

RESEARCH ARTICLE

Evidence for density-dependent effects on body composition of a large omnivore in a changing Greater Yellowstone Ecosystem

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Abstract

Understanding the density-dependent processes that drive population demography in a changing world is critical in ecology, yet measuring performance–density relationships in long-lived mammalian species demands long-term data, limiting scientists' ability to observe such mechanisms. We tested performance–density relationships for an opportunistic omnivore, grizzly bears (*Ursus arctos*, Linnaeus, 1758) in the Greater Yellowstone Ecosystem, with estimates of body composition (lean body mass and percent body fat) serving as indicators of individual performance over two decades (2000–2020) during which time pronounced environmental changes have occurred. Several high-calorie foods for grizzly bears have mostly declined in recent decades (e.g., whitebark pine [*Pinus albicaulis*, Engelm, 1863]), while increasing human impacts from recreation, development, and long-term shifts in temperatures and precipitation are altering the ecosystem. We hypothesized that individual lean body mass declines as population density increases (H1), and that this effect would be more pronounced among growing individuals (H2). We also hypothesized that omnivory helps grizzly bears buffer energy intake from changing foods, with body fat levels being independent from population density and environmental changes (H3). Our analyses showed that individual lean body mass was negatively related to population density, particularly among growing-age females, supporting H1 and partially H2. In contrast, population density or sex had little effect on body fat levels and rate of accumulation, indicating that sufficient food resources were available on the landscape to accommodate successful use of shifting food sources, supporting H3. Our results offer important insights into ecological feedback mechanisms driving individual performances within a population undergoing demographic and ecosystem-level changes. However, synergistic effects of continued climate change and increased human impacts could

Francesca Cagnacci and Frank T. van Manen equally co-advised this work.

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lead to more extreme changes in food availability and affect observed population resilience mechanisms. Our findings underscore the importance of long-term studies in protected areas when investigating complex ecological relationships in an increasingly anthropogenic world.

KEYWORDS

body mass, environmental change resilience, feeding tactic, individual performance, life-history strategy, *Ursus arctos*

1 | INTRODUCTION

The importance of density dependence in influencing demographic processes of populations is well established (Reznick et al., 2002). When population density of long-lived mammals increases toward carrying capacity (Stephens et al., 2019), a sequence of changes in life-history traits has been postulated to occur. First, the mortality rate of immature animals increases, followed by an increase in age of first reproduction (i.e., primiparous females), a reduction in the reproductive rate of adult females, and, lastly, an increase in the mortality rate of adults (Eberhardt, 2002). However, quantifying variations in life-history traits of long-lived mammalian populations can take decades (Western, 1979), potentially limiting the ability to detect the emergence of density-dependent effects. Alternatively, body mass and body composition (lean body mass and percent body fat) are indicators of individual performance directly related to fitness of mammals: larger or fatter individuals usually have a higher probability of survival and a greater capacity to invest energy in reproduction (Stearns, 1992; Stephens et al., 2009; Wilder et al., 2016). This particularly applies to long-lived mammal species that rely on energy accumulation for long-term survival and reproduction (Oftedal, 2000). Individual performance and population density are therefore intrinsically linked through a feedback mechanism: to grow larger and thus enhance fitness, individuals must acquire proportionally more resources, the availability of which often decreases as density increases because of intraspecific competition (Chesson, 2000).

Density-independent factors, such as landscape perturbations or extreme weather, may affect this feedback by lowering carrying capacity due to reduction in resource availability (Skogland, 1985; Woodworth-Jefcoats et al., 2017), which can amplify the impact of high densities on life-history traits (e.g., birth rates, survival rates, and age at reproductive maturation; Fowler, 1981). In the face of competition or perturbations, animals may adopt different behavioral, reproductive, or feeding tactics to maintain high individual performance (Fattebert et al., 2019; Kruuk & Parish, 1982; Pettorelli et al., 2005; Taylor & Norris, 2007). The adaptive capacity to respond to spatiotemporal environmental changes varies substantially among species. Clavel et al. (2011), for example, observed that generalist species are outperforming and gradually replacing specialist species globally because of their plasticity in responding to rapid climate and

land use change. Omnivory, a common trait among generalist species, may be a beneficial strategy in a rapidly changing environment because it enables animals to shift their diet when a resource becomes temporarily depleted, allowing recovery of the resource and ultimately stabilizing the system (Kratina et al., 2012). Large omnivores in particular have access to a wider range of resources in the landscape and have slower life histories, both of which improve their ability to adapt to environmental changes relative to smaller members of their guild (Jackson et al., 2022; Kratina et al., 2012), while having higher energy requirements (Atanasov, 2007). This could give large omnivores an evolutionary advantage in buffering spatiotemporal environmental fluctuations (Liao et al., 2020), but as population density increases, this adaptive capacity may be constrained by growing competition with conspecifics, affecting individual performance. By examining variation in body mass and composition among individuals across a range of local population densities and during periods of environmental change, we can gain important insights into the resilience of large-bodied omnivores.

The Greater Yellowstone Ecosystem (GYE), home to most of North America's large mammal species, is no exception to current environmental fluctuations. Despite being one of the world's least anthropized temperate ecosystems (Kennedy et al., 2019), pronounced environmental changes have occurred in recent decades due to increased human impacts from recreation, development, and climate change (Gude et al., 2007; Hansen & Phillips, 2018; Hostetler et al., 2021; Romme et al., 2016). Within the large mammal community, the grizzly bear (*Ursus arctos*, Linnaeus, 1758), commonly referred to as brown bear outside of the interior of North America, has received significant attention for over 60 years. These bears have not been subjected to regulated hunting since 1975, the year of its listing as threatened under the U.S. Endangered Species Act. Their diet primarily consists of natural foods following the closure of open-pit garbage dumps during 1968–1979 (Gunther et al., 2014; Haroldson et al., 2008). One of the world's largest terrestrial omnivores, grizzly bears consume food resources across multiple trophic levels depending on availability (Gunther et al., 2014). Omnivory in grizzly bears is a functional adaptation, allowing them to live in a broad range of environments (i.e., Holarctic distribution; McLellan et al., 2017) and exploit a wide variety of food sources (Coogan et al., 2018). Besides their opportunistic feeding strategy, grizzly bears are long lived (>25 years) and are thus exposed to habitat

variability and competition over many years. They are also non-territorial, can track temporally variable food resources over extensive areas, and have no natural predators except for conspecifics and humans. An important aspect of their life-history strategy is the need to acquire and store sufficient energy reserves in the form of body fat during their active months to support 3–7 months of denning and hibernation. They are slow life-history strategists with small litter size and long maternal care (1.5–2.5 years). For reproductive-age females, stored energy must also be adequate to support pregnancy and lactation while denning (>20% body fat; Robbins et al., 2012). Consequently, grizzly bear body mass varies considerably within their annual cycle, from lows in early to mid-summer to substantial mass gain prior to denning and at the onset of hibernation in November (Kingsley et al., 1983). Additionally, because grizzly bears grow rapidly during their first years of life and subsequently plateau with age (i.e., growth asymptote; Bartreau et al., 2011), age-related changes in body mass are particularly significant during early life cycle stages.

The conservation status of the GYE grizzly bear population markedly improved from 1970s to present, driven by concerted management efforts that resulted in relatively high survival rates for several decades (Schwartz et al., 2006). More specifically, the grizzly bear population increased from perhaps fewer than 250 to around 1000 individuals (van Manen et al., 2022; Figure 1a), and the occupied range expanded (Figure 2). Population growth has slowed since the early 2000s in the presence of density-dependent effects, primarily due to lower immature (<2 years old) survival rates, with intraspecific killing by male bears playing a likely role, as well as lower fecundity of females (van Manen et al., 2016). However, it remains uncertain to what extent intraspecific competition (i.e., density-dependent factors) influenced individual performance such as sex-specific growth and body composition (van Manen et al., 2016). This is timely and relevant to be singled-out, because density-independent factors, such as landscape-level perturbations induced by climate change and human impacts (Gude et al., 2007; Hansen & Phillips, 2018; Hostetler et al., 2021; Romme et al., 2016; Figure 1c) and involving declines in several high-calorie food sources (Figure 1b), have occurred in recent decades in the GYE. For example, starting in the early 2000s, mature whitebark pine (*Pinus albicaulis*, Engelm, 1863) trees (seeds of which are a high-calorie food source during late summer and fall; Macfarlane et al., 2013; van Manen et al., 2016) experienced extensive mortality, primarily from a large-scale mountain pine beetle (*Dendroctonus ponderosae*, Hopkins, 1902) outbreak (Shanahan et al., 2016), with masting events moderating over time (Haroldson, 2021; Figure 1b). Climate variables were linked to this outbreak and models indicate climate change will likely provide favorable conditions for future beetle outbreaks (Buotte et al., 2016). Furthermore, elk (*Cervus canadensis*, Erxleben, 1777) populations in core areas of the GYE began to decline in the mid-1990s (Christianson & Creel, 2014; Figure 1b), whereas bison (*Bison bison*, Linnaeus, 1758) numbers increased (Geremia, 2022; U.S. Department of Interior and National Park Service, 2021; Figure 1b). Also, cutthroat trout (*Oncorhynchus clarkii*, Richardson, 1836), a high-calorie food

for grizzly bears residing near tributary streams to Yellowstone Lake (Haroldson et al., 2005; Reinhart & Mattson, 1990), were reduced to 10% of historical levels because of predation by non-native lake trout (*Salvelinus namaycush*, Walbaum, 1792), whirling disease (*Myxobolus cerebralis*, Hofer, 1903), and prolonged droughts (Koel et al., 2003, 2005; Figure 1b). Overall, food availability for grizzly bears in the GYE was greater during the first decade (2000–2009) than the second decade (2010–2020) (Figure 1b; Supporting Information S1).

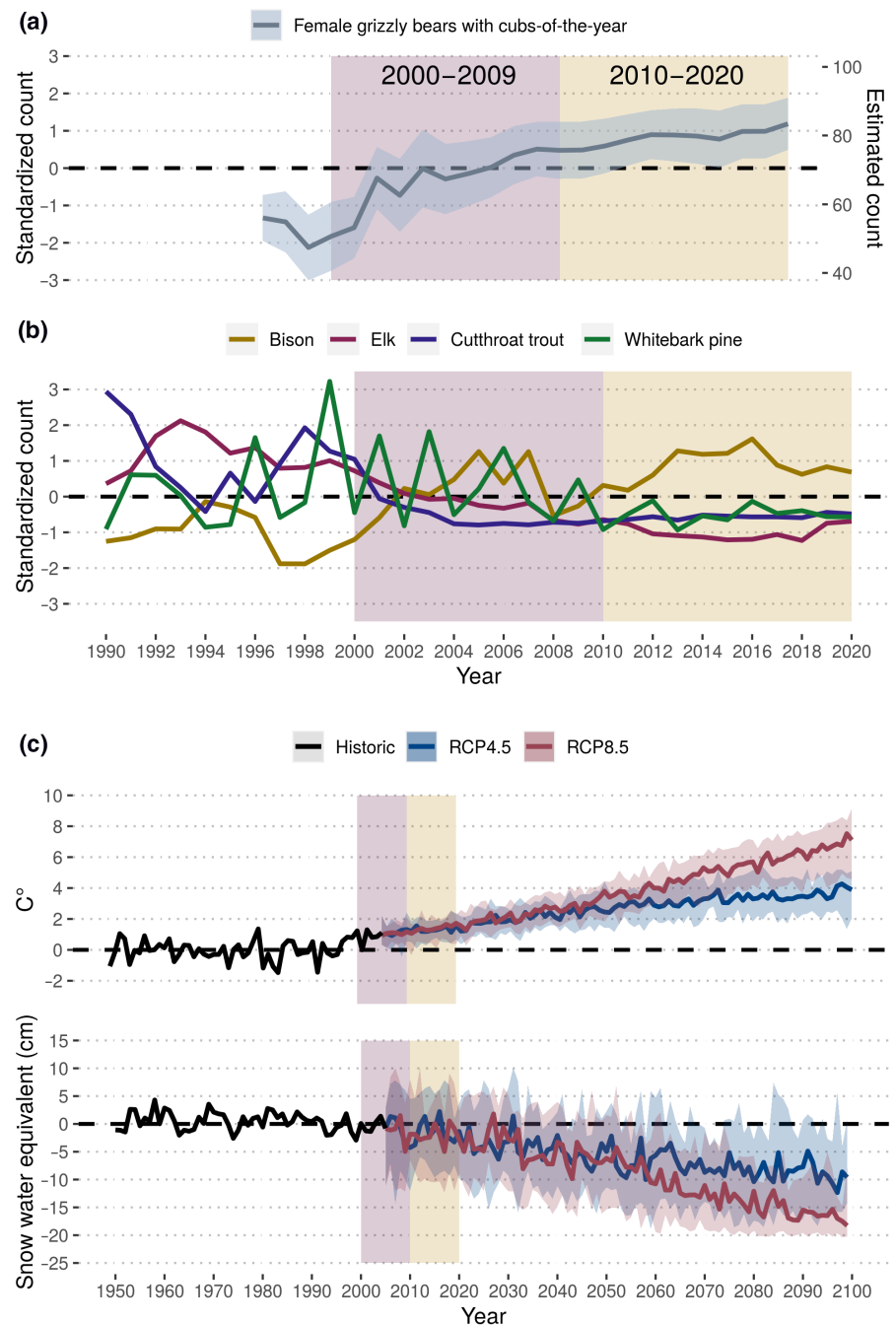
Using a dataset of grizzly bear body composition estimates (lean body mass and percent body fat) spanning 2000–2020, and a matching temporal array of a spatially explicit index of bear population density, we investigated relationships among individual performance and intrinsic and extrinsic factors at the population level (Table 1). Specifically, we examined lean mass and percent body fat as proxies for performance because they allometrically scale with fitness (Stearns, 1992; Stephens et al., 2009; Wilder et al., 2016), respectively measuring long- and short-term responses to environmental conditions and local population density. We hypothesized that individual lean body mass of grizzly bears declines as population density increases (H1), and that population density has an age-dependent effect on lean body mass (H2). Furthermore, because body fat is essential for grizzly bear hibernation and for female reproduction and offspring care, bears seasonally prioritize fat storage over increasing lean body mass when allocating energy from food consumption (Belant et al., 2006). This is especially important for a capital breeder (Jönsson, 1997; Stephens et al., 2009) such as grizzly bears, who depend on energy stored during the fall of the previous year to sustain hibernation and reproductive investment. Accordingly, we hypothesized that individual grizzly bear body fat levels are independent from population density and environmental changes (H3). We tested these three hypotheses by assessing the following predictions: (i) lean body mass of bears is negatively correlated with grizzly bear population density, (ii) lean body mass of growing individuals, more so than mature individuals, is negatively correlated with population density, and (iii) percent body fat is constant as grizzly bear population density increases, across two decades characterized by different resource availability (Table 1).

2 | METHODS

2.1 | Study area and field data collection

The study area consisted of occupied grizzly bear range in the GYE (70,468 km² in 2020) and included Yellowstone and Grand Teton National Parks, portions of five national forests, and state and private lands in Wyoming, Montana, and Idaho. The GYE consists of a high-elevation plateau surrounded by 14 mountain ranges with elevations greater than 2130 m and contains the headwaters of three continental-scale rivers. Summers are short and most of the average annual precipitation (50.8 cm) falls as snow. Vegetation transitions from low-elevation grasslands through conifer forests at mid-elevations, reaching alpine tundra at around 2900 m.

FIGURE 1 (a) Standardized (left y-axis) and estimated (right y-axis) count of female grizzly bears with cubs-of-the-year and 95% confidence interval (1997–2020) based on annual population monitoring (van Manen et al., 2022). (b) Standardized temporal trends (1990–2020) of high-calorie food sources for grizzly bears in the Greater Yellowstone Ecosystem, specifically bison (dark yellow line), elk (dark red line), cutthroat trout (dark blue line), and whitebark pine (dark green line). Details regarding data used for each trend are provided in [Supporting Information S1](#). (c) Historical (1950–2005, black line) and projected (2005–2100) changes in annual temperature (C°, top plot) and amount of water stored in the April 1 snowpack (i.e., snow water equivalent [cm], bottom plot) in the Greater Yellowstone Ecosystem as deviations from the 1900–2005 and 1950–2005 mean, respectively (Hostetler et al., 2021). Projected trends are based on two future greenhouse gas emission scenarios (Representative Concentration Pathways, RCPs, 4.5 and 8.5), which, respectively, indicate significant emissions mitigation (blue line) and no emissions mitigation (red line) (Hostetler et al., 2021). For each plot (a–c), the dashed line represents the overall mean and the shaded vertical areas the two decades of data (i.e., 2000–2009 and 2010–2020)



Grizzly bears were captured during 1975–2020 as part of a long-term research and monitoring program. Captures were conducted 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 permits from the National Park Service, and state wildlife agencies of Wyoming, Montana, and Idaho. Capture and handling 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). Grizzly bear captures were conducted with the aim of obtaining adequate coverage across the distribution of bears

at the time of sampling, and a representative sample by sex, age class, and other factors that influence demographics (Schwartz et al., 2006).

Starting in 2000, as part of a suite of morphometric measurements, we obtained body mass using an electronic scale (Artech Model 20210-2K s-beam load cell, Artech Industries Inc. and 4406 indicator A&D Co., Ltd.) and estimated percent body fat with Bioelectrical Impedance Analysis (BIA; Quantum II, R.J.L. Systems). We determined total body water and body lipid content using equations for brown bears following Farley and Robbins (1994). We calculated lean body mass (kg) by subtracting body fat mass from total body

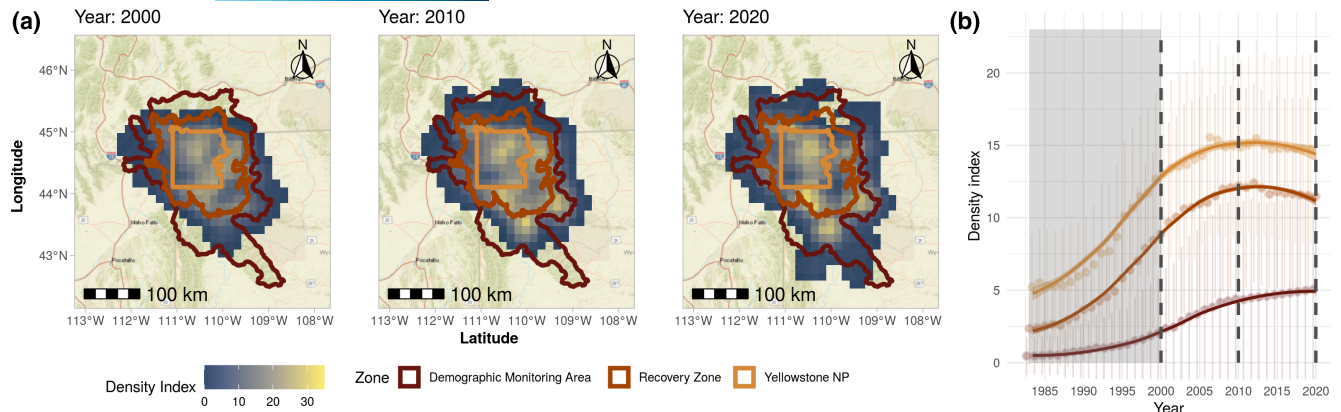


FIGURE 2 (a) Changes in bear density index in three different geographic zones in the Greater Yellowstone Ecosystem during 2000–2020. The relative population density of grizzly bears was calculated on a pixel-by-pixel basis (196-km² square grid). Annual index of local population density was based on a comprehensive dataset that included >45 years of capture and location data of >1000 individual bears. (b) Smoothed trend and 95% confidence intervals (*loess*) of mean density index by zone during 1985–2020. Mean values and standard deviations for each zone and year are displayed in the background. The gray shaded area represents the years before this study's analysis, and the vertical dashed lines serve as a reference for the density index maps on the left (2000, 2010, and 2020). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

mass. We extracted a vestigial, first premolar tooth for age estimation based on cementum annuli (Matson's Laboratory; Matson et al., 1993).

2.2 | Analysis

2.2.1 | Overview of the methodological approach

We tested our hypotheses (Table 1) by examining factors that may influence individual variation in lean body mass and body fat of grizzly bears. We estimated sex-specific lean body mass growth using von Bertalanffy growth curves (Bartreau et al., 2011; Kingsley et al., 1983) and examined whether individual variation in lean body mass for two life stages (growing and mature individuals) was associated with a spatially explicit covariate of local population density (H1 and H2). Because of different land ownership and management practices, the history of population dynamic processes varies within the study area: Yellowstone National Park is the core strictly protected area where grizzly bears have always been present at relatively higher densities. Conversely, the presence of grizzly bears outside the national park was reduced until conservation measures were implemented and densities began to increase in adjacent areas starting in the mid-1980s, and peripheral areas of the ecosystem were re-occupied only in the last two decades (Figure 2) (van Manen & Haroldson, 2017). Therefore, we controlled for spatial heterogeneity of population dynamic histories by using estimates of local density, as described under the *covariates* subsection below. We used measurements from the beginning of the fat accumulation phase in June through October, just prior to the onset of hibernation, to study the influence of population density and life stage on body composition, using

decade (2000–2009 vs. 2010–2020) as a control for variation in high-calorie food resources (H3; Figure 1b).

2.2.2 | Lean body mass and sex-specific growth (H1, H2)

Grizzly bear fat reserves fluctuate over the course of the active season (April–November; Kingsley et al., 1983), which can cause substantial seasonal influence on body mass. Consequently, we focused on lean body mass for our analysis of growth because it is seasonally invariant. We preliminarily tested this assumption by calculating the Kendall rank correlation coefficient between lean body mass of mature bears and months of the active season.

We used lean body mass data obtained during captures conducted from May to October. We excluded bears that were captured for conflict management purposes, individuals whose age was not estimated via cementum annuli, and any values identified as statistical outliers for which we had evidence of measurement or transcribing errors. We used lean body mass of bears of all ages to estimate growth, but we excluded dependent-age (<2 years old) individuals to estimate body fat gain. Because proximity to carcass redistribution sites (used primarily for deposition of ungulates killed in vehicle collisions on park roads) was positively correlated with lean body mass in some males (see Supporting Information S2), we also excluded 52 male grizzly bears captured in proximity (<2000 m) of such sites from analysis. In total, we compiled 566 (210 females, 356 males) body mass measurements for 418 individual bears (146 females, 272 males) born between 1978 and 2019 and captured from 2000 to 2020 (USGS ScienceBase catalog; Haroldson et al., 2023).

We estimated body mass growth by fitting the von Bertalanffy growth function:

TABLE 1 Hypotheses and predictions tested in the study on population-scale drivers of individual grizzly bear body mass and composition, together with the ecological principles from the literature that led to their formulation.

Ecological principle	Hypothesis	Prediction	Supported
Population regulatory mechanisms in long-lived mammals are mediated by individual performance ^{a,b}	H1 Individual grizzly bear lean body mass declines as population density increases	(i) Lean body mass of bears is negatively correlated with grizzly bear population density	Yes
Population regulatory mechanisms in long-lived mammals mainly affect younger age classes ^b	H2 Population density has an age-dependent effect on lean body mass	(ii) Lean body mass of growing individuals, more so than mature individuals, is negatively correlated with population density	Only for females
Omnivory buffers energy intake from variations in intrinsic and extrinsic factors ^{c,d}	H3 Individual grizzly bear body fat levels are independent from population density and environmental changes	(iii) Percent body fat is constant as grizzly bear population density increases, across two decades characterized by different resource availability	Yes

^aReznick et al. (2002).

^bEberhardt (2002).

^cClavel et al. (2011).

^dChubaty et al. (2014).

$$E[W|t] = W_{\infty} (1 - \exp^{-k(t-t_0)}), \quad (1)$$

where $E[W|t]$ is the expected lean body mass at age t , W_{∞} is the asymptotic average maximum body mass, k is the growth coefficient, and t_0 is the hypothetical age at which the average body mass is zero. We performed the curve-fitting procedure following the approach outlined by Ogle (2016), using the Levenberg–Marquardt nonlinear least-squares algorithm provided in the R package `minpack.lm` (Elzhov et al., 2016). Because body size in grizzly bears is sexually dimorphic (i.e., males are larger than females; Bartareau et al., 2011; Kingsley et al., 1983), we fit population-level, sex-specific growth curves with data from bears captured between 2000 and 2020 and born from the 1970s to the 2010s. We excluded measurements from same-year recaptures by randomly selecting one body composition estimate within that year, but used multiple measurements from the same animal when collected over several years. Regardless, the majority of the measurements were from grizzly bears that had only been captured once and the sex-specific growth curves were assumed to be representative of the population. We identified the age at which 95% of sex-specific asymptotic lean body mass was obtained according to the von Bertalanffy growth functions, and defined growth-phase and mature bears as those younger and older than that age, respectively. We derived confidence intervals for the growth function parameters via bootstrapping ($n=999$ iterations) and estimated overall goodness-of-fit by measuring the correlation between observed and expected values.

2.2.3 | Body fat levels and rate of accumulation (H3)

We estimated individual body fat levels of grizzly bears at capture as the percentage of fat mass in total body mass (see Section 2.1). In contrast to lean body mass, body fat levels increase over the active season and we used this metric as a proximate response to environmental conditions (see *below*). We used fat measurements from the same individual grizzly bears included in H1 and H2 to test this hypothesis.

We estimated the rate of accumulation as the amount of body fat gained by grizzly bears throughout the active season. We first determined the month in which the lowest body fat level is reached (i.e., the inflection point) for each sex to estimate the physiological start of the fattening period. Exploratory analysis indicated June as the physiological start for all bears: for both decades, females had the lowest percent body fat between May and June (mean = 16.5%), whereas males continued to lose body fat after den emergence, reaching their lowest condition in June (mean = 18.3%). Therefore, we examined fat accumulation from June until the start of the denning season in late October. Because fat accumulation is linear with time following the inflection point, as previously shown for this species (McLellan, 2011), we estimated sex-specific gains using linear regression analysis.

2.2.4 | Covariates

To examine the spatiotemporal relationships of body composition with local population density, we used a grizzly bear density index developed for the GYE by Bjornlie et al. (2014). The basis of that index was a spatiotemporal population reconstruction using extensive long-term capture and telemetry data, calculated for 14 × 14-km grid cells (196 km²; approximate annual home range of female bears) for 1983–2020. The index effectively tracked population density changes through time and space (Figure 2). A more detailed description of the methods and the sample's geographic distribution is available in Bjornlie et al. (2014).

To account for spatial heterogeneity of population dynamic processes associated with different land ownership and management, we used three geographic zones as a control variable in our analysis (Supporting Information S3, Figure S3): Yellowstone National Park where bears have always been present and at relatively higher densities; the area outside of the national park but within the Grizzly Bear Recovery Zone where bear densities increased between the mid-1980s and the mid-2000s; and the area outside the recovery zone but within the Demographic Monitoring Area, most of which was re-occupied over the last two decades (Figure 2).

We controlled for the decades of 2000–2009 (2000s) and 2010–2020 (2010s) in our analysis as a temporal proxy for changes in the availability of high-calorie foods considered important for grizzly bears in the Greater Yellowstone Ecosystem (Figure 1b). Because body fat accumulation is largely a function of current conditions, whereas lean body mass is a result of past conditions that cannot be tracked to the time of capture, we only examined time-dependent relationships between food source availability and body fat.

2.2.5 | Hypothesis testing

We used generalized additive mixed models (GAMMs) with a Gaussian error distribution to test our first two hypotheses (H1 and H2) by simultaneously estimating individual lean body mass (Lean Mass) and accounting for sex-specific growth, local grizzly bear density index, and life cycle stage (growing vs. mature individuals), while also controlling for geographic zones. To match the sex-specific von Bertalanffy growth curves, we used a natural log transformation for age (Age) and fitted it with a thin plate regression spline that was optimally implemented using GAMM. We included grizzly bear density index (Density) and geographic zones (Zones) as fixed terms, and year of capture (Year) as a random intercept to account for inter-year variability (ζ). Because the density index indicated different changes over time in the three geographic zones (Figure 2), we included an interaction term (Density × Zones). We also included life cycle stage (Life Stage) as a fixed term and an interaction term between density and life cycle stage (Density × Life Stage) to evaluate the local density relationship of growing versus mature bears. We scaled and standardized ($\mu=0$, $\sigma=1$) the response variable and all continuous explanatory variables associated with each sex and

checked for multicollinearity ($|r| < 0.7$; Dormann et al., 2013), thereafter fitting sex-specific GAMMs using the functions from R package mgcv (Wood, 2011). We started by fitting the full model as:

$$Y_{\text{Lean Mass}} \sim \beta_0 + \beta_1 \log(\text{Age}) + \beta_2 \text{Density} + \beta_3 \text{Zones} + \beta_4 \text{Life Stage} + \beta_5 (\text{Density} \times \text{Zones}) + \beta_6 (\text{Density} \times \text{Life Stage}) + \zeta_{\text{Year}} + \varepsilon \quad (2)$$

for females and males, separately, then gradually reduced models by removing terms (except for Age) to have various combinations of fixed-effect terms, including a null model (without Age; Supporting Information S4), and assessed the best model to predict lean body mass using the second-order Akaike's information criterion (AIC_c). To assess model fit and the stability of parameter selection in the best-fitting model (lowest AIC_c score), we also fitted full models and performed bootstrap analysis ($n=999$ iterations) and compared the outputs.

We used generalized linear mixed models (GLMMs) with a Gaussian error distribution to test hypothesis H3, by estimating body composition (i.e., percent body fat; Body Fat) and accounting for linear daily gain (McLellan, 2011), local grizzly bear density index, and life cycle stage, while also controlling for decade of capture (i.e., 2000–2009 and 2010–2020). To account for intra-year fat accumulation, we included Julian day (Julian) as a fixed term in all models with body fat as the response variable. We added grizzly bear density index (Density) and life cycle stage (Life Stage) as fixed terms and an interaction term (Density × Life Stage). We added decade of capture (Capture Decade) as a fixed term and an interaction term with day of the year (Julian × Capture Decade) for modeling the annual rate of gain. We again included a random intercept term for year of capture (Year) to account for inter-year variability (ζ) and scaled and standardized ($\mu=0$, $\sigma=1$) the response variable and all continuous explanatory variables associated with each sex. We fitted the model as:

$$Y_{\text{Body Fat}} \sim \beta_0 + \beta_1 \text{Julian} + \beta_2 \text{Capture Decade} + \beta_3 \text{Density} + \beta_4 \text{Life Stage} + \beta_5 (\text{Julian} \times \text{Capture Decade}) + \beta_6 (\text{Density} \times \text{Life Stage}) + \zeta_{\text{Year}} + \varepsilon \quad (3)$$

for females and males separately. Finally, using AIC_c, we identified the best model to predict percent body fat similarly to the lean body mass model, with Julian as the constant term across reduced models (other than the null model; Supporting Information S4). We again assessed model fit and the stability of parameter selection by comparing the output of the best-fitting model to that of the full model and bootstrap analysis. We performed all statistical analysis in R 4.0.0 (R Core Team, 2020) under Ubuntu 16.04.3 LTS (Canonical Ltd.) and visualized the fitted regression models with the visreg package in R (Breheny & Burchett, 2017).

3 | RESULTS

3.1 | Lean body mass model

The von Bertalanffy growth function accurately described the growth pattern of Yellowstone grizzly bears, fitting well to female ($\rho_{\text{female}}=0.76$; $W_{\infty}=94.77 \pm 1.43$, $k=0.39 \pm 0.05$, $t_0=-0.44 \pm 0.30$)

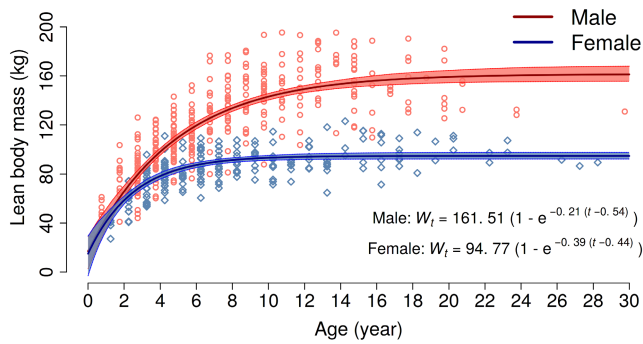


FIGURE 3 Sex-specific von Bertalanffy growth curves fitted to lean body mass (kg) as a function of Age (year) of grizzly bears from captures in the Greater Yellowstone Ecosystem during 2000–2020. Each symbol (blue diamond for females, red circle for males) represents an individual lean body mass measurement (146 females, 272 males). Solid lines (blue for females, red for males) indicate the von Bertalanffy growth function fitted to the data, whereas corresponding shaded areas represent the 95% confidence intervals estimated via bootstrapping ($n=999$ iterations). The sex-specific von Bertalanffy growth equations are shown for reference (right bottom).

and male ($\rho_{\text{male}}=0.84$; $W_{\infty}=161.51 \pm 3.42$, $k=0.21 \pm 0.02$, $t_0=-0.54 \pm 0.27$) lean body mass data (Figure 3). Sex-specific growth showed that females reach physical maturity at the age of 7 (90 kg), whereas males reach physical maturity at the age of 14 (153 kg). We verified that lean body mass measurements were invariant over the active season for males ($\rho=-0.06$, $p=.61$) and for females during June–October ($\rho=0.11$, $p=.23$) (Figure S5); inclusion of May data for females indicated a slight trend in monthly estimates ($\rho=0.18$, $p=.04$) but sample size was low ($n=8$), and a higher proportion of females with dependent offspring (63%) were captured in this month, which typically have a lower lean body mass than lone females (Hilderbrand et al., 2000).

Lean body mass was related to age in all bears, as expected, confirming the relationship predicted by the von Bertalanffy growth function (Figure 3; Supporting Information S6). Dropping age as a model term resulted in a notable increase in ΔAIC_c score (females: $\Delta\text{AIC}_c=169.38$; males: $\Delta\text{AIC}_c=417.78$, compared with null model; Table 2), but despite its significance as a predictor variable, variation in lean body mass could not be explained solely by age (females: $\Delta\text{AIC}_c=26.73$; males: $\Delta\text{AIC}_c=16.80$, compared with best-fitting model; Table 2). Instead, female and male lean body mass were negatively related to grizzly bear population density, supporting prediction (i) (H1, Table 1). Specifically, there was strong support for the addition of the density index covariate (females: $\Delta\text{AIC}_c=17.49$, males: $\Delta\text{AIC}_c=16.80$; Table 2) and those models were considerably more parsimonious (Table 2). Bear density was the only predictor other than age to be included in the best-fitting model for both sexes (Table 3), and had a larger effect size than any of the other predictors (females: $b_{\text{Density}}=-0.38$ (-0.51 to -0.25); males: $b_{\text{Density}}=-0.13$ (-0.18 to -0.07); Table 3).

Model selection indicated the interaction term for density and life stage was strongly supported for females, but there was limited

support for such an interaction for males ($\Delta\text{AIC}_c=3.08$ compared with best-fitting model) (Table 2). When considering the best-fitting model for females, the effect of density on lean body mass differed between life cycle stages ($b_{\text{Density:Life Stage(Mature)}}=0.32$ (0.15–0.49); Table 3). Thus, density showed significantly stronger relationships with body mass of growing individuals than mature individuals, but primarily in females (Figure 4a), partially supporting prediction (ii) (H2, Table 1). There was no support for the inclusion of geographic zones, and adding them as a fixed factor made the models less parsimonious even when compared with lean body mass as a function of age (females: $\Delta\text{AIC}_c=0.61$, males: $\Delta\text{AIC}_c=1.99$) (Table 2). The output of the full models (Supporting Information S7, Table S7) showed that the estimated coefficients were similar to those of the best-fitting model (Table 3), as also supported by bootstrap analysis (Figure S7.1), suggesting that the selected models were a good fit for the data. Based on the fitted regression for females, we detected an estimated 27 kg difference in lean body mass for growing individuals at high versus low density (Figure 4a), corresponding to 30% of female asymptotic lean body mass. Among males, the negative relationship of density with lean body mass was similar for both life stages, with an estimated overall effect size across the range of density of 22 kg (Figure 4b), representing about 14% of male asymptotic body mass.

3.2 | Percent body fat model

Julian date was the only variable strongly associated with percent body fat in both females and males, as evidenced by model selection (Table 2). When modeling body fat as a linear function of day of the year (females: $b_{\text{Julian}}=0.51$ (0.39–0.63); males: $b_{\text{Julian}}=0.48$ (0.38–0.58); Table 3), we observed that from June 1 to October 31 (152 days), females and males gained 15.3% and 16.8% body fat, respectively, a daily increase of 0.10% (Figure 5b–d), regardless of capture decade. Neither female or male body fat accumulation rates were related to grizzly bear population density (females: $\Delta\text{AIC}_c=2.49$; males: $\Delta\text{AIC}_c=2.62$; Table 2), nor to capture decade (females: $\Delta\text{AIC}_c=2.95$; males: $\Delta\text{AIC}_c=3.34$; Table 2), supporting prediction (iii) (H3, Table 1). Importantly, mature females maintained their reproductive potential by achieving over 20% body fat (30) by the onset of the denning season (i.e., October; Figure 5a,b, top panels). The results of the full models (Table S7) generally corroborated the outputs of the best-fitting models for body fat accumulation rates (Table 3), except for the female life stage term for which there was only marginal statistical evidence over the bootstrap sample (Figure S7.2).

4 | DISCUSSION

Our analyses indicate that intrinsic factors were greater drivers of lean body mass of GYE grizzly bears than extrinsic factors. Analyzing individual data collected over two decades (Figure 3)

TABLE 2 Model selection results for models of lean body mass and percent body fat of female and male grizzly bears in the Greater Yellowstone Ecosystem, 2000–2020. Response and explanatory variables, deviance, second-order Akaike's information criterion (AIC_c) scores, delta AIC_c (ΔAIC_c), and AIC_c model weight (w) are reported for each model. Models are ranked by AIC_c scores and AIC_c model weight for each response variable and sex.

Response	Sex	Explanatory variables ^a	Deviance	AIC_c	ΔAIC_c	w	
Lean body mass	Female	log(Age) + Density + Life Stage + Density:Life Stage	74.96	393.71	0	0.93	
		log(Age) + Density + Zones + Life Stage + Density:Zones + Density:Life Stage	73.78	399.16	5.45	0.06	
		log(Age) + Density	78.14	402.95	9.24	0.01	
		log(Age) + Density + Zones + Density:Zones	77.83	406.08	12.37	0	
		log(Age)	84.31	420.44	26.73	0	
		log(Age) + Zones	83.92	420.81	27.10	0	
		log(Age) + Life Stage	84.34	422.11	28.40	0	
		~1	195.59	591.49	197.78	0	
		Male	log(Age) + Density	92.68	556.69	0	0.63
	log(Age) + Density + Zones + Density:Zones		90.22	559.01	2.32	0.20	
	log(Age) + Density + Life Stage + Density:Life Stage		92.59	559.77	3.08	0.14	
	log(Age) + Density + Zones + Life Stage + Density:Zones + Density:Life Stage		90.10	562.28	5.59	0.04	
	log(Age)		97.58	573.49	16.80	0	
	log(Age) + Life Stage		97.70	575.63	18.94	0	
	log(Age) + Zones		97.03	575.77	19.08	0	
	~1		326.39	993.55	436.86	0	
	Percent body fat		Female	Julian	473.42	488.21	0
		Julian + Life Stage		470.93	490.23	2.02	0.19
Julian + Density		470.03		490.70	2.49	0.15	
Julian + Capture Decade		472.83		491.16	2.95	0.12	
Julian + Capture Decade + Julian:Capture Decade		472.11		494.80	6.59	0.02	
Julian + Density + Life Stage + Density:Life Stage		465.26		494.94	6.73	0.02	
Julian + Capture Decade + Density + Life Stage + Julian:Capture Decade + Density:Life Stage		464.05		501.82	13.61	0	
~1		530.89		539.63	51.42	0	
Male		Julian		751.90	768.23	0	0.61
		Julian + Density	748.32	770.85	2.62	0.17	
		Julian + Capture Decade	750.51	771.57	3.34	0.12	
		Julian + Life Stage	751.65	772.06	3.83	0.09	
		Julian + Capture Decade + Julian:Capture Decade	750.14	775.96	7.73	0.01	
		Julian + Density + Life Stage + Density:Life Stage	747.73	778.36	10.13	0	
		Julian + Capture Decade + Density + Life Stage + Julian:Capture Decade + Density:Life Stage	745.85	786.09	17.86	0	
		~1	827.66	837.58	69.35	0	

^aYear of capture was always included as a random intercept term in the model formula.

TABLE 3 Parameter estimates of the most parsimonious models based on model selection (Table 2) of lean body mass (predictions *i*, *ii*) and percent body fat (prediction *iii*) of female and male grizzly bears in the Greater Yellowstone Ecosystem, 2000–2020. The estimated standardized coefficient values (*b*), the 95% confidence intervals, and *p*-values are reported for each covariate. The Growing Phase represented the reference category for the categorical variable Life Stage.

Response	Explanatory variables	Females			Males		
		Est.	CI (95%)	<i>p</i>	Est.	CI (95%)	<i>p</i>
Lean body mass	(Intercept)	-0.04	-0.24 to 0.15	.675	0.01	-0.06 to 0.08	.817
	log(Age) ^a			<.001			<.001
	Density	-0.38	-0.51 to -0.25	<.001	-0.13	-0.18 to -0.07	<.001
	Life Stage(Mature)	0.02	-0.31 to 0.36	.890			
	Density×Life Stage(Mature)	0.32	0.15 to 0.49	<.001			
	Observations	208			351		
Percent body fat	(Intercept)	-0.02	-0.21 to 0.17	.849	-0.00	-0.10 to 0.10	1.000
	Julian	0.51	0.39 to 0.63	<.001	0.48	0.38 to 0.58	<.001
	Observations	191			292		

^aThere is no single estimate since smooth terms have several coefficients, that is, one for each basis function.

during which substantial changes in population density (overall increasing, Figure 2), food sources (several decreasing, Figure 1b), and environmental perturbations (Figure 1c) occurred, we observed density-dependent effects. Lean body mass was negatively associated with locally higher grizzly bear densities, as hypothesized (H1, H2, Table 1), particularly in young female bears (Figure 4a), suggesting density-dependent feedback controls. Importantly, the relative influence of density on lean body mass was notably greater for females (30%) than for males (14%) (Figure 4). These results corroborate and integrate findings of previous grizzly bear research in the GYE that population growth slowed as juvenile mortality increased, with infanticidal males likely playing a role, and female reproductive rate declining, particularly in areas with higher bear densities (van Manen et al., 2016). Conversely, rate of body fat accumulation was relatively constant (Figure 5) with respect to local population density and declines in several high-calorie food sources over the last two decades (Gude et al., 2007; Hansen & Phillips, 2018; Hostetler et al., 2021; Romme et al., 2016; Figure 1b). This shows omnivory-mediated plasticity as a stabilizing driver for body condition across decades, supporting the hypothesis that bears prioritize fat storage over lean body mass when allocating energy from food consumption in preparation for hibernation (H3, Table 1).

The density-dependent relationship with lean body mass for younger female bears suggests a potential mechanism for population regulation. The observed lower reproductive performance at the population level, particularly the lower probability of reproductive transition from having no offspring to cubs (van Manen et al., 2016), may be attributed to the slower growth of young females at higher population densities (Figure 4a). This could be related to the bears' reproductive biology, with body mass early in life influencing female lifetime reproductive success (Zedrosser et al., 2013). Female dominance and philopatry may also play a role in competition for resource acquisition in high-density areas, potentially leading to socially induced reproductive suppression of younger, but fertile,

females (Støen et al., 2006) and hence additional growth regulation at the population level. Thus far, despite the intrinsic driver of density-dependent feedback on lean body mass, our data indicate younger female bears in the GYE show compensatory growth and attain typical body mass as they mature (Figure 4a). For brown bears in Scandinavia, Zedrosser et al. (2006) suggested such compensatory mechanisms may include delayed reproduction or possibly dispersal to areas with lower densities. In the long term, however, the negative relationship between lean body mass and local population density may also lead to a population with smaller individuals, on average. This can be expected for a non-territorial species with plastic feeding strategies exposed to density dependence (e.g., dwarfism of large herbivores on islands; McNab, 2010) and considerable body mass variability (mean body mass range of 152–271 kg for males and 91–196 kg for females across populations in North America; Cameron et al., 2020).

Once females reach physical maturity, though, the capacity to reach adequate fat storage (Figure 5a,b) ensures individual survival and reproductive success (i.e., sufficient body fat to sustain pregnancy and lactation; Robbins et al., 2012). The consistent fat accumulation rate across the two decades supports the notion that the capital breeding strategy (Jönsson, 1997; Stephens et al., 2009) of grizzly bears was maintained as extrinsic factors varied, as also indicated by long-term trend data for the number of females with cubs-of-the-year (van Manen et al., 2022; Figure 1a). Fat accumulation from fall hyperphagia also appeared adequate to support the post-denning breeding activity of adult males, as early spring fat levels remained high (Figure 5c). This capital breeding strategy by males is adaptive. In spring, when large-bodied males travel extensively searching for mates, they have a limited intake rate and physiological capacity by subsisting on scarce and low-calorie foods (Costello et al., 2016; McLellan, 2011). Males thus use their energy reserves in the spring and start accumulating fat in the summer and fall once higher-calorie foods become available. The age at which females and

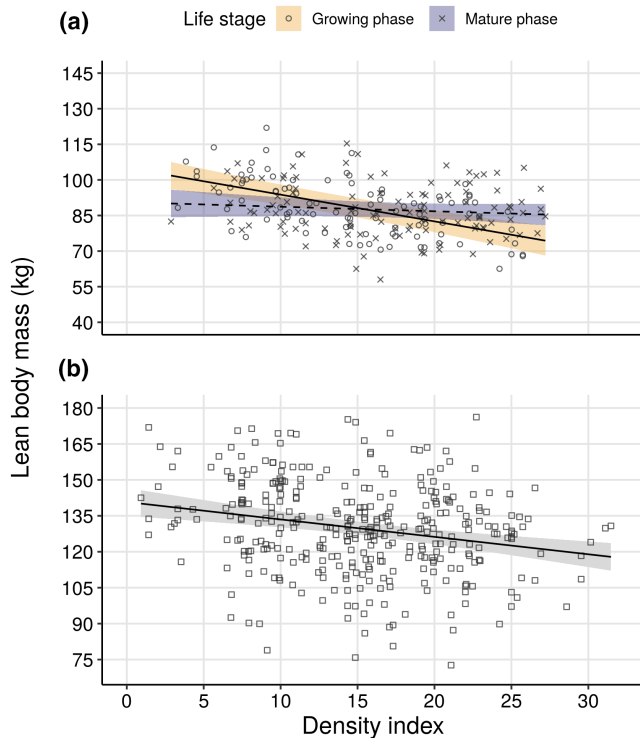


FIGURE 4 (a) Fitted regression lines with 95% confidence bands, estimated via generalized additive mixed models, of the empirical relationship between lean body mass, grizzly bear density index, and life cycle stage (growing vs. mature individuals, shown in yellow and purple, respectively) based on captures of *female* grizzly bears in the Greater Yellowstone Ecosystem during 2000–2020. We defined mature female bears from the age of 7. Each symbol (open circles for growing individuals, x for mature individuals) represents an individual measurement of lean body mass. The regression coefficients are derived from the best-fitting model (Table 2). (b) Fitted regression lines with 95% confidence bands, estimated via generalized additive mixed models, of the empirical relationship between lean body mass and grizzly bear density index based on research captures of *male* grizzly bears in the Greater Yellowstone Ecosystem during 2000–2020. Each symbol (square) represents an individual measurement of lean body mass.

males reached 95% of the asymptotic lean body mass (Figure 3, see also above) coincided with their respective reproductive strategies. Of all nulliparous females observed in this study, 97% had produced cubs by age 7, further supporting compensatory growth mechanism (Zedrosser et al., 2006). Conversely, males, although sexually mature by age 4, do not reach their reproductive prime until they reach sufficient body mass to compete successfully for breeding opportunities (Schwartz et al., 2006; Zedrosser et al., 2007).

Grizzly bear omnivory and capacity to shift feeding tactics are potential key factors for density dependence of lean body mass and fat accumulation stability as intrinsic and extrinsic factors change. First, grizzly bears maximize energy intake while optimizing macronutrient consumption of proteins, carbohydrates, and lipids (Costello et al., 2016; Erlenbach et al., 2014). On an energy-rich, high-protein diet (e.g., ungulates), bears are able to gain lean body mass and body fat, whereas consumption of low-protein foods

(i.e., rich in lipids or carbohydrates) favors body fat accumulation (McLellan, 2011). Grizzly bear local densities increased across portions of the GYE since the 1980s (Figure 2), in part driven by an increase in male survival (van Manen et al., 2016). Consequently, younger individuals, particularly immature females, may have experienced reduced access to high-energy foods because of competition with dominant, physically mature bears (Costello et al., 2016), thus limiting their ability to use excess calories to build up lean body mass. This is also consistent with grizzly bears prioritizing fat storage over lean body mass when allocating energy from food consumption according to seasonal and reproductive requirements (Belant et al., 2006). The constant rate of body fat accumulation throughout the last two decades (Figure 5b–d) suggests that individuals were able to obtain adequate calories with a mixture of foods, despite increased competition and substantial changes in food sources (Figure 1b). Supporting this interpretation, recent studies indicated a functional response of GYE grizzly bears to declines in whitebark pine (Costello et al., 2014) and cutthroat trout (Fortin et al., 2013), while compensating for the loss of these foods through diet shifts (Ebinger et al., 2016; Schwartz et al., 2014). Dietary plasticity allowed individual bears in the GYE to achieve similar percent body fat despite substantial disparities in total lean body mass. This is consistent with other studies on the feeding plasticity of brown bears across their range, resulting in different body sizes as a function of the quality and quantity of food resources in different ecosystems (Belant et al., 2006; Hilderbrand et al., 2018; Mangipane et al., 2018). These responses may ultimately result in adaptive eco-evolutionary processes: a decrease in lean body mass proportionally reduces individual energy intake needs, while achieving percent body fat necessary to successfully hibernate and reproduce. A study on sympatric American black bears (*Ursus americanus*, Pallas, 1780) in British Columbia, Canada, which were smaller but got proportionately fatter than grizzly bears, provides support for this notion. This suggests an evolutionary adaptation in survival and reproductive tactics associated with competition and food availability (McLellan, 2011).

While the plasticity of grizzly bears is crucial to their success in a changing ecosystem, their capacity for adaptation may be insufficient in the face of more extreme and long-term perturbations. For example, the GYE is experiencing a profound warming trend that started in the 2000s (Heeter et al., 2021; Figure 3c). Changes in climate and fire regimes may exceed the resilience of forest ecosystems and lead to widespread regeneration failures and thus changes in food resources (Rammer et al., 2021). In parallel, exurban development has increased in the GYE (Gude et al., 2007) and is expected to continue in regions with high proportions of protected lands (McDonald, 2007). These extrinsic factors could gradually limit resources available to bears, potentially reducing the carrying capacity of the ecosystem with negative feedback on density dependence and exacerbating density effects. Consequently, in the future, the reduction in individual performance (decrease in juvenile survival and female reproductive rate, van Manen et al., 2016; decrease in lean body mass growth, particularly of immature females, this study)

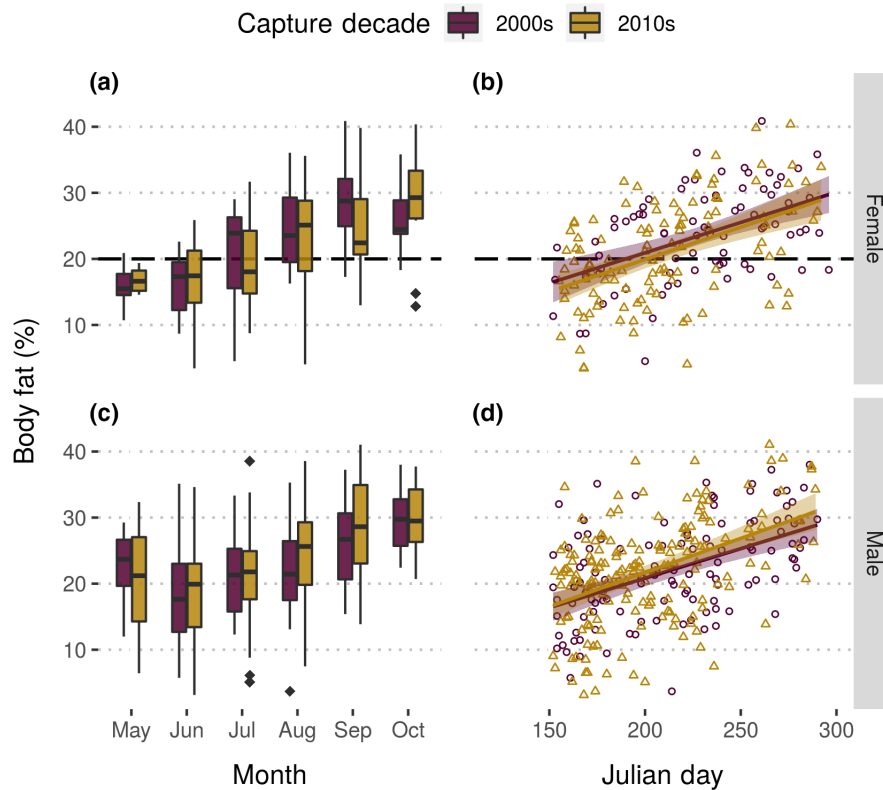


FIGURE 5 (a–c) Boxplots of percent body fat from May to October of independent-age (≥ 2 years old) grizzly bears captured in the Greater Yellowstone Ecosystem over two decades (2000–2009 and 2010–2020). (b–d) Fitted regression lines and 95% confidence bands, estimated via generalized linear mixed model, for the empirical relationship between percent body fat and Julian day over two decades, from June (physiological start of the fattening season) to October (beginning of the denning season). Each symbol (purple circle for 2000–2009, dark yellow triangle for 2010–2020) represents an individual measurement of percent body fat. On plots (a) and (b), the horizontal dashed line marks the 20% threshold required for females to support reproduction (Robbins et al., 2012). We divided predictions into capture decades (which were not included in the best model, as indicated by model selection; Table 2) to show how body mass and composition remained consistent across time.

could emerge at a comparatively lower local density than currently observed if projected perturbations occur in the future.

At the landscape and population level, so far grizzly bears seem to have sufficient space to disperse (lowering local density via dispersal; Figure 2). However, the resulting range expansion has also led to increased human–wildlife conflict potential (e.g., livestock depredation) on the periphery of occupied range, where anthropogenic influences are greater. As dispersal of bears continues into more human-dominated areas, conflicts and mortality may intensify. Monitoring data support this, with demography primarily driven by intrinsic, density-dependent factors within the core area and anthropogenic factors (i.e., human-caused mortality) on the periphery of occupied range (van Manen et al., 2016; van Manen & Haroldson, 2017). We observed these patterns under legal protection of the species for almost five decades. During this time, the large area of Yellowstone National Park functioned as a refugium, providing critical habitat and landscape conditions for the population to recover and thrive. This emphasizes the importance of extensive protected areas for large vertebrate species, where population dynamics are less influenced by anthropogenic mortality (Bischof et al., 2018) and disturbance (e.g., Europe; Chapron et al., 2014).

Generalists have an evolutionary advantage in environments where food availability can be temporally and spatially unpredictable because they can maintain loose links with numerous food sources (Kratina et al., 2012; Pimm, 1982) and optimize their foraging, while exhibiting multi-food functional responses (Morozov & Petrovskii, 2013). Our study adds to the body of knowledge that generalist species with slow life-history traits can accommodate short-term environmental changes (Jackson et al., 2022). Particularly, when the movement of omnivores is unrestricted (i.e., there are no movement barriers or territorial boundaries), species are able to track and acquire high-quality foods based on local availability. Nevertheless, this eventually leads to an increase in local population density and competition for limited resources, potentially resulting in reduced body size and individual performance (Bright Ross et al., 2020; Dennis & Otten, 2000; Mobæk et al., 2013; Young, 2020). On the other hand, because of their ability to buffer short-term changes in foraging opportunities, density-independent perturbations are less likely to have strong effects on generalist species compared with specialists. Yet, as more extreme and long-term perturbations may occur in the future (Dakos et al., 2019), long-lived species may be more vulnerable as their

slow life-history strategies require longer times to adapt (Gamelon et al., 2014).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the USGS ScienceBase catalog at <https://doi.org/10.5066/P9QLQSVX>, (Haroldson et al., 2023).

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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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