Ornithology, 2024, 142, 1–8
https://doi.org/10.1093/ornithology/ukae050
Insight

Ornithology

OXFORD

Use of anthropogenic landscapes in a wild *Columba livia* (Rock Dove) population

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ABSTRACT

Despite the role of many domestic animals as model organisms, our understanding of their undomesticated conspecifics is comparatively poor. This limits our ability to infer the eco-evolutionary context of phenomena studied in the laboratory and to explore domestication. The domestic pigeon's wild form is the Rock Dove (*Columba livia*). By studying 5 global positioning system–tagged wild Rock Doves in Scotland's Outer Hebrides, we present the first individual-level assessment of undomesticated Rock Dove movements, revealing extensive use of anthropogenic habitats in both a roosting and foraging context. This association with humans provides tantalizing opportunities for research into the pre-domestication human–pigeon relationship. More generally, this work highlights the value of researching laboratory model species in nature.

Keywords: *Columba livia*, domestication, movement ecology, pigeons, synanthropism

How to Cite

Smith, W. J., S. J. Portugal, and M. T. Jezierski (2024). Use of anthropogenic landscapes in a wild *Columba livia* (Rock Dove) population. Ornithology 142:ukae050.

LAY SUMMARY

- Despite the importance of laboratory model organisms, our understanding of their wild forms is comparatively poor.
- Researching the wild forms of model organisms could enhance our understanding of the ecological and evolutionary context of phenomena studied in captivity.
- Here we describe individual-level movements of Rock Doves (*Columba livia*), the wild form of domestic pigeons (a model organism in behavioral research).
- We outline the movements of 5 global positioning system–tagged birds from Scotland's Outer Hebrides, where Rock Doves rarely interbreed with domestic pigeons.
- We show that all individuals were closely associated with humans in both a roosting and foraging context, providing insights into this species' pathway into domestication.

Utilisation des paysages anthropiques par une population sauvage de *Columba livia*

RÉSUMÉ

Malgré le rôle de plusieurs animaux domestiques comme organismes modèles, notre compréhension de leurs congénères non domestiqués est assez limitée. Cela limite notre capacité à déduire le contexte éco-évolutif des phénomènes étudiés au laboratoire et à explorer la domestication. La forme sauvage du pigeon domestique est le pigeon biset (*Columba livia*). En étudiant 5 individus sauvages de *C. livia* marqués par GPS dans les Hébrides extérieures écossaises, nous présentons la première évaluation au niveau individuel des mouvements de *C. livia* non domestiqué, révélant une utilisation extensive d'habitats anthropiques dans des contextes de repos et de recherche alimentaire. Cette association avec les humains offre des opportunités intéressantes pour la recherche sur la relation homme-pigeon avant la domestication. Plus généralement, ce travail met en évidence la valeur de la recherche sur les espèces modèles de laboratoire dans la nature.

Mots-clés: *Columba livia*, domestication, écologie des déplacements, pigeons, synanthropisme

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Submission Date: June 11, 2024. Editorial Acceptance Date: September 19, 2024

INTRODUCTION

Domestic pigeons originate from the neolithic domestication of Rock Doves (both *Columba livia*) (Johnston and Janiga 1995). Today, domestic pigeons represent a source of recreation (Baker 2013) and food (Chang et al. 2023), and are used to study cognition (Watanabe 2001), collective behavior (Dell'Ariccia et al. 2008), navigation (Benvenuti and Wallraff 1985), and social hierarchies (Portugal et al. 2017). Their superabundant and cosmopolitan 'feral pigeon' descendants are used to study urban evolution (Carlen and Munshi-South 2021), phenotypic polymorphism (Hetmański and Jarosiewicz 2008), epidemiology (Nebel et al. 2020, Nimri 2019, Scaglione et al. 2015), and human–wildlife interactions (Capoccia et al. 2018). Such attention has not been afforded to wild, undomesticated Rock Doves, which live in coastal/mountainous areas of Afro-Eurasia, and usually nest and roost in caves (Goodwin and Gillmor 1970). Scientists have suggested that this lack of attention may be because of (1) the "remoteness" of colonies (Johnston and Janiga 1995) and (2) ongoing wild–feral hybridization, which made it unclear whether "true" undomesticated Rock Doves still persisted and led to a lack of interest in putative populations, which were dismissed as "wild-feral hybrids" (Smith et al. 2022a). Although genetically distinct Rock Doves may persist in various regions around the world (Johnston et al. 1988, Smith 2023b), it is difficult to morphologically distinguish them from feral/hybrid individuals (Smith 2023a). The only contemporary undomesticated Rock Dove population that has been genetically confirmed to have experienced negligible wild–feral genetic admixture exists in the Outer Hebrides of Scotland (Smith et al. 2022b).

The value of studying the "wild" forms of model species is increasingly recognized (Alfred and Baldwin 2015). Although there are known behavioral and morphological differences between wild and domestic rats (*Rattus norvegicus*) (Modlinska et al. 2015, Stryjek et al. 2012) and mice (*Mus musculus*) (Renaud et al. 2024, Savriama et al. 2022, Vogt et al. 2024), comparisons are mostly made in captivity. Model organism research rarely incorporates an understanding of their wild context, reducing our ability to generalize beyond the laboratory (Alfred and Baldwin 2015). Given that domestic pigeons are used in studies of movement (Biro et al. 2006, Portugal et al. 2017, Sasaki and Biro 2017), wild-living Rock Doves could provide a natural context within which to understand the ecology and evolution of avian navigation, flocking patterns, and general movements.

The first attempts to quantify wild Rock Dove movements were based on flock observations at Capo Caccia, Sardinia (Baldaccini et al. 2000). While feral pigeon intrusion (Baldaccini 2020, Skandrani et al. 2016) renders this colony less representative of wild birds, these studies have demonstrated the nature of the species' characteristic "commuting flights" (Goodwin and Gillmor 1970). These twice-daily commuting flights represent foraging movements (i.e., crossing unsuitable foraging habitats, such as moorland or forest, to move between roosting and feeding sites), rather than nomadism or migration as had been previously thought (see e.g., Toschi 1939). Within the Outer Hebrides, Rock Doves are common in Uist (Gray 1871, Smith 2023b), where they feed on seeds (Anderson 1913) and potentially snails (Gray 1871, Harvie-Brown et al. 1888), and roost/nest in caves (Beveridge 1911, Cunningham 1979). Many roost on the rocky east coast, commuting west (over moorland) to forage within *machair* and surrounding agricultural land (Guthrie 1920). Machair is a type of meadowland sustained by low-input agriculture, found within a wider arable/pasture matrix along parts of the Atlantic fringe of the British Isles (see Angus and Dargie 2002). Putative Rock Dove commuting flights are regularly observed, both within Uist and between Uist and its outlying islands; the Monach Isles (Hepburn et al. 1977, Outer Hebrides Natural History Society 2014) and Haskeir (Harvie-Brown et al. 1888, Ritchie 1920, Outer Hebrides Natural History Society 2004).

Currently, many Rock Doves in Uist occupy human structures (usually derelict houses but also modern barns) (e.g., MacDonald 2014). This is likely a recent occurrence in Uist, at least as a frequent behavior, since buildings from the 1900s (see Course 2019) are taller, representing safer roosts when derelict than the older (and shorter) "blackhouses" (see Hance 1951). Whereas wild, undomesticated Rock Doves around the world have long been known to inhabit buildings where available (e.g., a castle on Kerrera, Scotland; Johns and Owen 1882), older references from Uist (e.g., Beveridge 1911, Elton 1938, Kearton 1895, Peel 1901, Buchanan 1883, MacGillivray 1841) only describe them as cave-nesters. This is a particularly notable omission given that *Passer domesticus* (House Sparrow; Harvie-Brown et al. 1888, MacGillivray 1841) and *Sturnus vulgaris* (European Starling; Beveridge 1918) were said to use buildings. Historical hunting pressure (Peel 1901) may also have prevented roosting in the west, where the human population is (and has long been) highest (killing wild Rock Doves, as opposed to feral pigeons, is now illegal in the UK). Today, because most derelict buildings are in the west (adjacent to farmland), it is possible that some birds cease commuting (i.e., they can roost and nest directly within their feeding areas, without having to cross areas of habitat that are unsuitable for foraging). This is common in feral pigeons, which often roost in buildings and forage within a kilometer radius (Johnston and Janiga 1995). Although human-associated Rock Doves, in general, have been discussed before (Baldaccini 2020), unknown levels of wild–feral–domestic admixture across the world have made this difficult to quantify. Uist's unadmixed population provides a rare opportunity to identify anthropogenic associations in a population that has escaped extensive feral and domestic influence.

Individual-level Rock Dove movements remain to be studied. Global positioning system (GPS) tracking (e.g., Rose et al. 2006b, Rose et al. 2006a) has been used to study feral pigeons, but not wild, undomesticated Rock Doves. Here, we perform the first characterization of individual-level movements in wild Rock Doves, to test for the existence of "resident" individuals that have ceased the regular commutes that are considered to be a characteristic behavior of this species. We GPS-tracked 5 doves to investigate daily movements by calculating home ranges and distance traveled. We also examine habitat use to test for associations with anthropogenic structures. This allows us to discuss the potential role of this human association in the incipient domestication of this species, and the importance of work on wild Rock Doves to developing *C. livia* as a model organism.

METHODS

Since 2019, we have been monitoring Rock Doves in Uist. For this study, we focused on a small colony (of around 3 resident pairs) at Clachan Farm, North Uist (57.669417,

–7.230342). Here, doves roost in a stone building within agricultural land. Nesting happens at the site each year (*C. livia* can breed throughout the year, but birds in Uist generally avoid nesting from November to March), but there were no active nests during our GPS-tagging visit. We used NANO tags, which transmit data to a base station (HUB) (Interrex, Poland). Seven birds were caught and tagged before midnight on July 10, 2023. Five had been genetically sexed as part of their inclusion in prior studies (Smith and Clegg 2023, Smith et al. 2022b, 2023). We attached GPS tags using Araldite (see Urquia-Samele and Portugal 2022). Based on trials with domestic pigeons, we expected tags to fall off after a few weeks. The tag (3.7 g), Araldite (<0.5 g), metal (0.78 g), and color (0.3 g) rings, fell below 3% of body mass (see Portugal and White 2022 for discussion on this threshold). Tags recorded location every 2 hr (the BOOST option enabled more regular localization when solar charging allowed, up to one per minute). The HUB failed and was not fixed until September 08, 2023 (by which time tags had fallen off). We obtained data from 5 tags using the *Ecotopia* phone app (Druid, Shenzhen, China) as a backup, on July 13, 2023, and August 11, 2023. The mobile phone application has a significantly lower detection and download range than the HUB (~50 m as opposed to ~1,000 m), which likely explains why we did not get data from the 2 remaining birds. Five birds have been recaptured so far, in good condition, during subsequent visits (carried out as part of our long-term mark–recapture study of the Uist Rock Dove population). This is a satisfactory recovery rate and suggests minimal impact of the tags on the doves.

We used R v. 4.2.3 (R Development Core Team 2010) for data processing, with *tidyverse* v. 2.0.0 (Wickham et al. 2019) and *sf* v.1.0-15 (Pebesma 2018). We filtered the dataset to remove fixes using <3 satellites, and with high (>4) horizontal and vertical dilution of precision (see Rempel and Rodgers 1997, Wasserlauf et al. 2023). We retained data from the morning after tagging (from July 10, 2023; birds had ~6 hr to recover from handling) to the day on which tags stopped transmitting. One tag continued transmitting for 2 weeks after falling off (as identified by a lack of movement; we recaptured this bird subsequently). For this tag, we included records until it stopped moving. Maps were obtained from the Esri Data & Maps database, Natural Earth and Google, using *ggmap* v. 4.0.0 (Kahle and Wickham 2013), or by downloading it from the provider's webpage.

To summarize tracking data, we calculated the number of days for which we had data for each bird. We extracted the total distance travelled per day by each pigeon, by using *st_distance*() that calculates distances between 2 GPS fixes in a straight line and then summing these distances. To ensure that the day after tagging did not skew our results due to different behavior, we compared the mean distance traveled for a dataset with and without July 10, 2023, using the Wilcoxon nonparametric test. To depict home ranges, we used (1) autocorrelated kernel density estimator (AKDE) (Fleming et al. 2015), applied with the package *ctmm* (Calabrese et al. 2016); and (2) minimum convex polygons (MCP) of observations (Mohr 1947), applied with the package *adehabitatHR* (Calenge and Fortmann-Roe 2015). The latter method was used to compare data on Rock Dove movements with comparable studies on feral pigeons (Rose et al. 2006a, Carlson et al. 2011). We extracted MCP home range using *mcp*(). AKDE home ranges were estimated for each bird using functions *ctmm.guess*() and *ctmm.fit*(). To identify all potential (night-time) roost sites, we have used GPS fixes between 22:00 and 4:00 and used adjacency matrix graphs from the package *igraph* v.2.0.3 (Csardi 2013) to demarcate other potential roost sites, identifying 2 other sites. We then cross-examined these with known buildings/structures, and all corresponded to known roost sites (based on the long-term study) of Rock Doves within the area. We tested for differences in range size between the Rock Doves and those ranges previously reported for feral pigeons, using the Wilcoxon nonparametric test. All results are presented as mean ± 1 standard deviation (SD).

As the number of GPS fixes varies with tag battery status (from 2 hr to 1 m per fix), we could not express habitat use as a proportion of points or time spent in the habitat, as Rock Doves could move substantial amounts while on low battery, making time inference imprecise. Instead, we divided the day into 30-min periods and focused on dove presence in a habitat during each time interval (see Wasserlauf et al. 2023). We used NatureScot data (https://opendata.nature.scot/datasets/snh::habitat-map-of-scotland/about) to overlap GPS fixes and habitat categories. We simplified habitat categories, as NatureScot data is layered where some habitats may be subdivided into others. Within the study region, most of the habitat is both "arable land" and "machair," but may also consist of other major subcategories used by Rock Doves (e.g., dunes). To this end, we kept only machair and arable land classification for otherwise unclassified land, retained "Atlantic *Cynosurus-Centaurea* pastures" various types of dunes and machair, and classed all other habitats as "unknown or other". In addition, we defined roost sites as a separate habitat. We expressed habitat use per 0.5-hr intervals of the day in the following way: (1) we assigned each GPS fix in a dove day (a tracking day of a dove) to a 0.5-hr interval of the day, and to a habitat type; and then (2) we summarized presence/absence in a habitat at a given interval across all dove days, and expressed it as a proportion. This method allowed us to represent habitat use while minimizing bias caused by the irregularity of data transmission. We inspected graphically to check for differences between the dataset with the day of tagging included, and without.

RESULTS

We obtained GPS data from 5 birds. These produced 4,012 filtered GPS fixes with a mean tracking time of 18.6 ± 13.4 days (Table 1). On average, doves traveled 2,926 ± 2,844 m day^{-1}. The high SD stems from Rock Doves sometimes travelling a very short distance during a day (<200 m from the roost site). We did not observe sex differences in distance traveled (although the small sample size precludes formal testing), and inclusion of the morning of tagging day had no significant impact on estimates of mean distance traveled for either all Rock Doves or each individual (all *P*-values >0.8). During the study period, the average AKDE 95% home range of a Rock Dove averaged 138.21 ± 108.53 ha. The 100% MCP home range was 129.007 ± 83.9 ha. The variation (in the form of high SDs) stems from 2 birds having smaller home ranges (Figure 1). Our Rock Doves had larger ranges, as tested using the Wilcoxon nonparametric test, than those previously reported for urban ($W = 7$, *P*-value = 0.018) (Rose et al. 2006a) ($MCP_{mean} = 35.71 \pm 53.63$ ha; $n = 12$), but not rural feral pigeons ($W = 32$, *P*-value = 0.823) (Carlson et al. 2011)

TABLE 1. Information on 7 GPS-tagged Rock Doves, including biometric data collected on the day of tagging. The number of tracking days and average distance traveled is reported post-filtering (see Methods). We also present home ranges: autocorrelated kernel density estimation (AKDE) at 95% contour, with minimum and maximum estimates; and minimum convex polygon (MCP) range at 100% contour.

Individual ID	Year of ringing	Sex	Wing chord (mm)	Body mass (g)	Days of tracking data	Average distance traveled (m day^{-1})	Standard deviation of distance traveled (m day^{-1})	Number of fixes	AKDE (95%) (ha)	MCP (100%) (ha)
EA49502	2019	M	232	390	29	3,620	2,803	1,692	103.13 [90.69–116.36]	218.68
EA49503	2019	M	236	389	27	2,207	1,852	287	147.28 [119.61–179.02]	129.18
EA49568	2020	M	235	340	4	4,928	2,704	232	66.60 [51.18–84.03]	34.63
EA49570	2020	F	219	339	4	7,055	4,710	310	321.17 [229.72–427.69]	206.07
EA49571	2020	F	231	400	29	1,647	2,338	1,491	53.37 [46.41–60.81]	56.47
EA49887	2022	?	239	398	–	–	–	–	–	–
EM32177	2023	?	227	386	–	–	–	–	–	–

($\text{MCP}_{\text{mean}} = 406.6357 \pm 589.5389$ ha; $n = 14$). All doves remained within agricultural areas and did not, therefore, have to move over unsuitable foraging habitats (i.e., commute) to travel between roosting and feeding sites. They also did not undertake multi-kilometer flights on a regular basis and did not move across areas of moorland.

Tracked doves used a diversity of habitats during daylight, but spent significant amounts of time at roost sites (Figure 2). In any 30-min window, Rock Doves would be located in a roost site in at least 20.5% of cases. During daylight, doves mostly associated with farmland: 7.4–50.0% of all dove days had them located in the machair in a 30-min window, 3.7–20.9% in Atlantic pastures, and 5.3–37.5% in other arable lands. During daylight, machair with no other habitat designations is the most visited foraging habitat, and it has to be noted that as per NatureScot data, effectively all habitats presented can be considered machair (see Methods). We observed no notable graphical differences between the presented Figure 2A and one based on a dataset without the day of tagging.

DISCUSSION

For centuries, is it very likely that almost all of Uist's Rock Doves would be "based" in eastern caves, crossing over large tracts of moorland (multiple kilometers) to forage in farmland in the west. Such "commutes" are a characteristic part of undomesticated Rock Dove biology (Goodwin and Gillmor 1970). Our study demonstrates that there is now an element of the population that is "resident" within the agricultural regions of the islands. This element of the population is able to forego long-distance commuting and become associated with humans in a roosting *and* foraging context. Of our GPS-tracked birds, there were limited daily movements, no individual was recorded >3 km from the roost, and Rock Doves would return to roost sites multiple times during the day. All of the doves roosted entirely within human structures, and almost all of their time was spent in agricultural habitats. Birds used various structures for roosting, from active barns to derelict buildings, and spent significant time at roost sites during the daytime (which would not be possible if they were commuters roosting in caves). The birds used different elements of farmland but concentrated on machair. Our results provide individual-level assessment of Rock Dove movements, revealing that the commuting behavior might be abandoned by some colonies in Uist's population. However, commuting Rock Doves are still observed today in Uist, either through observations of birds flying over moorland, or observations made during our mark–recapture study of roost sites of >30 birds in the caves of eastern Uist, many miles from suitable foraging habitat. This suggests that there are 2 "living quarters strategies," namely commuting and resident individuals, present within the population.

The resident living quarters strategy has resulted in populations that are almost entirely dependent on humans, making use of human-created habitats for roosting, nesting, and foraging. Given that the original domestication of the Rock Dove involved the use of roost sites for harvesting birds (Johnston and Janiga 1995), the association of undomesticated Rock Doves with humans in the Outer Hebrides might provide a window into the incipient phases of the domestication of this species. However, the divergent living quarters strategies require further study. First, the proportion of resident versus commuter individuals in the wider Uist population is unclear. As part of our wider mark–recapture efforts on the islands (which began in 2019), we currently capture 250–500 Rock Doves in Uist's barns and derelict buildings each year (birds nesting and roosting within a suitable foraging habitat, i.e., probable residents). While it is difficult to be confident (due to the challenges of accessing commuting colonies in the cliffs and caves of the east), we estimate the total Uist population to be 2,000–5,000 birds. This suggests that, at the very least, resident colonies make up a non-negligible proportion of the total population. A second point is that not all cave colonies will "commute," and not all building colonies will be "resident." A handful of suitable ruins are in moorland regions, and a stretch of coastline on western North Uist (i.e., adjacent to large tracts of agricultural land) has sea caves. Large dove flocks (100+) are seen throughout Uist in the autumn and winter, suggesting greater mobility at certain times, even by 'resident' individuals. The extent to which residency or commuting represent distinct strategies or a continuum is unclear, as is their value in terms of predation, energetics, disturbance, disease, and competition. Altogether, the resident–commuter dichotomy represents an exciting opportunity to explore the ecological and evolutionary benefits of such differing strategies.

Our findings are relevant to discussions about the pathway of Rock Doves into domestication. Plasticity in feral pigeon

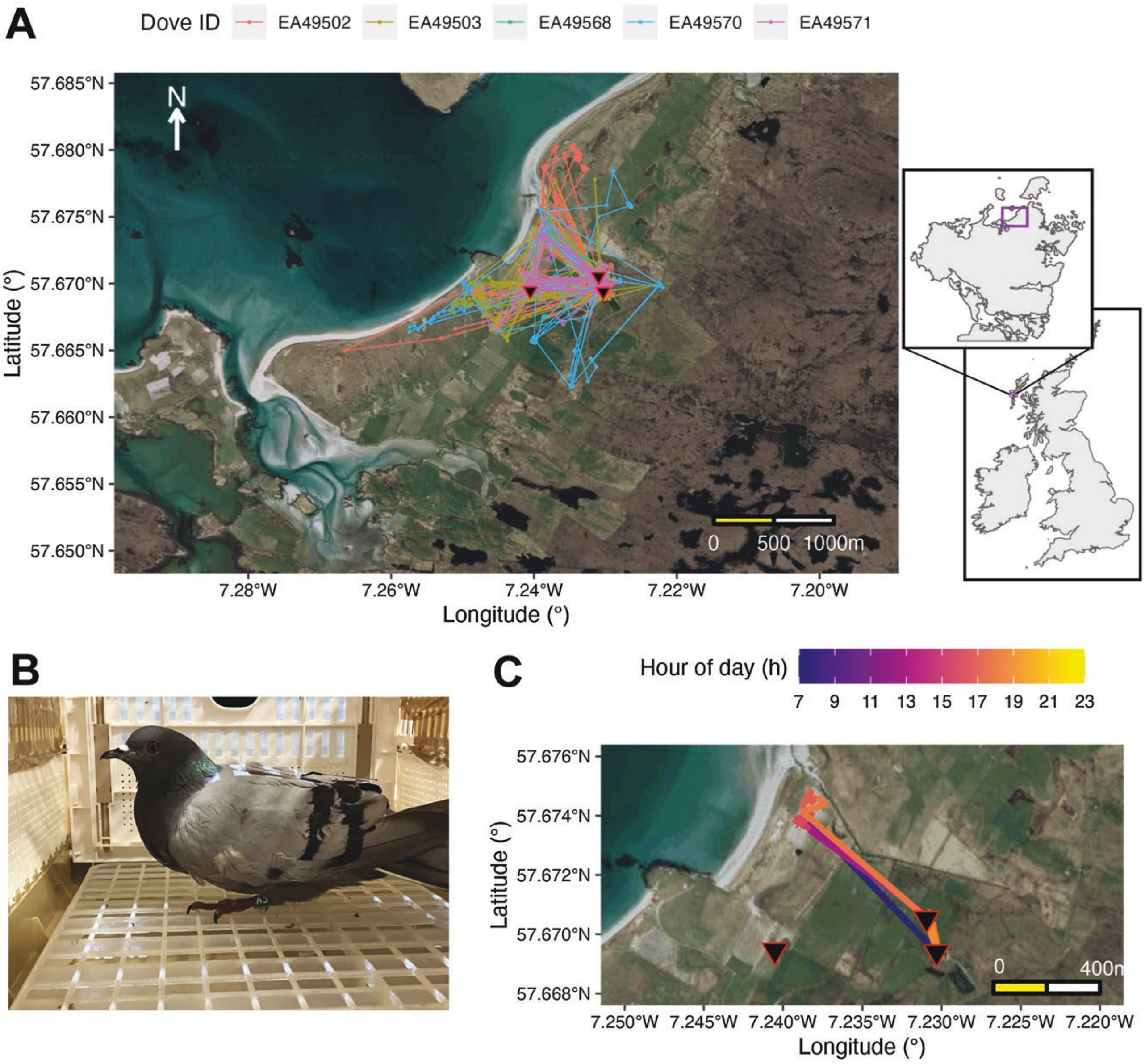

FIGURE 1. GPS tracks of undomesticated *Columba livia* (Rock Dove) demonstrate extensive use of human-dominated habitats, with no evidence of typical "commuting" behavior (i.e., having to move over large areas of unsuitable foraging habitat to travel between roosting and feeding sites). Instead, Rock Doves make brief movements among fields and machair patches to and from roost sites (triangles), which are already located within these suitable habitats. (**A**) Among the 5 birds, individuals did not travel farther than 3 km from roost site, remaining within agricultural parts and avoiding moorland regions to the east. Colors of tracks represent individual birds. Points represent GPS fixes, with lines linking consecutive fixes. Inset maps show the position of North Uist within the British Isles and the study site within North Uist. (**B**) Each individual in this study had a GPS tracker fixed to its back, alongside its metal British Trust for Ornithology leg ring, and its field-identifiable color ring. This bird, EA49568, was an adult male. (**C**) An example day track of Rock Dove EA49568, from July 12, 2023, showing movements to and from the roost site throughout the day. The bird foraged in a single field no farther than 400 m away from a roost site. Lines join consecutive GPS fixes, with colors indicating clock hour of the day of a GPS fix, starting at 07:00 and finishing at 23:00 British Summer Time. This "dove-day" consisted of 67 GPS fixes.

behavior—living on one street in cities versus commuting to outlying fields in small towns—has been seen as a driver of its success (Johnston and Janiga 1995). Agricultural land in Uist has allowed some doves to abandon commutes for more prolonged periods than the Capo Caccia birds, which did so sporadically after fruiting events (Baldaccini et al. 2000). Our observations challenge the assumption that Rock Dove and feral pigeon movements are different. We identified home range differences compared to urban (Rose et al. 2006a, Carlson et al. 2011) but not rural (Carlson et al. 2011) feral pigeons. Feral pigeons, mostly living in buildings, can also commute (Soldatini et al. 2006), and nest on cliffs (Maser 1975). We show that Rock Doves, despite mostly living in caves (Baldaccini 2020), can also use buildings and cease commuting. Across species, there is debate over whether domestication is driven by active "farming" or animals moving into human proximity. Uist's Rock Doves "moving in" to human habitats provides support for the latter "commensal" pathway (see Larson and Fuller 2014).

In conclusion, we present the first individual-level study of undomesticated Rock Dove movement ecology. We demonstrate that the presence of human constructions has allowed

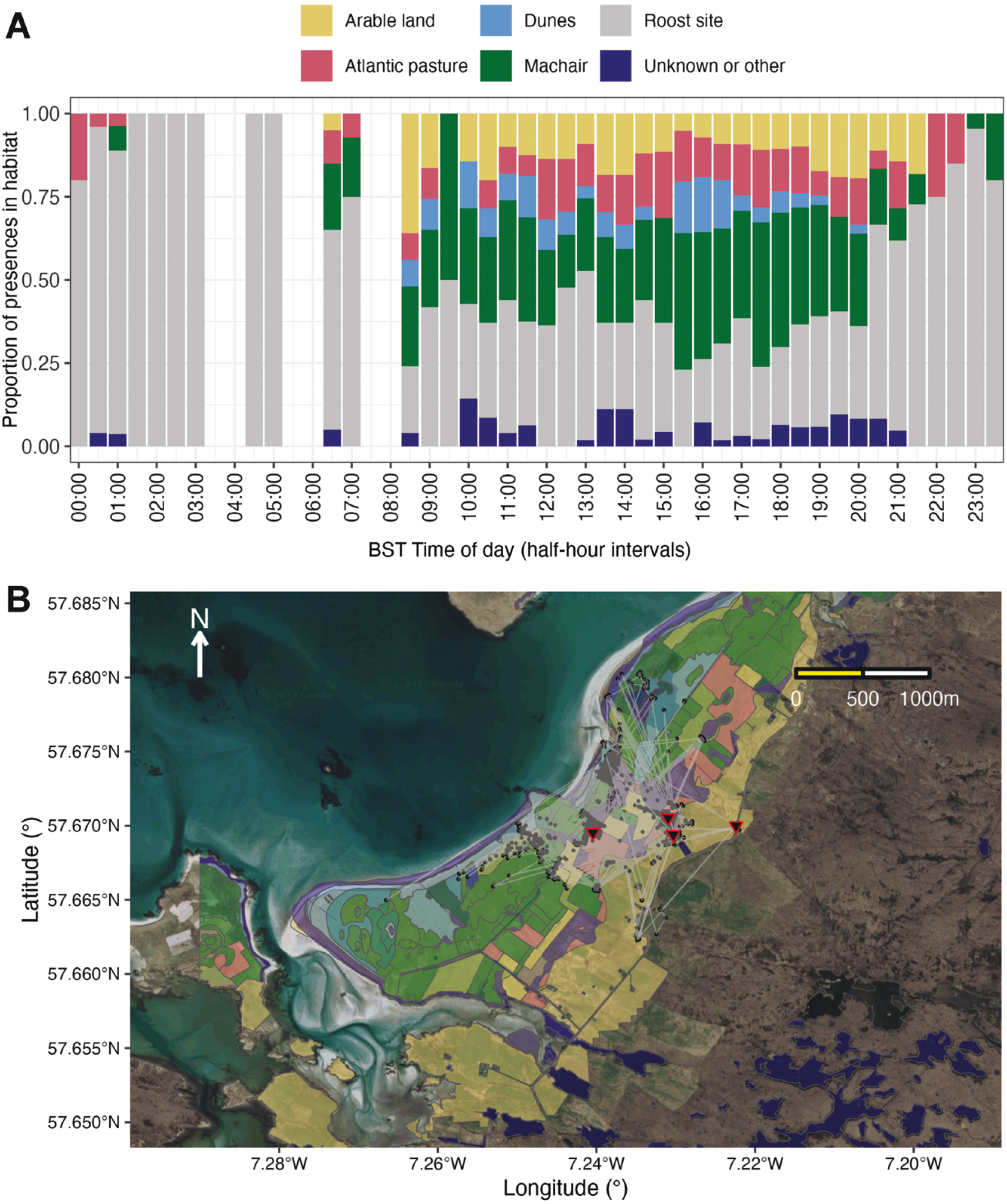

FIGURE 2. At any time of day, Rock Doves spend a significant amount of time in their (human-constructed) roost sites, and most of their activity outside of these sites occurs within agricultural environments. (**A)** Across all dove days (a tracking day of a Rock Dove), doves would be present in roost sites throughout any 0.5-hr interval of the day, with machair, arable, and pasture land accounting for the majority of habitat used by them, as shown by proportional presence (see Methods). Data presented is across all tracking days and doves in the study. Missing bars indicate absent data after filtering, due to low accuracy of data from the night (likely due to the stone walls of roost site buildings interfering with GPS signal). (**B)** All Rock Dove movements were clearly constrained to a few habitats, with Rock Dove roost sites located within a matrix of suitable agricultural habitats, as shown in this map of habitat categories overlaid on the satellite map (habitat type data is not available for much of the eastern moorland regions, although these sites were not used by our doves). All dove tracks are shown in Figure 1A, with roost sites labeled with triangles. Flight paths are shown in translucent gray for clarity. Colors of habitats match the legend in subplot **A**.

some doves to forego "commuting" flights and become more strongly associated with anthropogenic habitats. More generally, we highlight an opportunity to study the wild form of a model organism. This will facilitate future research allowing us to explore the representativeness of studies in captive domestic entities to the wider animal kingdom.

ACKNOWLEDGMENTS

We are grateful to DN and Andrew MacDonald for allowing us to work on their land. We thank Katja Rönkä, Rose Thorogood, and two anonymous reviewers for providing comments on a draft version of this work.

Funding statement

We acknowledge funding from the British Birds Charitable Trust, BTO, and Scottish Ornithologists' Club.

Ethics statement

Fieldwork was carried out under W.J.S.'s BTO ringing permit (A/6193), and permission from the BTO's Special Methods Technical Panel.

Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

W.J.S. conceived the idea, design, and experiment (supervised research and formulated question or hypothesis). W.J.S. and M.T.J. performed the experiments (collected data and conducted the research). W.J.S., M.T.J., and S.J.P. wrote the paper (or substantially edited the paper). M.T.J. and W.J.S. analyzed the data. W.J.S., M.T.J., and S.J.P. contributed substantial materials, resources, or funding.

Data availability

Analyses reported in this article can be reproduced using the data provided by Smith et al. (2024).

LITERATURE CITED

Alfred, J., and I. T. Baldwin (2015). New opportunities at the wild frontier. *eLife* 4:e06956.

Anderson, P. (1913). The birds of the island of Tiree. *The Scottish Naturalist* 21:193–200.

Angus, S., and T. Dargie (2002). The UK Machair Habitat Action Plan: Progress and problems. *Botanical Journal of Scotland* 54:63–74.

Baker, A. (2013). Pigeon racing clubs in Pas-de-Calais, France, 1870–1914. *Journal of Historical Geography* 41:1–12.

Baldaccini, N. E. (2020). The synanthropic status of wild Rock Doves and their contribution to feral pigeon populations. *Rivista Italiana di Ornitologia* 90.

Baldaccini, N. E., D. Giunchi, E. Mongini, and L. Ragionieri (2000). Foraging flights of wild Rock Doves (*Columba l. livia*): A spatio-temporal analysis. *Italian Journal of Zoology* 67:371–377.

Benvenuti, S., and H. G. Wallraff (1985). Pigeon navigation: Site simulation by means of atmospheric odours. *Journal of Comparative Physiology A* 156:737–746.

Beveridge, E. (1911). *North Uist: Its Archaeology and Topography, with Notes Upon the Early History of the Outer Hebrides*. William Brown, Edinburgh, UK.

Beveridge, F. (1918). The birds of North Uist. *The Scottish Naturalist* 83:245–254.

Biro, D., D. J. T. Sumpter, J. Meade, and T. Guilford (2006). From compromise to leadership in pigeon homing. *Current Biology* 16:2123–2128.

Buchanan, R. W. (1883). *The Hebrid Isles*. Chatto and Windus, London, UK.

Calabrese, J. M., C. H. Fleming, and E. Gurarie (2016). ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution* 7:1124–1132.

Calenge, C., and S. Fortmann-Roe (2015). adehabitatHR: Home Range Estimation. https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf

Capoccia, S., C. Boyle, and T. Darnell (2018). Loved or loathed, feral pigeons as subjects in ecological and social research. *Journal of Urban Ecology* 4:juy024.

Carlen, E., and J. Munshi-South (2021). Widespread genetic connectivity of feral pigeons across the Northeastern megacity. *Evolutionary Applications* 14:150–162.

Carlson, J. C., L. Clark, M. F. Antolin, and M. D. Salman (2011). Rock pigeon use of livestock facilities in northern Colorado: Implications for improving farm bio-security. *Human–Wildlife Interactions* 5:112–122.

Chang, L., Q. Tang, R. Zhang, S. Fu, C. Mu, X. Shen, and Z. Bu (2023). Evaluation of meat quality of local pigeon varieties in China. *Animals* 13:1291.

Course, M. (2019). Houses of Uist: Memory and dwelling in the Outer Hebrides. *Journal of the Royal Anthropological Institute* 25:51–65.

Csardi, M. G. (2013). Package "igraph." https://doi.org/10.32614/CRAN.package.igraph.

Cunningham, W. A. J. (1979). Birds of the Outer Hebrides: Terrestial birds and raptors. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences* 77:407–417.

Dell'Ariccia, G., G. Dell'Omo, D. Wolfer, and H.-P. Lipp (2008). Flock flying improves pigeons' homing: GPS-track analysis of individual flyers versus small groups. *Animal Behaviour* 76:1165–1172.

Elton, C. (1938). Notes on the ecological and natural history of Pabbay, and other islands in the Sound of Harris, Outer Hebrides. *Journal of Ecology* 26:275–297.

Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese (2015). Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology* 96:1182–1188.

Goodwin, D., and R. Gillmor (1970). *Pigeons and Doves of the World*. Trustees of the British Museum (Natural History), London, UK.

Gray, R. (1871). *The Birds of the West of Scotland: Including the Outer Hebrides, with Occasional Records of the Occurrence of the Rarer Species Throughout Scotland Generally*. T. Murray & Son, Glasgow, Scotland.

Guthrie, D. (1920). Some bird notes from South Uist. *The Scottish Naturalist* 99:45–48.

Hance, W. A. (1951). Crofting settlements and housing in the Outer Hebrides. *Annals of the Association of American Geographers* 41:75–87.

Harvie-Brown, J. A., T. E. Buckley, W. A. Smith, and R. F. Heddle (1888). *A Vertebrate Fauna of the Outer Hebrides*. D. Douglas, Edinburgh, Scotland.

Hepburn, I. R., P. Schofield, and R. A. Schofield (1977). The birds of the Monach Isles, Outer Hebrides. *Bird Study* 24:25–43.

Hetmański, T., and A. Jarosiewicz (2008). Plumage polymorphism and breeding parameters of various feral pigeon (*Columba livia* Gm.) morphs in urban area (Gdańsk, north Poland). *Polish Journal of Ecology* 56:683–691.

Johns, C. A., and J. A. Owen (1882). *British Birds in Their Haunts*. Society for Promoting Christian Knowledge, London, UK.

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

Johnston, R. F., and M. Janiga (1995). *Feral Pigeons*. Oxford University Press, New York, NY, USA.

Kahle, D., and H. Wickham (2013). ggmap: Spatial visualization with ggplot2. *The R Journal* 5:144–161.

Kearton, R. (1895). *British Birds' Nests: How, Where, and When to Find and Identify Them*. Cassell and Co., Ltd., London, UK.

Larson, G., and D. Q. Fuller (2014). The evolution of animal domestication. *Annual Review of Ecology, Evolution, and Systematics* 45:115–136.

MacDonald, F. (2014). The ruins of Erskine Beveridge. *Transactions of the Institute of British Geographers* 39:477–489.

MacGillivray, J. (1841). *Notes on the Zoology of the Outer Hebrides*. Published in Annals And Magazine of Natural History, Edinburgh, Scotland.

Maser, C. (1975). Predation by Common Ravens on feral Rock Doves. *The Wilson Bulletin* 87:552–553.

Modlinska, K., R. Stryjek, and W. Pisula (2015). Food neophobia in wild and laboratory rats (multi-strain comparison). *Behavioural Processes* 113:41–50.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *The American Midland Naturalist* 37:223–249.

Nebel, C., J. Harl, A. Pajot, H. Weissenböck, A. Amar, and P. Sumasgutner (2020). High prevalence and genetic diversity of *Haemoproteus columbae* (Haemosporida: Haemoproteidae) in feral pigeons *Columba livia* in Cape Town, South Africa. *Parasitology Research* 119:447–463.

Nimri, L. (2019). Fatal trichomoniasis in Feral Pigeons (*Columba livia f. domestica*) in the United Arab Emirates.

Outer Hebrides Natural History Society (2004). *Outer Hebrides Bird Report 2003*.

Outer Hebrides Natural History Society (2014). *Outer Hebrides Bird Report 2013*.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* 10:439–446.

Peel, C. V. A. (1901). *Wild Sport in the Outer Hebrides*. F.E. Robinson & Company.

Portugal, S. J., and C. R. White (2022). Externally attached biologgers cause compensatory body mass loss in birds. *Methods in Ecology and Evolution* 13:294–302.

Portugal, S. J., R. L. Ricketts, J. Chappell, C. R. White, E. L. Shepard, and D. Biro (2017). Boldness traits, not dominance, predict exploratory flight range and homing behaviour in homing pigeons. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372:20160234.

R Development Core Team (2010). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rempel, R. S., and A. R. Rodgers (1997). Effects of differential correction on accuracy of a GPS animal location system. *The Journal of Wildlife Management* 61:525–530.

Renaud, S., L. Amar, P. Chevret, C. Romestaing, J.-P. Quéré, C. Régis, and R. Lebrun (2024). Inner ear morphology in wild versus laboratory house mice. *Journal of Anatomy* 244:722–738.

Ritchie, J. (1920). *The Influence of Man on Animal Life in Scotland: Study in Faunal Evolution*. Cambridge University Press, Cambridge, UK.

Rose, E., P. Nagel, and D. Haag-Wackernagel (2006a). Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*). *Behavioral Ecology and Sociobiology* 60:242–254.

Rose, E., D. Haag-Wackernagel, and P. Nagel (2006b). Practical use of GPS-localization of Feral Pigeons *Columba livia* in the urban environment. *Ibis* 148:231–239.

Sasaki, T., and D. Biro (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications* 8:15049.

Savriama, Y., C. Romestaing, A. Clair, L. Averty, J. Ulmann, R. Ledevin, and S. Renaud (2022). Wild versus lab house mice: Effects of age, diet, and genetics on molar geometry and topography. *Journal of Anatomy* 240:66–83.

Scaglione, F. E., P. Pregel, F. T. Cannizzo, A. D. Pérez-Rodríguez, E. Ferroglio, and E. Bollo (2015). Prevalence of new and known species of haemoparasites in feral pigeons in northwest Italy. *Malaria Journal* 14:99.

Skandrani, Z., A. C. Prevot, N. E. Baldaccini, and J. Gasparini (2016). On the interplay between phylogeny and environment on behaviour of two urban bird species, *Columba livia* and *Corvus corone* (Aves). *Italian Journal of Zoology* 83:98–102.

Smith, W. J. (2023a). Rapid assessment of the extent of feral introgression in British and Irish Rock Dove (*Columba livia*) populations. *Ibis* 165:1432–1439.

Smith, W. J. (2023b). The undomesticated Rock Dove in Britain and the Isle of Man. *British Birds* 116:70–76.

Smith, W. J., and S. M. Clegg (2023). Hybridisation and genomic diversity in British and Irish pigeons *Columba livia*. *European Journal of Wildlife Research* 69:94.

Smith, W. J., M. T. Jezierski, J. C. Dunn, and S. M. Clegg (2023). Parasite exchange and hybridisation at a wild-feral-domestic interface. *International Journal for Parasitology* 53:797–808.

Smith, W. J., S. J. Portugal, and Michał T. Jezierski (2024). Data from: Use of anthropogenic landscapes in a wild *Columba livia* (Rock Dove) population. *Ornithology* 142:ukae050. https://doi.org/10.5061/dryad.pvmcvdnvq [Dataset].

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

Smith, W. J., A. T. Sendell-Price, A. L. Fayet, T. M. Schweizer, M. T. Jezierski, C. van de Kerkhof, B. C. Sheldon, K. C. Ruegg, S. Kelly, L. A. Turnbull, and S. M. Clegg (2022b). Limited domestic introgression in a final refuge of the wild pigeon. *iScience* 25:104620.

Soldatini, C., D. Mainardi, N. Baldaccini, and D. Giunchi (2006). A temporal analysis of the foraging flights of feral pigeons (*Columba livia f. domestica*) from three Italian cities. *Italian Journal of Zoology* 73:83–92.

Stryjek, R., K. Modlińska, and W. Pisula (2012). Species specific behavioural patterns (digging and swimming) and reaction to novel objects in wild type, Wistar, Sprague-Dawley and Brown Norway Rats. *PloS One* 7:e40642.

Toschi, A. (1939). *Richerche ed osservazione sul Colombo selvatico (Columba livia L.)*. Tipografia Compositori, Bologna, Italy.

Urquia-Samele, A., and S. Portugal, J. (2022). Homing pigeon (*Columba livia*) dominance hierarchies are stable over time and resistant to perturbation. bioRxiv:2022.2004.2018.488671.

Vogt, C. C., M. N. Zipple, D. D. Sprockett, C. H. Miller, S. X. Hardy, M. K. Arthur, A. M. Greenstein, M. S. Colvin, L. M. Michel, A. H. Moeller, and M. J. Sheehan (2024). Female behavior drives the formation of distinct social structures in C57BL/6J versus wild-derived outbred mice in field enclosures. *BMC Biology* 22:35.

Wasserlauf, Y., A. Gancz, A. Ben Dov, R. Efrat, N. Sapir, R. Dor, and O. Spiegel (2023). A telemetry study shows that an endangered nocturnal avian species roosts in extremely dry habitats to avoid predation. *Scientific Reports* 13:11888.

Watanabe, S. (2001). Van Gogh, Chagall and pigeons: Picture discrimination in pigeons and humans. *Animal Cognition* 4:147–151.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, et al. (2019). Welcome to the Tidyverse. *Journal of Open Source Software* 4:1686.