Body size plasticity in North American black and brown bears

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Citation: Cameron, M. D., G. V. Hilderbrand, K. Joly, J. H. Schmidt, D. D. Gustine, L. S. Mangipane, B. Mangipane, and M. S. Sorum. 2020. Body size plasticity in North American black and brown bears. Ecosphere 00(00):e03235. 10.1002/ecs2.3235

Abstract. Body size reflects realized physiological niche width at the population level and provides insights into the potential resiliency of a species to natural and anthropogenic perturbations to ecosystems. We analyzed patterns of American black and brown bear body size through a meta-analysis of data from 18 studies conducted across North America, to evaluate the effects of species, sex, latitude, sympatry, and harvest. We used a bootstrap model selection procedure, which accounted for differences in sample size and population variation between studies, to investigate patterns in body mass. As expected, we found that brown bears were generally larger than black bears and both species were sexually dimorphic (i.e., males were generally larger than females). Black bear body size was not related to latitude, whereas brown bear body size was greatest at intermediate latitudes, possibly due to the presence of salmon. Neither sympatry nor harvest was associated with body size for either species at the geographic scale of our meta-analyses, but both may warrant consideration at the local scale. Body size, as an index of population health, reflects phenotypic plasticity within species and populations and may serve as a useful indicator of niche utilization. Indeed, understanding large-scale physiological patterns such as these can assist in understanding past, present, and future changes to realized niches and subsequent resiliency of species and populations.

Key words: bootstrap model selection; grizzly bear; harvest; latitudinal variation; niche variation; sympatry; *Ursus americanus*; *Ursus arctos*.

Received 15 April 2020; accepted 18 May 2020; final version received 23 June 2020. Corresponding Editor: James W. Cain III.

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INTRODUCTION

Adaptability and plasticity can enhance the resiliency of populations as they respond to environmental change, alterations to habitat and climate, and direct human effects (e.g., harvest or exclusion from preferred habitat); and plasticity in body size is an effective means for enhancing resiliency (Van Valen 1965). Variation in body size has been assessed across a wide range of vertebrate taxa including fish (Jeffrey et al. 2017), birds (Hudin et al. 2016), small mammals (Gür and Gür 2012), ungulates (Sand et al. 1995), and carnivores (Stahler et al. 2013). Further work has focused on the influence of both intra- and inter-specific competition on the ability of individuals, and thus
populations, to fully utilize available resources and maximize their realized niche (Svænback and Bolnick 2007, Bolnick et al. 2003, 2007, 2010). Broader realized niche space may buffer populations in times of change. However, consideration of body size in the context of phenotypic niche width has not been fully investigated.

In North America, black (Ursus americanus) and brown (U. arctos) bears are sexually dimorphic (Garshelis 1994, McLellan 1994, Hilderbrand et al. 2018b) and exhibit significant variation in diet, morphology, and productivity (Garshelis 1994, McLellan 1994, Hilderbrand et al. 1996, 2018b, Mowat and Heard 2006, Bojariska and Selva 2012, Mangipane et al. 2018). The nutritional ecology of bears has been broadly studied (see Robbins et al. 2004), and the relationship between food quality and abundance, body size, and population productivity is well established. Dominance hierarchies that exist across sexes and species tend to govern utilization of preferred but limited resources resulting in broader niches at the population level relative to the individual level (Jacoby et al. 1999, Belant et al. 2006, 2010, Fortin et al. 2007, Schwartz et al. 2014, Lafferty et al. 2015, Hilderbrand et al. 2018b).

Brown bears tend to dominate high-quality, defensible food resources such as carcasses or stretches of salmon (Oncorhynchus spp.) spawning streams (Belant et al. 2006). Additionally, dominant male brown bears tend to be more carnivorous than females (Jacoby et al. 1999), which can result in females spending less time at concentrated food resources to reduce risk (Ben-David et al. 2004). While access to nutrient-dense foods leads to larger body sizes (Hilderbrand et al. 1999a, b), sympatric adult females of both species are able to achieve similar levels of percent body fat despite differences in diet (Lafferty et al. 2015, Mangipane et al. 2018). This suggests female bears are more likely to diversify their behavioral niche to expand their range of dietary resources when access to preferred foods is reduced. In addition to dietary niche partitioning (Jacoby et al. 1999, Belant et al. 2006), density-dependent processes can shape various aspects of bear population ecology within species (Garshelis 1994, McLellan 1994). Thus, it is reasonable to assume that species overlap may further confound these effects and potentially influence resiliency.

Mammals generally adhere to Bergmann’s Rule, with body size increasing with latitude as an adaptation of thermoregulation (Ashton et al. 2000, Meiri and Dayan 2003, Meiri et al. 2004), although evidence of this phenomenon in black and brown bears is mixed. Kennedy et al. (2002) examined body size in black bears ranging from the Eastern United States to Canada and found the largest bears residing in the southern states of Louisiana, Mississippi, and Texas. Both Rausch (1963) and Kojola and Laitala (2001) found that brown bears do adhere to Bergmann’s Rule with the caveat that the influence of salmon must be considered (Meiri et al. 2004). A broad perspective on the relationship between bear body size and latitude is informative as context for managers as they assess geographic, regional, and local drivers of body size.

Human harvest can exert selective pressure on phenotype which can affect behavior and population structure (Close and Seigel 1997, Hundertmark et al. 1998, Swihart et al. 1998, Strickland et al. 2001, Singer and Zeigenfuss 2002, Garel et al. 2007, Bunnefeld et al. 2009). Throughout much of North America, bear populations are exposed to harvest which has the potential to affect bear body size in a variety of ways: (1) If large trophy animals are harvested, selective pressure may tend toward smaller body-sized animals, (2) if harvest targets prime-aged animals, the population structure may shift toward younger or smaller individuals, or (3) if harvest reduces population density, it may allow for a broader utilization of available phenotypic niches due to reduced competition. Thus, harvest also has the potential to affect the realized niche and resiliency of bears.

Sympathy of black and brown bears across much of the latitudinal gradient occupied by bear populations in North America provides an opportunity to explore the potential effects of intra- and inter-specific competition on niche width across their respective distributions. To better understand how intra- and inter-specific competition, sex, harvest, and latitude may impact bear body size, we conducted a meta-analysis to investigate patterns in black and brown bear body size across North America. While incorporating differences between species and sex, we developed the following hypotheses: (1) Body size increases with latitude, (2) body size is lower when species are sympatric, and (3)
body size is lower in harvested populations. We expected that an exploration of these hypotheses at the continental scale would improve our understanding of the factors affecting bear body size and help to inform bear research and management in the future.

**METHODS**

We focused our meta-analysis on reported body mass and body length data from adult black and brown bear studies from across North America (Fig. 1). We began by conducting a literature review to identify studies that reported either metric for North American black and brown bears. We searched Wildlife and Ecology Studies Worldwide [https://www.ebsco.com/products/research-databases/wildlife-ecology-studies-worldwide](https://www.ebsco.com/products/research-databases/wildlife-ecology-studies-worldwide) for titles and keywords that included the terms: black bear, brown bear, body size, body mass, or body length. From the results of our literature search and previous experience with existing sources such as agency reports, we included any studies that reported either body measurement for either species. Our goal was to obtain information at a representative spatial extent for populations of both species that were allopatric and sympatric as well as harvested and non-harvested across their range, rather than an exhaustive search. While some studies reported additional metrics (e.g., skull measurements or lean mass), not enough studies reported these measurements to allow comparative analyses. Data reported in previous studies for both body mass and body length varied in format, and we used raw data when available. Some studies required us to use summary data or to estimate values from high-resolution published figures. Because body mass varies seasonally, we only used body mass measurements collected prior to July 1 because this preceded the annual hyperphagic period (Hilderbrand et. al. 1999a, 2000, Belant et al. 2006). Each study population was categorized as either allopatric or sympatric based on overall species range (brown bears, McLellan et al. 2017; black bears, Garshelis et al. 2016) and as harvested or non-harvested based on information contained in the original article or subsequent reviews of local harvest regulations. For each study, we recorded the mean and standard deviation for each available metric (body mass and body length) by sex.

To test for evidence that species, sex, latitude, harvest, and sympatry were correlated with black and brown bear mass across North America, we needed to account for differences in sample size and reported variation between studies. Thus, we developed a bootstrap model selection procedure. For each iteration, we randomly drew sex-specific mass values ($n =$ reported sample size) from a normal distribution defined by the mean and standard deviation reported in each study. We truncated each distribution at 0 so all weights were positive. Then, we fitted a candidate set of biologically plausible mixed-effects models to this generated data with bear populations unique to each study as a random intercept term (39 total models, Appendix S1: Table S1), ranked models based on Akaike information criterion for small sample sizes ($AIC_c$), and saved the model rankings, $AIC_c$ weight, and $\Delta AIC_c$ (Burnham and Anderson 2002). We limited our candidate models to having 10 or fewer parameters to avoid over parameterization due to the relatively small number of studies. We repeated this process 1000 times. For model fitting, we standardized latitude (one value for each study) by mean centering and dividing by the standard deviation. We judged model fit based on the average values of model ranking, $AIC_c$ weight, and $\Delta AIC_c$ across all 1000 iterations for the candidate set (Hurvich and Tsai 1989, Burnham and Anderson 2002). We used our top performing model and re-ran the bootstrap 1,000 times to calculate the parameter estimates and reported the average values for the coefficients and standard errors. Our analysis was conducted in R version 3.6.0 (R Core Team 2019) using the packages lme4 (Bates et al. 2015) and AICcmodavg (Mazerolle 2019). Across sexes and species, body mass was strongly correlated with body length ($r^2 = 0.94$). Therefore, we presented summary information on body mass and body length but limited our analyses to body mass as this metric was available more consistently across the populations we assessed.

**RESULTS**

We compiled body size data from 18 published sources representing 18 studies of black bears...
and 14 studies of brown bears (Table 1, Fig. 1). Seven of the 18 black bear populations were sympatric with brown bears, and 14 were subjected to some level of harvest, whereas nine of the 14 brown bear populations overlapped black bear range and eight could be legally harvested under applicable harvest regulations (Table 1). In general, brown bears were larger than black bears and males were larger than females in both species (Table 1).

Our top performing model for body mass included an interaction between species and sex and a species-specific quadratic latitude term. This model ranked as the top model in all 1000 bootstrap iterations and received virtually all of the AIC\textsubscript{c} weight (average AIC weight = 1.0, range 0.97–1.00, Table 2). The two next best performing models averaged over 13 ΔAIC\textsubscript{c} (Table 2), giving us confidence to interpret coefficients from only the top model. In this top

Fig. 1. Distribution of studies for which data were used on black (Ursus americanus; Garshelis et al. 2016) and brown (U. arctos; McLellan et al. 2017) bear body sizes across North America.
Table 1. Body mass (kg) and length (cm) of black (Ursus americanus) and brown (U. arctos) bears from select North American populations reported as mean ± SD.

| Population          | Latitude | Male Body Mass | Male Body Length | Female Body Mass | Female Body Length |
|---------------------|----------|----------------|------------------|------------------|-------------------|
| **Black bears**     |          |                |                  |                  |                   |
| Allopatric          |          |                |                  |                  |                   |
| Florida             | 26       | 144.7 ± 27.6   | ...              | 74.6 ± 6.6       | ...               |
| Mexico              | 29       | 106.7 ± 22.8   | ...              | 51.6 ± 5.9       | ...               |
| Georgia             | 31       | 103.3 ± 29.7   | ...              | 53.3 ± 11.3      | ...               |
| Florida             | 31       | 138.5 ± 25.5   | ...              | 64.6 ± 14.8      | ...               |
| Virginia/NC         | 37       | 148.1 ± 25.2   | 188.1 ± 107.5    | 62.5 ± 8.0       | 146.2 ± 63.0      |
| Maine               | 46       | 122.1 ± 28.7   | 172.2 ± 10.7     | 68.9 ± 12.0      | 151.6 ± 9.6       |
| Quebec              | 47       | ...            | ...              | 85.0 ± 20.7      | ...               |
| New Brunswick       | 47       | 127.7 ± 30.1   | 169.2 ± 12.6     | 64.7 ± 12.0      | 143.6 ± 11.4      |
| Quebec              | 47       | 104.2 ± 26.0   | 167.3 ± 13.9     | 53.5 ± 7.4       | 140.4 ± 9.1       |
| Ontario             | 48       | 126.7 ± 25.3   | 188.5 ± 11.0     | 64.0 ± 9.6       | 160.6 ± 7.1       |
| Newfoundland        | 49       | 157.8 ± 42.9   | 181.7 ± 16.8     | 84.6 ± 24.6      | 165.7 ± 11.2      |
| **Sympatric**       |          |                |                  |                  |                   |
| Yellowstone         | 44       | 101.4 ± 26.1   | ...              | 67.0 ± 23.8      | ...               |
| Southeast B.C.      | 50       | 93.7 ± 17.7    | ...              | 58.4 ± 9.1       | ...               |
| Kenai 1947 burn     | 60       | 95.5 ± 26.2    | ...              | 55.9 ± 7.1       | ...               |
| Kenai 1969 burn     | 60       | 116.4 ± 40.6   | ...              | 61.7 ± 8.9       | ...               |
| "Alaska"           | 60       | 123.9 ± 23.0   | 179.2 ± 11.9     | 68.1 ± 11.7      | 157.7 ± 9.3       |
| Northern Canada     | 62       | 116.7 ± 25.3   | 172.2 ± 18.5     | 87.6 ± 22.2      | 156.5 ± 17.1      |
| Denali             | 62       | ...            | ...              | 86.1 ± 19.6      | ...               |
| **Brown bears**     |          |                |                  |                  |                   |
| Allopatric          |          |                |                  |                  |                   |
| Kodiak Island       | 57       | ...            | ...              | 183.1 ± 28.3     | 190.2 ± 9.4       |
| SE Alaska           | 57       | 271.2 ± 84.8   | ...              | 176.0 ± 54.8     | ...               |
| Katmai             | 59       | ...            | ...              | 172.9 ± 28.1     | 186.3 ± 13.0      |
| Northern Canada     | 64       | 185.9 ± 34.1   | 198.1 ± 12.9     | 108.0 ± 21.1     | 171.2 ± 8.4       |
| Western Brooks      | 68       | 165.3 ± 27.4   | ...              | 112.0 ± 22.5     | ...               |
| **Sympatric**       |          |                |                  |                  |                   |
| Yellowstone         | 44       | 193.3 ± 22.0   | ...              | 134.5 ± 13.5     | ...               |
| Southeast B.C.      | 50       | 182.0 ± 33.0   | ...              | 112.0 ± 33.8     | ...               |
| Lake Clark          | 60       | 226.5 ± 94.4   | 199.4 ± 14.2     | 129.3 ± 28.0     | 178.8 ± 9.4       |
| Kenai              | 60       | ...            | ...              | 155.0 ± 24.0     | ...               |
| Denali             | 62       | ...            | ...              | 196.1 ± 24.7     | ...               |
| NC Alaska Range     | 64       | 257.4 ± 32.0   | 212.6 ± 11.3     | 114.2 ± 13.9     | 179.0 ± 7.5       |
| Gates of the Arctic| 67       | 151.6 ± 46.2   | 183.2 ± 9.0      | 91.3 ± 13.5      | 164.2 ± 9.6       |
| Noatak             | 67       | 202.8 ± 30.3   | 193.7 ± 18.8     | 111.1 ± 15.5     | 174.4 ± 10.0      |

**Notes:** Harvested populations are noted in bold type. Ellipses indicate data was not available for a given metric. Letters in superscript indicate sources: a, Maehr et al. (2001); b, Dobey et al. (2005); c, Hellgren and Vaughan (1994); d, Mahoney et al. (2001); e, Samson and Huot (1995); f, Schwartz et al. (2014); g, McLellan (2011); h, Schwartz and Franzman (1991); i, Bartareau et al. (2012); j, Belant et al. (2006); k, Hilderbrand et al. (2018); l, Titus and Beier (1993); m, Bartareau et al. (2011); n, Reynolds and Hechtel (1989); o, Blanchard (1987); p, Hilderbrand et al. (1999a); q, Reynolds (1989); r, Ballard et al. (1990).

model, female black bears were the reference category (average intercept = 65.7 kg) and male black bears were on average 47.7 kg larger than female black bears, but the species did not exhibit a significant latitudinal trend (Fig. 2) as the confidence intervals overlapped zero for the 1st order term (average $\beta = -5.0$, average SE = 7.4) and the 2nd order term (average $\beta = -1.0$, average SE = 5.6; Table 3). Female brown bears were on average 96.6 kg larger than female black bears, and male brown bears exhibited even stronger sexual dimorphism than male black bears.
bears (an average of 25.3 kg) in the interaction term of species and sex (Table 3). Brown bears exhibited a significant latitudinal trend, with mass initially increasing with latitude (1st order term average $\beta = 41.1$ kg, average SE = 8.9) and then decreasing at the northern-most latitudes (2nd order term average $\beta = -56.0$, average SE = 15.9), although we note that this effect was largely influenced by the two studies in Yellowstone. The resulting relationship from this model highlights the greater sexual dimorphism evident in brown bears compared to black bears along a latitudinal gradient as well as the notable latitudinal trend for brown bears (Fig. 2). We found no evidence for a direct effect of harvest or sympatry for either species.

**DISCUSSION**

Overall, our results confirmed and extended evidence that brown bears are generally larger than black bears and that males are typically larger than females for both species across North America. Also confirming past work, we found no evidence for a latitudinal gradient in body size for black bears, while brown bears tended to be largest at middle latitudes. Although we expected sympatry and harvest to influence body mass, we found no evidence of these effects. We expect this was due to the dominant influences of the quality and diversity of nutritional resources (e.g., Fortin et al. 2007) on body size and, by extension, of niche width (Bolnick et al. 2010), though small sample sizes may have played a role as well. Lastly, our work quantified the broad patterns in body size for both brown and black bears of both sexes at the continental scale. Understanding

### Table 2. Top 5 models from bootstrap model selection analysis for body mass (kg, body mass) of black (*Ursus americanus*) and brown (*U. arctos*) bear body sizes across North America.

| Model | Avg Rank (SD) | Avg AICc† weight | Avg $\Delta$AICc (SD) |
|-------|---------------|-----------------|----------------------|
| Body Mass $~$Species $\times$ Sex $+$ Species $\times$ Latitude $+$ Species $\times$ Longitude | 1.0 (0.0) | 1.0 | |
| Body Mass $~$Species $\times$ Sex $+$ Species $\times$ Latitude | 2.4 (0.7) | < 0.01 | 13.4 (2.4) |
| Body Mass $~$Species $\times$ Sex $+$ Species $\times$ Latitude $+$ Overlap | 3.6 (0.8) | < 0.01 | 14.1 (2.8) |
| Body Mass $~$Species $\times$ Sex $+$ Species $\times$ Latitude $+$ Harvest | 4.7 (0.9) | < 0.01 | 14.7 (2.4) |
| Body Mass $~$Species $\times$ Sex | 5.1 (2.0) | < 0.01 | 15.9 (4.9) |

*Notes:* Multiplier ($\times$) denotes an interaction between 2 variables, and all models include a random intercept term for the study which data were used from.
† Akaike information criteria for small sample sizes.

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**Fig. 2.** Predicted results from the top performing mixed-effects model for black (*Ursus americanus*) and brown (*U. arctos*) bear body mass. Estimated fit and upper and lower 95% confidence intervals are depicted by the colored bands and are the averaged predicted values from 1,000 bootstrap iterations of data generation and model fitting. The models were cut off 2 degrees of latitude beyond the northern-most and southern-most studies due to a lack of data. Reported averages from each study are plotted as points following the same coloration for sex.
these patterns can be helpful in understanding changes in the realized phenotypic niche in relation to variation in ecological conditions or anthropogenic impacts as the ability to respond to such changes may reflect, to an extent, the resiliency of a population.

**Sex and species**

As expected, we found that bears of both species were sexually dimorphic (Tables 1 and 2; Fig. 2), possibly due to differences in behavioral strategies between the sexes as they balance risk vs. resource availability and differentially invest in the energetic costs of body growth vs. supporting offspring (Farley and Robbins 1995, Jacoby et al. 1999, Ben-David et al. 2004, Hilderbrand et al. 2018a, b). Within gender, brown bears generally achieved larger body sizes than black bears regardless of latitude, sympathy, or harvest (Tables 1 and 2; Fig. 2). Our meta-analysis results provide useful estimates for these differences (between species and sexes) at the continental scale, and our hope is that these are beneficial for future research.

**Latitude**

Our findings generally support prior work that black bear body size does not appear to be positively related to latitude (Kennedy et al. 2002, Meiri et al. 2004). At a continental scale, we did not observe a significant trend in black bear body mass from studies ranging from 26° to 62° N (Table 3, Fig. 2). As with salmon, abundant mast crops have the capacity to support very large individual black bears (e.g., Alt 1980); however, our findings suggest this may be a localized effect. Bonin et al. (2019) did find that trophic position and dietary niche width was positively correlated with latitude over a 15° latitudinal gradient in Quebec, Canada, though this was at the northern edge of the distribution of black bears in Eastern North America. Conversely, brown bears exhibited a significant relationship in body size, which increased from their southern range extent at 44° N to ~57° N and then decreased at their northern extent up to 68° N (Table 3, Fig. 2). We interpret this relationship as support for brown bear body size being driven by food quality and quantity, especially salmon, in contrast to a purely latitude-driven climate effect such as Bergmann’s Rule. Salmon are more abundant in the diet of brown bears at mid-latitudes, and the occurrence of smaller individuals at higher latitudes is likely related to resource limitations (Hilderbrand et al. 1999b, 2018a, b, Mowat and Heard 2006). The broad scale of our meta-analysis permitted us to identify this relationship, but we were unable to establish causality and expect body size determinants are population- and, potentially, individual-specific.

**Sympathy**

We did not find direct evidence for an effect of sympathy on body size in this study, and we suspect that we had limited power to do so based on the distribution of allopatric/sympatric studies between the 2 species. However, the clear latitudinal trend of body mass detected in brown bears (Fig. 2), which was not evident in black bears, suggests that brown bears could be taking advantage of a latitudinal resource gradient which black bears are not. If so, this would support prior findings that brown bears may out-compete or exclude black bears from preferred food resources as evidenced by their larger body size where they were sympatric (Jacoby et al. 1999, Belant et al. 2006, 2010, McLellan 2011). We speculate that when black bears are present, with their higher relative levels of productivity (Garshelis 1994, McLellan 1994), they help create a floor for niche realization of brown bears. At

### Table 3. Bootstrapped parameter estimates from the top model associated with black (*Ursus americanus*) and brown (*U. arctos*) bear body mass across North America.

| Variable          | β (SD)   | Standard Error (SD) |
|-------------------|----------|----------------------|
| Intercept         | 65.7 (1.3) | 6.3 (0.3)             |
| Species—Brown     | 96.6 (3.8) | 9.5 (0.4)             |
| Sex—Male          | 47.5 (1.5) | 2.1 (0.1)             |
| Species—Brown: Sex—Male | 25.3 (3.2) | 3.0 (0.1)             |
| Species—Black: Latitude | −5.0 (2.9) | 7.4 (0.3)             |
| Species—Black: Latitude² | −1.1 (1.7) | 5.6 (0.3)             |
| Species—Brown: Latitude | 41.1 (5.7) | 8.9 (0.3)             |
| Species—Brown: Latitude² | −56.0 (4.9) | 15.9 (0.8)           |

**Notes:** Estimates are reported as the average fitted coefficient (β) and standard error values across 1,000 iterations, and standard deviation (SD) is reported for each in parentheses. Intercept represents black bear females, and latitude was standardized by mean centering and dividing by the standard deviation.
the same time, brown bears, as they are the more dominant species, help create a ceiling for niche realization of black bears when they are sympatric. Regardless, the potential effect of sympatry and allopatry likely warrants additional consideration as morphometric data accumulate across the range of both species.

**Harvest**

Most populations included in our study were harvested, likely limiting our ability to detect any harvest effects that may have been present. Additionally, we had no measure of harvest pressure; therefore, each population was simply categorized as either harvested or unharvested. Our metric of harvest was a coarse indicator of mortality owing to the continental scale we adopted, and populations experience other forms of mortality that may be selective for certain demographic classes (such as human conflict and management removals). Finally, many areas include harvest restrictions that differentially protect females (e.g., no harvest of females with dependent offspring). Thus, our study likely had low power to detect any effect of harvest on body size at broad geographic scales. We suggest detailed local studies are likely required to assess the potential effects of harvest on body size at the population level (e.g., Bartareau et al. 2011, 2012, Hilderbrand et al. 2018b). For example, Brockman et al. (2020) assessed the effects of elevated harvest designed to reduce predation on moose by an interior Alaskan brown bear population. Over a 13-yr period of elevated harvest (8–15% annually) that reduced the population by 25–40%, Brockman et al. (2020) did not detect changes in skull size or age structure of the harvested bears relative to the prior 10 yr under a more conservative, sustained yield-based harvest regime.

**Integration**

A mechanistic understanding of the interaction between species and their habitats is critical to contemporary wildlife management and conservation. In particular, effective wildlife management depends on clearly defined management objectives and an understanding of the carrying capacity of the ecosystem and population productivity. North American black and brown bear populations are currently managed with myriad of objectives (e.g., natural state, sustained yield, localized recovery, range expansion, predation reduction). For brown bears, lean mass and skull size in naturally regulated systems can vary 2- to 3-fold in adult females and 3- to 4-fold in adult males (Hilderbrand et al. 2018b), indicating broad ecological and physiological niche utilization. This within-population variation can occur despite disparate food resource availability across study areas (Hilderbrand et al. 2018b). Growth curves depict similar levels of variation in adult body size within populations of black and brown bears (Mahoney et al. 2001, Bartareau et al. 2011, 2012). Additional work is needed to assess whether sympatry between black and brown bears can impact within-population variation in these metrics and, thus, the breadth of niche utilization. Although we did not find differences between harvested and unharvested populations, other studies suggest that harvest impacts on body size at the population level warrant consideration by wildlife managers (Coltman et al. 2003, Fenberg and Roy 2008, Allendorf and Hard 2009). Clarifying large-scale physiological patterns may assist in understanding past, present, and future changes to realized niches in relation to environmental, ecological, and anthropogenic changes and subsequent resiliency of species and populations.

**Acknowledgments**

J. Lawler, J. Rasic, H. Golden, and 2 anonymous reviewers provided reviews of earlier drafts that improved the final manuscript. Funding and staff support were provided by the National Park Service and U.S. Geological Survey. All authors attest they have no conflicts of interest to declare. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U. S. Fish and Wildlife Service. Use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

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