CHAPTER 8

Dog conservation and the population genetic structure of dogs

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8.1 Introduction

The domestication of dogs likely began 12,500–30,000 years ago, giving dogs more time to evolve and diversify than any other domesticated species (Clutton-Brock, 2012). Over the course of just 5,000–10,000 generations, dogs adapted to a variety of environments and niches, a process accelerated in many populations by artificial selection. The wide assortment of shapes, sizes, temperaments, and behaviors in modern dogs testifies to the power with which human-directed selection can transform the dog genome to produce novel and desirable phenotypes suited to diverse tasks and predilections. The ubiquitous distribution of dogs across the globe testifies to the dogs' own ability to adapt to a wide array of anthropogenic niches.

In this chapter, we summarize what is known about the genetic and phenotypic distinctiveness of modern breed dogs and free-breeding dog populations, both truly feral populations (like dingoes) and the more common 'village' dog populations that are found throughout much of the world (see Box 8.1 for an explanation of terms). Because of the relatively recent origin (in evolutionary time-scales) of the dog, no dog population can fairly be described as a separate biological species. In fact, dogs can freely interbreed with wolves (*Canis lupus*) and coyotes (*C. latrans*) (Leonard et al., Chapter 7), and hybridization and introgression within the genus can make it difficult to neatly apply traditional species concepts (vonHoldt et al., 2011). Nevertheless, isolation and local adaptation created genetically distinct village dog populations, some of which are now threatened by the encroachment of non-indigenous dogs. On top of this, even genetically similar modern breed dogs demonstrate substantial phenotypic diversity that could interest conservation biologists. In this chapter, we begin by addressing the questions of what one might want to conserve and why. We then proceed to summarize the current state of dog diversity. Finally, we suggest ways to determine which populations should be conserved and present ideas on how to conserve them.

8.1.1 What are we conserving?

As wolves transformed into dogs, they arguably became integrated into our lives in a deeper and more complex manner than any other animal. We maintain working relationships of all sorts with dogs, using them to help us hunt, herd, guard, carry burdens, clear landmines, find missing persons, assist disabled individuals, find illicit substances, and detect cancers (e.g., VerCauteren et al., Chapter 9; Woollett et al., Chapter 10; Koster and Noss, Chapter 11). Depending on the culture of an area, dogs are also used as food and companions. Given this diversity of uses, it is unsurprising that specific kinds of dog are bred to have phenotypic and, perhaps, genetic advantages in performing one or another of these functions. For example, Poodles seem to contain more transcribed olfactory genes than Boxers, probably due to stronger selection on Poodles' ability to smell game and truffles (Tacher et al., 2005). In these cases, conserving dogs with unique abilities will conserve the genetics underpinning them and allow for their continued use and study.

Free-Ranging Dogs and Wildlife Conservation. Edited by Matthew E. Gompper

Box 8.1 Terminology

To clarify our use of terms and to distinguish our use of these terms from other, sometimes conflicting, uses of the same terms, we provide the following guide to terminology used throughout this chapter.

Dogs: Canis familiaris including modern breed dogs, village dogs, New Guinea singing dogs, and dingoes, but not including wolves or coyotes despite their ability to occasionally, albeit rarely, interbreed with dogs.

Breed/Purebred dogs: Dogs that have restrictive breed books and are generally recognized by kennel clubs (groups of dog owners that collectively focus on the breeding, maintenance, and promotion of particular breeds of dogs). Most dog breeds underwent a bottleneck during breed formation with some breeds encountering subsequent bottlenecks and/or inbreeding. *Modern dog breeds* come predominantly from Europe (see Figure 8.2) and developed closed breeding populations sometime during or after the Victorian era of the mid–late 1800s. Boxers and Poodles are examples.

Ancient breed dogs: In ancient times, some dogs were deliberately bred for certain characteristics, although not necessarily with the rigorously maintained pedigree records of modern purebreds. Ancient breed dogs today are purebred dogs with genetic signatures inherited from those dogs, signatures that are identifiably separate from the modern European breeds. Basenjis and Salukis are examples.

Land races: Dogs that exhibit physical traits and behavioral tendencies characteristic of dogs originating in a particular place. These characters have developed over hundreds or thousands of years though adaptation to the local environment, possibly with breeding interference by humans (artificial selection), but without official studbooks (and thus despite interbreeding with sympatric or parapatric dog populations). In many ways they are similar to ancient breed dogs but their breeding is less closely controlled and in most cases (e.g., the Africanis) it seems like the original land races were mostly or completely genetically swamped by modern breed dogs brought to these areas. In other cases these land races may just be local village dogs that happen to comport to a certain physical appearance (e.g., the Indog).

Village dogs: Dogs that live relatively free-breeding and oftentimes partially free-ranging existences as human commensals or mutualists in many places around the world. These dogs are not usually undergoing strong programs of human-directed breeding, but people may preferentially feed, shelter, or cull certain individuals. These dogs' relationship with the local humans and other animals varies greatly depending on cultural and ecological context. They tend to show a genetic signature of their place of origin and tend not to be closely related to major European dog breeds, although in some places (e.g., Central Namibia and much of the Western Hemisphere) they show significant admixture with European-derived dogs (Boyko et al., 2009; Castroviejo-Fisher et al., 2011). We use the term *indigenous village dog* to refer to a village dog that has little admixture with non-native dog breeds and *admixed village dog* to refer to a village dog that has significant admixture with non-native (usually European) dog breeds. Compared to land races, village dogs have a much wider variety of physical appearances within a location. Free-breeding city-dwelling dogs in Russia and India fit this definition, as well as dogs living at the margins of Egyptian society or living in rural villages in Uganda and elsewhere. Populations of admixed village dogs may be consistently replenished by new stray dogs while indigenous village dog populations are usually self-perpetuating, not requiring newly released dogs to maintain their populations.

Feral dogs: Dogs living completely or nearly completely free from human-derived resources (such as trash), for example dingoes. For our purposes of identifying conservation targets based primarily on genetics, we differentiate populations of feral dogs from village dogs based on the interactions most individuals have with people.

Free-breeding dogs: Dog populations with a substantial proportion of dogs that often choose mating partners for themselves, including village dogs and feral dogs. While we acknowledge that there is a range of dog breeding and husbandry practices across the globe, in general village dog breeding involves more sexual/natural selection and less artificial selection than modern breed dog breeding practices. This difference has important implications for the level of genetic and phenotypic diversity found in these populations, and for the diversity found between different populations and breeds. We prefer this term to *semi-feral dogs* because it encapsulates the most important difference between village dogs and breed dogs from a conservation standpoint, which is their mating system and its effects on genetic diversity and adaptation. It is also a more accurate term, as some village dog populations contain individuals that have nearly no interaction with people (truly semi-feral) while others contain mostly individuals that interact extensively with a human owner, but in general most bitches in these populations are either allowed to breed freely with other local dogs or are bred with locally available sires in such a way

continued

Box 8.1 *Continued*

as to not overly skew the variance in reproductive success between males and females or quickly diminish the population's genetic variation.

Introgression: The incorporation of portions of the genome from individuals of one species/population to another through admixture or hybridization and back-crossing.

Species: For sexually reproducing organisms, the biological unit consisting of similar individuals capable of interbreeding and reproductively isolated from other such groups. In dogs, some extreme breeds (Chihuahua and Great Dane) may be physically incapable of interbreeding, but are still genetically compatible and therefore considered the same species. Conversely, although wolves, coyotes, and dogs are all capable of interbreeding and producing fertile hybrids, they are often considered separate species on the basis that hybridization under natural conditions is rare. Where these species are sympatric, they remain genetically distinct even though some hybridization may occur (Leonard et al., Chapter 7).

Artificial selection: Human-controlled selective breeding of individuals for particular traits. In this chapter, we generally use the term to refer to directed breeding of particular individuals or the intentional killing or spaying/neutering of certain individuals, as opposed to the more subtle selection that occurs by favoring some individuals with higher quality resource provisioning.

Nevertheless, for the most part the phenotypic diversity of modern dog breeds is decoupled from the diversity of roles dogs can fulfill. Some phenotypes, like skin wrinkling in Shar Peis or brachycelphaly in Bulldogs, became more extreme during the last century as fewer dogs fulfilled working roles and breeding was driven more by aesthetics. For many of these visible morphological traits, artificial selection for novelty itself, accelerated by careful breeding with managed populations, has generated spectacular phenotypic diversity through the selection and fixation of a small number of genetic variants with major phenotypic effects (Figure 8.1; Boyko et al., 2010). In these cases, conserving these dogs would conserve the unique products of extreme artificial selection, which could help elucidate biological pathways and evolutionary processes.

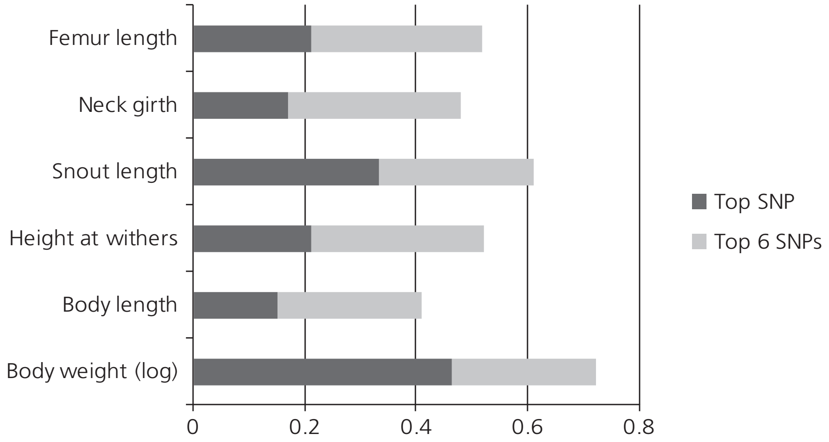

Figure 8.1 Mean proportion of between-breed phenotypic variance in various traits explained by the single nucleotide polymorphism (SNP) with greatest effect and the top six SNPs by effect size. Breed dog phenotypic traits are largely determined by a few SNPs of great effect. This figure shows the proportion of phenotypic variance between 80 breeds of dog (breed average phenotypic values derived from 890 dogs) explained by the SNP with the highest explanatory power and the top six SNPs in terms of explanatory power. For most traits, the top SNP explains about 20% of the variance and the top six SNPs explain more than 40% of the variance for all traits. Except for body size, all of these traits were allometrically scaled against ln (body size). Data are from Boyko et al. (2010).

Beyond morphological differences, dogs vary phenotypically in other ways, most notably in behavior. Surely genetics plays a large role in the distinct aptitudes of herders, pointers, and retrievers, but the genes underlying these traits have not yet been discovered. Still, in many cases various breeds of dogs can perform functions equally well (e.g., markedly reducing depression and negative health outcomes through companionship with nursing home residents, acquired immunodeficiency syndrome patients, and other groups; Nimer and Lundahl, 2007; Perelle and Granville, 1993; Siegel et al., 1999). Conserving a variety of dogs with different abilities and temperaments will give science time to better understand the genetic underpinnings of mental processes and behavioral traits before that remarkably diverse study system is lost forever.

In many regions, village dogs perform jobs such as guarding crops and livestock. For example, the presence of village dogs has been shown to reduce attacks on livestock grazing in northern Kenya by 63% (Treves and Karanth, 2003; Woodroffe et al., 2007). In at least two societies in Ethiopia, 'nurse dogs' help raise babies and small children, cleaning the children and providing warmth and companionship (Fuller and Fuller, 1981). Even free-ranging dogs scavenging human-derived foods might perform valuable roles for human communities. Evidence from India suggests that village dogs consume most of the available human-derived foods in and around agricultural areas, excluding native foxes from the agricultural areas and thus, perhaps, mitigating the potential conflict between foxes and farmers (Vanak and Gompper, 2009). Village dogs could theoretically reduce populations of pest species such as rodents. However, leftover dog meals could also attract rodents (Masi et al., 2010) and dogs themselves carry or transmit some human parasites (Macpherson, 2005). The degree to which genetics has adapted village dogs to perform their various duties is unclear.

At the very least, many of these village dog populations contain genetic adaptations for survival in their local environment. Desert dogs are almost universally lanky, presumably facilitating heat dissipation. Other populations likely contain unique genetic variants to help them survive harsh winters, food shortages, high altitudes, unique diets, parasitic infections, and other biotic and abiotic stresses. Only by careful study of indigenous populations of village dogs fulfilling their natural roles in intact human communities will we be able to discover the genetic basis of their adaptation to these various niches over thousands of years. Village dogs may also perform important sociocultural functions in many societies, and may contain important genetic and behavioral clues for improving our understanding of the evolutionary history of dogs and the process of domestication. Conserving these village dogs will conserve any local adaptations and preserve the selective and demographic history written into their genes.

8.2 An overview of dog diversity

Dogs have diversified in size, shape, and behavior perhaps more than any other mammal (Figure 8.2). This diversification recently accelerated as dog breeders established closed populations for various breeds and deliberately selected some lines for novel or exaggerated phenotypes according to the distinctive standards of each breed. Depending on one's viewpoint, the 400 or so modern breeds of dog persisting today represent either the perfection or the perversion of the canine form, drastically expanding the range of phenotypic diversity present in the dog's wild progenitor, the gray wolf.

Genetic analysis of purebred dogs and wild canids shows that most breeds trace back relatively recently with only a few breeds—the Basenji and a smattering of Asian, Middle Eastern, and Nordic breeds—showing more ancient roots or unique signatures of wolf admixture (Larson et al., 2012; Parker et al., 2004; vonHoldt et al., 2010). Certainly, distinct 'kinds' of dogs were present in ancient times, but most of these either died out (e.g., the English Turnspit dog, Morris, 2002; the Salish Wool dog of the Pacific Northwest, Crockford, 1997) or admixed with other dogs sufficiently to destroy much of their ancient or localized heritage (e.g., Rhodesian Ridgebacks and Pharaoh Hounds; Boyko et al., 2009; Parker et al., 2004, 2007).

Neolithic dogs likely had similar relationships to the humans that lived with them as present-day village dogs do, having fulfilled varied roles in the human communities they associated with. It seems unlikely that they were bred in the same manner as current breed dogs, with closed breed books or

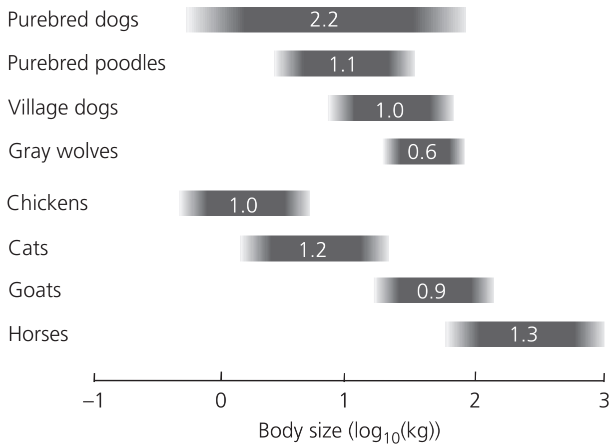

Figure 8.2 Size variation within various groups of dogs, gray wolves, and several domesticated species. Size variation within purebred dogs varies over 2 orders of magnitude, from Chihuahuas weighing less than 1 kg to Great Danes weighing 80 kg. Even within single breeds formed within the last two centuries, size variation can be extreme and similar to the variation found in other domesticated animals (e.g., Poodles vary across 1.1 orders of magnitude). In contrast to breed dogs, the order of magnitude variation in size in free-ranging village dogs is similar to that observed in other domesticated animals. This variation still exceeds that observed across all extant gray wolf subspecies. Data taken from Carroll and Huntingtom (1988), Wayne and Ostrander (1999), Galal (2005), Brooks et al. (2010), Hunter (2011), Henderson (2012), and Boyko et al. (unpublished data).

similar strict protocols guarding the line's purity. Ancient dog populations or breeds that could not be kept isolated from the emerging 'modern' European breeds lost their genetic distinctiveness, a process accelerated in populations with close proximity to populations of modern breeds or with attributes such as small body size that made them easy to transport (Larson et al., 2012; Pires et al., 2009). Deliberate interbreeding of ancient breeds with modern stock also occurred in some lineages, particularly those with breed-defining dominant mutations like the Rhodesian Ridgeback or the Mexican Xoloitzcuintli (Fox, 2003), or those facing dwindling numbers as their utility waned (e.g., Irish Wolfhounds and Finnish Spitzes).

Yet, most dogs throughout history and even today are not breed dogs in any sense, but are free-breeding human commensals (Coppinger and Coppinger, 2001). The population history of these village dogs is potentially much richer than that of modern breeds, which largely reflect genetic variation present in a few dogs in Europe several centuries ago. Village dogs have a nearly global distribution, with most continental populations first established millennia ago. Notably, these village dogs reflect the ancestral stock for all dog breeds, and may represent an important genetic resource for reinvigorating some purebred lineages using outbred individuals related to the breed founders.

Like many modern breeds, some populations of village dogs are also genetic mixtures of several modern European breed dogs that were relatively recently imported to those areas (e.g., Puerto Rican and central Namibian village dogs; Boyko et al., 2009). These dogs resumed a scavenging, free-breeding existence (they are 'secondarily free-breeding'), but they retain little or no localizable genetic signature and do not contain unique genes resulting from local adaptation over millennia. We refer to these dogs as admixed village dogs. Other village dog populations, however, have much more ancient roots and are likely to be very informative for deciphering the origin of dogs and the movement of early dog populations across the globe (e.g., Ugandan village dogs; Boyko et al., 2009). These indigenous village dogs also represent unique genetic resources for understanding local adaptation and may provide unique services to the humans that live with them.

In many ways, indigenous village dogs are intermediate between purebred dogs and wolves. Village dogs, living off human scraps, are mostly freed from the demands of needing to hunt prey and thus have reduced selective pressure on many functional traits. However, without strict breeding controlled by humans, they still must compete for mating opportunities. Even in cases where humans control breeding for some village dogs, sympatric scavenging dogs that are not under human control also contribute to the dog population. Further, these dogs are generally selected for functional traits like greater hunting aptitude, which tends to decrease genetic diversity less than breeding for conformation (Pedersen et al., 2013). Given this, village dogs exhibit more diversity in their behavior and morphology than do wolves, but nothing like what could be seen in an afternoon at the Westminster Kennel Club Dog Show (but see de Caprona and Savolainen, 2013, who argue that a high level of phenotypic diversity co-occurs with a high level of genetic diversity in southern Chinese village dogs). Likewise, even though all dogs (village dogs and purebred dogs) descend from the same ancestral stock, the lack of strong artificial selection in most village dog populations means they have more genetic variants and genome characteristics (e.g., a high level of heterozygosity) in common with the first domestic dogs (and also modern wolves) than purebred dogs, which rapidly lost their genetic diversity in the last few decades or centuries (Calboli et al., 2008). Finally, whereas wolves are a keystone species and clearly an important conservation target from an ecological perspective (Fortin et al., 2005) and purebred dogs are not generally ecologically important (e.g., a keystone species), free-breeding dogs, because they interact with both humans and the natural environment, present an interesting intermediate case. They can potentially mediate the interactions between humans, other domestic animals, and wildlife (Woodroffe et al., 2007; Ritchie et al., Chapter 2; Vanak et al., Chapter 3, Butler et al., Chapter 5) and, at least in some animal communities, act as an important predator species (e.g., dingoes, Johnson et al., 2007; Zimbabwean village dogs, Butler et al., 2004).

Dogs are the only domesticated species that pre-dates the origin of agriculture, and rural free-breeding dog populations likely live a similar lifestyle to that of the very first dogs, mostly choosing their own mating partners while relying on scavenging food from humans (Coppinger and Coppinger, 2001). Whether dogs 'pre-adapted' humans for the Neolithic revolution or not, the fact remains that village dogs have filled an important niche (guard/companion/scavenger) ever since farming communities first existed. As human populations expanded and diversified, so did dog populations, with dogs serving as hunters, sentries, shepherds, warriors, and food animals. Thus, genetic analysis of village dog populations could shed light on theories of dog origins and also yield unique anthropological insights and improve our understanding of the genetic basis of natural and artificial selection.

As dogs spread across the globe, they encountered different geographical features, ecological contexts, and historical events. These led to different selection regimes and demographic histories of the dog populations in different areas. Due to this, the dogs on each continent are not equally useful for preserving the genetic diversity of dogs as a whole. In the following sections we will examine extant dog genetic diversity on each continent, which will inform the discussion of dog conservation that follows.

8.3 Africa

The prototypical image of the proud, independent Basenji of Central Africa evokes a sense of rugged independence and hunting prowess maintained since ancient times. For many Africans, however, a more typical image would be dogs foraging on trash, waste, and animal carcasses on the periphery of human settlements. African dogs have a complex relationship with the humans and wildlife with which they share the continent and an equally complex genetic background. Because of this, there is no simple answer to the question of which African dog populations are especially worthy of conserving.

8.3.1 History of dogs in Africa

Mummified dogs have been found in Egyptian tombs, sometimes sleeping curled at their master's feet, dating from around 4,500 years ago (Ikram, 2005). With deserts, dense forests, and tsetse fly infested savanna to cross, it took about 3,000 more years for dogs to make their way to South Africa (Larson et al., 2012). Thus, no southern African dog has a truly ancient distinctive genetic makeup in the context of the 15,000-plus year history of the dog. However, the diseases and terrain that slowed dogs' initial advance across the African continent also served as a buffer against the subsequent intermixing with European dogs that overwhelmed the local diversity in many places across the globe (Diamond, 1997). This allowed some African dogs to maintain relatively distinctive genetic lineages that provide a glimpse of some of the dog genetic diversity that existed prior to the formation of European breed clubs that instituted closed breed books and ultimately sharply reduced the genetic diversity of European dog populations (Calboli et al., 2008; Larson et al., 2012).

By the time Europeans first visited the Cape of Good Hope in 1652, indigenous people were using dogs to assist in hunting, guarding, and herding throughout the continent (Gallant, 2002). Ridged dogs were present in southern Africa as well as Basenjis north of them in the Congo basin (Gallant, 2002). Both Basenji fanciers and southern African breed (Rhodesian Ridgeback and Africanis) enthusiasts today claim ancient breed status, but recent genetic studies only back-up the claim for Basenjis (Bannasch et al., 2005; Boyko et al., 2009; Larson et al., 2012).

8.3.2 A case study from Namibia

To understand why some ancient dog populations maintained their distinctive genetic signatures while others now appear genetically identical to modern European breed dogs, we consider the distribution of dogs in Namibia. Namibia provides a particularly instructive example in how climate and geography interact with chance historical events to influence dog population histories.

In the late nineteenth century, European immigrants displaced the native peoples and established ranches in the most productive and easily exploited land in German South-west Africa (present-day Namibia). European settlement covered much of the southern 80% or so of the country while the northern area of the country experienced colonial administration without large immigrant-owned ranches (Meischer, 2012). European and South African authorities limited the movement of farm animals from the North to the South of Namibia to prevent livestock disease from spreading to European-owned ranches, eventually building a physical chain-link fence across the country after the Second World War (Meischer, 2012).

The Namibian fence (also called the Red Line) did nothing to prevent dogs from moving freely about the country prior to its physical substantiation and did not actually prohibit their crossing after its construction. However, the fence created a sharp delineation between tropical Africa, with its agriculturally poorer soils and high tropical disease burdens that ethnic Europeans (and their dogs) were not accustomed to, and the more temperate southern lands that were suitable for ranching and harbored fewer tropical ailments.

Although there are now a few modern European breed dogs south of the Red Line, most dogs today on both sides of the fence appear to be 'typical' village dogs, similar to those found throughout much of rural Africa (Figure 8.3): tan, prick ears, short hair, and about 15 kg (Boyko et al., 2009). Since canids naturally have large home ranges, high gene flow, and low genetic differentiation among populations, one would expect Namibian dogs, which are not prevented from crossing the Red Line, to show low genetic differentiation between populations north and south of the Red Line (Wayne et al., 1992). This is especially true given the phenotypic similarity and small geographic distance between dogs on either side of the fence. However, dogs north of the fence averaged 87% indigenous African dog ancestry while those south of the fence had

Figure 8.3 A young bitch (about 1 year old) in Boende, Democratic Republic of the Congo, July 2012. This dog has a standard village dog appearance. Photo credit: Julia A. Randall.

only 9% indigenous African ancestry on average, the rest coming from recent imports of European dogs (Figure 8.4; Boyko et al., 2009). This result is confirmed by other studies that have found southern African dog breeds (e.g., Rhodesian Ridgeback and Africanis) to have significant recent European ancestry and low genetic diversity (Bannasch et al., 2005; Larson et al., 2012). Clearly if one cares about preserving indigenous genetic lines, African dogs north of the Red Line represent a good conservation target. However, within that area, less is known about which populations are genetically distinct; we explore that question below.

8.3.3 Current status of dog diversity in Africa

Outside of southern Africa, relatively little data exist to determine which village dog populations have primarily indigenous ancestry. East Africa had fairly intensive European settlement in some areas and the dogs there may have significant European ancestry, though this is not addressed by any studies to date. Dogs in Giza, Egypt have some European ancestry, though not nearly as much as dogs from southern Namibia (Boyko et al., 2009). A Y chromosome study is consistent with indigenous ancestry for Basenjis as well as some Middle Eastern dogs, supporting the notion that North African village dogs may be primarily indigenous (Bannasch et al., 2005). Mitochondrial DNA evidence shows high levels of diversity in Moroccan dogs as well, although there is likely some European admixture with these dogs given their proximity to Iberia (Pires et al., 2006). Thus, these dogs may be diverse, but that diversity is likely partially due to having a mix of mitochondrial DNA from the African village dog line and from modern European breeds. Given the abundance of nearby modern European breed dogs, these populations are unlikely, at first glimpse, to be the most useful conservation targets for preserving African village dog lineages. Mitochondrial studies have also confirmed that Malagasy village dogs are closely related to indigenous African village dogs and show a higher genetic diversity than other island populations that have been sampled (Oskarsson, 2012). Dogs on the island of Madagascar thus represent another viable African indigenous village dog population.

Outside of the periphery of Africa (southern Africa, Madagascar and other offshore islands, the Mediterranean Coast, and part of East Africa that had colonization featuring European emigrant owned ranches), African dogs may be a generally panmictic population with some fairly small

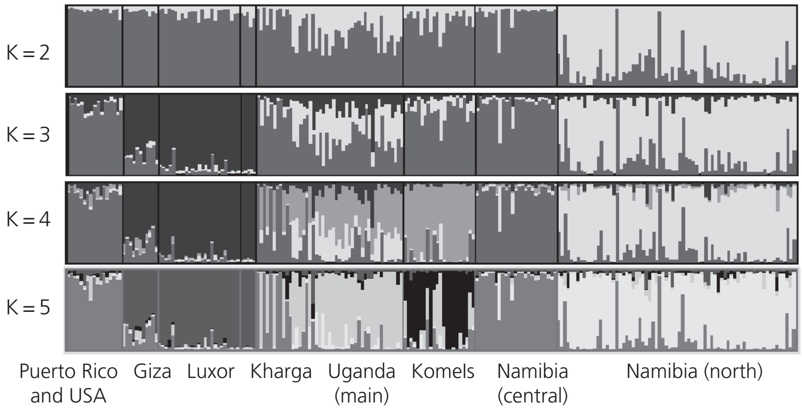

Figure 8.4 STRUCTURE analysis across 389 SNP and microsatellite loci in African village and American mixed breed dogs. Each column represents an individual dog, with dogs grouped by population. Each color represents one of *k* populations, and individuals are colored according the proportion of their genome assigned to each population by the program. Despite being separated by only a few kilometers, central Namibian dogs do not cluster genetically with northern Namibian dogs but rather with European breed-admixed street dogs from Puerto Rico and elsewhere. This figure is based on a STRUCTURE analysis across 389 SNP and microsatellite loci in 223 unrelated African village dogs and 17 American mixed breed dogs (from Boyko et al., 2009).

variations due to natural dispersal barriers such as lakes and deserts. Supporting this idea, dogs from northern Namibia and Uganda, 2,900 km apart, varied little (Fst = 0.025, Boyko et al., 2009). However, dogs from islands in Lake Victoria did vary some from the Ugandan mainland dogs 10–20 km away (Fst = 0.038). Similarly, dogs from the Kharga Oasis in Egypt showed some differentiation from the dogs 230 km away in Luxor (Fst = 0.09). Still, it seems that this variation is most likely due to founder effects and genetic drift and does not represent any lineages distinct from the ones inhabiting most of sub-Saharan Africa above the Red Line. Given the low coverage of genetic studies on African dogs to date, isolated populations representing unique lineages may still be found in remote regions there.

Of course, genetic heritage is only one factor to consider when determining populations to target for conservation. Ridged dogs in southern and western Africa have distinctive appearances and many dedicated enthusiasts and Basenji lovers hold special esteem for rural Congolese dog populations. In southern Africa, just as in more northern sub-Saharan Africa, dogs are used for hunting and may be locally adapted. Dogs in urban environments are often larger and have different temperaments than dogs in rural environments, which enable them to physically compete against other dogs and animals while remaining fearful of, and keeping their distance from, people (R. Boyko and A. Boyko, pers. obs.). These dogs may benefit local people by reducing the number of trash-eating and disease-carrying small animals living in the cities and villages, although little research has been done on the overall effect of dog populations on disease aside from rabies. Some research has shown that having guard dogs may mitigate human–wildlife conflict near the borders of national parks (Saj et al., 2001). Conversely, dogs in some areas can kill wildlife and spread disease to wildlife and people (Ritchie et al., Chapter 2; Knobel et al., Chapter 6).

8.4 Oceania and Island South-east Asia

8.4.1 Dingoes and New Guinea Singing Dogs

Dingoes and New Guinea Singing Dogs (NGSDs) are well-known examples of truly feral dog populations, and are already given some status as conservation targets (Koler-Matznick et al., 2007; Letnic et al., 2012). Genetically, these groups are sister taxa, clearly descended from domestic dogs, but separated from other dog populations for over 4,000 years (Ardalan et al., 2012; Fillios et al., 2012; Oskarsson et al., 2012; Savolainen et al., 2004). No archeological evidence for these dogs exists before this time, so it is likely they were introduced sometime after Australia and New Guinea were separated by rising sea levels approximately 8,000 years ago.

These feral dogs share many ‘primitive’ characteristics, including annual estrus and a lack of barking, suggesting they retain (or, less likely, have regained) characters found in pre-Neolithic and early Neolithic dogs that have been subsequently lost in modern mainland populations. Both dingoes and NGSDs show relatively low levels of genetic diversity, likely due to strong founder effects or low population sizes, and they are at extreme risk of genetic contamination from interbreeding with modern dogs (Corbett, 1995). A recent study found that only 12.5% of the 24 sampled dingoes in south-east Australia had <25% modern European breed dog ancestry (Claridge et al., 2009), though earlier studies using morphological instead of genetic measures suggest that dingoes may be less mixed with modern breed dogs elsewhere on the Australian continent (Stephens, 2011). Indeed, a microsatellite study involving nearly 4,000 dingoes across Australia revealed that a majority of dingoes in central and western Australia, including 87% of dingoes in the Northern Territory, were pure dingo and not hybrid (Stephens, 2011). NGSDs are extremely rare in the wild, limited to elevations above 4,000 m, and captive populations are small and at high risk for inbreeding (Koler-Matznick et al., 2007). Genome-wide analysis of 48,000 single nucleotide polymorphism (SNP) markers showed that dingoes and NGSDs are highly diverged from other dogs (vonHoldt et al., 2010) despite some admixture from European-derived dogs, at least in dingoes. Although distinguishing dingoes/NGSDs from other dogs based on genetic markers is relatively simple due to their strong divergence, so far no studies have identified genetic differences underlying unique dingo and NGSDs traits.

8.4.2 Other dogs in Oceania and Island South-east Asia

In contrast to the truly feral and highly diverged dingo and NGSD, the village dogs found throughout Oceania are behaviorally and genetically much closer to other dog lineages (Irion et al., 2005; Runstadler et al., 2006). Even village dogs in the highlands of Papua New Guinea share more genetic affinity with mainland village dogs than they do with NGSDs (Boyko et al., unpublished data), suggesting perhaps multiple waves of dog migration through Oceania, with the isolation of NGSDs and dingoes prior to the most recent migrations.

The urban street dogs on the island of Bali were one of the first village dog populations to be analyzed genetically, and were found to be intermediate between mainland Asian dogs and dingoes based on microsatellite data (Irion et al., 2005). Despite living on an island of approximately 5,600 km^2 containing fewer than 1 million dogs, Bali street dogs had much more mitochondrial, Y chromosome, microsatellite, and dog leukoctye antigen (DLA; a series of genes involved in dogs' immune function) diversity than the dingoes of 7.6 x 10^6 km^2 Australia, and harbored several unique haplotypes not found in modern dog breeds (Brown et al., 2011; Irion et al., 2005; Runstadler et al., 2006). These data show that dogs were introduced to Bali over 3,000 years ago and have subsequently been isolated from other dog populations (Brown et al., 2011).

Because of their isolation, indigenous island dogs are potentially highly informative for ancestral dog diversity and also human migration patterns and trade routes. Recent analysis of mtDNA shows that modern-day Polynesian street dogs are most closely related to Indonesian and Melanesian dogs, and not to dogs from Taiwan or the Philippines (Oskarsson et al., 2012). However, reaching definitive conclusions about the spread of early dogs in the region based on this relatedness is complicated since some of these mtDNA haplotypes were likely introduced in modern times. Island dog ancestry has implications for understanding the spread and trade networks of Polynesians, although studies using genomic markers will be required to determine whether contamination with modern breeds needs to be taken into account when estimating colonization history. Beyond ancestry analysis, genome-wide datasets from indigenous island dog populations will be particularly useful for detecting signatures of selection that may underlie genetic adaptations to local conditions. Thus far, few island dogs have been analyzed to this resolution, and many island dog populations are still completely uncharacterized.

8.5 Mainland Eurasia

Dogs evolved from Eurasian gray wolves (Vilà et al., 1997; Wayne, 1993). This continent is clearly the cradle of dog origins, and likely contains the oldest free-breeding dog populations. These dogs may carry important clues regarding the evolutionary process and population history of the dog. Mitochondrial and chromosome Y haplotypes in East Asian village dogs, particularly those in southern China, are especially diverse, making this region a diversity hotspot and perhaps the center of origin for the species (Ding et al., 2011; Pang et al., 2009; Savolainen et al., 2002). Southern Chinese village dogs may also exhibit high phenotypic diversity for village dogs (de Caprona and Savolainen, 2013), but systematic, quantitative comparisons with other village dog populations to demonstrate this have not been attempted thus far. Because village dogs are found throughout South-east Asia but Asian dog breeds disproportionately hail from China and Japan (and some of these, such as the Chinese Crested and Pekinese, have mixed Asian–European ancestry; Larson et al., 2012), genetically analyzing village dogs will be particularly valuable for providing a finer-scale geographic pattern to this East Asian center of diversity. Indeed, Brown et al. (2011) recently found mtDNA and Y chromosome diversity as high in village dog populations in far South-east Asia as in southern China, extending the geographic area of known high diversity in Asian dogs. Many potentially important areas (e.g., Myanmar and Bangladesh) have not yet been studied and most other populations have only been studied with uniparentally inherited markers (chromosome Y and the mitochondrion), so there is still much to learn about them.

8.5.1 Asian dogs

Genetic clustering of Asian village dog populations reveals two major groupings: South-east Asian dogs and Middle Eastern dogs (Brown et al., 2011; Ding et al., 2011). The diverse South-east Asian dogs show some affinity with the dogs of Oceania (including dingoes and NGSDs) whereas the Middle Eastern populations, home of the oldest archeological evidence for dogs, share some affinity with European and African dogs (Larson et al., 2012) (although Y chromosome evidence supports a closer relationship between Asian and European dogs than between Middle Eastern and European dogs; Brown et al., 2011). Between these clusters, India has large populations of village dogs (sometimes referred to as 'pariah dogs') that have been studied in terms of anatomy and behavior, as well as a diverse assortment of indigenous breeds. These Indian dog populations have yet to be well characterized genetically. Genetic analysis of Middle Eastern dogs revealed lower overall levels of diversity than in East Asia, but also evidence of localized mtDNA haplotypes (Ardalan et al., 2011; Brown et al., 2011; Pang et al., 2009; but see vonHoldt et al., 2010 who found similar levels of nuclear DNA variation between Middle Eastern and East Asian dogs).

Genome-wide analysis of Middle Eastern dogs and wolves shows that they clearly interbred in the past, and that genes from these wolves may have been critical for the evolution of some dog traits like small body size or limb dwarfism (Gray et al., 2010; Parker et al., 2009; vonHoldt et al., 2010). Thus, Middle Eastern dog populations represent an important genetic resource for understanding dog evolution. The Canaan dog, a land race from the eastern Mediterranean area around Israel and Lebanon, clusters genetically with Middle Eastern purebreds (Afghan Hounds and Salukis) but with lower genetic diversity in the imported stock, suggesting that genetic analysis on dogs in the Middle East will be highly informative (Shiboleth, 2004; vonHoldt et al., 2010). Y chromosome studies also show Canaan Dogs have relatively high haplotype diversity and Canaan Dogs and Salukis have deeply rooted Y chromosome haplotypes, supporting a lengthy evolutionary history with significant population size for these dogs (Bannasch et al., 2005).

In addition to Asian village dogs, Asian Spitz-type dogs, such as the Akita and Chow Chow, also contain some haplotypes not seen in most modern breeds (Larson et al., 2012; Parker et al., 2004). These 'ancient' breeds tend to be strongly diverged from other breeds, which could be a consequence of long-maintained genetic separation from other dogs or simply a product of strong inbreeding (Parker et al., 2004). Dogs appeared in the fossil record over 12,000 years ago in northern China and the Russian Far East, so current Asian Spitz-type dogs and other northern Asian dogs may have a lengthy history apart from other dogs (Cui and Zhou, 2008; Dikov, 1996; Jing 2010a, b). Scientists have not yet tested whether or not any free-breeding populations of northern Asian dogs retain genetic signatures of local, ancient heritage, though this seems likely given the area's social and geographic separation from Europe. Likewise, dogs living in relatively inaccessible places like the high altitudes of Tibet have admixed little with modern breed dogs and exhibit high genetic diversity (Li and Zhang, 2012).

8.5.2 European dogs

Village dogs also occur in many European countries, presenting a possible conservation problem by interbreeding with endangered gray wolf populations (Verardi et al., 2006; Vilà et al., 2003; Leonard et al., Chapter 7). Early European village dog populations were likely some of the founder stock for many of our modern dog breeds. But as the popularity of purebred dogs grew, homogenization of these village dog populations through interbreeding with purebred dogs likely greatly reduced European village dog populations' genetic diversity and distinctiveness, especially in urban areas. Nevertheless, unstudied pockets of ancestral genetic diversity may exist, with isolated free-breeding dog populations and indigenous working dog breeds the most likely candidates to harbor that diversity. Although modern breed dogs with European ancestry continue some ancient European dog genetic lineages, some regions of the continent have few if any representatives in modern kennel clubs. For these regions, studying intact village dog populations or ancient DNA samples are the only methods available to assess their early dogs' genetic history.

The Arctic region of Europe was also important in creating some modern dog lineages. Spitz-type dogs were likely developed here thousands of years ago, in part through accidental or deliberate interbreeding with local wolves (Klütsch et al., 2011; Parker, 2012; Parker et al., 2004; Savolainen, 2006; vonHoldt et al., 2010). In fact, the modern breed descendents of these dogs carry clear mtDNA signatures of this interbreeding with local wolves, having a private haplogroup found almost exclusively in Spitzes (Klütsch et al., 2011; Savolainen, 2006). These village dog populations essentially disappeared as tribal cultures were replaced with modern societies in this region, but through the extraordinary efforts of some individuals, some of their genetic legacy lives on in breeds such as the Finnish Spitz (Morris, 2002).

8.6 The Americas

Before its discovery by Europeans, the American continents teemed with village dogs, including some land races with distinctive phenotypes, such as the hairless Xoloitzcuintli (Morey, 2010; Schwartz, 1998). These dogs were not independently domesticated from North American gray wolves, but were instead brought from Asia by early Americans (Leonard et al., 2002). European colonization not only destroyed great American tribes and empires, but also led to the extinction of nearly every single Native American dog breed, including extremely unique breeds like the Salish Wool Dog of British Colombia (Crockford, 1997). Many dogs likely disappeared as their niches at the feet and trash heaps of Native American peoples collapsed. In other cases, the local dogs may have bred with European-derived dog stock to the point where the pre-Colombian American dog genetic signature was completely lost. The Mexican hairless (Xoloitzcuintli) and its hairless Peruvian counterpart live on, but since hairlessness is a dominant mutation, it is likely that hairlessness survived by introgression of hairless dogs with European stock, leaving the modern American hairless breeds' genomes primarily derived from European breed dogs (Vilà et al., 1999). While one study found no evidence of pre-Colombian American dog mtDNA in 19 Xoloitzcuintli (Leonard et al., 2002), another found some evidence for pre-Colombian American dog mtDNA in the Xoloitzchintli, Chihuahua, and Peruvian hairless (Oskarsson, 2012). Further research will be required to quantify the amount of ancient American dog heritage in these breeds.

8.6.1 Current state of dog diversity in the Americas

The human population of Central and South America today has approximately 10–50% Native American ancestry depending on the country analyzed, with the rest of its genetic heritage coming from European or African ancestors. Thus, in a sense, even tribes that have been lost since European contact, like the Taíno of Puerto Rico, live on in the genomes of the modern population (Bryc et al., 2010; Young, 2011). The Native American dogs, however, did not fare so well. Diagnostic mitochondrial haplotypes discovered through ancient DNA analysis of Native American dog burials are almost completely absent from modern populations, with perhaps the exception of some Arctic sled dogs and possibly a few dogs around the Yucatán Peninsula (Brown et al., 2013; Castroviejo-Fisher et al., 2011; Leonard et al., 2002). At most, 5% of the surveyed dogs descend from ancient American dogs, and the true number is likely much lower (possibly zero). While the 2011 study of Castroviego-Fisher et al. analyzed 400 modern dogs from several isolated areas across the Americas, the sampling emphasized some geographic areas over others and the study only included 13 ancient Latin American samples. It is still possible that certain areas with relatively few modern dogs sampled (such as the south-eastern USA, where the 'American Basenji,' or Carolina Dog, is found) may yield greater levels of Native American dog DNA, or that increased sampling of ancient American dogs will lead to reinterpretation of the study's results. Indeed, a recent study found that all tested Carolina Dog mtDNA haplotypes belonged to East Asian or universal clades, including 37% private haplotypes not found in any other dogs (Oskarsson, 2012). This study lends credence to the hypothesis that feral, free-breeding Carolina Dogs are remnant populations of pre-Colombian American dogs (Brisbin and Risch, 1997). Once again, thorough analysis of isolated dog populations, including the use of genome-wide DNA markers to detect admixture proportions, will be key for determining how much, if any, genetic legacy from this profoundly interesting evolutionary branch still survives.

The Native American Arctic dogs may have fared better than their more southern counterparts. The Alaskan Malamute shows evidence of ancient heritage, forming, along with the Siberian Husky, a distinct clade separate from modern European breeds (Parker et al., 2004; vonHoldt et al., 2010). Modern Malamutes contain significant admixture with modern breeds, but likely retain some ancestry from early American dog lineages such as the Pre-Columbian working dogs of the native Iñupiat people in Alaska's far north-west (Brown et al., 2013; Cummins, 2002). Competitive sled dogs derive over 50% of their DNA from this Malamute–Husky lineage that likely includes some ancient Inuit sled dog ancestry (Huson et al., 2010, 2012). A new study of modern and ancient mtDNA in Arctic dogs shows that modern Eastern Arctic Inuit sled dogs, to a much greater extent than even Malamutes, retain the mtDNA haplotypes found in the pre-Columbian dogs of region (Brown et al., 2013). Most likely, they will serve as a useful population for understanding the history of the dog.

8.7 Conserving dog diversity

As noted in the above sections, the patterns of genotypic and phenotypic diversity in dogs around the world do not match. Phenotypic diversity—at least for the most obvious traits like size, shape, and specialized behavior—is concentrated in breed dogs generally held in developed countries, whereas genotypic diversity is concentrated in indigenous village dogs living mostly in developing countries. This pattern is not unusual for domestic animals. For example, goats are far more numerous in the Asia-Pacific and African regions than in Europe (75% of the goats live in the Asia-Pacific and African regions versus 4% which live in Europe), but Europe has the largest number of described breeds of any region (33%) (Galal, 2005). It does appear, however, that the disconnect between population size (and likely high genetic diversity) and number of breeds (and likely high phenotypic diversity) is particularly large in the case of the dog, as Europe boasts over 80% of the Fédération Cynologique Internationale-recognized breeds while probably containing less than 10% of all individuals (Figure 8.5).

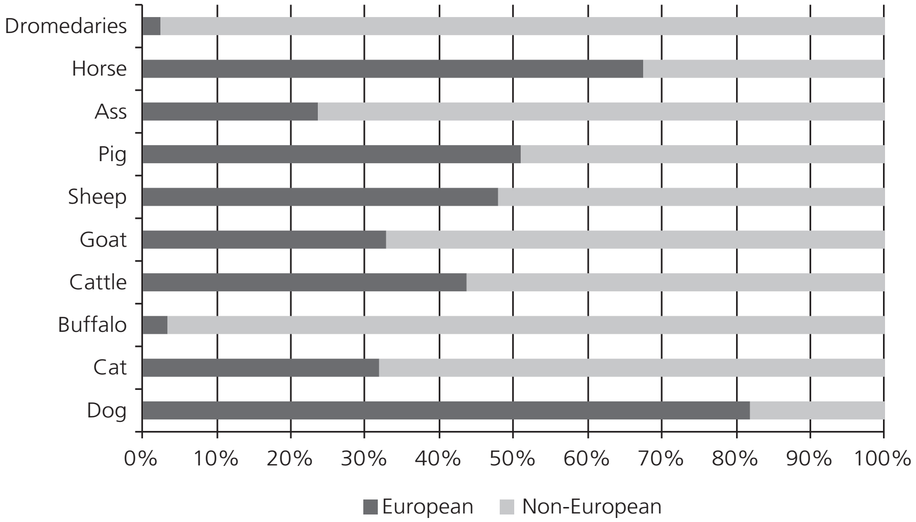

Figure 8.5 Percentage of breeds in each species or species group with European origin. Despite the fact that Europe has <25% of the individual animals of each of these species (Coppinger and Coppinger, 2001; Galal, 2005), it is often the birthplace of half or nearly half of the breeds. In fact, in every one of these domesticated species, Europe has more breeds for every million animals than any other continent. However, that rate is particularly high for dogs, where Europe is home to 82% of the dog breeds recognized by the Fédération Cynologique Internationale. Sources: Galal (2005), The International Cat Association, Fédération Cynologique Internationale.

8.7.1 Conserving village dog diversity

Indigenous village dogs have locally distinct genotypes that are the result of successive founder events, genetic drift, and probably local adaptation, although little progress has been made in identifying signatures of genetic adaptation in these populations. To the extent that these dogs adapted to their different environments, preserving their genetic diversity is important for maintaining healthy populations of well-adapted village dogs across their current geographic range. In fact, undiscovered genetic variants in village dogs could be used to breed disease resistance and other traits into established dog breeds in response to new ecological, economic, or sociocultural factors, as has been considered for other plants and animals of agricultural importance (Oldenbroek, 1999). Separately, there would be some benefit to preserving many modern breeds of dog as well, for the genetic structure of breeds makes it easier to identify the genetics underlying various traits and diseases, including some genetic diseases affecting humans (see Box 8.2).

Box 8.2 The value of dogs as genetic resources

In addition to preserving dogs for intrinsic reasons or for their ecological, economic, and sociocultural value, dogs provide useful genetic resources for studying people and evolutionary processes. Some examples of recent work using dogs to study genetic processes in people and other organisms include:

- *Mapping canine disorders*: Because modern dog breeds are highly inbred with successful males siring dozens of litters, their genomes have long runs of linkage disequilibrium and low heterozygosity (Lindblad-Toh et al., 2005). Taking advantage of this genomic architecture, scientists have mapped the genetic underpinnings of a number of canine disorders much more simply than they could map similar human diseases. In a number of cases, such as narcolepsy and epilepsy, similar human diseases have proven to be caused by similar mutations in loci that correspond to the canine disease variants (Lin et al., 1999; Lohi et al., 2005; Seppälä et al., 2011).
- *Acting as models for gene therapy*: For example, dogs with one form of progressive retinal atrophy that causes blindness were successfully treated using a recombinant virus that then proved successful in treating the human form of the disease (Acland et al., 2001; Ostrander, 2012).
- *Understanding complex inheritance patterns*: Given the genomic resources available for studying dogs, including published genomes, microsatellites and SNP genotyping arrays, as well as the breed structure and extreme phenotypic diversity of dogs, dogs are a model system for understanding the genetic architecture of traits with complex inheritance (Boyko et al., 2010; Wayne and Ostrander, 2007). Multigenic traits in particular are much easier to map in dogs than many other animals (Ostrander, 2012).
- *Understanding artificial selection*: Village dogs are a group of geographically widespread domesticated animals that do not undergo strong artificial selection. Studying their genetics could elucidate the differences between natural and artificial selection, as has been done for selection on size. Between dog breeds, one locus, IGF1, explains 50% of the variation in size (Boyko et al., 2010). The situation is similar in other domestic animals (e.g., four loci explain 83% of the size variation in horses; Makvandi-Nejad et al., 2012). In village dogs, however, the top three SNPs explain only 38% of the variation in body mass (Boyko et al., 2010). While this does not approach the complexity of size determination in humans (697 genes are estimated to explain 15.7% of the variation in human height; Allen et al., 2010), it does suggest that village dogs may be something of an 'in between' in terms of artificially and naturally selected animals. After undergoing an initial domestication event bottleneck they have since been impacted by both human and natural selective pressures. Thus village dogs could elucidate the genomic changes associated with domestication bottlenecks versus those that are the result of continuing, strong artificial selection.
- *Understanding local adaption processes*: Dogs underwent dietary and lifestyle changes during and after domestication. They inhabit nearly every place humans do and share similar food to humans. Genetic analysis of diverse dog populations might help researchers find local adaptations to diet and physical conditions, such as altitude. It may also help us understand complex disease

continued

Box 8.2 *Continued*

processes. For example, dogs are the only animal besides humans to regularly suffer prostate cancer as they age. This likely has to do with their dietary overlap of red meat and fats as well as phytoestrogens in Western food and environmental factors (Coffey, 2001). High fat diets can also cause pancreatitis that can lead to diabetes in dogs (Rand et al., 2004). Studying obesity and metabolic syndrome in dogs helped point out directions for human research into diabetes and related conditions and could do so for other conditions (Kaiyala et al., 2000; Kim et al., 2003).

- *Understanding genomic integrity*: Canids are the only mammals that do not have functional PRDM9 genes which, for all other mammals including humans, localize recombination hotspots in their genomes (Oliver et al., 2009). Dog genomes also contain a highly active, canine-specific SINE_Cf transposable element. Disruptive SINE insertions underlie many important dog phenotypes and possibly contribute to structural instability in some genomic regions (Kirkness et al., 2003). Studying dog genomes will further our understanding of evolutionary processes involved in genomic integrity.

Conserving village dog populations represents a unique challenge. Unlike other canids, village dogs are often found at much higher densities and thrive in urban environments. Traditional canid conservation strategies tend to focus more on keeping population numbers healthy than on preventing admixture between native free-breeding animals and nonlocal purebred or admixed animals (e.g., Ginsberg and Macdonald, 1990). Additionally, attempts at preserving breeds of other domestic animals take advantage of their artificially created population structure and controlled breeding, meaning village dogs require different methods to conserve them. For example, studies on protecting cattle show that native cattle breeds have far smaller population ranges than village dogs, enabling conservation efforts over smaller geographic areas using different tools than required for village dog conservation (e.g., 49 African cattle breeds, Reist-Marti et al., 2003; 20 North European cattle breeds, Kantanen et al., 2000).

Given the inadequate models of conservation available, how should we approach village dog conservation? Because dogs vary so much phenotypically and maintain the ability to interbreed with each other and even with some other canids, recent literature has widely varied in their classification schemes (e.g., in 2012 alone, dingoes have been called *Canis lupus dingo* (Ardalan et al., 2012), *Canis dingo* (Smith et al., 2012), and *Canis familiaris dingo* (Kutt, 2012)). Given the relatively short evolutionary time-scale of the dog and the disconnection between genetic and phenotypic diversity in dogs, we cannot rely on traditional taxonomic units to target which populations to conserve. Systems incorporating ecological differentiation (e.g. Crandall et al., 2000), extinction risk to domestic breeds (e.g., Reist-Marti et al., 2003; Simianer et al., 2003), or evolutionarily significant units (Moritz, 1994) are potentially more viable. However, the amount of ecological differentiation between village dog populations and the factors that increase extinction risk (other than widespread contact with Western breed dogs) are poorly understood. Which ecological interactions need to be considered when conserving dogs is also unknown. In some places dogs may play important roles in their ecosystems. For example, 6% of the dogs in one area in Zimbabwe fell prey to leopards over the course of a year, possibly increasing leopard density and affecting the density of traditional leopard prey (Butler et al., 2004). However, when the alternatives are indigenous village dogs or admixed village dogs living in an area, it is not yet established that a change in the dogs' genetic profiles would have an important effect on the ecosystem.

At this time, we do not have enough genetic, ecological, or sociocultural data to know the geographic extent of various indigenous village dog populations, the number of individuals in the population, the ecological and phenotypic distinctiveness of each population, or the external extinction risk factors for the population. We also do not have enough experience conserving village dog populations to know how expensive this would be, even if we could decide what constituted a single population and which populations we wanted to conserve. Simple answers, such as, 'conserve the ancestral population' do not work, since 'ancient' dog breeds and village dog populations generally derive from isolated areas, not areas with ancient (i.e., archeological) dogs or areas where the dogs' progenitor, the gray wolf, lives (Larson et al., 2012).

With the above caveats in mind, we will try to make some suggestions regarding populations that deserve consideration from conservationists. It seems clear that in the postcolonial era, countries geographically closest to developed countries are the most at risk for losing their indigenous village dog populations to swamping gene flow (e.g., northern Egyptian dogs had relatively high levels of admixture with European dogs; Boyko et al., 2009). Urban dog populations found in large cities that maintain global trade networks are also likely highly admixed. In addition to having a high volume of global trade, urban areas often have spay-and-neuter programs aimed at preventing dog overpopulation and the accompanying public health and safety problems. These programs likely hasten the replacement of indigenous dogs with admixed ones as they prevent many indigenous street dogs from reproducing while allowing owned dogs with nonlocal ancestry to contribute disproportionately to the next generation of street dogs. Isolated or peripheral populations such as those on islands in the Indonesian archipelago (Irion et al., 2005), those on the Tibetan plateau (Larson et al., 2012), those in and around Iran (Brown et al., 2011), those in eastern Arctic North America (Brown et al., 2013; Darwent 2013), and those in Central Africa (Boyko et al., 2009) are most likely to be genetically distinct from modern European breed dogs. However, many village dog populations, like gray wolf populations, are interconnected over large ranges (e.g., African village dogs in Uganda and northern Namibia, separated by >2,000 km, are very similar genetically; Boyko et al., 2009). More work on dog abundance, phenotypic distinctiveness, and genetic relatedness in free-breeding populations is needed to determine where conservation considerations are warranted. Clearly, though, there are some possible target populations on most, if not all, continents.

Deciding which particular populations in each geographic area to conserve and how to do so depends on the goals and resources available. Targeting the most vulnerable populations could have the biggest impact in terms of maximizing the number of distinct dog populations remaining on Earth, but would require an immediate investment of significant resources to fight the forces currently threatening those populations. Conserving currently unthreatened populations would presumably be cheaper and require fewer resources, at least for the moment. Determining which populations are most threatened requires population abundance estimates for dog populations around the world, which currently do not exist, but could be accomplished with reasonable effort. Regardless of which populations are targeted, conserving them could focus on conserving their genetic lineage, conserving most of their extant genetic diversity in a viable population, or conserving them across much of their current range.

The cheapest and easiest solution for 'saving' a population is to choose several non-admixed individuals in the population to form a new dog breed, and then begin to breed them in the traditional manner. To slow the loss of genetic diversity, one could allow some outbred crosses with other non-admixed individuals from the population for as long as the free-breeding population survives. This would preserve some of the unique local genetic information and adaptations, but could result in a highly inbred population and would certainly cause the loss of much of the current population's genetic variation. It would also prevent that lineage from continuing to evolve with changing ecological conditions as dogs have done quite successfully for millennia.

Preserving a viable free-breeding population somewhere within its current range is somewhat more complex, but would enable much of the population's genetic variability to be maintained and allow the population to continue to evolve in response to ecological changes. Such efforts would require the buy-in of the local human population and active efforts to prevent non-local dogs from entering the local breeding population. To achieve that would require public education on the value of local dogs over imported ones, which might also improve the welfare of local animals. Depending on the location, it might involve significant trade-offs regarding spay-and-neuter dog control programs and other conservation and public health and safety projects.

Saving a dog population across most or all of its current range seems prohibitively difficult and expensive given current interest in dog conservation. It would require extensive genetic surveillance and programs tailored to the local social and ecological context across wide geographic areas. In many places, local efforts are already underway to try to conserve indigenous village dog populations (which are often referred to as land races), but current efforts are primarily focused on preserving just a sliver of the present genetic diversity through local breed formation. However, conservation requires effort and money, and these are potential quick and easy wins for conservation if saving particular genetic lineages is an important goal. For example, the Indian Indog, the South African Africanis, and the Indonesian Kintamani dog (Puja et al., 2005) make attractive conservation targets because local people are willing to put the time and effort into conserving them although, in the case of the Africanis, finding enough non-admixed individuals to form a viable breed may be challenging. Geneticists and conservationists could work with these groups to identify dogs that have a high proportion of indigenous DNA and, to the extent possible, represent the range of genetic and phenotypic diversity of local dogs. These dogs could then form the basis of a closed or partially closed breeding group. However, the history of numerous breeds demonstrates that conserving a particular phenotype in a breeding line is much simpler and cheaper than conserving high genetic diversity. It is not clear that dog fanciers would be willing to pay the higher costs and go through the additional effort to conserve a large enough breeding population to encompass most of an indigenous breed's genetic diversity. If long-term conservation of dog populations is important, efforts to save viable populations of free-breeding dogs will need to be undertaken and will most likely need to be led by conservationists coordinating with local dog enthusiasts (Box 8.3).

8.7.2 Conserving breed dog diversity

While conserving purebred lineages is beyond the scope of this chapter, we note that some such lineages (particularly those of ancient or indigenous dog breeds) may be the only genetic descendants left for some endangered or extinct free-ranging or free-breeding dog populations. For example, in the absence of Latin American dog populations with significant Native American dog ancestry, preserving Xoloitzcuintlis or Chihuahuas might be the only way to perpetuate at least some of the early American dog gene pool. Even this would likely preserve only a small portion of the pre-Colombian American dog genetic diversity, mostly that centered on the genes responsible for the phenotypic traits that distinguish these dogs (Leonard et al., 2002; but see Oskarsson, 2012 who argues that there may be more ancient American dog ancestry in today's free-breeding populations than previously thought). In general, genetic distinctiveness is a good measure for identifying breeds that are potential targets for conservation, though extinction risk, phenotypic distinctiveness, and other criteria could also be used as supplemental criteria in identifying breeds for conservation efforts.

Fortunately, there are many individual dog fanciers and breed organizations that can afford to undertake the great efforts necessary to conserve dog breeds. For example, one man, Hugo Roos, single-handedly rescued the Finnish Spitz from extinction in the late nineteenth century, carefully breeding some of the last remaining native Spitz-type individuals (Morris, 2002). The Portuguese Water Dog was also saved largely through the work of one man, Vasco Bensaude, in the 1930s (Braund, 1997). More recently, the Basenji Club of America has opened its studbook twice (in 1990 and 2009–13) to newly imported dogs from the Congo to preserve the breed in the face of genetic disorders very common in American Basenjis due to founder effects (Bell, 2007). These efforts have included difficult and expensive trips to the Democratic Republic of the Congo to bring back native Basenjis. Clearly, there is money available to conserve at least some breeds, though care must be taken not to conserve merely one particular phenotype at the expense of genetic diversity, or worse, attempt to reconstruct a phenotype by the selective breeding of unrelated stock.

8.7.3 Conserving dingoes and New Guinea Singing Dogs

Dingoes serve an important role as top-predator across much of Australia (Johnson et al., 2007; Letnic et al., 2009, 2012; Ritchie et al., Chapter 2). They are genetically distinct from all other dog lineages except NGSDs (Savolainen et al., 2004; vonHoldt et al., 2010). They are also culturally important to Australian aboriginal populations (Meggitt, 1965). In parts of Australia, they are at risk from pest control measures such as baiting and hunting, but in many areas they are most at risk from admixture with local, modern breed dogs (Elledge et al., 2006). Current conservation efforts focus on identifying and removing dingo–dog hybrids as well as mitigating the impacts of human and livestock encroachment on dingo lands (Claridge and Hunt, 2008; Elledge et al., 2006). Understanding dingo behavior and ecology better will also improve dingo conservation. For example, their large home ranges suggest that larger dingo conservation areas are warranted (Claridge et al., 2009).

Although NGSDs are genetically distinct from other non-dingo dog lineages, less work has been completed on NGSD conservation (Koler-Matznick et al., 2007; vonHoldt et al., 2010). These dogs have unique behavioral, ecological, and cultural significance, and are threatened by small population size and hybridization with dogs (Koler-Matznick et al., 2003, 2007). At this point little is known about their population size, except that it is extremely small, probably shrinking, and limited to high altitudes (Koler-Matznick et al., 2007). Indeed, the last confirmed sighting of an NGSD by a scientist occurred in 1989, though there have been a number of reports of sightings by Papuans in remote mountain areas since then (Koler-Matznick et al., 2007). More research is clearly needed.

Box 8.3 Future directions for free-breeding dog conservation

Dogs are a well-studied model species for a number of genetic conditions, but relatively little is known about many of the most threatened dog populations, hampering efforts to conserve non-breed dog populations. The following are some areas in which more study and action could prove particularly useful for conserving dogs.

- More studies are needed characterizing genetic diversity across diverse populations of free-breeding and indigenous breed dogs, particularly for the majority of the genome that is biparentally inherited (unlike the mitochondrion and chromosome Y). Whereas mitochondrial and Y chromosome studies have contributed greatly to our understanding of dog population history, genome-wide studies can detail the role of selection in shaping genetic diversity and provide finer resolution for parameterizing models of demographic history and identifying distinct free-breeding dog populations versus populations that are amalgamations of imported, non-native dog lineages.
- More archeological DNA studies of ancient dogs, particularly in the Americas, are required to better understand what diversity existed and to perhaps start to understand how displacement with modern breed dogs occurred and how that can be avoided in the future.
- Studies of gene expression in various village dog populations could uncover specific phenotypic adaptations these dogs harbor that might make certain populations higher priority conservation targets (e.g., adaptations to specialized diet, extreme altitudes, etc.). These studies may also prove useful for understanding human and other animal adaptations to similar environmental stressors.
- Breeding programs that increase the genetic diversity in certain breeds would better protect the health of individual animals and enable the long-term survival of currently highly inbred breeds.
- Studies are needed to identify breeds facing the threat of extinction and determine which are worthy targets of conservation based on genetic and phenotypic distinctiveness, particularly in breeds that were founded from free-ranging dog populations that have subsequently gone extinct (e.g., Finnish Spitz and Xoloitzcuintli).
- Continued efforts should be made to improve dingo and New Guinea Singing Dog (NGSD) conservation. For dingoes, this involves improving the ability to identify and remove hybrids as well as addressing human encroachment. For NGSDs this involves more basic research in identifying their distribution and numbers and identifying

continued

Box 8.3 *Continued*

threats to the population's survival in any pockets of territory in which it still persists. If no viable populations are found in the wild, zoo breeding programs and possible reintroduction to the wild could be considered.

- Studies demonstrating what benefits local people obtain from keeping indigenous village dogs could be used to convince local people to prefer those dogs over imported ones and could also help galvanize outside individuals and groups to contribute to indigenous village dog conservation.
- More research is required to determine the positive and negative effects that village dogs and feral dogs have on other species' populations (e.g., by fulfilling a top-predator niche or by competing with endangered or threatened carnivore species). Without this, conservation efforts could cause unintended consequences and ultimately fail if, for example, an increase in village dogs in an area reduces populations of the endangered African wild dog, *Lycaon pictus*.
- Investments in vaccination programs in cities and research into better vaccine delivery systems would reduce the negative impact of village dogs, which is a prerequisite for any large-scale attempt to conserve them. Designing and implementing spay/neuter programs that do not result in decreased indigenous dog representation in the next generation is also important to mitigate the conflict between public health and safety and indigenous village dog conservation.

8.8 Conclusions

Over the past several millennia, village dogs spread across the globe and diversified as genetic drift and selection acted upon isolated populations. Particularly in areas with relatively large populations that avoided breeding with imported dogs in recent times, village dog populations maintained a genetic diversity that was lost in modern breeds. These populations bear unique genetic signatures that arose in geographic areas not represented by modern breeds. Unfortunately, many important village dog populations have already been lost, including nearly all of the dog populations that lived in the New World and Polynesia prior to European contact and colonization.

Currently, village dogs still inhabit much of the globe. Some, such as the street dogs in many large cities, are undoubtedly mixes of various indigenous and imported dogs, but many others still occupy traditional niches in the community and retain localized genetic signatures and physical features. The patterning of genetic diversity in these 'indigenous' populations is largely based on geographic separation over centuries or millennia. Particularly in isolated and peripheral dog populations, these dogs likely harbor important undiscovered genetic variants contributing to local adaptation. These adaptations that are not present in modern breeds warrant further study before these populations are lost in our increasingly urban and interconnected world.

Breed dogs also deserve conservation consideration. While most modern breeds are closely related to each other, many harbor unique genetic variants underlying extreme phenotypic differences. Additionally, several ancient breeds from peripheral areas of the dog's range harbor distinct genes derived from older, isolated dog populations or local wolf populations. Some breeds are also particularly useful for biomedical research on the genetic components of disease processes.

Dingoes and NGSDs are free-ranging dogs that represent distinct genetic lineages from all other modern dogs. These dogs require different kinds of conservation efforts than other dogs, as they have been completely free-ranging for millennia. Dingoes, and possibly NGSDs, also play important ecological roles in their environments. Given this, conservation of these dogs is important for maintaining healthy ecosystems and can be accomplished using more traditional conservation methods than will be required for the conservation of other dog populations.

Effective dog conservation requires better definition of the goals of such efforts. Merely maintaining the range of genetic lineages found in modern dogs requires identifying distinct village dog populations and genetically distinct breeds and then conserving a large enough representative sample of these populations. This could potentially be done through the formation of 'new' internationally recognized breeds of dogs from indigenous village dog populations, as is being done in India with the Indog.

Preserving viable free-breeding populations that would conserve genetic diversity, evolutionary potential, and the ecological and sociocultural roles of indigenous village dogs where they are found now would require more intensive conservation efforts aimed at keeping modern breed dogs out of areas with indigenous village dogs. It would also require working with local human populations to balance dog conservation with the conservation of nearby wildlife and with public health and safety. This would be most helpful in areas still practicing traditional hunting, farming, or ranching, where indigenous village dogs directly assist people and are not at such high population sizes that they constitute a significant risk to public safety.

However, in some areas individuals may prefer to breed their dogs with modern breed dogs that are often larger or have other desirable traits. In these areas, local support for conservation of indigenous village dogs may be harder to achieve and might crucially depend on trying to change the hearts and minds of individual dog owners to believe that owning local dogs is preferable to owning imported ones. If this cannot be achieved, we note that rapid evolution and successive waves of colonization have been the norm for dogs as long as they have existed. The continuation of free-breeding populations in areas where they currently exist, even if those populations are already admixed or become admixed in the future, would allow dogs to continue to adapt to these local conditions. Given the demonstrated ability of dogs to adapt to a wide variety of human-associated niches, the conservation of indigenous village dogs' ecological and sociocultural roles may not necessarily require the conservation of indigenous village dogs themselves. However, indigenous village dogs adapted to local conditions over many centuries or millennia, and their ancestral populations presumably started with more genetic diversity than modern breeds have. Therefore, conserving indigenous village dogs does seem preferable wherever possible.

Ultimately, conservationists must decide if saving those indigenous populations is feasible, or if they should instead focus on conserving dogs' roles in a local community. If conservationists do not protect indigenous free-breeding populations, some benefit might come from creating a new breed by saving a few representative members of an indigenous village dog population before it is swamped by modern breed dogs.

Alternatively, a focus on preserving phenotypic variation in dogs would require a greater focus on conserving modern breed dogs as well as efforts to find genes responsible for local adaptation and other distinctive traits in indigenous village dog populations. Such a focus would preserve specific alleles of large effect and allow dogs to continue to serve as a model system for understanding artificial selection and for discovering the genes underlying many interesting traits. It would, however, reduce dog genetic diversity and likely limit their potential to evolve new adaptations and traits of interest in the future. It would also make it nearly impossible to use genetics to detail the history of the dog. Further, many of the breeds with the most distinctive traits are not currently in danger of extinction and conservation efforts for most breeds are probably unnecessary.

As a broader point, biologists should consider dogs' remarkable adaptability when planning conservation efforts. Dogs followed humans across the globe and thrive in a remarkable number of niches in every environment humans live in. They exhibit enormous phenotypic variation. Conservation efforts aimed at merely maintaining the status quo, such as by forming local breeds with closed breed books and strict phenotypic conformation standards, short circuit dogs' hallmark trait of adaptability. The extent to which conservationists should prevent continuing genetic change, or even prevent the spread of non-native dog genetic material in indigenous populations, is an open question without a clear objective answer. Interventions aimed at mitigating human impacts, such as reducing the number of modern breed dogs breeding with indigenous village dogs, are probably more defensible than those aimed at reducing the effects of more localized or 'natural' population processes, but even these need to consider the wishes of the local human population and the fact that dogs have been colonizing and recolonizing territories for many millennia to produce the present-day distribution of dogs (e.g., Li and Zhang, 2012).

Regardless of what people choose to conserve, more research is needed to fully catalogue the genetic diversity found in modern dogs and to understand the range of uses people in different areas of the world have for their dogs. Once that is completed, it will be easier to identify distinct populations and choose appropriate conservation goals. A closer working relationship between dog enthusiasts, conservationists, and scientists would make it easier to coordinate in making these decisions and allocate funds to the most pressing conservation issues.

Dogs will undoubtedly live on in the world for centuries to come. However, most of the genetic diversity found in dogs will be lost if the diverse indigenous village dog populations alive today vanish or are replaced with non-native imported modern breed dogs. Without a concerted effort, some populations will certainly be lost as globalization brings more competition from non-native imported dogs and changes the structure of the human communities to which native dogs have adapted. In many cases the imported dogs and their purebred or admixed offspring may benefit from human breeding and dog control practices, such as spay/neuter programs. Given the sentimental, economic, and sociocultural value of dogs to many people, and their value as a model organism for studying the genetic underpinnings of biological processes, it is clear that humanity would lose much if we did not save at least some of these unique populations.

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