

Wild Furbearer Management and Conservation in North America



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CHAPTER 16: GENETICS FOR FURBEARER MANAGEMENT AND CONSERVATION



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Chapter 16: Genetics for Furbearer Management and Conservation

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GENETICS FOR FURBEARER MANAGEMENT AND CONSERVATION

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A chapter on genetics was absent from *Wild Furbearer Management and Conservation in North America* (Novak et al. 1987) because, at the time, biologists were only beginning to recognize the importance of genetic factors in maintaining wildlife populations and the potential for genetic tools to provide insight into the ecology and evolution of these species. Since then, the relatively nascent field of **conservation genetics**, and its expansion to **conservation genomics**, has developed into an integral component of furbearer management and conservation (see Box 16.1 for a glossary of terms presented in bold text throughout this chapter). The field is quickly evolving, and the past decade has included particularly rapid advances in genetic understanding, techniques, and tools that open exciting new avenues for research and application, but also incite bewilderment at the dizzying array of changing and emerging approaches. In this chapter, we provide some foundational information on deoxyribonucleic acid (DNA) and its use in furbearer management and conservation to help biologists. Specifically, this includes: 1) gaining familiarity with key terms and concepts needed to effectively communicate and collaborate with geneticists, 2) increasing awareness of the types of questions DNA can help address and some specific empirical examples, and 3) providing resources to help make informed decisions when designing or conducting research where genetic samples may be appropriate.

THE BASICS OF DNA

Like other methods for studying furbearers, such as camera-traps, track-plates, or traps, the use of DNA has strengths and limitations that are important to understand and consider for deciding if it is an appropriate tool for the application (Taberlet et al. 1999, Mills et al. 2000, Waits and Paetkau 2005). DNA encompasses some key features that make it a particularly useful and flexible tool to study furbearers and other organisms. First, DNA is a universal molecule and serves as the blueprint that influences the structure and function of all living organisms. Thus, advances

made to study humans or other model organisms often may be transferable to non-model, rare, novel, or under-studied species. Indeed, the management and conservation of some furbearing species has been catapulted ahead by leveraging genetic resources developed in closely related model organisms. For example, genetic studies of bobcats (*Lynx rufus*; Reding et al. 2012, Fraser et al. 2018, Tucker and Broman 2024 [Chapter 36]) and Canada lynx (*Lynx canadensis*; Schwartz et al. 2002, Rueness et al. 2003, Cardoza et al. 2024 [Chapter 37]), and similarly, coyotes (*Canis latrans*; Sacks et al. 2004, DeCandia et al. 2019, Gese and Patterson 2024 [Chapter 28]) and gray wolves (*Canis lupus*; Roy et al. 1994, vonHoldt et al. 2016, Boyd et al. 2023 [Chapter 32]), have benefited from the high quality and early availability of **genetic markers** (i.e., molecular markers) and sequenced genomes for the domestic cat (*Felis catus*; Menotti-Raymond et al. 1999, 2005; Pontius et al. 2007) and domestic dog (*Canis lupus familiaris*; Ostrander et al. 1993, Breen et al. 2001, Debenham et al. 2005), respectively.

A second key feature of DNA is that it is abundant in biological material. There may be >1 trillion cells that make up an individual organism, and nearly all of these cells contain DNA molecules. Moreover, except for rare mutations, each of these cells contains identical DNA. Organisms constantly shed DNA-containing cells (e.g., from skin, hair, saliva, urine, and feces) into the environment, leaving signatures of their presence (Thomsen and Willerslev 2015). Thus, a wide range of source material can be selected to best meet the question and situation at hand.

Another important feature of DNA in mammals (and more broadly, in eukaryotes) is that it occurs as two different genomes: **nuclear DNA** (nDNA) and **mitochondrial DNA** (mtDNA). Although these two distinct genomes co-occur in cells, they differ in evolutionary origins and mutation rates, inheritance patterns, size and abundance, and other features. Although most of the DNA (2–4 billion base pairs; Gregory 2005) in a mammal cell is found in the nucleus,

BOX 16.1. GLOSSARY OF COMMONLY USED TERMS IN THE FIELD OF GENETICS.

adaptive genetic variation: Genetic variation detected at genetic markers under natural selection, meaning they have a direct effect on fitness. Adaptive genetic variation is generally more difficult to sample and does not reflect demographic processes as neutral variation does, but is important for examining phenotypic traits and the adaptive potential of populations. See also neutral genetic variation.

ancient DNA (aDNA): DNA extracted from old biological material that can originate from archaeological material, museum skins or skeletal material, or paleontological remains and range in age from tens of years to hundreds of thousands of years old. Ancient DNA is often more degraded and contaminated in comparison with contemporary genetic material.

conservation genetics: A field of biology that uses genetic markers to help conserve biodiversity and manage species and populations. Traditional genetic markers include allozymes, microsatellites, and targeted gene sequences obtained by Sanger sequencing.

conservation genomics: A field of biology that uses genome-wide information to help conserve biodiversity and manage species and populations. Genomic data consist of thousands to millions of loci across the genome of a sample of organisms and are derived from high-throughput sequencing technology. Examples include whole genome resequencing and targeted approaches, such as genotyping-by-sequencing, exome sequencing, single nucleotide polymorphism (SNP) genotyping, and transcriptome sequencing.

direct sample: Tissues collected from live-captured animals, animal carcasses, or museum specimens, which requires handling of a live or dead animal or its body parts (Fig. 16.2). See also noninvasive sample.

effective population size (N_e): The size of a so-called ideal population (e.g., number of males and number of females is equal, all individuals can reproduce and produce an equal number of offspring, mating is random, and the population size remains constant) that would have the same rate of inbreeding or loss of genetic diversity due to genetic drift as the actual population of interest. For most organisms, N_e is substantially lower than the actual population size. N_e is a key statistic for summarizing past population history, assessing current genetic health, and predicting future risk of extinction.

environmental DNA (eDNA): DNA that can be extracted from environmental samples (e.g., air, soil, water), without first isolating any target organisms. eDNA is characterized by a complex mixture of genomic DNA from many different organisms and by possible degradation (i.e., DNA molecules are broken into small fragments by abiotic and biotic factors; Fig. 16.2).

evolutionary significant unit (ESU): A population or group of populations for which genetic and ecological distinctiveness warrant separate conservation priority.

genetic marker: Also called molecular marker, an alteration in a piece of DNA that can be readily detected and used in the laboratory to identify different cells, individuals, populations, or species. Common types of genetic markers include single nucleotide polymorphisms (SNPs) and microsatellites.

genetic monitoring: An approach that uses genetic markers to quantify temporal changes in population genetic metrics (e.g., genetic variation, effective population size [N_e], mixture proportions, population structure, gene flow) or other population and demographic parameters (e.g., distribution and abundance, survival and recruitment, hybridization, pathogens and parasites, social dynamics, and diet).

genetic tagging: An approach that uses DNA, usually obtained from noninvasive samples, to generate genotypes at multiple, independent genetic markers such that each individual animal can be uniquely identified and monitored over space and time. The approach can provide information on abundance, dispersal, pedigree reconstruction, recruitment, space use, and survival.

genome-wide association study (GWAS): An approach used to evaluate genetic markers across the genomes of many individuals to identify genomic variants that are statistically associated with a particular trait.

genotyping: The determination of the nucleotide or length polymorphisms from targeted sites (i.e., genetic markers) previously identified as variable within a population.

introgression: The incorporation of novel genes or alleles from one population or species into another via hybridization and repeated backcrossing of descendants of the first-generation (F1) hybrid individual with individuals from one of the pre-hybridization populations or species.

invertebrate-derived DNA (iDNA): A type of environmental DNA where terrestrial vertebrates (e.g., amphibians, birds, mammals, reptiles) can be detected via their DNA that was ingested by invertebrates (e.g., carrion flies, leeches, mosquitoes, sandflies, ticks).

management unit (MU): A local population that ideally is managed as a distinct unit because of its demographic independence.

metabarcoding: An approach that simultaneously identifies multiple species from a mixed sample (e.g., gut contents, scats, soil, water) by using universal primers and next generation sequencing (NGS) to target standardized, variable gene regions (i.e., barcodes) useful for taxonomic assignment across a range of taxa.

microbiome: The collection of all microorganisms (e.g., archaea, bacteria, fungi, protists, viruses) and their genes that occur together in a particular environment, including in or on vertebrates.

microsatellite: Simple, short repetitive DNA sequences that are ubiquitous across the non-coding regions of eukaryotic genomes (Fig. 16.3). Microsatellites have high rates of mutation and follow simple models of evolution, making them highly polymorphic and informative.

mitochondrial DNA (mtDNA): DNA located in the mitochondria of a eukaryotic organism. It usually consists of 100–1,000 copies/cell, is circular in structure, and is haploid and maternally inherited (Fig. 16.1). See also nuclear DNA (nDNA).

monomorphic: A genetic marker that is not variable across surveyed individuals within a species. See also polymorphic.

nuclear DNA (nDNA): DNA contained within each cell nucleus of a eukaryotic organism. It usually consists of diploid copies of linear chromosomes, one inherited from each parent (Fig. 16.1). See also mitochondrial DNA (mtDNA).

neutral genetic variation: Genetic variation detected at neutral genetic markers, meaning they do not have any direct effect on fitness, and thus are selectively neutral. Neutral genetic variation is widely used for investigating gene flow, historical population sizes, population structure, relatedness, and other characteristics. See also adaptive genetic variation.

next-generation sequencing (NGS): Also called high-throughput sequencing (HTS), NGS is a term used to describe several different modern sequencing platforms that perform sequencing of millions of small fragments of DNA in parallel. These technologies allow for sequencing of DNA much more quickly and at much lower cost than the previously used Sanger sequencing, and as such has revolutionized research in many biological fields.

noninvasive sample: A source of the DNA that is deposited by an animal and can be collected without capturing or directly handling the animal (Fig. 16.2). Examples of sources include hair, saliva, scat, shed skin cells, and urine. See also direct sample.

polymerase chain reaction (PCR): A laboratory technique used to amplify (i.e., copy) a specific DNA target from a mixture of DNA molecules.

polymorphic: A genetic marker with multiple variants that are distinguishable across surveyed individuals within a species. See also monomorphic.

Sanger sequencing: A method that sequences one DNA fragment at a time, and was the most widely used sequencing method for approximately 40 years, before NGS technologies emerged. Sanger sequencing remains in wide use for smaller-scale projects, for validation of NGS results, and to achieve longer sequence reads (i.e., >500 base pairs).

sequencing: The determination of the nucleotide sequence of one or more regions of the genome, including variable nucleotides and non-variable nucleotides.

single nucleotide polymorphism (SNP): A common type of DNA variation where a substitution of a single nucleotide occurs at a specific position in the genome (usually found as only two alleles; Fig. 16.3).

species: A group of organisms that are deemed evolutionarily distinct from other such groups, the specific criteria of which vary depending on species concept (e.g., biological, evolutionary, phylogenetic). All such concepts include that members of a species can reproduce with one another and produce fertile offspring.

subspecies: Groupings of populations within species that share a unique geographic range or habitat and are distinguishable by morphological, ecological, or genetic traits. Although frequently given legislative status, there is no single definition or consistent criteria used by taxonomists to describe subspecies.

zoonotic disease: Infections with the potential to spread between humans and animals.

these linear chromosomes are present in only two copies: one maternally inherited and one paternally inherited (Fig. 16.1). The sex chromosomes (as opposed to autosomal chromosomes) are an important exception, in which the Y chromosome is generally present as a single paternally inherited copy and X chromosome as a single maternally inherited copy in male mammals. In contrast, the much smaller, circular mitochondrial genome (about 17,000 base pairs) may be present in dozens to thousands of copies in a single cell and is maternally inherited (Fig. 16.1).

The abundant copies and maternal inheritance made mtDNA the primary tool for genetic analysis for decades (Avisé 2004). There are several other desirable features associated with mtDNA, including simple genetic structure passed on without rearrangement, elevated mutation rate relative to nDNA (excluding microsatellites and other mutational hotspots), and juxtaposition of conserved regions showing little difference in DNA sequence across taxa with variable regions showing substantial difference between and even within species. It is technically easier and less expensive to

amplify and sequence mtDNA compared to nDNA, and mtDNA provides universal markers that can be readily applied to virtually any mammal species without prior sequence knowledge, provides marker options suitable for intraspecific comparisons as well as deep divergences, and is well-suited for tracing lineages to illuminate phylogenetic histories (Avisé 2004, Ladoukakis and Zouros 2017).

Although mtDNA still plays an important role in genetic studies today, recent technological advances have made nDNA more accessible than previously. The use of nDNA is advantageous in that it provides many independent molecular markers, more accurately reflects **introgression**, is biparentally inherited and thus reveals movement patterns of both sexes, and provides a mix of markers that influence fitness or are selectively neutral (Ballard and Whitlock 2004). Because of their different features, mtDNA and nDNA are best suited to different questions, and studies may use data from both genomes to provide complementary information.

DNA is relatively stable in the environment, degrading more slowly, for example, than protein molecules, which facilitates the use of ancient, historical, or noninvasively collected samples (i.e., partially degraded sources). Although DNA is subject to degradation, particularly in warm, moist, and ultraviolet-exposed environments, usable DNA has been recovered from subfossils dating as far back as 1.2 million years before present (i.e., **ancient DNA** [aDNA]; van der Valk et al. 2021) and from permafrost sediments dating back at least 2 million years before present (Kjær et al. 2022). More commonly, furbearer research has included DNA from museum specimens (e.g., bone, claws, hair, skin, teeth) dating back a century or more to gain insight into temporal questions or extinct populations (e.g., Leonard et al. 2005, Schwartz 2007, Aubry et al. 2009, Brown et al. 2013, McDonough et al. 2018).

Similarly, samples collected from biological materials found in the field (e.g., hair, scat, deposited saliva) or from environmental samples (e.g., soil, snow around tracks, in waterways, from air) provide potentially valuable sources of DNA. However, the viability of partially degraded DNA sources varies tremendously depending on ambient conditions before specimens were collected as well as how they were handled during the curation process or after collection from the field. Because mtDNA is more abundant and potentially more stable than nDNA (Foran 2006), it is often the marker of choice for highly degraded samples. Pilot studies to assess DNA quality may be beneficial prior to embarking on large-scale projects using ancient, environmental, or museum sources of DNA that are likely to be degraded. Additionally, special handling and training in laboratory and analysis procedures are needed when working with degraded DNA to guard against contamination and misleading results (Taberlet et al. 1999, 2012; Wandeler et al. 2007).

One final feature we wish to highlight is that only some regions of the genome code for proteins or other molecules, whereas much of the genome is non-coding (e.g., introns, intergenic regions, microsatellites). In furbearing (and other) species, we can examine **adaptive genetic variation** in functional regions that may be under selection and influence important traits such as pelage and skin coloration (e.g., gray wolf [Schweizer et al. 2016], red fox [*Vulpes vulpes*; Vage et al. 1997, 2003],

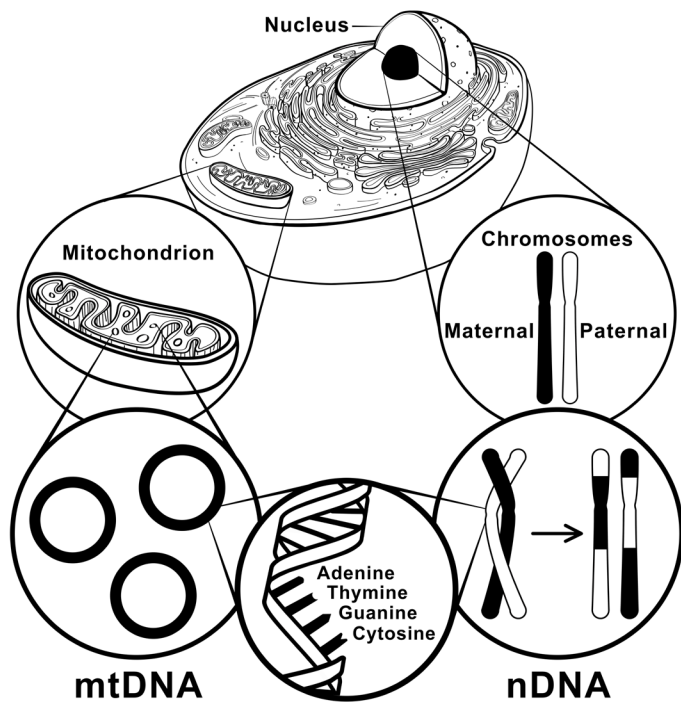


Fig. 16.1. Mammal cells carry two different genomes: nuclear DNA (nDNA) and mitochondrial DNA (mtDNA). The larger nDNA genome is found within the nucleus as linear chromosomes that are generally present in only two copies: one maternally inherited and one paternally inherited. As nDNA is passed on to offspring, the maternal (black) and paternal (white) chromosomes can exchange genetic material to create different combinations of genes. In contrast, the much smaller, circular mitochondrial genome is found within mitochondria, may be present in dozens to thousands of copies in a single cell, and is maternally inherited. Its simple genetic structure is passed on without rearrangement. Although both genomes consist of double-stranded DNA held together by bonds between the four types of nucleotide bases (adenine, thymine, guanine, and cytosine), differences in the abundance, structure, inheritance, and evolution of nDNA and mtDNA often make them suited to address different questions. Image by A. Allen, Photon Illustration, Michigan, USA.

Virginia opossum [*Didelphis virginiana*; Nigenda-Morales et al. 2018]), immune function (e.g., northern raccoon [*Procyon lotor*; Kyle et al. 2014], wolverine [*Gulo gulo*; Rico et al. 2015]), or hypoxia resistance (American pika [*Ochotona princeps*; Lemay et al. 2013]; gray wolf [Schweizer et al. 2016]). More commonly, we access non-functional or neutral regions that simply serve as markers recording population history. Such **neutral genetic variation** can be used as DNA fingerprints to identify unique individuals or distinguish family relationships, or they can be used to inform us of current or historical (and changes in) population parameters, such as genetic diversity, gene flow, **effective population size**, and hybridization and introgression.

SOURCES OF DNA

The utility of DNA as a tool for furbearer management and conservation depends on the collection of samples from which DNA can be isolated. Robust samples of DNA are most reliably collected from blood or tissue samples, but can also be collected from materials deposited in the environment by the species of interest (Fig. 16.2). When samples are collected directly from animals (e.g., blood, biopsy-punched ear tissue, buccal swabs, plucked hair or whiskers), we use the term **direct samples**. Direct samples also include tissue collected opportunistically from mortalities, such as hunter-harvested carcasses, vehicle-struck animals, or other remains, such as museum specimens. We note that Taberlet et al. (1999) used the terms nondestructive and destructive to differentiate between these two types of direct samples.

Samples from feces (Höss et al. 1992), saliva deposited on prey or substrates (Ernest and Boyce 2000, Wengert et al. 2014), snagged hair (McDaniel et al. 2000), and urine (Valiere and Taberlet 2000, Akins et al. 2018) are termed **noninvasive samples** because the source material remains after presence of an animal and it can be collected without capturing or disturbing that animal (Taberlet et al. 1999). However, we note the term minimally disruptive samples may be more appropriate when collection of the source material could impact the behavior and fitness of the animal (Lefort et al. 2019). An emerging subcategory of noninvasive DNA sampling, known as **environmental DNA** (eDNA), can be used to detect DNA of furbearers in samples of air, snow, soil, water, or blood-sucking parasites (sometimes called **invertebrate-derived DNA** [iDNA]), such as carrion flies, leeches, and mosquitoes (Dalén et al. 2007; Taberlet et al. 2012, 2018; Carroll et al. 2018; Franklin et al. 2019).

The collection of DNA through direct sampling requires handling a live or dead animal or its body parts. For a live animal, this involves capturing and handling an animal by following strict protocols to minimize stress and harm to that animal (e.g., Sikes et al. 2016). Tissue samples (e.g., blood, ear via biopsy punch) from live animals can provide robust DNA extracts. Biopsied tissue and whole-blood samples provide the highest quality sources of DNA and in quantities that lend to any application. These specimens can be archived for long-term use by many laboratories and most natural-history collections. Given the high value of such specimens, consideration of their collection should be integrated into animal handling protocols whenever possible, regardless of whether DNA is needed for the immediate objectives of the study (DeYoung and Honeycutt 2005).

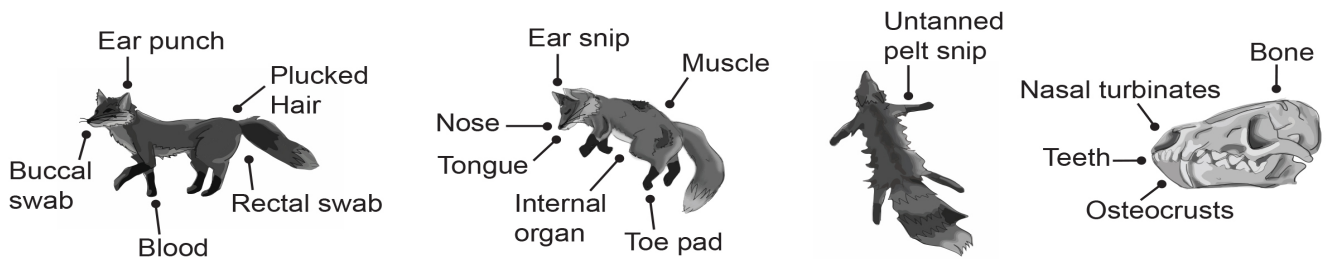
One may also pluck hair (hair follicle must be intact) or obtain buccal-swab samples (Ernest and Boyce 2000) from a captured individual; whereas this kind of sample can produce sources of DNA adequate for many immediate objectives, it is less than ideal for archiving or for several genomics approaches that require greater quantities of DNA. Rectal-swab samples from live-captured animals can also be useful, though primarily for obtaining DNA from microorganisms to investigate pathogens or **microbiome** diversity. Various tissue samples are available from hunter-harvested or vehicle-struck carcasses, including nose, ear tip, toe pad, tongue, any muscle tissue, or visceral organ tissue. When possible, it is best to collect fresh tissue and avoid rotting and exposed tissue that may have degraded and contaminated DNA.

Recently prepared (and untanned) pelts can provide high-quality DNA from toe pads or a small piece of the pelt itself ($\leq 3 \text{ mm} \times 3 \text{ mm}$ [0.1 in \times 0.1 in] is often sufficient). Tissue remaining on bones or gum tissue scraped from teeth can also be a useful source of DNA. Museum specimens are more technically challenging for obtaining viable DNA (Wandeler et al. 2007), and museum collections require justification for using those samples rather than other sources, as museums are responsible for safeguarding resources over the long term. However, if destructive sampling is justified and permitted, sampling dried tissue remaining on the cranium (osteocrusts), drilling into claws or teeth, or extracting scroll-like bones in the nasal passages (nasal turbinates) may provide viable DNA (Wisely et al. 2004, McDonough et al. 2018; Fig. 16.2). Collection of such samples requires very careful handling techniques to avoid contamination. Laboratories that are equipped to handle low-quality and low-quantity DNA, and the unique challenges they pose, are critical in the successful use of such samples (Wandeler et al. 2007).

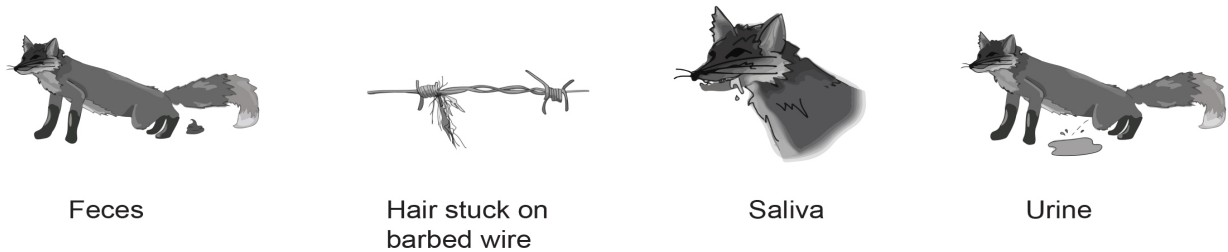
Noninvasive sampling of DNA takes advantage of biological materials that remain after an animal is no longer present (Taberlet et al. 1999, Long et al. 2008). This is advantageous over invasive collection in that there is no need to capture or handle animals, and consequently, no associated stress on wildlife or handlers. This type of sampling has become routine and is informative for furbearer management and conservation (Gese 2001; Gompper et al. 2006; Long et al. 2008, 2011; De Barba et al. 2014). However, noninvasive samples are exposed to environmental factors that degrade and contaminate DNA as soon as they are deposited. Thus, they are often a short-lived resource, and even when collected promptly can produce low-quality and low-quantity DNA, and therefore require additional work in the laboratory to ensure robust results (Taberlet et al. 1999, Pompanon et al. 2005).

Fecal DNA has been used quite successfully to understand movements of individuals, estimate population sizes, and assess relatedness among individuals, which may provide the best option for long-term monitoring of some rare and secretive furbearing species (Lonsinger et al. 2018, Quinn et al. 2019). Salivary DNA has been collected from varied substrates, including bait stations (Statham et al. 2012), depredated carcasses or eggs (Ernest and Boyce 2000, Williams et al. 2003, Blejwas et al. 2006,

Direct



Noninvasive



eDNA

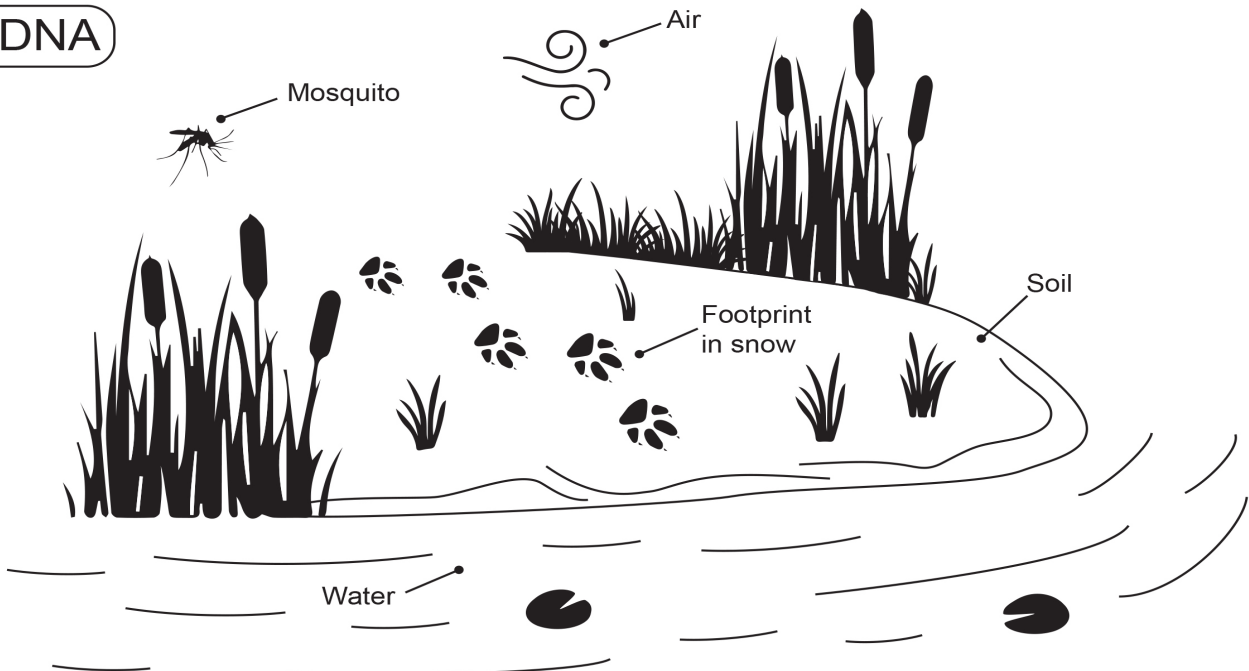


Fig. 16.2. Sources of DNA for studying furbearer management and conservation include direct (invasive) and noninvasive samples. Direct sample (e.g., biopsy-punched ear tissue, blood, buccal or rectal swabs, plucked hair) can be taken from a live-captured animal or collected opportunistically from mortalities such as harvested or vehicle-struck animals; skulls and untanned pelts; or other remains, including museum specimens. Noninvasive samples include source material deposited by an animal (e.g., feces, saliva, snagged hair, urine) and can be collected without capturing or directly handling the animal. A specific type of noninvasive sample, environmental DNA (eDNA), can be used to detect furbearer DNA in samples of snow, soil, water, air, or blood-sucking parasites. Image by A. Peterson, Luther College, Iowa, USA.

Wengert et al. 2013, Hopken et al. 2016), twigs (Nichols et al. 2012, 2015) and other plants that have been fed upon (Saito et al. 2008), and clothing from human attack incidents (Meredith et al. 2020). Salivary DNA degrades quickly but has been found to successfully amplify in 50% of samples ≤ 12 weeks after deposition in some cases (Nichols et al. 2012).

Numerous studies of carnivores have included collection of hairs from barbed-wire fencing or various hair-trap mechanisms placed in the environment by investigators (e.g., McDaniel et al. 2000, Zielinski et al. 2006, Kierepka and Latch 2016a). Successful isolation of DNA from hair requires obtaining follicles, which provide a range of DNA quality depending on the species. All types of noninvasive samples require careful handling throughout the sampling process to avoid contamination and to ensure preservation of DNA. Also, these sample types require special consideration in laboratory procedures to minimize genotyping error, including specific handling protocols, technical replication, quality controls, and analytical consideration of errors that occur with low-quality, low-quantity DNA (Taberlet et al. 1999).

Noninvasive sampling includes eDNA, whereby DNA from a target species or from multiple species is collected from air, snow, soil, water, or other environmental sources (Taberlet et al. 2012, 2018). Because mtDNA is more abundant in cells and more persistent in the environment, it is typically the focus of studies involving collection of eDNA; mtDNA is most useful for detecting rare species and invasive species in newly invaded areas, and as part of efforts to document the absence of a species after control efforts. Environmental sources of DNA are rarely of sufficient quality or quantity to obtain nDNA as is required for individual identification or sex (but see Adams et al. 2019). More so than other forms of noninvasive DNA, eDNA has highly variable persistence that varies by species and by habitat conditions. Successful collection of eDNA is also influenced by abiotic factors (e.g., diffusion, dispersion, pH, turbidity), and careful consideration of sampling scheme is critical for increasing the probability of detection (Goldberg et al. 2016).

The field of eDNA has largely focused on water samples, and thus on aquatic species. Because furbearing species generally are either semi-aquatic or terrestrial, eDNA is still a novel approach for these species, with each new study adding to our understanding of the applications and utility of this tool. For example, detection of a terrestrial invasive species, feral swine (*Sus scrofa*), using eDNA has proven to be a powerful management tool for sensitive and efficient surveillance (Williams et al. 2017, 2018). The utility of this approach for furbearing species was demonstrated for coyotes through detection of their DNA in water sources (Rodgers and Mock 2015). Additionally, the methods of eDNA concentration have been applied to melted snow from tracks of furbearers to identify rare carnivores, such as Canada lynx and wolverines (Franklin et al. 2019). The field of eDNA is still new and boundaries are presently being pushed into new sampling approaches, including the sampling of air to detect the presence of terrestrial mammals (Clare et al. 2022, Lynggard et al. 2022).

STORAGE OF DNA

All samples require some form of preservation, such as through freezing, storage with silica beads to adsorb water to inhibit DNases (i.e., enzymes that degrade DNA) and avoid growth of DNA-consuming bacteria, addition of buffer or $>95\%$ ethanol to preserve DNA, or placement onto filter paper, such as Nobuto strips (Cole-Parmer, Vernon Hills, Illinois, USA) or Whatman FTA® cards (GE Health Care, Piscataway, New Jersey, USA). There are many options available for sample collection, transport, and storage, with the optimal combination contingent on source material, field and logistical conditions, downstream application, and to some degree, personal preference. Therefore, it is advisable to consult with a genetics laboratory prior to sample collection to discuss options and preferences of particular labs. Below we present some general guidelines for storage of DNA.

For directly collected samples, the most appropriate storage for optimal DNA preservation is freezing the sample soon after collection in a manually defrosting freezer. Avoid using self-defrosting freezers, particularly for long-term storage, as the freeze-thaw cycle shears DNA. When freezing within a few hours is not feasible, directly collected blood and tissue samples can be collected into sterile vials or Whirl-paks® (Nasco Sampling, Madison, Wisconsin, USA) and preserved through the addition of buffer or $>95\%$ ethanol that protects DNA from degradation. Blood may also be smeared onto Nobuto strips or Whatman FTA cards, but these methods provide only small amounts of mammalian DNA because mature red blood cells lack nDNA and thus are not ideal sources for genomic approaches (Love Stowell et al. 2018).

Noninvasive samples can be collected by swabbing substrates for traces of blood, saliva, or urine, or from collecting feces, hair, or whiskers. These samples may be obtained by systematically searching the environment for their presence, often through the use of detection dogs (e.g., Thompson et al. 2012, Gese et al. 2023 [Chapter 15]), or they may be obtained through the use of lures or bait stations. For example, olfactory attractants often elicit a defecation response from some species (e.g., Statham et al. 2012). Noninvasive samples are susceptible to rapid degradation, and thus associated DNA must be immediately stabilized through methods mentioned above. Hairs and whiskers can be placed in paper envelopes, or in tubes with desiccant or $>95\%$ ethanol to avoid breakage of the bulb that forms the base of the follicle, and shipped to a laboratory. These samples are fairly robust and may tolerate months to years of storage if kept dry and out of direct sunlight. However, degradation can still occur, particularly after 6 months, so it is best to extract and store DNA from hair samples soon after collection (Roon et al. 2003).

There is a large body of literature on the collection and use of fecal DNA (e.g., Santini et al. 2007, Panasci et al. 2011, Lonsinger et al. 2015, Miles et al. 2015, Nakamura et al. 2017, Monterrosa et al. 2019), and the appropriate approach depends largely on the research question and whether the target DNA is that of the defecating individual (e.g., for species, sex, or individual identification) or other organisms (e.g., prey or forage for diet analysis, bacteria or viruses for disease detection).

For example, when interested in DNA from the defecating individual, the surface of fecal samples can be swabbed or scraped to preferentially obtain shed epithelial cells (Panasci et al. 2011). However, when interested in DNA from prey or microorganisms, subsampling multiple locations from or homogenizing the entire fecal sample may better capture the taxonomic diversity (Gosselin et al. 2017).

There are two approaches to collecting water samples for analysis of eDNA: 1) filtering water and preserving the DNA on the filter substrate, or 2) collecting water and using centrifugation or precipitation with chemicals in the laboratory to isolate the DNA in the sample (e.g., Valiere and Taberlet 2000, Ficetola et al. 2008, Goldberg et al. 2011, Foote et al. 2012). The first approach requires field personnel to carry pumps, or specific eDNA collection units (e.g., eDNA Sampler; Thomas et al. 2018), whereas the second approach requires collection and transport of water samples (60 mL–2 L); either way, these samples require immediate preservation through freezing or by adding a buffer that preserves DNA (Renshaw et al. 2015, Williams et al. 2016).

MOLECULAR MARKERS

Historically, products of DNA variation were surveyed indirectly through protein polymorphisms (allozymes) or karyotypic differences. Advances in direct DNA amplification and sequencing, in particular the advent of the **polymerase chain reaction (PCR)**, have displaced these approaches in favor of more powerful molecular markers that survey variation at the level of individual nucleotide base pairs (i.e., adenine [A], cytosine [C], guanine [G], thymine [T]; Fig. 16.3). By surveying changes in the DNA bases directly, DNA-based markers provide a more representative survey of variation across the genome than protein-based markers that survey only the subset of variation that results in changes to protein composition or function. Being able to resolve evolutionary relationships using the number of differences between two sequences as an indicator of how recently those two individuals shared a common ancestor is another major advantage of DNA-based markers.

There are several approaches for surveying DNA variation that fall into two broad, non-mutually exclusive categories: **sequencing** and **genotyping** (Fig. 16.3). DNA sequencing involves collecting the nucleotide sequence of one or more regions of the genome, including sites that have different nucleotides present within or among individuals (variable or **polymorphic**) and those that are identical across all sequences (non-variable or **monomorphic**). Genotyping typically refers to collecting the nucleotide or length-polymorphism (see below) information from targeted sites previously identified as variable. The key distinction is that although sequencing can reveal novel mutations or alleles not previously known to occur, genotyping generally is limited to known sites of variability. With advances in sequencing technology, it has also become feasible to combine features of these two approaches in reduced-representation sequencing methods, such as genotyping-by-sequencing (GBS) or restriction site-associated DNA (RAD) sequencing (reviewed by Davey et al. 2011).

DNA can be sequenced using traditional **Sanger sequencing** or **next-generation sequencing (NGS)**. In principle, these two sequencing approaches are similar in that a DNA polymerase adds nucleotides one at a time onto a growing DNA template strand. The incorporated nucleotides are detected using fluorescence or other tags to read the sequence of the strand. The primary difference between Sanger and NGS is in the volume of sequence data produced. Whereas the Sanger method sequences one DNA fragment at a time, NGS is massively parallel, sequencing millions of fragments simultaneously. NGS yields hundreds to millions of sequenced loci at once. Regardless of the approach used, the resulting sequences can be compared across individuals or populations for myriad applications, from taxonomy to forensics.

Genotyping typically refers to assaying a set of previously identified variable markers in the nuclear genome. An autosomal genotype can refer to a single locus (marker), in which case it is heterozygous (two alleles, a different allele inherited from each parent) or homozygous (one allele, the same allele inherited from each parent). Use of multiple loci produces a multilocus genotype, which, if loci are sufficiently variable or numerous, provides a unique combination of alleles that enables the individual to be identified. This principle is much the same as from a fingerprint, but because they reflect Mendelian inheritance, a genotype also contains information on familial relationships with other genotyped individuals.

Markers used for genotyping can vary in fragment size (e.g., microsatellites) or in the nucleotide present at a specific site (**single nucleotide polymorphisms [SNPs]**). Markers that vary in fragment size can be separated by gel electrophoresis, and most notably include microsatellites (Fig. 16.3). Microsatellites are simple, short, repetitive DNA sequences that are ubiquitous across the non-coding regions of eukaryotic genomes. They have high rates of mutation and follow simple models of evolution, making them highly polymorphic and informative. Microsatellites are not typically under the influence of natural selection, and thus represent the outcome of mutation, migration, and random genetic drift, which all are evolutionary processes important to the management and conservation of populations.

A suite of 10–20 moderately variable microsatellites is often sufficient to differentiate individuals and populations and quantify gene flow between populations. However, microsatellites are not without limitations (Zhang and Hewitt 2003, Selkoe and Toonen 2006). One limitation of microsatellites, and all fragment size-based molecular-marker systems, is that the ancestral state is not typically known, making it difficult to infer genealogy. In addition, because their mutation rates are high, microsatellites are not generally useful for high-level systematics. Microsatellite genotyping also requires the development of species-specific primer sequences that target the appropriate regions for amplification, which adds a step to the process if markers have not previously been developed. However, NGS can be used to efficiently characterize microsatellites (Castoe et al. 2012) and genotype individuals at many markers (De Barba et al. 2017).

Another common marker used in genotyping is the SNP, a single site within the DNA sequence at which the nucleotide varies, usually between two alleles (Fig. 16.3). Depending on objectives, tens to tens of thousands of SNPs are surveyed and compared across individuals. SNPs are common across the genome, for example occurring about once every 1,000 base pairs in humans, and found in both coding and noncoding regions. Until recently, identifying and characterizing SNP loci was expensive and tedious, and often required some knowledge of the genome of the target species. One benefit of NGS is that it has alleviated previous limitations, which makes SNP discovery and genotyping more efficient. For example, reduced-

representation approaches (e.g., RAD-Seq) subsample a fraction of the genome using restriction enzymes to cut genomic DNA into fragments that are then sequenced using NGS and aligned to detect SNPs. Targeted capture approaches (reviewed in Jones and Good 2016) can be used to specifically target SNPs in or near coding regions (e.g., ultraconserved elements [UCEs] that are highly conserved across diverse taxa; Faircloth et al. 2012), or in other genomic regions of interest to genotype orthologous sites across species for comparative study (Smith et al. 2014), to better understand functional genetic variation (Linnen et al. 2013, Donaldson et al. 2017), or to capture desired fragments from poor-quality samples (e.g., RAD capture; Ali et al. 2016).

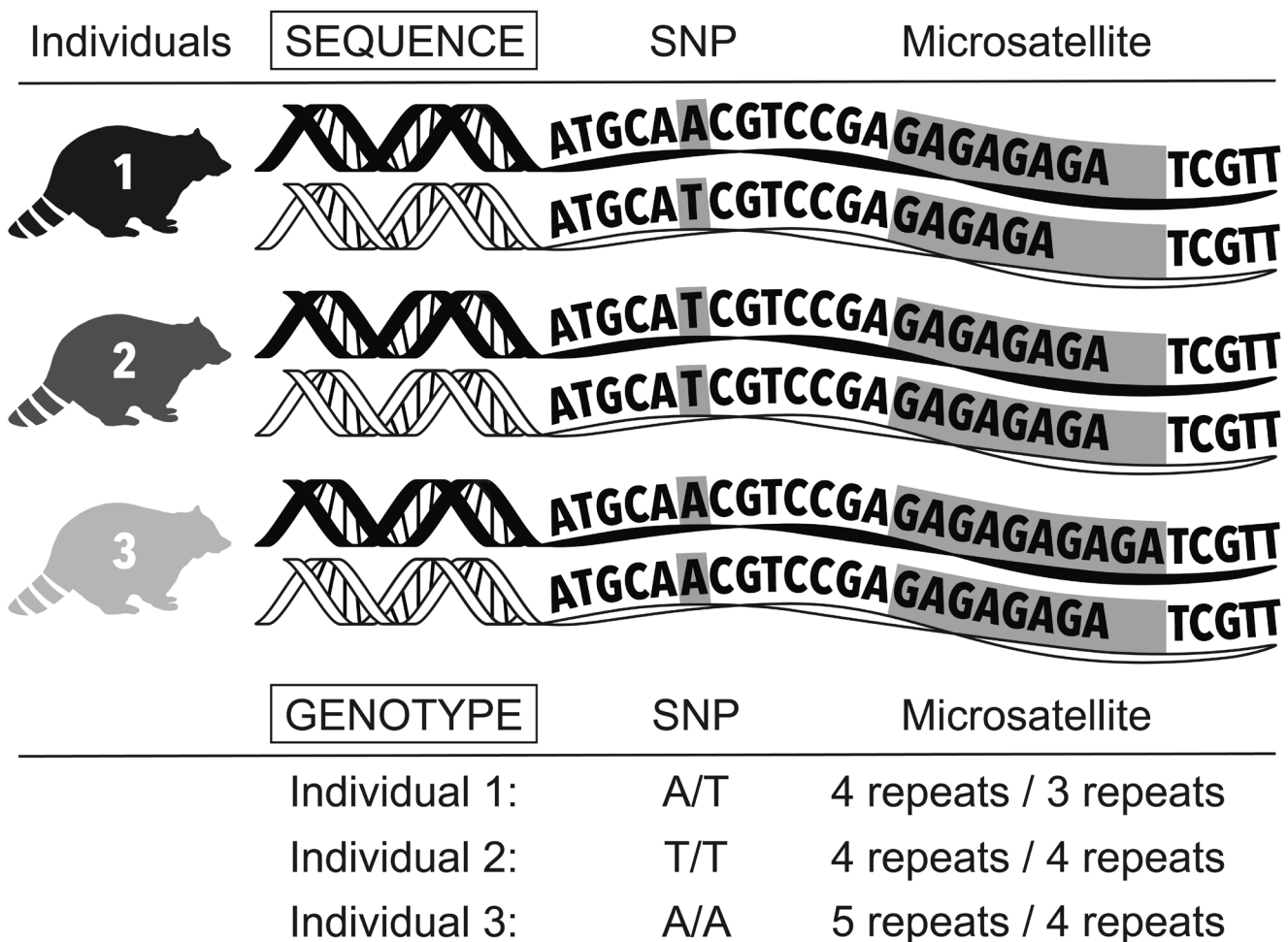


Fig. 16.3. Genetic information for three hypothetical individuals of northern raccoon (*Procyon lotor*) demonstrates the two types of approaches for surveying DNA variation: sequencing and genotyping. DNA sequencing involves collecting the nucleotide sequence of a region of the genome, including sites that have different nucleotides present within or between individuals (variable; highlighted in gray) and those that are identical across all sequences (non-variable; not highlighted). Each northern raccoon has sequence data for two autosomal chromosomes: maternally inherited (black) and paternally inherited (white). Genotyping refers to collecting information from targeted sites (markers) previously identified as variable. Markers can vary in the nucleotide present at a specific site (single nucleotide polymorphisms [SNPs]) or in fragment size due to differences in number of short tandem repeats (microsatellites). An autosomal genotype can be heterozygous (two alleles, a different allele inherited from each parent) or homozygous (one allele, the same allele inherited from each parent). Image by A. Allen, Photon Illustration, Michigan, USA.

USE OF DNA IN MANAGEMENT AND CONSERVATION OF FURBEARERS

There are many potential research questions that DNA can help address, some of which have been reviewed in detail (e.g., Carroll et al. 2018, Lamb et al. 2019). Here, we highlight a few common areas where DNA has been particularly useful in informing furbearer management and conservation.

Sex Identification

Accurate sex identification is vital for understanding individual-level behaviors as well as population-level demographic parameters. Particularly relevant to furbearer management and conservation, sex identification is used to characterize harvest and population structure, which is integral to models used to assess population responses to harvest or make other management decisions (Hiller et al. 2014). When a live-captured animal or carcass is available for examination by biologists or furtrappers, notable external differences (e.g., body size, genitalia) may allow the sexes to be easily distinguished by properly trained personnel. However, such telltale features may be subtle or nonexistent in juveniles or monomorphic species, particularly for felids (e.g., bobcats) and North American beavers (*Castor canadensis*), which are notoriously challenging due to relatively small external testis size or lack of external genitalia, respectively (see White et al. 2024 [Chapter 14]). Indeed, significant errors in sex identification based on external observation have been reported for a variety of species (e.g., American marten [*Martes americana*; Belant et al. 2011], bobcat [Williams et al. 2011, Hiller et al. 2014], North American beavers [Williams et al. 2004]). Furthermore, when intact organisms are not available for inspection (e.g., partial or degraded carcasses or noninvasive samples), sex determination based on physical examination is precluded.

To identify or verify the sex of individuals, researchers often turn to PCR tests designed to take advantage of the fact that male mammals possess a Y chromosome (XY genotype), whereas females do not (XX genotype; reviewed in Hrovatin and Kunej 2017). Some tests rely on Y-chromosome-specific genes for which only males produce an amplification product (e.g., SRY locus; Palsbøll et al. 1992). When used alone, negative results can be misleading when degraded samples that simply fail to amplify result in classification as female. To circumvent this problem, Y-chromosome sex markers can be integrated in assays with additional loci (e.g., microsatellites), which serve as controls for poor-quality DNA samples.

Other tests amplify gene regions present in slightly different forms (i.e., paralogous) on both the X and Y chromosomes so that both sexes produce a positive, but differential result. For example, Pilgrim et al. (2005) designed two different tests in felids where the Y-chromosome copy of the amelogenin gene (AMELY) has a 20-base-pair (bp) deletion and the zincfinger gene (ZFY) a 3-bp deletion when compared with the respective X-chromosome copies (AMELX and ZFX). Thus, each of these two tests provide positive results for males (two amplification products of different length) and females (one product) when PCR products are visualized

using gel electrophoresis. In addition to insertions or deletions, tests could also take advantage of sequence differences such as SNPs between the X and Y copy, which could be discerned through a variety of techniques, such as quantitative PCR with sequence-specific primers and probes (O'Neill et al. 2013), high-throughput sequencing of PCR amplicons (De Barba et al. 2017), or restriction enzymes that cut one sequence but not the other (Ortega et al. 2004, Statham et al. 2007).

For the most part, these DNA-based tests are reliable and treated as the gold standard for sex-identification methods. However, it is important to be aware of some technological limitations, anomalies, and potential for errors. First, some tests are designed to amplify across a broad range of taxa. Although this can be a beneficial feature that allows flexibility in applying the test across a diverse set of species, it can also lead to errors when non-target DNA is amplified. For example, females may potentially test positive for a Y-marker in the presence of human male DNA due to accidental contamination from field or laboratory technicians, or, if the testing material was scat, in the presence of DNA from male prey items (Murphy et al. 2003). In addition, males could erroneously be identified as females because of null alleles or allelic dropout. Whereas an apparent YY genotype would be flagged as suspicious, an XX genotype would simply seem to be female and may result in misclassification. However, studies have shown that long alleles tend to drop out more frequently because PCR is more efficient in amplifying shorter sequences (Wattier et al. 1998), thus designing tests with the shorter allele on the Y chromosome may be expected to reduce the risk of males being incorrectly genotyped as females. In addition, sex reversals and intersex scenarios in mammals can create authentic mismatches between chromosomal sex (XY or XX), gonadal sex (testis or ovary), and thus phenotypic sex (male or female; reviewed in Parma et al. 2016). Given uncertainty in accuracy of some molecular tests and typically a lack of known-sex individuals for verification, it is often advisable for studies to use two independent genetic tests to help confirm the validity of the genotype calls (Pilgrim et al. 2005, Robertson and Gemmill 2006).

Individual Identification

As with a fingerprint, every individual has a unique genome, which enables discrimination of individuals using DNA markers (i.e., genetic or molecular tags). Improving on a fingerprint, however, DNA additionally contains information on familial relationships among individuals. Like physical tags and tracking devices, the use of genetic tags from noninvasive samples, such as hair or scats, enables identification of individuals repeatedly in space and time. This facilitates capture-recapture estimation of abundance; information on space use, dispersal, and pedigree reconstruction; and survival and recruitment. For some rare species of furbearers, such genetic tagging may offer the most feasible means of long-term population monitoring (e.g., Lamb et al. 2019, Quinn et al. 2019).

Although there are many factors that affect the success of studies that utilize individual-based noninvasive genetic tagging, most factors can be adequately planned for with the aid of pilot studies to anticipate and optimize genotyping success and information content of the resulting genotypes. Factors affecting

genotyping success include the study environment (climate, weather), species, diet, freshness of sample (particularly scats), preservation method, and laboratory procedures. Genotyping success rates can range from about 30% to >85%, which affects how many field samples are required to meet study objectives.

With respect to scats, genotyping success is typically much higher with very fresh samples than with older samples. Therefore, where feasible, such as when sampling scats from den sites for monitoring purposes, only fresh samples (still moist with the mucous layer identifiable) should be collected (e.g., Rutledge et al. 2009, Stansbury et al. 2014). However, in most applications, such as when sampling widely to estimate abundance, few very fresh scats are typically encountered; it is difficult to consistently differentiate scats that are 1–2 days old from those that are 1–3 weeks old. Therefore, it is rarely feasible to be selective about which scats are collected, which leaves preservation method as the primary factor in control during collection in the field.

Despite some of the associated inconveniences (e.g., prone to leakage, flammable, hazardous, makes tissues brittle, requires alcohol-resistant markers for labeling), 95–99% ethanol seems to be among the most reliable media for preserving DNA in fecal samples (Murphy et al. 2002, Frantz et al. 2003, Piggott and Taylor 2003, Beja-Pereira et al. 2009, Panasci et al. 2011, Tende et al. 2014). Alternatively, DET buffer (dimethyl sulfoxide saline solution; Seutin et al. 1991) avoids some of these drawbacks and also seems to be highly effective at preserving DNA in fecal samples (Frantzen et al. 1998, Panasci et al. 2011, Wultsch et al. 2015).

Factors affecting the information content of successfully genotyped samples depend on study objectives, but minimally include classification accuracy of the suite of markers used. Classification accuracy, in turn, relates to resolution (Mills et al. 2000) and genotyping accuracy (Creel et al. 2003). Resolution of a suite of markers depends both on the genetic diversity in the population under study (intrinsic to the subject) and on the type and number of markers used (methodological variable). Smaller, isolated populations contain less genetic diversity than larger, more connected populations, and therefore require more markers to obtain the necessary resolving power for accurate pedigree reconstruction. Because microsatellite loci typically exhibit 5–20 alleles, whereas SNPs typically have only two alleles, fewer microsatellite than SNP loci are required to achieve a comparable resolution for individual identification. Conversely, technologies for SNP genotyping enable many more loci (e.g., ≥ 96) to be genotyped in a single assay (Fabbri et al. 2012, Nussberger et al. 2014, Kraus et al. 2015, von Thaden et al. 2017), compared to ≤ 12 microsatellite loci in a single reaction (Sacks et al. 2016a). A common measure of the resolution of a marker or marker set is in terms of the probability of two distinct individuals sharing identical genotypes by chance (probability of identity [PID]). The probability of two siblings sharing a genotype by chance (PIDSibs) is higher than that for two randomly selected individuals in the population, and therefore serves as a more conservative benchmark, with PIDSibs <1% usually considered an acceptable level (Waits et al. 2001). This amounts to a <1% misclassification rate stemming from resolution of the marker set.

The other type of misclassification error, incorrectly assigning two samples from the same individual as two distinct individuals, occurs due to a mismatch in genotypes stemming from genotyping error (Creel et al. 2003). The traditional approach to reducing this type of classification error has been to repeat the genotyping reaction many times with the goal of eliminating genotyping error (Taberlet et al. 1999). To minimize the probability of obtaining any errors in a genotype, it was also standard practice to use only as many loci as was required to achieve the desired resolution (e.g., PIDSibs <1%; Waits and Leberg 2000, Waits and Paetkau 2005). This trade-off between resolution and genotyping error, however, applies only to classification schemes that assume zero genotyping error. If this assumption is relaxed and genotyping error explicitly accounted for, there is no such trade-off and the use of many loci can reduce both types of classification error to negligible levels (e.g., Quinn et al. 2019; see Box 16.2). Use of many loci also facilitates familial relationships and pedigree reconstruction, which are not usually feasible with smaller numbers of loci, but greatly expands the functionality of genetic data sets for a variety of monitoring purposes (Flanagan et al. 2018, Lamb et al. 2019).

Depending on the objectives associated with identification of individuals, other forms of information content include sample size and independence. Estimates of population abundance or density based on capture-recapture approaches require larger sample sizes for larger populations to obtain sufficient numbers of resamples from individuals. Pedigree reconstruction also requires more samples from more abundant populations to maximize the number of parents included in the dataset. Because statistical estimates of population abundance or density assume that the population is closed during the sampling period (or primary sampling period, if robust-design population models are employed), and that samples are collected randomly (with or without stratification) and are independent of one another, violations of these assumptions can bias results. Therefore, the use of sound sampling design is as important for genetically based capture-recapture studies as for traditional ones (Brinkman et al. 2011, Thompson et al. 2012, Efford and Fewster 2013, Murphy et al. 2018). In very small, isolated populations, it may sometimes be feasible to sample all (or most) individuals repeatedly over time, which enables detailed monitoring of abundance, births, deaths, inbreeding, and outbreeding of the population (Hedrick et al. 2019, Quinn et al. 2019).

An advantage to some protocols based on noninvasive collection of data, such as scat sampling, over traditional approaches, such as invasive mark-recapture studies, is that detection probabilities should be relatively homogenous among individuals using the sampling area and over time. In contrast, similarly to trapping, individuals can vary substantially in their probabilities of detection when sampled using baited hair-traps that require the animal to both approach the bait and come into sufficient contact with adhesive, barbs, brushes, or snares to collect data (Marucco et al. 2011, Gese et al. 2023 [Chapter 15]).

BOX 16.2. DETERMINING INDIVIDUAL IDENTIFICATION FROM SAMPLE GENOTYPES.

The principle is one of discrimination. All that is observed is a similarity between sample genotypes (i.e., proportion of alleles shared across all loci). We must infer whether two sample genotypes reflect the same individual or two different individuals. The traditional approach is to assume 0% genotyping error and to use 100% similarity as the decision rule. However, each of these possibilities (i.e., same individual or different individuals) can be represented generally in terms of a binomial probability distribution that described likelihoods associated with similarities ranging from 0 to 100%, with the number of discrete categories depending on number of loci. In general, two sample genotypes from the same individual will tend to have a mode at or very close to 100%, but because of genotyping error, have a tail that extends in the direction of 0%. Two sample genotypes from, say, siblings, may have a mode of about 60%, but because of chance inheritance of alleles, have tails that extend in either direction. When a small number of loci (e.g., 6) is used, unless genotyping error has been truly eliminated, and a conventional PIDsibs (probability of two siblings sharing a genotype by chance) threshold achieved, these distributions can overlap considerably, causing an unavoidably and potentially unacceptably high misclassification rate. Conversely, if many loci are used, the range of similarities over which two sibling genotypes are expected to occur (i.e., with some confidence level, e.g., 99%) becomes much narrower. Likewise, although the number of genotyping errors in a genotype is expected to increase in proportion to the number of loci used (Waits and Leberg 2000), the variance in the similarity of two genotypes from the same individual declines with increasing numbers of loci, such that this distribution also narrows. Importantly, these distributions can be estimated using the PID (probability of two distinct individuals sharing identical genotypes by chance), PIDsibs, or both, and the genotyping error rate, both in conjunction with the binomial formula (e.g., Lounsbury et al. 2015, Furnas et al. 2018, Quinn et al. 2019). The result is a larger margin of error in terms of identifying a threshold value for genotype similarity. For example, when using 6 loci assuming a PIDsibs of 1% and genotyping error rate of 5%, intuitively, it may not be unexpected to observe 83% similar genotypes (i.e., sharing 10 of 12 possible alleles) from two siblings or from a single individual with a few genotyping errors. However, when using 20 loci, a similarity rate of 83% implies matching at 33 alleles and mismatching at 7 alleles. This would be extremely rare from two samples from the same individual, assuming the same genotyping error rates. Moreover, if the average expected allele sharing of siblings was 60%, many fewer sibling comparisons would be expected to reach this high level of similarity with 20 loci (i.e., 83%) as they would with 6 loci.

Species Occurrence

Baited camera-trap surveys have long been the method of choice for broad-scale surveys of rare or endangered (and other) furbearer species to assess occupancy and monitor changes in distribution (e.g., Long et al. 2008). With improved technology enabling higher rates of genotyping success with lower-quality DNA samples, however, noninvasive DNA sampling for scats (De Barba et al. 2010; Lonsinger et al. 2015, 2018; Sacks et al. 2016a; Quinn et al. 2019), urine in snow (Akins 2017, Akins et al. 2018), iDNA from blood-sucking invertebrates (Kocher et al. 2017), and even tracks in snow (with and without eDNA methods; Dalén et al. 2007, Franklin et al. 2019) offer an increasingly practicable alternative approach. These two approaches are also complementary in that for many species, detection probabilities at baited camera-traps are highest during winter and lowest during summer, whereas

scat sampling is often most productive, particularly in remote and rugged locations, during summer or snow-free months. Where beneficial, scat searches can be aided by trained scat-detection dogs (Thompson et al. 2012). Use of DNA-based approaches additionally provide genetic data that can be used to assess sex, individuals, and population of origin.

Noninvasive DNA-based collection methods also are useful for detection of invasive species early in the invasion process or later after implementing control or eradication efforts to monitor those efforts. Environmental sampling through eDNA can be a useful tool for detecting species with low population densities, particularly involving aquatic systems, and more recently from air (Clare et al. 2022, Lynggard et al. 2022), but also requires a rigorous study design that takes into account the variability in eDNA in the environment and its persistence rate, the number of samples/site and across the sampling area to collect to achieve the maximum probability of detection, and the number and format of technical replication in the lab to minimize false positives and false negatives (Taberlet et al. 2018).

Forensics

Wildlife forensics applies validated tools, including DNA techniques, to provide robust evidence for investigations and sometimes legal cases involving biological evidence from wildlife species. Such an approach can be particularly useful when trying to identify predatory species involved in a depredation event. A depredation event may be identified through different kinds of evidence, such as: 1) eggshells from a nest; 2) items remaining at a kill or fight site (e.g., dog collar); 3) carcass; or 4) hair, urine, or fecal samples in proximity to a kill site, among other things. The use of forensics is also helpful in management of furbearers when illegal harvest is suspected, as animal remains and seized weapons can be tested for DNA (Ogden et al. 2009). When multiple populations are already well characterized through genetic tools such as microsatellites, SNPs, or DNA sequences, DNA from the sample in question can be assigned not only to species, but also to source population (Millions and Swanson 2006, Ogden and Linacre 2015). Such approaches have been particularly informative in the illegal trade of wildlife, where understanding the species that a product originated from, and its geographic locality of origin, can be useful in legal prosecution and management of poaching (Wasser et al. 2008).

Defining Conservation Units

Many species of furbearers are broadly distributed across North America, but management and conservation typically operate at the level of more localized jurisdictional units (e.g., state or provincial). In an ideal scenario, decisions associated with these units would reflect or be informed by the population structure that inevitably exists across the geographic distribution of a species. Indeed, most **species** are not comprised of a single, panmictic population, but rather some individuals are more likely to interact and interbreed than others. Recognizing this demographic and genetic structure is important because migration and gene flow (or

lack of) influence ecological and evolutionary phenomena, such as levels of genetic diversity, extinction risk, local adaptation, recolonization, and spread of disease. In addition, biologists are increasingly interested in preserving the unique genetic diversity harbored by different population segments as a means of maximizing the evolutionary potential of a species (i.e., capacity to evolve in response to changing environments; Frankham 2005, Sgró et al. 2011, Harrisson et al. 2014). However, because evolution is a continuous and complex process, it can be challenging to categorize taxa into discrete, hierarchical entities along the species-population continuum (Schaefer 2006).

How species and intraspecific units are classified can depend greatly on the definitions employed and criteria used for determining whether biologically significant differences exist. Although multiple sources of information (e.g., behavior, environment, geography, life history, morphology, socioeconomic value) can be used to help describe units for management and conservation, most definitions integrate **adaptive genetic variation**, **neutral genetic variation**, or both, but in different ways (Allendorf et al. 2013). For example, some definitions of **evolutionary significant units** (ESUs; Ryder 1986) stress long-term historical isolation and neutral divergence demonstrated by reciprocal monophyly at mtDNA and significant allele frequency differences at nuclear loci (Moritz 1994), whereas others emphasize evidence of adaptive divergence (Waples 1995, Funk et al. 2012, Prentice et al. 2019) or ecological and genetic inexchangeability (Crandall et al. 2000) between separate ESUs.

More recently, to consolidate these different approaches, a decision tree has been developed to help managers define these genetic units and thus facilitate meaningful management (Hoelzel 2023). Closer to the population end of the species-population spectrum, some definitions of **management units** (MUs) stress current population structure and allele frequency differences sufficient to reject panmixia (Moritz 1994), whereas others emphasize evidence for demographic independence based on the amount of population genetic divergence equivalent to <10% dispersal (Palsbøll et al. 2007).

When gathering genetic evidence of intraspecific population structure, important considerations in study design include sampling scheme (e.g., sampling pre-defined populations vs. sampling individuals, sample sizes, presence of missing populations or sampling gaps, whether close relatives are potentially included), number and type of genetic markers used (e.g., mtDNA vs. nuclear, microsatellites vs. SNPs, neutral vs. functional, handful vs. hundreds of thousands), and data analysis procedures employed (e.g., multivariate vs. model-based, aspatial vs. spatially informed). Because many furbearing species are continuously distributed rather than clumped into obvious a-priori populations, a useful approach is to sample individuals uniformly across a landscape and use the genetic data to determine the number, extent, and membership of populations (e.g., Reding et al. 2012, Kierepka and Latch 2016a). However, spatially biased sampling can impact genetic structure findings and needs to be carefully considered, particularly in individual-based studies (Schwartz and McKelvey 2008).

To provide the data and statistical power needed to reveal biologically relevant population divergence in a cost-effective manner, decisions on marker type and number should consider whether genetic markers have already been characterized for the species of interest, whether the focus is on broad versus fine-scale patterns, whether sex-specific patterns are of interest, and whether neutral or adaptive genetic variation is important. With whole-genome sequencing and genome sampling approaches offering unprecedented numbers of markers to resolve even the most fine-scale population structure, care is needed to distinguish biological versus statistical significance in order to avoid oversplitting units and misusing conservation resources (Isaac et al. 2004, Allendorf et al. 2013, Coates et al. 2018).

On the flip side, genomic approaches can provide improved statistical power to resolve cryptic population structure and allow for the integration of adaptive differences, which can help avoid undersplitting units and overharvesting populations (Funk et al. 2012, Allendorf et al. 2013). Finally, sampling and marker choices will dictate to a certain degree the data analysis methods suitable for a study, as samples with low quality and low quantity of DNA present challenges for many genomics approaches (Andrews et al. 2021), and some sampling schemes and markers may violate assumptions for certain analyses (Funk et al. 2012). When genetic studies offer seemingly conflicting views of population structure, it is best to consider the full range of complexity involved and evaluate whether the studies might actually provide complementary insight into real, complex patterns (Hoelzel 2023).

Investigations of population genetic structure in North American furbearers have revealed a wide array of patterns. In many cases, genetic data have not supported subspecies taxonomy based on geographic and morphological differences (Hall 1981), and instead suggest a collapsing of subspecific entities (e.g., American badger [*Taxidea taxus*; Kierepka and Latch 2016b], bobcat [Reding et al. 2012, Kitchener et al. 2017], mountain lion [*Puma concolor*; Culver et al. 2000, Kitchener et al. 2017]). In other cases, genetic data have revealed cryptic divergences, often due to Pleistocene climate fluctuations and historic isolation in fragmented glacial refugia (e.g., bobcat [Reding et al. 2012], Canada lynx [Prentice et al. 2019], gray fox [*Urocyon cinereoargenteus*; Goddard et al. 2015, Reding et al. 2021]) or to differences in prey-habitat specialization (e.g., gray wolf [Carmichael et al. 2001, Musiani et al. 2007]). Despite best attempts to classify taxonomic units, genetic and genomic tools also reveal that such boundaries are fluid, and introgression between species is likely more common than previously thought (Koen et al. 2014, vonHoldt et al. 2016, Coates et al. 2018).

Recolonization and Translocation

Many furbearer species have experienced extirpations from portions of their natural distribution, often due to the combined effects of historical overharvesting and habitat loss and fragmentation (see Lewis and Weir 2024 [Chapter 8]). Some of these species have returned to the landscape, either through natural recolonization (e.g., bobcat [Reding et al. 2012], wolverine [Moriarty et al. 2009]), or assisted through reintroduction efforts via translocation from one or several source

populations (e.g., American marten [Williams and Scribner 2010], Canada lynx [Devineau et al. 2010], fisher [*Pekania pennanti*; Stewart et al. 2017], North American river otter [*Lontra canadensis*; Mowry et al. 2014]), or potentially from a combination of reintroduction and recolonization (e.g., fisher [Proulx et al. 2018], North American beaver [Epps et al. 2021]).

In scenarios of natural recolonization, genetic information can be used to characterize regional population connectivity and dynamics, which can help identify factors (e.g., dispersal barriers, harvest rates) that can facilitate or hinder the recolonization process. When reintroduction efforts are under consideration, genetic information can be important for identifying and prioritizing the appropriate source populations to use and to monitor populations following reintroduction to assure restoration of genetic diversity (Serfass et al. 1998, Mowry et al. 2014). Historical and post-release genetic information can be invaluable for identifying the source(s) of contemporary populations to distinguish whether reintroduction efforts were successful, unwittingly reinforced pre-existing but undetected populations (i.e., augmentation), or were followed by cryptic recolonization, potentially seeded by the initial reintroduction. For example, genetic studies of expanding populations of fishers have revealed that unexpected and complex patterns can emerge when remnant, neighboring, and translocated populations can all potentially contribute to the genetic legacy of contemporary populations (Schwartz 2007, Stewart et al. 2017, Hapeman et al. 2017, Proulx et al. 2018).

Translocations can also be used to intentionally augment existing furbearer populations (Pacioni et al. 2019, Lewis and Weir 2024). Such efforts can potentially rescue remnant or reintroduced populations from deleterious consequences of small population size, including inbreeding depression, loss of genetic diversity, and skewed sex ratio or other problems associated with demographic stochasticity. To this end, translocations have succeeded in a range of cases (e.g., American badger [Kinley and Newhouse 2008], black-footed ferret [*Mustela nigripes*; Wisely et al. 2008], fisher [Lewis et al. 2012]). However, augmentation has also been criticized as costly, controversial, and ineffective (e.g., American marten [Manlick et al. 2017]), unnecessary when natural recolonization is possible (e.g., North American beaver [Epps et al. 2021]), and potentially detrimental when disease transmission (e.g., northern raccoon [Nettles et al. 1979]), outbreeding depression (e.g., grizzly bear [*Ursus arctos*; Shafer et al. 2014]), or the loss of native genetic diversity due to introgression and genetic swamping (e.g., Pacific marten [*Martes caurina*; Colella et al. 2019]) result (reviewed by Weeks et al. 2011).

Landscape Genetics

Landscape genetics aims to characterize the influence of landscape features on population genetic structure. Correlating patterns of spatial genetic structure with landscape features yields novel insights into how the environment shapes gene flow and local adaptation and guides the design of better strategies for management and conservation. For example, Garroway et al. (2011) used a landscape genetic approach to show that spatial genetic structure in a recently expanded population of fishers was driven by constrained gene flow

from anthropogenic impacts (i.e., road density) and seasonal variation in habitat conditions (i.e., snow depth, density of ice-free rivers), suggesting that management decisions might be better informed by considering habitat continuity during winter when juveniles disperse. Landscape genetics is well suited to addressing a variety of additional questions relevant to furbearer management and conservation, including detecting landscape barriers to gene flow (Latch et al. 2008, Garroway et al. 2011, Koen et al. 2012, Kierepka and Latch 2016a), investigating population dynamics (Sacks et al. 2016b), identifying movement corridors (Laurence et al. 2013), understanding functional connectivity (Reding et al. 2013, DeCandia et al. 2019, Epps et al. 2021), and mitigating disease spread (Cullingham et al. 2009, DeYoung et al. 2009, Root et al. 2009).

The application of genomic tools to landscape genetics is particularly exciting for understanding the structure of adaptive genetic variation across natural landscapes (Manel and Holderegger 2013, Hand et al. 2015). To date, there have been few studies of local adaptation in furbearing species. One well-conceived example surveyed both neutral and adaptive variation in coyotes along an urban-rural gradient to determine that small population size (genetic drift) was the primary driver of genetic diversity in a coyote population that had recently established in an urban area, rather than strong selection promoting adaptation to the urban environment (DeCandia et al. 2019). These data highlight the utility of surveying both neutral and functional variation, to the benefit of wildlife management, urban planning, and green design. As landscapes are transformed by urbanization and other rapid environmental changes, understanding how functional variation responds will be critical to maintaining furbearer populations.

Diet Analysis

Diet analyses can be an important tool in the management and conservation of furbearers. Diverse methodological approaches (e.g., direct observation, microscopic examination, stable isotope analysis) have traditionally been used for diet analysis, each with advantages and limitations. A genetic approach for studying animal diet is based on **metabarcoding**. Metabarcoding, a type of NGS technology, amplifies a specific gene fragment that can be compared across taxonomic groups (e.g., animals, fungi, plants) by simultaneously sequencing all orthologous (i.e., corresponding) DNA fragments extracted from a fecal or stomach-content sample (Valentini et al. 2009, Pompanon et al. 2012, Taberlet et al. 2012). Such an approach can precisely identify food items in a recent meal rather than broad food categories consumed over longer periods of time (i.e., stable isotope analysis), even if they lack hard remains or diagnostic features (i.e., direct observation and microscopic examination).

In conjunction with noninvasive sampling of the exterior of a single fecal sample, this can be a powerful tool to identify predatory species, individuals and their sex, as well as prey species. Such data can help elucidate predator-prey interactions, impacts of invasive species on native flora and fauna, and seasonal diet changes for furbearers. Moreover, gut content and fecal samples collected for diet analysis can serve a dual purpose by additionally providing insights into health status via pathogen testing and gut

microbiome analysis (e.g., Li et al. 2016, Grueber et al. 2020, Sugden et al. 2020, Gillman et al. 2022). For these studies, it is important that samples are fresh, handled with aseptic techniques, and preserved appropriately to maintain integrity of DNA of prey, predator, and microbiota.

Disease Monitoring

Disease is a major threat to the persistence of some populations of furbearing species, is costly to mitigate, and often poses substantial threats to human health (see Gillin et al. 2024 [Chapter 7]). Diseases relevant to furbearer populations that can be transmitted to humans include alveolar echinococcosis, giardiasis (beaver fever), leptospirosis, rabies, raccoon roundworm, and a variety of tick-borne diseases. Molecular data have transformed our ability to monitor disease presence, mitigate disease spread, and understand the effects of pathogens on wildlife population dynamics.

Pathogens can be detected using DNA collected from the infected individual, from the parasite or vector, or from the environment. For example, one might use barcoding markers and PCR amplification to detect *Amdoparvovirus* in blood (Glueckert et al. 2019) or identify *Echinococcus multilocularis* (a tapeworm) cestodes in fecal samples (Melotti et al. 2015). If molecular parasite detection is combined with DNA fingerprinting to identify the individual furbearer producing the scat, it could be used to monitor infection status over time (Liccioli et al. 2015) or predict disease spread (Cullingham et al. 2009). The environment can also be surveyed for disease, for example using eDNA from soil or water, or iDNA from blood meals from mosquitoes or other bloodsucking arthropod vectors. Combined with occupancy modeling, eDNA or iDNA surveys could be used to model the presence of disease across unsampled landscapes.

Although the use of fecal or environmental samples to survey for parasites can be a powerful, noninvasive tool for early detection of emerging diseases, the approach can be challenging. Pilot studies are essential for establishing robust best practices and to quantify sensitivity (probability of false-negative results) and specificity (probability of false-positive results). False negatives are particularly problematic when pathogens are in low abundance in the biological or environmental sample, whereas PCR-based surveys with universal primers (i.e., primers that are designed to amplify a larger group of organisms, e.g., all nematodes) are more prone to false positives. Robust detection of species from environmental samples typically requires molecular approaches with high specificity (Wilcox et al. 2013).

Recent research demonstrates the power of PCR-based tools with high specificity in environmental **zoonotic disease** monitoring. Environmental detection of the zoonotic pandemic virus SARS-CoV-2 RNA in human wastewater systems (e.g., Medema et al. 2020) sparked concern for exposure to novel wildlife species, which was subsequently confirmed using PCR tests. In North American furbearers, susceptibility to SARS-CoV-2 has been detected in a range of species, including American mink (*Neogale vison*; Shuai et al. 2021, Adney et al. 2022), red fox (Porter et al. 2022), northern raccoon (Francisco et al. 2022), and striped skunk (*Mephitis mephitis*; Bosco-

Lauth et al. 2021, Francisco et al. 2022). However, only some species (e.g., American mink [Shuai et al. 2021], striped skunk [Bosco-Lauth et al. 2021, Francisco et al. 2022], red fox [Porter et al. 2022]) seem to actively shed infectious viral particles, and American mink are the only furbearing species documented to date that maintains transmission in the wild (Oreshkova et al. 2020, Aguiló-Gisbert et al. 2021, Shriner et al. 2021).

Advances in genomics are transforming our understanding of wildlife disease. The increasing availability and affordability of NGS data facilitates **genome-wide association studies** (GWAS) to identify host genes related to disease resistance (DeCandia et al. 2020a, Weckworth et al. 2020a). Detailed tracking and characterization of pathogen variants at a continental scale will provide helpful information for developing vaccines for effective and sustainable interventions, and landscape genomic data on host movement will yield more accurate disease outbreak predictions (Fountain-Jones et al. 2021). Genomics is enriching our understanding of transmission dynamics in complex multi-host systems by helping to identify cryptic host species (Weckworth et al. 2020b), and gene expression studies are helping us to understand host-parasite interactions and immune responses (Davy et al. 2017).

Finally, advances in metabarcoding are paving the way for research on the role of host-microbiome relationships in health and fitness of furbearing species (e.g., DeCandia et al. 2020b, Sugden et al. 2020, Biles et al. 2021, Gillman et al. 2022, Lafferty et al. 2022). Given the importance of the coevolved microbiota on and within wild mammals for immune function, digestion, behavior, and other processes (reviewed by Suzuki 2017), the breakdown (i.e., dysbiosis) of this microbial community due to anthropogenic pressures such as land use change and shifts in food availability and quality can impact disease susceptibility and overall health (Trevelline et al. 2019). Monitoring gut microbiomes via scat could be used as a tool to assess population health in relation to human-mediated stressors (Sugden et al. 2020, Gillman et al. 2022, Lafferty et al. 2022), and future efforts for furbearer management and conservation may need to include consideration of protection or augmentation of host-associated microbial biodiversity (Trevelline et al. 2019, Gillman et al. 2020).

Genetic Monitoring

The use of individual-based noninvasive genetic tagging for monitoring furbearers and other wildlife populations over time across large spatial extents is a powerful and arguably underutilized tool (Carroll et al. 2018, Lamb et al. 2019). Since the first major review of **genetic monitoring** was published over a decade ago (Schwartz et al. 2007), several applications have emerged that illustrate the power of genetic tagging as a tool for monitoring both the genetic and demographic status of furbearer and other wildlife populations (Kendall et al. 2009, Carroll et al. 2018, De Barba et al. 2010, Åkesson et al. 2016, Bischof et al. 2016, Lonsinger et al. 2018, Hedrick et al. 2019, Lamb et al. 2019, Quinn et al. 2019). Although genetic monitoring can involve direct invasive methods to obtain genetic samples from live animals, most applications involve noninvasive sampling (Beja-Pereira et al. 2009).

Recent technological advances in molecular genetic methods have reduced the significance of previous obstacles to individual-based noninvasive genetic tagging (see section on Individual Identification). Genome-level datasets allow for monitoring locally adaptive genetic variation, with direct impacts on species management and conservation actions such as translocations, genetic rescue, or assisted gene flow (Flanagan et al. 2018). Today, the use of noninvasive samples, such as scat or hair, facilitates both localized, intensive, and regional-scale survey and monitoring programs that would be impractical or insufficient using traditional methods alone; noninvasive genetic approaches can provide information on changes in community composition, dispersal or connectivity, occupancy, population abundance, sex ratio, survival, reproduction, and territorial or other spatial dynamics (Kendall et al. 2009, Bischof et al. 2016, Lamb et al. 2019, Quinn et al. 2019). Noninvasive genetic monitoring can also provide information on habitat quality, such as those areas serving as sources or sinks, using spatially explicit inferences from abundance, demographic parameters, and dispersal movements.

Examples of individual-based noninvasive genetic monitoring of furbearer populations include Arctic foxes (*Vulpes lagopus*; Meijer et al. 2008), gray wolves (Caniglia et al. 2014, Stansbury et al. 2014, Åkesson et al. 2016), gray wolf × eastern wolf (*Canis lycaon*) hybrids (Hedrick et al. 2019), kit foxes (*Vulpes macrotis*; Lonsinger et al. 2018, Sacks and Milburn 2018), red wolves (*Canis rufus*; Bohling et al. 2016), Sierra Nevada red foxes (*Vulpes vulpes nicator*; Quinn et al. 2019), and wolverines (Brøseth et al. 2010, Bischof et al. 2016). Long-term individual genetic tagging programs of wolverines and wolves in Fennoscandia provide examples of demographic monitoring, including density dependence, population abundance trends, sex-specific survival, and territoriality (Brøseth et al. 2010, Åkesson et al. 2016, Bischof et al. 2016).

Individual genetic-tagging programs, because they enable pedigree reconstruction, provide direct evidence of genetic rescue, habitat connectivity, hybridization, inbreeding, and space use, along with estimates of population abundance and density, reproduction, survival, and sex ratio (Adams et al. 2003, Åkesson et al. 2016, Bohling et al. 2016, Hedrick et al. 2019, Quinn et al. 2019). For example, in an extremely small population of Sierra Nevada red foxes in California, annual genetic tagging was used to detect inbreeding depression and genetic rescue, and to track changes in both abundance and genetic composition of the population after immigration of two male red foxes from an expanding population (Quinn et al. 2019). Similar programs have been recommended for kit fox populations at the margins of their geographic distribution (Lonsinger et al. 2018, Sacks and Milburn 2018). Individual-based noninvasive genetic tagging also enables monitoring of recolonization dynamics, including hybridization, social dynamics, and source populations (Caniglia et al. 2014). The use of metabarcoding can be paired with genetic tagging to monitor changes in diets across years, which, in combination with demographic information, could illuminate key prey species affecting population dynamics.

Other Emerging Technologies

As sequencing technologies continue to improve, so will our ability to cost-effectively sequence and genotype more individuals at increasing numbers of molecular markers, including whole genomes. Such full-genome-scale data sets are already in use in wildlife studies and offer unparalleled resolution to examine the genetic health of populations through estimates of inbreeding (Saremi et al. 2019), infer past events such as range contractions and expansions due to climatic fluctuations (Colella et al. 2018), or test the notion of unique ancestry for protected populations (Sinding et al. 2018). It is possible to simultaneously sequence the same gene across broad taxonomic ranges from a single environmental sample (metabarcoding) with NGS, which is also revolutionizing our ability to assess biodiversity (Taberlet et al. 2018, Bohmann and Lynggard 2023).

In addition to DNA sequences, other -omic approaches are being used to unveil the genes that are actively turned on or off under various developmental or environmental conditions (transcriptomics; Fraser et al. 2018), the pattern of chemical modifications to the DNA and associated proteins that alter genome function (epigenomics; Meröndun et al. 2019), and the profile of compounds such as lipids and carbohydrates that represent the downstream products of metabolic reactions catalyzed by molecules encoded in the genome (metabolomics; Gossmann et al. 2019). These emerging approaches may offer insight into local adaptation when DNA sequence differentiation is lacking. Finally, cloning technologies are being used to restore lost genetic diversity of small, inbred populations via decades-old, cryopreserved cells harboring unique genomes (e.g., black-footed ferret; Sandler et al. 2021).

CONCLUSIONS

DNA has demonstrated its value as a tool in furbearer management and conservation, and further advances are on the horizon. We have highlighted some of the advantageous features of DNA, popular and promising research directions, as well as some common hurdles encountered in the field of conservation genetics with an emphasis on furbearing species. With myriad options available, a key takeaway is that there is no single best type of tissue, sampling design, storage method, molecular marker, or analytic method, but rather the optimal solution will depend on the question and system at hand. At the outset of study planning, we encourage biologists to consult with wildlife geneticists to discuss DNA collection and storage opportunities, even if no immediate genetic-related objectives are apparent. Several professional organizations associated with wildlife management have working groups focused on genetics (e.g., The Wildlife Society, Molecular Ecology Working Group; Society for Conservation Biology, Conservation Genetics Working Group; International Union for Conservation of Nature, Conservation Genetics Specialist Group) that can field questions and help with project planning. Greater insight into the ecology, evolution, management, and conservation of furbearers can be achieved by combining data from multiple disciplines and perspectives, including genetics.

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