Snow Leopard (*Panthera uncia*) Genetics: The Knowledge Gaps, Needs, and Implications for Conservation

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Abstract | Conservation geneticists apply genetic theory and techniques to preserve endangered species as dynamic entities, capable of coping with environmental change and thus minimizing their risk of extinction. Snow leopards are an umbrella species of High Asia, and a keystone for maintaining biodiversity within this fragile ecosystem. A clear understanding of patterns of snow leopard genetic diversity is critical for guiding conservation initiatives that will ensure their long-term persistence. Yet, a comprehensive analysis of snow leopard genetic variation is lacking. The number of published snow leopard genetic studies is far fewer than for other imperiled big cats. Here, I review the limited genetic work to date on snow leopards and the significant knowledge gaps to be filled. An emphasis must be placed on describing and understanding population genetic dynamics within and among meta-populations to provide information about the interactions between landscapes and the micro-evolutionary processes of gene flow and genetic drift. These results can be used to evaluate the levels and dynamics of genetic and demographic connectivity. A lack of connectivity, particularly in the low density, small populations that typify snow leopards, can lead to multiple demographic and genetic consequences, including inbreeding depression, loss of adaptive potential, and heightened susceptibility to demographic and environmental stochasticity. New efforts in conservation research on snow leopards should focus on this line of inquiry, and the opportunities and challenges for that are outlined and discussed to encourage the required, and considerable, transboundary partnerships and collaborations needed to be successful.

1 Introduction

Snow leopards are an umbrella species and a conservation keystone for maintaining biodiversity within their fragile High Asia habitat spanning 12 countries[55]. They prey primarily on wild sheep and goats, but also the livestock of the pastoralists who share the isolated, but increasingly less remote habitat. This can create significant human-snow leopard conflict, one of a myriad of anthropogenic threats[55(pp 59–136)]. They are keenly adapted to the extreme ruggedness, temperature, and hypoxic conditions of their mountain homes, yet much of their natural history remains undocumented[55]. Basic questions regarding population size, distribution, and connectivity remain unanswered, and much of their behavioral ecology can only be guessed at from anecdotal observations. There are few other large, charismatic species with such significant knowledge gaps. These gaps are substantial enough that the lack of knowledge is often cited as one of the primary conservation challenges for the species[55].

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This is due in part to the difficulties of studying them in their remote, harsh ecosystems, but also due to lack of funding for the research required. The snow leopard's current distribution is uncertain because much of its possible habitat has never been surveyed, or surveyed recently, using rigorous, standardized methods. Similarly, the size of the total snow leopard population is at best a rough estimate. Consistent range-wide scientific monitoring of snow leopards, their prey species, or of changes in habitat characteristics, has also been lacking, which hampers efforts to determine the effectiveness of conservation interventions[78]. No publications currently available provide a comprehensive review of snow leopard cause-specific mortality, and so among the challenges of poaching, retaliatory killings, loss of prey, habitat fragmentation, and climate change, we can only guess at which threats are the most critical to snow leopard persistence, and how those are likely to change across the species' range.

Genetic and genomic methods are powerful tools to study species ecology, evolution, and population dynamics, and inform and guide conservation efforts. Some recent felid examples utilizing these tools include; Indian tigers[59], jaguar[48], puma and jaguar[92], lions[15,53], lions and cheetah[10], and leopards[5,63]. However, the body of published snow leopard genetic research follows the general theme of snow leopard research generally, with significant knowledge gaps and lack of attention as compared to other charismatic species. In an assessment of all the big cats of the world, a literature search in Web of Science (performed on January 3rd, 2021) demonstrated how far behind snow leopards are in pure volume of publications. In a topic-based search combining two terms, first each big cat species' names (e.g. *Panthera uncia*, *Panthera tigris*, etc.) and then either "genetic*" or "genom*". The combined number of manuscripts that mention genetic* and genom* was 634 for tiger (*Panthera tigris*), 579 for lion (*P. leo*), 513 for puma (*Puma concolor*), 417 for cheetah (*Acinonyx jubatus*), 340 for leopard (*P. pardus*), 225 for jaguar (*P. onca*), and only 134 for snow leopard (*P. uncia*), demonstrating the clear lack of attention, as compared to other cats, that snow leopards get across this broad research topic search. This lack of genetic and genomic-related citations on snow leopards is surprising considering that the identified major knowledge gaps in understanding distribution, range, connectivity, and various ecological and evolutionary dynamics can all be addressed using genetics research methods and tools. Indeed, the field of conservation genetics was established, and continues to developed, as a discipline that provides the scientific approaches for understanding and harnessing knowledge on the dynamics of genes to inform conservation action and avoid extinction in species of concern (e.g.[51]). Herein, I explored how to define conservation genetics and needs for snow leopards, what limited genetic work has been done on these cats, and how the conservation community can promote and support an expanded utilization of this field of study and its related methods.

2 What is Conservation Genetics? A Theoretical Overview

To appreciate the context for how conservation genetics are poised to fill important knowledge gaps for snow leopards, we should first consider the origins and development of the field itself. Darwin[12] acknowledged concerns that small, isolated populations of deer in British wildlife parks could have detrimental losses in fitness. This was a nod towards the understanding of, if not in the molecular mechanics, how processes inherent in declining populations lead to deleterious demographic consequences, a process described almost a century later as the extinction vortex[25]. Our contemporary view of conservation genetics did not coalesce until the 1970s. In a landmark publication titled "Genetic conservation: our evolutionary responsibility", Frankel[20](p. 53) states that "…there is an urgent need for exploration and clarification of the genetic principles of conservation…the possibility of a virtual end to the evolution of species of no direct use to man raises questions of responsibility and ethics." To this end, Frankel[20] also acknowledges not only the necessity of utilizing genetic information as a research tool, but the importance of evolutionary processes and an evolutionary perspective in highlighting the grounds for conservation by providing a sense of permanence that other perspectives (e.g. ecological) may fail to reinforce. In a lesser known review on principles of genetic conservation in wildlife management, Greig[26](p. 57) outlines the philosophical, historical, and theoretical basis for conservation genetics. An excerpt from his eloquently succinct abstract summarizes a strategy that is still relevant four decades later: "…conservation of genetic variation should be the prime consideration in the implementation of nature conservation policy, for ecological, taxonomic and aesthetic reasons. This is best achieved by conserving the genetic integrity of population units somewhere between the hierarchical levels of deme and subspecies without unnecessary genetic admixture…The survival of

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life in a changing world depends upon evolution which in turn is completely dependent upon the existence of a full spectrum of genetic variation." This grounding in the tenets of evolution by both Frankel[20] and Greig[26] provides the foundation for the prominent theoretical field that informs conservation genetic principles, population genetics.

Population genetic research is derived from the study of micro-evolutionary forces, including gene flow, drift, selection, mutation and recombination. In conservation, the focus is primarily on gene flow and drift, as they have immediate, measurable, impacts on the small populations that typify endangered species such as snow leopards. Both in theory and in practice, the movement of individuals and their genes in geographic space has many important implications on species' ecology and evolution[31]. Gene flow determines the role of population structure in the evolutionary process[75,76,85,91]. This consequence of population dynamics has led to an emphasis on estimating the magnitude of gene flow through both direct and indirect methods[19,68,75]. Direct methods quantify the movement of genes by monitoring the means of gene flow, by either directly following marked individuals in space (e.g. radio-collaring), or through parentage analyses. Indirect measures of gene flow (reviewed in[75,77]) focus on the impact of gene flow on local differentiation of genetic markers.

Gene flow is generally regarded as an opposing force to evolution[8,54], with the premise that natural selection will tend to adapt a population to local environmental conditions, but immigrants from outside the population bring in new genes that are adapted to different environments, consequently controlling any differentiation between populations[18,85,89,91]. However, gene flow can also be a creative force in evolution. The movement of individuals, or even entire populations, can spread favorable genes throughout an entire species' range.

Gene flow also helps to overcome the demographic and molecular consequences of genetic drift[17,76]. Genetic drift is the random change in allele frequencies that occurs from one generation to the next because gametes transmit only a sample of the alleles present in the parental generation. Without the homogenizing effect of gene flow, isolated and fragmented populations can rapidly drift to significantly different allele frequencies[17]. Small populations in particular are especially susceptible to the loss and reorganization of genetic variation by drift[44]. In these small populations, increased inbreeding and drift lead to a higher probability of fixation of deleterious alleles and a related reduction in fitness, the extinction vortex.

The role of gene flow, drift, and selection in the persistence of species of concern, including snow leopards, is inherent and so the inclusion of population genetics into conservation planning is paramount[22,23]. To understand and evaluate population structures, interactions, or demography, these micro-evolutionary forces must be addressed. With an emphasis on factors of isolation, small population size, and reduced genetic variation, the field of population genetics provides a significant underlying body of theory to provision the application of conservation genetic methods in practice[1]. Thus, with roots in evolution and a body of theory in population genetics guiding it, conservation genetics in practice aims to understand (1) the deleterious effects of inbreeding (and conversely outbreeding) on survival, (2) the loss of genetic diversity and evolutionary potential, (3) fragmentation and gene flow, (4) defining conservation units, (5) applications in wildlife crime forensics, and (6) providing new insights into species ecology. See Frankham et al.[21] and Allendorf et al.[2], among others, for further insights and explanations on these topics. For the purposes of snow leopard conservation, I will define conservation genetics as the interdisciplinary field that aims to describe and understand the genetic dynamics of populations of concern to inform management and conservation policy action to prevent extinction.

3 Snow Leopard Research Needs and the Potential of Genetics

3.1 Non-Invasive Genetics and Survey and Monitoring of Snow Leopards

In snow leopard survey and monitoring efforts, camera traps are by far the most ubiquitous research tool used in field data collection[90]. The cameras are used primarily to identify occupancy in novel field sites, and to calculate density [e.g. spatial capture–recapture (SCR) approaches] in regions of particular interest. Non-invasive genetics methods[80], where the DNA template for analysis is acquired without direct interaction with the animal, provide similar information as camera traps, often with better precision and detail (e.g. sex determination). Further, surveys with camera traps require at least two trips into the field site, whereas a genetic survey can be done with a single site visit. In a study comparing camera trapping and non-invasive genetics methods for surveying tigers in Bhutan, Dhenup[14] found that, after controlling for sampling effort, non-invasive genetics

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performed better. However, in some cases, a non-invasive genetics approach may require increased field effort and a larger effective sampling area[14]. Additionally, the cold, arid environment of snow leopards likely allows for fecal material (the typical source for non-invasive DNA samples) to persist over a long time and aging a scat can be difficult or impossible. This has implications for analyses where there are assumptions of temporal closure (e.g. population estimates). Quantifying the decay rate of scats in the field would allow for correcting factors, but has yet to be calculated.

Non-invasive sampling of hair, feces, urine, saliva, and environmental DNA (eDNA) can be used to identify species presence, sex ID, and in some cases individual ID. The use of eDNA, DNA that is shed by an organism into the environment (inclusive of, but not limited to, other non-invasive sources), has long been used in aquatic systems and is a rapidly developing tool in terrestrial habitats[45,70,84]. Trace eDNA from snow tracks has been used to augment camera trapping efforts to more effectively distinguish between closely related, but rare cat species of management concern in North America (lynx and bobcat,[24]. The use of eDNA sampling has also been shown to improve on the performance of camera trap efforts with regards to false negatives, detecting species missed by cameras (e.g.[24,45]). These, and other advances in the use of non-invasive DNA samples (e.g.[41]) have allowed for an increasingly high level of sophistication of research applications. In the use of SCR approaches for estimating population sizes, the accurate identification of individuals is vital. A genetic metric for determining the robustness of discriminating among individuals is called the probability of identity (PID). This value is defined as the probability that two distinct individuals would have the same genetic profile. Janjua et al.[39] found that for a collection of 12 moderately variable microsatellite loci, PID in a small population of snow leopards in the Gobi Desert of Mongolia was calculated at 2.35×10^{-7}. For those same individuals using a modest number of single nucleotide polymorphisms (SNPs) the PID was calculated to be 1.55×10^{-168}. Both sets of genetic markers offer high confidence in discriminating the number of individuals in a dataset, and the sensitivity of SNPs is impressive. In contrast, the often subjective task of identifying individuals through spot patterns in camera trap photos can be less robust, with a recent study indicating even experts had a 10% rate of misclassifying individuals[40].

Additionally, while genetic detections can function in the same way as camera trap image detections, the individual ID genetic data also allow for the calculation of effective population size (N_e). N_e is a parameter driving genetic drift that reflects changes to population dynamics and can roughly be translated as a calculation of the number of breeders in a population that contribute genes across generations. N_e influences the rate of drift and evolutionary potential[49]. In practical terms, N_e is the size of an ideal population that loses genetic diversity at the same rate as the actual population being studied, yet, because wild populations typically depart from ideal conditions, N_e is usually smaller than a census population estimate (N_c). Measuring and monitoring changes in N_e and the N_e/N_c ratio is a powerful tool in conservation as a predictor of genetic diversity loss and population differentiation and detecting important changes in population demographics[49].

However, non-invasive samples are prone to some types of genotyping error, such as allelic dropout and null alleles[6,93]. To counter these inherent problems, lab protocols must be rigorous and results need to be demonstrated to be consistent across multiple independent replicates. When done properly, genetic approaches for snow leopard detections can be incredibly efficient for rapid assessments of snow leopard occupancy and abundance efforts (but see[79]), notwithstanding issues with temporal closure. Given the challenges of camera traps and genetics approaches, an idealized sampling scheme would combine both camera trap and genetic methods, where the benefit of two independent data sources, and their combined strengths, may overcome some of the collective shortcomings.

The individual IDs that go into calculations of effective population size and the inventory and monitoring uses above are calculated from the genetic profiles derived from microsatellite loci or SNPs. Of note, to date most individual IDs in non-invasive studies are done with microsatellites as achieving reliable SNP datasets from non-invasive DNA sources is largely still in progress (but see[60]). However, as noted earlier, the potential for SNPs is incredible, and SNPs data from other DNA sources have proven to provide incredible insights into carnivore population dynamics and connectivity (e.g.[10]). The same kind of genetic profiles, whether from microsatellites or SNPs, provide the fundamental units of information required to address avenues of hypothesis and application-driven research that can fill significant knowledge gaps important for snow leopard conservation.

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3.2 Connectivity, Meta-Population Dynamics, and Landscape Genetics

Snow leopards are a species that persists at low densities (in some habitats < 1 adult per 100 km[273]), and across the naturally fragmented landscapes of High Asia's mountain ranges. Small, fragmented populations are predicted to be particularly sensitive to changes in connectivity and require specific attention in species conservation planning[64,65]. Population genetics approaches provide a basis from which to evaluate gene flow, connectivity (or conversely, isolation), and genetic drift (e.g.[5,48]). A number of recent studies have modeled snow leopard habitat at the range-wide scale, and demonstrated a pattern of core habitat patches connected by narrow corridors throughout the range[47,66]. Li et al.[46] modeled how the size and number of these patches would be expected to change under different climate scenarios, looking both back in time to the most recent Pleistocene glacial maximum and forward in time to various climate warming models. The implications of these results are significant for informing conservation management and policy for snow leopards as it relates to protected area designation, corridor network design, and predicting range shifts and habitat needs under global climate change (e.g. in tigers[82]). Yet, while compelling and useful, the results are model outputs from a data-limited species, and may require validation and additional analysis to sufficiently embolden policy-makers and natural resource managers into appropriate action. Genetic data provides an ideal dependent variable against which to evaluate and test the model outputs, i.e. the models provide a series of testable hypotheses. Among the most pertinent routes that this hypothesis testing can inform snow leopard conservation are (1) identifying patterns of variability that are consistent with core, source populations versus regions of recent colonization or demographic sinks, (2) characterizing range-wide patterns of genetic diversity (i.e. phylogeography) to define appropriate conservation units, including important meta-populations (e.g. in tigers[58]), (3) identifying functional routes of connectivity among meta-populations, and (4) insight into what geographic, abiotic, biotic, and anthropogenic factors influence snow leopard gene flow (i.e. landscape genetics, e.g.[82]). A recent review of the history of molecular studies of tigers provides an overview of how genetics and genomic approaches have informed many of these similar issues for that species[51].

Meta-population theory defines systems of evolutionary ephemeral and genetically subdivided populations (i.e. subpopulations or patches) that persist through time by colonization and gene flow from neighboring patches[31,62]. These populations are connected by rates of gene flow that are low enough for drift to create genetic differentiation among the subpopulations, but high enough to rescue local populations from extinction[31]. The key point here being that this "rescue" effect depends on adequate connectivity and subpopulations with the demographic dynamics conducive towards dispersing individuals. Snow leopard populations have cycled through range contractions and expansions under large climatic events of the past[46], yielding a mosaic of habitat patches[47] threaded together into functioning meta-populations. As snow leopards face the ongoing, or impending, impacts of human infrastructure expansion, natural resource extraction, and anthropogenic climate change, the number of patches are predicted to increase[46] making connectivity all the more important, but increasingly challenged. When connectivity breaks down, the "rescue" effect fails, small populations become more isolated, genetic drift increases, and the demographic dynamics trend towards declining numbers and increased probability of local extirpation, the extinction vortex[25].

Amidst all of that, the questions remain, what is adequate connectivity for snow leopards, and what do those population demographics look like (e.g.[5])? What are the underlying evolutionary and ecological mechanisms driving the patterns of connectivity that allow for population persistence (e.g.[48])? To answer these question, we can look towards the fields of population genetics and landscape ecology, and in the relatively recently emerged field of landscape genetics that combines the theory and statistical tools of those two disciplines (e.g.[57,83]). Landscape genetics provides information about the interaction between landscape features and micro-evolutionary processes such as gene flow, genetic drift, and selection[52] and can play an important role in the management and conservation of species[71].

Given the precariousness of the fragile high elevation ecosystems where snow leopards persist, successful snow leopard conservation will require an understanding of meta-populations and landscape genetics. However, there remain significant knowledge gaps in these topics with fundamentally no rigorous work yet published on snow leopards at meta-population and landscape scales (reviewed in[7,67], but see below). Filling those gaps must be a priority to insure wildlife managers and policy-makers have the scientific backing to

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inform the scale-appropriate conservation measures needed to prevent snow leopard population declines.

4 Snow Leopard Genetics to Date

Caragiulo et al.[7] reviewed the status of snow leopard genetics research up to 2015, summarizing that the published work was largely focused on (1) the snow leopard's place within the greater Felid phylogenetic history (e.g.[13]), (2) the development of molecular tools and markers (e.g.[36,86]), and (3) the use of those tools for individual identification for occupancy and diet analyses (e.g.[34,35,56]). Caragiulo et al.[7] noted that as of their publication date, there had been no well-sampled, rigorous studies addressing important conservation genetic issues such as population genetics, landscape genetics, or snow leopard phylogeography. They called for an increased emphasis in filling those knowledge gaps for future snow leopard research programs. In the 5 years since the publication of Caragiulo et al.[7], this call for increased research attention has largely gone unheeded.

In a literature review for snow leopard genetics from 2016 to 2021 (using same search criteria as noted above), again genetic tools were more widely used for species and individual identification in support of diet analysis (e.g.[28,74,88]) and occupancy/density/distribution studies (e.g.[9,30,42]). Only four additional papers have been published that present data towards explaining population genetic processes[4,37,50,74]. Only two of those clearly demonstrated the proper criteria, multiple PCR replications of individual ID, required to be confident in the data produced and analyzed[37,74]. Additionally, a common issue with many genetics studies, including these, is sampling design. A cluster sampling design with a small number of loci at low, or even moderate, levels of allelic diversity has been modeled to perform poorly in successfully identifying the generating demographic or landscape processes responsible for observed patterns of genetic diversity[61], thus the results of these population, landscape, and connectivity analyses should be interpreted cautiously. Of those, only Janecka et al.[37] used enough microsatellite loci to provide the statistical power required to have confidence in the results. Yet, whatever the shortcomings of the papers above, all of the efforts made to employ genetics approaches for snow leopard research is encouraging, and with improved funding, partnerships, and knowledge-sharing (see Sect. 5 below), the initial success of many of these pilot projects can be built upon with greater rigor in both field sampling and lab and data approaches.

Janecka et al.[37] offered the first ever range-wide analysis of snow leopard genetic diversity and incorporated the largest sample size, to date, of any snow leopard genetic research project. Many of the co-authors are representatives from snow leopard range countries, and the publication is a clear demonstration of how multi-institutional collaborative efforts are key towards producing impactful and scale-appropriate studies on this low-density, wide-ranging mammal. In their study, Janecka et al.[37] analyzed 70 individuals with 33 microsatellite loci and summarized a variety of population genetic metrics that described patterns of snow leopard genetic variability across their range. Among the results, their primary conclusions were that (1) snow leopards experienced a population bottleneck ~ 8000 years ago, coinciding with post-Pleistocene warming in the Holocene epoch, and (2) snow leopard populations segregate into three distinct phylogenetic units representing distinct subspecies. The latter conclusion is quite controversial. Subspecies concepts in general are keenly debated and hotly contested[29], and the conservation implication of accepting their taxonomic revision of subspecific diversity for snow leopards is that each would require its own IUCN Red List assessment[33].

In a formal response to this controversy, Senn et al.[72] cited, among other concerns, significant sampling gaps and lack of mitochondrial DNA (mtDNA) diversity, in addition to the uncertainty that surrounds objective definitions of subspecies[29], as evidence against accepting the new classification. In response, Janecka et al.[38] counter-argued in support of their original claims of three subspecies by citing that their sampling was consistent with similar taxonomic revisions of other felids[43] and noting some of the potential shortcomings of mtDNA diversity and its use in taxonomy and phylogeography. Both responses make valid points and articulate strong arguments, which is consistent with the pendulous nature of most debates on subspecies (e.g.[11,87]). Nevertheless, a strong argument can be made for improved sampling[61] and the utility of mtDNA[69], as well as the need for incorporation of other independent measurements for phylogenetic evaluation (e.g. morphology, behavior, genomic data). As such, Janecka et al.[37] can best be utilized as a benchmark study of snow leopard phylogeography and population genetics that provides a set of hypotheses (e.g. subspecific diversity) to be tested with increased sampling and alternative approaches.

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5 Challenges and Opportunities for Moving Forward

As noted previously, among the world's high-profile and charismatic species, the snow leopard remains significantly understudied with genetic approaches or otherwise. The lack of information and published studies can likely be attributed to the difficulty in undertaking direct study of snow leopards and their ecosystems. They persist in harsh and remote environments that are difficult to access logistically and sometimes politically. The remoteness and severity of their habitat has likely helped to isolate them from similarly significant losses of habitat and population pressures that other Asian distributed species have experienced over the last century, for example, the tiger has lost over 90% of its historic range. The snow leopard has never been an abundant species, and although over time its IUCN Red List status may change up and down a spectrum of classifications, its natural history makes it a species always on the razor's edge of extinction, with little margin for error. Consequently, as human populations expand (in numbers and in need for natural resources), even the nearly inhospitable climes where snow leopards dwell are experiencing new and amplified anthropogenic threats. The need to improve our knowledge of snow leopards is essential, and genetic approaches can be fundamental towards filling the knowledge gaps. We must then understand why the gaps in use of genetics remain, how to resolve those challenges, and what are the opportunities to improve[32].

The incorporation of genetics into conservation planning has been a lost opportunity globally[65]. In New Zealand, Taylor et al.[81] surveyed 148 conservation practitioners in the country's Department of Conservation on their attitudes, knowledge, and experiences with genetics in a conservation framework. Across conservation issues, they found that insufficient awareness, expertise, and funding were the primary barriers for increased application of genetic methods in conservation practice. It is likely these same challenges, and some unique to snow leopards and their range countries, impede the use of genetics methods in rigorous, scale-appropriate snow leopard conservation efforts. Below, I outline some of these challenges and related opportunities.

(1) Challenge: lack of awareness of the applications of genetics methods to snow leopards

Opportunity: the snow leopard conservation community must be educated on the value, efficacy, and power of genetic data and related analyses. The use of camera traps in snow leopard research has been revelatory in rapidly expanding our understanding of the species, and in the same vein that we cannot imagine studying snow leopards without camera traps, conservation organizations and range state wildlife agencies must promote genetic tools as equally indispensable.

(2) Challenge: lack of expertise in designing/implementing projects, analyzing data, and interpreting results

Opportunity: there are potentially two opportunities to pursue to overcome this challenge

(a) Many snow leopard range countries have active and advanced molecular facilities and practitioners capable of doing the needed genetic work, but that expertise is focused on human health systems or academic pursuits on model organisms. Inroads, in both academic and government agency laboratories, must be made to promote wildlife and conservation genetics practices and take advantage of the expertise already in place. Fostering better communication among these institutes via workshops and interdisciplinary conferences could catalyze improvements in developing expertise and expand the scope of practice of genetic labs already in place.

(b) A concerted effort by the snow leopard conservation community must be made to build in-country capacity for genetics practitioners. A common theme, to date, is that scientists from Western countries and institutions lead the majority of wildlife/snow leopard genetics projects. Long-term viability and acceptance of genetic methods will require that genetics research is done by scientists from range countries. They must first receive the proper training and skillsets with which to lead genetics research and manage regional collaborations. The more established and experienced institutions and scientists (from range countries and abroad) may help to provide the training and facili-

tate the exportation of their knowledge and skills.

(3) Challenge: inadequate funding to cover expensive lab analyses.

Opportunity: conservation funding is always limited and remains a significant challenge that hinders progress along any research or mitigation activity. However, the molecular methods used for most genetic, and genomic, tools have significantly dropped in cost over the past 20 years, and continue to get cheaper, with more data coming out of the same unit of cost per lab effort. Survey costs, for example, can be the same or less than the camera trapping equivalent (with all the value added, as per above). Genetics approaches also may allow for accessing novel sources of fundraising that were previously unavailable. Conservation organizations need to invest in genetic methods at equal, or increased, levels as their camera trap programs. In addition to these three challenges that are likely general to conservation efforts irrespective of species, there are additional, sequential challenges specific to the needs for snow leopard conservation.

(4) Challenge: difficulty in obtaining representative sampling range-wide and continuous sampling at landscape levels.

Opportunity: proper sampling is crucial for achieving suitable context and statistical power to fill the knowledge gaps described above. Getting that sampling is essentially impossible for a single individual or institution. Adequate sampling will require building and maintaining expansive collaborative networks among academic, government, and NGO institutions. Competitive or exclusionary approaches to snow leopard conservation will always stymy progress and limit the potential to scale up research design and achievement. The complexities of these collaborative arrangements are notable, but it must be a priority of snow leopard conservation leaders.

(5) Challenge: inability to export samples to labs outside of range countries.

Opportunity: in the case where a range country does not have the capacity to perform the needed laboratory work on genetics projects, samples are often shipped to outside labs (e.g. to the United States or Europe), however, there is increasing sensitivity on the use and exportation of genetic materials, such that exporting samples, whether raw non-invasive material or even DNA extractions, is becoming prohibitive. This leads once again towards emphasizing in-country capacity building and improved collaborative efforts with in-country institutions to organize, fund, and build appropriate lab facilities.

(6) Challenge: standardizing datasets among labs to allow for meta-analysis at larger spatial scales.

Opportunity: in snow leopard non-invasive genetics work, microsatellite markers are used for producing the individual identification data, but are inherently difficult to standardize between labs, thus challenging the prospects of reliably combining independent datasets. An approach to mitigate this is having each lab use the same positive control samples; however, if samples cannot be exported this is not possible. Next generation sequencing (NGS) methods are increasingly available in non-model organisms[16,27] and utilize SNPs as a marker for individual ID. SNPs have the potential to provide considerably increased statistical power over microsatellites[39], and are more easily reproducible across labs, although they are not without their own challenges[3]. Presently, reliably amplifying SNPs from non-invasively collected DNA templates (e.g. feces) remains a significant challenge, although there is some progress[60]. Snow leopard research programs in molecular research should emphasize developing SNPs to improve analytical approaches, the capacity building for NGS technologies in snow leopard range states, and building of collaborative networks to standardize these approaches and allow for future meta-analyses.

(7) Challenge: The feasibility of seizing on any of the opportunities above will vary greatly from one snow leopard range state to the next as well as across snow leopard conservation organizations, both local and international, due to resource limitations. Resources needed for conservation inevitably outstrip availability. Thus, adding molecular approaches to snow leopard conservation will require either new fundraising efforts or a redirection of resources already invested in other conservation activities. In the latter case, careful consideration must be made to ensure that the value added by incorporating genetics projects is not at a greater cost to important conservation needs.

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Opportunity: Genetics and genomic tools are not a panacea to conservation challenges. As with any tool, only when used properly can it contribute to improving on knowledge and outcomes. Genetics approaches should be evaluated first in how they can complement or strengthen ongoing programs. Examples might include, camera trapping for occupancy and abundance, diet analysis to better understand human-snow leopard conflict, or validating connectivity of habitat models. For some range countries, where the necessary technological infrastructure required for doing genetics/genomics work is not readily available, this may give motivation to improve transboundary collaboration and partnerships with other range states that already have those capabilities in place.

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Conflict of interest

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Dr. Byron Weckworth joined Panthera in 2012 following studies in conservation and biology through his undergraduate degree at the University of Montana, a M.S. at Idaho State University, and his Ph.D. at the University of Calgary. His research experience has involved fieldwork across a variety of ecosystems from North Carolina swamps to the mountains of High Asia, on an equally varied number of species, including wolves, black bears, caribou, moose, and, of course, wild cats. His research aims to address a wide spectrum of ecological and evolutionary questions pertinent to successful conservation. Byron's goals are to help produce rigorous scientific research and to work collaboratively to make such research accessible and applicable to the people and partner organizations that have the influence to impact conservation.

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