



Investigation of bed and den site selection by American black bears (*Ursus americanus*) in a landscape impacted by forest restoration treatments and wildfires



Susan M. Bard^a, James W. Cain III^{b,*}

^a Department of Fish, Wildlife, and Conservation Ecology, New Mexico State University, P.O. Box 30003, MSC 4901, Las Cruces, NM 88003, USA

^b U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation Ecology, New Mexico State University, P.O. Box 30003, MSC 4901, Las Cruces, NM 88003, USA

ARTICLE INFO

Keywords:

Bed site
Black bear
Den site
Forest restoration
Habitat selection
New Mexico
Thinning
Ursus americanus

ABSTRACT

The combined effects of long-term fire suppression, logging, and overgrazing have negatively impacted many southwestern U.S. forests, resulting in decreased habitat quality for wildlife, and more frequent and severe wildfires. In response, land management agencies are implementing large-scale forest restoration treatments, but data on how wildlife respond to restoration treatments and wildfires are often limited. We investigated bed and den site selection of American black bears (*Ursus americanus*) using GPS location data and a use/available study design to assess the influence of habitat characteristics, including wildfires, prescribed burns, and thinning treatments on bed and den site selection in the Jemez Mountains, New Mexico. The most supported models suggested that black bears were more likely to select bed sites with a combination of low horizontal visibility ($\beta = -0.007$, SE = 0.002; $P = 0.002$) and high stand basal area ($\beta = 0.013$, SE = 0.005; $P = 0.004$). The highest-ranking model for den site selection indicated that black bears were more likely to select den sites with low horizontal visibility ($\beta = -0.0102$, SE = 0.004; $P = 0.006$). Black bears used all disturbed sites to varying degrees (45% of study area), although 48% of bed sites were located in undisturbed habitat (55% of study area) while only 11% and 2% of bed sites were located in thinned and prescribed burn sites, respectively. Thirty-nine percent of bed sites were located in previous wildfire locations; however, 67% of these sites were in areas with low burn severity. Thirty-eight percent of den sites were located in previously disturbed habitat, 8 of these sites were burned by wildfires. In order to develop effective management plans for black bears, it is essential to understand responses to landscape-scale habitat disturbances due to wildfires and restoration activities, all of which are becoming more prevalent and widespread across southwestern forests. Accounting for the timing, size, and proximity of future restoration efforts would aid in mitigating potential short-term negative effects on black bears.

1. Introduction

Forests in the southwestern United States have been altered by over a century of livestock grazing, timber harvest, and fire suppression (Swetnam and Betancourt, 1990; O'Connor et al., 2014). These anthropogenic changes have interacted with climatic variation to disrupt natural fire cycles and homogenize forest structure resulting in increased density of small diameter trees, increased canopy cover, a reduction in biodiversity, and diminished habitat quality for many wildlife species (Covington and Moore, 1994; Touchan et al., 1996; Moore et al., 2004). Many forest types in the Southwest are adapted to frequent, low to moderate-severity wildfires (Allen et al., 1996;

Swetnam and Baisan, 1996; Rother, 2010). However, altered forest conditions have resulted in a shift to fire regimes characterized by large, high-severity fires (Ellis, 2001; Grissino-Mayer et al., 2004). The frequency of catastrophic, stand-replacing wildfires in the western U.S. has resulted in a demand to restore historical forest structure, plant species composition, and fire regimes (Allen et al., 2002). If southwestern forests are not restored to conditions that are more resilient to wildfires, the increased temperatures, drier winters, and earlier springs predicted for the Southwest under various climate change scenarios are likely to increase severe wildfire activity further (Westerling et al., 2006; Abatzoglou and Williams, 2016).

Common restoration techniques used to mitigate wildfire risk focus

* Corresponding author.

E-mail address: jwcain@nmsu.edu (J.W. Cain).

on fuel reduction, either by conducting prescribed burning, hand thinning trees, or removal of fuels through mechanical thins (Agee and Skinner, 2005; North et al., 2007). Restoration projects frequently involve use of multiple treatment types on the project area (e.g., thinning followed by prescribed fire). These treatments have been shown to reduce the severity of subsequent wildfires (Stephens, 1998; Pollet and Omi, 2002); however, the long-term efficacy of these treatments is still being investigated in many areas of the Southwest, including Arizona and New Mexico (Schultz et al., 2012). Although prescribed burns and thinning are frequently implemented to enhance habitat conditions for many wildlife species, the effects of these activities are rarely investigated (Block et al., 2001). Therefore, the direct and indirect consequences of these restoration efforts are largely unknown for many wildlife species.

Although many aspects of the ecology and life history characteristics of American black bears (*Ursus americanus*) are commonly investigated, our knowledge regarding responses of black bears to habitat disturbance including wildfires and forest restoration treatments is limited. Within the last decade there has been an increase in research related to human-wildlife interactions, including how humans have influenced bear movements (Baruch-Mordo et al., 2008; Cristescu et al., 2013; Duquette et al., 2017), food habits (Merkle et al., 2013; Kirby et al., 2016; Murphy et al., 2017), and population dynamics (Lewis et al., 2014). Relatively little is known regarding the responses of black bears to wildfire, prescribed burns, or thinning (but see Stratman and Pelton, 2007; Yaklin, 2017).

Wildfires, prescribed burns, and thinning treatments can cause substantial changes to habitat conditions, reducing cover (White et al., 2001; Tredick et al., 2016), and increasing fragmentation (Mitchell and Powell, 2003), which can result in increased interactions with hunters and other black bears (Linnell et al., 2000; Stewart et al., 2013). Wildfires and forest restoration treatments may create unfavorable environmental conditions at least for the short-term as they temporarily reduce forage availability, basal area, and horizontal cover, which may result in avoidance of treated areas by bears until sufficient post-disturbance vegetation recovery has occurred (Hellgren et al., 2005; Baruch-Mordo et al., 2014). For example, forage availability for black bears varies across seasons as a result of precipitation patterns and rate of vegetation maturation, and these factors interact with bear nutritional requirements resulting in seasonal shifts in forage consumption (Pelchat and Ruff, 1986; Auger et al., 2005). Grasses and forbs typically emerge first at higher elevations that receive more moisture, and they are easily digested following prolonged periods of fasting in the den. Therefore, increased grass and forb production following fires may provide better forage conditions during early spring when forage species with higher nutritional content are limited. Hard mast species such as oak (*Quercus* spp.) mature slowly and are not available as forage until late summer and early autumn. The availability of hard mast species also coincides with black bear hyperphagia during autumn and has a large influence on black bear reproductive success in the Southwest (Costello et al., 2003).

Wildfires and forest restoration treatments often reduce these essential food sources for black bears until regeneration occurs after treatments are completed. Thinning and prescribed fire treatments, used alone or in combination, can also result in temporary reduction in total vegetation cover, and shrub cover in particular (Busse et al., 2000; Dodson et al., 2008; Busse et al., 2009; Willms et al., 2017). The duration of post-treatment vegetation recovery may vary between plant species, burn severity, and post-treatment climatic conditions that influence the rate of vegetation recovery (Bartel et al., 2016). Regionally, these treatments may have variable effects on black bears which have been documented in studies of prescribed burns (Stratman and Pelton, 2007; Yaklin, 2017). These studies suggest black bears avoid burned sites immediately post-fire, while the longer-term (e.g., 5–25 years) responses differed, likely due to the rate of post-fire changes in forage productivity and concealment cover in forests with differing

environmental conditions.

In the boreal forests, black bears during the non-denning period were reported as selecting for regenerating clear-cut stands (6–20 years old) within their home ranges and avoiding mature coniferous forest with open understories; regenerating stands provided the most horizontal cover and highest density and biomass of berries (Brodeur et al., 2008). However, the time between a disturbance and black bear use likely varies in different forest types (Bartel et al., 2016). Additionally, black bear habitat use varied across sex and age classes (Cunningham and Ballard, 2004; Garneau et al., 2008), reproductive status (Schooley et al., 1994; Benson and Chamberlain, 2010), and black bear densities and competition (Oli et al., 2002; Garneau et al., 2008). Studies also suggest that black bear body condition can also influence habitat use patterns (Hellgren et al., 1989; Hellgren et al., 1993).

Denning is an evolutionary strategy for black bears to avoid inclement winter weather conditions and periods of reduced forage (Hellgren, 1998). Den sites are critically important for the survival and productivity of black bears; dens serve as parturition sites and provide a secure area for extended maternal care of altricial cubs until conditions for den emergence are favorable. Bears are particularly vulnerable to disturbances while in the den (Linnell et al., 2000); displacement from dens sites is energetically costly, and den abandonment can lead to increased cub mortality (Goodrich and Berger, 1994; Swenson et al., 1997).

Identifying large scale habitat selection patterns cannot account for individual variation at smaller spatial scales. Black bear microhabitat selection is likely dependent on occurrence, quality, and local abundance of cover and forage, and may be influenced by age, sex, body condition, reproductive status, and competition with conspecifics (Morris, 1992; Dahle and Swenson, 2003; Rode et al., 2006). Determining microhabitat selection of black bears including selection of bed sites (i.e., resting sites) and den sites can aid in identifying habitat characteristics that are critical for maintaining and increasing fitness (Mollohan, 1987; Cristescu et al., 2013). Because forage resources may be limited seasonally, their effects on habitat selection are likely to become more pronounced as a result of habitat disturbances (Reynolds-Hogland et al., 2007). Additionally, the availability of suitable cover is significant in providing thermal cover for both bed and den sites as well as decreased susceptibility from threats such as hunter harvest, interspecific strife, and infanticide (LeCount and Yarchin, 1990). Reduced cover and forage may result in displacement and or increased competition with conspecifics. Therefore, evaluating habitat characteristics at these scales can contribute to development of mitigation efforts where necessary.

Our specific objectives were to assess: 1) seasonal bed site selection; and 2) den site selection by male and female black bears. We aimed to investigate both site selections in relation to a suite of habitat covariates commonly associated with black bear habitat selection and any influence of wildfires and forest restoration treatments. Based on previous black bear studies, we expected that bed sites would be selected in areas of denser cover, areas providing sufficient escape and thermal cover. During spring and early summer, we expected that black bears would utilize areas within recent burns which likely provide abundant grasses and forbs when soft and hard mast resources are not yet available, and that hard mast resources would influence bed site selection of black bears in autumn. We predicted that that den sites would be selected in areas with decreased horizontal visibility, and that females would select dens with more cover than those used by males. Investigating bed and den selection of black bears after natural and anthropogenic disturbances will augment our understanding of how black bears may respond to future habitat disturbances, allowing managers to make more informed recommendations to mitigate potential negative short-term impacts of treatments and facilitate long-term improvement of habitat conditions for black bears.

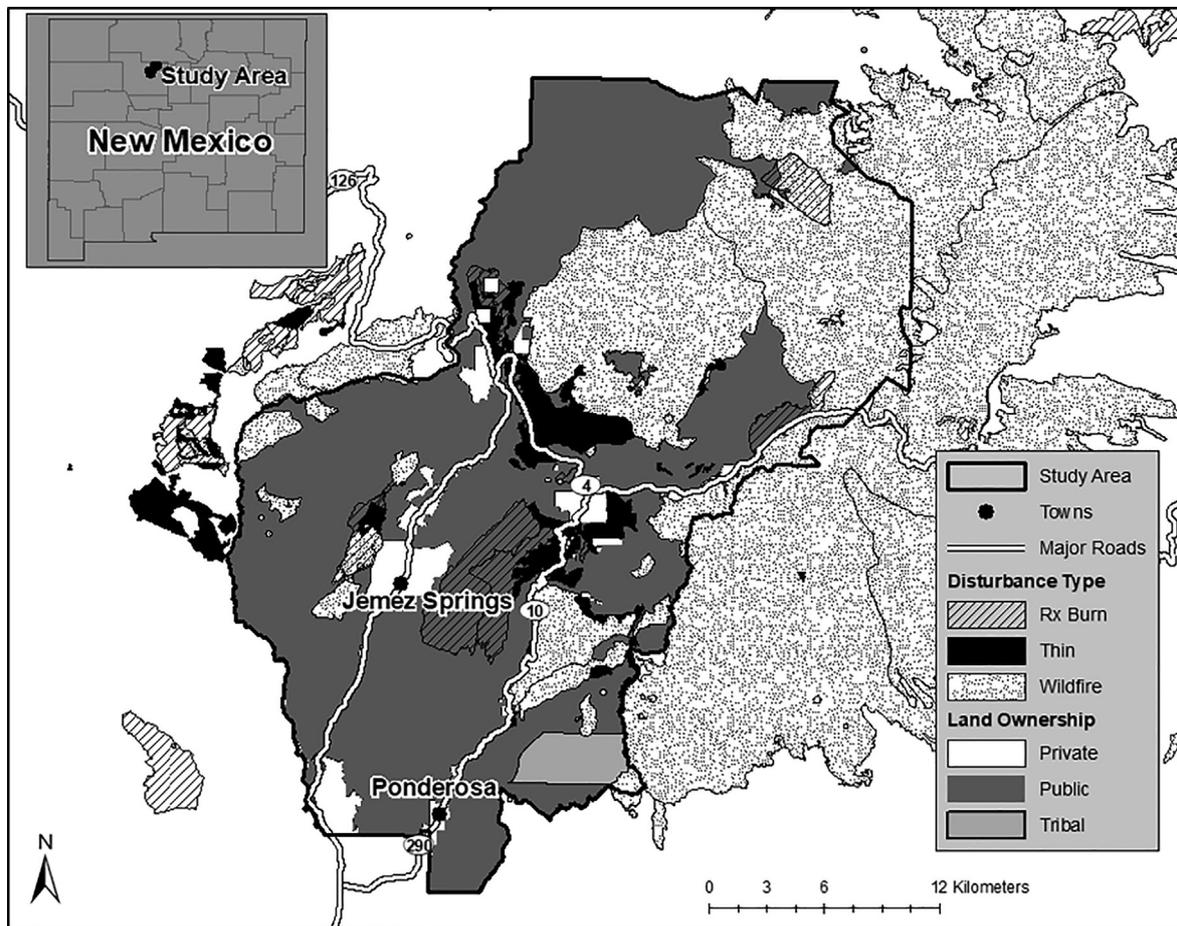


Fig. 1. Study area located in the Jemez Mountains of north-central New Mexico where bed and den site selection of black bears (*Ursus americanus*) was investigated during 2015–2016. Within the last decade, this area was heavily impacted by natural and anthropogenic disturbances including wildfires, prescribed burns, and thinning treatments.

2. Materials and methods

2.1. Study area

We conducted our study during 2015–2016 in the 85,000 ha Collaborative Forest Landscape Restoration Program (CFLRP) area in the Jemez Mountains, New Mexico, USA (Fig. 1). Lands are primarily managed by the Santa Fe National Forest (SFNF; 44,690 ha) and the Valles Caldera National Preserve (VCNP; 34,880 ha), but also includes tribal lands owned by the Jemez Pueblo (1560 ha). Topography varied from resurgent volcanic domes surrounded by grasslands in the VCNP, to steep ridges, rock outcrops, canyon-lands, and mesas in the SFNF; elevation ranged from 1795 to 3431 m. Due to elevational changes and broken topography, vegetation types were diverse and interspersed. Mesic, high elevation sites associated with mixed conifer communities, including *Abies arizonica*, *A. concolor*, *Picea engelmannii*, *P. pungens*, and *Pseudotsuga menziesii*, and ponderosa pine (*Pinus ponderosa*) forests at moderate elevations characterized the VCNP, while the SFNF within the study area was predominately ponderosa pine forest and pinyon-juniper (*Juniperus deppeana*, *J. monosperma*, *J. osteosperma*, *Pinus edulis*) woodlands at more xeric, low elevation sites. Oak shrublands and quaking aspen (*Populus tremuloides*) stands were often located in mixed vegetation communities at moderate to high elevations (U.S. Geological Survey Gap Analysis Project, 2016).

Common black bear forage included bear corn (*Conopholis americana*), wild raspberry (*Rubus* spp.), wild strawberry (*Fragaria vesca*), juniper seed cones, Gambel oak (*Quercus gambelii*), pinyon pine nuts, gooseberry (*Ribes uva-crispa*), chokecherry (*Prunus virginiana*), New

Mexico locust (*Robinia neomexicana*), desert prickly pear (*Opuntia phaeacantha*), as well as various mushroom, conifer seeds, grasses, sedges, and forbs. Bears also foraged on various insects such as Formicidae, Vespidae, and Apoidea, as well as carrion, and elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) neonates (Kindschuh et al., 2016). The SFNF is open to fall black bear harvest outside the VCNP.

Climate is semi-arid, with average yearly precipitation ranging from 43 cm (SD = 25 cm) at low elevations (e.g., 2195 m) to 58 cm (SD = 25 cm) at higher elevations (e.g., 2471 m). Average snowfall ranged from 73 cm (SD = 40 cm) to 305 cm (SD = 97 cm) at low and higher elevations, respectively (Western Regional Climate Center, 2016). The climate is characterized by a monsoon precipitation cycle with most rainfall occurring from June through September (National Oceanic and Atmospheric Administration, 2016). Average daily high temperatures at low elevations range from 31 °C (SD = 1.0) in July, to average daily low temperatures of −6 °C (SD = 1.9) in January. At high elevations, the average daily high temperature is 25 °C (SD = 0.9) in July and the average daily low temperature is −14 °C (SD = 2.1) in January.

Primary land uses of the area are cattle grazing, recreation and commercial logging, which are administered by the U.S. Forest Service (USFS) and VCNP. Currently, prescribed burning and thinning treatments are being implemented to restore forest structure and natural fire regimes following two decades of intense and frequent wildfires. Thinning treatments were restoration cuts designed to restore historical forest structure. Extensive efforts were made by contractors to remove most of the thinned trees off site for biomass utilization, even small

diameter trees that would typically be considered unmerchantable in commercial timber sales; thus, little slash remained after restoration thinning treatments. The most notable recent wildfires are the Las Conchas Fire in 2011, and the Thompson Ridge Fire in 2013, which burned 63,371 ha and 9698 ha, respectively (Fig. 1); the Las Conchas Fire was mostly a high severity, stand replacing fire, whereas the Thompson Ridge Fire was mixed severity. The CFLRP aims to promote the reintroduction of natural fire regimes, making forests more resilient to climate change (Schultz et al., 2012). The CFLRP restoration treatments were established in 2010 and are anticipated to be completed by 2020–2021. During 2010–2017, 23,067 ha (27% of the 85,000 ha project area) were treated with either prescribed fire or thinning.

2.2. Capture and monitoring

We captured black bears during the spring and summer of 2015 and 2016 using Aldrich foot snares and culvert traps placed throughout the study area. Black bears were chemically immobilized using a mixture of 4.4 mg/kg ketamine (Ketaset, Fort Dodge Animal Health, Overland Park, Kansas, USA) and 2 mg/kg xylazine (AnaSed, Lloyd Inc., Shenandoah, Iowa, USA) or a mixture of 3 mg/kg tiletamine-zolazepam (Telazol, Zoetis Inc., Kalamazoo, Michigan, USA) and 2.2 mg/kg xylazine (Kreeger and Arnemo, 2012) via a CO₂ dart pistol (Dan-Inject, Børkop, Denmark), or pole syringe (Tomahawk, Hazelhurst, Wisconsin, USA). Adult black bears were fitted with global positioning system (GPS) telemetry collars equipped with a VHF transmitter and a breakout device (G2110E, Advanced Telemetry Systems, Isanti, MN, USA). Collars were programmed to collect locations every 3 h, and to transmit locations every 72 h via Iridium satellite. Collars were also programmed with a 12-hr mortality signal. Cubs, yearlings, and subadult (i.e., 2–3 years old) bears were not radio-collared because of relatively rapid weight gain and neck growth, and to avoid any GPS bias due to natal site fidelity during their first few years of independence (Costello, 2010). We checked the fit of collars on all previously captured bears while in the den during January–March of 2016 and 2017. Collars were adjusted, replaced, or removed as necessary. Upon completion of handling, we administered 0.15 mg/kg yohimbine (Tocris Bioscience, Minneapolis, Minnesota, USA) or 2 mg/kg tolazoline hydrochloride (Zoopharm, Windsor, Colorado, USA) to reverse the effects of xylazine. When necessary, we monitored black bears from the ground using hand-held directional antennas (Telonics, Inc., Mesa, AZ). All animal handling procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocols # 2011-028 and 2015-022) and followed acceptable methods (Sikes, 2016).

2.3. Microhabitat of bed sites

Using GPS data transmitted through the Iridium satellite system and a cluster identification code in program R (R Version 3.3.1, R Core Team, 2016; Daniel and Kindschuh, 2016; Kindschuh et al., 2016), we identified locations that formed a cluster, indicating the location of potential bed sites. Clusters were defined as ≥ 2 GPS locations within 50 m of each other recorded ≤ 24 h apart. Clusters with GPS locations that were not consecutive were unlikely a result of bedding activity, but rather more indicative of foraging activities. Therefore, to increase the chance of encountering a bed site in the field, we only investigated clusters characterized by consecutive GPS locations. Clusters with ≥ 3 GPS locations that included failed GPS fix attempts were only visited if at least 2 locations were consecutive. We randomly selected a minimum of four cluster sites/bear per month for field visitation. Bed sites were classified by season (summer [mating, dispersal: Jun–Aug], autumn [hyperphagia: Sep–Dec]). Bed sites were visited within 2 weeks of cluster formation to ensure that no significant changes in vegetation occurred between the date a bed site was used and data collection.

Presence of hair aided in identification of bed sites, however, we

also considered a site to be a bed if body prints were observed within the substrate, or if a depression was excavated. Other signs used to identify bed sites included trees scraped of their bark, material raked into clumps, claw marks on tree trunks, and scat piles in the area (Mysterud, 1983). Before approaching these sites, we used a hand-held telemetry antenna to confirm whether a bear was in the area to minimize disturbance and to reduce bias by altering bear movements. We did not visit sites that occurred within 50 m of a site already surveyed for an individual bear. If more than one bed site was observed at a cluster, we surveyed the bed site that was closest to the collected GPS location.

We collected data on physical and vegetative characteristics at bed sites and paired random locations. We determined the location of random sites by selecting a random distance (i.e., 50–250 m) and random azimuth (i.e., 1–360°) from the used site. Straight-line distance traveled by black bears within a 1-hour period averaged 250 m (based on movement rates of bears previously radio-collared in the study area [$n = 28$]). The maximum distance of the random location increased the likelihood that available sites occurred in similar land cover types as the used sites, thus more accurately depicted the area available to the bear when it decided to bed down. We chose the minimum distance of 50 m to minimize overlap with habitat conditions recorded at bed sites. We placed two, 30 m perpendicular lines (oriented north-south and east-west, respectively) at the intersection of the bed site or center of paired random site (Mollohan, 1987; Grovenburg et al., 2010) to estimate abundance of down woody debris using the line intercept method. We recorded the total number of woody debris ≥ 15.1 cm in diameter that intersected the transect lines (Reynolds, 1966); larger decayed logs are frequently occupied by colonial invertebrates (e.g., termites and ants) which are a major food source for black bears (Raine and Kansas, 1990; Noyce and Garshelis, 1997). Fire and forest thinning induced changes in habitat structure can result in a reduction of these detritivores (Buckingham et al., 2015) and concealing cover. Black bears are likely to select cover with or near available forage. Black bear forage has been shown to be limited for several years post disturbances. However, use increased with high forage diversity and abundance 3–6 years after; these sites were avoided as stands further matured (Lindzey et al., 1986; Hamer, 1996; Brodeur et al., 2008). We placed a 1-m² quadrat at 5 m and 15 m north and south along the transect line to visually estimate the percent cover of grasses, forbs, soft (*Juniperus* spp. and other berries) and hard mast (*Quercus* spp. and *Pinus* spp.), and bare ground using Walker's (1976) ranking method (i.e., 0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99%, and 100%). Visibility, canopy cover, and stand basal area are all reduced by wildfires and forest restoration treatments. We used a collapsible (63 cm tall \times 38 cm diameter; approximate bear resting height) cylinder with 2, 31.5 cm sections (1 white and 1 blue to distinguish both sections easily) made with spring wire and light cloth to estimate horizontal visibility. This was a slightly modified version of the cylinder used by Ordiz et al. (2009). We placed the cylinder in the bed or plot center, and separately estimated the proportion of the upper and lower sections that were visible from 10 m away along each cardinal direction when viewed from 1 m above the ground. The categories for estimating visibility were: 0 if not visible at all, 1 if $\leq 25\%$, 2 if 26–50%, 3 if 51–75%, and 4 if $\geq 76\%$ visible. To estimate the percentage of horizontal visibility for each site, we divided summed visibility values by the maximum possible value (i.e., 32; the value without any obstructing cover). We also measured the minimum distance at which the cylinder was no longer visible from the four cardinal directions; we averaged the four distances for each site (Ordiz et al., 2009). Percent canopy cover was estimated using a spherical densiometer (Forestry Suppliers, Inc., Jackson, MS, USA) while facing away from the site at 5 m in each cardinal direction (Cook et al., 1995). Stand basal area (m²/ha) was estimated in a 360° area while standing in the bed or plot center using a 10-factor prism (Jim-Gem® Rectangular Prisms, Forestry Suppliers, Inc., Jackson, MS, USA; Grovenburg et al., 2010; Smith et al., 2015), and if a bear bedded against a tree, the

Table 1
Structure of a priori models used to assess the influence of habitat characteristics and disturbances on bed and den site selection of American black bears (*Ursus americanus*) in the Jemez Mountains, New Mexico, 2015–2016.

Site	Model No.	Model Structure ^a
Bed, Den	1	Wildfire
Bed, Den	2	Thin
Bed, Den	3	Rx
Bed, Den	4	Basal Area
Bed, Den	5	Canopy
Den	6	Northness
Bed	7	Vegetation
Bed, Den	8	Visibility
Den	9	VRM
Den	10	Slope + Canopy
Den	11	Slope + Elevation + Northness
Bed, Den	12	Visibility + Basal Area
Bed, Den	13	Visibility + Canopy + Basal Area
Bed	14	Visibility + Hard Mast
Bed	15	Visibility + Vegetation
Bed	16	Visibility + Wildfire
Bed	17	Visibility + Thin
Bed	17	Visibility + Rx Burn
Den	18	Visibility + Elevation + Northness
Den	19	Visibility + Northness
Bed	20	Visibility + Grass + Forb + Water
Bed	21	Visibility + Grass + Forb + Water + Sex × Visibility + Sex × Grass + Sex × Water
Bed, Den	22	Visibility + Road + Visibility × Road
Bed, Den	23	Visibility + Road + Visibility × Road + Sex × Road
Den	24	Visibility + Road + Visibility × Road × Sex
Bed, Den	25	Wildfire + Sex × Wildfire
Bed, Den	26	Thin + Sex × Thin
Bed, Den	27	Rx + Sex × Rx
Bed, Den	28	Wildfire + Rx + Thin
Bed, Den	29	Wildfire + Thin + Rx + Wildfire × Sex + Thin × Sex + Rx × Sex
Bed, Den	30	Wildfire + Vegetation + Wildfire × Vegetation
Bed, Den	31	Visibility + Sex × Visibility
Bed, Den	32	BasalArea + Sex × BasalArea
Bed, Den	33	CanopyCover + Sex × CanopyCover
Bed, Den	34	Visibility + Basal Area + Sex × Visibility + Sex × Basal Area
Bed	35	Vegetation + Sex × Vegetation
Bed	36	Wildfire + Severity + Wildfire × Severity × Sex
Bed, Den	37	Visibility + Vegetation + Sex × Visibility + Sex × Vegetation
Den	38	Northness + Sex × Northness
Den	39	Visibility + Northness + Sex × Visibility + Sex × Northness
Den	40	VRM + Sex × VRM
Den	41	Visibility + Elevation + Northness + Sex × Visibility + Sex × Elevation + Sex × Northness
Den	42	Slope + Canopy + Sex × Slope + Sex × Canopy
Bed	43	Wildfire + Thin + Rx + Sex × Visibility
Bed	44	Visibility + Rx + Sex × Visibility + Sex × Rx
Bed	45	Visibility + Wildfire + Sex × Visibility + Sex × Wildfire
Bed	46	Visibility + Hard Mast + Sex × Visibility + Sex × Hard Mast
Bed	47	Visibility + Canopy + Basal Area + Sex × Visibility + Sex × Canopy + Sex × Basal Area

^a Variable notation: Basal Area = stand basal area, m²/ha; Canopy = percent canopy cover; Northness = northness index; Vegetation = vegetation type; Visibility = percent horizontal visibility; VRM = vector ruggedness measure; Slope = percent slope; Elevation = elevation of site (m); Hard Mast = average percent cover of hard mast species; Wildfire = site burned by wildfire; Rx Burn = prescribed burn site; Grass = percent grass cover; Forb = percent forb cover; Water = distance to nearest perennial water (m); Road = distance to nearest road (m).

diameter at breast height (DBH [cm]) was recorded (Mysterud, 1983). We measured the percent slope and aspect of the surrounding area (i.e., 15 m radius) using a clinometer and compass (Suunto, Vantaa, Finland). We used 30 × 30-m resolution Digital Elevation Models (DEM; The National Map, 2016) to calculate aspect. Aspect was converted to values between −1 and 1 where north = 1 and south = −1 using the following equation: $\cos \frac{\text{aspect} \times \pi}{180}$, (Wallace and Gass, 2008; ArcMap 10.3.1 [Esri, 2002]). We created a Vector Ruggedness Measure (VRM; neighborhood size 3) layer within GIS using the Benthic Terrain Modeler (Walbridge et al., 2018) to determine a ruggedness value for each site. Vegetation types were classified as: ponderosa, mixed-conifer, pinyon-juniper, oak, aspen, grassland, or other by determining the dominant cover type (e.g., ≥ 50%) within a 15 m radius from the center of each site; our mixed conifer classification included spruce-fir cover. We determined the distance (m) to nearest perennial water source using GIS. Water sources included perennial streams, lakes, wildlife drinkers,

and cattle tanks and were identified based on geospatial data obtained from the USFS and VCNP. Sites were also classified as thinned, prescribed burn, wildfire, or untreated (i.e., not subjected to wildfire, thinning or prescribed burns) based on geospatial data from the SFNF and VCNP. We classified wildfires as unburned, burned 2–3 years ago, and burned ≥ 4 years ago; there were no wildfires in the year immediately prior to sampling. Wildfire severity was determined by a GIS layer created by the USFS, and classified as either low, moderate, or high. Thinned sites were classified as unthinned, thinned 1–2 years ago, and thinned ≥ 3 years ago. Prescribed burns were classified as either burned or unburned because all prescribed burns in the study area were conducted within the previous 2–3 years of data collection. We conducted post-hoc single factor ANOVAs to determine whether use of vegetation types was significantly different and to determine if a relationship existed between percent horizontal visibility and the time since disturbance. Disturbance data included activities that

occurred during 1995–2016.

2.4. Microhabitat of den sites

To assess microhabitat characteristics at den sites, we monitored GPS locations intensively starting in early October until mid-December. Once GPS locations and transmissions ceased, we visited the last collected fix location and used VHF radio-telemetry to locate the den site. We waited at least a month post den entry to locate the den to minimize disturbance and to reduce the chance of den abandonment.

Dens used by male black bears, and females expected to have yearlings were visited in January, while females expected to have cubs of the year were not visited until March. Observations throughout the previous summer and autumn (e.g., cub sign at visited GPS locations) aided in determining the status of offspring. To increase the number of dens surveyed, we also located den sites from black bears ($n = 9$) fitted with GPS collars during 2013 and 2014 as part of a different investigation within the study area. We recorded the dominant vegetation type, slope, and aspect within a 15-m radius, elevation, canopy cover, stand basal area, and horizontal visibility. The cover cylinder was placed in front of the den entrance to estimate horizontal visibility from 10 m away in the 4 cardinal directions (Libal et al., 2012). We noted whether the site was located in a burned or thinned area. Using ArcMap, we determined the distance to the nearest disturbance. Wildfires, prescribed burns, and thinned areas were categorized as described above. We created a VRM for all den sites as described for bed locations. A paired random site within 200–700 m of the den site was also surveyed for the same microscale characteristics (Martorello and Pelton, 2003). This buffer distance aimed to reduce overlap of habitat characteristics that may be found within 200 m of the used site but should still have represented an area where a bear could choose to den. To obtain an accurate representation of cover present when the bear first entered the den, visibility data were collected during autumn when the bear entered the den, and the remaining data were collected during the winter at a den visit. If surveyed in the spring, there would likely have been higher visibility estimates because winter conditions reduce herbaceous vegetation. To assess den site selection on a larger scale, we calculated 95% fixed kernel home ranges using Geospatial Modeling Environment (0.7.4, Beyer, 2016) for each bear and used each individual's home range to create a buffer around each den site using ArcMap 10.3.1 (Pigeon et al., 2016). Within each buffer we generated 10 random locations then extracted covariate values to these random locations in GIS.

2.5. Data analysis

For both bed and den site selection analyses, we tested predictor variables for multicollinearity using the Pearson correlation coefficient (r). If any variables were correlated ($r \geq 0.6$), then they were not used in the same model. We then created a set of *a priori* models (Table 1) to assess the influence of habitat characteristics and disturbances on bed and den site selection; we used the same *a priori* model set to assess the influence of habitat variables and disturbances on den selection at the 95% home range scale. We developed a suite of core models based on factors we believed could influence selection of bed or den sites by black bears. To determine if there were differences in the most supported models for bed and den site selection of male and female bears, we added interaction terms between sex and habitat covariates included in each model. Because we did not have sufficient data to implement models with sex \times season \times habitat covariate interactions, we subset the data to determine if the influence of habitat characteristics and disturbances on selection differed by season.

For bed site selection, the minimum distance the cover cylinder was visible and horizontal visibility were correlated (i.e., ≥ 0.697). The latter was considered more biologically meaningful, therefore minimum distance values were not included in the analysis. References

levels for categorical covariates included aspen for vegetation type, low for burn severity, and unthinned or unburned for thinning, wildfire and prescribed burns. We then used mixed effects conditional logistic regression using the *mclogit* package in program R (Elff, 2016, R Version 3.3.1, R Core Team, 2016), with bear ID as a random effect (Duchesne et al., 2010). For den site selection, none of the variables were highly correlated ($r \geq 0.6$). We used the R package *mclogit* (Elff, 2016, R Version 3.3.1, R Core Team, 2016) to run conditional logistic regression to evaluate *a priori* models (Table 1).

Model support was assessed using Akaike information criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson, 2002). We used model weights (w_i) as an indication of support for each model (Burnham and Anderson, 2002). Competing models were evaluated for uninformative parameters following Arnold (2010). When competing models performed poorer than the highest ranking model with the addition of a single predictor variable, we considered the more complex model to contain an uninformative parameter (Arnold, 2010) and excluded these models unless the change in deviance supported the additional parameter. These models with uninformative parameters were discarded (Arnold, 2010).

3. Results

3.1. Microhabitat of bed sites

We analyzed data from 24 radio-collared bears (10 F, 14 M) marked during 2015 and 2016. We surveyed 302 used bed sites, and 302 paired random locations; 169 sites were used by female black bears (87 in summer and 82 in autumn), and 133 were used by males (82 in summer and 51 in autumn). The number of clusters surveyed among individuals varied due to collar placement date, collar failures, hunter harvest, and periodic movements to inaccessible tribal lands. Individual black bears demonstrated repeated use of the same bed sites; this was determined by different age and composition of scats present at the sites, and GPS data which indicated the bear had visited sites more than once.

The majority of bed sites (33%) were located in mixed conifer forest (28% of study area), while the remaining bed sites were found in ponderosa (22.5%; 38% of study area), oak (22.5%; 1% of study area), pinyon juniper (14%; 15% of study area), aspen (7%; 3% of study area), and grassland (1%; 13% of study area). Other vegetation types consisted of 2% of the study area; there were no bed sites within these cover type. Mean horizontal visibility at bed sites differed by vegetation type ($F_{3,240} = 2.71$, $P = 0.03$); visibility was 27% (SE = 1.89) in mixed conifer forest; 33% (SE = 2.17) in ponderosa forest; 34% (SE = 4.97) in oak patches, 16% (SE = 6.97) in pinyon-juniper, and 37% (SE = 4.75) in aspen. Forty-eight percent of the sites were located in unburned or unthinned locations (55% of the study area), while 39% of used sites were located in previous wildfire areas (32% of the study area), 11% in thinned areas (6% of the study area), and only 2% of used sites were located within a prescribed burn (7% of the study area). The majority of bed sites located within previous wildfire areas were in areas that burned at a low severity (67%; 44% of study area burned by wildfire), while moderate (19%; 33% of study area burned by wildfire) and high (14%; 23% of study area burned by wildfire) severity burn sites were used less frequently. Mean horizontal visibility at bed sites located within wildfire areas differed by age of the fire ($F_{1,118} = 4.60$, $P = 0.03$); however, there was no difference in horizontal visibility between different forest thinning ages ($F_{1,31} = 0.67$, $P = 0.42$). Horizontal visibility in wildfire sites that burned 2–3 years prior to bed use was 33% (SE = 2.32); in sites that burned ≥ 4 years prior, visibility was an average of 24% (SE = 3.16). In thinned locations treated 1–2 years prior to bed use, the mean horizontal visibility was 40% (SE = 4.81); at sites that were thinned ≥ 3 years prior, mean visibility was 47% (SE = 6.39). The average visibility at undisturbed sites was 27%. Used sites were generally well concealed; sites were no longer visible after a mean distance of 12 m (SE = 2.10), canopy cover

Table 2

Five highest ranking *a priori* models for American black bear (*Ursus americanus*) bed site selection in the Jemez Mountains, New Mexico, 2015–2016. Maximized log likelihoods, total parameters (K), Akaike's information criterion adjusted for small sample sizes (AIC_c), ΔAIC_c , and Akaike weights (w_i) are given.

Model Structure ^a	K	Log-likelihood	AIC_c	ΔAIC_c	w_i
Visibility + Basal Area	3	-618.775	1241.6	0.00	0.578
Visibility + Canopy + Basal Area	4	-618.579	1243.2	1.62	0.257
Visibility + Hard Mast	3	-620.877	1245.8	4.21	0.071
Visibility	2	-623.008	1248.0	6.46	0.023
Basal Area	2	-623.423	1248.9	7.29	0.015

^a Variable notation: Visibility = percent horizontal visibility; Basal Area = stand basal area, m²/ha; Canopy = percent canopy cover; Hard Mast = average percent cover of hard mast species.

averaged 65%, and in instances where a bear bedded against a tree, the mean DBH was 53 cm (SE = 4.68) suggesting that larger diameter trees are selected to provide additional cover. The mean minimum distance that random locations were no longer visible was 21 m (SE = 1.87) and average canopy cover at random locations was 60%.

The highest ranked bed site model included horizontal visibility and basal area ($w_i = 0.58$) and the second highest ranking model ($w_i = 0.26$) included horizontal visibility, basal area, and canopy cover; however, the highest ranking model had over two times more support than the second ranking model (Table 2). Models including interaction terms between sex and habitat covariates ranked lower than the reduced model structures without interaction terms indicating little support for sex-specific differences in the influences of habitat characteristics on bed site selection by black bears; parameter estimates for interaction terms also had 95% confidence intervals that encompassed zero. Black bear bed sites were more likely to occur in areas with decreased horizontal visibility and increased basal area (Table 3). Based on the second highest ranking model, bed sites were also more likely to occur in areas with higher canopy cover (Table 3). Models including covariates for wildfires or restoration treatments were not among the most supported models, most likely because bed site-random site pairs were typically in the same disturbance class, thus including these covariates in the models were not particularly informative to assess bed site selection at the spatial scale used in our study. We did not include coarse woody debris, percent cover of bare ground or percent cover of soft mast in any models as there were too few sites with these components.

The highest-ranking model for summer bed sites included horizontal visibility and basal area ($w_i = 0.41$), and the highest-ranking model for autumn locations surveyed was basal area ($w_i = 0.31$; Table S.1, Supplementary material). Model structures of the highest ranking models for both summer and fall were almost identical to those models

Table 3

Parameter estimates, standard errors, and P -values for the five highest ranking models for American black bear (*Ursus americanus*) bed site selection in the Jemez Mountains, New Mexico, 2015–2016.

Model No.	Covariate	Estimate	SE	P
12	Visibility	-0.007	0.002	0.002
	Basal Area	0.013	0.005	0.004
13	Visibility	-0.007	0.002	0.003
	Canopy	0.002	0.003	0.532
	Basal Area	0.012	0.005	0.014
14	Visibility	-0.008	0.002	0.002
	Hard Mast	0.047	0.023	0.041
8	Visibility	-0.008	0.002	0.002
4	Basal Area	0.014	0.005	0.003

^aVariable notation: Visibility = percent horizontal visibility; Basal Area = stand basal area, m²/ha; Canopy = percent canopy cover; Hard Mast = average percent cover of hard mast species.

that combined seasons (Table 2). While the same variables were in the top models when evaluating selection irrespective of season, subsetting data by season resulted in lower model support for the top-ranking model. However, the magnitude and direction of the parameter estimates were similar (Table S.2, Supplementary material).

3.2. Microhabitat of den sites

We surveyed 26 dens sites which were used by 23 black bears (10 F, 13 M). Most den sites were associated with boulders ($n = 21$), nine of which required digging to construct a cavity, while eight required little effort other than adding bedding materials to an existing cavity. The remaining four rock dens were natural caves. Dens not located within a rock cavity were all constructed by female bears and were excavated into the side of a slope ($n = 4$) and into a large (≥ 51 cm) downed decaying tree ($n = 1$). Of the den sites surveyed, 38% were located in a previously disturbed area (45% of the study area); eight (i.e., 31%) dens were located within a previous wildfire site (32% of the study area). Of the dens located in previous wildfire areas, four were in low severity (44% of area burned by wildfire), three were in moderate severity (33% of area burned by wildfire), and one was in high severity burn (23% of area burned by wildfire). These wildfire sites were burned during 2011 or 2013. There were no den sites located in prescribed burned areas (7% of study area), and only two were located in thinned areas (6% of study area). Both den sites located in thinned areas were selected just months after the thinning treatment occurred. The majority of dens (38%) were in mixed conifer (28% of study area), while the remaining sites were in oak (23%; 1% of study area), ponderosa (23%; 38% of study area), pinyon juniper (12%; 15% of study area), and aspen (4%; 3% of study area).

The highest-ranked model for den site selection included only horizontal visibility ($w_i = 0.682$, Table 4) and had almost 8 times the support of the second highest ranking model ($w_i = 0.086$, Table 4), which included horizontal visibility, canopy cover and basal area. Models with interaction terms between habitat covariates and sex had more support than in the bed site models, but were still relatively unsupported ($w_i = 0.027$ – 0.029 , Table 4), compared to the two highest ranking den site models. Black bears selected for den sites with less visibility (Table 5). The 95% fixed kernel home range scale did not elucidate den site selection either; all models were not well supported and 95% confidence intervals for all parameter estimates in highest ranking models included zero (Tables S.3, S.4, Supplementary material).

4. Discussion

Following our investigation of numerous habitat characteristics, bed site selection was most related to horizontal visibility and basal area. Decreased visibility at sites due to obstruction from boulders, vertical and horizontal vegetation cover, downed logs and increased stand basal area were most strongly related to bed site selection by black bears. We did not detect any important differences when modeling bed site selection between sexes and seasons, suggesting that both male and female black bears select bed sites in a similar manner and require sufficient cover, or that differences in selection between sexes may have been related to habitat characteristics unsampled during our study. Mollohan (1987) reported similar results of bed sites selected by black bears in Arizona. Black bears in this study primarily selected for security cover and 64% of sites had less than 5 m of visibility. Cunningham et al. (2003) surveyed habitat characteristics at paired used and random locations, however their random locations were generated within a larger scale and placed throughout their entire study area. Yet, despite the extensive distance between used and random locations used by Cunningham et al. (2003), their results also indicated that black bears selected for increased cover. Black bears in our New Mexico study demonstrated repeated use of sites, suggesting that areas

Table 4

Five highest ranking *a priori* models for American black bear (*Ursus americanus*) den site selection in the Jemez Mountains, New Mexico 2013–2016. Maximized log-likelihoods, number of parameters (*K*), Akaike's information criterion adjusted for small sample sizes (AIC_c), ΔAIC_c, and Akaike weights (*w_i*) are given.

Model Structure ^a	<i>K</i>	Log-likelihood	AIC _c	ΔAIC _c	<i>w_i</i>
Visibility	1	−49.965	102.0	0.00	0.682
Visibility + Canopy + Basal Area	3	−49.901	106.1	4.14	0.086
Visibility + Northness + Visibility × Sex + Northness × Sex	4	−49.878	108.3	6.32	0.029
Visibility + Basal Area + Visibility × Sex + Basal Area × Sex	4	−49.957	108.5	6.48	0.027
Visibility + Road + Visibility × Road + Sex × Road	4	−49.961	108.5	6.49	0.027

^aVariable notation: Visibility = percent horizontal visibility; Canopy = percent canopy cover; Basal Area = stand basal area m²/ha; Northness = northerly aspect value; Visibility × Sex = interaction effect between visibility and sex of bear; Northness × Sex = interaction effect between northness value and sex of bear; Basal Area × Sex = interaction effect between basal area and sex of bear; Road = distance to nearest road (m); Visibility × Road = interaction effect between visibility and the distance to nearest road (m); Sex × Road = interaction effect between the sex of bear and the distance to nearest road (m).

Table 5

Parameter estimates, standard errors, and *P*-values for the five highest ranking models for combined American black bear (*Ursus americanus*) den site selection in the Jemez Mountains, New Mexico, 2013–2016.

Model No.	Covariate	Estimate	SE	<i>P</i>
8	Visibility	−0.010	0.004	0.006
13	Visibility	−0.010	0.004	0.008
	Canopy Cover	0.003	0.010	0.733
	Basal Area	0.003	0.025	0.903
39	Visibility	−0.010	0.005	0.054
	Northness	−0.007	0.332	0.982
	Visibility × Sex	0.001	0.008	0.934
	Northness × Sex	0.136	0.454	0.764
34	Visibility	−0.010	0.005	0.054
	Basal Area	0.003	0.023	0.896
	Visibility × Sex	−0.001	0.008	0.982
	Basal Area × Sex	−0.003	0.043	0.943
23	Visibility	−0.010	0.005	0.006
	Road	0.00009	0.001	0.929
	Visibility × Road	−0.00001	0.0001	0.999
	Sex × Road	0.0001	0.001	0.932

^aVariable notation: Visibility = percent horizontal visibility; Canopy = percent canopy cover; Basal Area = stand basal area, m²/ha; Northness = northerly aspect value; Visibility × Sex = interaction effect between visibility and sex of bear; Northness × Sex = interaction effect between northness value and sex of bear; Basal Area × Sex = interaction effect between stand basal area, m²/ha and sex of bear; Road = distance to nearest road (m); Visibility × Road = interaction effect between visibility and the distance to nearest road (m); Sex × Road = interaction effect between the sex of bear and the distance to nearest road (m).

of sufficient cover for bed sites, and or areas with sufficient cover near forage resources may be limited throughout the year. Alternatively, black bears may simply be displaying site fidelity to specific bed sites.

Categorical covariates for wildfires, prescribed burns and thinning treatments were not among our most supported models for either bed or den site selection likely because of the paired data collection at used and random sites. We constrained our paired random sites to less than 250 m for bed sites and 700 m for den sites because we wanted to make sure that our available sample was drawn from within an area that could reasonably be considered as available to our study animals at the time they used the bed or den sites. However, this constraint resulted in most of our used-random site pairs having the same classification for thinning, wildfire and prescribed fires, thus reducing the utility of these covariates in distinguishing between used and random sites in our models. However, because wildfires and restoration treatments can reduce understory vegetation, a primary structural component affecting horizontal cover in our study, as well as basal area (Busse et al., 2000; Dodson et al., 2008; Busse et al., 2009; Wilms et al., 2017), both disturbance types may temporarily affect availability of areas with conditions suitable for black bear bed sites. Sites that were burned 2–3 years prior to use had higher horizontal visibility than sites that were burned ≥4 years. This change in visibility was likely a result of

vegetation growth in the understory following the fires. Therefore, older age burned areas are likely to provide more cover for black bears than recent burn sites. Areas thinned 1–2 years prior to bed use had similar horizontal visibility as sites thinned ≥3 years prior (40% vs. 47%) which is potentially related to slower regeneration times in thinned areas. Mechanical treatments can disturb the soil through scarification, skidding logs, and piling slash, which does not closely simulate natural phenomenon; rather, this process can impact the rhizomes and root crowns of reproducing vegetative plants, resulting in their overall decline (Zager et al., 1983). Additionally, some thinned areas were burned 3–5 years after thinning treatments to remove residual woody debris. Therefore, these prescribed fires could increase visibility.

Black bears may have been able to meet some of their foraging needs by selecting bed sites in close proximity to areas with forage. For example, during fall 2015, five radio-collared females used the same ridge for several weeks bedding and feeding on acorns that were relatively patchy in distribution. Concurrently, most male bears were found at lower elevations foraging on pinyon pine nuts, prickly pear, and acorns, all of which were more abundant in their distribution. However, because bear forage was commonly located near both used and random sites, covariates associated with forage were not informative in predicting bed site selection, at least not at the scale of our analyses. However, many bed sites (i.e., 64%) were within or adjacent to forage sites, providing habitat characteristics associated with both security cover and foraging opportunities. For example, many downed woody debris were found recently torn apart, likely the result of black bears searching for invertebrates within these logs. Typically, these areas had less vegetation, and a bear would bed against the logs which provided considerable cover. Also, a high percentage of grass, forbs, and most producing shrubs provided sufficient cover and forage. Similarly, Mollohan (1987) classified 40% of sites sampled as feeding-bedding sites; these sites had increased cover compared to sites only used for feeding. LeCount and Yarchin (1990) reported similar results from a separate black bear population in Arizona; bed sites had denser cover than feeding sites.

Overall, few studies have investigated bed site selection in bears. Although black bear bed site selection has been described previously, most studies relied on VHF radio-collars, resulting in low sample sizes (Wenzelides, 1998; Cunningham et al., 2003), sites that were not surveyed on the ground (Rayl et al., 2014), or sites that were surveyed for only one sex (Mollohan, 1987). In addition, some studies only surveyed the most accessible sites, or focused on surveying sites used during certain time frames (i.e., 0830–1800, 0900–1500; Huusko, 2012; Skuban et al., 2017). Regardless of some of the differences in sampling designs in previous studies, selection of bed sites by bears has most often been associated with increased horizontal cover and steeper slopes (Mollohan, 1987; LeCount and Yarchin, 1990; Cunningham et al., 2003). However, only one study has described bed areas in relation to a wildfire (Cunningham et al., 2003), and none to our knowledge have described black bear bed site selection in relation to

forest thinning or prescribed burn treatments.

Variation in significant covariates for black bears between our study and those in Arizona may have been due to habitat differences as a result of wildfires and restoration treatments. [Cunningham et al. \(2003\)](#) found that the number of food-plant species available, horizontal cover, shrub density, and vegetative cover within 0.91 to > 4.6 m were all greater at mid-day used sites compared to random locations. [Mollohan \(1987\)](#) and [LeCount and Yarchin \(1990\)](#) did not report any wildfire activity, and neither reported details regarding forest restorations. Thirty-nine percent of our bed sites were within an area burned by a wildfire (32% of the study area), most of which were located in areas that burned at a low severity (44% of the study area). Vegetation frequently has slower regeneration times in areas subjected to high severity fires compared to areas that burn at low severity ([Chambers et al., 2016](#)), which could explain the lower number of bed sites in areas with high burn severity in our study. Several prescribed burn and thinning treatments occurred after a wildfire had already disturbed the landscape, and there were very few used bed sites located within these areas. If a prescribed burn or thinning treatment occurred within the same year as a wildfire, then that site was classified as a wildfire. While previous wildfire sites provided thick horizontal cover several years post burn, prescribed burn sites did not have this response as they were treated more recently and vegetation responses were mostly limited to herbaceous vegetation providing little security cover. Thinned sites used by bears in our study were subjected to additional treatments, and many did not have time for sufficient recovery of the shrub layer that would provide the most horizontal cover for black bears. Thus, black bears likely avoided bedding in recent prescribed burn and thinning sites due to reduced horizontal cover. These sites were essentially large areas of open understory with little horizontal cover. However, the VCNP conducted salvage logging post wildfire. Although this removed significant amounts of timber, a considerable amount of slash was left behind. For the few sites surveyed in areas subjected to post-fire salvage logging, horizontal cover in the form of slash may have been a substantial factor for black bears in those areas. However, most thinning projects in the study area, were restoration thins and extensive efforts were made to remove all usable biomass from the site, even small diameter trees that would be left behind during typical salvage logging operations.

Decreased horizontal visibility was the most informative habitat characteristic distinguishing den sites. Additional covariates included in the analysis were not useful for predicting den site selection at either spatial scale we assessed, and we did not detect any differences between sexes. Dense cover at den sites likely provided increased security and thermal cover ([LeCount and Yarchin, 1990](#)) and is consistent with previous studies on den site selection of black bears which documented selection of dens with increased horizontal cover. For example, [Waller et al. \(2013\)](#) investigated den site selection at three spatial scales (i.e., 15 m, 100 m, 1000 m), and detected selection for increased cover at the 100 m spatial scale. In North Carolina where forestry practices are extensive, black bears have adapted to using brush and nest dens, which had a greater cover density, including taller shrubs and increased stem densities ([Martorello and Pelton, 2003](#)). A few brown bear studies have also collected data at fine scales to assess the selection process and have reported similar results ([Libal et al., 2012](#); [Pigeon et al., 2016](#)). Although there was some variation in habitat characteristics related to selection among these studies, all suggest that cover is a key habitat component for selection of den sites. Den sites in our area may not be limited in their availability due to an abundance of rocky terrain and canyons; however, the increased removal of vegetative cover from wildfires and restoration treatments may result in more black bears using rock sites for denning. [White et al. \(2001\)](#) documented changes in den use when resources were limited in an area managed for timber. Because few trees in this managed area ever reached a suitable condition for denning (e.g., large diameter), black bears instead denned on the ground, while bears in a wildlife refuge not managed for timber

denned exclusively in tree cavities. Disturbances such as wildfires and restoration treatments are likely to influence den site selection of black bears to some degree, although bears have demonstrated a strong capacity for adaptability. Continued monitoring of den site selection in these areas will aid in restoring and preserving suitable cover near den sites.

5. Conclusions

This study represents the first research conducted on bed and den site selection of black bears in New Mexico and is based on a large sample size from both male and female black bears in a forested landscape subjected to repeated disturbances from wildfires, prescribed burns, and thinning treatments. Black bears in this study have demonstrated selection of increased cover patches despite the extensive distribution of previously disturbed areas. With an increasing footprint of restoration treatments and large-scale wildfires, black bears may be required to adjust to changes in horizontal cover and perhaps vertical cover as well. While small disturbances are beneficial because they create a mosaic of habitat types and stand ages, large-scale, homogenous treatments may result in altered distribution and habitat use patterns of black bears until sufficient cover has regenerated following the disturbances. Managers may consider the timing and scale of restoration treatments to minimize their effects on black bear bed and den sites. Because their resources are spatially and temporally isolated across the landscape, identifying significant habitat components is critical for pragmatic management decisions. Strategic planning for future treatments may include preserving patches of suitable bear forage (e.g., hard [oak], and soft mast producing species) and cover within large prescribed fire and thinning treatments. Additional data, monitoring the time between treatments and other disturbances and use by black bears would also be informative for predicting long-term use by bears.

CRedit authorship contribution statement

Susan M. Bard: Conceptualization, Methodology, Data curation, Writing - review & editing. **James W. Cain:** Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Santa Fe National Forest, Valles Caldera National Preserve, and T&E, Inc. which provided funding and access to complete field work. E. Reiling provided assistance with bed site investigations, NMDGF personnel assisted during den captures, and D. Wilkens assisted with all aspects of field work. S. Murphy assisted with data analysis. J. Gedir and two anonymous reviewers provided constructive comments on an earlier draft of this article. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.117904>.

References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western U.S. forests. *Proc. Natl. Acad. Sci.* 113, 11770–11775. <https://doi.org/10.1073/pnas.1517707113>.

- doi.org/10.1073/pnas.1607171113.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>.
- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of south-western ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433. [https://doi.org/10.1890/1051-0761\(2002\)012\[1418:EROSPP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2).
- Allen, C.D., Touchan, R., Swetnam, T.W., 1996. Overview of fire history in the Jemez Mountains, New Mexico, in Goff, F., Kues B.S., Rogers M.A., McFadden L.D., Gardner J.D. (Eds.), *The Jemez Mountains region*. New Mexico Geological Society, Forty-Seventh Annual Field Conference, September 25–28, 1996, pp. 35–36.
- Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.* 74, 1175–1178. <https://doi.org/10.2193/2009-367>.
- Auger, J., Heward, J.D., Black, H.L., Wallace, G., 2005. Movements of Utah black bears: implications for management and conservation. *Western Black Bear Workshop 8*, pp. 72–80.
- Bartel, S.F., Chen, H.Y.H., Wulder, M.A., White, J.C., 2016. Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *For. Ecol. Manage.* 361, 194–207. <https://doi.org/10.1016/j.foreco.2015.11.015>.
- Baruch-Mordo, S., Breck, S.T., Wilson, K.R., Theobald, D.M., 2008. Spatiotemporal distribution of black bear-human conflicts in Colorado, USA. *J. Wildl. Manage.* 72, 1853–1862. <https://doi.org/10.2193/2007-442>.
- Baruch-Mordo, S., Wilson, K.R., Lewis, D.L., Broderick, J., Mao, J.S., Breck, S.W., 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. *PLoS One* 9, e85122. <https://doi.org/10.1371/journal.pone.0085122>.
- Benson, J.F., Chamberlain, M.J., 2010. Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *J. Wildl. Manage.* 71, 117–126. <https://doi.org/10.2193/2005-580>.
- Beyer, H.L., 2016. Kde (Kernel density estimation). <https://www.spatial ecology.com/gme/kde.htm/> (accessed 4 Jan 2016).
- Block, W.M., Franklin, A.B., Ward Jr., J.P., Ganey, J.L., White, G.C., 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restor. Ecol.* 9, 293–303. <https://doi.org/10.1046/j.1526-100x.2001.009003293.x>.
- Brodeur, V., Ouellet, J., Courtois, R., Fortin, D., 2008. Habitat selection by black bears in an intensively logged boreal forest. *Can. J. Zool.* 86, 1307–1316. <https://doi.org/10.1139/Z08-118>.
- Buckingham, S.B., Murphy, N., Gibb, H., 2015. The effects of fire severity on macro-invertebrate detritivores and leaf litter decomposition. *PLoS one* 10, e0124556. <https://doi.org/10.1371/journal.pone.0124556>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer-Verlag, New York, New York.
- Busse, M.D., Cochran, P.H., Hopkins, W.E., Johnson, W.H., Riegel, G.M., Fiddler, G.O., Ratcliff, A.W., Shestak, C.J., 2009. Developing resilient ponderosa pine forests with mechanical thinning and prescribed fire in central Oregon's pumice region. *Can. J. For. Res.* 29, 1171–1185. <https://doi.org/10.1139/X09-044>.
- Busse, M.D., Simon, S.A., Riegel, G.M., 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *For. Sci.* 46, 258–268. <https://doi.org/10.1093/forestscience/46.2.258>.
- Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. *For. Ecol. Manage.* 378, 57–67. <https://doi.org/10.1016/j.foreco.2016.07.001>.
- Cook, J.G., Stutzman, T.W., Bowers, C.W., Brenner, K.A., Irwin, L.L., 1995. Spherical densitometers produce biased estimates of forest canopy cover. *Wildl. Soc. Bull.* 23, 711–717.
- Costello, C.M., 2010. Estimates of dispersal and home-range fidelity in American black bears. *J. Mammal.* 91, 116–121. <https://doi.org/10.1644/09-MAMM-A-015R1.1>.
- Costello, C.M., Jones, D.E., Inman, R.M., Inman, K.H., Thompson, B.C., Quigley, H.B., 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus* 14, 1–16.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47. <https://doi.org/10.1093/jof/92.1.39>.
- Cristescu, B., Stenhouse, G.B., Boyce, M.S., 2013. Perception of human-derived risk influences choice at top of the food chain. *PLoS One* 8, e82738. <https://doi.org/10.1371/journal.pone.0082738>.
- Cunningham, S.C., Ballard, W.B., 2004. Effects of wildfire on black bear demographics in central Arizona. *Wildl. Soc. Bull.* 32, 928–937. [https://doi.org/10.2193/0091-7648\(2004\)032\[0928:EOWOBB\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2004)032[0928:EOWOBB]2.0.CO;2).
- Cunningham, S.C., Ballard, W.B., Monroe, L.M., Rabe, M.J., Bristow, K.D., 2003. Black bear habitat use in burned and unburned areas, Central Arizona. *Wildl. Soc. Bull.* 31, 786–792. <https://doi.org/10.2307/3784601>.
- Dahle, B., Swenson, J.E., 2003. Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *J. Anim. Ecol.* 72, 660–667. <https://doi.org/10.1046/j.1365-2656.2003.00737.x>.
- Daniel, D.L., Kindschuh, S.R., 2016. AnimalClusters.R source code (Version 1.1) [Source code]. business.nmsu.edu/departments/economics/.
- Dodson, E.K., Peterson, D.W., Harrod, R.J., 2008. Understorey vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. *For. Ecol. Manage.* 255, 3130–3140. <https://doi.org/10.1016/j.foreco.2008.01.026>.
- Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed conditional logistic regression for habitat selection studies. *J. Anim. Ecol.* 79, 548–555. <https://doi.org/10.1111/j.1365-2656.2010.01670.x>.
- Duquette, J.F., Belant, J.L., Wilton, C.M., Fowler, N., Waller, B.W., Beyer, D.E., Svoboda, N.J., Simek, S.L., Beringer, J., 2017. Black bear (*Ursus americanus*) functional resource selection relative to intraspecific competition and human risk. *Can. J. Zool.* 95, 203–212. <https://doi.org/10.1139/cjz-2016-0031>.
- Elff, M., 2016. mclogit: Mixed Conditional Logit. R package version 0.4.4. <http://cran.r-project.org/web/packages/mclogit/index.html>.
- Ellis, L.M., 2001. Short-term response of woody plants to fire in a Rio Grande riparian forest, Central New Mexico, USA. *Biol. Conserv.* 97, 159–170. [https://doi.org/10.1016/S0006-3207\(00\)00108-7](https://doi.org/10.1016/S0006-3207(00)00108-7).
- Garneau, D.E., Boudreau, T., Keech, M., Post, E., 2008. Habitat use by black bears in relation to conspecifics and competition. *Mamm. Biol.* 73, 48–57. <https://doi.org/10.1016/j.mambio.2006.11.004>.
- Goodrich, J.M., Berger, J., 1994. Winter recreation and hibernating black bears *Ursus americanus*. *Biol. Conserv.* 6, 105–110. [https://doi.org/10.1016/0006-3207\(94\)90354-9](https://doi.org/10.1016/0006-3207(94)90354-9).
- Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L., Hanna, D.D., 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85, 1708–1724. <https://doi.org/10.1890/02-0425>.
- Grovenburg, T.W., Jacques, C.N., Klaver, R.W., Jenks, J.A., 2010. Bed site selection by neonate deer in grassland habitats on the Northern Great Plains. *J. Wildl. Manage.* 74, 1250–1256. <https://doi.org/10.2193/2009-399>.
- Hamer, D., 1996. Buffaloberry [*Shepherdia Canadensis* (L.) Nutt.] fruit production in fire-successional bear feeding sites. *J. Range Manage.* 49, 520–529. <https://doi.org/10.2307/4002293>.
- Hellgren, E.C., 1998. Physiology of hibernation in bears. *Ursus* 10, 467–477.
- Hellgren, E.C., Onorato, D.P., Raymond Skiles, J., 2005. Dynamics of a black bear population within a desert metapopulation. *Biol. Conserv.* 122, 131–140. <https://doi.org/10.1016/j.biocon.2004.07.007>.
- Hellgren, E.C., Rogers, L.L., Seal, U.S., 1993. Serum chemistry and hematology of black bears: physiological indices of habitat quality or seasonal patterns? *J. Mammal.* 74, 304–315. <https://doi.org/10.2307/1382385>.
- Hellgren, E.C., Vaughan, M.R., Kirkpatrick, R.L., 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia – North Carolina. *Can. J. Zool.* 67, 1837–1850. <https://doi.org/10.1139/z89-262>.
- Huusko, J., 2012. *The Effects of Habitat and Human Activity on Daybed Selection in Brown Bears*. M.S. thesis. University of Helsinki, Helsinki, Finland.
- Kindschuh, S.R., Cain III, J.W., Daniel, D., Peyton, M.A., 2016. Efficacy of GPS cluster analysis for predicting carnivory sites of a wide-ranging omnivore: the American black bear. *Ecosphere* 7. <https://doi.org/10.1002/ecs2.1513>. art e01513.
- Kirby, R., Alldredge, M.W., Pauli, J.N., 2016. The diet of black bears tracks the human footprint across a rapidly developing landscape. *Biol. Conserv.* 200, 51–59. <https://doi.org/10.1016/j.biocon.2016.05.012>.
- Kreeger, T.J., Arnemo, J.M., 2012. *Handbook of Wildlife Chemical Immobilization*, fourth ed. Published by authors, Wheatland, Wyoming.
- Esri, 2002. ArcMap GIS. Ver. 10.3.1. Environmental System Research Institute, Inc, Redlands, California, USA.
- LeCount, A.L., Yarchin, J.C., 1990. Black Bear Habitat Use in east-central Arizona: A Final Report. Arizona Game and Fish Department, Research Branch Technical Report 4, Phoenix, Arizona.
- Lewis, D.L., Breck, S.W., Wilson, K.R., Webb, C.T., 2014. Modeling black bear population dynamics in a human-dominated stochastic environment. *Ecol. Model.* 294, 51–58. <https://doi.org/10.1016/j.ecolmodel.2014.08.021>.
- Libal, N.S., Belant, J.L., Marja, R., Leopold, B.D., Wang, G., Marshall, S., 2012. Microscale den-site selection of grizzly bears in southwestern Yukon. *Ursus* 23, 226–230. <https://doi.org/10.2192/URSUS-D-12-00002.1>.
- Lindzey, F.G., Barber, K.R., Peters, R.D., Meslow, E.C., 1986. Responses of a black bear population to a changing environment. In: *Bears: their biology and management*, Vol. 6, a selection of papers from the 6th International Conference on Bear Research and Management. February 1983, Grand Canyon, Arizona, USA, pp 57–63. <https://doi.org/10.2307/3872806>.
- Linnell, J.D.C., Swenson, J.E., Andersen, R., Barnes, B., 2000. How vulnerable are denning bears to disturbance? *Wildl. Soc. Bull.* 28, 400–413. <https://doi.org/10.2307/3783698>.
- Martorello, D.A., Pelton, M.R., 2003. Microhabitat characteristics of American black bear nest dens. *Ursus* 14, 21–26.
- Merkle, J.A., Robinson, H.S., Krausman, P.R., Alaback, P., 2013. Food availability and foraging near human developments by black bears. *J. Mammal.* 94, 378–385. <https://doi.org/10.1644/12-MAMM-A-002.1>.
- Mitchell, M.S., Powell, R.A., 2003. Response of black bears to forest management in the southern Appalachian Mountains. *J. Wildl. Manage.* 67, 692–705. <https://doi.org/10.2307/3802676>.
- Mollohan, C.M., 1987. Characteristics of adult female black bear daybeds in northern Arizona. In: *Bears: their biology and management*, Vol. 7, a selection of papers from the 7th International Conference on Bear Research and Management. February and March 1987, Williamsburg, Virginia, USA, pp 145–149. <https://doi.org/10.2307/3872620>.
- Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *For. Sci.* 50, 162–176. <https://doi.org/10.1093/forestscience/50.2.162>.
- Morris, D.W., 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evol. Ecol.* 6, 412–432.
- Murphy, S.M., Ulrey, W.E., Guthrie, J.M., Maehr, D.S., Abrahamson, W.G., Maehr, S.C., Cox, J.J., 2017. Food habits of a small Florida black bear population in an

- endangered ecosystem. *Ursus* 28, 92–104. <https://doi.org/10.2192/URSU-D-16-00031.1>.
- Mysterud, I., 1983. Characteristics of summer beds of European brown bears in Norway. In: *Bears: their biology and management*, Vol. 5, a selection of papers from the 5th International Conference on Bear Research and Management. February 1980, Madison, Wisconsin, USA, pp. 208–222. <https://doi.org/10.2307/3872540>.
- National Oceanic and Atmospheric Administration, 2016. Climate data online search. <https://www.ncdc.noaa.gov/cdo-web/search/> (accessed 5 Feb 2016).
- North, M.P., Innes, J.C., Zald, H.S.J., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. *Can. J. For. Res.* 37, 331–342. <https://doi.org/10.1139/X06-236>.
- Noyce, K.V., Garshelis, D.L., 1997. Influence of natural food abundance on black bear harvests in Minnesota. *J. Wildl. Manage.* 61, 1067–1074. <https://doi.org/10.2307/3802103>.
- O'Connor, C.D., Falk, D.A., Lynch, A.M., Swetnam, T.W., 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *For. Ecol. Manage.* 329, 264–278. <https://doi.org/10.1016/j.foreco.2014.06.032>.
- Oli, M.K., Jacobson, H.A., Leopold, B.D., 2002. Pattern of space use by female black bears in the White River National Refuge, Arkansas. *USA. J. Nat. Conserv.* 10, 87–93. <https://doi.org/10.1078/1617-1381-00010>.
- Ordiz, A., Støen, O., Langebro, L.G., Brunberg, S., Swenson, J.E., 2009. A practical method for measuring horizontal cover. *Ursus* 20, 109–113. <https://doi.org/10.2192/08SSC031.1>.
- Pelchat, B.O., Ruff, R.L., 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. In: *Bears: their biology and management*, Vol 6, a selection of papers from the 6th International Conference on Bear Research and Management. February 1983, Grand Canyon, Arizona, USA, pp. 81–92. <https://doi.org/10.2307/3872809>.
- Pigeon, K.E., Cote, S.D., Stenhouse, G.B., 2016. Assessing den selection and den characteristics of grizzly bears. *J. Wildl. Manage.* 80, 884–893. <https://doi.org/10.1002/jwmg.1069>.
- Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *Int. J. Wildland Fire* 11, 1–10. <https://doi.org/10.1071/WF01045>.
- Raine, R.M., Kansas, J.L., 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. In: *Bears: their biology and management*, Vol 8, a selection of papers from the 8th International Conference on Bear Research and Management. February 1989, Victoria, British Columbia, Canada, pp. 297–304. <https://doi.org/10.2307/3872932>.
- R Core Team, 2016. R: a Language and Environment for Statistical Computing. R foundation for statistical computing, R Vienna, Austria Version 3.3.1. <https://www.R-project.org/>.
- Rayl, N.D., Fuller, T.K., Organ, J.F., McDonald Jr., J.E., Otto, R.D., Mahoney, S.P., 2014. Den abandonment and traditional day bed use by black bears *Ursus americanus* in Newfoundland. *Wildl. Biol.* 20, 222–228. <https://doi.org/10.2981/wlb.00020>.
- Reynolds, H.G. 1966. Slash cleanup in a ponderosa pine forest affects use by deer and cattle. U.S. Forest Service Research Note RM-64, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, pp. 3.
- Reynolds-Hogland, M.R., Mitchell, M.S., Powell, R.A., Brown, D.C., 2007. Selection of den sites by black bears in the southern Appalachians. *J. Mammal.* 88, 1062–1073. <https://doi.org/10.1644/06-MAMM-A-329R1.1>.
- Rode, K.D., Farley, S.D., Robbins, C.T., 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87, 2636–2646. [https://doi.org/10.1890/0012-9658\(2006\)87\[2636:SDRSAH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2636:SDRSAH]2.0.CO;2).
- Rother, M.T., 2010. Influences of Climate and Anthropogenic Disturbances on Wildfire Regimes of the Zuni Mountains, New Mexico, U.S.A. M.S. thesis. University of Tennessee, Knoxville, Tennessee, USA.
- Schultz, C.A., Jedd, T., Beam, R.D., 2012. The collaborative forest land restoration program: a history and overview of the first projects. *J. For.* 110, 381–391. <https://doi.org/10.5849/jof.11-082>.
- Schooley, R.L., McLaughlin, Matula Jr., G.L., Krohn, W.B., 1994. Denning chronology of female black bears: effects of food, weather, and reproduction. *J. Mammal.* 75, 466–477. <https://doi.org/10.2307/1382569>.
- Sikes, R.S., 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild animals in research and education. *J. Mammal.* 97, 663–688. <https://doi.org/10.1093/jmammal/gyw078>.
- Skuban, M., Find'o, S., Kajba, M., 2017. Bears napping nearby: daybed selection by brown bears (*Ursus arctos*) in a human dominated landscape. *Can. J. Zool.* 96, 1–11. <https://doi.org/10.1139/cjz-2016-0217>.
- Smith, J.B., Grovenburg, T.W., Jenks, J.J., 2015. Parturition and bed site selection of bighorn sheep at local and landscape scales. *J. Wildl. Manage.* 79, 393–401. <https://doi.org/10.1002/jwmg.843>.
- Stephens, S.L., 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed-conifer forests. *For. Ecol. Manage.* 105, 21–35. [https://doi.org/10.1016/S0378-1127\(97\)00293-4](https://doi.org/10.1016/S0378-1127(97)00293-4).
- Stewart, B.P., Nelson, T.A., Laberee, K., Nielsen, S.C., Wulder, M.A., Stenhouse, G., 2013. Quantifying grizzly bear selection of natural and anthropogenic edges. *J. Wildl. Manage.* 77, 957–964. <https://doi.org/10.1002/jwmg.535>.
- Stratman, M.R., Pelton, M.R., 2007. Spatial responses of American black bears to prescribed fire in northwest Florida. *Ursus* 18, 62–71. [https://doi.org/10.2192/1537-6176\(2007\)18\[62:SROABB\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2007)18[62:SROABB]2.0.CO;2).
- Swenson, J.E., Sandegren, F., Brunberg, S., Wabakken, P., 1997. Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biol.* 3, 35–38. <https://doi.org/10.2981/wlb.1997.005>.
- Swetnam, T.W., Baisan, C.H., 1996. Historical fire regime patterns in the Southwestern United States since AD 1700, in Allen, C.D. (Ed.), *Fire Effects in Southwestern Forests*, In: *Proceedings of the 2nd La Mesa Fire Symposium*. U.S. Forest Service General Technical Report RM-GTR-286, Fort Collins, Colorado, pp. 11–32.
- Swetnam, T.W., Betancourt, J.L., 1990. Fire-southern oscillation relations in the southwestern United States. *Science* 249, 1017–1020. <https://doi.org/10.1126/science.249.4972.1017>.
- Touchan, R., Allen, C.D., Swetnam, T.W., 1996. Fire history and climatic patterns in ponderosa pine and mixed-conifer forests of the Jemez Mountains, northern New Mexico, in *Fire Effects in Southwestern Forests*. In: *Proceedings of the 2nd La Mesa Fire Symposium*. March 29–31, 1996, Los Alamos, NM, pp. 33–46. <https://doi.org/10.2737/RM-GTR-286>.
- Tredick, C.A., Kelly, M.J., Vaughn, M.R., 2016. Impacts of large-scale restoration efforts on black bear habitat use in Canyon de Chelly National Monument, Arizona, United States. *J. Mammal.* 97, 1065–1073. <https://doi.org/10.1093/jmammal/gyw060>.
- U.S. Geological Survey Gap Analysis Project, 2016. Download land cover data. https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/land-cover-data-download?qt-science_center_objects=0#qt-science_center_objects (accessed 6 Feb 2016).
- U.S. Geological Survey The National Map, 2016. Elevation. <https://www.nationalmap.gov/elevation.html/> (accessed 15 Feb 2016).
- Walbridge, S., Slocum, N., Pobuda, M., Wright, D.J., 2018. Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler. *J. Geosci.* 8, 94. <https://doi.org/10.3390/geosciences8030094>.
- Walker, B.H., 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.* 6, 1–32.
- Wallace, C.S., Gass, L. 2008. Elevation derivatives for Mojave Desert tortoise habitat models. U.S. Geological Survey Open-File Report 2008-1283, Reston, Virginia. <https://doi.org/10.3133/ofr20081283>.
- Waller, B.W., Belant, J.L., Leopold, B.D., Evans, D.L., Young, B.W., Simek, S.L., 2013. Scale-dependent den-site selection by American black bears in Mississippi. *Mammal Study* 38, 211–216. <https://doi.org/10.3106/041.038.0309>.
- Wenzelides, L., 1998. *Bedding Sites of Grizzly Bears (Ursus arctos horribilis) and Black Bears (Ursus americanus) in Avalanche Chutes and Adjacent Timber*. M.S. thesis. Braunschweig University of Technology, Braunschweig, Germany.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. wildfire activity. *Science* 313, 940–943. <https://doi.org/10.1126/science.1128834>.
- Western Regional Climate Center, 2016. Western U.S. climate historical summaries. <https://www.wrcc.dri.edu/Climsum.html/> (accessed 5 Feb 2016).
- Willms, J., Bartuszevige, A., Schwilk, D.W., Kennedy, P.L., 2017. The effects of thinning and burning on understory vegetation in North America: a meta-analysis. *For. Ecol. Manage.* 392, 184–194. <https://doi.org/10.1016/j.foreco.2017.03.010>.
- White Jr., T.H., Bowman, J.L., Jacobson, H.A., Leopold, B.D., Smith, W.P., 2001. Forest management and female black bear denning. *J. Wildl. Manage.* 65, 34–40. <https://doi.org/10.2307/3803274>.
- Yaklin, D.M., 2017. The effects of prescribed fire on black bear forage availability, resource selection, and distribution in the interior highlands. Ph.D. dissertation, Oklahoma State University, Stillwater, Oklahoma, USA.
- Zager, P., Jonkel, C., Habeck, J. 1983. Logging and wildfire influence on grizzly bear habitat in northwestern Montana. In: *Bears: their biology and management*, Vol. 5, a selection of papers from the 5th International Conference on Bear Research and Management. February 1980, Madison, Wisconsin, USA, pp. 124–132. <https://doi.org/10.2307/3872529>.