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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 (≥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 wild-life 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 Frääs, 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 \sim 800 km² of intensively managed boreal forest in Dalarna and Gävelborg 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 Frääs, 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 Besparingsskog 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 \sim 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,

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