

Evaluating mountain goat population structure in Glacier National Park and Waterton Lakes National Park

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Key words

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Abstract

Mountain goats are an iconic, climate-sensitive species across their North American alpine range. Among its nearly complete complement of native wildlife, no single species embodies Glacier National Park (GNP) more than the mountain goat. They play an important role as an alpine food source for many of the park's carnivores including wolverines, mountain lions, and grizzly bears. Mountain goats face many increasing threats, particularly at the southern extent of their range. These include changes in precipitation and temperature, shifts in forage and fire frequency and intensity, and rapidly increasing visitation and recreation. Although the high latitude and elevations of GNP offer refugia, the mountain goat population likely declined between 2008 and 2019 and may also have a smaller distribution. In Montana, many other native mountain goat populations are also declining or have disappeared entirely. Using a combination of staff and citizen scientists, we collected fecal pellets across GNP in Montana, USA, and adjoining Waterton Lakes National Park (WLNP) in Alberta, Canada, between 2019 and 2023. We used genotypes of 6 to 19 loci microsatellites to identify individuals and assess isolation by distance, genetic structure, and genetic diversity. We found no evidence of genetic structure and only limited isolation by distance. This suggests that mountain goats in GNP and WLNP can be considered a single population, so samples can be combined across the area to estimate a single population size. Genetic diversity was similar to recent mountain goat studies conducted in other regions; allelic richness was 3.54 and inbreeding coefficients (F_{IS}) ranged from 0.01–0.19, with values >0.11 only in the Livingston Range in the northwest of the study area. The high F_{IS} in the Livingston Range suggests several closely related groups with little interchange, and perhaps a

recent decrease in gene flow, both of which are consistent with a recent population decline in that area. We detected a high number of closely related individuals throughout our study area, consistent with the high adult survival, low reproductive success life history of goats, but also suggesting that we sampled much of the overall population.

Introduction

Mountain goats (*Oreamnos americanus*) are alpine specialists adapted to living on cliffs and in cold regions with persistent snowpacks (White et al. 2024). Mountain goats are icons of the peaks and glaciers of the northern Rocky Mountains, feature prominently on logos for all Glacier National Park's (GNP) official partners, and sightings and photographs of them are avidly sought by visitors to the park and the region. In Montana, many native populations are declining or have been extirpated (Smith and DeCesare 2017). Populations to the north, in adjoining Waterton Lakes National Park (WLNP), may presently be stable, but anecdotally have declined from amounts seen prior to the start of regular surveys in 2000. Suspected reasons for these declines include overharvest, droughts, reduced snowpacks, high-intensity fires, changes in forage, and increasing pressure from human recreation (White et al. 2025).

Enthusiasm for goats and their rugged peaks is linked to increasing recreation use of once secure goat haunts and to habituation of goats, both of which influence goat behaviors, movement and predator avoidance (Sarmiento and Berger 2017). Mountain goats live at the highest available elevations and depend on steep cliffs and talus to avoid predation, such that their options for shifting habitat in response to recreation or other stressors are extremely limited. Climate change models predict the observed changes of (i) earlier melt-off of snow patches in alpine environments (Fagre et al. 2003), (ii) upward shift of vegetation types (e.g., Klasner and Fagre 2002); and (iii) changes in phenology, species composition, and timing of plant nutrients in alpine environments (Berman et al. 2020). Increasingly frequent and severe wildfires are also removing cover in areas traditionally used for shelter and access to natural mineral licks. Thus, mountain goats may be the species in GNP and surrounding areas most threatened by climate change (Beever and Belant 2011). New research suggests that climate change may affect both the distribution and population persistence of goats (White et al. 2018, White et al. 2024). GNP's population is at the southern edge of the range of native mountain goat populations and native goat populations southeast of GNP in the neighboring Bob Marshall Wilderness have declined substantially, shrinking to ~25% of their population size since the 1940s (Smith and DeCesare 2017). Many other nearby native populations that may have previously formed part of a metapopulation are small, isolated demographically and genetically, and are also declining or have disappeared, including in the adjacent Whitefish range. Declines are documented across much of the southern portion of the species' native range (Côté and Festa-Bianchet 2003, Festa-Bianchet and Côté 2008, Smith 2014), including 50% declines in British Columbia, Canada (BC Mountain Goat Management Team 2010) and 60% declines in Washington, USA (Rice and Gay 2010).

Glacier National Park (GNP) has been conducting citizen science-based monitoring of mountain goats at 37 sites across the park since 2009 (Belt and Krausman 2012, Graves et al. 2025). These efforts have revealed a 45% (95% Credible Intervals (CRI) = 32%, 57%) decline in median number of goats per site from 77.8 (95% CRI = 64.4, 95.1) in 2008 to 42.3 (95% CRI = 34.3, 52.2) in 2019, with the largest declines between 2008 and 2015 (Graves et al. 2025). This decline

over only two generations exceeds International Union for Conservation of Nature (IUCN) criteria for classifying a population as vulnerable (a 30% decline across three generations; IUCN 2024). Results indicated that the Livingston Range, in the northwest portion of GNP, has relatively few goats remaining (median goats predicted to use a site is <30 for all but one site) compared to sites with the highest use, such as between Logan Pass and Gunsight Pass (median goats predicted to use a site 79-155; Graves et al. 2025). Especially since 2015, credible intervals around the predicted number of goats per site are relatively large (Graves et al. 2025), mirroring a pattern typical for small populations wherein trends become more difficult to assess as populations decline (e.g., Barnes 2002).

Past efforts to evaluate population size have been based on extrapolations that were either unclear or made strong assumptions. Belt and Krausman (2012) had the most transparent approach based on single year N-mixture estimates of the number of goats/site. They compared estimates from volunteers, biologists, and aerial counts. Confidence intervals were large. The 2009 estimate from the paper used by park officials when asked about the number of goats had a mean of 2,027 goats, with a 95% confidence interval of 1,397-2,657. The interval overlaps with the ~1,500 minimum goats identified by Chadwick, which was based on an unclear approach to extrapolation of densities from counts he conducted in the Many Glacier area and other counts in southern portions of the park, including at the Walton mineral lick (Chadwick 1977, Singer 1975). Chadwick (1977) notes that his number is nearly double the ‘traditional estimates exemplified by Calhane’s (1948) figure of 870’, which has no information on methodology. The method used by Belt and Krausman (2012) estimated the number of goats using each site across the full season, which provides information on the relative densities across different sites. However, it assumes closure (i.e., that none of the goats counted in one area moved to another counted area). Although grid sizes used in the sample design relate to home range size, goats select for escape terrain and thus home ranges of goats are often long and linear, following the contours of upper elevations, which could violate the closure assumption. Since that study, animals with GPS collars have moved between some of the citizen science sites illustrating clear violation of the closure assumption. These areas, including between Logan Pass and Gunsight Pass, had some of the highest predicted goats/site (Graves et al. 2025). Thus, when extrapolating across the ~1,685 km² of escape terrain in the park, this approach could double or possibly even triple-count goats in areas with the highest goat densities in the park. The study design was targeted at monitoring goat densities and trend using average count at sites and the authors acknowledge that extrapolation to parkwide population size was subject to violation of assumptions about population closure. However, given those are the most transparent estimates, we used those to coarsely assess population size as of 2020 assuming limited declines in population size between 2008 and 2009 (Graves et al. 2025). Calculation of a 57% decline (trend credible interval) from the lower 95% population CI (1,397) and a 32% decline (trend credible interval) in the upper population CI (2,657) yields an extrapolated range between 601 and 1,807 goats as of 2020 (Graves et al. 2025).

When populations have small effective population sizes (<500-1,000 animals), a loss of evolutionary potential can occur (Frankham 1980, Frankham et al. 2014, Jamieson and Allendorf 2012; Pérez-Pereira et al. 2022). Alpine ungulates typically exhibit a small effective population size (broadly defined as the number of breeding individuals in a population) and limited ability to disperse to new areas (Forbes and Hogg 1999). Effective population size for a population can

be lower than the number of adult animals in a population when mating is not random, sex-ratios are uneven, generations are not discrete, and breeding is structured by age, which all apply to goats generally. However, limited spatial structure and migration from neighboring populations may increase effective population size (Waples 2025). Thus, knowing both population size and movement patterns can aid in the status assessment of wildlife populations.

Understanding whether goats in the GNP-WLNP contiguous, protected, transboundary area comprise a single population or are subdivided into smaller subpopulations will provide context on the ecological importance of this apparent decline. Smaller and less genetically diverse populations are more vulnerable to catastrophic events and extinction (Slatkin 1977, Hebblewhite et al. 2010, Johnson et al. 2011). Information on mountain goat status can be used to guide proposed infrastructure and regulations under consideration in the Going to the Sun Road Corridor Management Plan and the Backcountry Management Plan that could influence goats (Glacier National Park 2019, Glacier National Park 2021, R. Found and M. Biel written communication, 5/13/2025). Goats are included in GNP's Foundation documents, WLNP's park management plan, and studying goats from ecological and human interaction perspectives is a goal of both parks (e.g., Glacier National Park 2021, R. Found and M. Biel written communication, 5/13/2025).

Nonetheless, goats remain poorly studied in GNP, WLNP, Montana, and throughout their range (White et al. 2024, DeCesare and Smith 2018). Limited understanding exists of goats generally and population structure specifically, in part because of challenges of observing them in their steep alpine habitats and even collecting genetic samples in some places (Shackleton 1997, Gude et al. 2022). GNP and WLNP seek to minimize administrative overflights and aircraft and pilots with required certifications do not exist locally, restricting commonly used techniques for monitoring via air such as repeat counts of animals, capturing animals, or collecting pellets or other samples via helicopter or fixed-wing platforms (Glacier National Park 2022). Monitoring using aerial surveys also requires substantial cost for large landscapes, leading to a lack of statistical rigor for many goat populations (e.g., DeCesare and Smith 2018). WLNP appears to be topographically connected and has conducted helicopter counts periodically but genetic structure or diversity have not been evaluated. Understanding population structure (i.e. whether a population is subdivided) provides context to identify the degree of threat to a population from stressors. Stressors that have been documented as increasing include visitation, off-trail recreation use, increasing habituation of goats, encroachment, changes in forage, and changes in thermal refugia (i.e., snow fields; White et al. 1998, DeCesare and Smith 2018). In addition to the documented declines, and a generally small effective population size, mountain goats respond slowly demographically (because of their low reproductive potential) to improvements in their habitat and thus management actions may require many years to achieve results. Therefore, the results of this work can help resource managers prioritize needs for goat conservation and identify adaptive management approaches for GNP and the region.

Through this project we collected fecal pellets across both parks to support two primary goals: 1) assess genetic structure and diversity, and 2) determine a minimum number of goats for the study area. Data collection also will support two long term objectives of estimating mountain goat numbers and evaluating mountain goat diets (e.g., Poole et al. 2011, Scoresby et al. 2025).

METHODS AND STUDY AREA:

Study Area

This study was conducted within predicted mountain goat habitats within GNP and WLNP, which together comprise the Waterton-Glacier International Peace Park (Hop et al. 2007). This World Heritage Site protects an area containing headwaters for three oceans, many unique flora and fauna including high profile species such as grizzly and black bears, wolves, mountain lions, and several ungulates including mountain goats (<https://whc.unesco.org>). Mountain goat habitat generally includes subalpine and alpine ecosystems above ~7,000 ft. (Figure 1; Flesch and Belt 2017). Much of GNP's primary goat habitat is accessible using the >700 miles of trail combined with off-trail scrambling, but some areas require multiple days of off-trail travel to access (Belt and Krausman 2012). Weather conditions, especially in the alpine, can be volatile as the study area spans two competing weather systems on the continental divide, resulting in high precipitation and winds (Hop et al. 2007). Snow persists at high elevations in some years and places into July, creating travel safety challenges.

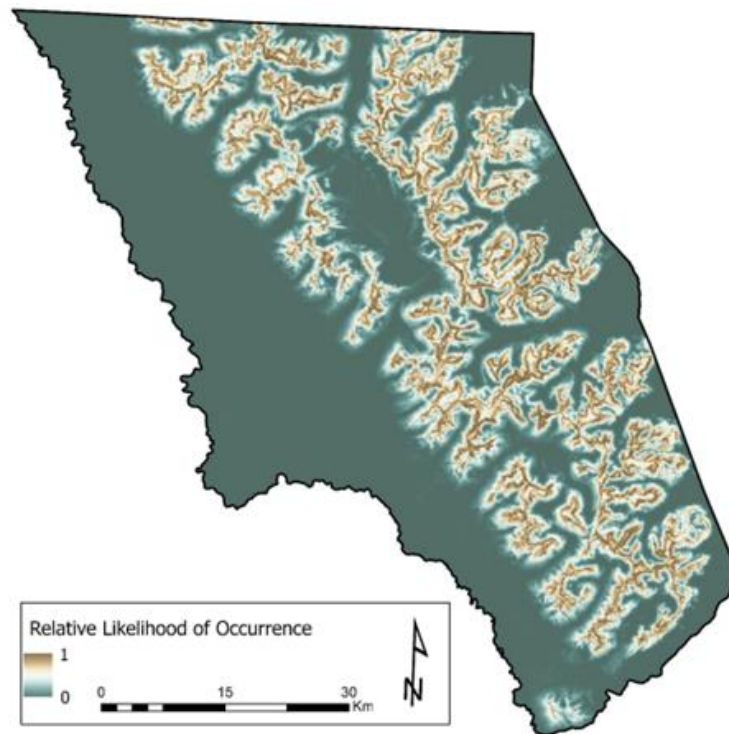


Figure 1: Relative likelihood of occurrence for mountain goats in Glacier National Park, Montana (Don White Jr., University of Arkansas, written communication, 2021).

Data Collection

In 2019, we conducted an opportunistic pilot survey to assess challenges with collecting goat pellets, assess protocols and training of citizen scientists, and evaluate genotyping success based on various methods (Scoresby et al. 2025). Sampling included the region between the Sperry Glacier basin and Gunsight Pass, an area known to have high numbers of mountain goats

exhibiting high levels of habituation, a few natural mineral licks, and a few off-trail routes. Overall results from this opportunistic sampling were reported in Scoresby et al. (2025).

In 2022, we attempted to collect fecal pellets evenly across the area inhabited by goats. Sampling evenly supports consistent data collection where a species of interest exists. It can avoid inducing structure due to gaps in sampling for genetic structure classification approaches. Sampling evenly can also facilitate assessments of isolation by distance by leading to data at a wide range of pairwise distances between goats. We first split GNP into four quadrants based on the Going to the Sun Road (separating north from south) and a combination of potential barriers to large scale movements of goats (Figure 2). The northern half was split by the Waterton Valley, comprised of a large lake in the north and mostly forested terrain further south. The southern half was split through a series of valleys west of the Continental Divide that were also primarily heavily forested and lower elevation. Within each quadrant, we chose sets of 10 target survey routes in areas with high predicted goat occupancy and habitat suitability (Flesch and Belt 2017, Don White Jr., University of Arkansas, written communication, 2021). We selected survey routes that included: a) relatively safe routes to ridges and peaks (<class 3 on the Yosemite Decimal System mountaineering scale) and b) trails that in combination with routes would provide consistent coverage of goat habitat across GNP. In addition, we prioritized sampling at mineral licks known to be used by mountain goats (Schoenecker et al. 2015). Many mineral licks occur at lower elevations and could be safely accessed in May and June in alignment with peak use (Jokinen et al. 2014). We sought to collect at least 30 mountain goat samples in each quadrant of the park to support a reasonable sample size for up to four subpopulations.

In 2023, the citizen science program conducted additional pellet surveys targeting spatial gaps in sampling from 2022. In 2022 and 2023, staff from WLNP in Canada also conducted surveys opportunistically in mountain goat habitat within that park. We conducted surveys in 2022 between May 1st to October 16th, with most effort in July and August, in part due to a spring that was relatively cool. Surveys in 2023 spanned from June 16th to September 3rd. Timing of surveys at specific locations largely depended on accessibility due to weather conditions and persistent snow.

Fecal Pellet Collection

Technicians (U.S. Geological Survey [USGS], GNP, WLNP) and citizen science volunteers in GNP collected fecal pellets. The GNP citizen science program worked with two types of volunteers. The first group of volunteers, sent to trails likely to have goat pellets, had either limited off-trail experience or desire to go off-trail, but demonstrated strong interest and ability to collect high-quality data and samples. We also identified a small group of highly experienced volunteers with the skills, abilities, and interest to search for pellets along backcountry routes. This group included retired park service employees, members of the Nordic Backcountry Ski Patrol, and members of the Glacier Mountaineering Society. USGS and GNP technicians primarily targeted off-trail and longer routes, prioritizing projected gaps in sampling and mineral licks. WLNP used experience staff only to collect pellets exclusively in high alpine, off-trail areas.

All surveyors attended an in-person training covering project objectives, goat identification, pellet identification, study design, and sampling protocols. We used a Survey123 app

(Environmental Systems Research Institute) to record the date, time, and surveyor, as well as the location of samples, a barcode for the sample, recent weather, mountain goat presence, and details about the age, color, and condition of the scat. Once in goat habitat, surveyors scanned the immediate travel route for pellets. They also scanned surrounding areas for mountain goat trails to search, using binoculars to seek more distant areas for the presence of game trails and mountain goats. We prioritized samples without mold or dry cracks and collected 6 pellets per pile of pellets. Based on results from the pilot project related to both genotyping success and ease of implementation, we placed most pellets directly into a 15-mL vial with 95% ethanol for preservation (Appendix A; Scoresby et al. 2025). However, when surveyors ran out of vials or if surveyors were unwilling to carry vials, samples were placed into coin envelopes and dried. In one case when neither container was available, pellets were wrapped in clean tinfoil and frozen within 4 hours. Data collectors recorded their routes using Survey123, on GPS units, or on other apps on cellular devices (e.g., Gaia, Strava, OnX). The routes traveled represented goat pellet search effort and they can be used for planned spatial capture-recapture population estimates.

Mountain goat sample genotyping

We analyzed three pellets from each sample at the Epps Population Genetics Lab at Oregon State University. Pellets in ethanol were placed into weigh boats in a fume hood for a minimum of one night to dry. Once pellets were dried, lab technicians scraped the exterior of pellets (Wehausen et al. 2004) to collect epithelial cells. DNA was then extracted using the AquaGenomic Stool and Soil protocol (Multitarget Pharmaceuticals, Salt Lake City, UT, USA).

To meet genetic structure assessment goals, we selected ~33 of the 2022-2023 samples from each of the four GNP quadrants, plus 10 samples from WLNP, distributed as evenly as possible with preference for samples identified by the collector as fresh or green in color where present (Scoresby et al. 2025). For these samples, we attempted to amplify 20 markers (19 microsatellites and 1 sex identification marker) using PCR and three replicate reactions per sample. These markers had previously been shown to amplify and be variable in studies of other mountain goat populations (Mainguy et al. 2005, Shafer et al. 2011, Poole et al. 2011). Amplicons were run on an ABI 3730 DNA Analyzer (Applied Biosystems, Waltham, Massachusetts) at the Center for Quantitative Life Sciences at Oregon State University and scored using Genemapper v.6 (Applied Biosystems, Waltham, Massachusetts). We tabulated allele frequencies and determined that a minimum of 6 loci were required to maintain a cumulative probability of identity (P_{ID}) of $<1 \times 10^{-3}$ and $P_{ID_{siblings}}$ of <0.05 . Because bighorn sheep (*Ovis canadensis*) and mountain goat pellets were not easily distinguished in the field, we identified species based on microsatellite allele profiles and excluded bighorn sheep from further analysis. Subsequent funding supported genotyping of all samples collected in 2022 and three from 2023 by species and individual (≥ 6 loci). Some of these samples had more extended genotypes considered useful for evaluating potential issues such as null alleles.

Genetic structure and diversity analyses

Data analysis was conducted in R v.4.4.3 (R Core Team 2025) and RStudio v.2024.12.1.563 (Posit team). We used genotypes from all individuals identified across 2019-2023 with at least 6 loci to evaluate genetic structure and diversity. We assessed genetic diversity overall and in four hypothesized subpopulations based on GNP quadrants. We calculated allelic richness (corrected for uneven sample size), observed and expected heterozygosity, inbreeding coefficient (F_{IS}), and

genetic distance (F_{ST}) among the four putative subpopulations using the R package *hierfstat* v.0.5-11 (Goudet and Jombart 2022).

To evaluate whether subpopulation structure existed in the parks, we assessed support for a range of genetic clusters (K), from two to ten. We used program STRUCTURE v.2.3.4 (Pritchard et al. 2000) with no prior information on population or sampling location to assign individual ancestry proportionally across multiple potential subpopulations. STRUCTURE uses a Bayesian framework and assumes Hardy-Weinberg proportions and linkage equilibrium across populations. We used a burn-in of 50,000 iterations and 100,000 Monte Carlo Markov Chain sampling iterations with ten replicate runs. To improve accuracy of inferences, we used an initial alpha value of 0.25, or $1/K$, with K in this instance representing our originally hypothesized number of subpopulations ($n=4$, Wang 2017). We averaged assignment probabilities, q , across these runs in CLUMPAK beta version (Kopelman et al. 2015). To determine the largest substantiated number of clusters (subpopulations) in the dataset, we used the High Assignment Criterion (HAC) which supports the highest value of K at which at least 1 individual is assigned at high confidence ($q > 0.90$) to each cluster (Epps et al. 2018). We also compared the difference in the likelihoods across K (ΔK , Evanno et al. 2005) and probability of K (Pritchard et al. 2000, Puechmaille 2016).

We mapped the average assignment probabilities for each sampled individual in our dataset at increasing values of K to evaluate alternative hypotheses that STRUCTURE assignment had spatial cohesion (i.e., formed mostly discrete groups). We used the R package *adeigenet* v.1.3-1 (Jombart 2008) to test for deviations from Hardy-Weinberg proportions by population and locus to check for evidence of selection processes or further population structuring. To test for isolation by distance, we plotted Euclidean distance and genetic distance between each pair of individuals and performed a Mantel test of correlation against the portion of shared alleles using the R package *vegan* v.2.6-8 (Oksanen et al. 2024).

We assessed relatedness using the Lynch-Ritland method in the R package *related* v.1.0 (Lynch and Ritland 1999, Pew et al. 2015) to evaluate whether we a) needed to exclude any samples from STRUCTURE analysis and b) had abnormally high numbers of highly related individuals. We also compared this relatedness metric with geographic distance using the Mantel test in *vegan* as a further assessment of isolation by distance. The fecal pellet data that support this study are available in Graves et al. (2025).

RESULTS

Sample collection

Between May 1 and October 16 of 2022, 60 surveyors comprised of 50 citizen scientists, 6 trained USGS staff, and 4 trained NPS staff conducted at least 221 surveys, with 129 conducted by ≥ 1 trained USGS or NPS staff and 111 surveys conducted solely by citizen scientists. Between June 17 and September 9 of 2023, 19 surveys were conducted: 4 surveys were completed by ≥ 1 trained NPS staff and 15 surveys were completed solely by citizen scientists. Surveyors covered at least 1,890 kilometers throughout GNP in 2022, divided approximately as 16% in the northwest, 27% in the northeast, 26% in the southeast, and 31% in the southwest (Figure 2) quadrants. Surveyors in GNP in 2023 covered an additional 127 kilometers with 74%

in the northwest, 4% in the northeast, 17% in the southwest, and 5% in the southeast quadrant. Only a few gaps in sampling remain around Vulture and Anaconda Peak (fire closure in 2022) and the Mount Doody and the Cloudcroft Peaks area in the southwest quadrant.

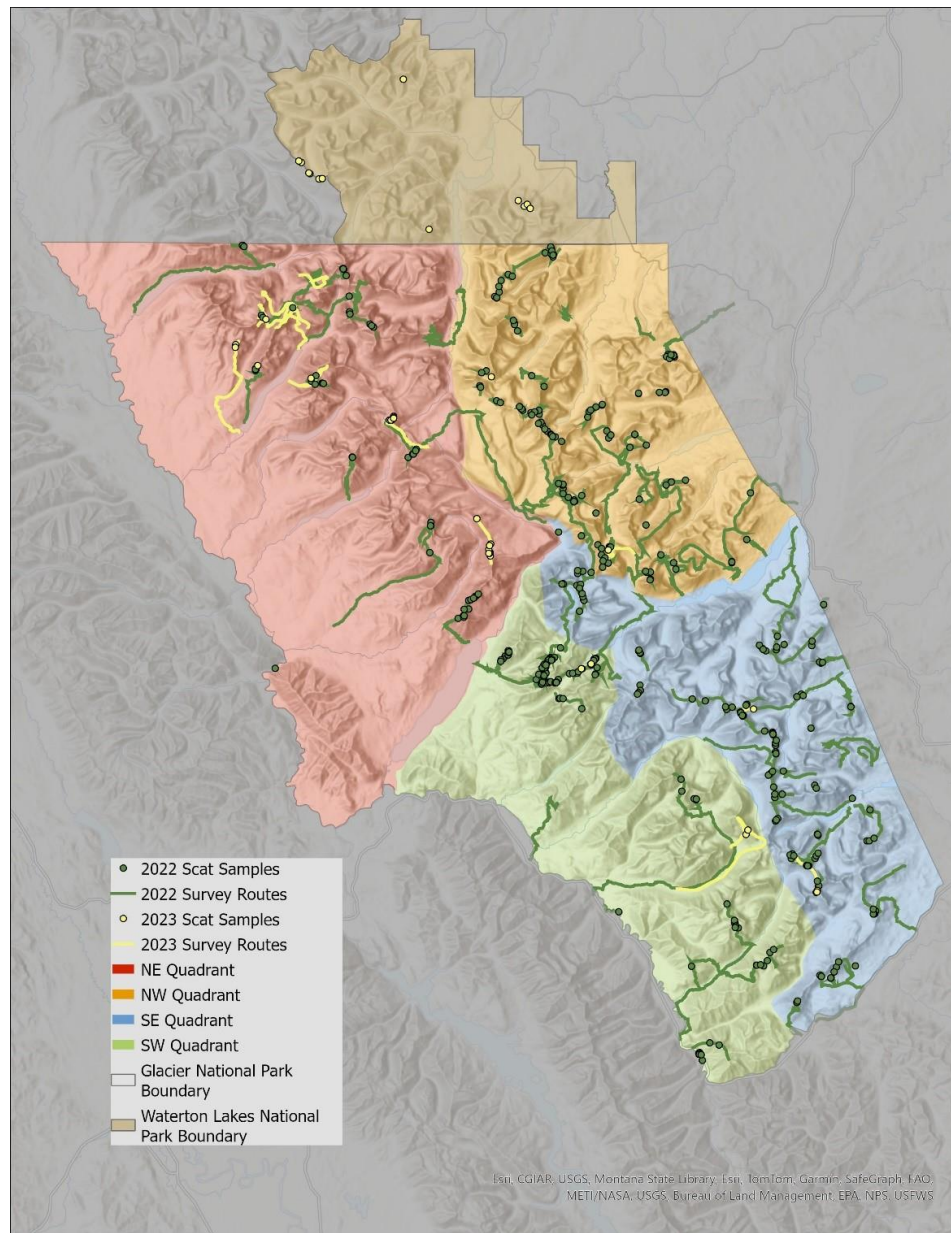


Figure 2. Map of Glacier National Park and Waterton Lakes National Park showing sampling quadrants, survey routes and sample collection locations in 2022 and 2023. Background map from Esri. North is at the top of the map.

In 2022, 606 samples were collected, including 548 from GNP and 58 from WLNP (Table 1, Figure 2). Of the 606 samples collected in 2022, surveyors collected 252 dry samples, 351 ethanol samples, and 3 frozen samples. Most samples collected in GNP were collected by USGS or NPS staff (n=378), with citizen scientists collecting the other 170 samples (Table 1). The

southwest quadrant in GNP had the most samples (n=176), with many collected between the Sperry Glacier Basin and Gunsight Pass (Figure 2). The northeast (n=144) and southeast quadrants (n=159) had reasonable sample sizes, but fewer samples were collected in the northwest (n=69), primarily due to persistent snow limiting accessibility. Although strong preference was given to collecting the freshest scat possible, pellets estimated to be less than 1 day old were the least-collected age class (n=133), with most pellets estimated as older than 1 day, but fresher than 1 week (n=282; Table 1). At the end of the season, 597 scat samples were accounted for with full data collected. There were 5 samples for which data had been collected but were not physically accounted for; 1 of these missing samples was from WLNP staff, 1 was from USGS staff, and the remainder were initially collected by citizen scientists.

In 2023, surveyors collected 61 samples (37 from GNP and 24 from WLNP; Table 2). Staff collected 44 samples and citizen scientists collected 17 samples, primarily using the dry protocol (n=47) and ethanol (n=14; Table 2). Most samples collected in GNP in 2023 focused on addressing spatial gaps in surveying and were collected in the northwest quadrant of GNP (n=26), with the other quadrants having 5 or fewer samples collected (Table 2). At the end of the season, 59 of these samples were accounted for with 2 missing from GNP citizen scientists.

Genotypes with ≥ 6 -loci yielded from samples included 60 genotypes from 2019, 248 from 2022, and 2 (of 3 samples submitted) from 2023. Numerous samples were identified through genotyping as duplicates from the same goats. After we removed duplicates, 33, 174, and 2 individual goats remained from 2019, 2022, and 2023, respectively, for use in these analyses. Extended genotypes (≥ 12 loci) included 33 unique goats from 2019, 136 from 2022, and 2 from 2023. Genotyping yielded 311 total samples distributed thus by quadrant (NE = 59, NW = 43, SE = 64, SW = 145) representing 209 individuals with ≥ 6 -loci, distributed thus by quadrant (NE = 50, NW = 32, SE = 47, SW = 79). These individual results include WLNP as part of the NE quadrant.

Genetic structure and diversity

Allelic richness by quadrant ranged from 2.68-2.82 and was 3.54 over the full dataset. Observed heterozygosity ranged from 0.36 in the northwest quadrant (Livingston Range) to 0.44 and expected heterozygosity ranged from 0.42 to 0.45 with large differences between expected and observed in the northwest (0.06) and southwest (0.04) quadrants, which also had positive inbreeding coefficients (0.19 and 0.11 respectively, Table 3). F_{ST} values between quadrant pairs were all low (0.01-0.04) suggesting low differentiation and high mixing.

Although diversity metrics using different markers are not directly comparable, metrics in this dataset were intermediate compared to several populations of goats in Alaska (White et al. 2020) and across Washington and southern British Columbia (Parks 2023).

Tests for deviation from Hardy-Weinberg equilibrium showed that all loci were in Hardy-Weinberg proportions after applying the Bonferroni correction for multiple loci. We found limited but statistically significant support for isolation by distance based on pairwise comparisons of the proportion of shared alleles (*Mantel* $r = -0.06$, $p = 0.01$) and Euclidean distance using pairwise relatedness (*Mantel* $r = -0.05$, $p = 0.001$). This small isolation by distance effect on relatedness was similarly small for female only (*Mantel* $r = -0.05$, $p = 0.01$) and male only (*Mantel* $r = -0.05$, $p = 0.02$) pairwise comparisons.

Table 1. Number and percent of fecal pellet samples summarized by quadrant of Glacier National Park and Waterton Lakes National Park (WLNP) and by preservation method, personnel, collection month, and estimated pellet age for samples collected in 2022.

	NE (N=144)	NW (N=69)	SE (N=159)	SW (N=176)	WLNP (N=58)	Overall (N=606)
Preservation Method						
Dry	63 (43.8%)	23 (33.3%)	59 (37.1%)	62 (35.2%)	45 (77.6%)	252 (41.6%)
Ethanol	81 (56.3%)	45 (65.2%)	100 (62.9%)	112 (63.6%)	13 (22.4%)	351 (57.9%)
Freeze	0 (0%)	1 (1.4%)	0 (0%)	2 (1.1%)	0 (0%)	3 (0.5%)
Personnel						
Staff (≥ 1)	77 (53.5%)	58 (84.1%)	101 (63.5%)	142 (80.7%)	58 (100%)	436 (71.9%)
Volunteer	67 (46.5%)	11 (15.9%)	58 (36.5%)	34 (19.3%)	0 (0%)	170 (28.1%)
Month						
May	1 (0.7%)	0 (0%)	1 (0.6%)	15 (8.5%)	1 (1.7%)	18 (3.0%)
June	20 (13.9%)	2 (2.9%)	34 (21.4%)	2 (1.1%)	3 (5.2%)	61 (10.1%)
July	44 (30.6%)	27 (39.1%)	55 (34.6%)	36 (20.5%)	16 (27.6%)	178 (29.4%)
August	59 (41.0%)	17 (24.6%)	46 (28.9%)	89 (50.6%)	8 (13.8%)	219 (36.1%)
September	20 (13.9%)	23 (33.3%)	22 (13.8%)	32 (18.2%)	14 (24.1%)	111 (18.3%)
October	0 (0%)	0 (0%)	1 (0.6%)	2 (1.1%)	16 (27.6%)	19 (3.1%)
Age of Scat						
<1day	21 (14.6%)	11 (15.9%)	30 (18.9%)	63 (35.8%)	8 (13.8%)	133 (21.9%)
>1day	61 (42.4%)	39 (56.5%)	73 (45.9%)	87 (49.4%)	22 (37.9%)	282 (46.5%)
>1week	60 (41.7%)	18 (26.1%)	55 (34.6%)	25 (14.2%)	28 (48.3%)	186 (30.7%)
Missing	2 (1.4%)	1 (1.4%)	1 (0.6%)	1 (0.6%)	0 (0%)	5 (0.8%)

Table 2. Number and percent of fecal pellet samples summarized by quadrant of Glacier National Park and Waterton Lakes National Park (WLNP) and by preservation method, personnel, collection month, and estimated pellet age for samples collected in 2023.

	NE (N=2)	NW (N=26)	SE (N=5)	SW (N=4)	WLNP (N=24)	Overall (N=61)
Preservation Method						
Dry	2 (100%)	16 (61.5%)	1 (20.0%)	4 (100%)	24 (100%)	47 (77.0%)
Ethanol	0 (0%)	10 (38.5%)	4 (80.0%)	0 (0%)	0 (0%)	14 (23.0%)
Personnel						
Staff	1 (50.0%)	15 (57.7%)	4 (80.0%)	0 (0%)	24 (100%)	44 (72.1%)
Volunteer	1 (50.0%)	11 (42.3%)	1 (20.0%)	4 (100%)	0 (0%)	17 (27.9%)
Month						
June	0 (0%)	3 (11.5%)	0 (0%)	0 (0%)	0 (0%)	3 (4.9%)
July	0 (0%)	17 (65.4%)	0 (0%)	0 (0%)	7 (29.2%)	24 (39.3%)
August	2 (100%)	0 (0%)	5 (100%)	2 (50.0%)	10 (41.7%)	19 (31.1%)
September	0 (0%)	6 (23.1%)	0 (0%)	2 (50.0%)	7 (29.2%)	15 (24.6%)
Age of Scat						
>1day	1 (50.0%)	8 (30.8%)	2 (40.0%)	0 (0%)	1 (4.2%)	12 (19.7%)
>1week	1 (50.0%)	18 (69.2%)	2 (40.0%)	1 (25.0%)	23 (95.8%)	45 (73.8%)
<1day	0 (0%)	0 (0%)	1 (20.0%)	3 (75.0%)	0 (0%)	4 (6.6%)

Every goat in the sample had at least one close relative (relatedness > 0.25) and 206 (>98%) of the 209 goats had relatedness values suggesting at least one parent or sibling was genotyped (relatedness > 0.50). Of the 21,736 pairs of goats in this analysis, 2,572 pairs (12%) had relatedness > 0.25 and 600 (3%) had relatedness > 0.50.

Because we could not remove all the highly related goats and still conduct an assessment of population structure, we removed the 152 goats with the highest number of closely related (> 0.4) pairs and re-analyzed the remaining 57 goats in STRUCTURE. Nearly all, 55 of the remaining 57 goats (96%), still had at least one relative with relatedness > 0.25 and 36 goats (63%) had a relative with relatedness > 0.5. We found no support for subpopulation subdivision either with or without those 152 goats ($Prob(K=1) = 1$, Figure 3).

Table 3. Genetic diversity metrics overall and by quadrant for mountain goats in Glacier National Park, Montana, USA and Waterton Lakes National Park (WLNP), Alberta, Canada. WLNP samples are included in the NE quadrant.

	n	Allelic Richness	Observed Heterozygosity	Expected Heterozygosity	Inbreeding Coefficient (F_{IS})
Overall	209	3.54	0.41	0.45	NA
NE	50	2.82	0.44	0.44	0.01
NW	33	2.69	0.36	0.42	0.19
SE	47	2.68	0.42	0.44	0.03
SW	79	2.79	0.41	0.45	0.11

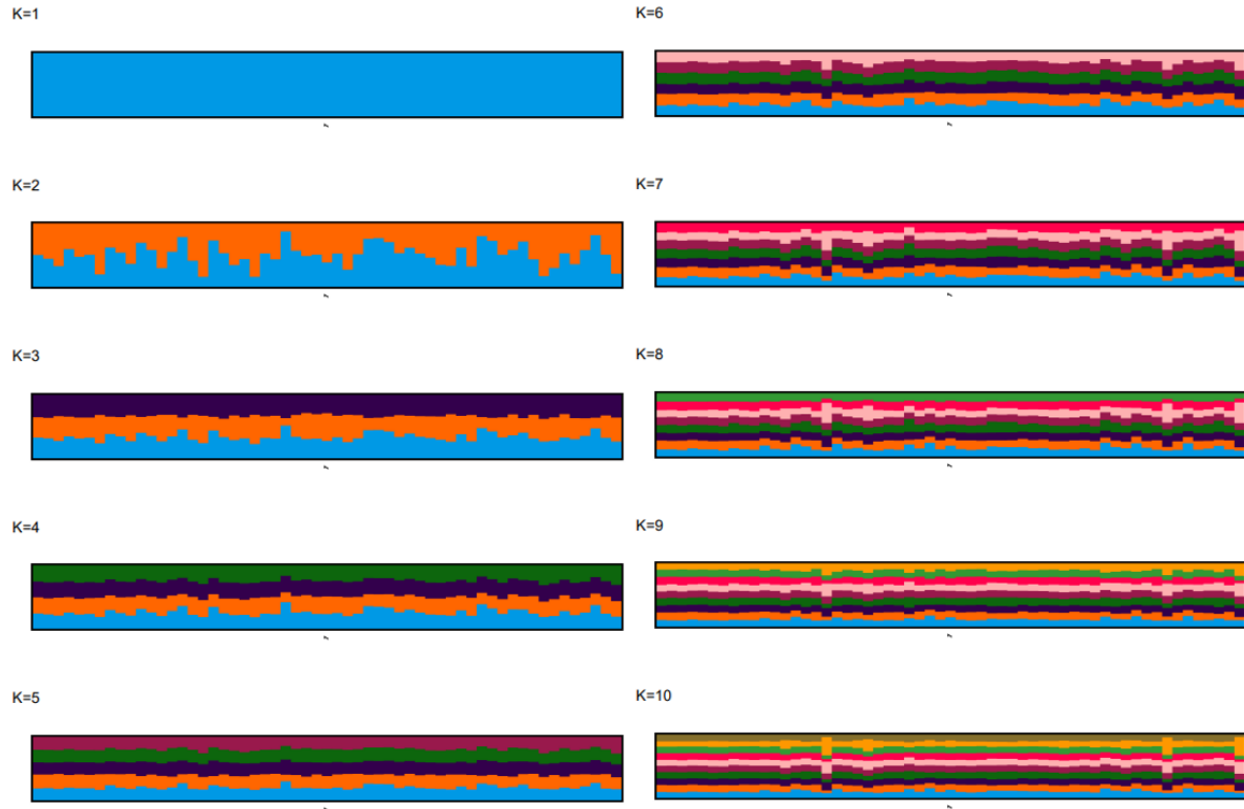


Figure 3. Bar charts illustrating lack of genetic structure in mountain goats in Glacier National Park and Waterton Lakes National Park based on fecal pellets collected from 2019-2023. Each vertical bar in each chart illustrates ancestry assignments for 57 goats with ≥ 6 locus microsatellite genotypes. The 152 goats with the most near-relatives are not included in this figure. If the population had subdivisions, some individuals would show larger proportions of a single color and these individuals would be located spatially near each other. Bar charts including all goats similarly showed no subdivisions.

Discussion

Our findings indicate that mountain goats in GNP and adjacent WLNP are well mixed genetically and can be considered a single population rather than a metapopulation. The very limited isolation by distance suggests consistent dispersal at this relatively large spatial extent. However, the high F_{IS} in the Livingston Range (northwest quadrant) suggests that in that area we collected samples from several closely related groups with little interchange. This may also indicate a recent decrease in gene flow. Both patterns are consistent with a recent population decline documented for most of the northern half of the park (Graves et al. 2025). We also detected a high number of closely related individuals throughout the study area. This is consistent with the high adult survival, low reproductive success life history of mountain goats, but also suggests that we sampled much of the overall population (Festa-Bianchet and Côté 2008). Few similar studies have reported proportions of highly related individuals along with population size however, so we cannot use this information to infer the implications of this for population size, another metric used to support management of this mountain goat population. The lack of strong signals of subdivision in mountain goats contrasts with genetic patterns in the same study area for bighorn sheep, the other primary mountain ungulate in GNP. Assessments of

bighorn sheep subdivision consistently show at least two barriers with limited movement (St. Mary Lake and Waterton Lake: Tosa et al. 2023, Flesch et al. 2020, Graves et al. 2023). Bighorn sheep rarely occur on the west side of the Continental Divide and perhaps are more constrained to areas without canopy cover (Graves et al. 2023).

Using citizen scientists in this research greatly increased our ability to gain even coverage of sampling, especially given short summers when accessing goat habitat is relatively safe. However, technicians collected nearly 75% of samples in parkwide sampling in 2022, and GNP restricts sharing the locations of mineral licks to protect that important resource. Thus, we expect technician data collection to continue to play a role in any planned repeat sampling. Because differentiation between bighorn sheep and goat scat is not possible in the field, additional sampling effort in areas with species overlap, as we did here, could lead to more similar sample sizes across GNP quadrants. Areas with fewer animals or that are harder to reach (e.g., Livingston Range, Mount Doody/Cloudcroft) also may require additional effort for repeat sampling if possible changes in gene flow are a concern and the population continues to decline.

We met our objectives to evaluate genetic structure and diversity and collect data to support a planned assessment of the population size of goats in GNP and WLNP (e.g., Schmidt et al. 2022, Epps et al. 2024). The need for this estimate was motivated by declines estimated between 2008 and 2019, increasing threats to their habitat, and originally coarse assessments of population size that with the estimated declines suggest the population could be below 500 animals (Chadwick 1983, Belt and Krausman 2012, Graves et al. 2025). Because the cause of declines is not well understood, an approach that uses these data to concurrently evaluate covariates related to density, habitat selection, and movement, such as spatial capture-recapture approaches, could be especially informative for management (Chandler and Clark 2014, Royle et al. 2013, Carroll et al. 2024).

This research complements recent and ongoing research in GNP on goats. The first GPS collar study (2013-2016) focused on Logan Pass in the center of the park where goats are accessible and mostly habituated (Sarmiento et al. 2016, Sarmiento et al. 2019, Sarmiento and Berger 2020). Recent research (2018-2021) expanded collar deployment to include not only the Logan Pass area and the area around Mount Brown and the Sperry Chalet, but also near two natural mineral licks in the south-central area of GNP (Hayes 2023, Hayes and Berger 2023). These recent studies evaluated the thermal ecology of goats and refugia such as snowbanks and topographic shade using data from 20 GPS collared goats, which were genetically sampled during capture. GNP currently has plans for additional collaring near the Goat Lick to address concerns about river recreation impacts on the mountain goats that frequent this area. Our research also complements Montana Fish Wildlife and Parks investigations of goats across several study areas in the state. As the only large, non-hunted, native population of goats in Montana, research on goats in GNP and WLNP can serve as a benchmark for regional and statewide studies.

Roles

TAG, MB, and JB identified initial objectives. TAG, JB, and RF managed project including oversight of technicians, with JB coordinating citizen science components and Survey123 form creation. CWE, RSC, and HT led genotyping. LD conducted initial summaries. ES conducted statistical analyses with guidance from TAG and CWE. TAG and ES drafted initial report. All authors reviewed the report.

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Appendix A: Protocol provided to citizen scientists participating in the fecal pellet study.



Glacier National Park High Country Citizen Science Fecal Pellet Collection Tech Protocol Version 2.0



Equipment:

- ☐ Ethanol vials
- ☐ Sampling envelopes
- ☐ Desiccant packets
- ☐ Pencil

- ☐ Sharpie
- ☐ Smartphone with Gaia, Survey 123 app, camera
- ☐ Timepiece
- ☐ Rocks (found in field)
- ☐ Ziploc bags (keep closed until use)

Label Protocol for All Fecal Sample Collection

1. Initiate Survey 123 on your smartphone, initiate a new "survey" in the app, and prepare to complete relevant fields in the app. If possible, use the ethanol vial sample collection directly below, if not available, use the dry sample collection protocol (see Dry Protocol)
2. Collect pellets from a single defecation event. Usually there is a single pile of pellets.
3. Write date, location, sample number from Survey123 (i.e. 1,2,3 etc.), and surveyor initials on envelope

Major Principles to Observe

1. **Avoid contaminating samples with DNA** (goats, bighorns, you, plant matter). Don't reuse collection materials. Don't touch the rocks you use to collect pellets, or the pellets themselves with bare hands/your skin or the inside of collection vials/envelopes.
2. **For DNA analysis, Pellets must be relatively fresh** - usually less than a week old, not rained on.
3. **For stress analysis, only observed depositions will work. Pellets must be kept in cooler OR placed in ethanol vials immediately.**

If you observe a goat or bighorn pooping, please collect 2 sets of samples: 1 for goat DNA & 1 for glucocorticoid. Unless prohibited by a lack of supplies, please follow the ethanol collection protocol. While timing of collection is important, try not to push off goats from their established areas.

Protocol for Ethanol Vial Fecal Sample Collection

1. Initiate Survey 123 on your smartphone, initiate a new "survey" in the app, and prepare to complete relevant fields in the app.
2. Use permanent marker to write date, location (i.e. "Rockwell"), sample number from Survey123, and surveyor initials on white section of vial.
3. Collect pellets from a single defecation event. Vial will have c. 9 mL 95% ethanol. **Collect at least 6 pellets.**
 - a. Use small rocks to push pellets into the vial. Don't handle the ends of rocks that will touch the pellets.
 - b. **DISPOSE OF ROCKS AFTER EACH SAMPLE** to prevent contamination.

- c. If pellet groups are mixed on the ground, (this can occur in high-use areas), collect **ONLY** pellets in discrete piles.
 - 4. Close vial securely. Store in a dry, cool place. If available, store in cooler.
 - 5. Once you have returned from the field, **DO NOT OPEN SAMPLES**. Return to office to place ALL samples in -80 freezer immediately.
- If you find yourself in the field **without adequate ethanol vials**, proceed to protocol for **dry fecal sample collection**

Protocol for Dry Fecal Sample Collection

- 1.) Initiate Survey 123 on your smartphone, initiate a new "survey" in the app, and prepare to complete relevant fields in the app.
- 2.) Collect pellets from a single defecation event (10-15 pellets per sample is ideal).
 - a. Use small rocks to push pellets into the envelope. Don't handle the ends of rocks that will touch the pellets. **DISPOSE OF ROCKS AFTER EACH SAMPLE** to prevent contamination of genetic material.
 - b. If pellet groups are mixed on the ground, (this can occur in high-use areas), collect **ONLY** pellets in discrete piles.
2. Tape the envelope closed with the dots provided or fold the top of the envelope securely, **DO NOT LICK** the envelope flaps. Place in Ziploc bag with the desiccant envelope and close bag tightly.
3. Make sure pellet samples dry completely on the day you collect them. **Mold will cause sample to be DISCARDED**. Check to see whether outside of envelope is completely dry without squishing pellets. The samples need to remain dry for optimal genotyping. If you are in the field, and it is warm/dry, you can spread them out to dry at night inside your tent. Beware of dew. Putting them on your dashboard on a warm day for a short period of time works very well.
4. Otherwise, once you return from the field remove sample envelopes from Ziploc to dryer oven. **DO NOT OPEN SAMPLE ENVELOPES**.
5. Once dry, place envelopes into a dry envelope or paper bag. Store the samples at room temperature in a sealed box with generous amounts of fresh desiccant pellets.

Tips for Scat Collection

- **Freshly** deposited fecal samples can be obtained by the "**watch and wait**" method. Observe the animal until it deposits some fecal pellets. This method allows for accurate identification of species and accurately record time that the sample was deposited. Wait until the animal has **moved away at least 25 yards** before collecting sample.
- Collect samples from different locations if possible. Ultimately, we like to have at least 15 samples from each drainage, and more is better.
- It is better to collect a questionable sample than no sample at all, especially if you're in a remote area.