

Tree rubbing by Yellowstone grizzly bears *Ursus arctos*

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Tree rubbing or marking by bears has been observed throughout the northern hemisphere. Even so, this behaviour has rarely been studied. We documented 93 sites where grizzly bears *Ursus arctos horribilis* rubbed on 116 trees during 1986-1992, in the Yellowstone Ecosystem. We used logistic regression and information-based estimation and selection criteria to specify models that explained selection of sites and individual trees for rubbing by bears in our study area. The probability of rubbing peaked during May and June, the period of mating and moult, and declined thereafter. At the landscape level, grizzly bears selected for gentle south-facing slopes, forest/non-forest ecotones with sparse deadfall, and forest stands dominated by lodgepole pine *Pinus contorta* or Douglas-fir *Pseudotsuga menziesii*. Among the trees at sites where bears rubbed, we found strong selection for large diameters but no indication of selection for species. Rubbed trees were highly associated with travel routes likely used by bears, including game trails, recreation trails and forest edges. Rubbing was often oriented towards these likely travel routes. Short trails of entrenched pad-shaped marks leading up to rubbed trees were recorded at 58% of the sites where rubbing occurred. Contrary to reports of black bears *Ursus americanus* clawing and biting trees, we found shredded or bitten bark at only 9% of sites with rubbed or otherwise marked trees. Circumstantial evidence suggests that bears used trees primarily for rubbing their back and shoulders. Our findings are consistent with previous arguments that rubbing serves as a means of chemical communication.

Key words: grizzly bears, marking, rubbing, rub tree, *Ursus arctos horribilis*, Yellowstone

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Rubbing of trees by brown bears *Ursus arctos* has been documented throughout the Northern Hemisphere. Tschanz, Meyer-Holzapfel & Bachmann (1970) described rubbing by a group of captive brown bears in Bern, Switzerland. Adult bears rubbed primarily their shoulders, neck and back of the head while facing away from trees. Males rubbed most frequently during the mating season while females rubbed most frequently during moult. The two genders shared some sites for rubbing while others were used only by a single sex. Tschanz et al. (1970) presented evidence that bears used rubbed trees for orientation, but concluded that the primary function of rubbing was communication by chemical means. Colmenares & Rivero (1983) confirmed this interpretation by observations of bears in the Madrid Zoo.

There has been a great deal of speculation about the function of rubbing by bears under field conditions. Schaffer (1971) monitored rubbing of trees in the Apgar Mountains of Glacier National Park, Montana, USA, and reported that most trees had straight trunks with few branches. He did not observe increased frequency of rubbing during the mating season and concluded that rubbing was a form of stretching or a response to external stimuli such as insect bites. In the Ahnuhati River drainage in coastal British Columbia, Canada, bears favoured the use of Amabilis fir *Abies amabilis* for rubbing. Rubbed trees were often associated with well-developed bear trails (sequences of entrenched pad prints; Lloyd (1979)). Lloyd (1979) speculated that this combination of bear trails and rubs reduced strife by assisting bears to space themselves within confined valley bottoms near concentrated food sources (spawning salmon *Oncorhynchus* spp.). Murie (1981) reported bear trails in conjunction with rubbed trees in Mount McKinley (Denali) National Park, Alaska, USA. In the absence of trees, he observed bears to rub boulders, downed poles and even the ground. Murie (1981) concluded that bears rubbed primarily to massage themselves and discounted the importance of rubbing in communication. All three of these authors reported only incidental clawing and biting of trees.

Observations of wild brown bears in northern Europe and Asia are equally inconsistent. Krott (1962) noted rubbing of trees in the Alps and in Finland and Sweden and concluded that it functioned only in 'personal hygiene'. Novikov (1956), Stroganov (1962) and Novikov, Airapet'yants, Pukinskii, Timofeeva & Fokin (1969) reported that bears in the former U.S.S.R. scratched trees with their claws, but made no mention of rubbing or burnishings. Stroganov (1962) speculated that the scratchings functioned to sharpen or abrade the bears' claws, whereas Novikov et al. (1969) suggested that markings

were used in intra-species communication. Bromlei (1965) described rubbing by bears during spring and early summer in the Amur region of Russia and considered it to be a response to biting insects. Sharafutdinov & Korotkov (1976) referred to trees "used for scratching" in the Bashkir State Forest Preserve, but it is unclear whether this was synonymous with 'rubbing'.

American black bears *U. americanus* have been reported to claw and bite trees throughout their North American range (Grinnell, Dixon & Linsdale 1937, Rogers 1977, Spencer 1966, Willey 1978, Burst & Pelton 1983). American black bears have also often been observed to strip bark from conifers early in the growing season to consume sugar-rich cambium (Glover 1955, Poelker & Hartwell 1973, Mason & Adams 1989, Barnes & Engeman 1995). Reports of tree rubbing are infrequent. Burst & Pelton (1983) and Rogers (1977) reported that clawing and biting peaked prior to August. Rogers (1977) attributed this early-season activity to males, which evidenced high levels of blood serum testosterone during spring and early summer (McMillin, Seal, Rogers & Erickson 1976). He also suggested that black bears marked trees to reduce mutually harmful conflicts among males.

We documented rubbing of trees by grizzly bears *U. a. horribilis* in the Yellowstone region of the USA during an intensive study of foraging behaviour by radio-marked bears during 1986-1992. We used our field observations and the observations of other researchers, summarized above, to develop several hypotheses that focused our analysis and aided in the selection of candidate variables for explanatory modelling. Because we assumed that our study bears primarily rubbed their backs, we expected: 1) that marking by clawing or biting was infrequent and 2) that the maximum height of burnished rubbing surfaces approximately corresponded to the contour body length of adult bears captured during our study. We also expected that rubbing would be positively associated with: 3) tree diameter, absence of limbs and the presence of bear trails; 4) forest/non-forest ecotones; 5) gentle slopes and landforms such as ridges and bottoms; and 6) the mating and moulting seasons.

Material and methods

Study area

We documented tree rubbing by grizzly bears throughout their 23,300-km² range in the Yellowstone region. This ecosystem includes parts of the states of Wyoming, Montana and Idaho and spans Universal Transverse

Mercator (UTM) grids 450,000-650,000 m East and 4,815,000-5,050,000 m North. The area contains Yellowstone and Grand Teton National Parks, parts of five adjacent National Forests, and privately owned land. Most of the study area lies between 2,000 and 2,400 m a.s.l. and consists of high-elevation plateaus surrounded by rugged mountain ranges.

Winters were long and cold, and summers were short and cool. The average annual temperature at Mammoth, Wyoming was 4.4°C; seasonal means varied from -5°C for January-March to 15°C for July-September (Dirks & Martner 1982). Much of the 30-75 cm of average annual precipitation fell as snow during the mid-winter months, with accumulations reaching 20-260 cm before melting during March-June, depending on elevation and latitude (Dirks & Martner 1982). A rain-shadow caused xeric conditions in the Yellowstone Valley to the north and in the Shoshone National Forest east of Yellowstone National Park (Baker 1944).

Coniferous forests covered >75% of the study area. Extensive non-forest areas occurred primarily in the alpine zone or in low-elevation valleys. Most forests were in early- to mid-successional stages of development dominated by lodgepole pine *Pinus contorta*. Low elevation late-successional forests were dominated by Douglas-fir *Pseudotsuga menziesii*, whereas late-successional forests above 2,400 m were dominated by whitebark pine *Pinus albicaulis*, subalpine fir *Abies bifolia*, or Engelmann spruce *Picea engelmanni*. Aspen *Populus tremuloides* and limber pine *Pinus flexilis* were abundant in only a few low-elevation areas (Despain 1990).

Field methods

Bears were trapped, marked and radio-relocated according to methods described by Knight & Eberhardt (1985) and Blanchard & Knight (1991). At the time of each capture, bears were sexed and measured with a steel tape (Blanchard 1987). Seven body measurements were taken including the length of dorsal body profile from tail to nose. Bears were located by aerial telemetry from fixed-wing aircraft at approximately 4-day intervals.

Field crews collected data from rubbed trees during field visits to aerial-telemetry locations of radio-marked bears during 1986-1992. A large study area, lack of road access, and administrative or legal restrictions on helicopter use forced us to representatively rather than randomly select aerial locations for field visits (Mattson 2000). We measured and otherwise described site parameters as well as the bear's activity at each visited site. We collected information that included location (UTM), landscape position (ridge, upper slope, mid-slope, low-

slope, bottom and flat), elevation (m), slope (°), aspect (° from the North), distance to forest/non-forest edge (m), estimates of abundance of coarse woody debris (i.e. deadfall in the categories 0-7, indicating none to very heavy), and description of site physiognomy. For forested sites, we included an ocular estimate of percent forest overstory and a measure of basal area (Avery 1975: 169) for live and dead trees, by species (m² ha⁻¹; Mattson 1997). While en route to and from radio-telemetry locations, we described sites where we encountered signs attributable to unknown bears by the same measures we used to describe radio-telemetry locations.

For rubbed trees, we recorded species, diameter at breast height, presence of clawing or biting, age of most recent rubbing, compass direction of rubbing (°), maximum height of rubbing (dm), percent of tree circumference rubbed, presence and dimensions of associated bear trails (i.e. series of pad shaped depressions), association with game or human recreation trails, and orientation of rubbing with respect to these trails (i.e. the difference in compass degrees between orientation of the rubbed surface and a perpendicular from the rubbed tree to the trail). We aged rubbing activity by the brittleness and bleaching of hair snagged on the bark of rubbed trees, the liquidity of sap exuded from tree wounds, and the freshness of other bear signs such as faeces, urinations and tracks. We also sketched or photographed most rubbed trees.

Analysis methods

We specified multi-variable logit-based models (Hosmer & Lemeshow 2000) to explain the probability that rubbing had occurred at a site, versus not, as a function of site features. We considered Julian date, dominant tree species in the surrounding forest stand, distance to forest edge, total basal area, dead standing basal area, basal areas of lodgepole pine and whitebark pine, amount of deadfall, stand age, slope, aspect and landform as candidate variables for models explaining selection of sites for rubbing. We only analyzed activity sites where total basal area was >0 for this model based on the premise that trees needed to be present in order for grizzlies to exercise choice in rubbing. We specified two models using two different data sets: 1) sites where signs had been found that were attributable to an unknown grizzly bear, excluding telemetry locations of radio-marked bears; and 2) sites solely associated with telemetry locations, including sites where no signs of feeding, bedding or rubbing had been found. Because few incidents of rubbing were found at telemetry locations, we relied more heavily on data set 1) for inferences.

We also specified a multi-variable model to explain

Table 1. Estimates and standard errors (SE) of β parameters for multi-variable logit-based models explaining the probability that a grizzly bear in the Yellowstone region had rubbed a tree versus all other types of activity during 1986-1992. The importance of explanatory variables is indicated by Δ AIC (change in Akaike's Information Criterion with deletion of the variable).

Explanatory variable	Parameter estimates		Δ AIC
	β	SE	
Constant	-11.1	4.66	
Dominant tree species			6.3
Douglas-fir (DF)	3.26	0.8	
Lodgepole pine (LP)	2.26	0.53	
Spruce/fir (SF)	0.92	1.13	
Non-forest (NF)	0.64	1.14	
Whitebark pine (WB)	-7.09 ^b		
Julian date	0.11	0.055	2.9
Julian date squared	-0.00034	0.00016	4.0
Distance to forest/non-forest edge (m) ^a	-0.39	0.14	6.5
Amount of deadfall (index) ^a	-1.11	0.41	5.7
Slope (°)	-0.1	0.045	9.5
Aspect (° from the north) squared	0.000079	0.000026	8.4

^a Parameters were estimated using natural log transformations ($\ln[x + 1]$) of the data.

^b This parameter was calculated as the difference between zero and the sum of other parameters for the effect of dominant tree species.

Results

the selection of individual trees for rubbing. We considered species, diameter at breast height and plot as candidate explanatory variables. We considered trees to be 'available' if they fell within a variable-radius plot centered on the rubbed tree. We weighted each tree in the analysis by a factor that corrected for bias in probability of detection that was inversely related to tree diameter, subject to the constraint that the sums of weighted and unweighted observations were equal. This constraint guarded against inflating degrees of freedom.

We chose variables for inclusion in models so as to minimize the sample-size-corrected version of Akaike's Information Criterion (AIC_c ; Burnham & Anderson 1998). Parameters were estimated by maximum likelihood. We expressed the relative importance of given explanatory variables in final models by the change in AIC_c with their piece-wise deletion (Δ AIC). A relatively large change in AIC_c indicated greater explanatory information. Once we identified important explanatory variables in the context of multi-variable models, we used logistic regression plots to illustrate the nature of univariate or bivariate relations.

During 1986-1992 field crews visited 1,225 forested sites where a radio-marked bear had been located by aerial telemetry. Feeding, bedding or rubbing activity attributable to unknown grizzly bears was documented at an additional 779 forest sites. At 93 sites we observed signs of at least one grizzly bear rubbing some object. Of the seven radio-marked grizzly bears known to rub trees, four were females and three were males.

Grizzly bears rubbed or otherwise marked a total of 116 trees, one trail marker post, the side of a backcountry barn, and the front porch posts of two backcountry cabins. Of the sites where rubbing occurred, 61 had one rubbed tree, 15 sites had two rubbed trees, two sites had three rubbed trees, and four sites had four rubbed trees. Of the 116 rubbed trees, 76 were lodgepole pine, 18 were Englemann spruce, 12 were Douglas-fir, seven were sub-alpine fir, and three were whitebark pine.

Effects of site and landscape features

The explanatory model based on observations of signs from unknown grizzly bears exhibited a good fit to the data ($R_L^2 = 0.86$, $N = 693$, $df = 681$, $G^2 = 139.0$, $P[\text{goodness-of-fit}] = 1.00$). Of the individual effects, those of

Table 2. Non-parametric summary statistics for variables included in models explaining differences between sites where Yellowstone grizzly bears had versus had not rubbed a tree during 1986-1992, for sites where some signs of feeding or bedding had been observed, including sites not associated with a radio-telemetry location.

Variable	Rubbing site		Not a rubbing site	
	Median	Interquartile range	Median	Interquartile range
Distance to forest edge (m)	10	0 - 40	50	5 - 200
Calendar date	15 June	27 May - 14 July	21 July	10 June - 30 August
Amount of deadfall (index)	1	0 - 2	2	1 - 4
Site slope (°)	5	3 - 10	9	4 - 16
Aspect (° from the north)	124	96 - 159	47	20 - 94

slope (negative), orientation away from the north aspect (positive), and distance from forest edge (negative) were strongest (Tables 1 and 2, Fig. 1). The species of dominant trees in the surrounding forest stand also had a strong effect, with rubbing most likely where Douglas-fir or lodgepole pine were dominant, and least likely where whitebark pine was dominant (see Table 1). Based on the first derivative of the univariate relation with date (see Fig. 1A), the probability of rubbing peaked around Julian date 158 (= 7 June). Collectively,

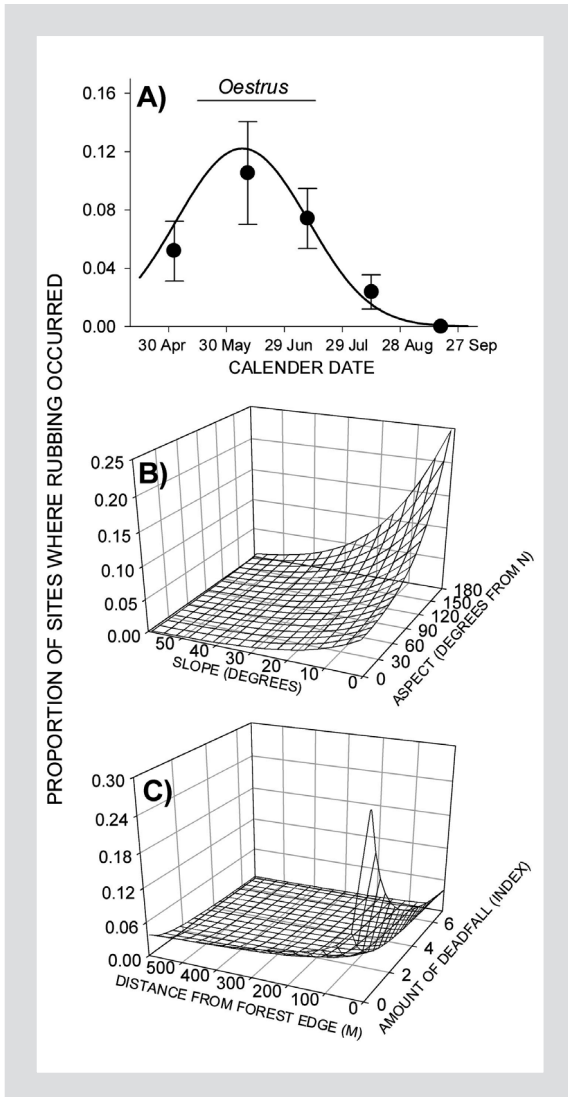


Figure 1. The probability that rubbing activity was recorded at forested activity sites of Yellowstone grizzly bears during 1986-1992, as a function of A) date, B) slope (in $^{\circ}$) and aspect ($^{\circ}$ from the north), and C) distance to forest edge (in m) and amount of deadfall (indexed). In A) circles and associated standard error bars are for mean probabilities estimated for quintiles of the data and are shown to illustrate goodness-of-fit, and the period of oestrus is also demarked (roughly mid-May through mid-July; Craighead et al. 1995).

factors associated with vegetation structure (distance to forest edge, amount of deadfall, and overstory dominant species) had the greatest effects on probability of rubbing (Δ AIC = 26.7), followed by the effects of factors associated with physical site (slope and aspect; Δ AIC = 15.3) and the effect of the polynomial of date (Δ AIC = 4.9).

The explanatory model based on sites where radio-marked bears had been located by aerial telemetry also fit well ($R_L^2 = 0.94$, $N = 1,201$, $df = 175$, $G^2 = 45.7$, $P[\text{goodness-of-fit}] = 1.00$). The sole explanatory variable was Julian date (JD; Δ AIC = 2.2). The model was: $\text{logit}(p) = 8.62 - 2.64\ln(\text{JD} + 1)$, where $\text{logit}(p)$ was the logit-transformed probability that rubbing had occurred at a site.

Features of rubbed trees and rubbed tree surfaces

Of sites where rubbing had occurred, 70% were associated with recreation trails, 16% were associated with game trails, and 12% had no trail association. Rubs were not oriented independently of these trails ($df = 2$, $G^2 = 21.58$, $P < 0.05$). The centers of 63% of rubbed surfaces faced towards ($\pm 22.5^{\circ}$) trails, whereas 13% were oriented away from ($\pm 22.5^{\circ}$), and 24% were oriented parallel to ($\pm 22.5^{\circ}$) trails.

Entrenched linear sequences of bear pad marks (i.e. bear trails) were documented at 58% of the sites where rubbing had occurred. These bear trails occurred independently of the presence of human recreation trails ($df = 1$, $G^2 = 2.43$, $P > 0.10$). The mean length of 46 bear trails measured at 37 sites was $6.17 \text{ m} \pm 4.55$ ($= 1 \text{ SD}$). Trails averaged 2.0 ± 0.36 pad prints per meter of bear trail. Individual pad prints averaged $3.2 \text{ cm} \pm 1.3$ deep ($N = 399$).

All trees marked by grizzly bears during this study were rubbed. Evidence of clawing or biting was noted on only 9% of rubbed trees. On average, $52\% \pm 24.3$ ($= 1 \text{ SD}$) of the tree circumference was rubbed ($N = 77$). The average maximum height of rubbing was $1.73 \text{ m} \pm 0.21$. This height was not appreciably different from contour body lengths of adult bears captured during this study (males = $1.88 \text{ m} \pm 0.20$; females = $1.70 \text{ m} \pm 0.15$). Rubs were not oriented independently of the four ordinal directions (north, east, south and west; $df = 3$, $G^2 = 8.94$, $P < 0.05$). The greatest proportion of rubbed surfaces (37%) was oriented towards the east and the smallest proportion (14%) was oriented towards the west. Of the 36 trees where the rubbed surface was described in detail, 16 had a smooth rubbed surface free of all branches, four exhibited a lean towards the rubbed surface, 11 had both an inward lean and a smooth

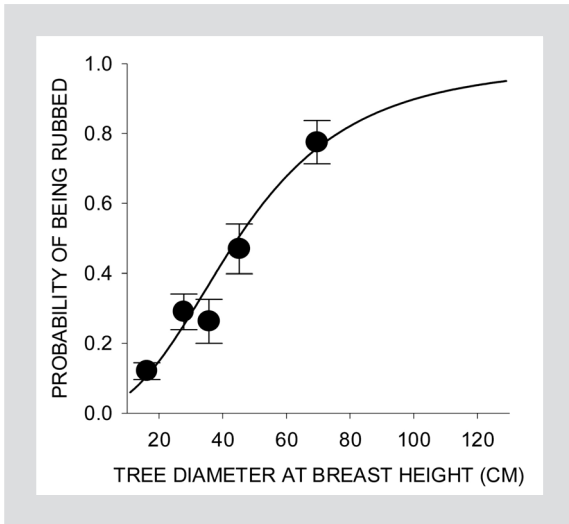


Figure 2. Relation between diameter at breast height (cm) and probability that a tree had been rubbed by Yellowstone grizzly bears, considering all trees measured in plots centered on known rubbed trees during 1986-1992. Circles and standard error bars are for mean probabilities estimated for quintiles of the data and are shown to illustrate goodness-of-fit.

rubbed surface, and seven had a burl or other rounded protuberance at the center of the rubbed surface.

We found no evidence that grizzly bears selected for tree species or that plot identity had an effect on selection. However, the probability that a tree was rubbed increased markedly with tree diameter ($R_L^2 = 0.30$, Somer's $D = 0.11$; $N = 411$, $df = 283$, $G^2 = 280$, $P[\text{goodness-of-fit}] = 0.54$; Fig. 2). Correspondingly, the mean diameter of rubbed trees at 1.4 m above ground level ($45.0 \text{ cm} \pm 1.2$ [= 1 SE]) exceeded the mean diameter of unrubbed trees ($33.8 \text{ cm} \pm 1.1$; $r^2 = 0.652$, $df = 92/318$, $F = 6.47$, $P < 0.001$).

Discussion

Our results suggest that Yellowstone grizzly bears used trees primarily to rub the dorsal parts of their body while standing erect. This interpretation is supported by the correspondence between maximum heights of rubbing on trees and contour body lengths of adult bears, together with the paucity of claw and bite marks. This conclusion is also consistent with descriptions by Tschanz et al. (1970) and analyses of rubbed trees by Krott (1962), Bromlei (1965), Schaffer (1971), Lloyd (1979) and Murie (1981). The propensity for rubbing among grizzly bears is in contrast to the frequent evidence of clawing and biting on trees visited by American black bears (Grinnell et al. 1937, Spencer 1966, Rogers

1977, Willey 1978, Burst & Pelton 1983). This difference may either reflect fundamentally different marking behaviours by the two species, or be an artifact of insufficient investigation of bear marking and rubbing behaviours. Complicating things, descriptions of trees clawed and bitten by brown bears in Eurasia (Stroganov 1962, Novikov 1956, Novikov et al. 1969, Putschkovsky 1991) match descriptions of trees clawed and bitten by American black bears and contradict the hypothesis that brown and black bears employ different marking techniques. Further investigation of bear anatomy and bear behaviours associated with marking or rubbing will be required to resolve or explain these inconsistencies.

Our results suggest that once Yellowstone grizzly bears were at a suitable site, they selected trees of larger diameter for rubbing irrespective of species. This positive effect of tree diameter is consistent with the results of Putschkovsky & Mityukhina (2001). By contrast, Lloyd (1979) and Putschkovsky & Mityukhina (2001) found that brown bears in their study areas preferred species of true fir, i.e. *Abies* spp. We did not quantify other aspects of rubbed trees such as irregularities in the bole, amount of limbs, or lean of the tree. Even so, almost all trees were free of limbs in the area of rubbing, and many had irregularities such as burls that were the apparent focus of rubbing. A number of other trees exhibited a slight lean, typically towards the side that was rubbed. Together, these features suggest that bears in our study area selected trees to enhance the pleasurable sensations of rubbing.

The high incidence of rubbed trees along recreation and game trails could have been caused partly by observer bias in that we often used recreation and game trails while travelling to and from telemetry locations of radio-marked bears. However, this potential bias was mitigated, in part, by the fact that we modelled selection on the basis of all bear signs found en route to and from telemetry locations. Presumably all such locations would have been affected by the same bias towards travel routes. Moreover, the close association of rubbing with trails in our study area was consistent with the location primarily along travel routes of trees rubbed or clawed by black and grizzly bears in other study areas (Grinnell et al. 1937, Schaffer 1971, Rogers 1977, Lloyd 1979, Murie 1981, Burst & Pelton 1983). Our results are also consistent with observations from other study areas suggesting that rubbing and clawing were oriented towards trails (Schaffer 1971, Rogers 1977, Lloyd 1979, Murie 1981, Burst & Pelton 1983). This affinity for travel routes probably explains the positive association of rubbing by Yellowstone grizzly bears with forest edges. Our field observations suggest that forest edges

also tended to funnel the travel of large vertebrates in the Yellowstone region, including grizzly bears.

Yellowstone grizzly bears selected sites for rubbing based on features in addition to trails (i.e. gentle slopes and sparse deadfall) that apparently facilitated ease of access. It was undoubtedly easier for bears to approach rub trees and engage in the physical act of rubbing when trees were located on gentle slopes in forest stands with relatively little interfering deadfall. The positive association of rubbing with south-facing slopes is not as easily understood. However, we speculate that this orientation could have arisen from greater volatilization of turpinoids or other potentially attractive chemicals produced by bears or trees, caused by the greater exposure of trees on south versus north slopes to incident radiation. The likelihood of this happening was increased by the occurrence of most rubbed trees along forest edges.

Differences in levels of rubbing activity between whitebark pine-dominated stands and stands dominated by lodgepole pine or Douglas-fir were likely the partial result of differences in distributions of seasonal foods. Whitebark pine stands in the Yellowstone ecosystem were sought out by bears to forage on whitebark pine seeds principally during the fall of the year (Mattson, Blanchard & Knight 1991, Mattson, Kendall & Reinhart 2001), after rubbing activity had largely stopped. On the other hand, Douglas-fir-dominated stands were concentrated at lower elevations (Despain 1990) where grizzly bears intensively foraged for foods such as ungulate carrion during the same time of year that rubbing was common (Green, Mattson & Peek 1997). The high proportion of sites with rubbing activity in lodgepole pine-dominated stands may have been partly an artifact of limited feeding opportunities. Lodgepole pine cover types were relatively underused for feeding by Yellowstone grizzly bears because of the scarcity of foraging opportunities within them (Mattson 1997), which may have accentuated the relative importance of rubbing in these types of forests.

Peak rubbing activity coincided with the moulting and mating seasons, both of which began in late May and extended into July (Novikov 1956, Pearson 1975, Craighead, Sumner & Mitchell 1995). As such, this result does not suggest which was the primary impetus for rubbing. However, repeated use of specific trees and associated development of entrenched bear trails is inconsistent with bears rubbing merely in response to external stimuli. With abundant trees available for rubbing, the focus on specific trees and bear trails suggests a more refined purpose such as intra-specific communication (Tschanz et al. 1970). The differences in rubbing activity among bears

of different sex and age observed by Tschanz et al. (1970) and Rogers (1977), as well as gender-specific differences in responses to rubbing sites (Tschanz et al. 1970), also suggest functions other than hygienic maintenance. If spatial orientation was the sole motivation for rubbing by bears, then rubbing should have continued unabated through the active season, in contrast to the marked seasonal peak in rubbing activity observed during a time when indices of movement for Yellowstone's grizzly bears were lowest (Blanchard & Knight 1991). Conversely, the use of traditionally-rubbed trees by bears for intra-specific communication does not exclude the additional benefits of alleviating external irritants and offering points of orientation within a bear's home range.

In short, our results are consistent with previous conclusions that rubbing is a form of social communication (Tschanz et al. 1970) that serves as a form of marking similar in function to that of other mammalian species (Gosling 1982). If tree rubbing is a form of marking behaviour, then the disturbance or removal of traditionally rubbed trees could disrupt communication among bears. Also, rub trees could affect the reproductive success of trans-located bears. Bears that are moved by managers between regions face not only the prospect of learning effective foraging strategies but also may face the challenge of learning potential benchmarks of communication such as traditionally rubbed trees. Such knowledge could affect mating opportunities, especially for males. If so, the importance of rubbing is probably greater in low-density populations where finding mates and synchronizing encounters with oestrus is predictably more chancy. If management aims include minimizing conflicts with humans and maintaining socially 'healthy' populations of bears, then the presence of traditionally rubbed trees should be an additional factor in management deliberations.

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