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ARTICLE

Animal Ecology

Mountain goat declines in a protected, interior, native population

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Abstract

A shifting climate poses threats to alpine-adapted species including mountain goats. We used long-term (12 years) citizen science monitoring data and Bayesian N-mixture modeling to estimate population trends and drivers of population metrics among mountain goats in Glacier National Park (GNP). Median goats per site ($n = 37$ sites) declined by 45% (95% credible interval [CRI] = 32%, 57%) from 77.8 (95% CRI = 64.4, 95.1) in 2008 to 42.3 (95% CRI = 34.3, 52.2) in 2019, with consistent declines from 2008 until 2015, when the number of estimated goats stabilized. The decline exceeds IUCN criteria for classifying a population as vulnerable, >30% declines over only two generations. Across years, relatively few goats occupied northwestern GNP. Goat numbers declined the most at northeastern sites, trended toward decline in most southern sites, and increased at only two west-central sites. The proportion of permanent snow and glaciers, the presence of natural mineral licks, and habituation strongly increased the initial abundance of goats in the area. Weather variables had the greatest influence on population growth rates, particularly precipitation between May 15 and June 15 of the previous summer, the neonatal period. Lower growth occurred with less snow water equivalent and lower mean winter temperature, early summer temperature, and early summer precipitation. Projected reductions of permanent snow, increasing spring and summer temperatures, and insufficient and variable spring precipitation raise concerns for the future of native goats in this region. Our analyses reveal ways to improve detection rates of goats during surveys, which is important for optimizing the precision of estimates and the power to detect future trends. Detection increased with goat habituation, retention of observers with experience, use of binoculars, and conducting surveys at lower temperatures and earlier dates. Improving detection will be particularly important given the lower number of goats currently observed in the park. Research

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Tabitha A. Graves and Jami Belt contributed equally to the work reported here.

to estimate park-wide population size, evaluate genetic structure and diversity, assess changing habitat, human recreation levels and forage, and forward-project climate effects on persistence will be crucial to understanding the context of these results and conserving this iconic, metapopulation at the southern edge of the distribution of native mountain goats.

KEYWORDS
citizen science, climate, conservation concern, demographic, Glacier National Park, hierarchical model, IUCN, mountain goat, N-mixture, *Oreamnos americanus*, population declines, ungulate

INTRODUCTION

Species living in the extreme conditions of high mountain ecosystems often have specific adaptations, allowing them to thrive in these typically cold areas that often have high precipitation and seasonality. While distributions of many species will likely shift in response to new climatic conditions (Bateman et al., 2016; Hovick et al., 2016), species at upper elevations may not be able to shift upwards and will consequently decline or become locally extinct (Parmesan, 2006). Because mountainous areas are changing rapidly, alpine species are among the most sensitive species to climate change (Pepin et al., 2022; Nogués-Bravo et al., 2007). Therefore, recent studies have sought to examine the sensitivity of mountain ungulate populations to climate effects (Grignolio et al., 2004; Harris et al., 2024; Rattenbury et al., 2018) and project future changes in populations (Lovari et al., 2020; Riquelme et al., 2020). However, for many species, only a few studies have been completed and much remains to be learned about variation in responses across the ranges for all mountain ungulates (White et al., 2024).

Native mountain goats (*Oreamnos americanus*) represent one of North America's mountain ungulates most threatened by climate change (Johnston et al., 2012). Mountain goats generally live at the highest available elevations and depend on steep cliffs to avoid predation (Sarmento & Berger, 2020), such that their options for moving upwards or otherwise shifting habitat in response to warming temperatures or other stressors are extremely limited. As the human population grows, more people are moving into and recreating in remote areas. This can result not only in habitat loss and degradation but also increased disturbance that can decrease access to resources needed by goats, increase stress, or result in habituation that can lead to human–wildlife conflicts or increased concentrations that may alter disease risk, but which may also shield animals from predation (Bejder et al., 2009; Festa-Bianchet & Côté, 2008; Sarmento & Berger, 2017; St-Louis et al., 2013). Climate change models predict earlier melt-off of snow patches in alpine environments, upward shifts and encroachment of forest vegetation types (e.g., Klasner & Fagre, 2002); and changes in phenology, species composition, and timing of plant nutrients in alpine environments (Berman et al., 2020; Lovari et al., 2020). Increasingly frequent and severe wildfires are removing cover in areas traditionally used for shelter (Westerling, 2016). Changes in the composition and configuration of vegetation may also alter predation risk associated with access to mineral licks, which provide an important resource for bone and horn development and nutrient absorption (Hebert & McTaggart Cowan, 1971).

Recent research suggests that climate change can affect both the distribution and population persistence of goats (White et al., 2011, 2018). 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 & Hogg, 1999). In addition, mountain goat populations have a slow life history strategy with a late age of primiparity, small litter size, and reproductive pauses that lead to overall low population growth rates and therefore require many years for population recovery after declines (Festa-Bianchet & Côté, 2008; Shafer et al., 2011, 2012). Thus, management actions may require many years to achieve results.

Glacier National Park (GNP) is at the southern edge of the range of native populations. No trend estimates exist to evaluate population fluctuations for this region and prior assessments of population size for this region did not incorporate detection probability and involved extrapolation across the park (Belt & Krausman, 2012; Chadwick, 1977; Graves, Stein, et al., 2025). Researchers have documented declines in many other mountain goat populations across the southern portion of the species' native range (Côté & Festa-Bianchet, 2003; Festa-Bianchet & Côté, 2008; Smith, 2014), including 50% declines in British Columbia (BC Mountain Goat Management Team, 2010) and 60% declines in Washington (Harris et al., 2024;

Rice & Gay, 2010). Native goat populations south of GNP in the neighboring Bob Marshall Wilderness shrank to 25% of their population size in the 1940s (Smith & DeCesare, 2017). Other nearby native populations that likely previously formed part of GNP's metapopulation are small, isolated demographically and genetically, and are also declining or, as in the adjacent Whitefish Range, have disappeared (Smith & DeCesare, 2017). As a population without harvest, GNP provides a valuable benchmark for understanding broader regional declines in native populations (Gude et al., 2022).

Mountain goats and many of the world's 37 mountain ungulates can be difficult to monitor in remote areas, particularly where aerial access is limited (Shackleton, 1997). They are highly mobile and inhabit steep and inaccessible terrain, which leads to high costs and difficult logistics for collaring goats. GNP limits flights to maintain wilderness values and is quite remote. Therefore, in 2008, GNP instituted a citizen science program targeted toward monitoring changes in the goat population (Belt & Krausman, 2012). The program recruited and trained volunteers to conduct timed counts of all goats at 37 sites representing the full distribution of goats across the park. These systematic counts have continued every year since 2008 to present and have been the primary method for monitoring goat trends at a park-wide scale in GNP.

Here, we use the long-term citizen science observations to evaluate trends in the population size in GNP over time, assess climate and other factors that contribute to the distribution of goats and changes in population size, and evaluate ways to improve the citizen science monitoring through improvements in goat detection.

METHODS

Study area

Over 400,000 ha in northwestern Montana, GNP was established in 1910 and is managed by the National Park Service (Hop et al., 2007). It is adjacent to Alberta and British Columbia in Canada, and forms part of the Waterton–Glacier International Peace Park. Sitting along the spine of the Continental Divide, the Pacific maritime climate dominates the western side of the park, while a drier, continental climate exhibits strong easterly winds on the east side. The Waterton River and McDonald Creek drainages partially separate the Livingston Range in the northwest region of the park from the Lewis Range which encompasses the rest of the mountainous terrain in the park. Named for the many glaciers formed during the Pleistocene, GNP's steep peaks, active glaciers, glacial lakes, moraines, and cirques provide substantial goat habitat. Elevations in the park range from 960 to 3185 m and heavy winter snowfall at high elevation feeds three major river watersheds, flowing into Hudson Bay, the Mississippi River, and the Pacific Ocean (Hop et al., 2007).

Mountain goats provide a unique experience for many of the ~3 million park visitors annually (https://irma.nps.gov/Stats/Reports/Park/GLAC, accessed May 23, 2025). The Going-to-the-Sun Road bisects the park, running west to east. Visitors stopping at the top of the road at Logan Pass, a popular subalpine location for many park visitors, can often easily see goats up close (GNP, 2019). High visitation combined with the availability of salt from human sources (e.g., urine, sweat, roads) here and in some backcountry areas has led to habituation and goats using humans as shields from native predators including bears, mountain lions, and wolves (Sarmento & Berger, 2017). In addition to anthropogenic mineral salt sources, goats, especially females with kids, also use several patchily distributed natural mineral licks (Singer, 1978). Many of these licks and the other peaks that are primary goat habitat can be accessed by humans only through the >1100 km (700 miles) of trail or with off-trail route-finding and scrambling.

GNP's High Country citizen science program began in 2008 and 2009, with research comparing the value of trained staff and aerial mountain goat surveys to citizen scientists (Belt & Krausman, 2012). After demonstrating that ground counts from volunteers, ground counts from biologists, and aerial surveys yielded similar and overlapping estimates (Belt & Krausman, 2012), GNP determined that continuing the program was the most cost-effective and realistic way to continue long-term monitoring of population trends (J. Belt, verbal communication, January 2020).

At the onset of the program, researchers identified 37 sites using a representative, random, optimized design (Belt & Krausman, 2012). First, researchers placed an 8 km × 11 km grid over the park. This represented the maximum goat home range size (Rideout, 1977). Goats spent 76.7% of their time in escape terrain ≥40° (Chadwick, 1977) and the maximum line-of-sight distance for reliable goat identification is 3.2 km. Therefore, within each grid cell, researchers randomly selected one 2 km trail segment from those including views of terrain with ≥40° slope. The viewshed included areas not blocked by topographical features within a 3.2 km buffer. Next, researchers walked the entire segment and chose the place with the greatest viewshed of escape terrain ≥25° slope, the slope angle defined as escape terrain by other goat research (Gross et al., 2002; Varley, 1994) as the center of the 6.4 km × 6.4 km observation grid (Figure 1). Across all 37 sites, 9% (149 km^2) and 43.9% (727 km^2) of the area of escape terrain ≥25° in GNP

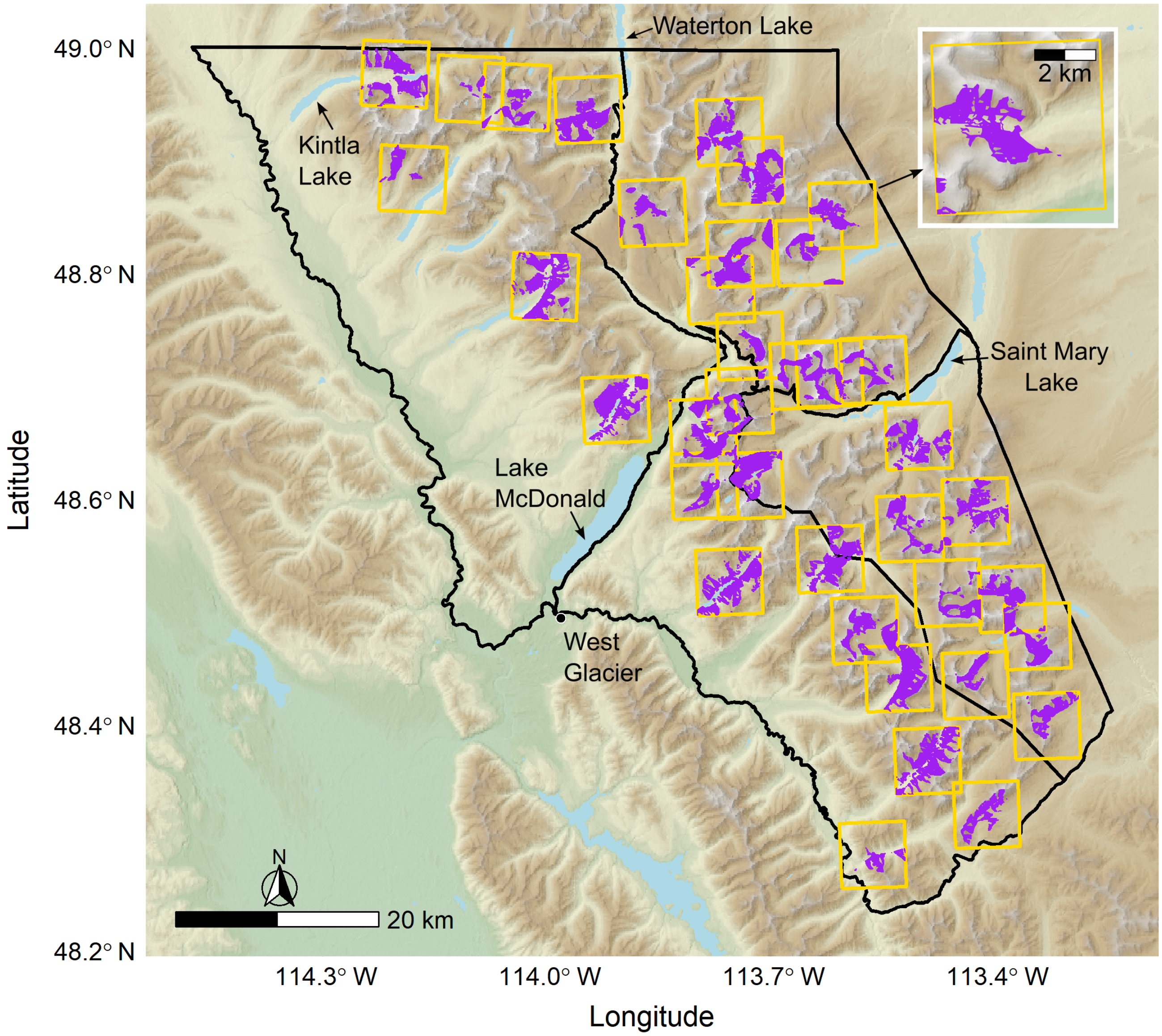

FIGURE 1 Glacier National Park study area map with the regions outlined in black, 6.4 × 6.4 km observation grid cells outlined in yellow and viewsheds filled with purple. The Going-to-the-Sun Road runs east–west through the park, dividing the northern and southern regions. Basemap from NASA 30 m Digital Elevation Model (Farr et al., 2007).

is within sampled viewsheds and observation grids, respectively.

Each year, coordinators recruited and trained volunteers to complete ≥3 surveys per site per year, supplementing citizen science visits with staff visits, particularly for distant and unpopular sites (Graves, Janousek, et al., 2025). During surveys, volunteers used binoculars and spotting scopes to conduct ground counts of the entire viewshed for 1 h. Each year, the park's program hosted a "Goat Days" event around August 16th, attempting to survey all sites within 3 days. In the first two years, during research on the effectiveness of citizen science, 49 surveys included 72 observations by paired volunteers and biologists (Appendix S1: Table S1). We included only observations between June 1 and October 31 ($n = 6$) to focus on the time period between birthing (May–June) and rut (November–December) when large movements by goats are less likely to occur (Chadwick, 1977; Festa-Bianchet & Côté, 2008). Logistics and detection of goats also decline with variable and snowy conditions common and widespread outside this time frame.

Statistical approach

We implemented N-mixture models (Royle, 2004) to estimate population trend following the general approach outlined in Hostetler and Chandler (2015) with the class of hierarchical models described by Dail and Madsen (2011). We included consecutive stages of model selection for the: (1) abundance distribution, (2) detection covariates, (3) population dynamics model form, (4) initial abundance covariates, and (5) population growth covariates, all conducted using a maximum likelihood framework within the "unmarked" package (Fiske & Chandler, 2011). We then fit our best model in a Bayesian modeling framework to obtain site- and year-specific 95% credible intervals [CRI]. For all stages, we created a priori models and compared them using Akaike information criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002). For the abundance distribution, we compared Poisson, zero-inflated Poisson, and negative binomial distributions, testing the robustness of the negative binomial distribution using increasing upper bounds of $K = 80$, 120, 160, 200, 300, and 400, as described in Kéry (2018). To evaluate the best form for population growth, we compared a null model of no growth with an autoregressive model and models for exponential growth, Ricker growth, and Gompertz growth curves. The last two models evaluate density dependence (Hostetler & Chandler, 2015). We tested each with and without a term for the average number of immigrants to a site per year (Brommer et al., 2017; Hostetler & Chandler, 2015). For all models, we used a finite upper bound of 200 goats per site. Each stage of the modeling process (detection, initial abundance, and population growth) had comparisons of multiple spatially and temporally varying covariates defined at one of four scales: the full study area (time-varying for population growth only), a region of the park (NW, NE, SW, SE), the 6.4 km × 6.4 km observation grid centered on the observation point, or the viewshed within the observation grid (Figure 1).

For each stage of the modeling process, we used correlations, variance inflation factors, initial univariate comparisons with a null model, and comparisons of related covariates quantifying an ecological process to reduce the number of variables to carry forward. For example, for detection we examined several ways of evaluating observer experience, but only carried forward the best performing covariate (i.e., log(Observer Experience)). Within each process stage, we categorized groups of variables and carried the best model for the category forward to a comparison of all possible combinations for the process.

We considered many variables for detection to provide information on how the citizen science program might be able to improve power in the future. Variables covered five categories: observer characteristics, survey equipment, abiotic conditions, viewshed effects, and goat habituation (Appendix S1: Table S2). For observer characteristics, we compared several indices reflecting experience, including the maximum number of surveys previously conducted by any observer present, the log number of the maximum number of surveys, and categorical covariates when observers had conducted more than 5, 10, or 20 surveys. We evaluated the number of observers and its quadratic plus categories for observer type (e.g., citizen scientist, wildlife staff). We assessed equipment used; although volunteers were instructed to use binoculars and spotting scopes during all surveys, 14.1% of surveys were conducted without a scope, or scope information was not recorded, and 2.9% of surveys were conducted without binoculars (~half of which had a scope; Appendix S1: Tables S3 and S4). We evaluated several abiotic survey conditions. Sky cover included the presence of fog, smoke, or precipitation. We considered whether detection of goats might change based on Julian date and its quadratic, the number of days since the date of peak green up of vegetation, or temperature. The visibility of goats might decrease during higher temperatures if goats moved to forested areas or rugged micro-terrain for shade. We also assessed the largest previously observed group of goats at a site to index sites where goats might be more easily observed. Within the viewshed effects category, we considered total viewshed area, the area of viewshed with slopes ≥25°, the area of non-forested landcover in the viewshed, and the area of non-forested landcover in the viewshed that also had slopes ≥25°. Because several sites in the park have a long history of habituation (Rideout, 1977), which could increase visibility, we assigned sites as having no history of habituation, occasional reports, and frequent reports of habituated goats based on the expert opinion of GNP biologists.

For initial abundance, we assessed categories for spatial unit, habitat, proportion of permanent snow, mineral lick presence, and habituation (Appendix S1: Table S5). We compared two hypotheses for spatial units. In the first, we evaluate the Livingston Range, in the northwest of the park, as a unit with different initial abundance because the Livingston Range is smaller with forested valleys ~2 km wide separating it from the Lewis Range and park biologists generally see fewer goats in the Livingston Range. For the second hypothesis, we divided the park into four regions based on mountain ranges, ecological differences across the Continental Divide (splitting west and east), and a potential barrier to movement during the summer months when traffic volumes increase: the Going-to-the-Sun Road (splitting north and south). Thus, the NW region was the Livingston Range, the NE region was the Lewis Range north of the Going-to-the-Sun Road, and the SW and SE regions encompassed the rest of the Lewis Range split along the Continental Divide (Figure 1). For the habitat category, we compared the area of escape terrain (slope ≥ 25°, based on 30-m resolution, National Elevation Dataset) with the sum of values of predicted high occupancy from Flesch and Belt (2017). We also considered the proportion of permanent snowfield and glaciers in the observation cell (Fagre & Peitzsch, 2010; Fagre et al., 2017, 2019), the presence of a mineral lick in the observation cell, and the three levels of habituation described above. Because habituated goats may be in places where humans act as a predator shield, we also evaluated whether more goats might be in areas with more habituation.

For the population growth process, we considered categories associated with winter conditions (October–April), summer conditions (July–August), drought (of the prior year or of the prior summer), neonatal conditions of the prior year (May 15–June 15), and non-climate (Appendix S1: Table S7). Because goat summer and winter locations likely differ, we compared winter conditions at the study area scale (i.e., the park), which varied only by year, and the regional scale, which varied by year and across the park. White et al. (2011) found that goat survival in their coastal study area was negatively influenced by total annual snowfall. Because our study area is mid-continent rather than coastal, we evaluated additional covariates that might better describe effects, including total snowfall, average temperature, average snow depth, and average snow water equivalent along with its quadratic, all derived from SNODAS (National Operational Hydrologic Remote Sensing Center, 2004). We summarized covariates describing summer conditions, drought, and early summer conditions for each observation grid. We evaluated summer precipitation, average daily temperature (White et al., 2011), warm summer days (>12.8°C, the temperature at which respiration increases, Sarmento et al., 2019), and hot summer days (>15.6°C, White et al., 2011). We also considered the variance of the peak green-up date and the range of the peak green-up date (eMODIS, Jenkerson et al., 2010) to evaluate the effect of local heterogeneity in forage timing on goat population growth (Pettorelli et al., 2007). Because drought severity is increasing and we have observed changes in vegetation likely to influence protein content, even at high elevations in drought years (Berman et al., 2020; Whitlock et al., 2017), we compared the average drought across the last year and the average drought for the previous summer (July–September). Cold, wet conditions during the neonatal period (May 15–June 15); based on average birth dates from Chadwick (1977) might decrease newborn goat survival or influence forage quality and quantity and we therefore considered early summer precipitation and temperature (Butler & Garrott, 2012; Hamel et al., 2010; Théoret-Gosselin et al., 2015). Other variables included the open escape terrain area, region to allow us to assess different population change in each part of the park, the proportion of permanent snow and glaciers, and habituation.

We fit the top-ranked model from the maximum likelihood analysis in a Bayesian framework in JAGS (Kellner, 2019) and the statistical software R (v.4.3, R Core Team, 2023), using diffuse normal priors for explanatory parameters except the growth rate intercept and immigration terms which used a uniform distribution. We added a binary variable to represent the potential for different detection rates during the 2008 and 2009 study years, which had more surveys and paired observations compared to later years 2010–2019. During the early study period, we hypothesized and examined whether observers' knowledge of being tested could have increased motivation and detection. Thus, we competed this model against a model with a random effect for detection for each year. Bayesian models used four MCMC chains and ran for 50,000 iterations. We retained 35,000 values per chain, after discarding 15,000 for adaptation and burn-in. We calculated a Bayesian p value to assess goodness of fit (Kéry & Schaub, 2011).

To evaluate abundance, N-mixture models assume that detections of individuals are independent of each other. If individual detection is not independent, estimates of abundance will be biased high (Martin et al., 2011). Because mountain goats often live in groups and kids typically stay with their mother for their first season, we avoid estimating overall population abundance and instead focus on population change over time. When evaluating population growth, changes in the degree of association could affect the interpretation of the apparent trend. To address this concern, we assessed whether group size changed over time by fitting a Poisson model of group size as a function of year, habituation level, Julian day (as quadratic), and temperature during the survey with a random effect of site. N-mixture models of abundance further assume that individuals are counted only once per survey. To account for this, during surveys, citizen scientists tracked goats once detected to avoid double counting.

N-mixture models also assume that the population is demographically and geographically closed within replicates for a year and site. We limited surveys to the time between birth and rut, which also excluded most migrations to winter ranges. In other populations, most mortalities occur after the rut or shortly after birth (White et al., 2011). Although observation grids were chosen to provide an even distribution across the park, topographic restrictions and limited trail access led to some overlap for five observation grids. Therefore, to assess the sensitivity of our results to the inclusion of these overlapping observation grids, we refit models after alternately removing the grids excluded by Belt and Krausman (2012) and the opposite grids. To evaluate coverage of goat habitat at survey sites, we compared the distributions of aspect and elevation within viewsheds to predicted occupied goat habitat (Flesch & Belt, 2017).

RESULTS

Dataset summary

From 2008 to 2019, between June 1 and October 31, staff and citizen scientists conducted 1961 surveys: 194 in 2008, 294 in 2009, and an average of 147 surveys year^{-1} from 2010 to 2019, resulting in a mean of 4.42 surveys site^{-1} year^{-1} (SD = 2.62, range = 0–23; Appendix S1: Table S1). The citizen science program met sampling objectives of at least 3 surveys site^{-1} in 80.4% of site-years and had at least 2 surveys site^{-1} in 93.5% of site-years. No surveys occurred at only 2% of the 444 site-years, 3 sites in 2008 during program initiation, and 3 sites each in 2015 and 2016 due to fire and resulting inaccessibility (Appendix S1: Figure S1). The number of surveys overall and also for each site generally increased through mid-August, peaking during the annual "Goat Days" event and then declining thereafter (Appendix S1: Figure S2).

Best model

Although the negative binomial formulation best described the distribution of goat counts, it exhibited the issues outlined in Kéry (2018) of estimates increasing as the input parameter for the upper limit of goats per site increased. As a result, we used the next most supported model (Poisson) for the abundance distribution. The best-supported population growth model was exponential with an immigration term. We confirmed similar estimates for the best unmarked model and our initial Bayesian formulation and report results for the Bayesian formulation.

The mean detection probability for an individual goat was 0.045 (95% CRI = 0.011, 0.12). The best detection model included all 5 categories with 19 terms representing relationships among 9 variables (Table 1; Appendix S1: Tables S2 and S3), namely the log of observer experience, observer class, binocular presence, scope presence, temperature during survey, Julian day of survey, the largest previously observed group size at the site, an interaction between the area of the viewshed and the area of open escape terrain, and habituation level. Model selection supported inclusion of the quadratic of Julian day of survey and interactions among it with the log of observer experience and temperature. Habituation of goats had the largest effect on detection of goats during surveys. Detection probability was 1.3 times larger at sites with occasional ($n = 9$) and 2.3 times larger at sites with moderate/frequent reports ($n = 4$) of habituated goat behavior than at sites with a reference level of no habituation ($n = 24$). Compared to those conducting a survey for the first time, detection rates are 1.6, 2.0, 2.3, and 2.6 times larger for observers who conducted 10, 20, 50, and 100 surveys, respectively, but were not statistically different by observer class (Appendix S1: Figures S3 and S4). Detection was 1.5 times higher when surveys were conducted at temperatures of 10 versus 27°C. Detection was highest early and very late in the season (Appendix S1: Figure S5). Compared to the average survey date of August 6, detection probability was 2.7 times larger on June 1 and 1.5 times larger on July 1.

The most parsimonious initial abundance model included three variables: a random intercept for the region of the site, the proportion of the site covered by snow or glacier, and the presence of known mineral lick(s) in the observation grid (Appendix S1: Figure S6). The initial abundance was lowest in the Livingston Range in the northwestern region of the park, with significantly more in the southeast, southwest, and northeast regions (Figure 2; Appendix S1: Figure S7). Models that also included either the sum of probability of occupancy for the observation grid or the level of habituation were similarly supported (<2 AIC; Appendix S1: Table S6). We used the most parsimonious model in subsequent modeling steps.

The model predicts large population declines, especially after the first two years of the study, with continued more moderate declines until around 2015, when estimated goats per site appear to stabilize at relatively low numbers (Figures 2 and 3). Median goats per site declined by 45% (95% CRI = 32%, 57%) from 2008 to 2019 and by 28% (95% CRI = 18%, 38%) from 2010 to 2019. Predicted growth (λ) was statistically below $\lambda = 1$ (declining) for 5 of the years, was never statistically above $\lambda = 1$ (growing) and the median goats per site declined from 77.76 (95% CRI = 64.44, 95.12) in 2008 to 42.27 (95% CRI = 34.32, 52.22) in 2019 (Figure 3). Because we included spatially and temporally variable covariates, abundance at each site could change independently of other sites. We found statistically supported declines over the study period at 18 of the 37 sites, with 14 of those in eastern quadrants (Figure 4). The northeast had the largest declines, with a site near Logan Pass having the greatest decline. This site (Haystack Butte) had an estimated median decline nearly twice the average site-level rate, decreasing from 134 to 22 goats (Graves, Janousek, et al., 2025; Graves, Stein, et al., 2025). The median number of goats increased statistically at two west-central sites. An additional 11 sites, primarily in southern quadrants,

TABLE 1 Estimated coefficients for final N-mixture model of mountain goats in Glacier National Park, USA.

Model/variable	Effect (95% CRI)
Detection	
Startup years effect (habituation = none)	0.19 (0.03, 0.35)
Julian date	−1.97 (−2.47, −1.51)
Julian date^2	1.79 (1.32, 2.29)
No binoculars	−0.33 (−0.59, −0.08)
No scope	0.09 (−0.02, 0.2)
Observer class = CS	−3.68 (−3.88, −3.46)
Observer class = CScasual	−3.69 (−4.05, −3.36)
Observer class = GNPstaff	−3.33 (−3.57, −3.09)
Observer class = outreach	−3.61 (−3.86, −3.35)
Observer class = WLBT	−3.41 (−3.63, −3.19)
Observer class = WLBTother	−3.45 (−3.69, −3.21)
Observer class = WLBToutreach	−3.56 (−3.89, −3.23)
Observer experience (log)	0.29 (0.25, 0.32)
Observer experience × Julian date	0.41 (0.09, 0.72)
Observer experience × Julian date^2	−0.39 (−0.7, −0.07)
ETOpen (viewshed)	1.01 (0.74, 1.27)
ETOpen2 (viewshed)	−1.08 (−1.38, −0.77)
Area (viewshed)	0.16 (0.05, 0.27)
ETOpen (viewshed) × Area (viewshed)	−0.06 (−0.25, 0.14)
ETOpen2 (viewshed) × Area.VS (viewshed)	0.18 (−0.06, 0.41)
Temp hourly	−0.15 (−0.18, −0.11)
Largest group to date	0.12 (0.06, 0.18)
Temp hourly × Julian date	0.48 (0.12, 0.83)
Temp hourly × Julian date^2	−0.44 (−0.78, −0.08)
Habituation (moderate/high)	1.00 (0.74, 1.25)
Habituation (occasional)	0.54 (0.35, 0.73)
Growth	
Intercept	0.92 (0.89, 0.95)
Regional SWE	0.02 (−0.02, 0.05)
Regional winter temp	0.05 (0.01, 0.10)
Neonatal temp	0.05 (0.02, 0.09)
Neonatal precipitation	0.08 (0.04, 0.13)
Regional SWE × Winter temp	−0.04 (−0.08, −0.01)
Initial abundance	
Park region = Northeast	4.71 (4.51, 4.93)
Park region = Northwest	2.68 (2.17, 3.13)
Park region = Southeast	3.90 (3.61, 4.17)
Park region = Southwest	4.26 (4.01, 4.50)
Proportion SnowGlac (grid)	0.13 (0.04, 0.23)
MineralLick (grid)	0.15 (0.08, 0.22)

Abbreviations: CRI, credible interval; CS, citizen scientist; ET, escape terrain; SnowGlac, snow and glacier cover; SWE, snow water equivalent; Temp, temperature; VS, viewshed; WLBT, wildlife biological technician.

had declining median goats per site, and 6 sites primarily in the northeast had increasing median goats per site; but changes were not statistically supported (Figure 4). In general, as the number of predicted goats at a site declined, the variance around estimates decreased, consistent with use of the Poisson distribution for abundance (Pearson $r = 0.86$; Figure 4; Appendix S1: Figure S8).

The best model for population growth included only four variables, all recorded at the region level: snow water equivalent, mean winter temperature, early summer temperature, and early summer precipitation, along with an interaction between snow water equivalent and mean winter temperature (Table 1; Appendix S1: Figure S9). Lower growth occurred with less snow water equivalent, lower mean winter temperature, and lower early summer temperature and precipitation. The strongest variable influencing population growth rate was early summer precipitation (0.08, 95% CRI = 0.04, 0.13; Table 1, Figure 5). This effect was 1.3 times larger than the next strongest predictor, early summer temperature during the neonatal period (0.05, 95% CRI = 0.02, 0.09). We found no evidence of a lack of fit (Bayesian p value = 0.55).

Evaluation of assumptions

Group size decreased slightly over time from 2.26 (CI = 1.98, 2.51) in 2008 to 1.99 (CI = 1.78, 2.25) in 2019 with no significant differences by habituation level. Age ratios did not decrease over time or correlate highly with population growth ($r = 0.19$). Kid-to-nanny ratios tracked population growth rates during the decline from 2008 to 2015 but were generally low in later years when the population appears to have stabilized at lower numbers (Figures 3 and 6). The removal of overlapping grid cells from the analysis resulted in decreased precision due to smaller sample size and slightly smaller predicted declines because the removed sites were those with large declines. However, in all cases, population growth was significantly negative with CRIs that did not overlap 0.

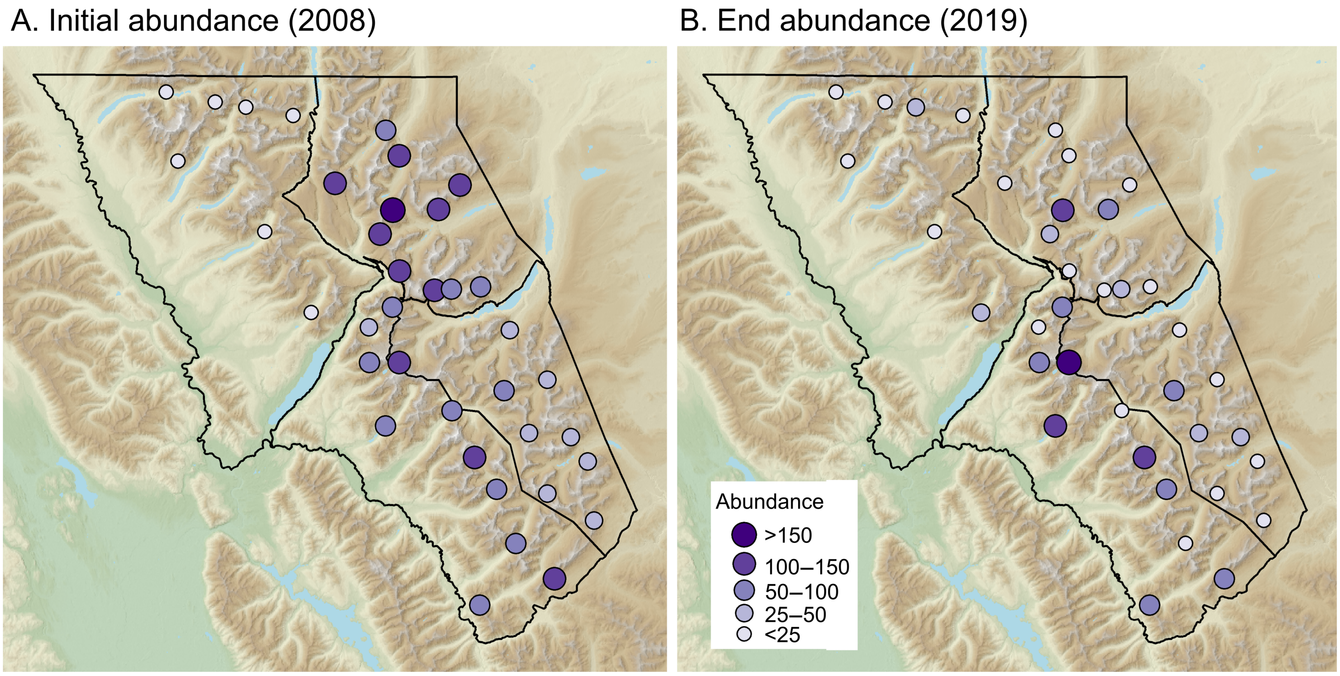

FIGURE 2 Median site-level goat abundance for 2008 and 2019. Outlines indicate the four regions in Glacier National Park, Montana, USA, used to define covariates in this study. Basemap from NASA 30 m Digital Elevation Model (Farr et al., 2007).

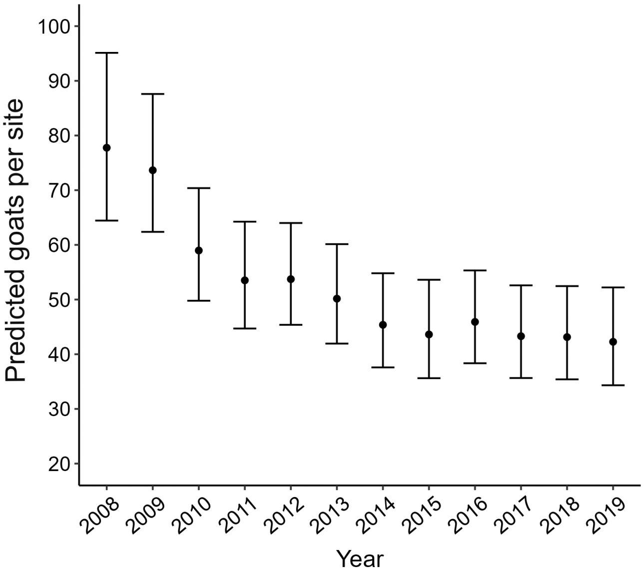

FIGURE 3 Median number of goats per site and the associated 95% credible interval over years.

Observation viewsheds represented areas predicted to be occupied by goats by Flesch and Belt (2017) very well, with viewsheds skewed slightly toward better-than-average goat habitat and with greater coverage of the northerly aspects, higher elevations, and steeper slopes that goats might be expected to use more frequently with higher temperatures (Appendix S1: Figure S10).

DISCUSSION

We found a very large, 45%, decline in the population of mountain goats in GNP. As the largest non-hunted, native population in the contiguous United States, this raises concern about native mountain goat populations at the southern extent of the range. The population steadily declined from 2008 to 2015, with numbers appearing to stabilize at a much lower population size thereafter. Relatively few goats were present in the Livingston Range (northwestern GNP) across the study period. By the last year of the study, the numbers of goats had declined in most eastern and southwestern sites, with the largest declines in the northeast. Our hierarchical model identified positive relationships for initial abundance with permanent snow and mineral licks and several climate variables for population growth that may have counteracting effects on goat demography, and thus require forecasting to predict future trajectories. Although some variables positively associated with growth rates might support GNP's goat population, declines in permanent snow, interactions between snow characteristics and temperature, and projected increases in the frequencies of drought raise concerns.

Climate projections in the park consistently predict increasing temperatures across all seasons, but projections for precipitation vary substantially across models, across seasons, and across the study area (Abatzoglou, 2012; Climate Change Response Program, 2024; Whitlock et al., 2017).

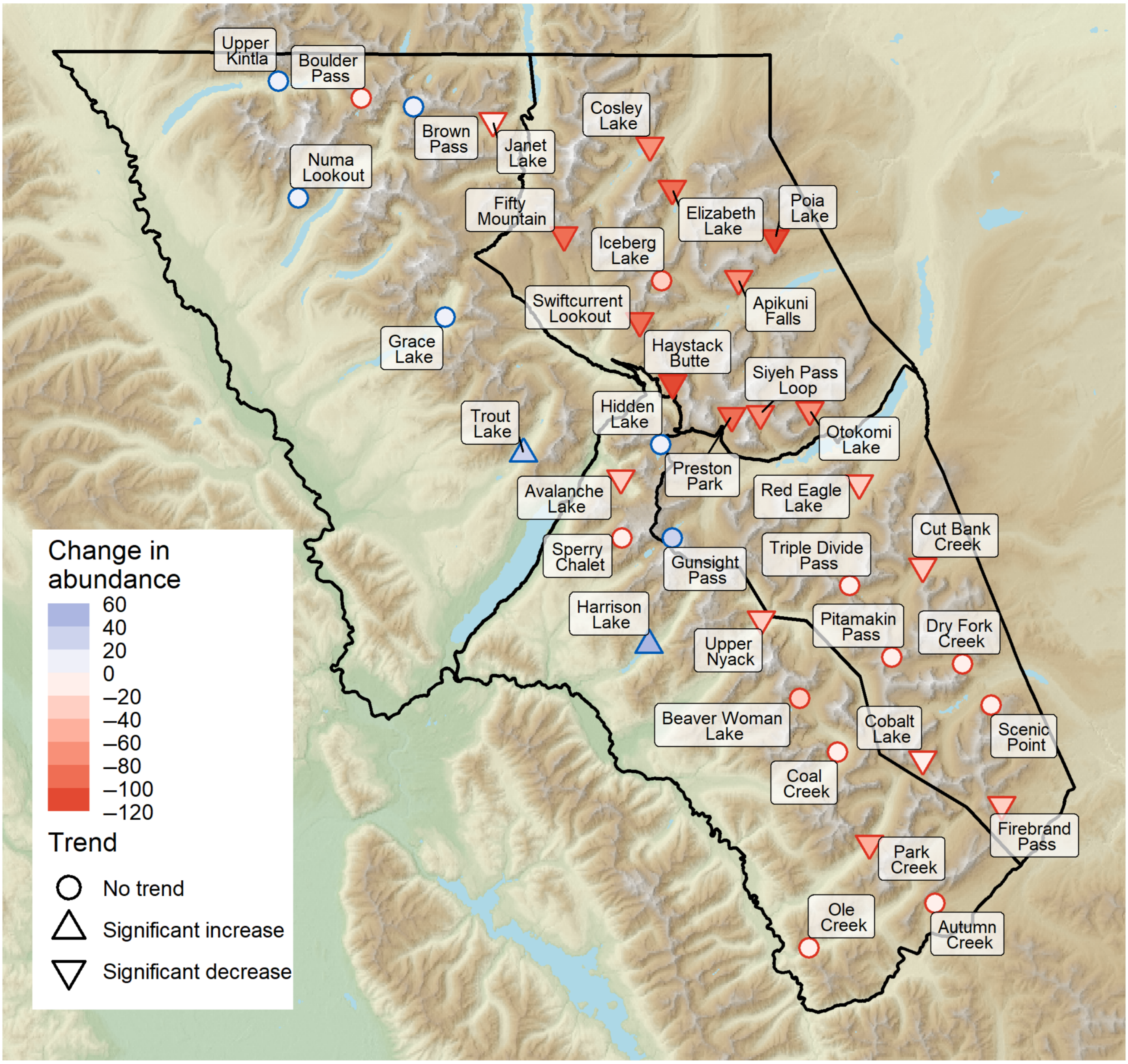

FIGURE 4 Predicted site-specific change in mountain goat abundance 2008–2019. Site names reflect local features. Outlines indicate the four regions in Glacier National Park, Montana, USA, used to define covariates in this study. Basemap from NASA 30 m Digital Elevation Model (Farr et al., 2007).

We found increased spring temperatures supported population growth, but temperature increases can also lead to more evaporation, less soil moisture, and drought, which generally decrease forage quality and quantity and are tied to declines in survival in Washington, USA (Harris et al., 2024). Snow water equivalent and temperature interacted in the population growth level of our model. Snow has low thermal conductivity and thus deep snow can limit negative effects of cold air temperatures (Zhang, 2005). However, deep snow also significantly changes energetic costs of movement and the availability of winter forage (Dailey & Hobbs, 1989), which negatively influences demographics (Parker et al., 2009). Snow characteristics (e.g., density) may shift the negative effects of deep snow (Reinking et al., 2022), but we did not have data to evaluate detailed features of the snowpack. Our model indicates the proportion of persistent snowfields and glaciers positively influenced initial goat abundance. We could not evaluate the effect of declining persistent snow area on population growth because our snow data reflected a single temporal snapshot, though persistent snowfields and glaciers have decreased and will

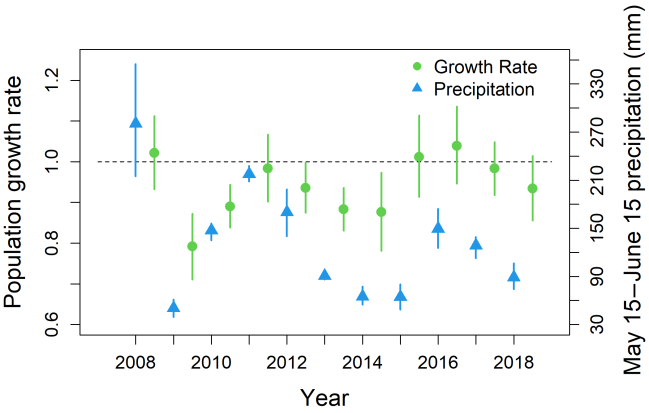

FIGURE 5 Predicted population growth rate between years and precipitation during the neonatal period of the prior summer over time in Glacier National Park, Montana, USA. Dashed horizontal line is growth rate = 1, the value at which a population is stable. Error bars represent 95% credible interval region for growth rate estimates and the 5th and 95th percentiles for annual summaries of neonatal precipitation.

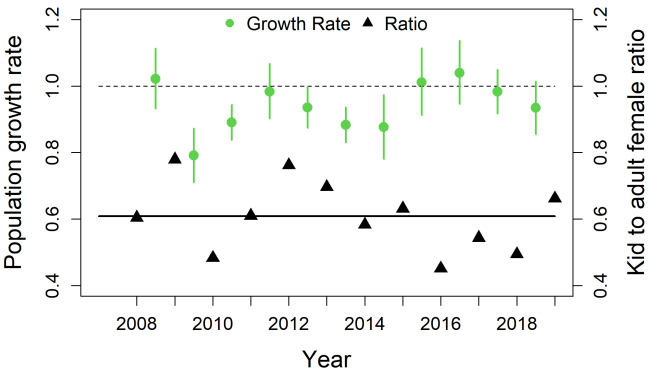

FIGURE 6 Predicted growth rate and 95% credible interval (error bars) reflecting the interval prior to the year plotted and kid to nanny ratio across biologist-only observations for the summer of the year plotted in Glacier National Park, Montana, USA. Dashed horizontal line is growth rate = 1, the value at which a population is stable, and the solid line is the mean ratio.

continue to decrease (Bosson et al., 2019; Martin-Mikle & Fagre, 2019). In addition, mineral licks exist due to processes related to water flow and evaporation, but the geohydrology and influence of climate change on the lick resources in the park have not been evaluated.

Behavioral changes may be an important way for goats to adapt in place in the short term given that they cannot shift in space to higher elevations (Beever et al., 2017; Thurman et al., 2020). Sarmento et al. (2019) suggested that, during summer, thermal stress occurs at high enough levels in the park to cause goats to modify their behavior. Goats selected areas with snow or forest cover during the heat of the day in the summer. Cooler temperatures, cloud cover, and the use of snow patches reduced goat respiration and observed heat stress (Sarmento et al., 2019). In addition, behavioral modification may reduce available forage (Michaud et al., 2024). In many species, heat stress alone or in combination with nutritional stress can also affect reproductive hormones (Seijan et al., 2011). Biologists in GNP have found carcasses in forested areas in recent years. Evaluating the potential that goats using forested areas in GNP experience higher predation would help us learn whether changing behavior to thermoregulate could sometimes be an ecological trap.

Our analyses do not identify which demographic changes (reproduction, mortality, or emigration) drive the declines we documented or allow us to parse out the mechanism by which covariates such as early summer precipitation influence population growth. However, the relationship of kid to nanny ratios and predicted growth estimates suggests that pregnancy or very early kid survival rates contribute to variation in the annual survey counts and the estimated population growth rate. Less early summer precipitation may decrease forage quality or quantity, which could influence the energy balance of this mountain ungulate leading to decreased reproduction of nannies or decreased survival of goats through harsh winters (Aublet et al., 2009; Fox, 1991; Pettorelli et al., 2007; Théoret-Gosselin et al., 2015). Harris et al. (2024) found that populations had lower survival in low precipitation and drought years. Early-season forage conditions may have particularly strong effects on nannies and their offspring because of the high energetic costs of late gestation and lactation (Hamel et al., 2010; Loudon, 1985). For example, at Caw Ridge in Alberta, Canada, most kid mortality occurred between birth and the end of June (Hamel & Côté, 2007). Similarly, shifts in avalanche frequency and depth or changes in snow conditions could change forage availability in winter ranges (Jenkins et al., 1990; White et al., 2009). Combined, this suggests that further research into the effects of forage on vital rates may be fruitful.

Other mortality sources may also play a significant role in goat demographics. In a recent study of radio-collared mountain goats in GNP, 5 of 24 individuals died (M. Biel, personal communication April 9, 2021; ~79% naïve survival). While this high proportion of deaths is consistent with our declining estimates, the sample size is small and goats were collared in only a few areas. Many of the carcasses were found in avalanche chutes, but the cause of mortality is unknown. Elsewhere, avalanches have been documented to be an important cause of mountain goat mortality (White et al., 2024). In our study region, the frequency, severity, and characteristics of avalanches have changed over time and are expected to continue shifting with climate change going into the future (Peitzsch et al., 2021), but how this translates into goat survival in the park is not yet understood.

Other variables we did not evaluate could also influence population declines. For example, if forage quality varies with distance to escape terrain, as it does in Caw Ridge, Alberta, interannual variation in forage quality may alter trade-offs associated with females choosing between safety from predators and forage (Hamel & Côté, 2007; Tosa et al., 2023). Delude-de-Broin et al. (2019) demonstrated stress-induced breeding suppression in mountain goats from predation risk. We did not have data to support modeling predation pressure. We also had limited information on the spatial distribution of increasing human recreation and other activities that could influence habitat loss, lead to avoidance of high-quality habitat, increase stress or increase habituation (i.e., human disturbance as a form of predation risk; Frid & Dill, 2002). Along with disturbance, visitor urine can bring nitrogen, caffeine, antibiotics, and hormones to alpine habitats (Baron et al., 2023). In GNP, visitation has increased from 2 million visitors per year in 2010 to over 3 million in 2019, with a large increase of over 600,000 visitors from 2015 to 2016 associated with nationwide marketing to celebrate the centennial of NPS and has stayed near 3 million since then (Kernan, 2019). These stressors could amplify climate-related effects and warrant further study, including examination of adaptive management strategies.

Without a precise population estimate, it is difficult to place these declines in context. An extrapolation of densities from the Many Glacier and Walton Goat Lick study areas suggested that the park might have had ~1500 mountain goats in the late 1970s (Chadwick, 1977). However, our analysis suggests that those study areas were among the most densely populated areas of the park in 2008 when our research began. Belt and Krausman (2012) used N-mixture site estimates for 2009 to extrapolate an estimate of 2027 (95% CI = 1397, 2657) goats across the park. The count of goats observed during surveys varies substantially and this high natural variance challenges precision in N-mixture models. Also, the non-independent detection of kids with nannies can positively bias annual N-mixture analysis estimates of site population size. In our assessment of assumptions for our trend estimate, we detected relatively small, ~12%, declines in goat group size that could lead to a higher bias in initial than later annual estimates (Martin et al., 2011). This could reduce but would not eliminate the large declines we estimated. As herding is an anti-predation adaptation, smaller group sizes are also consistent with population decline. Projecting the upper and lower 95% CLs of the 2009 estimate paired with the 95% CRI here leads to extrapolations of between 601 and 1807 goats in GNP for the year 2020.

Approaches that use individual identification such as a repeated spatial capture–recapture approach based on fecal pellets (e.g., Epps et al., 2024; Kendall et al., 2019) or integrated population models that incorporate observational counts with individual identification-based approaches could provide more precise population and trend estimates (Schaub et al., 2007). This context may be needed for managers to understand and support challenging policy decisions associated with evidence reported here of substantial population decline. In addition to improved precision, these methods are less likely to be influenced by group size and offer a more effective approach when implemented over time to detect declines in small populations.

Population estimates need to be placed in the context of genetic structure given that separated, smaller populations can more easily succumb to an extinction vortex, where demographic, environmental, and genetic stochasticity can interact to mutually accelerate the extinction of small populations (Gilpin & Soule, 1986). Mountain goat populations often exhibit fine-scale structure (Parks et al., 2015; Shafer et al., 2011). Inclusion of the effects of genetic structure in mountain goats led to lower projected persistence even with very low harvest in isolated populations (White et al., 2021). Although goats in GNP cannot be legally harvested, if many animals move outside the park, susceptibility exists. Furthermore, ecological first principles suggest that small, isolated populations have less buffer to environmental stochasticity or random catastrophic events that elicit increases in natural mortality or declines in reproduction.

Our results emphasize the value of long-term monitoring, a strong initial study design, and the adoption of advanced statistical methods. Our well-distributed sites cover the entire park with a reasonable sample size, permitting inference at the population scale. Although the decline was large, the trend in the goat population was not obvious in the raw data, nor in single-year N-mixture model estimates conducted by park staff in intervening years (Appendix S1: Figure S11; J. Belt, personal communication, January 2020). Although this is not surprising based on initial power analyses conducted by Belt and Krausman (2012), our results highlight the benefits of incorporating data collected across many years and using models that represent the various processes of interest. The newer statistical techniques used here crucially improved inference and provided information on variables influencing detection.

The covariates describing detection suggest that potential improvements in data collection can be achieved and could increase precision and power to detect future declines. We found that observers with more experience detected more goats, which implies that retaining observers in the program can improve detection. Similarly, our analysis suggests a continued requirement of using optics including binoculars during surveys. Many sites have a viewshed that includes areas difficult to see without good optics. Inclusion of temperature in our model accounts for decreasing detection when goats become less visible through shifts to forest or micro-terrain in cliffs or reduced movement, but timing surveys during cooler temperatures such as in late evening or early morning could increase detection. Restricting survey times may be difficult to achieve with citizen scientist observers because most surveys occur by people on day hikes and hiking after dark is not recommended in areas inhabited by grizzly bears. Focusing surveys and the "Goat Days" event earlier or later in the season may also improve detection, but many of these sites are at higher elevations that are not easily accessible until late July when snowpack has decreased.

Our analyses suggest that the mountain goat population in GNP experienced a large decline during our 12-year monitoring period. Additional research could contextualize the decline and mechanisms behind it. Methods used here provided the power to detect this large decline of an iconic climate-sensitive species, despite challenges with collecting ground-based field data in remote, mountainous areas that include logistics and high variability in the data. Climate appears to play a large role with many mechanisms having the potential to shift populations (reviewed in White et al., 2024). Because we could not incorporate information on all possible stressors, this research raises several questions. At the low numbers we documented, it will also be more difficult to detect further declines and better identifying decline causes could take years. Given the relatively slow reproductive potential of mountain goats (Festa-Bianchet & Côté, 2008), it will likely take several years for any proactive management activities to reverse declines and to determine whether actions have been effective. While numbers may have stabilized at relatively low levels, increased attention to this vulnerable population in the forms of both research and management may be needed to ensure the persistence of this population and meet the NPS mission to preserve and protect resources for the enjoyment of future generations.

AUTHOR CONTRIBUTIONS

Jami Belt led data collection in most years. Jami Belt and Tabitha A. Graves conceived this manuscript. Michael J. Yarnall prepared and analyzed maximum likelihood models. William M. Janousek analyzed Bayesian models and prepared figures. Tabitha A. Graves wrote the first draft of the paper. All authors edited and approved the final version of the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Graves, Janousek, et al., 2025) are available from the USGS: https://doi.org/10.5066/P91GTUL3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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