A unified approach to long-term population monitoring of grizzly bears in the Greater Yellowstone Ecosystem

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ARTICLE INFO

ABSTRACT

Long-term wildlife research and monitoring programs strive to maintain consistent data collections and analytical methods. Incorporating new techniques is important but can render data sets incongruent and limit their potential to discern trends in demographic parameters. Integrated population models (IPMs) can address these limitations by combining data sources that may span different periods into a unified statistical framework while providing a holistic view of population dynamics. We developed an IPM in a Bayesian framework for grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem. We coupled demographic data with multiple, independent population count data to link annual changes in abundance with vital rates over 4 decades (1983–2023). Abundance increased threefold from an estimated 270 individuals in 1984 to 1030 individuals in 2023. Parameter estimates indicated survival of bears ≥2 years of age was high, contributing to robust population growth during the 1980s ($\lambda = 1.023$ [50 % interquartile range $= 0.993$–1.082]) and 1990s ($\lambda = 1.064$ [1.023–1.103]). A slowing of population growth started

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around 2000 (2000s: λ = 1.030 [0.989–1.068]) and continued into the 2010s (λ = 1.021 [0.985–1.057]), due primarily to reductions in survival of bears <2 years of age. These findings corroborate previous research that identified density-dependent effects as a likely cause. The IPM framework provided greater certainty and understanding regarding the dynamic demographic characteristics of the population and serves as a powerful monitoring tool for this long-lived species. Implementation of the IPM allows timely dissemination of demographic data to help inform adaptive management strategies and policy decisions necessary for the continued management and conservation of this population. This robust and flexible monitoring system allows scientists to investigate the effects of a changing ecosystem on population dynamics, incorporate new data sources and statistical models, and respond to changes in monitoring needs for the population. We highlight the efficacy of the IPM in estimating and tracking demographic parameters for a long-lived species, while accommodating shifts in monitoring techniques and data collections typical of long-term wildlife conservation programs worldwide.

1. Introduction

Population monitoring is a fundamental tool in global wildlife conservation and can be defined as the repeated, systematic collection of data to detect long-term changes in the populations of wild species (Moussy et al., 2022). Monitoring data can reveal drivers of population dynamics, provide insights toward the development of conservation actions, and produce metrics to assess the effectiveness of those actions. Long-term monitoring typically involves continuous collection and analyses of empirical data for at least 10 years (Lindenmayer and Likens, 2010), with longer time frames particularly relevant for species with slow life histories. Inherent in any long-term research and monitoring program is the difficulty to maintain a cohesive system of data collections and analysis (Pelton and van Manen, 1996). Interruptions in data collection and changes in monitoring techniques or objectives can reduce compatibility of data sets over time. These incongruencies are particularly impactful when monitoring demographic rates of long-lived species, for which the power to detect changes in trend is inherently low. Integrated population models (IPMs) can address these limitations by combining multiple data sources that may span different periods into a unified statistical framework (Abadi et al., 2010; Besbeas et al., 2002; Brooks et al., 2004; White and Lubow, 2002). Their synergistic nature allow IPMs to leverage information shared among vital rates estimated from demographic and count data, resulting in more precise parameter estimates and the ability to estimate latent (i.e., unobserved) parameters (Schaub and Abadi, 2011; Schaub and Kéry, 2021). Collectively, these properties enable monitoring programs to amalgamate data sets collected under various conditions and harness the full potential of long-term data.

The application of IPMs is well suited to species of conservation importance, as it can improve detection of changes in the population trajectory, accommodate different monitoring techniques and incomplete data, and refine management strategies (Schaub et al., 2007; Zipkin and Saunders, 2018). The grizzly bear (*Ursus arctos*) population of the Greater Yellowstone Ecosystem is an internationally recognized population of substantial conservation interest, and an ideal candidate for an IPM-based monitoring program. With some of the lowest reproductive rates among terrestrial mammals, grizzly bear populations are sensitive to mortality factors, particularly in relation to adult female survival (Bunnell and Tait, 1981; Eberhardt, 2002; Eberhardt et al., 1994; Knight and Eberhardt, 1985). Grizzly bears were eliminated from approximately 98 % of their historical range in the conterminous U.S. over a period of about 100 years (U.S. Fish and Wildlife Service, 2021). By the mid-1900s, grizzly bears in the Greater Yellowstone Ecosystem were the most southern population in North America, isolated and relegated largely to Yellowstone National Park. Grizzly bears in the conterminous U.S. were listed as threatened under the Endangered Species Act (ESA) in 1975 (U.S. Fish and Wildlife Service, 1975). In the early 1970s, due to uncertainty regarding the status of the population, the National Academy of Sciences was tasked to conduct a rigorous demographic review (National Academy of Sciences, 1974). One of the recommendations of the review led to the formation of the Interagency Grizzly Bear Study Team, a science consortium of Federal, State, and Tribal agencies charged with determining the status and trend of the population.

The monitoring program evolved over time, incorporating advancements in data collection and analysis techniques. The program has focused on tracking females with cubs-of-the-year (hereafter, females with cubs) under the assumption that trends in this recognizable segment of the population were representative of trends in the total population. This population segment was initially estimated based on counts of observed family groups, followed by techniques to identify unique family groups using litter size and a spatiotemporal ruleset (Knight et al., 1995). Because of imperfect detection, those counts were eventually coupled with a nonparametric, bias-corrected Chao estimator (Chao, 1989; Cherry et al., 2007; Keating et al., 2002) with trends inferred using linear and quadratic regressions (Harris et al., 2007). Demonstrated negative bias in the females with cubs estimate (Schwartz et al., 2008) prompted the development of a mark-resight estimator that was unbiased but imprecise due to sparse data (Higgs et al., 2013). Recently, a portion of the spatial ruleset used to differentiate unique family groups was updated to correct the underestimation bias, and new trend detection techniques were implemented using a generalized additive model (van Manen et al., 2022). Concurrently, the monitoring program amassed decades of other demographic data, such as survival and reproduction. These data were used in a benchmark study to estimate demographic rates and conditions associated with population growth during 1983–2001 (Schwartz et al., 2006) and to determine sustainable mortality limits within a designated demographic monitoring area (Interagency Grizzly Bear Study Team, 2012). These monitoring efforts continue today, providing essential data for recovery planning (van Manen et al., 2022) and insights into ecological questions germane to the ecosystem and the species (e.g., Corradini et al., 2023).

Changes in data collection and analysis techniques are not the only challenges presented by the evolution of a monitoring program.

Another limitation is that uncertainty associated with multi-pronged estimation procedures is not always fully propagated throughout the population analysis steps (Schaub and Kéry, 2021). Because there are separate estimation processes for parameters related to abundance, survival, and reproduction, interruptions in data collection for any one process can affect the ability to estimate other parameters. Additionally, preparing data sets and separately estimating various demographic parameters is time consuming and typically leads to period-based estimates of vital rates (i.e., Interagency Grizzly Bear Study Team, 2012; Schwartz et al., 2006) rather than annual updates.

Reliable monitoring data and accurate vital rate estimates are crucial to inform management objectives and identify potential changes in a timely manner. Into the foreseeable future and regardless of their legal status (i.e., ESA listed or delisted), grizzly bears in the Greater Yellowstone Ecosystem will require greater management attention than may be considered for many other wildlife species (Goble et al., 2012; Scott et al., 2005). Thus, it is important to maintain a rigorous but flexible monitoring system that can evolve with changing management objectives. The flexible structure and enhanced analytical capabilities of an IPM may offer important advancements to the demographic monitoring program. Our objective was to develop an IPM for the grizzly bear population in the Greater Yellowstone Ecosystem by combining over 40 years of monitoring data into a unified modeling framework, explicitly linking changes in population size over time with variation in vital rates.

2. Material and methods

2.1. Study area

The Greater Yellowstone Ecosystem is in the northern Rocky Mountains and characterized by several high-elevation plateaus (2400–2700 m) and mountain ranges (peaks: 3400–4200 m). We conducted our study in the demographic monitoring area (49,928 km^2; Fig. 1), which represents the area where abundance, mortality rates, and demographic recovery criteria are monitored
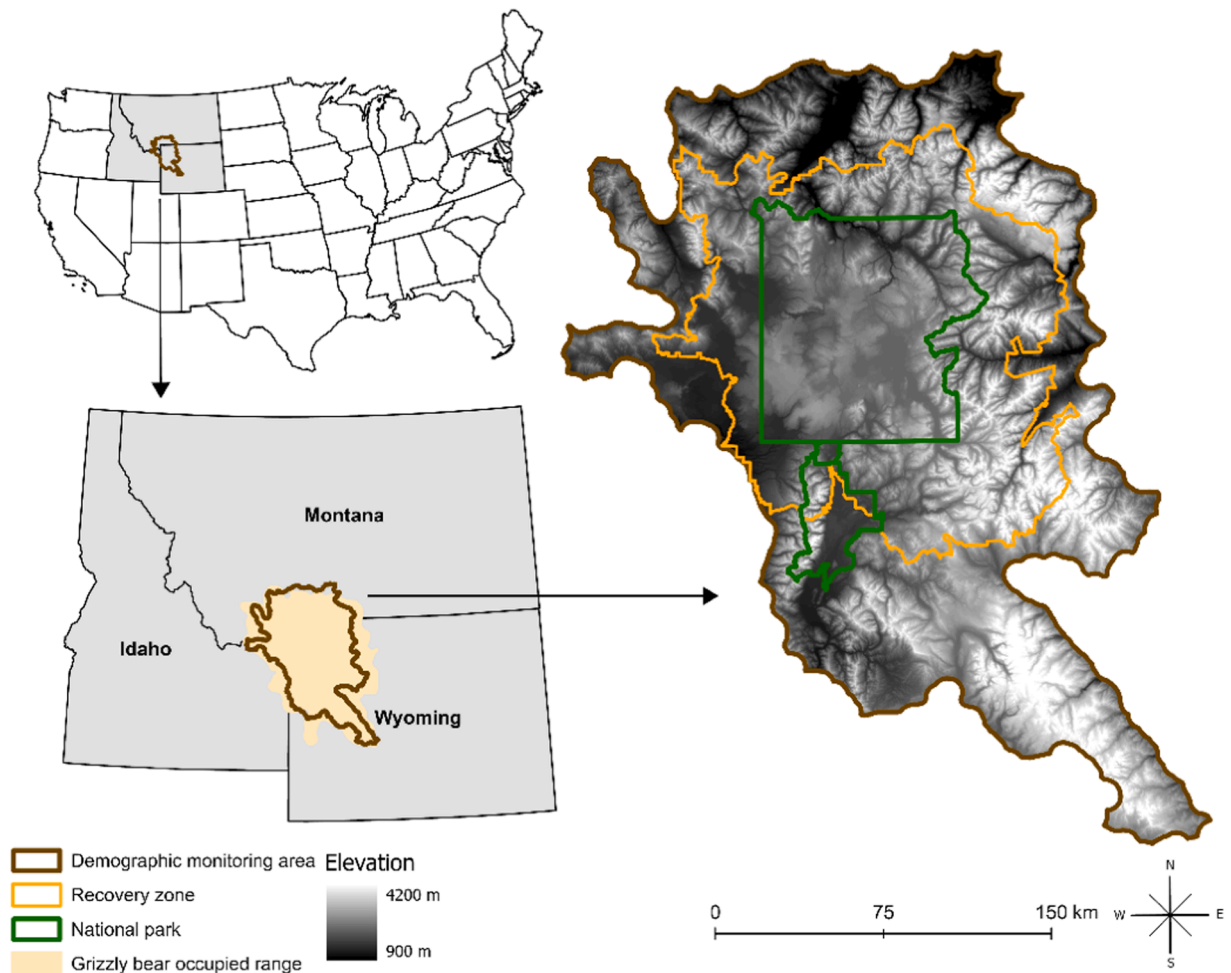

Fig. 1. Study area map showing the demographic monitoring area, recovery zone, and occupied range (2008–2022 data) for grizzly bears and administrative boundaries in the Greater Yellowstone Ecosystem, USA.

(Interagency Grizzly Bear Study Team, 2012; U.S. Fish and Wildlife Service, 2017). The study area encompassed lands across the three U.S. states of Idaho, Montana, and Wyoming, including five national forests (Beaverhead-Deerlodge, Bridger-Teton, Caribou-Targhee, Custer Gallatin, and Shoshone), two national parks (Grand Teton and Yellowstone), the Wind River Indian Reservation, and private lands. Grizzly bears occupied 70,101 km^2 within the ecosystem in 2022, including 97 % of the demographic monitoring area (Dellinger et al., 2023). Food resources for grizzly bears include whitebark pine (*Pinus albicaulis*) nuts, army cutworm moths (*Euxoa auxiliaris*), cutthroat trout (*Oncorhynchus clarkii*), elk (*Cervus canadensis*), bison (*Bison bison*), ants (*Camponotus* spp. and *Formica* spp.), graminoids, and forbs (Costello et al., 2014; Fortin et al., 2013; Gunther et al., 2014).

2.2. Modeling overview

An IPM links population-level count data with individual-based survival and reproductive data through a "state-space model" (Schaub and Kéry, 2021). A state-space model is composed of a process and observation submodel, with the former describing the true state of the population over time and the latter linking temporal changes of the population with count data. The process submodel is a matrix model whereby abundance in year $t+1$ is a function of abundance, survival, and reproduction in year t (Schaub and Kéry, 2021). The count data are conditional on ecological processes (e.g., reproduction and survival), and it is assumed that changes in count data track changes in abundance. Count data provide two benefits: 1) direct information on abundance over time and 2) indirect information on survival and reproduction because those parameters inherently control abundance (Schaub and Kéry, 2021). Because count data provide limited demographic information, survival- and reproduction-specific submodels are needed to estimate additional demographic parameters. By combining all data into a single analysis, more information is available to estimate parameters shared among the state-space model and the survival and reproduction submodels (Fig. 2; Hooten and Hobbs, 2015). Because parameters are linked among submodels, the estimation process is synergistic, resulting in "self-consistent estimates" that must reconcile with one another (Schaub and Kéry, 2021).

We implemented the IPM by analyzing each submodel separately and then generating distributions using annual estimates and their standard errors (Besbeas et al., 2002; Moeller et al., 2021; Schaub and Kéry, 2021). The IPM minimizes the deviation between the
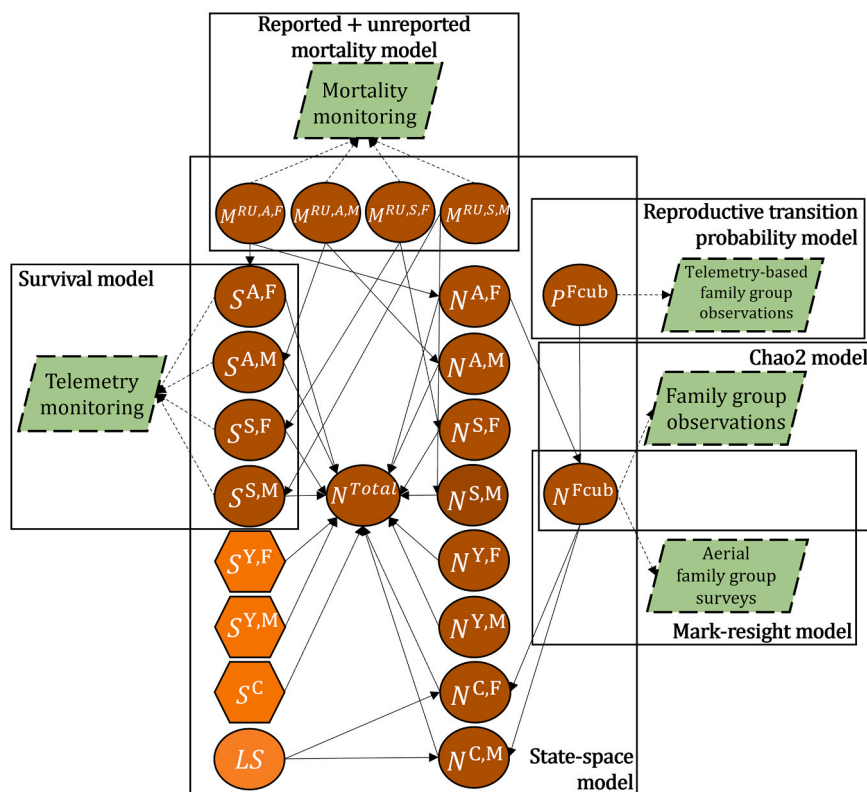
Fig. 2. Directed acyclic graph of an integrated population model used to monitor long-term demographics of grizzly bears in the Greater Yellowstone Ecosystem, USA. Demographic parameters are estimated (brown circles) using data (dashed-green nodes) or latently (i.e., unobserved; orange hexagons). Nodes represent parameters related to survival (S), abundance (N), and the proportion of adult females with cubs (P^{Fcub}). Superscripts represent sex (F = female, M = male) and age class (C = cub [0–1 yr], Y = yearling [1–2 yrs], S = subadult [2–3 yrs], A = Adult [≥3 yrs]). Dependencies among nodes are represented by directed arrows with dashed lines representing those informed by data. Submodels are depicted using solid outlined rectangles. All parameters are time varying, except litter size (*LS*).

model parameters and the data-derived estimates for each submodel, weighted by the relative precision of each estimate. Although this method does not incorporate the raw data into the IPM likelihood, as is customary in traditional IPMs, sampling and process errors are fully propagated throughout the model, while maintaining adequate chain mixing. This allows for more rapid prototyping, evaluation of multiple process model structures, and decreased model convergence time (McCaffery and Lukacs, 2016; Moeller et al., 2021).

2.3. Independent-age survival

2.3.1. Independent-age survival data

We captured grizzly bears and deployed very-high frequency and Global Positioning System radio collars during 1983–2023 on independent-age ($\geq$2 yrs; subadult [2 yrs], adult [$>$2 yrs]) bears as part of a long-term research and monitoring program (Blanchard, 1985; Jonkel, 1993). We achieved a representative sample of the population by distributing capture efforts across the study area and considering sex, age class, and reproductive status of captured bears. We monitored radio-collared bears with telemetry flights every 7–14 days during April–November. We reduced telemetry flights to once per month during December–March when most bears were hibernating (Haroldson et al., 2002). We attempted to observe bears located during flights or conducted a site visit when a radio collar was stationary and emitted a mortality signal to confirm the status of the individual (i.e., alive, cast collar, or mortality). We censored individuals that were captured in a conflict setting but were not already monitored as a research individual at the time of conflict; including these individuals could bias vital rate estimates (Schwartz et al., 2006).

Capture and handling procedures conformed to the Animal Welfare Act and to U.S. Government principles for the use and care of vertebrate animals used in testing, research, and training (U.S. Geological Survey ACUC no. 2021.1). We captured grizzly bears under U.S. Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40(b)], with additional research permits from Idaho, Montana, and Wyoming state wildlife agencies and the National Park Service for Grand Teton and Yellowstone National Parks.

2.3.2. Independent-age survival submodel

We used a nest survival (NS) style model to estimate monthly (m) survival (ϕ) for an individual (i) by age class (j: subadult [S] and adult [A]) and sex (k: female [F] and male [M]), where $y_{i,m}$ was the observed state (alive or dead) of individual i in month m. We augmented data for individuals with unresolved fates by assigning a fate (alive or dead) using the estimated mean monthly age- and sex-specific survival rate (Walsh et al., 2015). In estimating mean survival by age class and sex ($s_m^{j,k}$) on the logit scale, we included a random effect for year ($\varepsilon_t^{NS,j,k}$), assuming monthly survival rates were more similar among months within the same year than within the same month across years. For priors, we specified a normal (4, 1) distribution for the intercept ($s_m^{j,k}$) with a logit link. We hierarchically centered the random effect and specified a vague prior using a normal distribution, with a mean of zero and a vague uniform (0, 100) for the standard deviation hyper-parameter within the nest survival style model ($\sigma^{NS,j,k}$):

$$y_{i,m} \sim Bernoulli\left(\phi_m^{j,k}\right), \tag{1}$$

$$logit\left(\phi_m^{j,k}\right) = s_m^{j,k} + \varepsilon_t^{NS,j,k}, \tag{2}$$

$$\text{and } \varepsilon_t^{NS,j,k} \sim Normal\left(0,\ \left(\sigma^{NS,j,k}\right)^2\right). \tag{3}$$

We derived annual survival ($\nu_t^{j,k}$) by multiplying monthly age- and sex-specific survival rates. We entered these estimates as data into an observation model for annual survival by age class and sex ($S_t^{j,k}$) and its standard deviation within the IPM. We estimated mean annual survival by age class and sex ($\Theta_t^{j,k}$) on the logit scale using a normal distribution while including a random effect for year ($\varepsilon_t^{IPM,j,k}$), which we sampled from a normal distribution:

$$\nu_t^{j,k} \sim Normal\left(S_t^{j,k},\ SE(\nu_t^{j,k})\right), \tag{4}$$

$$logit\left(S_t^{j,k}\right) = \Theta_t^{j,k} + \varepsilon_t^{IPM,j,k}, \tag{5}$$

$$\text{and } \varepsilon_t^{IPM,j,k} \sim Normal\left(0,\ \left(\sigma_t^{IPM,j,k}\right)^2\right). \tag{6}$$

We specified informed priors for the intercept with a logit link, using a normal distribution for mean survival by age class ($\Theta_t^{j,k}$). The inverse logit of these values translated into a mean survival probability of 0.90 for adults and 0.88 for subadults using a standard deviation of 0.32 for both age classes (Schwartz et al., 2006). For the random effect, we specified a vague prior using a normal distribution, with a mean of zero and a vague uniform (0, 50) for the standard deviation hyper-parameter within the IPM ($\sigma_t^{IPM,j,k}$).

2.4. Reproduction

2.4.1. Reproduction data

During telemetry flights, we attempted to observe radio-collared females to determine their reproductive status and, if offspring were present, their age class (cubs, yearlings, or older offspring) and number of young.

2.4.2. Reproductive transition probability

We estimated the probability an adult female transitioned between reproductive states given her reproductive status the previous year (Schwartz and White, 2008). We assumed four reproductive states (N = alone, C = with cubs, Y = with yearlings, and T = with two-year-olds) leading to 16 transition probabilities. Six transitions are biologically impossible (N-Y, N-T, C-T, Y-Y, T-Y, T-T), which we fixed to a probability of zero. Because the transition from a single reproductive state to all other states must sum to one, we estimated six transition probabilities (N-C, C-C, C-Y, Y-C, Y-T, T-C) and derived the remaining four (N-N, C-N, Y-N, T-N) by subtraction. We used a categorical likelihood to analyze the transition probability data. Specifically,

$$y_{i,t+1}^{TP} \sim Categorical(\pi_{l,t}), \tag{7}$$

$$logit(\pi_{l,t}) = \beta 0_{l,t} + \varepsilon_{l,t}^{TP}, \tag{8}$$

$$\text{and} \quad \varepsilon_{l,t}^{TP} \sim Multivariate\ Normal\ (0_{1:t}, \Omega), \tag{9}$$

where $\pi_{l,t}$ is a probability matrix representing the probability of transitioning from a reproductive state l in year t to the observed reproductive state in $t+1$. The intercept ($\beta 0_{l,t}$) represents the mean probability for one of the six estimated transition probabilities (l) in year t on the logit scale and $\varepsilon_{l,t}^{TP}$ represents a random effect on year for one of the six estimated transition probabilities, which we sampled from a multivariate normal distribution. We made a biological assumption that transition probability varied over time, deviating from Schwartz and White (2008) who assumed transition probabilities reached a stable state distribution. We specified vague priors for $\beta 0_{l,t}$ using a normal distribution (0, 0.01). For the random effect, we used a multivariate normal distribution with a mean of zero and a variance-covariance matrix drawn from a Wishart distribution with seven degrees of freedom. We conducted an eigen analysis using the posterior of the MCMC run to derive the proportion of adult females with cubs (P^{Fcub}).

2.5. Count data

2.5.1. Count data – females with cubs, Chao2

We annually collected observations of females with cubs through 31 August based on systematic aerial surveys and opportunistic aerial and ground-based sightings. We distributed effort for systematic aerial surveys by using bear observation areas (BOAs) initially covering the recovery zone, with units added over time to accommodate expansion of occupied range (van Manen et al., 2014). Following a ruleset developed by Knight et al. (1995), evaluated by Schwartz et al. (2008), and updated by van Manen et al. (2022), we enumerated sighting frequencies for unique family groups based on the distance between sightings, dates of sightings, and litter size. We deemed sightings ≥16 km apart as unique family groups. Sightings <16 km apart were parsed into unique sightings if family groups were observed at different locations but similar times, if one or both females were radiocollared, or if litter sizes were different (Knight et al., 1995; van Manen et al., 2022). Because of imperfect detection, we accounted for individual sighting heterogeneity of unique family groups by entering their sighting frequencies into a nonparametric, bias-corrected estimator based on Chao (1989) to enumerate the total number of females with cubs in the demographic monitoring area ($Chao2_t$):

$$Chao2_t = m + \frac{(f_1^2 - f_1)}{2(f_2 + 1)}, \tag{10}$$

where in year t, m is the count of unique females with cubs and f_1 and f_2 represent the number of unique females with cubs sighted once and twice, respectively (Cherry et al., 2007; Keating et al., 2002). We used Chao2 estimates since 1997 as inputs to the IPM, reflecting the period during which data collections were most consistent (van Manen et al., 2022).

2.5.2. Count data – females with cubs, mark-resight

Higgs et al. (2013) developed a mark-resight model to estimate the number of females with cubs, while accounting for a limited number of radio-collared females and low resight probability. They assumed homogeneity in sighting probabilities over 16 years (1997–2012) of aerial surveys and modeled counts of marked and unmarked females with cubs as multinomial random variables, using the capture frequencies of marked females with cubs for inference regarding the latent multinomial frequencies for unmarked females with cubs. This framework provides an unbiased estimation of the number of female with cubs in the population and another source of count data for the IPM, albeit with relatively high variance (Higgs et al., 2013). We collected mark-resight data on females with cubs from biannual systematic observation flights conducted from late May through 31 August during 2001–2019. During a survey, we recorded all observed bears, documented the composition of family groups, and checked whether individuals were radiocollared (i.e., marked) using telemetry.

The mark-resight framework assumes that the geographic distribution of radio-collared females with cubs is representative of the distribution and density of the female with cubs population. In the southeastern portion of the ecosystem grizzly bears congregate on

alpine scree slopes from mid-July to late September to feed on army cutworm moths (Mattson et al., 1991). These congregations result in higher visibility and counts of individuals relative to the rest of the ecosystem, but because the remoteness and ruggedness of this region limits field sampling, radio-collared females are underrepresented. Because these moth sites are well-defined, we excluded observations of females with cubs <500 m from moth sites from the mark-resight analysis to reduce overestimation bias.

2.5.3. Count data – independent-age mortalities

We incorporated count data for independent-age population segments by documenting independent-age mortalities. We classified mortalities (1983–2023) based on their degree of certainty (Craighead et al., 1988). We classified management removals and observed or physically inspected carcasses as "known" mortalities. When evidence suggested a mortality had occurred, but no carcass was recovered, we classified the event as a "probable" mortality. We used both classifications in our analyses. Whereas radio-collared individuals should provide an accurate representation of survival, a portion of non-agency, human-caused mortalities are unreported and undocumented if the bear was not radiocollared at time of death, resulting in mortality estimates that are biased low (Cherry et al., 2002). We mediated this source of bias by estimating the number of reported and unreported mortalities of independent-age bears similar to Cherry et al. (2002):

$$Radio^{\text{reported}} \sim Binomial\left(Report^{\text{rate}},\ Radio^{\text{total}}\right). \tag{11}$$

Here, we used the number of radio-collared bear mortalities reported ($Radio^{\text{reported}}$) rather than discovered using telemetry, and the total number of radio-collared bears ($Radio^{\text{total}}$) to estimate the probability of a human-caused mortality being reported ($Report^{\text{rate}}$), excluding agency removals. We specified a vague conjugate prior for $Report^{\text{rate}}$ using a beta distribution ($\alpha = 1$, $\beta = 1$):

$$M_t^{\text{reported},j} \sim Binomial\left(Report^{\text{rate}},\ M_t^{\text{RU},j}\right), \tag{12}$$

$$M_t^{\text{RU},j} \sim Poisson\left(\mu^{\text{mort},j}\right), \tag{13}$$

$$\text{and } \mu^{\text{mort},j} = \frac{\rho}{Report^{\text{rate}}}. \tag{14}$$

We used the posterior distribution for $Report^{\text{rate}}$ in Eq. 11 as a prior for $Report^{\text{rate}}$ in Eq. 12 when estimating the number of reported and unreported mortalities ($M_t^{\text{RU},j}$) by sex j based on the observed number of reported mortalities ($M_t^{\text{reported},j}$) by sex j in year t. We specified an informed prior for $M_t^{\text{RU},j}$ using a Poisson distribution ($\mu^{\text{mort},j}$), where $\mu^{\text{mort},j}$ was derived by dividing ρ by $Report^{\text{rate}}$. We specified a vague uniform prior for ρ (1, 200). After fitting the model, we split estimated number of reported and unreported mortalities by sex and independent-age class based on the proportion of known mortalities by sex and independent-age class in year t.

2.6. Integrated population model

2.6.1. Biological process model

We structured the IPM by sex and age class to account for differences in survival and reproduction among cohorts (Figs. 2 and 3). On 1 January in year t, we classified individuals as cubs (0–1 yr; denoted by C), yearlings (1–2 yr; Y), subadults (2–3 yr; S), and adults ($\geq$3 yr, A) for female and male bears. Although female grizzly bears in the population typically first mate at age four and give birth at age five, 9.8–12.6 % of females mate at age three and give birth at age four (Schwartz et al., 2006; Schwartz and White, 2008). Thus, we classified all bears three years or older as adults.

We used a post-breeding transition matrix model (Caswell, 2001) to represent the stage-structured population dynamics:
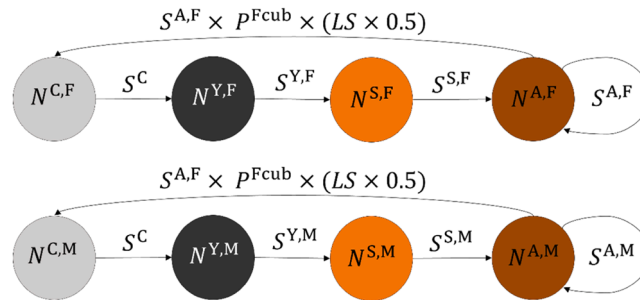

Fig. 3. Stage-structure life-cycle diagram for females (F, top panel) and males (M, bottom panel) serving as the basis for an integrated population model of grizzly bears in the Greater Yellowstone Ecosystem, USA. Nodes represent the abundance of age classes (C = cub [0–1 yr], Y =yearling [1–2 yrs], S = subadult [2–3 yrs], A = Adult [$\geq$3 yrs]), whereas transitions between nodes represent age-class specific survival (S) rates. Reproduction is the product of adult female survival ($S^{\text{A,F}}$), the proportion of adult females with cubs (P^{Fcub}), and litter size (LS), assuming an equal sex ratio at birth (0.5). All rates and parameters are time varying except litter size (LS).

$$\begin{bmatrix} N^{\text{C,F}} \\ N^{\text{C,M}} \\ N^{\text{Y,F}} \\ N^{\text{Y,M}} \\ N^{\text{S,F}} \\ N^{\text{S,M}} \\ N^{\text{A,F}} \\ N^{\text{A,M}} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & S^{\text{A,F}} \times P^{\text{Fcub}} \times (LS \times 0.5) & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S^{\text{A,F}} \times P^{\text{Fcub}} \times (LS \times 0.5) & 0 \\ S^{\text{C}} & S^{\text{C}} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S^{\text{Y,F}} & S^{\text{Y,M}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S^{\text{S,F}} & S^{\text{S,M}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S^{\text{A,F}} & S^{\text{A,M}} \end{bmatrix}_t \times \begin{bmatrix} N^{\text{C,F}} \\ N^{\text{C,M}} \\ N^{\text{Y,F}} \\ N^{\text{Y,M}} \\ N^{\text{S,F}} \\ N^{\text{S,M}} \\ N^{\text{A,F}} \\ N^{\text{A,M}} \end{bmatrix}_t \tag{15}$$

Parameters S^{C}, $S^{\text{Y,F}}$, $S^{\text{Y,M}}$, $S^{\text{S,F}}$, $S^{\text{S,M}}$, $S^{\text{A,F}}$, and $S^{\text{A,M}}$ are age- and sex-specific (except for cubs) survival rates; P^{Fcub} is the proportion of adult females with cubs; LS is litter size; and $N^{\text{C,F}}$, $N^{\text{C,M}}$, $N^{\text{Y,F}}$, $N^{\text{Y,M}}$, $N^{\text{S,F}}$, $N^{\text{S,M}}$, $N^{\text{A,F}}$, $N^{\text{A,M}}$ are cohort-specific abundance (N) estimates. Litter size was an estimated latent parameter drawn from an informed prior ($2.49/3 = 0.83$, annualization of a three-year reproductive cycle; Interagency Grizzly Bear Study Team, 2012) using a gamma $\left(\frac{0.83^2}{0.25}, \frac{1}{\frac{0.25}{0.83}}\right)$ distribution and represents female and male births combined. A latent parameter is estimated in the absence of direct data (i.e., unobserved) using inference from directly estimated parameters. Cub and yearling survival were also estimated latent parameters. We specified informed priors for cub and yearling survival, like independent-age survival, using normal distributions. The inverse logit of these values translated into a mean survival probability of 0.55 for cubs and 0.64 for yearlings using a standard deviation of 0.32 for both age classes (Schwartz et al., 2006). We assumed equal annual survival rates for female and male cubs.

We derived abundance of cohorts in year $t+1$ as a function of individuals that survived and entered their winter den in year t. We modeled transitions among cohorts and years stochastically as a normal approximation of a binomial distribution. The priors for these transitions were informative and taken from previous studies of age-specific survival (Schwartz et al., 2006). Annual process variance was incorporated using a random effect for year within the linear predictor of survival for each transition. We specified the random effect using a normal distribution centered on 0 with a standard deviation described by a uniform (0, 50) distribution:

$$N^{\text{Y,k}}_{t+1} \sim Normal\left(N^{\text{C,k}}_t \times S^{\text{C,k}}_t, \ N^{\text{C,k}}_t \times S^{\text{C}}_t \times \left(1 - S^{\text{C}}_t\right)\right), \tag{16}$$

$$N^{\text{S,k}}_{t+1} \sim Normal\left(N^{\text{Y,k}}_t \times S^{\text{Y,k}}_t, \ N^{\text{Y,k}}_t \times S^{\text{Y,k}}_t \times \left(1 - S^{\text{Y,k}}_t\right)\right), \tag{17}$$

$$N^{\text{A,k}}_{t+1} \sim Normal\left(\left(N^{\text{A,k}}_t + N^{\text{S,k}}_t\right) \times S^{\text{A,k}}_t, \ \left(N^{\text{A,k}}_t + N^{\text{S,k}}_t\right) \times S^{\text{A,k}}_t \times \left(1 - S^{\text{A,k}}_t\right)\right). \tag{18}$$

We modeled cub abundance in year $t+1$ stochastically as a function of the number of adult females that produced cubs (N^{Fcub}) multiplied by LS, while accounting for sex of the modeled cohort ($LS \times 0.5$) and assuming an equal sex ratio at birth using a normal approximation of a Poisson distribution:

$$N^{\text{C,k}}_{t+1} \sim Normal\left(N^{\text{Fcub}}_{t+1} \times (LS \times 0.5), \ N^{\text{Fcub}}_t \times (LS \times 0.5)\right). \tag{19}$$

We derived N^{Fcub}_{t+1} by multiplying the number of adult females that survived to the end of year t by the proportion of adult females with cubs in year $t+1$, P^{Fcub}_{t+1}:

$$N^{\text{Fcub}}_{t+1} = N^{\text{AF}}_t \times P^{\text{Fcub}}_{t+1}, \tag{20}$$

$$logit\left(P^{\text{Fcub}}_{t+1}\right) = \mu^{\text{Pfcub}} + \varepsilon^{\text{Pfcub}}_{t+1}, \tag{21}$$

$$\varepsilon^{\text{Pfcub}}_{t+1} \sim Normal\left(0, \ \left(\sigma^{\text{Fcub}}\right)^2\right), \tag{22}$$

where μ^{Pfcub} is the mean proportion of adult females with cubs on the logit scale and $\varepsilon^{\text{Pfcub}}_t$ is a year random effect. We specified an informed prior for μ^{Pfcub} using a normal (-0.969, 277) distribution and a vague prior for σ^{Fcub} using a uniform (0, 50) distribution. We used a normal approximation for binomial and Poisson distributions to increase reliability and speed of model runs (Brooks et al., 2004). We assumed an initial population size of approximately 250 bears based on White et al. (2017) using a normal $\left(250, \frac{1}{(250 \times 10)}\right)$ distribution.

2.6.2. Observation model

We linked the count data (*Chao2*, *MR*, and M^{RU}) with cohorts in the process submodel using count-specific observation models that assume observation error. We specified a negative binomial model to link N^{Fcub}_t with Chao2-estimated (*Chao2$_t$*) number of females with cubs in year t under the assumption that *Chao2$_t$* estimates limit the risk of overestimation and, on average, slightly underestimated the number of females with cubs in the population, as documented in van Manen et al. (2022):

$$Chao2_t \sim NegativeBinomial(p_t, \ q), \tag{23}$$

$$p_t = \frac{q}{(q + N^{\text{Fcub}}_t)}, \tag{24}$$

where p_t is the probability of success and q controls the amount of extra dispersion in the observed count of adult female bears with cubs. We chose a vague uniform (0, 1500) prior for q. We also specified an observation model to link the N_t^{Fcub} to the mark-resight estimated number of females with cubs (MR_t) in year t as:

$$MR_t \sim Normal\left(N_t^{\text{Fcub}}, \left(\sigma_t^{MR}\right)^2\right), \tag{25}$$

where, $\left(\sigma_t^{MR}\right)^2$ is the sampling variance from the mark-resight estimate. The Chao2 estimates represent a longer time series but with slight underestimation bias and inherent temporal variation (van Manen et al., 2022), whereas mark-resight estimates have high accuracy but are for a shorter period and with relatively low precision (Higgs et al., 2013). Combining both sources of count data in the IPM helps reconcile the different strengths and weaknesses of the count data with the other demographic estimates. Finally, we used a binomial model to link sex- and age class-specific abundance ($N_{t,\text{spring}}^{\text{j,k}}$) at the start of year t and survival in year t with the estimated number of reported and unreported mortalities ($M_t^{\text{RU,j,k}}$) by sex and independent-age class:

$$M_t^{\text{RU}},\text{k} \sim Binomial\left(1 - S_t^{\text{j,k}}, N_{t,\text{spring}}^{\text{j,k}}\right), \tag{26}$$

where $1 - S_t^{\text{j,k}}$ represents the estimated cohort-specific mortality rates.

2.7. Model fitting

We fit the survival submodel and the IPM in program R 4.2.1 (R Core Team, 2023) using rjags 4.13 (Plummer, 2022). For both, we ran three chains of 105,000 iterations and discarded the first 50,000 MCMC samples as burn-in. We fit the independent-age mortality model in program R 4.3.0 (R Core Team, 2023) using jagsUI 1.5.2 (Kellner, 2021). We ran three chains of 220,000 iterations and discarded the first 20,000 MCMC samples as burn-in. We conducted the mark-resight analyses using OpenBUGS code provided in Higgs et al. (2013). We ran three chains of 2000,001 iterations, discarded the first 5000 MCMC samples as burn-in, and thinned by 10. For all models, we considered convergence if the Gelman-Rubin $\widehat{R}$ statistic was < 1.1 (Gelman and Hill, 2007), we attained sufficient effective samples, and if the chains were mixed well after visually inspecting and checking for smooth unimodal posteriors. We estimated standard errors, 95 % credible intervals, and 50 % interquartile ranges based on posterior distributions.

Table 1
Summary and trend information for estimated parameters by decade for different sex (male, female) and age classes (cub [0–1 yr], yearling [1–2 yrs], subadult [2–3 yrs], and adult [≥3 yrs]) of grizzly bears in the Greater Yellowstone Ecosystem, USA, based on 1983–2023 data. A) Posterior summary of the estimated mean of a parameter over the specified decade. B) Comprehensive characterization of trends identified within the data using a two-pronged approach. The first metric, designated as "directional change," quantifies the average annual change of each parameter over the specified decade based on a geometric mean. The second metric, labeled "increase vs. decrease tendency," quantifies the parameter's propensity for positive or negative change. This latter value can be interpreted probabilistically; for example, a value of 0.80 for increase and 0.20 for decrease indicates that the model estimates an 80 % likelihood of a positive tendency relative to a 20 % likelihood of a negative tendency. Conversely, a value of 0.50 for both increase and decrease signifies a state of uncertainty around the estimate and indicates the trend is not meaningful. Through the combined analyses of "directional change" and "increase vs. decrease tendency," a more nuanced understanding of identified trends is achieved.

Parameter	Decade				
	1980s[a]	1990s	2000s	2010s	2020 s[a]
A. Posterior summary: mean (50 % interquartile range)					
Survival[b]					
Adult female	0.95 (0.95–0.96)	0.95 (0.95–0.96)	0.95 (0.94–0.96)	0.95 (0.95–0.96)	0.96 (0.95–0.96)
Adult male	0.94 (0.93–0.95)	0.94 (0.94–0.95)	0.94 (0.93–0.95)	0.94 (0.93–0.94)	0.94 (0.94–0.95)
Subadult female	0.95 (0.94–0.95)	0.95 (0.94–0.95)	0.95 (0.94–0.95)	0.95 (0.94–0.95)	0.95 (0.94–0.95)
Subadult male	0.93 (0.92–0.94)	0.93 (0.92–0.94)	0.93 (0.92–0.94)	0.93 (0.92–0.94)	0.93 (0.92–0.94)
Yearling female	0.57 (0.42–0.72)	0.62 (0.50–0.79)	0.55 (0.40–0.69)	0.53 (0.38–0.67)	0.57 (0.44–0.71)
Yearling male	0.67 (0.52–0.80)	0.71 (0.60–0.85)	0.65 (0.50–0.77)	0.63 (0.47–0.74)	0.67 (0.55–0.79)
Cub female/male	0.52 (0.42–0.62)	0.54 (0.45–0.66)	0.51 (0.41–0.60)	0.50 (0.40–0.59)	0.52 (0.43–0.62)
Population growth rate	1.023 (0.993–1.082)	1.064 (1.023–1.103)	1.030 (0.989–1.068)	1.021 (0.985–1.057)	1.034 (1.001–1.067)
B. Trend: directional change; increase vs. decrease tendency					
Survival					
Adult female	0.001; 0.86 vs. 0.14	0.001; 0.84 vs. 0.16	0.002; 1.00 vs. 0.00	0.001; 0.95 vs. 0.05	0.001; 0.62 vs. 0.38
Adult male	0.002; 0.85 vs. 0.15	0.001; 0.84 vs. 0.16	0.003; 1.00 vs. 0.00	0.001; 0.95 vs. 0.05	0.001; 0.62 vs. 0.38
Subadult female	0.000; 0.51 vs. 0.49	0.000; 0.57 vs. 0.43	0.000; 0.64 vs. 0.36	0.000; 0.49 vs. 0.51	0.001; 0.58 vs. 0.42
Subadult male	0.000; 0.51 vs. 0.49	0.000; 0.57 vs. 0.43	0.000; 0.65 vs. 0.35	0.000; 0.48 vs. 0.52	0.001; 0.59 vs. 0.41
Yearling female	0.053; 0.62 vs. 0.38	0.060; 0.85 vs. 0.15	0.011; 0.49 vs. 0.51	0.095; 0.90 vs. 0.10	0.003; 0.52 vs. 0.48
Yearling male	0.044; 0.67 vs. 0.33	0.050; 0.89 vs. 0.11	0.011; 0.53 vs. 0.47	0.080; 0.92 vs. 0.08	−0.007; 0.55 vs. 0.45
Cub female/male	−0.005; 0.44 vs. 0.56	−0.011; 0.42 vs. 0.58	−0.039; 0.22 vs. 0.78	0.017; 0.64 vs. 0.36	0.010; 0.50 vs. 0.50
Population growth rate	0.007; 0.75 vs. 0.25	−0.001; 0.49 vs. 0.51	−0.003; 0.28 vs. 0.72	0.003; 0.75 vs. 0.25	0.003; 0.56 vs. 0.44

[a] Data from 1983–1989 and 2020–2023 inform the 1980s and 2020s decadal estimates, respectively.
[b] Survival estimates were rounded to two digits, resulting in the median matching the lower or upper credible limit for estimates with narrow credible intervals.

3. Results

3.1. Captures and individuals

We captured, radiocollared, and monitored under a research status 192 female (adult: 160, subadult: 32) and 332 male (adult: 288, subadult: 44) bears based on age at first capture, constituting 719 female (adult: 587, subadult: 132) and 863 male (adult: 725, subadult: 138) bear years. From our radio-collared sample of adult females, we observed 155 females with cubs, 111 females with yearlings, and 43 females with two-year-olds, representing 226, 135, and 52 bear years, respectively. We documented 99 female (adult: 91, subadult: 8) and 135 male (adult: 113, subadult: 22) mortalities of independent-age bears monitored under research status.

3.2. Demographic rates

The median proportion of adult females with cubs ranged from 0.29 (95 % credible interval = 0.26–0.31) to 0.30 (0.28–0.32) and median litter size was 2.34 (1.85–2.86) cubs. For both sexes, annual survival rates over the study period were highest for adults (range: females = 0.93 [0.91–0.95] to 0.96 [0.95–0.97], males = 0.92 [0.89–0.93] to 0.95 [0.93–0.96]), followed by subadults (females = 0.94 [0.92–0.96] to 0.95 [0.93–0.96], males = 0.93 [0.91–0.95]; no variation observed at this level of precision), yearlings (females = 0.42 [0.03–0.85] to 0.71 [0.41–0.99], males = 0.52 [0.05–0.90] to 0.79 [0.52–1.00]), and cubs (females and males = 0.44 [0.07–0.76] to 0.61 [0.39–0.97]). Estimated adult and subadult survival rates fluctuated little over the four decades, with slightly higher median annual survival for females than males. Annual survival rates for cubs and yearlings fluctuated substantially, increasing during the 1980s and into the 1990s before peaking in the late 1990s and declining throughout the 2000s. Survival rates for cubs and yearlings increased slightly during the 2010s before plateauing in the 2020s (Table 1; Fig. 4).

### 3.3. Abundance and population growth

Abundance increased from 270 (95 % credible interval = 206–344) bears in the year 1984 to 1030 (865–1230) bears in 2023 (Fig. 5). The proportion of adults in the population increased over the 40-year period from 0.29 to 0.37 for females and from 0.16 to 0.31 for males. The proportion of subadults ranged from 0.01 to 0.08 for females and from 0.02 to 0.05 for males, whereas the proportion of yearlings ranged from 0.01 to 0.05 for females and 0.02 to 0.05 for males. Cub proportions ranged from 0.04 to 0.08 for both sexes combined. The sex ratio (males:females; all bears) increased from 0.54:1.00 in 1983 to 1.02:1.00 in 2023 (Table 1; Fig. 6).
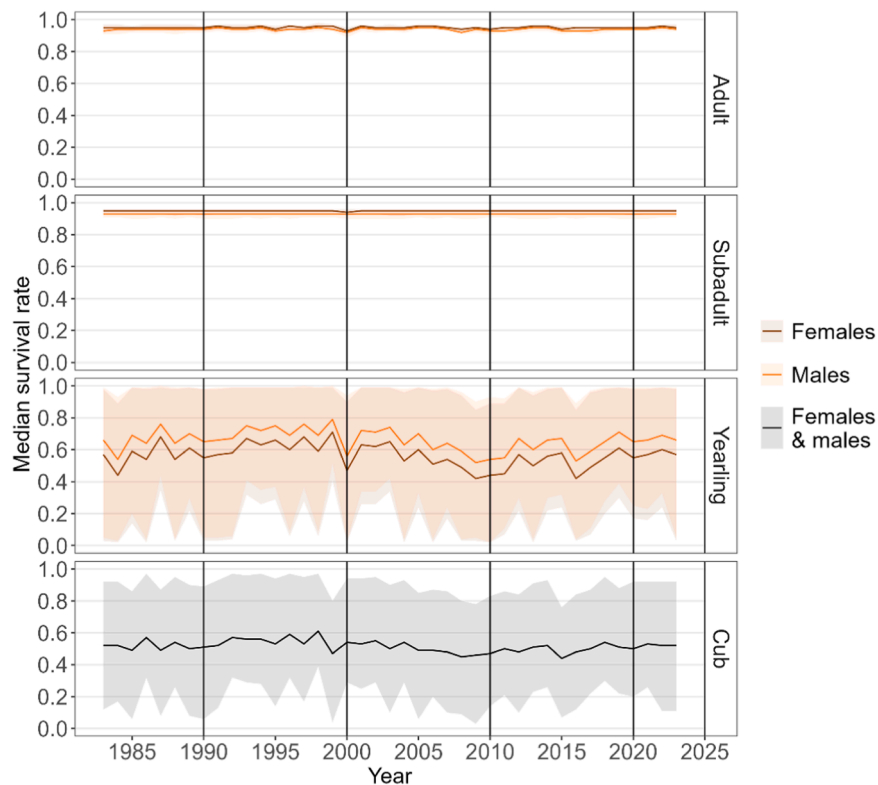
Fig. 4. Median survival rates (solid line = median, ribbon = 95 % credible interval) by sex and age class (cub [0–1 yr], yearling [1–2 yrs], subadult [2–3 yrs], adult [≥3 yrs]) for grizzly bears in the Greater Yellowstone Ecosystem, USA, based on 1983–2023 data.
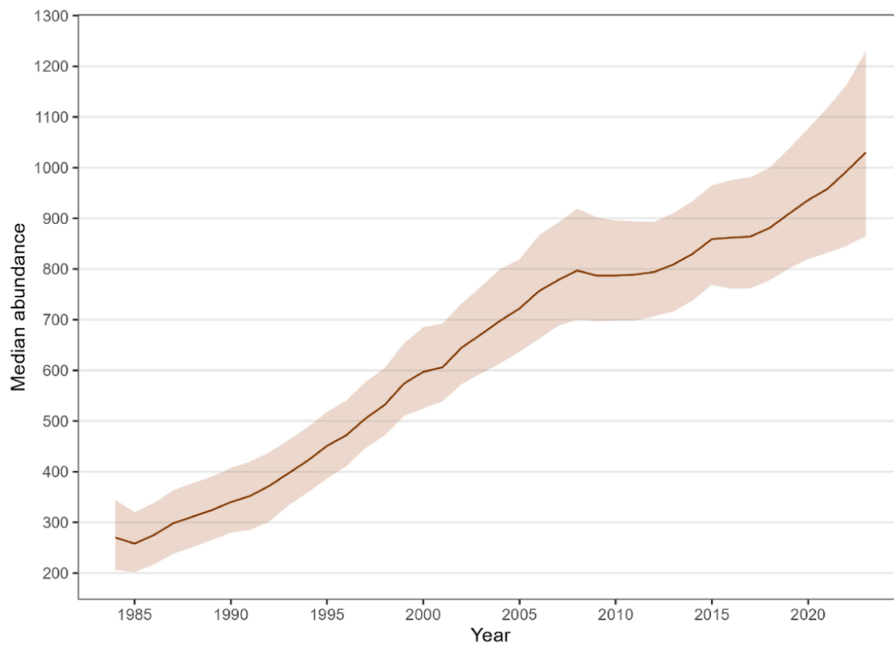
Fig. 5. Total abundance at den emergence (solid line = median, ribbon = 95 % credible interval) for grizzly bears in the Greater Yellowstone Ecosystem, USA, based on 1983–2023 data.
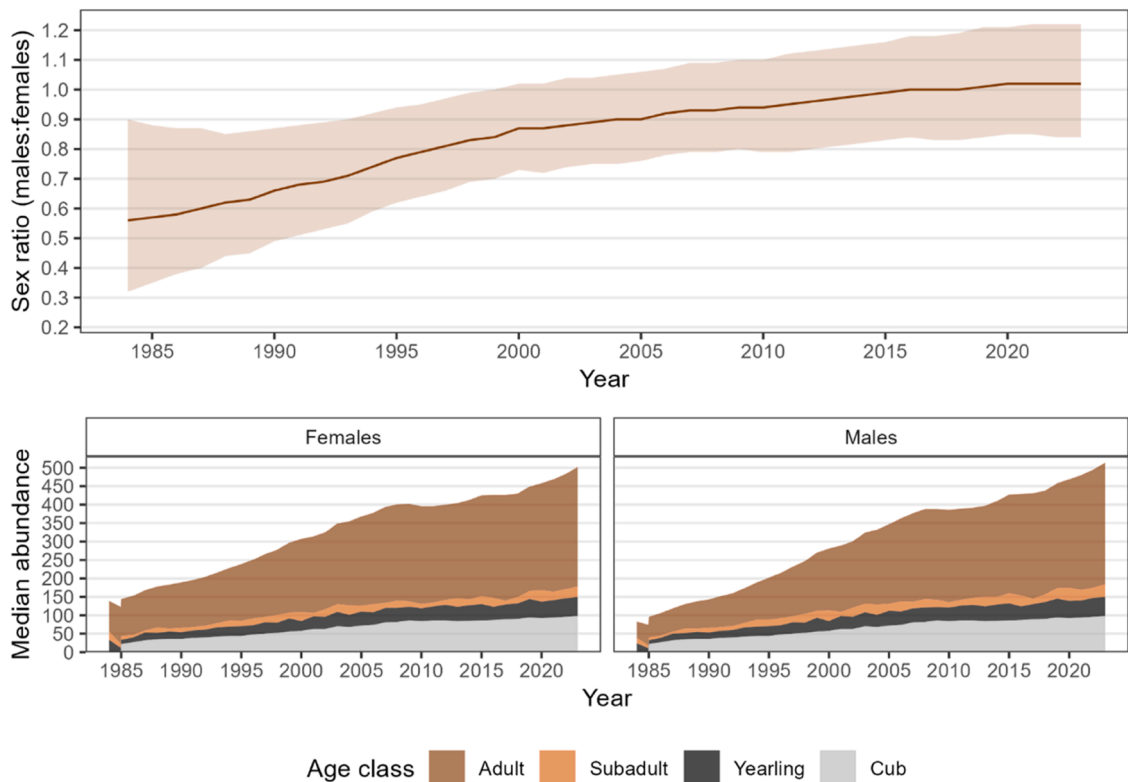

Fig. 6. Sex ratio (top panel; solid line = median, ribbon = 95 % credible interval) and median abundance (bottom panels) at den emergence by sex and age class (cub [0–1 yr], yearling [1–2 yrs], subadult [2–3 yrs], adult [≥3 yrs]) of grizzly bears in the Greater Yellowstone Ecosystem, USA, based on 1983–2023 data.

The median of mean annual λ was 1.023 (50 % interquartile range = 0.993–1.082) during the 1980s and increased to 1.064 (1.023–1.103) during the 1990s before slowing throughout the 2000s (λ = 1.030 [0.989–1.068]) and 2010s (λ = 1.021 [0.985–1.057]; Fig. 7). Since 2006, λ has oscillated around an annual mean of 1.022 (0.986–1.057).

4. Discussion

The IPM provides a flexible analysis framework that incorporates multiple data sources to estimate vital rates and abundance of grizzly bears in the Greater Yellowstone Ecosystem over four decades. The estimated proportion of females with cubs (range = 0.29–0.30) was similar to those previously reported for the population (0.29 for 1983–2003; Schwartz and White, 2008). Estimated median litter size was slightly higher than previous estimates of 2.04 (Schwartz et al., 2006) and 2.12 (Interagency Grizzly Bear Study Team, 2012). However, within the IPM framework litter size reflects the number of cubs born, whereas those previous estimates were based on first observation of litters and did not explicitly account for cub mortality prior to first observations, as has been documented for other brown bear populations (Schöll et al., 2024). Median litter size is similar to estimates reported for other grizzly bear populations in North America (range = 1.40–2.40; Haroldson et al., 2021). Annual survival estimates for adults and subadults were high and relatively constant, with female survival slightly higher than that of males for both age classes, comparable to previous estimates (Schwartz et al., 2006). Estimates of adult female survival were very similar to rates reported by Eberhardt (2002) for many other long-lived vertebrates, including several grizzly bear populations. High survival rates of independent-age males relative to other grizzly bear populations in North America, but similar to unhunted populations, likely reflect the protected status of the population (Keay et al., 2018; Sellers and Aumiller, 1994). Survival rates for cubs and yearlings started to decline in the late 1990s (probability of decreasing trend, 1998–2010: cubs = 0.88; yearling females = 0.76; yearling males = 0.72), and reflected patterns observed in Schwartz et al. (2006) and Interagency Grizzly Bear Study Team (2012). Although there is evidence in recent years (2011–2023) that cub and yearling survival has leveled off or increased slightly, respectively (probability of increasing trend: cubs = 0.54; yearling females = 0.73; yearling males = 0.74), survival rates of cubs and yearlings in this population are among the lowest reported estimates in North America (Haroldson et al., 2021).

Population growth has slowed concurrently with lower cub and yearling survival since the early 2000s. Slowing population growth during 2002–2011 relative to 1983–2001 was previously identified (Interagency Grizzly Bear Study Team, 2012), leading to further studies into possible factors contributing to this pattern. Increasing bear density or the decline of whitebark pine, a high-calorie food source in autumn, were investigated as possible drivers; an index of grizzly bear density, not whitebark pine mortality, was negatively associated with cub survival and, to a lesser degree, reproduction (van Manen et al., 2016). The slowing of population growth due to intrinsic rather than extrinsic factors was further supported by Corradini et al. (2023), who observed that individual lean body mass was negatively associated with population density, particularly for younger, growing-age females. Immature females are more likely to experience impacts from intra-specific competition with dominant bears for high-energy foods (Costello et al., 2016). Yet, population
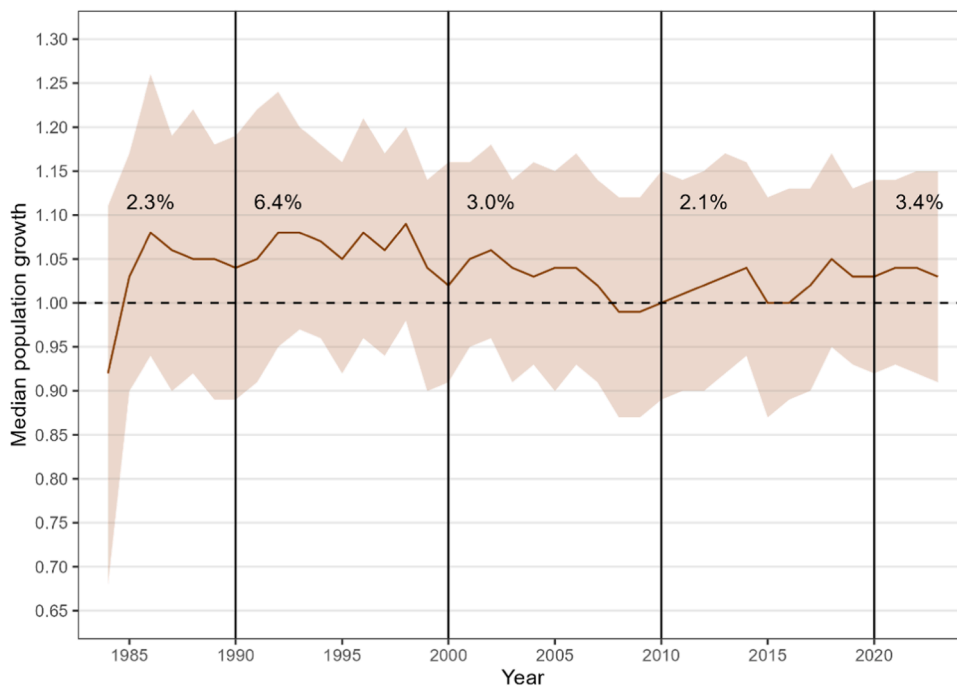
Fig. 7. Finite rate of annual population growth (solid line = median, ribbon = 95 % credible interval) and mean percent population growth rate (%) by decade (vertical lines) for grizzly bears in the Greater Yellowstone Ecosystem, USA, based on 1983–2023 data.

density did not have an association with body fat levels or the rate of seasonal body fat gain, suggesting sufficient food resources available to grizzly bears (Corradini et al., 2023). Combined, these studies provide evidence of an increasing role of intrinsic (i.e., grizzly bear density) rather than extrinsic factors on population demographics beginning around the year 2000. With high male survival, the population has trended towards an equal sex ratio. Because adult males are responsible for the majority of conspecific killings, and cubs in particular (McLellan, 1994; Steyaert et al., 2012), this supports the hypothesis that lower cub survival is associated with greater densities of males (van Manen et al., 2016). As predicted in van Manen et al. (2016) and following a predictable pattern for long-lived vertebrates (Caughley, 1970; Eberhardt, 2002), the slowing of population growth appears to have transitioned into an oscillating pattern around a long-term mean λ of 1.022 (50 % interquartile range = 0.986–1.057) starting around 2006. Caughley's (1970) study of Himalayan tahr (*Hemitragus jemlahicus*) revealed a similar sequence of growth patterns. Further supporting this interpretation, the probability of increasing or decreasing trend in λ over this period was 0.48 and 0.52, respectively. Estimates of total abundance for this period of relative stability (i.e., 2006–2023) ranged from 756 to 1030. The changes we documented in the population trajectory over four decades are to be expected in any previously suppressed wildlife population that recovers and re-occupies habitat areas; human activities limit where grizzly bears can be sustained on the landscape, which ultimately imposes constraints on population expansion and growth (Schwartz et al., 2010). Because density-dependent effects likely play a lesser role in peripheral areas of the demographic monitoring area (Interagency Grizzly Bear Study Team, 2012), overall population growth has remained positive. Annual estimates of λ are well below the theoretical maximum annual growth rate of $\lambda = 1.182$ for this population, as calculated based on the 2-stage version of Cole's equation (Cole, 1954; Hone et al., 2010). Maximum growth rates are rarely reached (Hone, 1999; Sinclair, 1997) and our estimates and trends of λ reflect the dynamic effects of extrinsic and intrinsic constraints on demographic parameters, and ultimately population growth.

We note that despite obvious growth of the population based on the trend in total abundance, lower 95 % credible intervals associated with estimates of λ bound 1.0. This uncertainty is primarily a function of the life history of grizzly bears, their low densities, and the logistical difficulties of studying them. Consequently, scientific quantification of trend will almost always result in the lower portion of the posterior distribution of lambda overlapping 1.0, even for a healthy population (Schwartz et al., 2006:62). Two potential scenarios could enhance statistical assessment: either λ is so high that the lower bound of the credible interval is above 1.0, or the interval is substantially narrowed. However, grizzly bears have extremely slow life histories and the maximum rate of population increase is modest, even for populations with robust demographic rates (maximum estimated $\lambda = 1.085$ for North American populations; Haroldson et al., 2021). Because of logistical constraints, obtaining sample sizes sufficiently large to narrow credible intervals for lambda would be cost prohibitive. Thus, estimates of λ alone are unlikely to yield documentation capable of rejecting a statistically plausible claim that the population has actually declined (Schwartz et al., 2006). We suggest managers instead consider the central tendencies of λ estimates (50 % interquartile range) and associated likelihood of positive or negative directional change, as shown in Table 1. Examining those tendencies for λ across the decadal periods supports the interpretations outlined in the previous paragraph.

The ability to track a suite of demographic parameters for this grizzly bear population is a result of commitments made by Federal, State, and Tribal agencies to monitor grizzly bears and implement conservation strategies following Endangered Species Act listing in 1975 (U.S. Fish and Wildlife Service, 1975). Changes in demographic parameters demonstrate the effectiveness of population and habitat management responses that were implemented, particularly after the formation of the Interagency Grizzly Bear Committee in 1983 (Strickland, 1990). The initial phase of population recovery was founded on implementation of science-based management and focused on reducing human-caused mortality, particularly among adult females (Knight and Eberhardt, 1984). The IPM data begin when implementation of those conservation actions just started to take effect: a population decline reversed in the mid-1980s, followed by robust population growth in the 1990s and continued, but slower, growth since the early 2000s. Concomitantly, occupied range increased by an average of 3.7 % per year, from 23,361 km^2 in 1990 to a range of 70,101 km^2 in 2022 (Dellinger et al., 2023). Combined with evidence of density-dependent mechanisms described previously, these data are indicative of biological recovery of grizzly bears in the Greater Yellowstone Ecosystem. These concerted conservation efforts played a crucial role in this recovery, but other factors contributed as well. Notably, the large, protected area at the core of the ecosystem (Yellowstone National Park and nearby wilderness areas) functioned as a refugium as the population reached its nadir (Pyare et al., 2004). Biological recovery was possible because enough adult females remained in that area to prevent the population spiraling towards extirpation, providing a basis for recovery once survival rates increased (Heppell et al., 2000). Subsequent collaborative efforts of agency, public, and private entities to protect vital habitats and reduce conflict potential between grizzly bears and humans were the key to the continued recovery and expansion of grizzly bears beyond the core recovery zone (Dellinger et al., 2023; Interagency Grizzly Bear Study Team, 2012; Lynch et al., 2008; Pyare et al., 2004). Proactive and reactive conservation efforts, coupled with extensive outreach and education campaigns, maintained and augmented public support for grizzly bears as they regained their former range. Recognizing the importance of protecting habitat and the ability to manage conflict is key to the long-term conservation and management of wide-ranging, large vertebrate species (Dickman, 2010; Leston et al., 2024).

As in any modeling framework, there are limitations and caveats to consider. In general, IPMs must adhere to submodel-specific assumptions, maintain independence among data sets, avoid over- or underfitting data, and accurately represent the ecology of the species (Schaub and Kéry, 2021). We mitigated these concerns by building the IPM upon a foundation of established modeling techniques and demographic analyses specific to this grizzly bear population (Cherry et al., 2002; Higgs et al., 2013; Interagency Grizzly Bear Study Team, 2012; Knight et al., 1995; Schwartz et al., 2006; Schwartz and White, 2008; van Manen et al., 2022). Dependency among data sets generally has a minor impact on parameter estimates, even in cases when dependency is strong (Abadi et al., 2010). Additionally, the inclusion of count data is paramount to the synergistic nature of IPMs through the sharing of information among data sets and parameters. The accuracy of parameter estimates is highly dependent on the quality of these count data. Inter-annual variation of the primary source of count data, adult females with cubs (*Chao*2), in the past has constrained population

monitoring (van Manen et al., 2022). However, through the state-space model, we were able to separate the true state process (number of females with cubs; N^{Fcub}) from the observation process; coupled with the self-reconciling properties of IPMs, this reduced the effects of inter-annual variation inherent in the *Chao*2 count data. The ability to include mortality data as a count source was also beneficial because it provided additional information on the realization of survival rates on abundance estimates. Cohort-specific mortality data enhanced inference of annual survival rates, particularly for less-represented cohorts such as subadult bears.

The IPM framework provides greater certainty and understanding regarding the dynamic demographic characteristics of the grizzly bear population and serves as a powerful monitoring tool to inform management decisions. It also highlights its efficacy in estimating and tracking the population dynamics of a long-lived species, despite shifts in monitoring techniques and interruptions in data collections; a common reality faced by long-term monitoring programs in support of wildlife conservation across the globe (Hostetler et al., 2021; Rolek et al., 2022). The modularity of IPMs allows users to assess spatial variation in demographic parameters, incorporate new techniques or data, and conduct simulations to evaluate population dynamics under different future conditions. Finally, IPMs can be used to assess the relative importance of different data sources and guide future data collections to enhance scientific inference and cost efficiency (Hostetler et al., 2021; Johnson et al., 2020).

5. Conclusions

Through implementation of the integrated population model (IPM), the demographic monitoring program for grizzly bears in the Greater Yellowstone Ecosystem provides resource managers with important annual updates on vital rates that influence population size and trend. Dissemination of timely information and inference is informing adaptive management strategies and policy decisions necessary for the continued conservation of this iconic population. An IPM-based monitoring system provides a versatile and powerful tool to investigate effects of changing ecosystems on population dynamics, incorporate new data sources and statistical models, and respond to changes in monitoring needs of wildlife populations.

Credit authorship contribution statement

All authors were involved in designing the research; JJN, HWM, and PML developed the IPM; MJG conducted the primary data analyses; MJG and FTvM wrote the paper; all authors reviewed and edited the paper.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Josh Nowak reports financial support was provided by U.S. Fish and Wildlife Service. the Interagency Grizzly Bear Committee, and National Park Service. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data in this study are available through the Interagency Grizzly Bear Study Team annual reports https://igbconline.org/grizzly-bear-study-team/

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