



A “clearcut” case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts



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ABSTRACT

Forest management alters habitat characteristics, resulting in various effects among and within species. It is crucial to understand how habitat alteration through forest management (e.g. clearcutting) affects animal populations, particularly with unknown future conditions (e.g. climate change). In Sweden, brown bears (*Ursus arctos*) forage on carpenter ants (*Camponotus herculeanus*) during summer, and may select for this food source within clearcuts. To assess carpenter ant occurrence and brown bear selection of carpenter ants, we sampled 6999 coarse woody debris (CWD) items within 1019 plots, of which 902 were within clearcuts (forests ≤ 30 years of age) and 117 plots outside clearcuts (forests > 30 years of age). We related various CWD and site characteristics to the presence or absence of carpenter ant galleries (nests) and bear foraging sign at three spatial scales: the CWD, plot, and clearcut scale. We tested whether both absolute and relative counts (the latter controlling for the number of CWD items) of galleries and bear sign in plots were higher inside or outside clearcuts. Absolute counts were higher inside than outside clearcuts for galleries (mean counts; inside: 1.8, outside: 0.8). CWD was also higher inside (mean: 6.8) than outside clearcuts (mean: 4.0). However, even after controlling for more CWD inside clearcuts, relative counts were higher inside than outside clearcuts for both galleries (mean counts; inside: 0.3, outside: 0.2) and bear sign (mean counts; inside: 0.03, outside: 0.01). Variables at the CWD scale best explained gallery and bear sign presence than variables at the plot or clearcut level, but bear selection was influenced by clearcut age. CWD circumference was important for both carpenter ant and bear sign presence. CWD hardness was most important for carpenter ant selection. However, the most important predictor for bear sign was the presence or absence of carpenter ant galleries. Bears had a high foraging “success” rate ($\geq 88\%$) in foraging CWD where galleries also occurred, which was assessed by summing CWD items with the concurrence of bear sign and galleries, divided by the sum of all CWD with bear sign. Clearcuts appeared to increase the occurrence of a relatively important summer food item, the carpenter ant, on Swedish managed forests for the brown bear. However, the potential benefit of this increase can only be determined from a better understanding of the seasonal and interannual variation of the availability and use of other important brown bear food items, berries (e.g. *Vaccinium myrtillus* and *Empetrum* spp.), as well as other primary needs for bears (e.g. secure habitat and denning habitat), within the landscape mosaic of managed forests.

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1. Introduction

Management of forest stands for production in the boreal region of Scandinavia has resulted in the alteration of stand characteristics and composition, nutrient cycles, and fire disturbance regimes (e.g. Zackrisson, 1977; Esseen et al., 1997; Östlund et al., 1997). Clearcutting, or complete logging of areas, is commonly used in the boreal landscape by commercial forestry and may be viewed as an anthropogenic replacement for, or emulation of, fire

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disturbance (e.g. McRae et al., 2001; Paillet et al., 2010), but not without limitation and/or criticism in implementation (e.g. Bergeron et al., 2002; Seymour et al., 2002). The response by wildlife to clearcuts varies among species (e.g. Potvin et al., 1999; Smith et al., 1999; Simon et al., 2002); some species obtain benefits such as increased cover, increased browse, and increased predation opportunities (e.g. Carey and Harrington, 2001; Newbury et al., 2007; Hebblewhite et al., 2009), whereas clearcuts can negatively influence others (e.g. direct loss of habitat, decreased reproductive success, increased predation) (e.g. Lomolino and Creighton, 1996; Deng and Gao, 2005; Courbin et al., 2009). Furthermore, a species can incur both benefits and disadvantages in response to clearcuts, e.g., caribou (*Rangifer tarandus*) may obtain increased forage, but this can become outweighed by the disadvantage of increased predation risk (Leclerc et al., 2014).

Also, within species, there is variable use of clearcuts among individuals and/or populations. Whereas previous research in North America has shown that brown bears (*Ursus arctos*) avoid clearcuts (Zager et al., 1983; McLellan and Hovey, 2001), they have more recently been shown to select them (Nielsen et al., 2004a; Moe et al., 2007; Linke et al., 2013) in both North America and Sweden. Clearcut selection appears to be influenced by human activity (e.g. Wielgus et al., 2002; Wielgus and Vernier, 2003; Ciarniello et al., 2007) and could also be influenced by the social organization of brown bears (Steyaert et al., 2013; Elfström et al., 2014). In Sweden, brown bears mainly select clearcuts during spring and during the crepuscular hours, likely owing to their foraging on ants (especially carpenter ants [*Camponotus herculeanus*]) (Ciarniello et al., 2014), while avoiding encounters with humans (Moe et al., 2007; Ordiz et al., 2014). Carpenter ants, which inhabit live and especially dead wood within cut out galleries (altogether composing the nest), are a preferred food source for brown bears in Sweden (Swenson et al., 1999).

Ant/termite-eating by mammals has been observed among at least 216 species, covering 43 families, wherein only approximately 22 are considered specialists (i.e. >90% of diet consists of ants and/or termites) (Redford, 1987), such as the giant anteater (*Myrmecophaga tridactyla*), the echidna (*Tachyglossus aculeatus*), and the aardvark (*Orycteropus afer*) (e.g. Redford, 1986; Abensperg-Traun and Boer, 1992; Taylor et al., 2002, respectively). Most mammalian species that feed on ants/termites appear to be opportunistic myrmecophages (Delsuc et al., 2014). Aside from a more specialized form in sloth bears (*Melursus ursinus*) and altogether absence in polar bears (*Ursus maritimus*) (Joshi et al., 1997), opportunistic myrmecophagy appears to be common place for bear species. It has been commonly described for American black bears (*Ursus americanus*) (e.g. Noyce et al., 1997), Asiatic black bears (*Ursus thibetanus*) (e.g. Yamazaki et al., 2012), and brown bears (e.g. Mattson, 2001). When myrmecophagy has been described for bear species, most studies deal with the use of ants by bears relative to their availability, without regard to potential factors determining ant availability.

Sanders (1970) asserted that carpenter ants nests are limited by the number of available potential nesting sites (i.e., coarse woody debris; CWD). Although intensive forest management has been linked to less CWD than otherwise found in unmanaged forests (Fridman and Walheim, 2000), the opening of the forest structure (e.g. increased light) favors carpenter ant colonization (Punttila et al., 1991). In order to better manage for biodiversity and meet policy, Swedish forest companies have implemented silviculture treatments, including the partial retention of snags, logs, and/or stumps (i.e. CWD) following clearcuts (Fridman and Walheim, 2000; Anders Fräas, personal communication, 2010), which most likely provide nesting habitat for carpenter ants.

Few studies of brown bear food resources in human-modified landscapes have recognized the need to understand the

determinants of resource availability, not just use (Nielsen et al., 2004a; Nielsen et al., 2004b). Furthermore, wildlife select habitats and their resources hierarchically (Johnson, 1980). Therefore, the choice of scale in determining both resource availability and resource selection is important (Boyce, 2006), because influential processes may be masked or inflated, due to an arbitrary or limited scope on scaling.

The aim of this study was to understand how forest management (i.e. clearcut characteristics) may influence brown bear utilization of a food resource (carpenter ants), and which variables may influence the availability of that food source. Predictor variables spanned three spatial scales: CWD item, plot and clearcut scales, whereas the response variable remained fixed to the CWD scale (i.e., binary presence-absence). Therefore, we explored which environmental variables best explained the presence-absence of carpenter ants in CWD and the selection of CWD by brown bears within a hierarchical framework of predictors. We also tested whether clearcuts provided a higher availability of carpenter ants and whether they had higher bear selection of CWD than surrounding forested habitats. We investigated the following hypotheses (H): (H1) there are more potential nesting sites (i.e., CWD) for carpenter ants inside than outside clearcuts; (H2a) absolute and (H2b) relative availabilities of carpenter ants are greater inside than outside clearcuts; (H3) Carpenter ant presence is best explained by the availability of CWD; (H4) the presence of bear sign on CWD is higher inside than outside clearcuts; (H5) brown bear selection of CWD on clearcuts is positively influenced by the presence-absence of carpenter ants; and (H6) bear selection on CWD is negatively influenced by proximity to human infrastructure (e.g. settlements and roads), denoting an avoidance of encounters with humans.

2. Materials and methods

2.1. Study area

The study area covered ~800 km² of intensively managed boreal forest in Dalarna and Gävleborg counties in south-central Sweden (61°N, 14°E). The dominant tree species were Scots pine (*Pinus sylvestris*; covered 82% of the area) and Norway spruce (*Picea abies*; 12%). Approximately 450–550 ha of forested stands are harvested per year (Anders Fräas, personal communication, 2010), with an approximate mean area for individual clearcuts of 25 ha (range: 0.1–425 ha) and a rotation age of approximately 120 years (Orsa Besparingskog forest company database 2009). The shrub layer typically consisted of common juniper (*Juniperus communis*), willows (*Salix* spp.), and dwarf birch (*Betula nana*). The field layer was dominated by dwarf shrubs, such as bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*), crowberry (*Empetrum* spp.), and heather (*Calluna vulgaris*). Soil surface was covered by mosses and lichens. The landscape is undulating with elevations ranging from 240 to 720 m. The growing season (mean temperature ≥5 °C) is 150–180 days, with winter and summer mean temperatures at –7 °C and 15 °C, respectively. Mean precipitation during the vegetation period is about 350–450 mm (Swenson et al., 1999), and snow cover is present from November until April or early May (Dahle et al., 1998). The road density (predominantly logging roads) was ~0.4 km km⁻² (within a search radius of 1 km; National Land Survey of Sweden, available at: “<http://www.lantmateriet.se>”) and human density was 4–7 inhabitants km⁻² (Ordiz et al., 2012). Bear density was ~30 bears 1000 km⁻² (Solberg et al., 2006).

2.2. Sampling design and model variables

We defined clearcuts as secondary forest stands ≤30 years of age (excluding bogs and impediments), managed for production,

where the previous stand had been anthropogenically harvested. Thirty-years was used as a cut-off, because silvicultural thinning regimes were soon after prescribed, which would have affected the availability of CWD. We selected 100 clearcuts from a digital map, based on the similarity of shape (i.e., regularity and roundness), area (4 classes: 0–10, 11–50, 51–100, >100 ha), and age (6 classes: 0–5, 6–10, 11–15, 16–20, 21–25, 26–30 years) (Table 1). We extracted tree age from the forest company database (Orsa Besparingskog), which was consistently two years after the previous harvest, giving time for the soil to “rest.” Therefore, we added two years to each database record of stand age to derive a more accurate clearcut age.

Within each clearcut, we set up sampling plots (10 m radius) along two perpendicular transects, running north–south and east–west, respectively. We maximized the clearcut area sampled via transect placement on a map. For clearcuts ≤ 10 ha and >10 ha, spacing between plots were 50 m and 100 m, respectively (Fig. 1). We took GPS coordinates for each plot with a precision of 10 m. To obtain forest characteristics in the area adjacent to a clearcut, we sampled one additional plot in each of the four cardinal directions, at 25 m and 50 m from the clearcut edge for clearcuts ≤ 10 ha and >10 ha, respectively. We sampled the clearcuts between 01 June and 06 August, 2003.

We removed plots located in water bodies, on roads, or within power-line clearings from analyses. We removed plots with missing variable information and incorrect GPS locations (rendering accurate variable extraction impossible in a geographic information system [GIS]). We also removed outside clearcut plots that were located in neighboring clearcuts (age ≤ 30 years). As we were concerned with how carpenter ants and bears selected CWD, we only included inside and outside clearcut plots that contained CWD, as selection cannot occur on an unavailable unit.

For each plot, we measured tree height (4 classes: 0–0.3 m; 0.3–1.5 m; 1.5–2 m; >2 m) and visually estimated canopy cover (to the nearest 5%). Tree height was used as a proxy for horizontal cover and classes were chosen based on a bear’s perspective, because, when assessing horizontal cover, it is important to address observation height relative to the target (Collins and Becker, 2001). In this case, the observation would be from the bear, and the target would be any potential threat. We categorized the field layer into 3 ordinal types, in decreasing order of productivity, using a modified dichotomous key for assessing ground- and field-layer productivity (Hägglund and Lundmark, 1982): (1-high) herbs and grasses (e.g. *Cirsium helenoides* and *Poa* spp.), (2-medium) soil without a field layer, sedge-horsetail (e.g. *Carex* spp. and *Equisetum* spp.), and bilberry, and (3-low) cowberry, crowberry-heather (*Empetrum* spp. and *Calluna vulgaris*), poor dwarf-shrub (e.g. *Betula nana*), peat moss (*Sphagnum* spp.) and lichen (*Lichen* spp.). Soil type (rock, gravel, sand, sandy-loam, clay-loam, clay, peat) was extracted from soil data in a GIS. CWD consisted of standing dead trees, dead and down trees and/or cut down trees (logs), and above-ground residual stumps (post-harvest), all of which were >14 cm in diameter. Within plots, we counted all CWD items

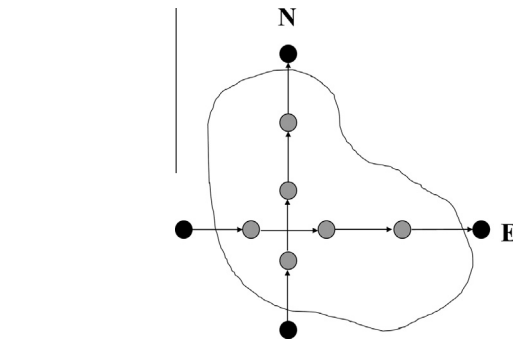


Fig. 1. Sampling plot design within an example clearcut. Plots (gray: inside clearcuts; black: outside clearcuts; radius = 10 m) are located on north–south and east–west perpendicular transects in a way that maximizes plot counts on clearcuts. Plots were spaced 50 m and 100 m apart on ≤ 10 ha and >10 ha clearcuts, respectively.

and recorded their circumference (cm, measurements at both ends of logs were averaged), species (pine, spruce, or deciduous), and hardness (3 categories; (1) little to no decay/hardest; (2) partly decayed/intermediate; (3) mostly decayed/softest). To identify hardness level and to ascertain the presence of carpenter ants, eggs, larvae, pupae, and carpenter ant galleries (hereafter galleries), we used an axe to split open the CWD. We also noted bear foraging of CWD (presence or absence) as CWD that was forcibly opened and/or excavated, yet lacking channeled excavations (e.g. caused by woodpeckers) or a crushed appearance (e.g. caused by forestry equipment) Time of occurrence (i.e. which year) was not determinable for galleries and bear sign on CWD.

Therefore, we used cumulative data for both carpenter ant galleries and bear sign for analyses, in which each was used as a proxy for carpenter ant presence and bear use, respectively. Due to the uncertain times of occurrence for galleries and bear sign on CWD and to increase confidence in our model output, we simulated what the frequency of occurrence for each gallery and bear sign would look like if it were constant over time, i.e. a constant rate across age intervals k (6 intervals: 0–5, 6–10, 11–15, 16–20, 21–25, 26–30 years). For each gallery and bear sign, we calculated this constant (C) by summing respective observed frequencies of occurrence (*Observed*) across age intervals ($k = 6$) and divided the sum by the total number of incremental time units, i.e., the sum of k age intervals (Eq. (1)). To calculate the frequency of occurrence for age interval k , this constant was multiplied by respective age interval values (k) in the series, in order to weigh it according to how many incremental time units had passed (Eq. (2)).

$$C = \frac{\sum \text{Observed}_k}{\sum k} \quad (1)$$

$$\text{Simulated}_k = C * k \quad (2)$$

We calculated a bear foraging “success” rate on all CWD items respective to inside and outside clearcuts; the sum of CWD items where both bear sign and carpenter ant galleries occurred (i.e. concurrence) were divided by the total number of CWD items with bear sign (Eq. (3)).

$$\text{Success Rate}_{\text{inside(OR outside)}} = \frac{\sum \text{CWD}_{\text{bear sign \& gallery present}}}{\sum \text{CWD}_{\text{bear sign present}}} \quad (3)$$

We calculated the volume of each individual CWD item (area calculated from circumferential radius \times length), the average CWD volume per plot and per clearcut, and we extrapolated plot count data of galleries, bear sign, and CWD to per hectare values for each clearcut. A geographic information system was used to extract elevation (in m) for all plots and to calculate the solar radiation in the

Table 1
The distribution of sampled clearcuts, stratified across clearcut age and area in south-central Sweden.

Area (ha)	Age (years)						Totals
	2–5	6–10	11–15	16–20	21–25	26–30	
2–10	7	5	4	5	5	2	28
11–50	7	10	8	5	5	6	41
51–100	0	3	5	4	3	3	18
>100	0	0	3	3	3	4	13
Totals	14	18	20	17	16	15	100

plots (in watt hours per m² for the summer solstice in 2003 using the ArcGIS 9.3 Spatial Analyst Solar Radiation toolset [ESRI 2010]), based on a digital elevation model (DEM, National Land Survey of Sweden, available at: '<http://www.lantmateriet.se>') and topographical maps (National Land Survey of Sweden, available at: '<http://www.lantmateriet.se>') (Table S1, Supplementary Materials).

For each 50 × 50 m raster cell, we derived the slope-aspect index (SAI) (Nielsen and Haney, 1998; Nielsen et al., 2004b), terrain ruggedness index (TRI) (Riley et al., 1999; Steyaert et al., 2011), and a road density (search radius = 1 km), which were extracted for each plot location. We calculated the Euclidean distance (m) of each plot to the nearest major road (i.e., highways and paved roads), lesser road (i.e., forestry roads), settlement (i.e., towns and villages with <200 inhabitants), and stand-alone building (i.e., cabins, farms), all of which and road density were used as proxies for human activity (Table S1, Supplementary Materials).

2.3. Statistical analyses

Our sampling design created an unbalanced sample size at the CWD level; $n = 6535$ inside and $n = 464$ outside clearcuts. Modeling of parameters inside and outside clearcuts was not possible, as the hierarchical spatial dependency of CWD sampled inside clearcuts (i.e., random factor levels of clearcut and plot ids) could not be appropriately applied to CWD sampled outside clearcuts. All plots inside a particular clearcut represent a specific habitat patch (3rd order; *sensu* Johnson, 1980), whereas by definition all plots outside clearcuts represent not only a different habitat patch (e.g. a plot north of a clearcut may consist of a bilberry field-layer with a mature pine over-story), but potentially several habitat patches. Plots representing these patches could vary substantially in species composition and structure (e.g. a plot east of the same clearcut in the previous example may consist of a lichen understory with a sparser mature pine over-story), yet have a sample size of only one for comparison. Therefore we only modeled CWD from inside clearcuts. For comparisons between inside and outside clearcuts, we pooled plots inside respective clearcuts and derived mean CWD, gallery and bear sign count data. Plots outside clearcuts retained their sampled count data. This strategy compromised resolution within clearcuts, but achieved a more balanced design (inside clearcuts: $n = 100$ plots; outside clearcuts: $n = 117$ plots), while satisfying the assumption of independence among observations for statistical analyses (i.e., the Mann-Whitney U test).

We used Mann-Whitney U tests to test all predictions comparing CWD figures between inside and outside clearcuts (predictions: H1–H2 and H4; Table 2). P -values were considered significant if less than $\alpha = 0.05$. To test whether (H1) availability of CWD was greater inside than outside clearcuts, we used the CWD count data at the plot level. To test whether (H2) the availability of galleries was higher inside than outside clearcuts, we used (H2a) an absolute (number of galleries per plot) and (H2b) a relative (i.e., frequency of occurrence: total count of CWD with galleries in a plot divided by the total count of CWD in a plot), definition for availability. To test whether (H4) bear sign was higher inside than outside clearcuts, we used the frequency of occurrence of bear sign per plot (total count of CWD with bear sign in a plot divided by the total count of CWD in a plot). We used the Fisher's Exact Test ($\alpha = 0.05$) (Agresti 2002) to identify whether bear foraging success rates on CWD differed between inside and outside clearcuts.

Predictions (H3, H5 and H6; Table 2) were tested by fitting generalized linear mixed models (GLMM) of the binomial family with a Laplace approximation. Our sampling design was a 1-sample presence-absence design, allowing us to fit the models directly using logistic regression (Johnson et al., 2006). All continuous model variables were standardized around their means for

Table 2

A summary and quick reference of hypotheses and predictions, H1–H6, comparing inside and outside clearcut counts of CWD, carpenter ant, and brown bear sign occurrence, in addition to understanding carpenter ant and bear selection of CWD.

Abbreviation	General scope	Hypothesis/prediction
H1	CWD: inside and outside clearcuts	There are more available potential nesting sites (absolute count of CWD) for carpenter ants within plots inside than outside clearcuts
H2a	Galleries: inside and outside clearcuts	There is a greater abundance of carpenter ant galleries (absolute count) within plots inside than outside clearcuts
H2b	Galleries: inside and outside clearcuts	There is a greater frequency of occurrence of carpenter ant galleries in CWD (relative count where CWD is controlled) within plots inside than outside clearcuts
H3	Carpenter ant selection on CWD: inside clearcuts	Carpenter ant selection on CWD is dependent on the availability of wood (for potential nesting)
H4	Bear sign: inside and outside clearcuts	There is a greater frequency of occurrence of bear sign in CWD (relative count) within plots inside than outside clearcuts
H5	Bear selection on CWD: inside clearcuts	The presence-absence of carpenter ants significantly affects brown bear selection on CWD
H6	Bear selection on CWD: inside clearcuts	Bears select CWD on plots farther away from human activity

computational efficiency and to improve model fit. We included a quadratic term for the variable 'age' and all 'distance' measurements (e.g. to roads), in order to account for potential non-linearity, as detected in other similar studies (Nielsen et al., 2004a; Nielsen et al., 2004b). Data exploration techniques were taken from the protocol developed by Zuur et al. (2010). No outliers were detected, and variables were considered collinear if their Pearson values were ≥ 0.7 and/or if their variance inflation factor values were ≥ 3 within individual candidate models.

We randomly partitioned the dataset inside clearcuts into a model training set (85%) and a model testing set (15%), the former for fitting the model, and both sets for assessing model fit and accuracy (Nielsen et al., 2004a). To account for spatial dependency in our data, we adopted the protocol by Zuur et al. (2013), in which the random component of the models is determined *a priori*. Therefore, we chose to include the clearcut and plot identifiers (IDs) as random factors on the intercept in all candidate models. Following the information-theoretic approach (Burnham and Anderson, 2002), we created two *a priori* candidate model sets, one for each of the two response variables: presence-absence of galleries and presence-absence of bear sign on CWD. The fixed-effect structures for the gallery and bear sign candidate model were grouped into 'model series,' which depict a common theme among models. For example, the gallery model series "microhabitat" contains several models controlling for microhabitat attributes (e.g. solar radiation, site productivity, and slope at the plot scale); all fixed-effect structures for gallery and bear sign models are shown in Tables S2 and S3 (Supplementary Materials), respectively.

We selected the parsimonious model with AICc Akaike's Information Criteria with a second-order bias correction (AICc-based diagnostics [Δ AICc: AICc difference values and AICc_w: AICc weights]) (Anderson, 2008). If Δ AICc was ≤ 4 between two or more models with the lowest AICc scores, then we performed model averaging (Anderson, 2008). A continuous variable or a factor level, relative to its reference level, was considered "informative" if its 95% confidence interval ($\beta \pm 1.96 * \text{standard error}$) did not include zero (*sensu* Arnold, 2010). The relative importance of each variable within the parsimonious models was determined by dropping each

variable and recalculating AICc. The difference (ΔAICc_i) between the parsimonious model $\text{AICc}_{\text{null}}$ (no variables dropped) and AICc_i , where variable i was dropped, was used to determine the relative variable importance of the dropped variables (i); the larger the ΔAICc_i , the more important the variable.

Because carpenter ants are dependent on the availability of nesting sites (Sanders, 1970) and possibly at a particular scale (e.g. CWD item, plot or clearcut), (H3) we predicted that one of the candidate models in model series “Available Wood” would be selected as the parsimonious model for galleries (Table S2). (H5) We predicted that brown bear selection of CWD would be substantially influenced by the availability of carpenter ants (galleries); in the parsimonious model for the bear sign candidate model set, we predicted that the variable representing gallery availability would be relatively important and informative. We predicted that brown bears would forage for carpenter ants within plots (H6) farther away from sites with human activity, i.e., major and lesser roads, settlements and buildings, and plots located in lower road density areas. We predicted that the parsimonious model for the bear sign candidate set would be the human model, expert or full model, all of which contained at least one human activity-related variable.

We validated the independence of the data within our parsimonious models, i.e., if the random effects properly handled the spatial autocorrelation from our sampling design, by plotting Pearson residuals against observed covariates (Zuur et al., 2013). We visually assessed whether there was a residual pattern by plotting smoothers (i.e., a generalized additive model, GAM, with the generalized cross-validation method) through the residuals against the covariates used in the parsimonious models. We considered the pattern to be significant if the smoother function was significant ($P < 0.05$). For the parsimonious models in respective candidate sets, we created Receiver Operating Characteristic (ROC) curves for both the training and test data sets. We integrated the Area Under the Curve (AUC) for the ROC curves (Robin et al., 2011), in order to assess model performance, where a value of 0.5 and 1.0 indicates no predictive power and perfect prediction, respectively (Boyce et al., 2002). We considered values between 0.5–0.7, 0.7–0.9 and ≥ 0.9 to represent ‘low’, ‘good’ and ‘excellent’ model accuracy, respectively (Nielsen et al., 2004b). We used the packages “lme4”, “pROC”, “mgcv”, “coeffplot2”, “ggplot2” and “lattice” in R 3.0.3 (R Development Core Team, 2014) for all analyses.

3. Results

3.1. Clearcuts, plots and CWD descriptions

We sampled 100 clearcuts and 1,381 plots, of which 981 plots were located within clearcuts and 400 outside clearcuts. The mean number of sample plots per clearcut was 9.6 ± 5.3 (SD) (range: 2–29). After plot removals (e.g. due to water bodies or human error with GPS handheld units), we used 1109 plots (902 inside and 117 outside of clearcuts) and 6999 CWD items (6535 inside and 464 outside of clearcuts) for analysis. Mean clearcut area and age were 43.1 ± 47.2 ha (range: 1.8–205.1) and 15.4 ± 8.4 years (range: 2–30), respectively. Mean age of outside clearcut plots was 91.0 ± 34.8 years (range: 31–142).

3.2. Inside and outside clearcuts: CWD, galleries and bear sign

(H1) Plots inside clearcuts had a higher amount of CWD items (mean: 6.8, median: 6.7, range: 1–16.1) than those outside clearcuts (mean: 4.0, median: 3.0, range: 1–18; Mann–Whitney test: $W = 8630.5$, $P < 0.001$, $n_{\text{[inside]}} = 100$; $n_{\text{[outside]}} = 117$). Within plots, (H2a) the absolute availability of galleries was higher inside clearcuts (mean: 1.8, median: 1.1, range: 0–6.5) than outside them

(mean: 0.8, median: 0.0, range: 0–7; Mann–Whitney test: $W = 8476$, $P < 0.001$, $n_{\text{[inside]}} = 100$; $n_{\text{[outside]}} = 117$). Moreover, (H2b) the frequency of occurrence of galleries in CWD within plots was also higher inside clearcuts (mean: 0.3, median: 0.3, range: 0–1) than outside them (mean: 0.2, median: 0.0, range: 0–1; Mann–Whitney test: $W = 7853.5$, $P < 0.001$, $n_{\text{[inside]}} = 100$; $n_{\text{[outside]}} = 117$).

Although seemingly marginal (both median values were 0.0), (H4) the frequency of occurrence of bear sign on CWD in plots was higher within clearcuts (mean: 0.03, range: 0–0.3) than outside them (mean: 0.01, range: 0–0.7; Mann–Whitney test: $W = 7244$, $P < 0.001$, $n_{\text{[inside]}} = 100$; $n_{\text{[outside]}} = 117$). The success rates of bear foraging effort were not significantly different between outside (100%, $n = 8$ CWD items) and inside clearcuts (88%, $n = 203$ CWD items) (Fisher’s Exact Test, $P = 0.602$).

3.3. Carpenter ant and bear selection on CWD

The CWD-level candidate model was selected as the most parsimonious model (hereafter “parsimonious model”) for both carpenter ant gallery (G.CWD) and bear sign (B.CWD) candidate sets, respectively. Due to collinearity among the three variables, CWD hardness, tree height in plots, and clearcut age (Fig. S2, Supplementary Materials), we re-fitted both G.CWD and B.CWD parsimonious models, replacing CWD hardness with tree height in plots and then clearcut age. There was no difference for the gallery candidate set; CWD hardness remained in the parsimonious model. However, the parsimonious model for the bear candidate set changed to include clearcut age instead of CWD hardness ($\Delta\text{AICc} = 5$); therefore, we only report the bear parsimonious model including age and its quadratic term in our results. Clearcut and plot level model candidates received virtually no support. Model probabilities and AICc_w values were 1.0 for both the gallery and bear parsimonious models. None of the (GAM) smoothers of binned covariates were significant when plotted against binned Pearson residuals (Fig. S1, Supplementary Materials). Each parsimonious model for predicting galleries or bear sign on CWD had ‘good’ model accuracy (AUC range: 0.80–0.95) with both training and test data sets; all specificity and sensitivity values ranged between 0.71 and 0.91.

3.3.1. Important variables for carpenter ant selection on CWD

Carpenter ant selection of CWD was significantly and positively influenced by CWD circumference, but not by volume (Fig. 2). CWD hardness was most important for carpenter ant selection on CWD (Table 3), with intermediate CWD hardness appearing to have the highest probability of a gallery, followed by the softest and then the hardest CWD (Fig. 2).

There was high variation of selection around deciduous CWD (not shown; captured in standard errors around the intercept parameter estimate), most likely due to its lower sample size ($n = 117$), compared to pine ($n = 4862$) and spruce ($n = 575$). The species of CWD items was relatively unimportant for the gallery model (Table 3).

3.3.2. Important variables for bear selection on CWD

Bear selection of CWD was also significantly influenced by CWD circumference and not by volume (Fig. 2), with a positive relationship between the probability of bear sign and CWD circumference (Fig. 3). The oldest clearcuts appeared to have the highest probability for bear sign, leveling out at around 30 years, due to the quadratic term (Figs. 2 and 3). CWD circumference and clearcut age were both important for brown bear selection, but circumference was more important (Table 3). However, the presence or absence of galleries was the most important variable in the bear model (Table 3), with (H5) bear selection of CWD largely based on whether or not galleries were present (Fig. 2). Bear selection of

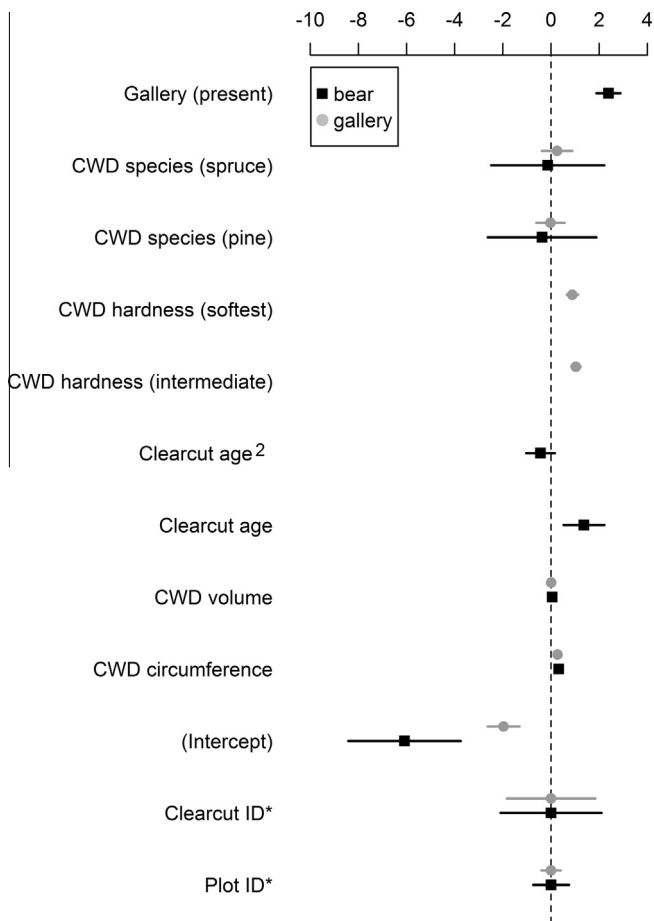


Fig. 2. Parameter estimates (gallery model variables: gray circles; bear model variables: black squares) with horizontal bars representing 95% confidence intervals for the parsimonious models for the probability of coarse woody debris (CWD) having galleries (G.CWD) and bear sign (B.CWD), respectively. Variables were considered important if their confidence interval did not contain zero. Reference levels of factors were “deciduous” for variable “CWD species”, “hardest” for variable “CWD hardness” and “absent” for variable “Gallery”. * Random intercepts “Clearcut ID” and “Plot ID” are not parameter estimates, but rather respective variances displayed with their center on zero ($\pm 1/2$ variance).

CWD was much higher in CWD with galleries, irrespective of clearcut age and CWD circumference, with little to no selection on CWD without galleries (Fig. 3). (H6) Models containing human-related

Table 3

The relative importance of variables in respective parsimonious models for carpenter ant galleries and brown bear sign in south-central Sweden. The dotted row shows the zero line, above which variable had increasing importance, and below which variables are of least importance and provide relatively little information for the model.

Variable; dropped	AIC _c _i	Δ AIC _c _i
<i>Parsimonious gallery model (G.CWD)</i>		
CWD hardness	5455.7	118.0
CWD circumference	5382.6	44.9
AIC _c _{null} (none dropped)	5337.7	0
CWD species	5337.1	-0.6
CWD volume	5335.7	-2.0
<i>Parsimonious bear sign model (B.CWD)</i>		
Gallery (presence-absence)	1326.2	124.0
CWD circumference	1213.1	10.9
Clearcut age	1205.7	3.5
Clearcut age ²	1202.9	0.7
AIC _c _{null} (none dropped)	1207.5	0
CWD volume	1200.9	-1.3
CWD species	1198.7	-3.5

variables (B.HUMAN, B.EXPERT and B.FULL) had little support for their importance in bear selection on CWD. The random effects variance was higher for clearcuts (“Clearcut ID”) than for plots (“Plot ID”) in both gallery and bear models (Fig. 2).

4. Discussion

In general, brown bear selection on CWD followed carpenter ant selection patterns on CWD inside and outside clearcuts. In support of prediction (H1), clearcuts had a higher amount of potential nesting sites for carpenter ants (i.e., higher count of CWD items) than outside them. Not surprisingly, with more nesting sites inside clearcuts, we also found (H2a) more galleries inside clearcut plots than outside them. Even after controlling for differences in the number of potential nesting sites (i.e., CWD count) carpenter ants colonized available nesting sites more frequently inside than outside clearcuts (H2b). This indicated that there are clearcut characteristics which provide advantages beyond just the availability of potential nesting sites, as proposed by Rolstad et al. (1998). Nest “quality,” which depends on microhabitat attributes surrounding CWD (Punttila et al., 1991), most likely plays a role in whether carpenter ants select CWD. However, none of the “Microhabitat” series candidate models (Table S2) provided strong evidence in affecting carpenter ant selection compared to the availability of nesting sites. Still, model variables in the parsimonious gallery model (G.CWD) may indirectly represent microhabitat attributes or mask them (e.g. the random factor plot id), such as those which enable carpenter ants to form nests and persist by way of, e.g., increased colonization of surrounding wood (including live wood), tunnel creation, competition, and localized climatic stability (e.g. Sanders, 1970; Hölldobler and Wilson, 1990; Punttila et al., 1994).

Our model selection results indicate that the CWD-scale predictors were most important for carpenter ant colonization on clearcuts, as compared to other candidate models (i.e., plot or clearcut scales). However, increased importance can be given to smaller scale variables when a spatial autocorrelation structure is incorporated into a model's error term (Boyce et al., 2002; Diniz-Filho et al., 2003). CWD hardness (or decay) and circumference were most important for carpenter ant colonization, which may also hold true for CWD outside clearcuts (not modeled), where different microhabitat attributes may interact with each nest site, but apparently yielding fewer advantages compared to those found within clearcuts. Overall, the gallery model results supported the prediction (H3) that carpenter ant selection of CWD depended on available wood (or nesting sites) (Rolstad et al., 1998). A higher CWD circumference may provide a more climatically stable nesting site or be a determinant factor in colony size, both of which may enhance colony persistence at a nest site (Hölldobler and Wilson, 1990). Carpenter ants appeared to be most prevalent in intermediately hard (partly decayed) CWD, and, in spite of the scale at which it was measured, we suggest that CWD hardness simultaneously captured multi-featured and multi-scaled influences on selection. For example, CWD hardness was measured on the CWD item scale, whereas tree height at the plot scale and age at the clearcut scale. Notwithstanding the limited levels (i.e. only “softest”, “intermediate” and “hardest”) of the factor hardness, its relatively smaller scale most likely captured more variation than that of the continuous variable age at the larger clearcut scale. Although appropriately not included in the same model, due to collinearity, CWD hardness, plot tree height, and clearcut age probably represented differential scalar components of the same theme, e.g., the effects of forestry, microhabitat, and time on nest quality. When re-fitting the parsimonious gallery model with each of these collinear variables, they three had the lowest AICc scores among all candidate models (results not shown). To demonstrate, the frequency of occurrence of both

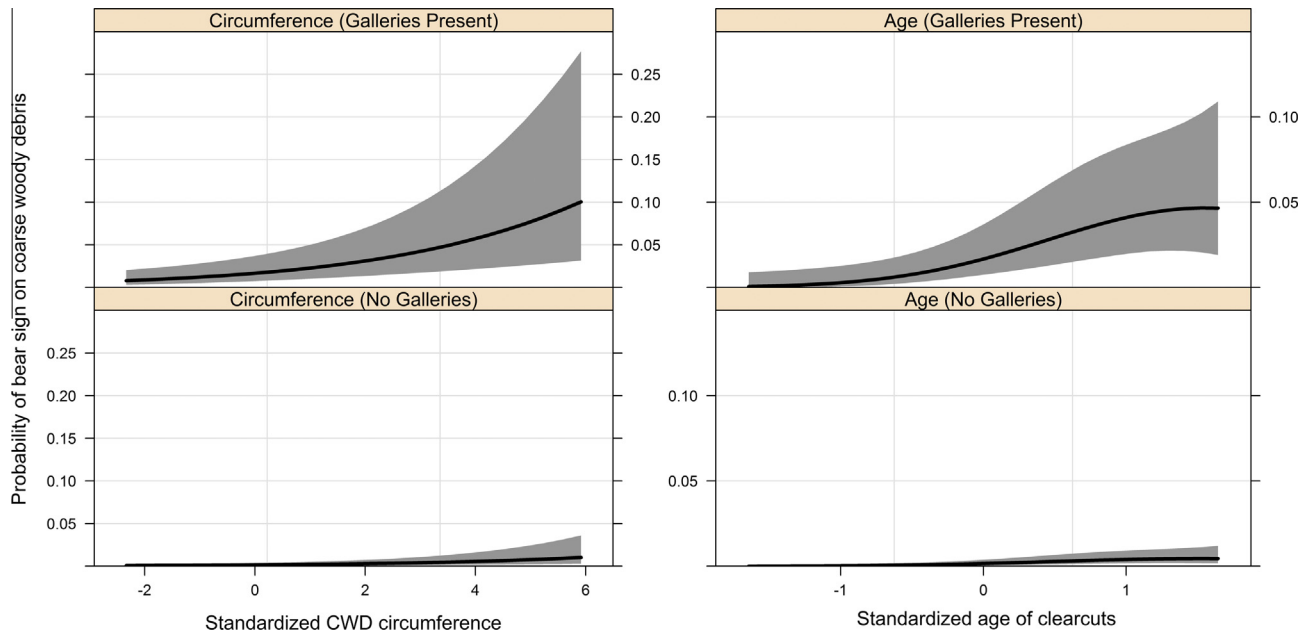


Fig. 3. The probability of brown bear sign presence on coarse woody debris (CWD) in relation to circumference size or clearcut age, based on whether or not carpenter ant galleries were present in south-central Sweden. Species was held constant at factor level “pine” and volume constant at its standardized mean value. Circumference and age were likewise each held at their mean values when using the other as a predictor. Brown bear sign had the highest probability of occurrence on CWD with larger circumferences and within older clearcuts when galleries were present (top left panel and right panel, respectively) and virtually no selection on CWD when galleries were not present, regardless of CWD circumference or clearcut age (bottom left and right panel, respectively).

galleries and bear sign followed relatively similar patterns across clearcut age (Fig. 4) and were parallel to that of relative CWD hardness levels, where galleries were most likely to be found in intermediate hardness (and age) (Fig. 2) and bear sign most likely on softer (or the oldest) CWD (Fig. 3).

The random factor variance for clearcut ID was higher than that for plot ID for both parsimonious gallery and bear models, suggesting that important large scale (3rd order; Johnson, 1980) explanatory variables may not have been included in the models beyond the spatial autocorrelation induced by our sampling design. These variables most likely represent a feature among clearcuts that gives them each variable characteristics, among which carpenter ants differentially select and persist (at the 4th order scale). For bears, the high variance in the clearcut ID random factor could be from a CWD selection process that is grouped at the clearcut level. This pattern could be caused by bears exhibiting fidelity toward certain clearcuts within their home ranges, due to successful foraging experience and higher security. Specifically, female bears with cubs may forage on clearcuts and close to humans, in order to avoid infanticide by adult males (Libal et al., 2011; Steyaert et al., 2013; Elfström et al., 2014). As a result, lacking individual bear identities in our models could mask the strength of a variable (e.g. proximity of a settlement to a clearcut), due to diluting effects from individual variation (i.e. some bears select whereas others avoid clearcuts closer to settlements). However, this effect would strengthen variables important for “nonselection” by individual bears and would not affect the selection of the CWD in our study. In other words, the results of this study should not necessarily be attributed to all bears as our data resulted from bear sign, i.e., those bears which decided to forage on CWD.

Similar to carpenter ants, our prediction (H4) that bears would select more CWD within clearcuts than outside them was supported. Clearcuts may provide characteristics that other forest types lack, such as the necessary habitat for carpenter ants to thrive, along with adequate cover from the early stages of secondary growth, under which bears can safely forage. Success rates were both high ($\geq 88\%$) and no difference was detected between

inside and outside clearcuts, but this is probably due to a low sample size outside of clearcuts ($n = 8$) for comparison.

Important predictors of bear selection of CWD paralleled those of carpenter ant selection of CWD (i.e., clearcut age compared with CWD hardness, and circumference and volume remaining the same) with one crucial difference, the availability of ants. Prediction (H5), that ant availability is a relatively strong predictor for bear use, was supported by the bear model, in which the presence or absence of galleries was the most important variable (Fig. 2; Table 3). There was a clear distinction between brown bear selection on CWD with and without galleries, the latter receiving virtually no use at all. This and the high success rate of bear foraging sign on CWD is a strong indication that bears knew whether or not ants were present in CWD when they decided to forage. However, this should be interpreted with caution, because it is possible that bears opened some CWD after carpenter ants had abandoned the nest.

However, there were differences in selection between bears and carpenter ants, as bears appeared to have a higher probability of selecting CWD in older clearcuts, which correlates with selecting softer CWD, whereas ants had a higher probability of selecting CWD of intermediate hardness (or medium aged clearcuts). Bears seemed to select CWD hierarchically, whereas ants less so. This was evident when we re-fitted both the gallery and bear models, using clearcut age in place of CWD hardness, and the parsimonious bear model exchanged hardness for clearcut age, but the parsimonious gallery model remained the same. Although the relative importance of clearcut age for bears was less than CWD-specific attributes (e.g. circumference and whether or not galleries were present) (Table 3), the selection of CWD was best shaped by clearcut characteristics, i.e., most likely captured by clearcut age. This is further supported by the lowered variance of the clearcut ID random intercept for the parsimonious model with clearcut age instead of CWD hardness (results not shown).

If brown bears expended less effort and time in opening softer CWD (on older clearcuts), these results are in line with optimal foraging theory, in which animals are able to recognize and

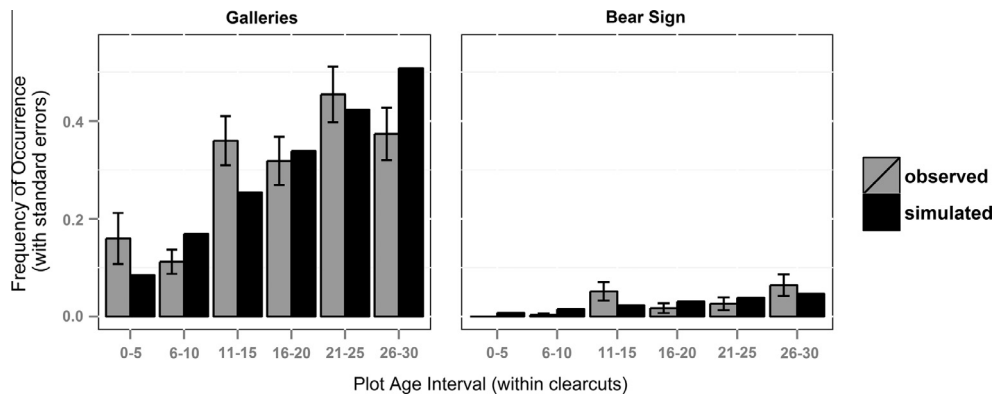


Fig. 4. Observed and simulated mean frequency of occurrence for carpenter ant galleries and brown bear sign in coarse woody debris (CWD), within clearcut plots across clearcut age intervals, in south-central Sweden. Simulated frequencies of occurrence assumed a constant, additive rate each year, based on the summed observed frequencies of all age categories, divided by total incremental time, then weighted by incremental time according to interval (e.g. interval “0–5” = 1 * constant rate, whereas “11–15” = 3 * constant rate).

maximize the profitability of prey (defined as net food yield per unit handling time) (Stephens and Krebs, 1986). However, old and fresh bear sign was indistinguishable, meaning it was not possible to know when the bears actually foraged on CWD; our models may be using improperly assigned age and hardness attributes to bear sign. Nonetheless, the expected accumulation of use up to a given year interval, when compared to the observed data, is congruent with results from the parsimonious models (Fig. 4). For example, the biggest disparities for gallery occurrence are during age intervals 11–15 (occurring more than expected) and 26–30 years (occurring less than expected), correlating with the variable hardness in our model output (Fig. S2), as ants selected more for CWD with intermediate hardness than the softest. Likewise, our bear models detected an increasing trend in CWD selection (if galleries were present); top right panel in Fig. 3) with increasing clearcut age, a pattern seen in both the observed and simulated data (Fig. 4), lending confidence to our model results.

Furthermore, CWD circumference had a positive relationship with bear foraging sign, presumably indicating that bears could find a higher abundance of ants there. Contrarily, CWD volume (collinear with CWD length), which may correlate with nest size and carpenter ant abundance, seemed unimportant for bears, suggesting that circumference may be linked to not just nest size, but the ease with which bears may forage a particular CWD item.

We found no evidence supporting (H6) that human activity-related variables influenced bear selection of clearcut CWD. It is likely that humans were avoided temporally (i.e., foraging during the crepuscular hours) rather than spatially (Moe et al., 2007; Coleman et al., 2013; Cristescu et al., 2013). Nevertheless, the social organization of brown bears may influence clearcut and CWD selection, as brown bears show spatiotemporal segregation, depending on season and social status in North America (e.g. Wielgus and Bunnell, 1994; McLoughlin et al., 2002; Rode et al., 2006) and in Scandinavia (Steyaert et al., 2013).

Brown bears have highly sensitive olfaction (e.g. Eisenberg and Kleiman, 1972; Rosell et al., 2011; Jojola et al., 2012) and they likely use it to locate carpenter ants. A question remains whether bears actively seek out only carpenter ants within clearcuts, or if they optimize their efforts and/or exhibit a functional response by utilizing multiple food sources in a preferential manner based on relative availability (Swenson et al., 1999). In Sweden, Swenson et al. (1999) determined that carpenter ants were preferred to other ant species in the summer, which was likely linked to their lower formic acid content with higher digestibility and fat. However, this preference and selection diminished, as another food source, i.e. berries, became available in autumn. In Scandinavia,

two berry species, bilberries and crowberries, are particularly important for bears in building fat reserves for hibernation (Elgmork and Kaasa, 1992; Swenson et al., 1999; Persson et al., 2001). Interannual and seasonal variation in berry abundance is, however, substantial (Selås, 2000; Selås, 2001; Nestby et al., 2011). Considering the high foraging success rate brown bears had on CWD and the low amount of CWD items bears selected (and foraged) relative to available CWD with galleries, brown bears may forage on more carpenter ants during years of poor berry crops.

In Alberta, studies have shown that forestry (e.g. forest design, site preparation, and silviculture) can affect the occurrence of grizzly bear foods in clearcuts, as well as clearcut selection by brown bears (Nielsen et al., 2004a,b). In our study, we show that forest management decisions, such as stand rotation age and target diameter of trees, may increase (or decrease) carpenter ant occurrence, and consequently, bear selection of CWD with ants. Nielsen et al. (2004a) determined that clearcut shape and clearcut area-to-perimeter ratios were important for brown bear clearcut selection in Alberta. This could also be true in Sweden. Even though our sampling design emphasized the interior of clearcuts, giving less weight to the edges, it is unlikely that this or the area-to-perimeter had a large effect in our study, because we selected clearcuts of similar shape (i.e. roundness) and included clearcut area as a variable. However, the variation of carpenter ant and bear selection of CWD at the clearcut level (i.e. variation of the clearcut ID random intercept), and the inclusion of clearcut age in the bear parsimonious model, may indicate differential features among the clearcuts, which could be attributed to more specific forest treatments (e.g. site preparation or stand tending prescriptions), but we did not have enough data to evaluate this.

Brown bears appeared to very efficiently select on CWD where carpenter ant galleries were present. The mechanism by which brown bears locate carpenter ants in CWD warrants more attention, as this could constrain or flexibly enable brown bears to exploit a food item under uncertain future effects from habitat modification and anthropogenic influence (e.g. forest management, hunting and climate change).

5. Conclusions

The probability of carpenter ant selection and brown bear selection on CWD revealed similar important factors on the CWD and clearcut scales that could be linked to forest management and microhabitat attributes. Carpenter ant gallery presence was most influenced by CWD hardness (which was related to tree height

and clearcut age) and circumference, whereas brown bear foraging on clearcut CWD was most influenced by whether or not galleries were present, CWD circumference and clearcut age.

Clearcuts appeared to increase the availability and selection of carpenter ants by brown bears within a managed forest mosaic. For the purposes of increasing a brown bear summer food item, it appears that target diameter of felled trees has the biggest influence on both carpenter ant presence and consequent selection by brown bears. Therefore, it may be possible to increase the availability of carpenter ants by adjusting stand rotation age and/or target diameters of trees.

However, one must guard against the assumption that clearcuts will always favor brown bears, even if it may favor a food item within this managed mosaic. In other words, it is unclear if clearcuts benefit brown bears in general in Sweden, as an understanding of the relationship between the seasonal and interannual variation of the availability of carpenter ants and other important food items (i.e. berries), in addition to other primary needs for bears (e.g. secure habitat and denning habitat), on the landscape scale, is lacking. For example, clearcuts may act as attractive sinks, particularly where human-caused mortality is high in relation to roads, which would counteract any short-term benefit bears may derive from the increased availability of food items (Nielsen et al., 2006; Nielsen et al., 2008). Nevertheless, if brown bears indeed consume more carpenter ants during poor berry crop years, i.e. due to localized unavailability (Swenson et al. 1999), adaptive silvicultural treatments within managed systems could be used to help buffer against future effects of climatic changes on brown bear food items.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.03.051>.

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