Divergence, convergence, and the ancestry of feral populations in the domestic rock pigeon

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Running head: Structure and phylogeny of domestic pigeons

SUMMARY

Domestic pigeons are spectacularly diverse and exhibit variation in more traits than any other bird species [1]. In *The Origin of Species*, Charles Darwin repeatedly calls attention to the striking variation among domestic pigeon breeds – generated by thousands of years of artificial selection on a single species by human breeders – as a model for the process of natural divergence among wild populations and species [2]. Darwin proposed a morphology-based classification of domestic pigeon breeds [3], but the relationships among major groups of breeds and their geographic origins remain poorly understood [4, 5]. We used a large, geographically diverse sample of 361 individuals from 70 domestic pigeon breeds and two free-living populations to determine genetic relationships within this species. We found unexpected relationships among phenotypically divergent breeds that imply convergent evolution of derived traits in several breed groups. Our findings also illuminate the geographic origins of breed groups in India and the Middle East, and suggest that racing breeds have made substantial contributions to feral pigeon populations.

RESULTS AND DISCUSSION

Genetic structure of domestic pigeon breeds

Charles Darwin was a pigeon aficionado and relied heavily on the dramatic results of artificial selection in domestic pigeons to communicate his theory of natural selection in wild populations and species [2]. "Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons," he writes in the *Origin* [2] (p. 20). Darwin notes that unique pigeon breeds are so distinct that, based on morphology alone, a taxonomist might be tempted to classify them as completely different genera [3], yet he also concludes that all breeds

are simply variants within a single species, the rock pigeon *Columba livia*.

Pigeons were probably domesticated in the Mediterranean region at least 3000-5000 years ago, and possibly even earlier as a food source [3, 6, 7]. Their remarkable diversity can be viewed as the outcome of a massive selection experiment. Breeds show dramatic variation in craniofacial structures, color and pattern of plumage pigmentation, feather placement and structure, number and size of axial and appendicular skeletal elements, vocalizations, flight behaviors, and many other traits [1-5]. Furthermore, many of these traits are present in multiple breeds. Today, a large and dedicated pigeon hobbyist community counts thousands of breeders among its ranks worldwide. These hobbyists are the caretakers of a valuable – but largely untapped – reservoir of biological diversity.

Here, as an initial step in developing the pigeon as model for evolutionary genetics and developmental biology, we address two fundamental questions about the evolution of derived traits in this species. First, what are the genetic relationships among modern pigeon breeds? Second, does genetic evidence support the shared ancestry of breeds with similar traits, or did some traits evolve repeatedly in genetically unrelated breeds?

To address these questions, we studied the genetic structure and phylogenetic relationships among a large sample of domestic pigeon breeds. Our primary goal was to examine relationships among traditional breed groups, to which breeds are assigned based on phenotypic similarities and/or geographic regions of recent breed development (Fig. 1) [4, 5, 8]. First, we used 32 unlinked microsatellite markers to genotype 361 individual birds from 70 domestic breeds and

two free-living populations. We next used the Bayesian clustering method in STRUCTURE software [9] to detect genetically similar individuals within the sample (Figs. 1 and S1). When two genetic clusters were assumed (K=2, where K is the number of putative clusters of genetically similar individuals; Fig. 1), the first cluster combined several breed groups with dramatically different morphologies. Principal members of this grouping included the pouters and croppers, which have a greatly enlarged, inflatable crop (an outpocketing of the esophagus); the fantails, which have supernumerary and elevated tail feathers; and mane pigeons, breeds with unusual feather manes or hoods about the head (Fig. 1).

The second ancestral cluster consisted mainly of the tumblers (including rollers and highflyers), the most breed-rich of the major groups (≥80 breeds recognized in the USA) [4, 8]. Tumblers are generally small-bodied and were originally bred as performance flyers, with many breeds still capable of performing backward somersaults in flight. In most modern tumbler breeds, however, selection is most intense on morphological traits such as beak size and plumage. Also included in this cluster are the owl and the wattle breeds (wattles are skin thickenings emanating from the beak). These two breed groups contrast dramatically in several key traits: owls are typically diminutive in body size, have a pronounced breast or neck frill, and have among the smallest beaks of all breeds, while the wattle breeds (English Carrier, Scandaroon, and Dragoon in our analysis) are larger-bodied, lack a frill, and have among the most elaborated beak skeletons of all domestic pigeons [4, 5, 10]. The homers (homing pigeons and their relatives) are included in the second cluster as well. The Carrier, Cumulet, and owl breeds – all members of this cluster – contributed to the modern homing pigeon during its development in England and Belgium approximately 200 years ago [5]. Consistent with this recent admixture, the owls and several

homer breeds continue to share partial membership in the same cluster at K=4 and beyond, and the Cumulet shares similarity with the homers and wattles at K=7. Numbers of clusters beyond K=9 reveals the structure of individual breeds, rather than lending additional insights about breed groups (Fig. S1). Notably, while allelic similarity is potentially indicative of shared ancestry, this analysis does not explicitly generate a phylogenetic hypothesis. Moreover, an alternative explanation for clustering is that large effective population sizes might result in an abundance of shared alleles.

We next used multilocus genotype data from a subset of breeds (those with >50% membership in a cluster at K=9) to calculate genetic distances among breeds and to generate a neighbor-joining tree (Fig. 2). Among the major groups, only subsets of the pouter, fantail, mane, tumbler, Modena and free-living European, and owl branches of the tree have strong statistical support (Fig. 2). Nevertheless, at the breed level we observed substantial genetic differentiation, suggesting that in many cases, hybridization among breeds has been limited (mean pairwise F_{ST} = 0.204 for all breeds, maximum F_{ST} = 0.446; potentially more reliable differentiation estimates considering the modest sample sizes for some breeds [11]: mean D_{est} = 0.156, maximum D_{est} = 0.421; Tables S4 & S5). As a comparison, mean pairwise differentiation among African and Eurasian human populations with historically limited gene flow is lower (mean F_{ST} = 0.106, maximum F_{ST} = 0.240 for the comparison between Pygmy and Chinese populations using a dense genome-wide SNP set) [12].

Taken together, our analysis shows both expected and unexpected genetic affinities among breeds. Like other domesticated animals such as dogs and chickens, pigeons probably have a

reticular rather than hierarchical evolutionary history, which is reflected in the complex genetic structure of many breeds and a star-shaped phylogeny. These findings probably result from hybridization that has occurred throughout the domestication history of the pigeon; this practice continues among some modern breeders as well, often with the goal of transferring a new color into an established breed, or "improving" an existing trait. Unlike the stringent regulations for registering purebred dogs, in which modern breeds are effectively closed breeding populations separated by large genetic distances [13, 14], no barriers exist to mixed ancestry or parentage of pigeons (average F_{ST}=0.33 between dog breeds [13] compared to 0.24 for pigeons). On the other hand, little genetic variation divides dog breeds into subgroups [14], and like our tree (Fig. 2), neighbor-joining trees of dogs show limited structuring of the internal branches [13, 14].

Convergent evolution of traits

Darwin classified 32 pigeon breeds into four major groups based primarily on morphological traits, especially beak size (Fig. 3A). We repeated our STRUCTURE analysis with 13 breeds from Darwin's study that were available to us and found that his morphological classification is broadly congruent with our genetic results (Fig. 3B). Beak size is only one of many traits that pigeon breeders have selected over the past several centuries, or in some cases, millennia. Feathered feet, head crests, and a multitude of color variants appear in many lineages [8] and must have evolved more than once (Fig. 4). Together, these findings suggest that traits do often, but not always, track the ancestry of breeds. This theme of repeated evolution is widespread in genetic studies of other natural and domesticated species as well [15-18].

Geographic origins of breeds

Modern breeds are frequently described as having origins in England, Germany, Belgium or elsewhere in Europe, but their progenitors were probably brought there from afar by traders or colonialists [3-5, 19, 20]. While we may never definitively know the sites of pigeon domestication, genetic data combined with historical records may provide new clues about the geographic origins of some of the major breed groups.

Most historical accounts trace the origins of the wattle breeds, owls, and tumblers to the Middle and Near East hundreds of years ago, with ancient breeds transported to Europe and India for further development by hybridization or selection [3, 5, 20-22]. Our genetic analyses are consistent with this common geographic origin, as these three groups share substantial membership in the same genetic cluster at K=2-3, and two of the three wattle breeds (English Carrier and Dragoon) retain high membership coefficients in the tumbler cluster through K=5 (Fig. 1).

The fantail breeds probably originated in India and have undergone less outcrossing than many other breeds [5]. In our STRUCTURE analysis, the Fantail (and the Indian Fantail to a lesser extent) shows a surprising affinity with the pouters at K=2-3, and these two groups share a major branch on the neighbor-joining tree (Figs. 1 & 2); these two groups are among the most morphologically extreme of all domestic pigeons, and among the most different from each other. European breeders have developed pouters for several hundred years [23, 24], and Dutch traders might have originally brought them to Europe from India [5]. Together, historical accounts and genetic similarity between fantails and pouters support the hypothesis of common geographic origin in India.

Ancestry of feral pigeon populations

Domestic rock pigeons were first brought to North America approximately 400 years ago and feral populations were probably established shortly thereafter [25, 26]. Likewise, some Eurasian and North African feral populations are probably nearly as old as the most ancient domestication events. In addition to the domestic breeds in our study, we also included a feral pigeon population (Salt Lake City, Utah). Escaped individuals from nearly any domestic breed have the potential to contribute to the feral gene pool, and feral birds showed highly heterogeneous membership across clusters at most values of K (Fig. 1). However, we expected that the Racing Homer would be a major contributor to the feral gene pool. Pigeon racing is an enormously popular and high-stakes hobby worldwide. While many birds in homing competitions are elite racers that reliably navigate hundreds of miles to their home lofts, some breeders report that up to 20% of their birds that start a race do not return. As predicted, pairwise D_{est} for the racing homer to feral comparison was among the lowest 0.1% of all pairwise comparisons (D_{est} =0.006), and pairwise F_{ST} was the lowest for any pairwise comparison (F_{ST} = 0.049). Therefore, feral pigeons and Racing Homers show very little genetic differentiation, and wayward Racing Homers probably make a substantial contribution to the genetic profile of this local feral population.

We also included samples of free-living rock pigeons (the existence of "pure" wild populations uncontaminated by domestics or ferals is questionable [27]) from Scotland to test for genetic similarities with domestic breeds, and with our North American feral sample. Consistent with previous studies [25, 28], European and North American free-living populations are highly

differentiated (D_{est} =0.162). The European sample groups with the Modena, a former-racing breed that was developed in Italy up to 2000 years ago [5] (Figs. 1 & 2). This suggests that either Modenas were developed from European free-living populations, or that, as in North America, wayward racers contributed to the local feral population, perhaps for centuries. Studies of additional feral populations will reveal whether strong affinities with racing breeds occur locally and sporadically or, as we suspect, almost everywhere.

The domestic pigeon as a model for avian genetics and diversity

Darwin enthusiastically promoted domestic pigeons as a proxy for understanding natural selection in wild populations and species, and pigeons thus hold a unique station in the history of evolutionary biology. More recently, domesticated animals have emerged as important models for rapid evolutionary change [29]. Feathered feet, head ornamentation, skeletal differences, plumage color variation, and other traits prized by breeders offer numerous opportunities to examine the genetic and developmental bases of morphological novelty in birds. These and other traits evolved repeatedly in many breeds, and a challenge arising from this study is to determine whether this distribution of traits resulted from selection on standing variation (either by hybridization between breeds or repeated selection on variants in wild populations), from *de novo* mutation in independent lineages, or both. In the first case, we would expect certain regions of the pigeon genome to share histories and haplotypes that reflect the transfer of valued traits between breeds. This hypothesis will be testable when we have more detailed information about genomic diversity in this species. Pigeons are also easily bred in the lab and morphologically distinct breeds are interfertile [2, 3, 30]. Therefore, hybrid crosses should be a fruitful method to

map the genetic architecture of derived traits, many of which are known to have a relatively simple genetic basis [4, 30].

The extreme range of variation in domestic pigeons mirrors, if not exceeds, the diversity among wild species of columbids (pigeons and doves) and other birds. Domestic pigeons and wild bird species vary in many of the *same* traits, so domestic pigeons provide an entry point to the genetic basis of avian evolutionary diversity in general [1, 31]. Changes in the same genes, and even in some cases the same mutations, have recently been shown to underlie similar phenotypes in both wild and domesticated populations [32, 33]. The genetic history of pigeons is a critical framework for the analysis of the genetic control of many novel traits in this fascinating avian species.

SUPPLEMENTAL DATA

Supplemental data include Supplemental Experimental Procedures, 1 figure, and 4 tables.

ACKNOWLEDGEMENTS

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FIGURE CAPTIONS

Figure 1. Genetic structure of the rock pigeon (*Columba livia*). Results from STRUCTURE analysis showing coefficients of genetic cluster membership of 361 individuals representing 70 domestic breeds and 2 free-living populations (European and North American, at the far left and far right of the plots, respectively) of rock pigeon. Each vertical line represents an individual bird, and proportion of membership in a genetic cluster is represented by different colors. Thin black lines separate breeds. At K=2, the tumblers, wattles, and owls are the predominant members of one cluster (blue), while other breeds comprise another cluster (orange). At K=3, the pouters and fantails (yellow) separate from the toys and other breeds, and at K=5, the fantails separate from the pouters. Pouters and fantails also share genetic similarity with the recently derived King, a breed with a complex hybrid background that probably includes contributions from Indian breeds [5]. At K=5, fantails are also united with the Modena, an ancient Italian breed, and a free-living European population. The latter two form a discrete cluster at K=9. At K=10 and greater (Fig. S1), some of the breed groups are assigned to different genetic clusters. This suggests that a number of assumed clusters beyond K=9 reveals the structure of individual breeds, rather than lending additional insights about genetically similar breed groups. Top row of photos, left to right: Modena, English Trumpeter, Fantail, Scandaroon, King, Cauchois. Bottom row: Jacobin, English Pouter, Oriental Frill, West of England Tumbler, Zitterhals (Stargard Shaker). Photos courtesy of Thomas Hellmann and are not to scale. See Fig. S1 for results from K=2-25, and Tables S1 and S2 for breed and marker information, respectively.

Figure 2. Consensus neighbor-joining tree of 40 domestic breeds and one free-living population of rock pigeon. The tree was constructed using pairwise Cavalli-Sforza chord genetic distances and includes the subset of breeds with >50% membership in one genetic cluster at K=9. Branch colors match cluster colors in Figure 1, except all tumbler breeds are represented with light blue for clarity. A notable incongruence between the STRUCTURE analysis and tree is the grouping of the English Pouter with a tumbler rather than with the other pouters; however, this grouping is not well supported. Percent bootstrap support on branches (≥50%) is based on 1000 iterations, and branch lengths are proportional to bootstrap values.

Figure 3. Comparison of Darwin's morphology-based classification and genetic structure analysis of domestic pigeon breeds. (A) Darwin classified 32 breeds into four groups: (I) the pouters and croppers, which have enlarged crops (also see Figs. 1 & 4); (II) wattle breeds, many of which have elaborated beaks, and the large-bodied runts; (III) an "artificial" grouping diagnosed by a relatively short beak; and (IV) breeds that resemble the ancestral rock pigeon "in all important points of structure, especially in the beak" [3] (p. 154). **(B)** Mean coefficients of genetic cluster membership for 14 domestic breeds represented in Darwin's classification and our genetic analysis. When two clusters are assumed (K=2), fantails are separated from all other breeds. At K=3, the breeds in Darwin's Group IV and the African Owl (Group II) share a high coefficient of membership in a new cluster. At K=4, the African Owl, Laugher, and (to a lesser extent) English Pouter share membership in a new cluster that includes members of three different morphological Groups. At K=5, the English Pouter and Jacobin form a cluster. While some genetic clusters span more than one morphological Group, others are consistent within a Group. For example, the wattle breeds (Group II), tumblers (Group III), and most of Group IV remain united with breeds of similar morphology at K=2-5. Taken together, these results confirm that morphology is a good general predictor of genetic similarity in domestic pigeons, yet they also show that breeds that share allelic similarity can be morphologically distinct. Darwin, too, recognized that breeds united in form were not necessarily united in ancestry and, conversely, that anatomically dissimilar breeds might be related. For example, he classified the short-beaked Barb (not in our genetic data set) with the long-beaked breeds of Group II. Darwin's tree reproduced from [3] (darwin-online.org.uk).

Figure 4. Distribution of several derived traits across groups of domestic pigeons.

Phylogenetic tree in Fig. 2 was converted to a cladogram format with equal branch lengths (far left). For beak size column, "+" indicates a substantial increase in size relative to the ancestral condition, and "O" indicates a decrease [4, 8]. For body mass, "+" indicates breeds with a maximum over 550 g, "O" indicates those under 340 g [4, 8]. Although a four-fold difference in body mass is depicted here, extremes in body mass among all known breeds differ by more than an order of magnitude. For crop, feathered feet, and head crest, "+" indicates fixed or variable presence of the trait (substantial departure from the ancestral condition [4, 8]). All traits shown were selected in multiple groups except an enlarged crop, which is confined to the pouters and croppers. A possible exception is the Cauchois (not included in the tree; see Fig. 1), a non-pouter breed with an enlarged and inflatable crop, thought to have been developed centuries ago from a cross between a pouter and large-bodied mondain breed [5, 34]. Our STRUCTURE analysis supports this hypothesis, with the Cauchois sharing 37.8-89.7% membership in the genetic cluster containing the pouters at K=2-9 (Fig. 1). Breeds shown (clockwise from upper left): African Owl*, Scandaroon, Norwich Cropper, Old German Owl, West of England Tumbler*, White Carneau, Budapest Short-face Tumbler (*photos courtesy of Thomas Hellmann). Scale bars = 10 cm.

Figure 1
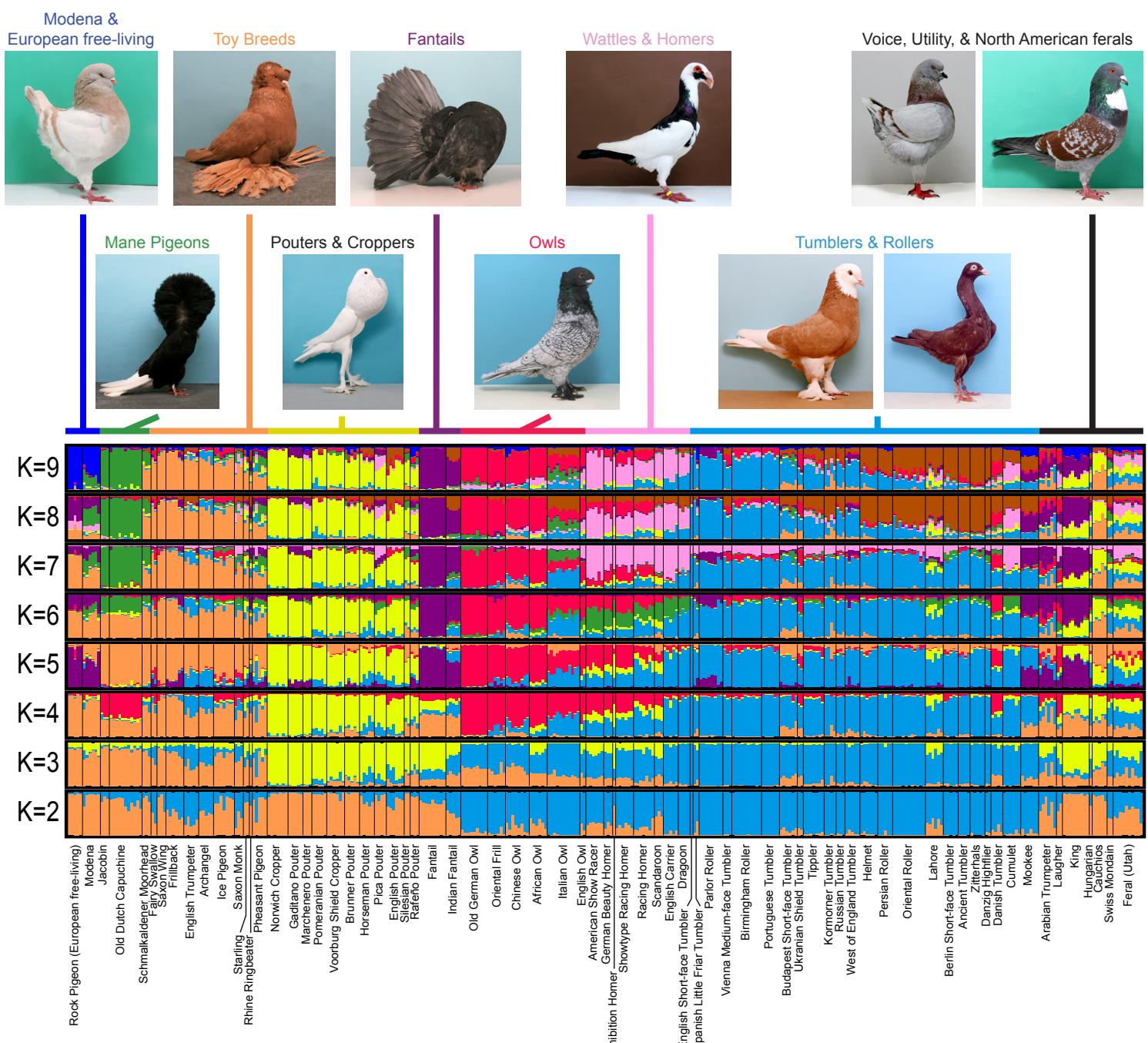
Figure 2

Figure 2
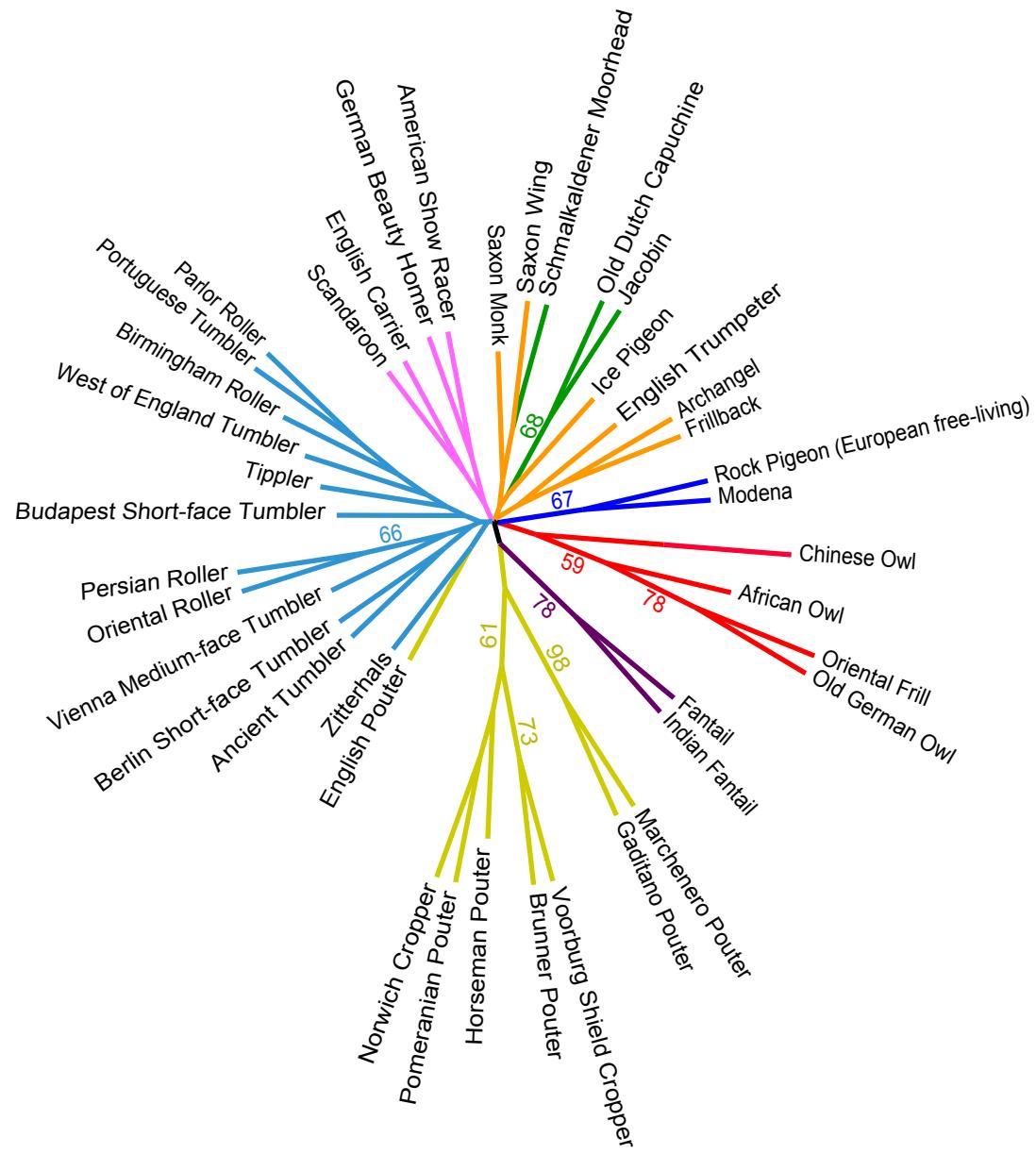
Figure 3

A

COLUMBA LIVIA or ROCK-PIGEON.
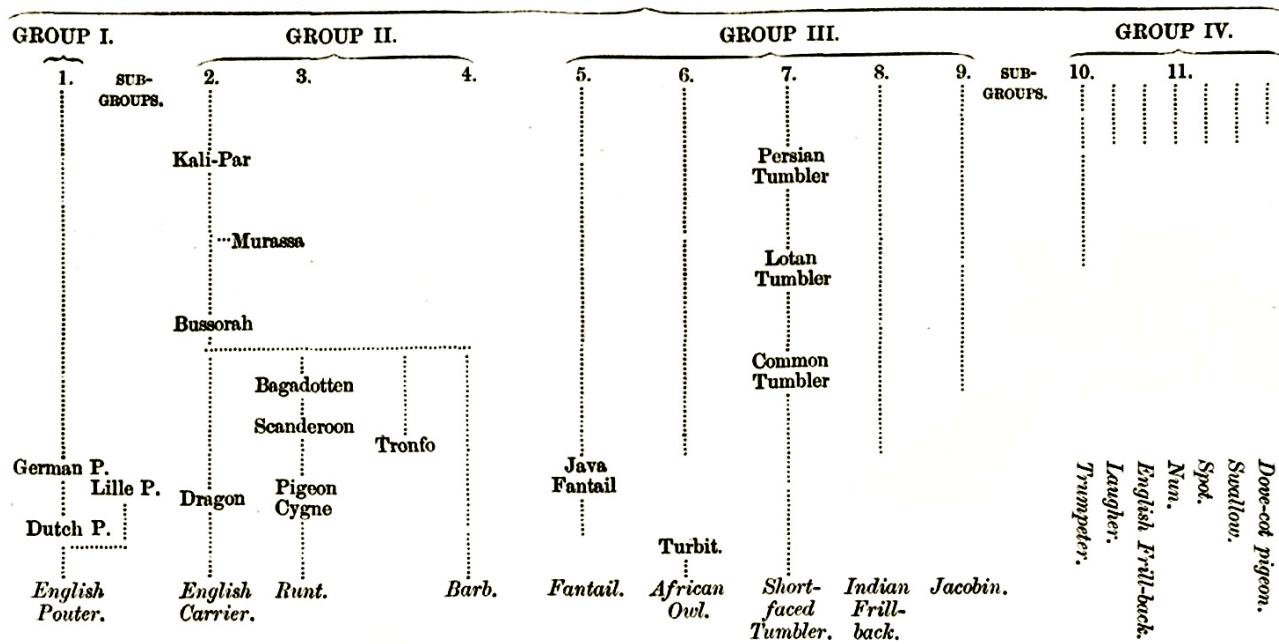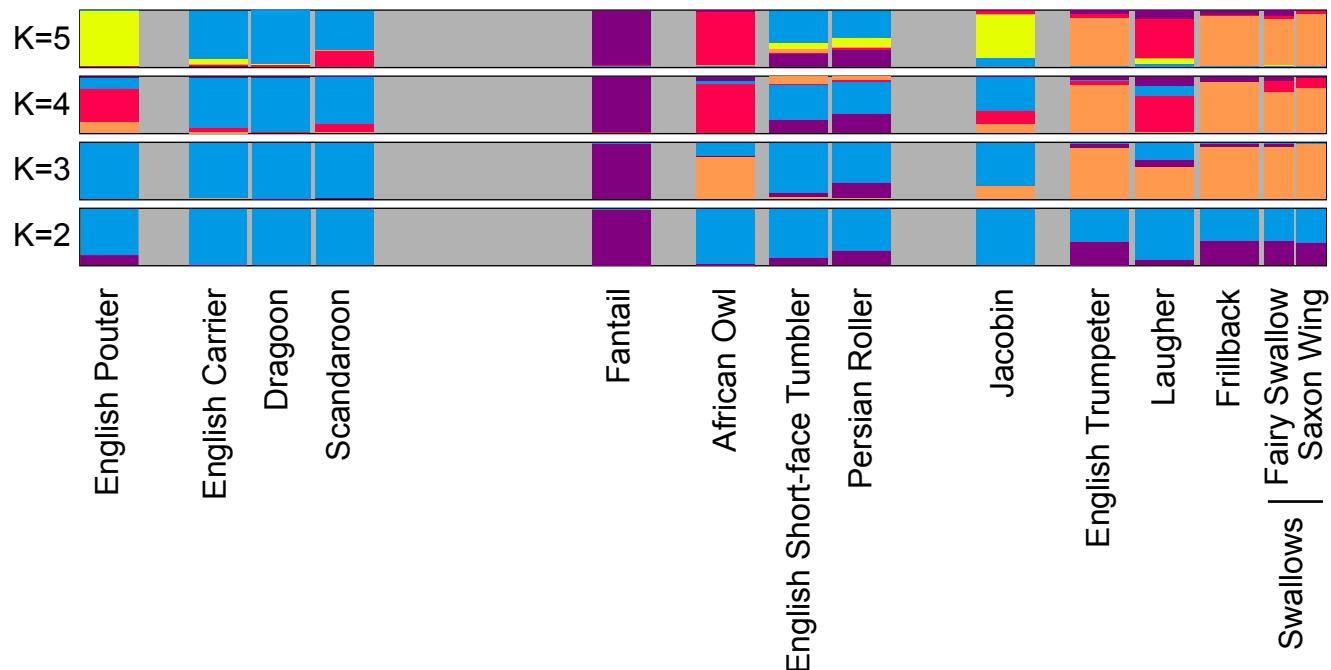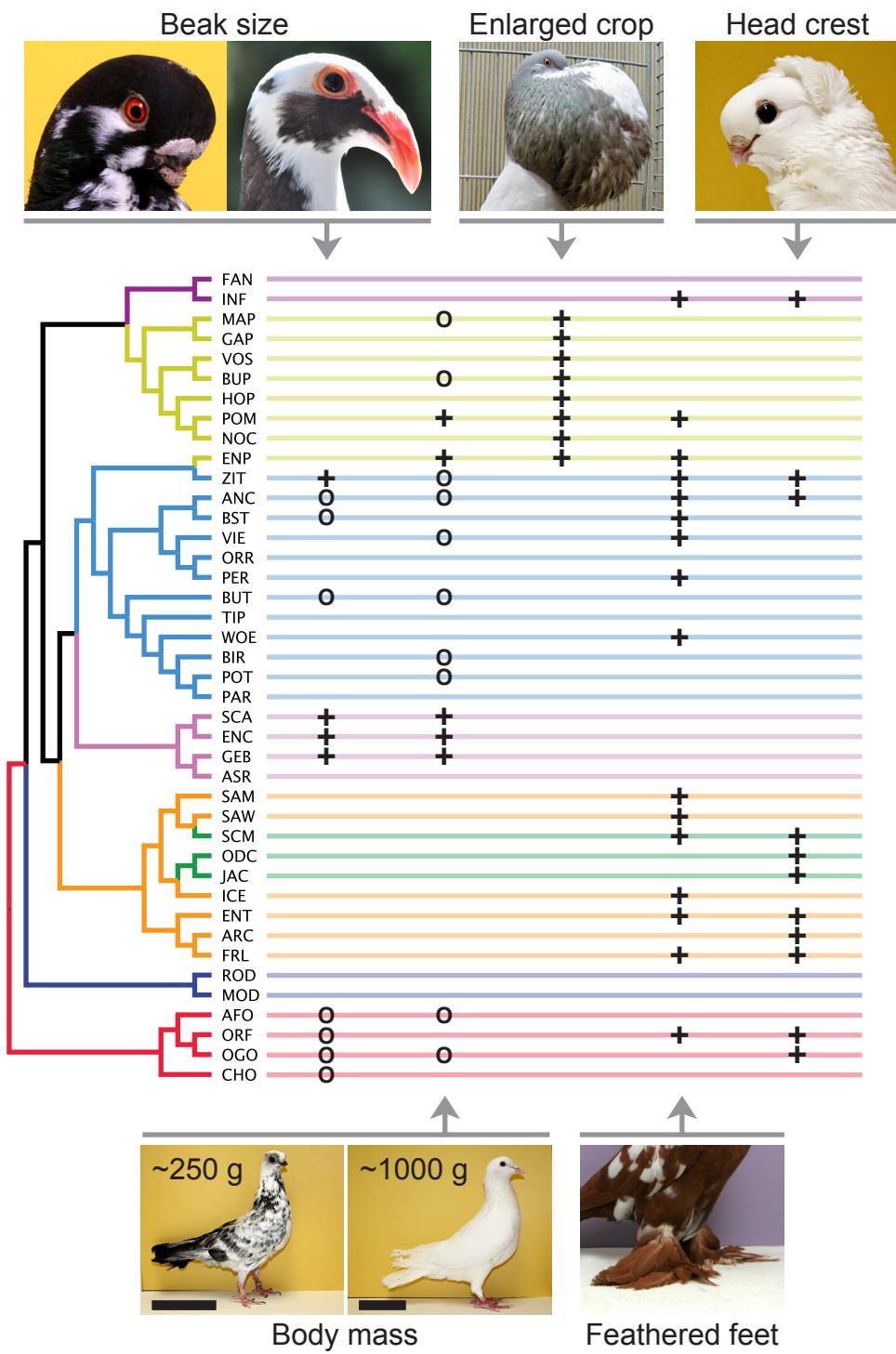
GROUP I. | GROUP II. | GROUP III. | GROUP IV.

SUB-GROUPS. 1. 2. 3. 4. 5. 6. 7. 8. 9. SUB-GROUPS. 10. 11.

Kali-Par

Murassa

Bussorah

Persian Tumbler

Lotan Tumbler

Common Tumbler

Bagadotten

Scanderoon

Tronfo

German P.
Lille P.
Dutch P.

Dragon

Pigeon Cygne

Java Fantail

Turbit.

Trumpeter.
Laugher.
English Frill-back.
Nun.
Spot.
Swallow.
Dove-cot pigeon.

English Pouter. | *English Carrier.* | *Runt.* | *Barb.* | *Fantail.* | *African Owl.* | *Short-faced Tumbler.* | *Indian Frill-back.* | *Jacobin.*

B

K=5
K=4
K=3
K=2

English Pouter
English Carrier
Dragoon
Scandaroon
Fantail
African Owl
English Short-face Tumbler
Persian Roller
Jacobin
English Trumpeter
Laugher
Frillback
Fairy Swallow | Swallows
Saxon Wing

Figure 4

Figure 4

Beak size   Enlarged crop   Head crest

Body mass   Feathered feet

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INVENTORY OF SUPPLEMENTAL INFORMATION

Supplemental Data

Figure S1, related to Figure 1. Coefficients of genetic population membership of 361 individuals representing 70 domestic breeds and 2 free-living populations of pigeon. Complete genetic structure results for K=2-25. A subset of these results are shown in the main text due to space constraints.

Table S1, related to Figure 1. Summary of populations. Contains a list of population abbreviations used in the paper and their corresponding full names, and well as the number of individuals genotyped, number of alleles, and heterozygosity statistics for each population.

Table S2, related to Figure 1. Locus information for 32 microsatellite markers. Contains a list of names, primer sequences, repeat motifs, number of alleles, heterozygosity statistics, and differentiation statistics for the 32 markers used in this study.

Table S3, related to Figure 1. Pairwise D_{est} values for breeds with N≥3 individuals. Genetic differentiation statistics for all breeds and populations in the study using a calculation optimized for smaller sample sizes.

Table S4, related to Figure 1. Pairwise F_{ST} values for breeds with N≥3 individuals. Genetic differentiation statistics for all breeds and populations in the study using a standard calculation method.

Supplemental Experimental Procedures

Subheadings: microsatellite identification, sample collection, DNA isolation, PCR and genotyping, data set filtering, linkage disequilibrium tests, genetic structure analysis, phylogenetic tree, genetic differentiation statistics.

Supplemental references

Includes 20 references pertaining to material in the supplemental data and experimental procedures.

Supplemental Information

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SUPPLEMENTAL DATA
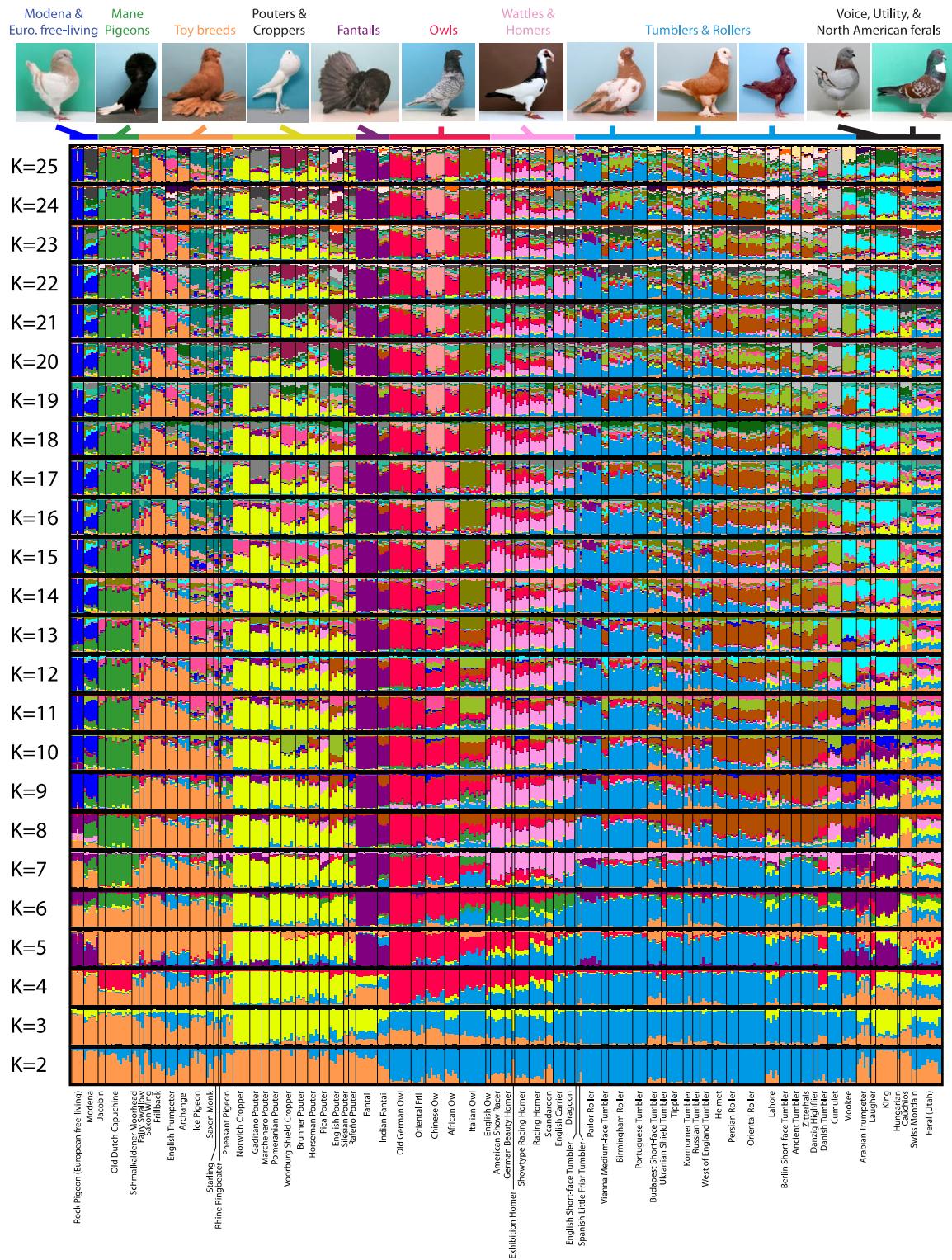
Figure S1, related to Figure 1. Coefficients of genetic population membership of 361 individuals representing 70 domestic breeds and 2 free-living populations of pigeon. Results are shown for K=2-25. Note that beyond K=9, small numbers of breeds (as few as one) from

2

several groups show memberships in new clusters. For example, at K=10, three pouter breeds show membership in a new group to the exclusion of other pouters. At K=11, the Italian Owl shows membership in a new group to the exclusion of other owls. Breeds pictured (left to right): Modena, Jacobin, English Trumpeter, English Pouter, Fantail, Oriental Frill, Scandaroon, English Short-face Tumber, West of England Tumbler, Zitterhall (Stargard Shaker), Show King, Cauchois. Photos courtesy of Thomas Hellmann and are not to scale.

Table S1, related to Figure 1. Summary of breeds.

Breed/Population #	Abbreviation	Name	N_{Ind}	N_A	H_O	H_E
1	AFO	African Owl	6	82	0.410	0.406
2	ANC	Ancient Tumbler	4	73	0.396	0.376
3	ARA	Arabian Trumpeter	6	89	0.357	0.434
4	ARC	Archangel	5	81	0.408	0.398
5	ASR	American Show Racer	6	85	0.402	0.418
6	BIR	Birmingham Roller	10	92	0.351	0.417
7	BST	Berlin Short-face Tumbler	5	79	0.360	0.405
8	BUP	Brunner Pouter	5	84	0.398	0.418
9	BUT	Budapest Short-face Tumbler	6	84	0.379	0.400
10	CAU	Cauchios	5	94	0.426	0.493
11	CHO	Chinese Owl	8	90	0.333	0.391
12	CUM	Cumulet	6	71	0.333	0.337
13	DAG	Dragoon	4	66	0.316	0.332
14	DAH	Danzig Highflier	2	45	0.246	0.168
15	DAT	Danish Tumbler	4	74	0.356	0.392
16	ENC	English Carrier	5	77	0.345	0.350
17	ENO	English Owl	2	62	0.448	0.344
18	ENP	English Pouter	6	51	0.140	0.257
19	ENT	English Trumpeter	5	83	0.414	0.419
20	EST	English Short-face Tumbler	1	36	0.161	0.078
21	EXH	Exhibition Homer	1	39	0.219	0.109
22	FAN	Fantail	9	80	0.321	0.358
23	FAS	Fairy Swallow	2	62	0.311	0.355
24	FER	Feral (Utah)	10	145	0.497	0.573
25	FRL	Frillback	6	93	0.363	0.442
26	GAP	Gaditano Pouter	5	61	0.373	0.303
27	GEB	German Beauty	3	74	0.326	0.378
28	HEL	Helmet	6	83	0.335	0.405
29	HOP	Horseman Pouter	5	89	0.415	0.421
30	HUN	Hungarian	1	41	0.323	0.156
31	ICE	Ice Pigeon	7	107	0.406	0.492
32	INF	Indian Fantail	5	74	0.288	0.378
33	ITO	Italian Owl	11	92	0.372	0.402
34	JAC	Jacobin	3	54	0.250	0.254
35	KIN	King	9	97	0.436	0.442
36	KOT	Kormorner Tumbler	4	71	0.276	0.379
37	LAH	Lahore	6	93	0.320	0.426
38	LAU	Laugher	2	52	0.379	0.246
39	MAP	Marchenero Pouter	3	52	0.181	0.234

4

			N_{Ind}	N_A	H_O	H_E
40	MOD	Modena	6	81	0.285	0.411
41	MOO	Mookee	6	89	0.407	0.442
42	NOC	Norwich Cropper	7	76	0.296	0.357
43	ODC	Old Dutch Capuchine	11	94	0.336	0.423
44	OGO	Old German Owl	9	88	0.353	0.383
45	ORF	Oriental Frill	6	84	0.303	0.388
46	ORR	Oriental Roller	11	96	0.334	0.438
47	PAT	Parlor Roller	8	76	0.329	0.358
48	PER	Persian Roller	5	61	0.257	0.312
49	PHP	Pheasant Pigeon	5	82	0.302	0.425
50	PIC	Pica Pouter	4	77	0.424	0.403
51	POM	Pomeranian Pouter	5	82	0.396	0.434
52	POT	Portuguese Tumbler	6	80	0.392	0.368
53	RAF	Rafeño Pouter	3	67	0.368	0.345
54	RAH	Racing Homer	7	105	0.493	0.485
55	RHR	Rhine Ringbeater	1	44	0.467	0.219
56	ROD	Rock Pigeon (European free-living)	5	74	0.640	0.416
57	RUS	Russian Tumbler	3	82	0.483	0.450
58	SAM	Saxon Monk	3	72	0.419	0.365
59	SAW	Saxon Wing	3	72	0.355	0.393
60	SCA	Scandaroon	3	56	0.279	0.260
61	SCM	Schmalkaldener Moorhead	3	60	0.241	0.296
62	SHH	Showtype Racing Homer	6	100	0.492	0.502
63	SIP	Silesian Pouter	2	57	0.452	0.309
64	SLF	Spanish Little Friar Tumbler	2	60	0.350	0.328
65	STA	Starling	2	74	0.516	0.441
66	SWM	Swiss Mondain	2	56	0.459	0.289
67	TIP	Tippler	7	102	0.436	0.466
68	UKS	Ukranian Shield	2	47	0.250	0.199
69	VIE	Vienna Medium-face Tumbler	3	58	0.286	0.264
70	VOS	Voorburg Shield Cropper	6	75	0.311	0.382
71	WOE	West of England Tumbler	5	86	0.326	0.395
72	ZIT	Zitterhals (Stargard Shaker)	5	64	0.208	0.315
		Mean	5.0	75.5	0.354	0.365
		Standard deviation	2.5	18.6	0.087	0.091

N_{Ind}, number of individuals; N_A, total number of alleles; H_O, observed heterozygosity, H_E, expected heterozygosity.

Table S2, related to Figure 1. Locus information for 32 microsatellite markers.

Loc	Marker	Fwd primer	Rev primer	Repeat motif	N_A	H_O	H_E	D_{est}	Source
L01	CliµT17	AGTTTTAATGAAGGCACCTCT	GTTTGATGGAGTTGCTATTTTGCT	GGAT	10	0.441	0.782	0.545	Traxler et al. (1999)
L02	CliµD32	GAGCCATTTCAGTGAGTGACA	GTTTGCAGGAGCGTGTAGAGAAGT	GT	12	0.553	0.858	0.660	Traxler et al. (1999)
L03	CliµD01	GATTTCTCAAGCTGTAGGACT	GTTTGATTTGGTTGGGCCATC	CA	25	0.607	0.877	0.644	Traxler et al. (1999)
L04	CliµD17	TCTTACACACTCTCGACAAG	GTTTCCACCCAAATGAGCAAG	CA	10	0.507	0.737	0.432	Traxler et al. (1999)
L05	UU-Cli10	CCCTCCAATTTGGCTAAACA	GCAGAAAGCAAGGAAACACC	GT	6	0.427	0.690	0.409	This study
L06	UU-Cli11	CCTTCAAAGGTCACCTAGTCC	TTCCTGAACACCTCAGTAAAAGG	CAAA	7	0.258	0.336	0.083	This study
L07	UU-Cli12	CGCCAGACTGTATTGTGAGC	AGCATGGCTGTTCTTTGAGG	CA	11	0.513	0.767	0.467	This study
L08	UU-Cli13	TGTGGAACCACACAATCAGG	CTTGGGATCAATTTGAAAAATAC	GT	14	0.457	0.741	0.408	This study
L09	UU-Cli16	CGAGTGGACTCAGCCTTAGC	TGTGCACTGCTTTATGACAGG	CA	4	0.386	0.598	0.299	This study
L10	CliµT02	AGTTTTAATGAAGGCACCTCT	TGTAGCATGTCAGAAATTGG	CATC	12	0.501	0.686	0.322	Genbank G73189.1 (Achmann et al., unpublished)
L11	UU-Cli03	CAAACAGAAAACCAACCAACC	CTGGGTCACTGTGTTTGGAAT	CA	4	0.070	0.111	0.027	This study
L12	UU-Cli04	TCCCAGAAATCTTCGTAACTGA	ATTCCAGGTGACAAAGAACCAT	CA	5	0.223	0.380	0.114	This study
L13	UU-Cli09	CCAAATCACATCTGTCAGTGC	AGCAGAGGTGCTGTTTGAGG	GT	7	0.099	0.130	0.046	This study
L14	UU-Cli14	CAGAACGTTTTGTTCTGTTTGG	TCTTGCTGCAGTCTTCATCC	GT	20	0.509	0.816	0.561	This study
L15	UU-Cli15	AGACGCCTTCAGGTTAGAGC	TGAGGGTGACAGAACACTGG	CA	7	0.191	0.356	0.179	This study
L16	UU-Cli17	TTGGGATCCTGACATTTATCC	TAGGTCCTGGATGGAACAGC	GT	11	0.249	0.753	0.576	This study
L17	UU-Cli05	TCCATGCGTCTGTCTGTCC	AGCTGTTGATTGCAGACTGG	GT	12	0.295	0.646	0.398	This study
L18	UU-Cli06	TTTGAAAAACATGGATTGTGC	AATTTGCAGAGGGTGAGTGG	CA	5	0.351	0.494	0.190	This study
L19	UU-Cli07	GCTGCCTGTTACTACCTGAGC	CTGGCCATGAAATGAACTCC	GT	10	0.276	0.448	0.191	This study
L20	UU-Cli08	GGCAGAATGAGCTATGTGACC	CAGCTCAGGGTAATATCAAAACG	CA	9	0.418	0.679	0.353	This study
L21	CliµT24	CCAGCCTAAGTGAAACTGTC	CCTTCCAACCCACATTATT	TGGA	9	0.601	0.812	0.471	Genbank G73196 (Achmann et al., unpublished)
L22	CliµT47	ATGTGTGTTTGTGCATGAAG	ATGAAAGCCTGTTAGTGGAA	TATC	9	0.457	0.658	0.356	Genbank G73190.1 (Achmann et al., unpublished)
L23	CliµD28	AAACCATCACTTATGCCAAC	ACTGATTCTGGTGACTCTGG	CA	3	0.044	0.129	0.092	Genbank G73192.1 (Achmann et al., unpublished)
L24	CliµD35	GGGAGCTTAAGGGATTATTG	ATTCCTTGCATGCCTACTTA	GT	7	0.262	0.413	0.136	Genbank G73199.1 (Achmann et al., unpublished)

L25	CliμD16	GCAGTGATAAAGTTCTGGAACA	GTTTGCCTCACCGTGACATCA	GT	21	0.472	0.730	0.398	Traxler et al. (1999)
L26	CliμD19	CCGTTTCTTCTAATGCAC	GTTTGGATTTCTGGGAGTGTATG	CA	9	0.099	0.653	0.401	Traxler et al. (1999)
L27	PG4	CCCATCTCCTGCCTGATGC	CACAGCAGGATGCTGCCTGC	TCCA	7	0.466	0.730	0.444	Lee et al. (2007)
L28	PG5	GTTCTTGGTGTTGCATGGATGC	AGTTACGAAATGATTGCCAGAAG	TTTG	3	0.139	0.234	0.083	Lee et al. (2007)
L29	UU-Cli02	TGGGCAAGGTACACTTTTAGGT	CTTTATGCTCCCCCTTGAGAT	CA	9	0.450	0.746	0.505	This study
L30	PG7	CATTGGTCAGGAGGAGGTGGTGGG	TCTGCCACTCACTCGCCCTC	TTG	6	0.420	0.703	0.432	Lee et al. (2007)
L31	UU-Cli01	TCCTTACTGCGTTTCTCTCCTC	AAAGAGAGGGCACTGATTTGAA	CA	4	0.370	0.555	0.262	This study
L32	CliμD11	CCAATCCCAAAGAGGATTAT	ACTGTCCTATGGCTGAAGTG	CA	12	0.485	0.783	0.434	This study Genbank G73194.1 (Achmann et al., unpublished)
	Mean				9.4	0.362	0.595	0.342	
	SD				5.1	0.159	0.224	0.177	

N_A, number of alleles per locus; H_O, observed heterozygosity; H_E, expected heterozygosity; D_{est}, estimator of actual differentiation [1].

Table S3, related to Figure 1. Pairwise D_{est} values for breeds with N≥3 individuals.

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ANC  0.125
ARA  0.132 0.155
ARC  0.191 0.150 0.132
ASR  0.107 0.127 0.164 0.216
BIR  0.073 0.094 0.099 0.120 0.124
BST  0.148 0.128 0.119 0.181 0.146 0.103
BUP  0.126 0.236 0.049 0.195 0.231 0.105 0.150
BUT  0.148 0.090 0.103 0.133 0.168 0.065 0.105 0.090
CAU  0.145 0.197 0.160 0.173 0.210 0.200 0.259 0.113 0.218
CHO  0.106 0.142 0.080 0.126 0.238 0.078 0.153 0.129 0.136 0.152
CUM  0.220 0.190 0.156 0.211 0.199 0.178 0.190 0.111 0.145 0.177 0.193
DAG  0.222 0.116 0.165 0.157 0.089 0.080 0.125 0.278 0.098 0.243 0.186 0.179
DAT  0.074 0.091 0.144 0.093 0.119 0.056 0.049 0.099 0.080 0.171 0.059 0.158 0.107
ENC  0.152 0.128 0.168 0.162 0.077 0.075 0.094 0.194 0.098 0.267 0.159 0.127 0.037 0.146
ENP  0.245 0.304 0.133 0.184 0.179 0.167 0.159 0.146 0.163 0.235 0.177 0.270 0.203 0.090 0.226
ENT  0.152 0.147 0.162 0.140 0.150 0.139 0.179 0.159 0.144 0.165 0.203 0.232 0.191 0.113 0.180 0.184
FAN  0.200 0.217 0.099 0.240 0.252 0.177 0.237 0.132 0.128 0.257 0.155 0.194 0.260 0.165 0.223 0.214 0.274
FER  0.085 0.128 0.067 0.099 0.106 0.036 0.093 0.036 0.066 0.113 0.098 0.146 0.102 0.071 0.025 0.156 0.084 0.166
FRL  0.210 0.213 0.155 0.131 0.241 0.224 0.202 0.233 0.125 0.232 0.180 0.332 0.205 0.160 0.167 0.200 0.120 0.173 0.128
GAP  0.218 0.302 0.153 0.270 0.275 0.170 0.206 0.170 0.256 0.223 0.249 0.264 0.243 0.175 0.309 0.179 0.327 0.162 0.150 0.314
GEB  0.086 0.190 0.104 0.165 0.073 0.122 0.169 0.184 0.203 0.160 0.116 0.151 0.080 0.087 0.072 0.179 0.131 0.197 0.064 0.171 0.173
HEL  0.107 0.107 0.053 0.134 0.160 0.060 0.053 0.107 0.062 0.210 0.111 0.162 0.116 0.078 0.088 0.161 0.144 0.150 0.076 0.145 0.236 0.140
HOP  0.088 0.158 0.073 0.133 0.118 0.063 0.137 0.071 0.119 0.121 0.100 0.194 0.145 0.078 0.136 0.110 0.141 0.166 0.049 0.160 0.137 0.070 0.079
ICE  0.167 0.161 0.086 0.145 0.232 0.120 0.166 0.118 0.145 0.098 0.063 0.201 0.181 0.115 0.139 0.159 0.135 0.138 0.067 0.123 0.228 0.158 0.112 0.088
INF  0.112 0.108 0.076 0.198 0.168 0.098 0.093 0.056 0.087 0.156 0.118 0.204 0.189 0.072 0.145 0.179 0.106 0.080 0.091 0.135 0.253 0.179 0.085 0.094 0.113
ITO  0.124 0.115 0.164 0.144 0.168 0.075 0.147 0.177 0.066 0.231 0.124 0.223 0.103 0.103 0.131 0.209 0.127 0.213 0.069 0.172 0.261 0.153 0.107 0.160 0.097 0.139
JAC  0.270 0.268 0.229 0.315 0.321 0.244 0.195 0.260 0.262 0.273 0.270 0.369 0.225 0.276 0.215 0.301 0.326 0.401 0.180 0.220 0.290 0.321 0.217 0.214 0.175 0.295 0.218
KIN  0.177 0.239 0.048 0.186 0.219 0.123 0.220 0.043 0.121 0.208 0.156 0.211 0.204 0.193 0.157 0.184 0.153 0.105 0.074 0.205 0.153 0.186 0.171 0.112 0.144 0.084 0.188 0.246
KOT  0.165 0.077 0.151 0.237 0.141 0.081 0.047 0.202 0.066 0.225 0.195 0.149 0.137 0.102 0.082 0.280 0.165 0.198 0.115 0.180 0.329 0.205 0.084 0.208 0.154 0.110 0.193 0.194 0.174
LAH  0.161 0.125 0.088 0.110 0.097 0.096 0.084 0.123 0.062 0.136 0.192 0.119 0.072 0.054 0.083 0.113 0.133 0.187 0.078 0.142 0.159 0.126 0.060 0.058 0.143 0.113 0.155 0.276 0.118 0.106
MAP  0.191 0.268 0.182 0.273 0.178 0.186 0.335 0.153 0.214 0.174 0.183 0.206 0.147 0.193 0.143 0.243 0.159 0.149 0.095 0.288 0.064 0.111 0.185 0.157 0.163 0.207 0.208 0.346 0.143 0.213 0.181
MOD  0.201 0.250 0.093 0.159 0.242 0.137 0.204 0.110 0.124 0.252 0.131 0.246 0.183 0.234 0.178 0.212 0.206 0.172 0.104 0.148 0.223 0.241 0.115 0.119 0.109 0.087 0.133 0.241 0.083 0.254 0.188 0.173
MOO  0.234 0.118 0.136 0.263 0.230 0.106 0.175 0.252 0.131 0.251 0.170 0.221 0.151 0.181 0.176 0.309 0.226 0.243 0.143 0.221 0.290 0.178 0.161 0.203 0.206 0.121 0.158 0.337 0.140 0.131 0.164 0.235 0.174
NOC  0.164 0.254 0.195 0.201 0.187 0.107 0.184 0.091 0.182 0.162 0.167 0.262 0.187 0.184 0.221 0.144 0.278 0.196 0.092 0.274 0.092 0.164 0.167 0.023 0.173 0.177 0.203 0.339 0.203 0.321 0.179 0.123 0.171 0.280
ODC  0.158 0.187 0.190 0.208 0.225 0.119 0.124 0.171 0.147 0.176 0.183 0.240 0.202 0.119 0.178 0.157 0.210 0.266 0.089 0.194 0.209 0.220 0.124 0.118 0.127 0.128 0.137 0.139 0.185 0.225 0.155 0.307 0.108 0.226 0.145
OGO  0.056 0.140 0.111 0.179 0.125 0.072 0.173 0.173 0.156 0.217 0.105 0.222 0.194 0.061 0.159 0.228 0.165 0.225 0.126 0.258 0.258 0.142 0.155 0.130 0.174 0.089 0.141 0.225 0.164 0.169 0.126 0.262 0.206 0.152 0.249 0.145
ORF  0.113 0.112 0.133 0.192 0.219 0.111 0.213 0.091 0.116 0.240 0.074 0.167 0.207 0.076 0.234 0.225 0.287 0.156 0.154 0.251 0.275 0.141 0.113 0.141 0.141 0.081 0.105 0.328 0.215 0.197 0.147 0.307 0.200 0.130 0.213 0.191 0.067
ORR  0.129 0.063 0.074 0.134 0.157 0.038 0.080 0.134 0.075 0.215 0.087 0.205 0.113 0.047 0.102 0.163 0.120 0.126 0.057 0.136 0.203 0.121 0.035 0.108 0.099 0.077 0.069 0.260 0.132 0.109 0.080 0.216 0.134 0.114 0.172 0.147 0.141 0.115
PAT  0.139 0.146 0.095 0.129 0.189 0.052 0.121 0.184 0.077 0.233 0.148 0.185 0.131 0.111 0.143 0.173 0.200 0.110 0.091 0.185 0.279 0.187 0.084 0.075 0.173 0.068 0.073 0.310 0.093 0.146 0.254 0.146 0.161 0.165 0.169 0.169 0.166 0.112
PER  0.193 0.089 0.114 0.172 0.140 0.048 0.119 0.191 0.048 0.221 0.087 0.203 0.093 0.126 0.081 0.144 0.170 0.125 0.109 0.124 0.317 0.135 0.081 0.165 0.114 0.105 0.103 0.261 0.137 0.088 0.093 0.245 0.107 0.069 0.255 0.191 0.174 0.144 0.028 0.097
PHP  0.139 0.102 0.080 0.144 0.139 0.106 0.113 0.091 0.144 0.121 0.159 0.226 0.191 0.119 0.081 0.184 0.158 0.162 0.039 0.186 0.222 0.150 0.125 0.143 0.087 0.053 0.159 0.190 0.120 0.094 0.135 0.179 0.130 0.209 0.239 0.160 0.138 0.173 0.104 0.115 0.139
PIC  0.181 0.243 0.094 0.222 0.136 0.144 0.222 0.128 0.156 0.133 0.137 0.213 0.166 0.161 0.089 0.201 0.198 0.145 0.054 0.223 0.063 0.102 0.160 0.085 0.128 0.166 0.197 0.285 0.102 0.216 0.099 0.005 0.154 0.206 0.128 0.195 0.180 0.250 0.131 0.232 0.114 0.107
POM  0.136 0.236 0.119 0.132 0.202 0.065 0.182 0.036 0.137 0.104 0.133 0.246 0.191 0.144 0.149 0.149 0.164 0.188 0.044 0.219 0.105 0.103 0.147 0.015 0.134 0.147 0.164 0.263 0.091 0.170 0.095 0.085 0.164 0.293 0.034 0.162 0.224 0.202 0.151 0.116 0.224 0.150 0.085
POT  0.150 0.092 0.075 0.130 0.173 0.067 0.186 0.187 0.104 0.210 0.157 0.197 0.105 0.165 0.096 0.215 0.202 0.214 0.078 0.240 0.255 0.227 0.058 0.126 0.199 0.157 0.116 0.343 0.134 0.121 0.124 0.208 0.182 0.154 0.199 0.207 0.157 0.176 0.120 0.073 0.139 0.181 0.206 0.133
RAF  0.142 0.159 0.075 0.149 0.136 0.084 0.147 0.126 0.135 0.146 0.085 0.259 0.151 0.149 0.160 0.107 0.141 0.136 0.043 0.143 0.067 0.082 0.159 0.088 0.098 0.158 0.083 0.237 0.124 0.234 0.141 0.052 0.093 0.117 0.084 0.165 0.206 0.144 0.116 0.158 0.076 0.093 0.039 0.106 0.147
RAH  0.080 0.092 0.083 0.088 0.065 0.044 0.104 0.102 0.061 0.139 0.102 0.155 0.045 0.054 0.050 0.112 0.099 0.167 0.006 0.113 0.205 0.050 0.082 0.026 0.096 0.068 0.056 0.215 0.087 0.085 0.042 0.136 0.108 0.112 0.092 0.094 0.089 0.087 0.062 0.085 0.088 0.068 0.105 0.068 0.070 0.033
ROD  0.278 0.284 0.222 0.241 0.303 0.234 0.316 0.197 0.189 0.316 0.193 0.265 0.291 0.208 0.326 0.257 0.274 0.162 0.234 0.421 0.240 0.239 0.268 0.229 0.247 0.270 0.382 0.200 0.332 0.261 0.323 0.146 0.273 0.313 0.265 0.328 0.260 0.224 0.308 0.188 0.211 0.304 0.305 0.329 0.249 0.224
RUS  0.101 0.045 0.058 0.125 0.174 0.037 0.094 0.052 0.065 0.097 0.083 0.171 0.163 0.054 0.183 0.249 0.021 0.237 0.009 0.152 0.242 0.112 0.064 0.100 0.137 0.085 0.161 0.220 0.144 0.061 0.119 0.197 0.134 0.121 0.203 0.113 0.125 0.151 0.037 0.123 0.129 0.087 0.161 0.065 0.078 0.120 0.097 0.250
SAM  0.101 0.193 0.140 0.212 0.091 0.111 0.155 0.126 0.082 0.159 0.172 0.223 0.160 0.071 0.152 0.154 0.107 0.174 0.037 0.170 0.249 0.130 0.104 0.148 0.067 0.081 0.098 0.274 0.155 0.126 0.058 0.141 0.144 0.182 0.253 0.131 0.125 0.155 0.119 0.140 0.066 0.062 0.125 0.228 0.154 0.082 0.074 0.252 0.124
SAW  0.172 0.256 0.115 0.167 0.186 0.246 0.161 0.163 0.188 0.182 0.206 0.216 0.343 0.214 0.239 0.280 0.163 0.243 0.124 0.173 0.283 0.176 0.201 0.251 0.100 0.152 0.205 0.243 0.122 0.218 0.157 0.358 0.158 0.279 0.407 0.196 0.187 0.262 0.194 0.208 0.190 0.121 0.235 0.241 0.260 0.254 0.210 0.300 0.188 0.054
SCA  0.217 0.222 0.205 0.210 0.167 0.123 0.090 0.213 0.141 0.234 0.180 0.245 0.099 0.132 0.060 0.244 0.166 0.280 0.087 0.303 0.277 0.188 0.122 0.215 0.180 0.188 0.172 0.273 0.196 0.123 0.146 0.151 0.226 0.240 0.238 0.220 0.128 0.296 0.165 0.251 0.212 0.118 0.110 0.162 0.141 0.137 0.073 0.387 0.143 0.192 0.356
SCM  0.220 0.195 0.229 0.242 0.234 0.190 0.181 0.117 0.140 0.266 0.193 0.321 0.267 0.152 0.230 0.194 0.249 0.293 0.177 0.140 0.293 0.231 0.169 0.194 0.171 0.167 0.209 0.147 0.204 0.170 0.140 0.318 0.233 0.236 0.304 0.213 0.293 0.243 0.147 0.273 0.150 0.178 0.239 0.189 0.303 0.122 0.134 0.354 0.165 0.164 0.122 0.219
SHH  0.094 0.161 0.097 0.130 0.031 0.105 0.124 0.125 0.099 0.179 0.127 0.180 0.085 0.071 0.050 0.154 0.151 0.158 0.017 0.140 0.208 0.068 0.094 0.089 0.131 0.133 0.141 0.298 0.114 0.142 0.053 0.181 0.120 0.117 0.143 0.183 0.067 0.068 0.095 0.149 0.074 0.098 0.071 0.139 0.127 0.048 0.021 0.197 0.067 0.082 0.193 0.083 0.196
TIP  0.092 0.053 0.089 0.081 0.098 0.007 0.065 0.107 0.017 0.161 0.073 0.145 0.051 0.034 0.040 0.155 0.179 0.138 0.023 0.160 0.217 0.134 0.020 0.092 0.081 0.082 0.033 0.202 0.129 0.046 0.093 0.117 0.084 0.165 0.206 0.144 0.116 0.158 0.076 0.093 0.039 0.106 0.147 0.052 0.021 0.197 0.067 0.082 0.193 0.083 0.196 0.068
VIE  0.195 0.110 0.008 0.148 0.164 0.075 0.111 0.019 0.044 0.175 0.090 0.166 0.097 0.170 0.132 0.254 0.237 0.161 0.037 0.237 0.166 0.078 0.076 0.099 0.144 0.117 0.071 0.268 0.090 0.159 0.190 0.154 0.109 0.075 0.115 0.216 0.216 0.121 0.035 0.098 0.056 0.125 0.161 0.143 0.120 0.036 0.047 0.224 0.062 0.131 0.188 0.241 0.207 0.121 0.030
VOS  0.163 0.241 0.207 0.212 0.298 0.187 0.194 0.042 0.138 0.137 0.181 0.227 0.259 0.151 0.219 0.146 0.185 0.237 0.096 0.216 0.170 0.289 0.197 0.088 0.129 0.136 0.179 0.240 0.172 0.308 0.132 0.195 0.174 0.289 0.097 0.121 0.234 0.205 0.180 0.201 0.209 0.150 0.158 0.083 0.221 0.106 0.120 0.242 0.123 0.161 0.209 0.295 0.180 0.220 0.173 0.215
WOE  0.150 0.130 0.053 0.068 0.152 0.026 0.147 0.075 0.018 0.158 0.120 0.199 0.155 0.111 0.107 0.116 0.080 0.144 0.039 0.116 0.265 0.169 0.054 0.190 0.121 0.080 0.109 0.294 0.104 0.108 0.059 0.253 0.136 0.134 0.214 0.148 0.114 0.126 0.045 0.089 0.037 0.088 0.148 0.130 0.075 0.133 0.052 0.205 0.038 0.063 0.158 0.131 0.211 0.098 0.013 0.081 0.181
ZIT  0.187 0.096 0.133 0.198 0.160 0.172 0.080 0.217 0.078 0.209 0.166 0.146 0.080 0.138 0.164 0.154 0.167 0.226 0.138 0.181 0.268 0.210 0.067 0.111 0.167 0.107 0.114 0.187 0.185 0.080 0.073 0.217 0.142 0.142 0.207 0.155 0.161 0.163 0.082 0.134 0.071 0.235 0.236 0.203 0.127 0.131 0.079 0.273 0.133 0.109 0.240 0.251 0.227 0.133 0.063 0.084 0.206 0.132
     AFO ANC ARA ARC ASR BIR BST BUP BUT CAU CHO CUM DAG DAT ENC ENP ENT FAN FER FRL GAP GEB HEL HOP ICE INF ITO JAC KIN KOT LAH MAP MOD MOO NOC ODC OGO ORF ORR PAT PER PHP PIC POM POT RAF RAH ROD RUS SAM SAW SCA SCM SHH TIP VIE VOS WOE
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Table S4, related to Figure 1. Pairwise Nei's F_{ST} values for breeds with N≥3 individuals.

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ANC  0.209
ARA  0.156 0.200
ARC  0.195 0.218 0.180
ASR  0.165 0.202 0.190 0.209
BIR  0.121 0.152 0.131 0.157 0.155
BST  0.202 0.195 0.171 0.209 0.173 0.138
BUP  0.179 0.245 0.176 0.217 0.212 0.174 0.204
BUT  0.193 0.173 0.169 0.202 0.183 0.122 0.161 0.205
CAU  0.164 0.207 0.166 0.201 0.170 0.168 0.214 0.149 0.196
CHO  0.142 0.193 0.136 0.184 0.216 0.133 0.202 0.184 0.181 0.165
CUM  0.227 0.246 0.218 0.250 0.225 0.188 0.245 0.200 0.220 0.203 0.222
DAG  0.226 0.228 0.203 0.225 0.179 0.129 0.218 0.290 0.170 0.236 0.223 0.267
DAT  0.149 0.217 0.166 0.171 0.159 0.103 0.139 0.197 0.159 0.169 0.132 0.210 0.212
ENC  0.203 0.213 0.204 0.213 0.171 0.130 0.181 0.235 0.177 0.213 0.202 0.242 0.156 0.218
ENP  0.289 0.332 0.211 0.274 0.243 0.210 0.235 0.255 0.226 0.258 0.236 0.323 0.319 0.211 0.303
ENT  0.179 0.220 0.194 0.184 0.175 0.174 0.192 0.211 0.185 0.182 0.203 0.241 0.247 0.169 0.221 0.252
FAN  0.215 0.225 0.160 0.226 0.240 0.198 0.237 0.176 0.192 0.194 0.198 0.239 0.269 0.198 0.250 0.281 0.232
FER  0.089 0.118 0.093 0.104 0.102 0.075 0.095 0.099 0.096 0.094 0.103 0.129 0.104 0.082 0.071 0.165 0.102 0.139
FRL  0.199 0.227 0.172 0.160 0.209 0.174 0.193 0.209 0.152 0.187 0.180 0.269 0.225 0.183 0.202 0.248 0.152 0.206 0.103
GAP  0.276 0.342 0.233 0.312 0.287 0.227 0.302 0.246 0.284 0.270 0.271 0.319 0.335 0.273 0.330 0.351 0.302 0.253 0.154 0.299
GEB  0.155 0.276 0.173 0.231 0.164 0.122 0.248 0.248 0.202 0.204 0.164 0.234 0.224 0.193 0.204 0.296 0.216 0.204 0.085 0.186 0.293
HEL  0.160 0.180 0.136 0.186 0.185 0.121 0.138 0.195 0.151 0.187 0.168 0.226 0.213 0.149 0.181 0.241 0.169 0.207 0.096 0.185 0.283 0.194
HOP  0.143 0.239 0.138 0.191 0.167 0.115 0.197 0.175 0.188 0.173 0.148 0.246 0.213 0.160 0.207 0.234 0.201 0.198 0.081 0.179 0.244 0.174 0.157
ICE  0.153 0.172 0.129 0.162 0.183 0.141 0.163 0.152 0.147 0.139 0.116 0.207 0.200 0.141 0.169 0.221 0.156 0.166 0.072 0.144 0.238 0.161 0.149 0.138
INF  0.176 0.203 0.169 0.222 0.185 0.147 0.177 0.180 0.153 0.201 0.176 0.249 0.249 0.169 0.211 0.273 0.156 0.143 0.096 0.175 0.300 0.228 0.173 0.183 0.148
ITO  0.150 0.165 0.157 0.168 0.180 0.125 0.166 0.190 0.122 0.194 0.166 0.225 0.149 0.129 0.162 0.227 0.160 0.208 0.101 0.167 0.249 0.158 0.152 0.161 0.135 0.156
JAC  0.275 0.322 0.233 0.316 0.274 0.201 0.265 0.276 0.272 0.253 0.250 0.354 0.349 0.314 0.288 0.377 0.330 0.309 0.129 0.242 0.391 0.385 0.261 0.255 0.188 0.308 0.196
KIN  0.168 0.198 0.117 0.171 0.190 0.136 0.194 0.119 0.157 0.162 0.175 0.196 0.189 0.160 0.171 0.242 0.171 0.154 0.087 0.176 0.194 0.162 0.170 0.146 0.149 0.133 0.176 0.210
KOT  0.223 0.215 0.193 0.241 0.208 0.152 0.150 0.245 0.168 0.207 0.207 0.232 0.236 0.201 0.202 0.318 0.221 0.106 0.193 0.342 0.248 0.175 0.236 0.166 0.204 0.179 0.317 0.172
LAH  0.177 0.194 0.149 0.183 0.156 0.139 0.154 0.177 0.168 0.176 0.186 0.221 0.169 0.131 0.178 0.193 0.179 0.210 0.099 0.182 0.255 0.192 0.139 0.143 0.165 0.184 0.181 0.252 0.137 0.179
MAP  0.253 0.351 0.231 0.324 0.275 0.199 0.346 0.255 0.269 0.241 0.229 0.315 0.339 0.326 0.347 0.383 0.377 0.154 0.120 0.280 0.222 0.294 0.263 0.264 0.210 0.311 0.224 0.466 0.181 0.347 0.265
MOD  0.212 0.248 0.164 0.202 0.225 0.166 0.230 0.186 0.180 0.200 0.189 0.267 0.235 0.227 0.221 0.289 0.208 0.214 0.110 0.184 0.273 0.228 0.197 0.183 0.148 0.176 0.173 0.268 0.135 0.243 0.190 0.246
MOO  0.201 0.177 0.171 0.221 0.204 0.140 0.196 0.220 0.154 0.203 0.187 0.245 0.188 0.179 0.201 0.290 0.213 0.231 0.107 0.199 0.279 0.187 0.189 0.197 0.154 0.187 0.182 0.279 0.193
NOC  0.226 0.282 0.224 0.252 0.225 0.177 0.251 0.191 0.220 0.201 0.235 0.302 0.270 0.230 0.263 0.272 0.261 0.252 0.133 0.260 0.235 0.239 0.237 0.111 0.209 0.251 0.227 0.325 0.215 0.293 0.226 0.248 0.242 0.264
ODC  0.175 0.184 0.164 0.203 0.189 0.155 0.159 0.165 0.163 0.170 0.189 0.230 0.184 0.133 0.183 0.213 0.166 0.232 0.111 0.174 0.239 0.179 0.163 0.137 0.137 0.157 0.166 0.142 0.168 0.191 0.153 0.224 0.162 0.194 0.207
OGO  0.107 0.193 0.155 0.208 0.173 0.124 0.181 0.178 0.194 0.184 0.145 0.229 0.200 0.114 0.205 0.256 0.181 0.243 0.109 0.205 0.278 0.162 0.180 0.157 0.156 0.148 0.167 0.209 0.177 0.191 0.161 0.246 0.215 0.170 0.255 0.167
ORF  0.160 0.206 0.205 0.240 0.232 0.163 0.225 0.203 0.217 0.220 0.155 0.226 0.263 0.175 0.248 0.298 0.256 0.206 0.129 0.247 0.302 0.213 0.208 0.210 0.171 0.197 0.154 0.309 0.187 0.242 0.213 0.311 0.240 0.204 0.258 0.188 0.129
ORR  0.143 0.119 0.103 0.143 0.156 0.091 0.115 0.151 0.109 0.149 0.135 0.192 0.136 0.098 0.129 0.186 0.141 0.157 0.079 0.144 0.207 0.123 0.083 0.122 0.123 0.117 0.114 0.187 0.135 0.127 0.113 0.184 0.154 0.124 0.191 0.162 0.163 0.153
PAT  0.194 0.203 0.152 0.199 0.216 0.103 0.176 0.219 0.118 0.230 0.196 0.245 0.197 0.172 0.200 0.261 0.213 0.199 0.112 0.197 0.312 0.209 0.159 0.176 0.187 0.164 0.162 0.283 0.197 0.174 0.198 0.291 0.215 0.192 0.252 0.197 0.215 0.222 0.138
PER  0.220 0.214 0.198 0.227 0.206 0.120 0.205 0.257 0.148 0.218 0.181 0.269 0.232 0.205 0.193 0.273 0.225 0.215 0.112 0.182 0.361 0.238 0.183 0.230 0.167 0.210 0.153 0.341 0.173 0.204 0.167 0.341 0.200 0.163 0.295 0.199 0.218 0.252 0.090 0.193
PHP  0.182 0.195 0.153 0.198 0.182 0.146 0.171 0.172 0.174 0.170 0.178 0.223 0.247 0.182 0.162 0.255 0.164 0.188 0.083 0.181 0.280 0.218 0.173 0.198 0.123 0.141 0.168 0.244 0.143 0.168 0.183 0.264 0.182 0.192 0.256 0.153 0.175 0.217 0.135 0.169 0.216
PIC  0.211 0.274 0.188 0.245 0.200 0.178 0.247 0.205 0.218 0.184 0.192 0.277 0.256 0.219 0.206 0.313 0.232 0.207 0.098 0.215 0.200 0.214 0.217 0.202 0.173 0.235 0.194 0.337 0.144 0.252 0.178 0.186 0.217 0.201 0.220 0.195 0.209 0.264 0.144 0.247 0.241 0.196
POM  0.178 0.255 0.171 0.196 0.199 0.137 0.213 0.162 0.193 0.166 0.191 0.259 0.247 0.195 0.215 0.265 0.211 0.224 0.099 0.212 0.234 0.226 0.200 0.124 0.167 0.204 0.170 0.288 0.127 0.226 0.176 0.239 0.203 0.223 0.157 0.171 0.196 0.233 0.154 0.187 0.265 0.191 0.189
POT  0.195 0.203 0.170 0.207 0.215 0.118 0.218 0.251 0.163 0.223 0.197 0.252 0.183 0.210 0.205 0.314 0.227 0.248 0.105 0.220 0.317 0.237 0.157 0.199 0.193 0.217 0.134 0.314 0.178 0.224 0.200 0.284 0.230 0.180 0.250 0.205 0.192 0.225 0.139 0.141 0.236 0.208 0.254 0.220
RAF  0.192 0.279 0.169 0.242 0.199 0.154 0.237 0.205 0.193 0.206 0.176 0.290 0.279 0.233 0.242 0.277 0.234 0.202 0.090 0.195 0.229 0.230 0.216 0.187 0.162 0.238 0.157 0.359 0.158 0.292 0.200 0.271 0.186 0.208 0.203 0.167 0.204 0.255 0.143 0.216 0.238 0.227 0.176 0.204 0.241
RAH  0.113 0.158 0.129 0.144 0.102 0.093 0.144 0.140 0.106 0.125 0.131 0.168 0.107 0.113 0.107 0.180 0.148 0.176 0.049 0.129 0.227 0.115 0.143 0.094 0.116 0.124 0.115 0.190 0.126 0.152 0.110 0.191 0.159 0.145 0.173 0.138 0.116 0.151 0.100 0.138 0.145 0.140 0.153 0.134 0.142 0.133
ROD  0.230 0.275 0.210 0.258 0.246 0.195 0.269 0.234 0.227 0.224 0.203 0.260 0.297 0.249 0.260 0.342 0.245 0.234 0.132 0.225 0.346 0.242 0.232 0.239 0.196 0.242 0.220 0.326 0.190 0.278 0.245 0.336 0.198 0.227 0.290 0.220 0.249 0.242 0.179 0.254 0.241 0.213 0.271 0.263 0.272 0.271 0.201
RUS  0.156 0.189 0.157 0.188 0.182 0.109 0.166 0.188 0.161 0.165 0.147 0.214 0.249 0.167 0.213 0.308 0.147 0.212 0.073 0.175 0.287 0.250 0.136 0.176 0.145 0.183 0.142 0.303 0.153 0.210 0.175 0.315 0.182 0.153 0.216 0.131 0.143 0.226 0.096 0.163 0.215 0.174 0.227 0.200 0.173 0.235 0.131 0.220
SAM  0.167 0.247 0.193 0.225 0.158 0.146 0.202 0.241 0.171 0.192 0.186 0.255 0.266 0.181 0.225 0.281 0.180 0.214 0.084 0.173 0.319 0.237 0.182 0.212 0.129 0.185 0.142 0.354 0.157 0.226 0.154 0.353 0.197 0.190 0.268 0.138 0.161 0.238 0.120 0.203 0.189 0.182 0.245 0.244 0.220 0.215 0.132 0.243 0.223
SAW  0.197 0.258 0.188 0.205 0.202 0.171 0.195 0.222 0.221 0.204 0.210 0.229 0.319 0.224 0.255 0.330 0.205 0.213 0.096 0.188 0.319 0.275 0.212 0.234 0.153 0.203 0.169 0.330 0.134 0.239 0.193 0.388 0.203 0.215 0.303 0.165 0.185 0.230 0.151 0.220 0.264 0.175 0.280 0.234 0.261 0.292 0.176 0.245 0.244 0.219
SCA  0.258 0.325 0.267 0.292 0.230 0.193 0.231 0.296 0.263 0.240 0.245 0.335 0.286 0.273 0.249 0.370 0.285 0.299 0.129 0.276 0.390 0.342 0.255 0.284 0.217 0.289 0.200 0.429 0.215 0.295 0.254 0.414 0.274 0.272 0.308 0.202 0.209 0.320 0.190 0.294 0.347 0.253 0.261 0.249 0.278 0.335 0.164 0.355 0.307 0.345 0.382
SCM  0.245 0.288 0.231 0.271 0.239 0.189 0.243 0.247 0.239 0.246 0.219 0.327 0.335 0.264 0.297 0.326 0.252 0.251 0.132 0.211 0.371 0.310 0.232 0.233 0.174 0.263 0.181 0.331 0.193 0.281 0.214 0.414 0.267 0.232 0.290 0.169 0.236 0.299 0.154 0.249 0.282 0.244 0.308 0.256 0.302 0.278 0.165 0.326 0.290 0.258 0.270 0.386
SHH  0.128 0.183 0.148 0.160 0.102 0.114 0.147 0.173 0.148 0.157 0.144 0.202 0.161 0.127 0.139 0.227 0.168 0.189 0.057 0.159 0.236 0.135 0.145 0.136 0.134 0.160 0.134 0.229 0.141 0.162 0.131 0.221 0.168 0.137 0.194 0.169 0.125 0.153 0.110 0.171 0.160 0.157 0.134 0.172 0.160 0.145 0.076 0.184 0.138 0.136 0.185 0.186 0.217
TIP  0.125 0.138 0.127 0.139 0.125 0.063 0.120 0.177 0.085 0.142 0.126 0.180 0.119 0.104 0.113 0.204 0.157 0.184 0.059 0.154 0.247 0.154 0.098 0.126 0.110 0.137 0.098 0.210 0.134 0.130 0.106 0.207 0.145 0.139 0.191 0.139 0.132 0.169 0.074 0.113 0.115 0.138 0.163 0.150 0.103 0.163 0.065 0.188 0.120 0.133 0.172 0.179 0.194 0.097
VIE  0.221 0.252 0.171 0.253 0.236 0.130 0.242 0.264 0.164 0.227 0.187 0.271 0.251 0.265 0.238 0.363 0.283 0.208 0.100 0.235 0.322 0.286 0.188 0.225 0.191 0.228 0.157 0.419 0.167 0.281 0.236 0.381 0.209 0.182 0.252 0.197 0.211 0.247 0.096 0.175 0.233 0.255 0.280 0.248 0.210 0.296 0.153 0.283 0.229 0.299 0.323 0.416 0.367 0.174 0.139
VOS  0.216 0.268 0.199 0.245 0.240 0.186 0.234 0.115 0.204 0.178 0.212 0.252 0.273 0.201 0.242 0.259 0.221 0.241 0.100 0.214 0.267 0.261 0.227 0.167 0.166 0.205 0.202 0.286 0.175 0.272 0.205 0.264 0.216 0.248 0.187 0.153 0.250 0.188 0.228 0.244 0.309 0.243 0.189 0.187 0.271
WOE  0.183 0.200 0.163 0.176 0.193 0.117 0.192 0.211 0.111 0.181 0.187 0.236 0.209 0.185 0.196 0.225 0.181 0.194 0.090 0.158 0.310 0.210 0.167 0.216 0.156 0.162 0.151 0.317 0.152 0.205 0.170 0.299 0.185 0.166 0.254 0.174 0.177 0.235 0.115 0.147 0.165 0.173 0.238 0.210 0.169 0.226 0.115 0.234 0.185 0.188 0.220 0.276 0.284 0.155 0.096 0.206 0.225
ZIT  0.236 0.237 0.191 0.260 0.222 0.178 0.202 0.252 0.176 0.226 0.216 0.253 0.237 0.226 0.266 0.268 0.227 0.268 0.130 0.222 0.348 0.281 0.189 0.211 0.202 0.214 0.176 0.315 0.212 0.226 0.169 0.378 0.222 0.201 0.285 0.186 0.198 0.240 0.134 0.218 0.203 0.250 0.304 0.261 0.222 0.250 0.153 0.287 0.218 0.222 0.286 0.362 0.311 0.177 0.154 0.253 0.271 0.207
     AFO ANC ARA ARC ASR BIR BST BUP BUT CAU CHO CUM DAG DAT ENC ENP ENT FAN FER FRL GAP GEB HEL HOP ICE INF ITO JAC KIN KOT LAH MAP MOD MOO NOC ODC OGO ORF ORR PAT PER PHP PIC POM POT RAF RAH ROD RUS SAM SAW SCA SCM SHH TIP VIE VOS WOE
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SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Microsatellite identification

Seventeen new microsatellite loci were identified by enriching genomic DNA for $(CA)_n$ dinucleotide repeats [2]. We purified 10 µg DNA from feral pigeon muscle tissue and digested with MboI. We enriched for repeats in the digest fragments using streptavidin beads and a biotinylated $(GT)_{15}$ probe [2], and the recovered fragments were cloned using a TOPO TA Cloning Kit (Invitrogen) and sequenced. Primers flanking microsatellites in the resulting sequences were designed using Primer 3 [3]. The new markers were deposited in Genbank, accession numbers GF111523 – GF111539. Nine additional published microsatellite markers [4, 5] and six unpublished markers deposited in Genbank (accessions in Table S2) were also included, for a total of 32 markers. An M13 sequence tag (5' CAC GAC GTT GTA AAA CGA C 3') was added to the 5' end of all forward primers to allow annealing of a fluorescently labeled oligonucleotide during PCR reactions [6, 7].

Sample collection

Blood samples were collected at local pigeon shows including the Utah Pigeon Club Premier Show (2009), the National Pigeon Association Grand National Pigeon Show (Salt Lake City, 2010), and at the homes of local pigeon fanciers. Additionally, breeders in the USA and elsewhere were contacted using online databases of pigeon organizations and submitted feather samples. Breeders interested in submitting samples were sent feather collection kits and detailed instructions, and samples were returned to us by mail. To increase the geographic scope of our sample, additional feather samples were collected in person at the Bund Deutscher

Rassegflügelzüchter annual show (Dortmund, Germany) in 2009. Collection protocols were approved by the University of Utah Institutional Animal Care and Use Committee, protocol 09-04015, and importation of samples from outside the USA was approved under USDA APHIS permit 110106 to MDS.

DNA isolation

Blood and feather samples from 735 individuals were selected for DNA extraction based on breed and geographical origin. DNA extraction from feathers was carried out using methods described by Bayer de Volo et al. [8]. This protocol was optimized for higher DNA purity with the following modification: after the addition of ammonium acetate and removal of supernatant, two additional spins were performed to remove additional keratin and protein. DNA extractions using blood were performed using 10 µL of blood and either standard phenol-chloroform methods or a DNeasy Blood and Tissue kit (Qiagen).

PCR and genotyping

PCR reactions contained 0.01 µM forward primer with an M13 tag on the 5' end, 0.4 µM each of reverse primer and M13 forward primer with a fluorescent label (FAM, VIC, NED, or PET) on the 5' end, 0.25 U Taq DNA polymerase, and 10 ng genomic DNA in a final volume of 10 uL. Thermal cycling was performed as described by Schuelke et al. [7] and Protas et al. [6]. PCR products were analyzed on an ABI 3100 and allele sizes were determined using GeneMapper v3.7 (Applied Biosystems) using the allele binning function. Each genotype call was also checked manually for accuracy.

To test for sex linkage, 478 samples with sex information were used in a chi-squared test to identify markers with differential overrepresentation of alleles between males and females. Although one marker, CliμD35, showed a statistically significant difference between males and females (p=0.02 after Bonferroni correction) it is probably not located in the sex-determining region of the genome. Only 3 of the 7 alleles exhibit this sex bias and both males and females are heterozygous at this locus ($H_{o(males)}$=0.182, $H_{o(females)}$=0.289, $H_{o(all birds)}$=0.236).

Data set filtering

We excluded individuals with missing genotypes at more than 12 markers, resulting in the retention of 581 of the 735 individuals. We also excluded multiple, related birds of the same breed from the same breeder to avoid overrepresentation of close relatives. Pedigree information was obtained directly from breeders either in person at shows, by phone, or by email. Multiple birds from the same breeder were excluded from the data set if: (1) they were confirmed siblings or parent-offspring pairs, (2) breeders could not positively rule out that birds were siblings or parent-offspring pairs, or (3) we could not contact breeders to establish relationships among their birds. Nearly all individuals in the data set are unrelated by grandparent. The only exceptions are confirmed first cousins in the following four breeds: Marchenero Pouter (2 individuals are cousins), Rafeño Pouter (3), Cumulet (2), and Spanish Little Friar Tumbler (2). The minimum allelic difference between cousins within these breeds is 26%. These samples were included in the final data set because seventeen other pairs of birds in the final data set have <26% allelic differences, including some pairwise comparisons between birds of different breeds. These filters resulted in a final data set of 361 birds from 70 domestic breeds and 2 free-living populations

(Salt Lake City, UT, and Isle of Skye, Scotland), with 90.7% of genotypes represented and a mean sample size of 5.0 individuals per breed.

Linkage disequilibrium tests

We used Arlequin v3.11 [9] to test for pairwise linkage disequilibrium (LD) between markers within breeds and the two free-living populations (number of permutations = 1000, number of initial conditions = 2). A mean of 8.2% of all within-breed pairwise comparisons (2914 of 35,712 overall) showed evidence of LD, but patterns of LD were inconsistent among breeds and were likely artifacts of small sample sizes and/or genetic structure in each breed. No pair of markers showed evidence of LD across all breeds. We also used the web interface of GENEPOP 4.0.10 [10] to test for LD between pairs of markers across *all* breeds simultaneously, which should circumvent LD due to genetic structure within breeds and potentially reveal real genomic linkage among markers. Using this approach, LD was not detected for any locus pair across all breeds. A contingency table could not be constructed for the CliμD28-PG5 pair in the all-breed analysis due to missing data, but these two markers were not in LD in any within-breed pairwise comparison.

Genetic structure analysis

We used STRUCTURE v.2.3.2 software [11] to determine genetic clusters in the entire set of 361 birds, and in a subset of breeds for comparison with Darwin's morphological classification. Both analyses used a 100,000-run burnin followed by 100,000 repetitions, and we used pilot runs to ensure that the burnin period was adequate to achieve stability of F_{ST}, Alpha, and r. Each value

of K was run 5 times using the admixture model and breed/population assignments as priors (LOCPRIOR model). Default settings were used for all other parameters. The Darwin data set was run from K=1-15 (one more than the number of breeds), and the complete data set was run from K=1-25. The number of K values simulated on the full data set was fewer than the number of breeds because our objective was to determine clusters of major breed groups, rather than to examine the structure of individual breeds. We used the web interface of STRUCTURE HARVESTER v0.6.8 [12] to generate concatenated individual and population Q-matrices from the five runs, and these files were used to align the runs using CLUMPP [13] (Greedy algorithm for K=1-6, LargeKGreedy algorithm from K=7-25, with 30,000 random input orders for both algorithms). Results of the five averaged runs for each value of K were plotted using DISTRUCT [14].

Determining the "true" value of K is difficult in STRUCTURE analyses, and many studies rely on biological relevance of the results to determine an appropriate value. Based on the expected number of breed groups, K=9 is appropriate for our data set. We also used the Evanno method [15] for determining K as implemented by STRUCTURE HARVESTER [12]. This method determines the most likely value of K using the rate of change between the log probabilities of the data between successive K values. STRUCTURE HARVESTER determined that K=2 is most likely for the complete data set and for the 40 breeds and one free-living population with >50% membership at K=9 (used to construct the tree in Fig. 2; see below). For the more limited Darwin data set in Fig. 3, we examined genetic structure at K=2, K=3 (the value suggested by the Evanno method in STRUCTURE HARVESTER [12]), K=4 (the same number as Darwin's morphological groups) and K=5.

Phylogenetic tree

Using STRUCTURE, we first identified all breeds that have >50% membership in a given ancestral cluster at K=9. Our goal was to determine relationships among major breed groups, so using a filtered data set could help reduce noise from breeds with complex hybrid ancestry spread across multiple genetic clusters. Individuals from this reduced data set were then grouped into their corresponding breeds and allele frequencies were calculated for each marker. Median allele values were filled in for markers without genotypes for the following breeds and markers (in parentheses): DAT (PG5), ENP (UU-Cli05, UU-Cli06, UU-Cli13, UU-Cli14, UU-Cli15), EST (UU-Cli01), HUN (CliμD19), JAC (CliμT24), LAU (PG5), PIC (PG5), RHR (CliμT17, CliμD28), and VIE (CliμD19). The added allele values account for less than 0.4% of genotypes in the data set and allow the inclusion of these breeds in the calculations of expected heterozygosity, genetic distance, and differentiation statistics. Pairwise Cavalli-Sforza chord genetic distances were calculated among all breeds using the *gendist* program in PHYLIP [16]. A neighbor-joining tree was then constructed using the *neighbor* program in PHYLIP. To assess the confidence of the tree, we generated a 1000-bootstrap data set and constructed a consensus tree using the *consense* program in PHYLIP. A tree graphic was generated using FigTree [17].

Genetic differentiation statistics

Estimated differentiation parameters for markers and populations were calculated using the SMOGD web interface [18]. The D_{est} statistic is especially well suited for genetic differentiation analysis without very large sample sizes in each population [1]. Nei's F_{ST} and heterozygosity statistics were calculated using the *adegenet* module [19] in R [20].

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