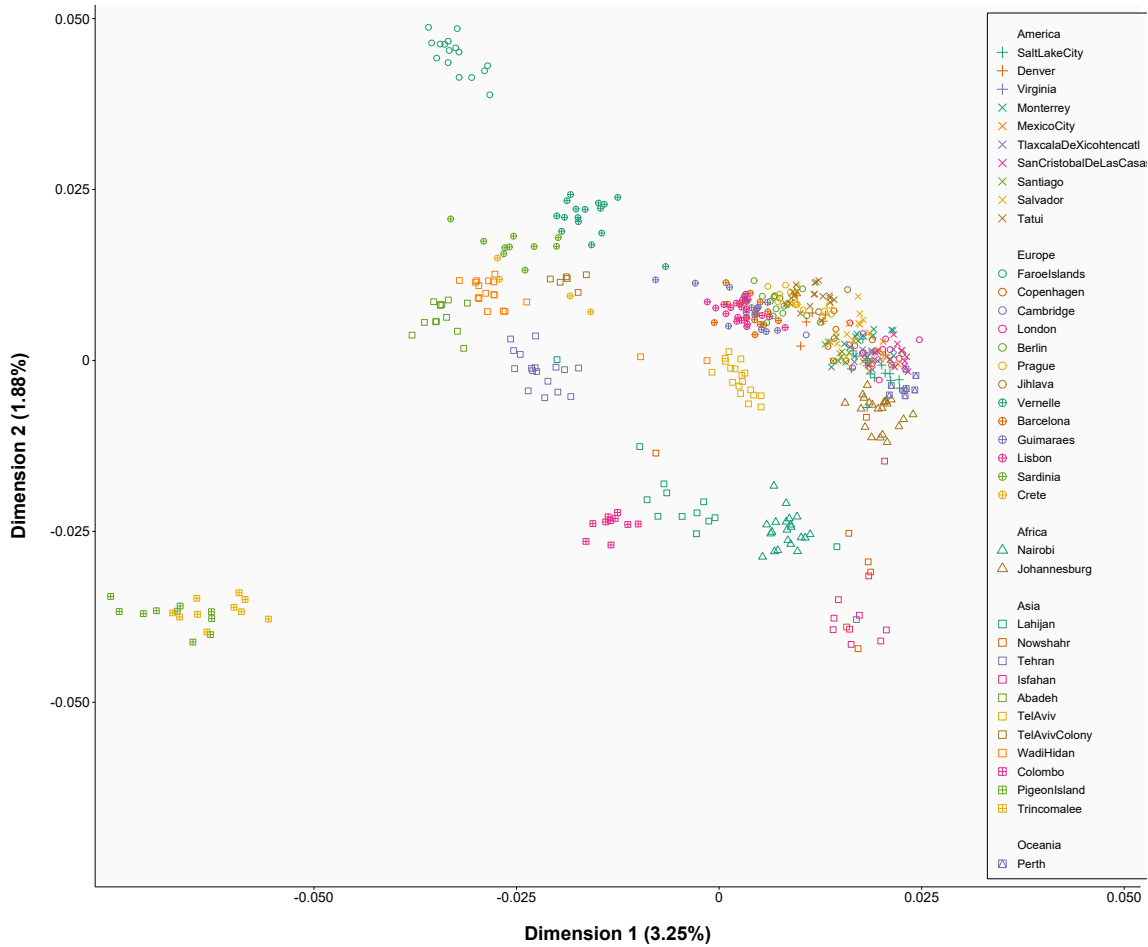


Fig. 4 Map of sampling effort. This is a trial attempt.

References

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Data Availability

All demultiplexed GBS sequencing data is publicly available at SRA (Project Number: PRJNA495951), as well as additional data uploaded to the University of Copenhagen's long term storage (https://sid.erda.dk/wsgi-bin/lis.py?share_id=aKqQoJvH4Y).

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Author Contributions

M.T.P.G. conceived the project and obtained financial support. M.T.P.G., G.P. and F.G.V. designed the study. G.P. led the project. M.T.P.G., G.P., M.T.O., T.dF.R., P.H., P.N., C.S., I.L.R., S.S.S., K.M., C. L.-F., G.S., R.F., J.D.,

J. F., N.H., F.K., R. D., A.H., M.B.A. M. C. A.-A. and P. R. E. contributed to sampling. M.D.S. collected and provided the breed samples. G.P. performed the vast majority of DNA extraction and QC. K.M. performed DNA extraction and QC on Sri Lanka samples. G.P. and F.G.V. conducted the computational analyses assisted by M.D.M. G.P., F.G.V., M.T.O. and M.T.P.G. interpreted the results. G.P. wrote the first draft of the manuscript with great input from M.T.P.G. and F.G.V. All authors critically reviewed and approved the final manuscript.

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Competing Interests

We have no competing interests.