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Human influences affect home range quality and nutritional condition of American black bears (Ursus americanus) in Rocky Mountain National Park, Colorado, USA

Las influencias humanas afectan la calidad del hábitat y la condición nutricional de los osos negros (Ursus americanus) *en el Parque Nacional de las Montañas Rocosas, Colorado, USA*

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ABSTRACT

Human impacts and policies affect carnivores, even within Protected Natural Areas (PNAs). Rocky Mountain National Park (RMNP) in Colorado conserves a small population of American black bears (*Ursus americanus*), where harsh high-elevation conditions restrict food availability and diversity, leading to historically low individual condition and demographic fitness. We used resource-area-dependence analysis to identify habitats associated with home range quality and related bear habitat associations at both the landscape and home range scales to nutritional condition of bears. Areas characterized by high human-use were the only habitats significantly positively related to the home range quality of bears in RMNP; bear condition was likewise positively associated with human-use areas during autumn, the season most important for fat accumulation in bears. While use of anthropogenic foods significantly increased individual and demographic fitness of bears in RMNP, use of human-use areas frequently leads to human-bear conflicts. Enhancing natural foraging habitats may help decrease bear dependence on human-use areas and conflicts in and around RMNP. However, contemporary and predicted future trends in key foraging habitats suggest that food availability will further decline for bears in RMNP. Only significant human-induced disturbance can alter this trajectory, but such management is unlikely given U.S. National Park Service non-intervention "ecological process management" (i.e., "natural regulation") policies.

Key words: American black bear; climate change; forest understory; home range quality; human conflicts; nutritional condition; Rocky Mountain National Park, *Ursus americanus*.

Relevancia:
Este estudio muestra que, incluso dentro de áreas naturales protegidas, las áreas sujetas a uso humano pueden mejorar la condición corporal de carnívoros, pero también aumentar el riesgo de conflictos, planteando retos clave para el manejo y la conservación

RESUMEN

Los impactos humanos y las políticas de manejo afectan a los carnívoros, incluso dentro de Áreas Naturales Protegidas (ANP). El Parque Nacional de las Montañas Rocosas (PNRM), en Colorado, conserva una pequeña población de osos negros (Ursus americanus), *donde las duras condiciones de gran altitud limitan la disponibilidad y diversidad de alimentos, generando históricamente baja condición individual y aptitud demográfica. Aplicamos un análisis de dependencia de*

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área-recurso para identificar hábitats asociados con la calidad del área de distribución y relacionamos estas asociaciones, tanto a escala de paisaje como de rango hogareño, con la condición nutricional de los osos. Las áreas de alto uso humano fueron los únicos hábitats significativamente asociados de manera positiva con la calidad del área de distribución; la condición de los osos también se relacionó positivamente con estas áreas en otoño, la estación más importante para la acumulación de grasa. Aunque el uso de alimentos antropogénicos incrementó la condición individual y la aptitud demográfica de los osos en el PNRM, la utilización de áreas humanas con frecuencia genera conflictos oso-humano. Mejorar los hábitats naturales de alimentación podría disminuir la dependencia de los osos de áreas humanas y los conflictos dentro y alrededor del parque. Sin embargo, las tendencias actuales y futuras de los hábitats clave de forrajeo sugieren una reducción continua en la disponibilidad de alimento. Solo una intervención humana significativa podría modificar esta trayectoria, aunque es poco probable dada la política de no intervención del Servicio de Parques Nacionales de EE. UU., basada en la "regulación natural".
Palabras clave: *Oso negro americano; cambio climático; sotobosque forestal; calidad del área de distribución; conflictos humanos; estado nutricional; Parque Nacional de las Montañas Rocosas,* Ursus americanus*.*

INTRODUCTION

Human influences have significant impacts on large carnivore populations (Gittleman, 2001; Terraube *et al.*, 2020; Cimatti *et al.*, 2021). While Protected Natural Areas (PNAs) are popularly considered to be refuges, intentional and unintentional human impacts and policies can significantly affect wildlife, including large carnivores, in PNAs (Terraube *et al.*, 2020).

Conservation of large carnivores, especially small populations, can be challenging for many reasons, including low reproductive rates, susceptibility to stochastic events, local habitat limitations, and negative interactions with humans (Gittleman *et al.*, 2001; Ray *et al.*, 2005).

Rocky Mountain National Park (RMNP) is a subalpine-alpine PNA located in north-central Colorado, USA, which conserves a small (20–24 individuals; Baldwin and Bender 2009a; Rocky Mountain National Park, 2012) population of American black bears (*Ursus americanus*) of unique ecological status (Baldwin, 2008; Baldwin and Bender, 2008a; 2009a,b). This high elevation population is challenged ecologically by many factors, particularly those limiting the production and diversity of natural foods (Baldwin and Bender, 2009b; Bretfeld *et al.*, 2019). Many of the habitats of RMNP (i.e., tundra, subalpine forests, etc.) lack important bear foods such as hard mast crops, and soft mast crops can be variable and scarce. High elevations (>2,400 m) also result in short growing seasons (6–7 months), limiting the time that bears have to accrue body reserves. High levels of recreational use, increased human development, and U.S. National Park Service (NPS) policies ("ecological process management" or "natural regulation"; Cole and Yung, 2010; NPS, 2014) that restrict habitat enhancements, are additional challenges that can significantly affect food availability and overall habitat quality for this population.

Food availability is a key determinant of habitat quality for black bears (Rogers, 1993), as virtually every individual fitness parameter of large mammals is related to nutritional condition (Hanks, 1981; Rogers, 1987; Eberhardt, 2002; Bender, 2020). Historic data collected from 1984–1991 in RMNP indicated that bear size was well below average, age of primiparity was delayed, litter sizes were reduced, reproductive pauses were extended, and female home range sizes were large (Baldwin, 2008; Baldwin and Bender, 2008a, 2009a,b). These characteristics were all indicative of severe malnutrition (Hanks, 1981; Rogers, 1987; McLoughlin *et al.*, 2000). Consequently, RMNP's bear population exhibited one of the lowest reproductive rates and densities recorded (Baldwin, 2008; Baldwin and Bender, 2009b).

Food-related challenges necessitate conserving habitats that provide for the nutritional needs of bears. Declines in key habitats (i.e., areas that supply high-quality and seasonally important foods) could lower individual and demographic fitness and lead to increased use of areas outside RMNP and consequent human conflicts (Beckmann and Berger, 2003b; Baldwin and Bender, 2009b; Baruch-Mordo *et al.*, 2014; CPW, 2015), which could further compromise the viability of RMNP's bear population (Beckmann and Berger, 2003a,b; Johnson *et al.*, 2020). Moreover, the importance of identifying and maintaining key habitats is increasingly relevant in light of long-term trends in forest understory (i.e., bear foods) (Bretfeld, *et al.*, 2019; Pelz and Smith, 2018; Kaczynski *et al.*, 2018; Pappas *et al.*, 2020) and the likely impacts of climatic warming on habitats of RMNP (Rocky Mountain National Park, 2008), neither of which is favorable for bear foraging environments.

Because habitat quality fundamentally drives the nutritional condition and, consequently, the fitness of bears (Bender, 2020), our primary goal was to determine which habitat characteristics most strongly influence the quality of bear home ranges and the nutritional condition of bears in RMNP. Consequently, we used resource-area-dependence analysis (RADA) to determine which habitat types significantly affected size of home ranges (Kenward *et al.*, 2018) during the 2003–2006 period. We indexed habitat quality using home range size because smaller home range sizes are indicative of greater resource availability and hence better habitat quality (Kenward *et al.*, 2018; Bender, 2020; Bender *et al.*, 2023). We further determined which habitat types and other metrics of the landscape and home ranges significantly affected nutritional condition of bears. Last, we relate our 2003–2006 data to contemporary (i.e., the last ca. 10 y) trends in bears and the landscape of RMNP resulting from natural processes, direct human impacts, and NPS policies.

MATERIALS AND METHODS

Study Area

RMNP is a 1,080 km^2 PNA located in the Rocky Mountain Front Range of north-central Colorado, USA (40.3330 N, 105.7090 W; Figure 1). Topography includes high mountainous peaks interspersed with small subalpine-alpine meadows, lakes, streams, and glaciers, with tundra at higher elevations. Elevations range from 2,400–4,345 m. The continental divide bisects

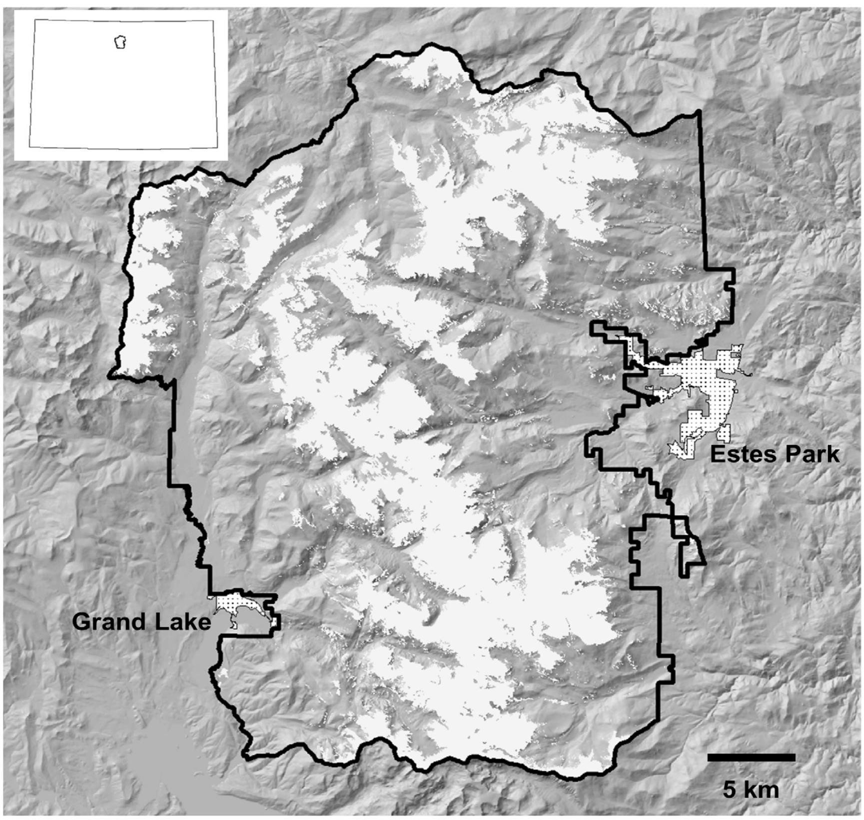

Figure 1. Topographic hillshade of Rocky Mountain National Park (RMNP), north-central Colorado, USA. Lighter areas are the highest elevation alpine habitats that produce little or no food for bears. Inset shows location of RMNP in Colorado, USA.

RMNP, creating different climatic patterns and vegetation types from east to west, with eastern RMNP being drier. Precipitation averages 35.1 cm in the town of Estes Park; 75% of precipitation falls from April to September. Mean daily high temperatures range from 7.2ºC in February to 27.8º C in July in Estes Park.

Vegetation includes herbaceous meadows and montane forests of lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) with drier sites dominated by ponderosa pine (*P. ponderosa*) and Douglas-fir (*Psuedotsuga menziesii*). Subalpine habitats are dominated by Engelmann spruce (*Picea englemannii*) and subalpine fir (*Abies bifolia*) with limber pine (*P. flexilis*) occasionally present. Elevations above timberline (ca. 3,500 m) are dominated by tundra and bare rock. Below treeline, wetland and riparian areas are comprised of a variety of species but are dominated by dense stands of spruce-fir and aspen in forested areas (Salas *et al.*, 2005). Recreational use by humans is high with >4 million visitors annually.

Capture and Monitoring

We captured bears using foot snares and culvert traps, 2003–2006. We anesthetized captured bears with a 5:1 mixture of ketamine hydrochloride (approximately 7.4 mg/kg body mass) and xylazine hydrochloride (approximately 1.3 mg/kg body mass) and fit bears with VHF radiocollars. We obtained relocations a minimum of weekly through observations of bears, or by circling bears to localize their location, from capture through the time of den entrance, and subsequently from May through den entrance annually. We constructed 95% and 100% minimum convex polygon (MCP) annual (number of locations = 24.5 [SE = 2.3]) and seasonal (number of locations: spring = 7.6 [SE = 0.7], summer = 10.2 [SE = 1.3], autumn = 9.4 [SE = 0.9]) home-ranges (Baldwin, 2008), respectively, for habitat analyses using ArcMap 10.0 (ESRI, Redlands, CA). For 95% MCP home ranges, we used the area-added approach to exclude outlier locations (White and Garrott,1990). We used the 100% MCP estimator for seasonal ranges because of the lesser number of locations.

Landscape and home range composition

We estimated 21 annual and 15–21 seasonal home ranges for 10 radio-collared bears (6 females and 4 males), representing approximately half of the population in RMNP during our study period (Baldwin and Bender, 2009a). We extracted habitat attribute data for annual and seasonal home ranges from GIS coverages of RMNP and surrounding areas (Salas *et al.*, 2005). We used habitat types and 6 landscape metrics (Table 1) to assess landscape-home range associations of bears annually and seasonally. For each individual annual and seasonal home range, we also calculated the proportion of locations in each habitat type (total number of locations in a habitat type divided by the total number of locations in the home range). We selected landscape metrics based on important landscape factors for bears (Linke *et al.*, 2005), and calculated landscape metrics (e.g., measures of patch, edge, diversity, etc.; Table 1) using the Patch Analyst extension (Elkie *et al.*, 1999). We also created a 400 m buffer around all human-use areas (trails, roads, campsites, ranger stations, and other developed areas) based on observed daily bear movements and human activity patterns to define a human-use habitat type and included this in habitat type analyses (Baldwin, 2008).

We used RADA (Kenward *et al.*, 2018) to assess home range quality by determining relationships between habitat type composition and home range size, specifically modeling ln(ah/A) as a function of ln(A), where A = area of home range and ah = area of home range comprised of individual habitat types. Habitat types were based on a vegetation classification and map developed for RMNP (Salas *et al.*, 2005), which provides a detailed and verified characterization of plant communities and land cover (Table 1). We determined all correlations between ln(ah's) and ln(A) and identified the habitat type with the strongest significant negative correlation using randomization tests following Kenward *et al.* (2018). We then successively repeated this process using a conditional probability approach. Specifically, if ln(ah1) had the strongest significant negative correlation with ln(A), we then (1) subtracted ah1 from A; (2) determined correlations between remaining ln(ah's) and ln(A–ah1) for all remaining habitat types; and (3) identified the strongest significant negative correlation from the remaining ah's. We repeated this process until there were no significant negative correlations remaining. If a habitat type was not present in a bear's home range, we

Table 1. Description of habitat types and landscape metrics used to evaluate black bear occurrence in Rocky Mountain National Park, Colorado, USA (Baldwin and Bender, 2008a,b; 2012).

Habitat type	Description
Herbaceous meadow	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Mesic shrubland	Shrublands lining streambanks and valley bottoms
Xeric shrubland	Shrub-dominated communities associated with drier sites
Krummholz	Characterized by stunted limber pine, Engelmann spruce, and subalpine fir at treeline
Dead and down	Characterized by fallen timber from wind, avalanches, or fire
Aspen	Forested site dominated by aspen
Mixed conifer with aspen	Canopy dominated by aspen and mixed conifer species
Riparian mixed conifer	Canopy dominated by spruce/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of two or more coniferous species including Engelmann spruce and subalpine fir
Lodgepole pine	Canopy dominated by lodgepole pine
Limber pine	Canopy dominated by limber pine
Ponderosa pine	Canopy dominated by ponderosa pine
Montane Douglas fir	Canopy dominated by Douglas fir though ponderosa pine can be codominant
Rock	Characterized by rock, bare soil, or snow
Non-vegetated surface	Included areas covered by roads, trails, and campsites
Patch density	Number of patches/km2
Edge density	Meters of edge/ha
Shannon’s diversity index	Measure of relative patch diversity
Shannon’s evenness index	Measure of patch distribution and abundance
Area-weighted mean shape index	Measure of shape complexity
Interspersion juxtaposition index	Measure of patch adjacency

set ah/A = 0.001 (Kenward *et al.*, 2018). We used RADA only to identify habitat types significantly related to home range size, and we performed analyses for annual and seasonal home ranges.

Condition-habitat relationships

We located and anesthetized (see above) collared bears in dens during early hibernation to assess the nutritional condition attained by bears during the previous year. We used bioelectrical impedence analysis (BIA) to assess percent body fat (BF) (Baldwin and Bender, 2010b). For resistance measurements, we placed bears on a plastic tarp (to eliminate conductivity issues associated with wet ground) and measured BIA multiple times to verify readings. We also determined a body condition index (BCI) for bears using straight-line body length (cm) and mass (kg; Cattet *et al.*, 2002; Baldwin and Bender, 2010b). BCI values are strongly correlated to true body condition ($r = 1.0$, $P < 0.001$; Cattet *et al.*, 2002) and reflect the combined mass of BF and lean muscle tissue of an individual relative to its body size (Baldwin and Bender, 2010b).

We correlated (Zar, 1999) BCI and BF with proportion of home-range composition (i.e., landscape scale) and proportion of home range locations (i.e., home range scale) of habitat types within individual bear ranges to identify positive associations with body condition. We performed separate analyses for annual and seasonal home ranges. We also included landscape metrics from home ranges to determine their influence on condition at the landscape scale.

RESULTS

RADA

Human-use areas were negatively related to bear home range size both annually ($r = -0.47$, $P = 0.089$) and during summer ($r = -0.39$, $P = 0.078$), indicating that home range quality improved (i.e., home range size decreased) as human-use areas increased within home ranges across both temporal scales. No other habitat types were significantly related to home range size annually or seasonally, although in all cases human-use ($r = -0.20 - -0.33$; $P > 0.184$) exhibited the strongest negative correlations with home range size. Human-use areas comprised 24–91% of bear annual home ranges in RMNP.

Habitat-condition associations

Human-use, aspen, and mesic shrubland were the habitat types most consistently and positively associated with bear condition in RMNP. Human-use areas were positively associated with BF at both the landscape ($r = 0.64$, $P = 0.062$) and home range scales ($r = 0.87$, $P = 0.056$), and with BCI at the home range scale ($r = 0.88$, $P = 0.048$), in autumn. Aspen was positively associated with BF (landscape: $r = 0.69$, $P = 0.083$) and BCI (landscape: $r = 0.81$, $P = 0.029$; home range: $r = 0.79$, $P = 0.033$) in spring. Mesic shrublands were positively associated with BF (home range: $r = 0.69$, $P = 0.065$) and BCI (home range: $r = 0.77$, $P = 0.025$) annually and with BCI (home range: $r = 0.85$, $P = 0.016$) during spring.

Other positive associations were: Douglas fir with BF (landscape: $r = 0.68$; $P = 0.095$) in spring; lodgepole pine with BCI (landscape: $r = 0.71$; $P = 0.070$) in spring; and mixed conifer with BCI (landscape: $r = 0.58$, $P = 0.091$) in autumn. No landscape metrics were associated with condition indices.

DISCUSSION

Human-use was the only habitat type positively associated with the quality of bear home ranges (i.e., was significantly negatively correlated with home range size), and this association highlighted the importance of anthropogenic foods to bears (Baldwin, 2008; Baldwin and Bender, 2009a) within RMNP. Food availability is the primary influence on bear habitat selection (Rogers, 1993), and this was further illustrated in seasonal habitat-condition associations in RMNP (see below). Because autumn is the season most closely tied to fat accrual in bears (Pelton, 2003), the positive association between human-use areas and bear condition during autumn was particularly important. During our 2003–2006 study period, we found a greater proportion of locations of radio-collared bears (70%) in human-use areas compared to historical records from 1984–1991 (51%; Baldwin 2008). Further, comparisons between recent and historic bear diets indicated that occurrence of anthropogenic foods was 15.2X higher during the recent period (Baldwin and Bender, 2009a). Anthropogenic foods are higher in calories, carbohydrates, proteins, and fats than most natural foods (Stringham, 1989), which would predict an increase in condition of bears from the historic to the recent period. In fact, nutritional condition of bears increased from historical levels in RMNP, which consequently resulted in increased individual size and productivity of bears (Baldwin, 2008; Baldwin and Bender, 2009b). Greater use of human-use areas and anthropogenic foods during autumn is frequently seen in urban/exurban bear populations and in poorer quality habitats (CPW, 2015; Johnson *et al.*, 2015), likely because of the importance of fat accrual prior to hibernation.

These results indicate that bears in RMNP have greatly increased use of human-use areas and anthropogenic foods, and derive substantial benefits (i.e., increased condition and individual fitness) from this use. The changing distribution of bears in RMNP towards areas with greater human influence (Baldwin and Bender, 2008a, 2010a) and increased individual size and population productivity of bears due to increased use of anthropogenic foods (Baldwin and Bender, 2009a,b; see also Johnson *et al.*, 2020) show that bears in RMNP have altered behaviors to access high yield resources associated with human-use areas. Throughout much of their distribution in North America, bears are increasingly using areas with greater human impacts and high levels of human activity, which often leads to conflicts between humans and bears, particularly in urban and exurban areas (Beckmann and Berger, 2003a,b; Baruch-Mordo *et al.*, 2014; CPW, 2015; van Manen *et al.*, 2019; Braunstein *et al.*, 2020). Increasing negative bear-human encounters in and around RMNP (CPW, 2015; Rocky Mountain National Park, 2021), including the first attack on a human (in 2003) since 1971, likely reflect increasing habituation to humans in order to exploit anthropogenic foods.

These behaviors are at least partially a response to the high elevation, food-limited environment of RMNP (Figure 1), which challenges bears to meet nutritional requirements as evidenced by malnutrition-related characteristics of the bear population in the historic period (see above; Baldwin, 2008; Bender and Baldwin, 2008a, 2009a,b). Much greater inclusion of anthropogenic foods during our study period has reversed those indicators of severe malnutrition (Baldwin and Bender, 2008a; 2009a,b). However, increased fitness came with a cost, i.e., increased incidence of human-bear conflicts, which in turn poses its own threat to the bear population (Beckmann and Berger, 2003b; Baldwin and Bender, 2009b; Barush-Mordo *et al.*, 2014; Johnson *et al.*, 2020). The trend of increasing bear-human conflicts has continued into the contemporary period (CPW, 2015); for example, 44 conflicts were reported in approximately one month in the Estes Park area in 2019 (Pialet, 2019), and bear-human encounters are increasing in human-use areas in RMNP despite a static bear population (Rocky Mountain National Park, 2012, 2021).

Consequently, conservation of bears in RMNP should strive to maintain increased fitness, but decrease dependence on anthropogenic foods and limit use of human-use areas (a common recommendation for bear conflict areas; Barush-Mordo *et al.*, 2014; CPW, 2015; Lewis *et al.*, 2015; van Manen *et al.*, 2019). Options to enhance the foraging attributes of natural habitats in RMNP are limited, however, because of productivity constraints and NPS policies, which favor (but do not mandate) a hands-off approach to wildlife management (Cole and Yung, 2010; NPS, 2014).

Productivity constraints largely confine conservation options to lower elevation habitats, preferably those positively associated with the availability of preferred natural foods and bear condition. The primary natural foods of bears in RMNP were green vegetation (58%), insects (47%), and soft mass (32%) during spring, summer, and autumn, respectively (Baldwin and Bender, 2009a); this was reflected in seasonal habitat-condition relationships. Despite being rare in RMNP (0.5% of land composition), aspen was positively related to condition of bears during spring at both landscape and home range scales, because of food abundance (Hellgren *et al.*, 1991; Costello and Sage, 1994; Lyons *et al.*, 2003). Aspen was also consistently overrepresented in home ranges and was the only natural habitat type positively associated with bear presence annually within home ranges in RMNP (Baldwin, 2008). Similarly, Douglas fir was positively related to condition during spring, and Douglas fir logs are preferred sites when foraging for ants (Bull *et al.*, 2001).

In summer, lodgepole pine was positively related to bear condition, and lodgepole pine stands contained a higher proportion of sites with ant resources than all other habitat types in RMNP (Baldwin, 2008). In autumn, condition was positively associated with mixed conifer (Table 1), and cover of soft mass-producing species was greatest in mixed conifer stands (39%; others < 14%) in RMNP (Baldwin, 2008). Last, mesic shrubland was positively related to condition of bears annually and in spring, likely because of its importance for spring foods, i.e., early phenology herbaceous vegetation (Baldwin, 2008). Such areas are used by bears during spring and early summer when herbaceous forages are highly digestible and relatively high in protein (Kelleyhouse, 1980; Graber and White, 1983; Stubblefield, 1993). Supporting this, we found that all bear locations in mesic shrublands in RMNP occurred before 24 July.

While the above identifies management opportunities, actual enhancement of foraging habitats in RMNP is challenging because NPS policies favor minimal interference with natural processes in National Parks (Cole and Yung, 2010; NPS, 2014). Consequently, most natural habitats in RMNP have changed little prior to or since our study with respect to forest understory (i.e., bear food related) attributes (Bretfeld *et al.*, 2019), despite natural disturbances such as wildfires and mountain pine beetle (*Dendroctonus ponderosae*) epidemics. Wildfires can benefit bear habitat, e.g., increase aspen regeneration (Pelz and Smith, 2018; Kaczynski *et al.*, 2018; Bretfeld *et al.*, 2019), but have affected little of the RMNP landscape. Moreover, local benefits are often compromised because of high levels of ungulate herbivory (Pelz and Smith, 2018; Kaczynski *et al.*, 2018), a result of high density large herbivore populations common to unhunted PNAs including RMNP (Powers *et al.*, 2016), which is also a consequence of non-intervention NPS policies. Aspen in particular requires continued disturbance to persist on the landscape, but without human-induced disturbance on a large scale (to swamp ungulate herbivory) significant regeneration is unlikely (Pelz and Smith, 2018).

Other natural disturbances such as long-term pine beetle epidemics have affected RMNP habitats to a much greater extent than wildfire, and likely will increase in size and intensity as the climate of RMNP warms (Rocky Mountain National Park, 2008). However, widespread overstory mortality in beetle-killed stands results in little bear use of such sites (Ivan *et al.*, 2018) or positive responses in bear foods (Pappas *et al.*, 2020); the primary understory response in RMNP has been an increase in graminoids rather than more valuable mast producing shrubs (Pelz and Smith, 2018; Bretfeld *et al.*, 2019; Pappas *et al.*, 2020). While a warming climate will decrease the extent of high elevation habitats (primarily tundra) considered mostly unsuitable for bears (Figure 1) as forest cover increases in elevation, the primary bear food in high elevation forests (limber pine) is expected to decline due to a drier climate, pine beetle infestation, and blister rust (Rocky Mountain National Park, 2008). Thus, natural bear foods have shown little or no increase since our 2003–2006 study period, and neither have bears. Given that most contemporary (and likely future) changes in the RMNP landscape are at least somewhat detrimental to bear habitat, bears may be even more dependent on anthropogenic foods currently and in the future. This is corroborated by increasing human-bear encounters and conflicts in RMNP (Rocky Mountain National Park, 2021) and adjacent areas (i.e., Estes Park [Pialet, 2019]).

CONCLUSIONS

Black bears sought areas with greater availability of preferred foods in the food-limited environment of RMNP, i.e., human-use areas, which consequently comprised 24–91% of bear home ranges annually. While use of these areas increased individual fitness of bears, their use may ultimately decrease survival or otherwise negatively affect the bear population because of conflicts with humans (Baruch-Mordo *et al.*, 2014; CPW, 2015), which continue to increase in the RMNP landscape, likely due to static or declining trends in natural bear foods/habitats (Bretfeld *et al.*, 2019; Pappas *et al.*, 2020). Because use of human-use areas is food driven (CPW, 2015; Johnson *et al.*, 2015; Lewis *et al.*, 2015; Braunstein *et al.*, 2020), bears in exurban areas use these areas less when natural foods are more abundant (Baruch-Mordo *et al.*, 2014; CPW, 2015; Johnson *et al.*, 2015; Lewis *et al.*, 2015). Thus, managing natural habitats to produce foods and structures related to bear foods is key to benefiting bear condition and potentially decrease use of human-use areas. NPS policies, however, disfavor most habitat management aside from prescribed natural fires (Cole and Yung, 2010; NPS, 2014).

Consequently, both human-related factors (e.g., NPS policies, human-bear conflicts) and natural factors (e.g., climate change, competition with abundant large herbivores) pose significant challenges to the viability of bears in RMNP, and these challenges are likely to intensify without large-scale habitat enhancements. Many of the natural habitat types positively associated with bear condition (e.g., aspen, etc.) can be enhanced by applied management actions to maintain or improve their quality as bear habitat. For example, prescribed burning, thinning, patch clearcutting (commonly used in fuels reduction programs in urban-interface areas), and a "let burn" policy toward wildfires (when safety permits) can increase the availability of early successional habitats such as aspen and understory vegetation that are important food sources for bears (Irwin and Hammond, 1985). Management actions like these can also promote the fractal habitat structure preferred by bears in RMNP (i.e., high habitat diversity and significant edge associated with small habitat patches; Baldwin, 2008) as well as provide features such as dead-and-down logs that support key bear foods (e.g., insects; Baldwin, 2008). Although these actions require direct habitat management at the Park level, they are not precluded by NPS "ecological process management" or "natural regulation" policies and align with recent acceptance of direct population management approaches such as culling overabundant large herbivores (Powers *et al.*, 2016).

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