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***Abstract:*** Several of the world's bear species exhibit tree-rubbing behavior, which is thought to be a form of scent-marking communication. Many aspects of this behavior remain unexplored, including differences in rub tree selection between sympatric bear species. We compiled rub tree data collected on Yellowstone National Park's Northern Range (USA) and compared rub tree selection of sympatric American black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) at local and landscape scales. During 2017 and 2018, we identified 217 rub trees and detected black bears at 117 rub trees and grizzly bears at 18 rub trees, based on genetic analysis of collected hair samples. Rub trees generally were located in areas with gentle slopes and close to existing animal trails. Trees selected by black bears were typically in forested areas, whereas trees selected by grizzly bears were in forested and more open areas. Use of rub trees varied seasonally and between sexes for black bears, but seasonal data were inconclusive for grizzly bears. Black bears showed preferences for certain tree species for rubbing, but we did not find evidence that rub tree selection by grizzly bears differed among tree species. Both bear species selected trees that lacked branches on the lower portions of tree trunks and the maximum rub height was consistent with the body length of the bear species that used the tree. Although the sample size for grizzly bears was small, identifying the species and sex of bears based on genetic analysis enhanced interpretation of rub tree use and selection by bears. Scent-marking by black bears and grizzly bears on similar rub objects in well-traversed areas likely serves to enhance communication within and between the 2 species.

***Key words:*** American black bear, grizzly bear, resource selection function, rub trees, *Ursus americanus*, *Ursus arctos*, Yellowstone National Park

Most forest-dwelling species of bears rub on trees and other objects, such as rocks and utility poles, a behavior thought to be a form of intraspecific communication via chemical scent-marking (Laurie and Seidensticker 1977, Karamanlidis et al. 2007, Latham et al. 2012, Nie et al. 2012, Sato et al. 2014, Tattoni et al. 2015, Filipczyková et al. 2017, Tee et al. 2020). These rubbing behaviors often involve repeated visits to trees, such that rubs are easily identified by their smooth, discolored bark and the presence of clumps of hair and bite and claw marks (Burst and Pelton 1983). Hair deposited by bears while rubbing provides a source of DNA for noninvasive

genetic sampling. Genetic material from bear hair can help address diverse ecological questions, ranging from abundance and density estimation to population structure, reproductive fitness, and connectivity (Mowat et al. 2005; Stetz et al. 2008, 2019; Proctor et al. 2012; Sawaya et al. 2012; Loosen et al. 2019; Morehouse et al. 2021).

Bear use of rub trees is not random (Sato et al. 2014) and several researchers have explored selection behavior of bears and characteristics associated with rub trees (Clapham et al. 2013, Morgan Henderson et al. 2015, Tattoni et al. 2015). Bears tend to select larger trees with few branches on the lower portions of the trunk, which likely facilitates rubbing (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014). They also tend to select living conifer trees that excrete more resin than do

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deciduous trees, which might allow scent marks to persist longer (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015). Bears usually select rub trees in areas that are easy to traverse, such as ridge tops or drainage bottoms with gentle slopes, and areas that coincide with animal trails or human hiking trails (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015).

In regions where multiple bear species occur, rub tree use and selection can vary among species, either in the timing of when trees are used or the number and type of marks left behind (Sawaya et al. 2012, Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015). For example, grizzly bears (*Ursus arctos*) have been found to rub mainly on trees during the spring mating season and in late autumn, leaving few bite or claw marks, whereas data from American black bear (*U. americanus;* hereafter, black bear) studies showed they rub on trees throughout the year and leave numerous marks (Green and Mattson 2003, Sawaya et al. 2012, Clapham et al. 2013, Sato et al. 2014). Both species of bear stand on their hind legs to rub their backs or chest on trees resulting in the maximum height of rub areas differing based on the bear species that is most common in the region (Burst and Pelton 1983, Clapham et al. 2013, Sato et al. 2014). Although rub tree studies have been conducted in areas with multiple bear species, there is a lack of information about species-specific differences in selection of rub trees (Green and Mattson 2003, Clapham et al. 2013, Morgan Henderson et al. 2015). A better understanding of potential differences in rub tree selection between sympatric bear species could be important for the design of studies relying on genetic samples of a specific bear species from rub trees.

Rub trees were used as 1 of 2 sampling methods to estimate the population density of bears on the Northern Range of Yellowstone National Park, with black bears occurring at higher densities than grizzly bears (Bowersock 2020). Both species were detected at rub trees, which provided an opportunity to examine species-specific use and selection at 2 spatial scales: landscape and individual rub tree. Based on differences in habitat selection of black and grizzly bears (Barnes and Bray 1967, Fortin 2011, Bowersock 2020), we predicted black bears would select rub trees in forested areas, whereas grizzly bears would select rub trees in both forested and open areas. Based on the findings of other rub tree studies (Sawaya et al. 2012, Sato et al. 2014, Kendall et al. 2015), we predicted that both species would select rub trees near roads and human hiking trails. In addition, we predicted black bears would leave more bite and claw marks on rub trees compared

with trees used by grizzly bears and that the height of the rub area would reflect the species that used the tree. We also predicted that the frequency of rub tree use varies seasonally for grizzly bears, but not for black bears. Lastly, we predicted that selection of tree species and size of rub trees differ between black and grizzly bears, with black bears using larger fir (*Abies* spp.) and spruce (*Picea* spp.) trees and grizzly bears using smaller pine (*Pinus* spp.) trees.

## Study area

The Northern Range covers a 1,530-km$^2$ area that includes the northern third of Yellowstone National Park and portions of southern Montana (Fig. 1), USA. We focused on the 1,000-km$^2$ area of the Northern Range within the borders of Yellowstone National Park. Elevations range from 1,590 to 3,360 m. Whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*) dominated forests at elevations of 2,600–2,900 m, whereas Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*) comprised lower elevation forests from 1,900 to 2,200 m. A mixture of sagebrush (*Artemisia* spp.), grasses, and sedges (*Carex* spp.) occurred in open meadows at the lowest elevations (Frank and McNaughton 1992, Singer et al. 1994). The Northern Range was used by 8 ungulate species, with elk (*Cervus canadensis*) and bison (*Bison bison*) being the most common, and hosted a suite of carnivores, including black bears, grizzly bears, gray wolves (*Canis lupus*), coyotes (*C. latrans*), and cougars (*Puma concolor;* White and Garrott 2005, Barber-Meyer et al. 2008).

## Methods
### Identifying rub trees

Field crews searched for rub trees throughout the Northern Range from May to August in 2017. These searches were designed to supplement collection of hair samples via hair snares for DNA-based density estimation of black bears (Bowersock 2020). Genetic sampling occurred within a contiguous area of 26 grid cells of 5 × 5 km, comprising 650 km$^2$. Searches for rub trees were conducted throughout the study area, with most search effort occurring away from designated hiking trails. We defined a rub tree as having ≥2 characteristics described by Burst and Pelton (1983): smooth, discolored bark, presence of bear marks (bite and claw marks); and bear hair on tree trunk. After locating a rub tree, we recorded tree species, condition (dead or alive), diameter at breast
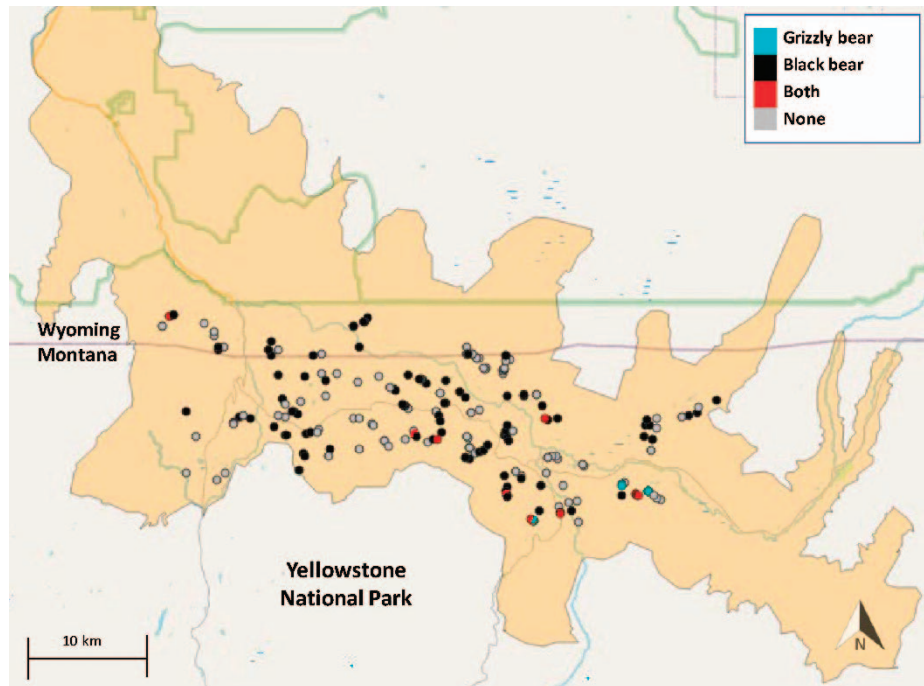
**Fig. 1.** American black (*Ursus americanus*) and grizzly (*U. arctos*) bear rub tree (*n* = 217) locations on the Northern Range (orange shading) of Yellowstone National Park, Montana and Wyoming, USA. We located and surveyed rub trees during 2017–2018. Each circle on the map represents a rub tree, with the color representing the bear species detected from collected hair samples.

height (DBH [cm]), distance from the ground to the lowest branch on the side of the tree with the rub surface (distance to lowest branch: [cm]), distance to nearest animal trail (m), and Universal Transverse Mercator coordinates. We also characterized the rub area by measuring the height of the bottom and top of the rub area (cm). In addition, we recorded the presence of bear sign (claw marks and bite marks) at each tree. We classified bear sign as fresh (<1 yr) if bite or claw marks were white or yellow in color and older (≥1 yr) if marks were dirty or dark in color. We visited all rub trees during May–September to collect hair samples, with visits occurring every 7–14 days in 2017 and 2018.

### Genetic analysis

When present on surveyed rub trees, we collected hair samples for genetic analyses. We then cleared the trees of hair using small butane torches to ensure we collected fresh hair samples for DNA mark–recapture analysis on subsequent visits and to track the frequency of use. We placed each hair sample in a paper coin envelope and stored samples in a plastic container with desiccant in a

climate-controlled room. Wildlife Genetics International (Nelson, British Columbia) conducted genotyping of hair samples collected from rub trees, using the G10J microsatellite marker to distinguish between samples from black and grizzly bears (Kendall et al. 2009). Based on these genetic data, we classified each rub tree as being used by a black bear, a grizzly bear, or both species. Following Sato et al. (2014), we calculated the probability of rub tree use (frequency of bear detection/no. of times a tree was sampled) for 4, 30-day periods within our annual sampling seasons.

### Selection of rub trees

**Landscape scale.** To assess landscape-scale selection of rub trees, we applied a use–availability sampling design and developed resource selection functions. We compared landscape characteristics associated with rub trees (used) with available (random) locations within the study area (second-order selection; Johnson 1980, Boyce and McDonald 1999, Manly et al. 2002). We generated random locations within the study area using the *st_sample* function in the *sf* package (Pebesma 2018) in

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Program R (R Development Core Team 2013), a similar ratio (~1:10) as Morgan Henderson et al. (2015) in northwestern Montana. We limited the extent of random locations to <13 km from roads because this was the greatest distance from roads at which we were able to search for rub trees.

To build the landscape models, we included topographic, vegetation, and anthropogenic covariates commonly associated with bear resource selection (Belant et al. 2010, Johnson et al. 2015, Morgan Henderson et al. 2015, Duquette et al. 2017). We used digital elevation models (U.S. Geological Survey 2017; 10-m resolution) to derive aspect (°), elevation (m), and slope (%). We converted aspect data to a ratio, with values ranging from 1 (northern aspects) to −1 (southern aspects; Deng et al. 2007). We used net primary productivity (NPP [kg carbon/m$^2$]), a measure of digestible energy from plant matter, during 2017 and 2018 to assess whether availability of herbaceous vegetation was associated with rub tree selection (250-m resolution; Xu et al. 2012, Numerical Terradynamic Simulation Group 2019). Additionally, we assessed potential differences in rub tree selection among vegetation communities using a Geographic Information System layer based on climatic overstory and understory plants (50-m resolution; Despain 1990, Yellowstone Spatial Analysis Center 2010). Human activities associated with hiking trails and roads can influence bear movements (Northrup et al. 2012, Morgan Henderson et al. 2015, Ladle et al. 2018), so we again used the *st_distance* function to measure distances to nearest hiking trails and roads using a geospatial layer of trails and roads (Yellowstone Spatial Analysis Center 2010, Pebesma 2018). We extracted these landscape data for the rub tree and random locations using the *raster::extract* function in *sf* package.

Before fitting models, we explored whether there was any correlation among pairs of covariates using the *cor* function in Program R and considered retaining only one of the pair of covariates for further analysis if the *r* value exceeded 0.7 (Dormann et al. 2013). To fit models at the landscape scale, we used generalized linear models with a binomial distribution and logit-link function using the *lmer4* package (Bates et al. 2019) and developed separate selection models for black and grizzly bears. We first built a global model that included all landscape covariates as additive effects, followed by backward variable selection to identify the most parsimonious model by removing variables that showed little association with rub tree selection ($P > 0.10$). We based our inference on effect sizes and associated confidence intervals. We checked for multicollinearity among model covariates using the variance inflation factor (VIF) *vif* function in Program R and considered removing covariates with VIF scores >10 (Dormann et al. 2013).

***Individual tree scale.*** We assessed selection at the level of individual trees by pairing each used tree with 1–5 available, but unused, trees within a 5-m radius that were ≥1.5 m tall (fourth-order selection; Thomas and Taylor 2006). This minimum height ensured we sampled trees that were large enough to potentially be used by bears for rubbing (Green and Mattson 2003, Sato et al. 2014, Morgan Henderson et al. 2015). At each available tree, we recorded the same tree characteristics as the used rub trees (i.e., tree species, tree condition, DBH, distance to lowest branch). For the distance to lowest branch measurement, we randomly chose a side of the tree based on one of the 4 cardinal directions. Available trees had not been used for rubbing, so we could not measure features associated with the rub area, such as bear marks or rub height. We excluded rub trees from analysis for which no available trees were present within a 5-m radius.

We used conditional logistic regression to assess selection at the individual tree scale, comparing characteristics of rub trees used by black bears or grizzly bears with paired available trees that were not used by bears (*coxme* package in Program R; Therneau and Lumley 2018). By explicitly pairing observations to match our data collection, selection was conditional on what was available to an individual bear at a specific location. We categorized tree species into 4 groups based on species or tree type (Douglas-fir, lodgepole or limber [*Pinus flexilis*] pine, Engelmann spruce [*Picea engelmannii*], and deciduous [trembling aspen]) to ensure sufficient sample sizes for inference. We again explored whether we needed to exclude parameters from our models by checking for potential collinearity among covariate pairs before running models. We then developed separate selection models for black and grizzly bears and began with a global model including 4 covariates: tree species group, tree condition, DBH, and distance to lowest branch. We selected these covariates based on previous research and hypothesized relationships, namely that bears typically rub on living coniferous trees with large circumference and with few to no branches on the lower portion (Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015). We then used backward variable selection to remove variables that showed little association with rub tree selection ($P > 0.10$), assessed multicollinearity using VIF scores, and again based inferences on effect sizes and associated confidence intervals.

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**Table 1.** Characteristics of rub trees used by American black bears (*Ursus americanus*) and grizzly bears (*U. arctos*), Northern Range, Yellowstone National Park, Montana and Wyoming, USA, 2017–2018. Four of 18 rub trees were used exclusively by grizzly bears (all were Engelmann spruce [*Picea engelmannii*], mean diameter at breast height [DBH] = 100 cm, maximum rub height = 171 cm, 3 of the 4 trees had bear marks).

| Tree species | *n* | DBH (cm) | | Max. rub height (cm) | | Bite marks | | | Claw marks | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SE | Mean | SE | No marks | Fresh | Old | Fresh | Old |
| Black bear | | | | | | | | | | |
| Douglas-fir | 22 | 83.8 | 5.5 | 158.9 | 2.6 | 15 | 1 | 1 | 1 | 6 |
| Engelmann spruce | 45 | 143.9 | 5.4 | 168.2 | 1.5 | 22 | 3 | 11 | 3 | 16 |
| Limber pine | 1 | 210.0 | — | 145.0 | — | 1 | 0 | 0 | 0 | 0 |
| Lodgepole pine | 41 | 127.6 | 3.8 | 165.7 | 1.8 | 5 | 5 | 14 | 9 | 25 |
| Rocky Mountain juniper | 4 | 69.1 | 2.2 | 167.1 | 2.0 | 0 | 1 | 1 | 1 | 3 |
| Subalpine fir | 1 | 95.0 | — | 112.0 | — | 0 | 0 | 0 | 0 | 1 |
| Trembling aspen | 1 | 110.0 | — | 142.0 | — | 0 | 0 | 0 | 1 | 0 |
| White spruce | 2 | 119.3 | 24.3 | 144.3 | 5.7 | 1 | 0 | 0 | 0 | 1 |
| Total or mean | 117 | 119.8 | 5.9 | 150.4 | 1.9 | 44 | 10 | 27 | 15 | 52 |
| Grizzly bear | | | | | | | | | | |
| Douglas-fir | 3 | 109.3 | 21.1 | 191.7 | 7.2 | 1 | 0 | 1 | 0 | 2 |
| Engelmann spruce | 14 | 147.0 | 8.3 | 179.2 | 3.4 | 6 | 2 | 4 | 2 | 4 |
| White spruce | 1 | 168.0 | – | 133.0 | – | 0 | 0 | 0 | 0 | 1 |
| Total or mean | 18 | 141.4 | 9.8 | 168.0 | 3.5 | 7 | 2 | 5 | 2 | 7 |

## Results

### Identifying rub trees and genetic results

Field personnel spent >900 survey hours searching for rub trees in 2017 and documented 217 rub trees. Between 2017 and 2018, hair samples were collected from 186 different rub trees, but bear genotyping was only successful for samples collected from 121 of those trees. We detected black bears (46 females, 54 males) at 117 rub trees and grizzly bears (3 females, 15 males) at 18 trees (Table 1). Of these, we detected both species at 14 trees: we documented an average of 2.5 (range = 1–6) black bear detections and 1.6 (range = 1–5) grizzly bear detections per tree. Only 4 trees had genetic samples exclusively from grizzly bears.

### Rub tree use

Black bears used trees with smaller DBH (mean = 119.8 cm, standard error [SE] = 5.9) compared with grizzly bears (mean = 141.4 cm, SE = 9.8). The maximum rub height at trees used by grizzly bears (mean = 168.0 cm, SE = 3.5) was greater than the rub height of trees used by black bears (mean = 150.4 cm, SE = 1.9; Table 1). Both bear species used rub trees that were in proximity to animal trails (black bear: mean = 57.1 m, SE = 4.9; grizzly bear: mean = 40.2 m, SE = 13.7). Overall, we found hair on 85.7% of rub trees, and rub trees used by black bears showed a higher frequency of claw marks than bite

marks (Table 1). Based on genetic samples, black bears showed seasonal patterns in rub tree use that varied by sex, with male bears using rub trees more frequently during spring and early summer, whereas females used rub trees more frequently in mid- to late summer (Fig. 2). Probability of rub tree use was low among female grizzly bears and showed no seasonal variation, whereas male probabilities were highest in spring and early summer but had substantial uncertainty (Fig. 2).

### Selection of rub trees

**Landscape scale.** Based on the 117 rub trees that black bears used (and the available [random] locations withing the study area), we found that aspect, elevation, slope, distance to nearest road, distance to nearest hiking trail, and vegetation community were important landscape features for selection (Table 2, Fig. 3) and did not find any evidence of collinearity or multicollinearity among model parameters. Black bears selected rub trees that were at lower elevations, on more gentle slopes, with southern aspects, and closer to roads and hiking trails (Table 2). Black bears selected rub trees found in mostly forested vegetation communities (except for subalpine fir–grass sedge [*Carex* spp.]) and were less likely to select rub trees found in big sagebrush (*Artemisia tridentata*)–grass sedge and Idaho fescue (*Festuca idahoensis*)–grass sedge communities, compared with big sagebrush–sticky
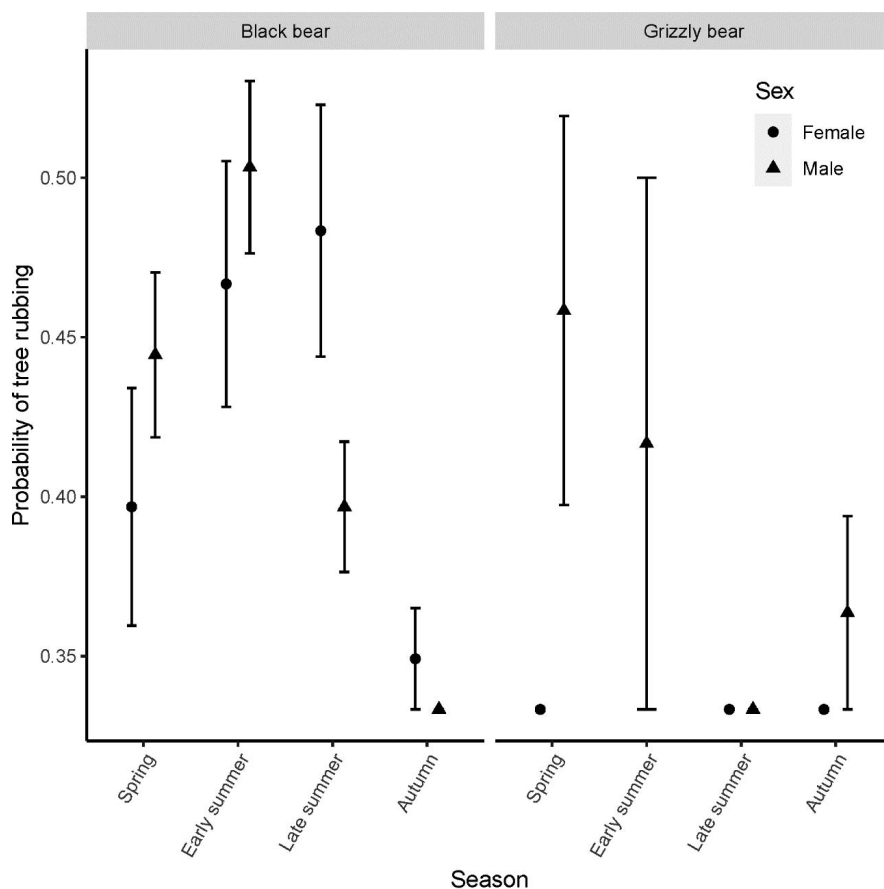
**Fig. 2.** Probability (means and standard errors) of rub tree use by American black (*Ursus americanus*) and grizzly (*U. arctos*) bears by season and sex, Northern Range, Yellowstone National Park, Montana and Wyoming, USA, 2017–2018. Probability of use was calculated as the frequency of bear detections divided by the number of times a tree was sampled within a 30-day period, which fell into 1 of 4 seasons: spring (15 May–14 Jun), early summer (15 Jun–14 Jul), late summer (15 Jul–14 Aug), and autumn (15 Aug–14 Sep).

**Table 2.** Parameter estimates from models characterizing selection of rub trees by American black (*Ursus americanus*) and grizzly (*U. arctos*) bears at the landscape scale, Northern Range, Yellowstone National Park, Montana and Wyoming, USA, 2017–2018. For the black bear model, we compared 117 used rub trees with 1,170 paired available trees. For the grizzly bear model, we compared 18 used rub trees with 180 paired available trees. Elevation, slope, distance to nearest road, and distance to nearest hiking trail were continuous variables. Aspect was scaled between 1 (north) and −1 (south). Vegetation community also was important for selection at the landscape scale (Fig. 3).

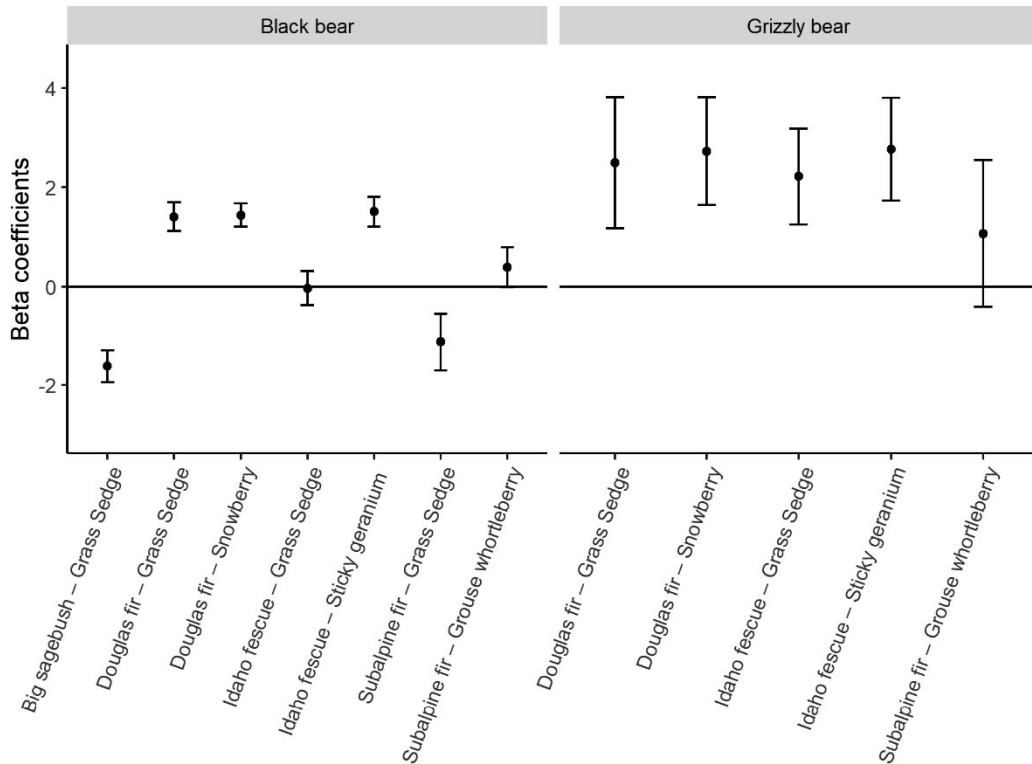| Landscape characteristic | Black bears | | | Grizzly bears | | |
|---|---|---|---|---|---|---|
| | Estimate | SE | *P* | Estimate | SE | *P* |
| Elevation (m) | −0.0037 | <0.001 | <0.001 | — | — | — |
| Aspect | −0.8876 | 0.108 | <0.001 | −0.5895 | 0.259 | 0.023 |
| Slope (%) | −0.0831 | 0.010 | <0.001 | −0.1605 | 0.042 | <0.001 |
| Distance to road (m) | −0.0003 | <0.001 | <0.001 | −0.0002 | <0.001 | 0.042 |
| Distance to trail (m) | −0.0003 | <0.001 | <0.001 | — | — | — |

**Fig. 3.** Parameter estimates (circles) and standard errors (vertical lines) based on models of characterizing selection of rub trees by American black (*Ursus americanus*) and grizzly (*U. arctos*) bears, specifically comparing vegetation communities at the landscape scale, Northern Range, Yellowstone National Park, Montana and Wyoming, USA, 2017–2018. The model for black bears included 117 rub trees (compared with 1,170 random locations) and the model for grizzly bears included 18 rub trees (compared with 180 random locations). Big sagebrush–sticky geranium (*Artemisia tridentata–Geranium viscosissimum*) was the reference level for both models. Elevation, aspect, slope, and distances to roads and trails also were important for rub tree selection at the landscape scale (Table 2).

geranium (*Geranium viscosissimum*; the reference community) or Idaho fescue–sticky geranium (Fig. 3).

Aspect, slope, distance to road, and vegetation community were the most important landscape features associated with the selection of rub trees by grizzly bears (Table 2, Fig. 3); and again, we did not detect any correlation or multicollinearity between model parameters. Similar to black bears, grizzly bears selected rub trees on more gentle slopes, with southern aspects, and closer to roads (Table 2). Grizzly bears selected rub trees in vegetation communities dominated by Douglas-fir and Idaho fescue over big sagebrush–sticky geranium (the reference community) or subalpine fir–grouse whortleberry communities (Fig. 3).

***Individual tree scale.*** We collected data on 169 used rub trees and 570 paired available trees. Some hair samples collected from these trees failed to produce a

genotype, leaving 98 rub trees for which we were able to identify the bear species, which were paired with 307 available trees.

For black bears, we compared characteristics of 94 used trees with 293 paired available trees. Black bears were more likely to select pine than Douglas-fir trees and were more likely to select Douglas-fir than deciduous trees (Table 3). However, we did not detect a difference in selection between Douglas-fir and spruce trees (Table 3). Black bears were more likely to select trees without branches on the lower portions of the trunk. We found little evidence that rub tree selected by black bears differed with tree diameter.

For grizzly bears, we compared characteristics of 13 used trees with 47 paired available trees. Similar to black bears, grizzly bears also were more likely to select trees without branches on the lower portions of the trunk

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**Table 3. Parameter estimates from models characterizing selection of rub trees by American black (*Ursus americanus*) and grizzly bears (*U. arctos*) at the individual tree scale based on conditional logistic regression, Northern Range, Yellowstone National Park, Montana and Wyoming, USA, 2017–2018. For the black bear model, we compared 94 used rub trees with 293 paired available trees. For the grizzly bear model, we compared 13 used rub trees with 47 paired available trees. Tree species was a categorical variable, with Douglas-fir (*Pseudotsuga menziesii*) as the reference group. The pine category included lodgepole (*Pinus contorta*) or limber pine (*Pinus flexilis*), spruce included Engelmann spruce (*Picea engelmannii*), and deciduous included trembling aspen (*Populus tremuloides*).**

| Species | Tree characteristic | β | SE | *P* |
|---------|---------------------|-----|------|--------|
| Black bear | Tree species—pine | 3.08 | 0.78 | <0.001 |
| | Tree species—spruce | 1.05 | 0.58 | 0.920 |
| | Tree species—deciduous | − 1.59 | 0.73 | 0.028 |
| | Distance to lowest branch | 0.004 | 0.001 | 0.004 |
| Grizzly bear | Distance to lowest branch | 0.015 | 0.005 | 0.007 |

(Table 3). We did not detect differences in rub tree selected by grizzly bears based on tree species group, tree condition, or DBH. Furthermore, we did not detect any collinearity or multicollinearity before or after running models for both bear species.

## Discussion

Using genetic data, we were able to characterize and compare use and selection of rub trees by 2 sympatric bear species. At the landscape level, black and grizzly bears showed similar patterns of selection. Both bear species on the Northern Range selected rub trees that were located mainly at lower elevations with low to modest slopes, consistent with the findings of other studies (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015). These areas represent typical travel corridors for bears because the terrain is easier to traverse (Carnahan et al. 2021) and may enhance detection of scent left at rub trees (Clapham et al. 2013, Morgan Henderson et al. 2015, Revilla et al. 2021). Similar to other studies (Sawaya et al. 2012, Sato et al. 2014, Kendall et al. 2015), we found that both species of bears selected for rub trees closer to hiking trails and roads. Although we did not find plant productivity (NPP) to be a good predictor of rub tree selection, rub trees were associated with vegetation communities containing food and cover resources that both bear species select (Barnes and Bray 1967, Fortin 2011, Schwartz et al. 2014, Bowersock 2020). In coastal British Columbia, Clapham et al. (2013) also found rub trees in areas associated with food resources, such as salmon (*Oncorhynchus* spp.) or fruiting vegetation.

We observed some differences in rub tree selection between the 2 bear species. Black bears selected rub trees in forested vegetation communities more often than did grizzly bears, which selected rub trees in both forested and nonforested vegetation communities, reflecting general patterns of habitat selection in the region (Barnes and Bray 1967, Fortin 2011, Bowersock 2020). Additionally, rub trees used by black bears had a maximum rub height similar to the average body length of black bears captured in this area (males: 164 cm, 95% CI = 150–177; females: 136 cm, 95% CI = 127–145; National Park Service, unpublished data). In comparison, the maximum rub height on trees used by grizzly bears matched the larger average body length of grizzly bears captured in Yellowstone National Park (males: 188 cm, 95% CI = 168–208; females: 170 cm, 95% CI = 155–185: Green and Mattson 2003).

In contrast to our prediction that black bears would use rub trees throughout the year, we found that the frequency of rub tree use varied seasonally for both female and male black bears. The probability of rub tree use among male black bears was highest in spring and early summer, which may reflect scent communication among competing males during the mating season (Taylor et al. 2015). However, contrary to other black bear studies that found female black bears use rub trees less often than do males (Sawaya et al. 2012, Taylor et al. 2015), we found that both sexes had similar probabilities of use during spring and early summer and females had higher probabilities of use in midsummer. In some cases, previous studies have relied on visual observation of bears using rub trees to make comparison between sex and age classes (Taylor et al. 2015, Revilla et al. 2021), which potentially underrepresented the frequency of female use of rub trees. For male grizzly bears, we found some evidence of greater use of rub trees during the spring mating season, consistent with other studies (Clapham et al. 2012, Sato et al. 2014, Lamb et al. 2017). However, we found little evidence of seasonal changes in rub tree use for female grizzly bears. In either case, our inference regarding seasonal use of
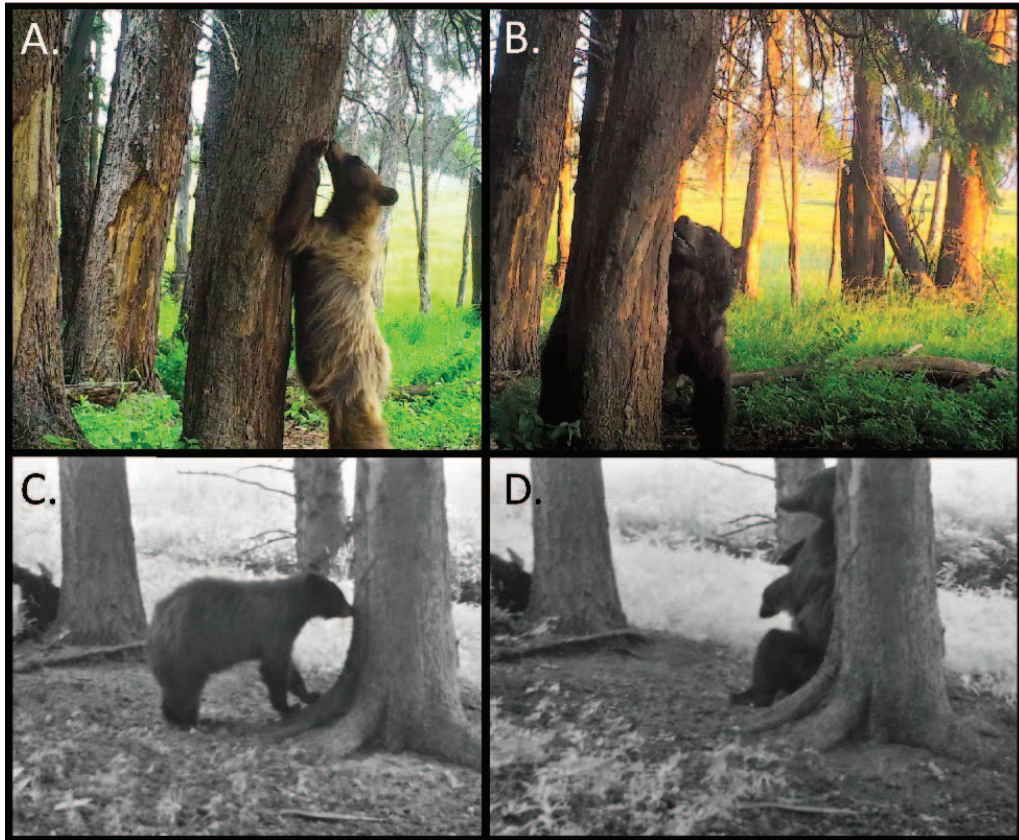
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**Fig. 4.   Remote camera pictures showing American black bears (*Ursus americanus;* A, C) rubbing on the same rub trees as grizzly bears (*U. arctos;* B, D) during July 2018, Northern Range, Yellowstone National Park, Montana and Wyoming, USA.**

rub trees by grizzly bears were limited because of small sample sizes.

At the individual tree scale, both bear species selected trees lacking branches on the lower portions of tree trunks. Whether a rub tree lacked branches on the lower portion of the trunk because of the trees' self-pruning or from bears and other animals breaking the branches off, these branch-free sections likely facilitate tree-rubbing (Shaffer 1971, Sato et al. 2014, Seryodkin 2014). We did not find evidence that tree condition or diameter were important factors for rub tree selection. Black bears selected coniferous over deciduous trees, which is consistent with other studies (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014). However, contrary to our predictions, black bears selected pine (mainly lodgepole pine) over spruce or fir trees, despite lodgepole pine–dominated forests being relatively uncommon in our study area. This selection could be because lodgepole pine trees self-prune

the lower branches in dense, mature forest (Anderson 2003), possibly making this tree species more desirable compared with other tree species. We did not detect differences in selection of tree species by grizzly bears, but the small sample size may have limited our ability to detect patterns. We also note that grizzly bears rubbed on utility poles more often than did black bears. Thus, the selection of lodgepole pine, which are less common on the Northern Range compared with other tree species, and utility poles may reflect that both bear species select conspicuous objects for rubbing, which is a common behavior among bears and other mammals for scent communication (Karamanlidis et al. 2007, Alberts 2011, Clapham et al. 2013, González-Bernardo et al. 2021).

Few studies have been conducted on rub tree use and selection by sympatric black bears and grizzly bears. Our findings are somewhat limited because of small sample sizes for grizzly bears, but broadly confirm those of other

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rub tree studies (Green and Mattson 2003, Clapham et al. 2013, Sato et al. 2014, Morgan Henderson et al. 2015). Furthermore, there are marked differences in black and grizzly bear densities on the Northern Range, reflecting differences in rub tree preferences we observed (Bowersock 2020,). Despite small sample sizes for grizzly bears, we detected multiple instances of both species using the same rub trees (Fig. 4). That finding was contrary to other studies (Mattson et al. 2005, Sawaya et al. 2012, Stetz et al. 2019) and suggests that interspecific communication may play a role, but further research is needed. Our findings also demonstrate that future rub-tree studies would benefit from including genetic sampling to enhance estimating the frequency of rub tree use and selection by different bear species and sexes. Additionally, bears of both species might frequently scent mark on similar rub objects in areas that are well-traversed by many animals to enhance communication within and between species.

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