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# The function of strategic tree selectivity in the chemical signalling of brown bears

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Large mammals select conspicuous objects on which to deposit their scent marks, which may function to supplement the olfactory signal, visually and/or chemically. Analysing marking sites is paramount to understanding whether signallers could mitigate potential fitness costs by placing scents strategically to reduce time and energy investment. The defining characteristics of marking sites are unclear across species, and variation in the literature concerning selectivity may be explained by behavioural plasticity. We took an evolutionary perspective on the selection and spatial distribution of marking trees by brown bears, *Ursus arctos*, to account for such variation. Our hypothesis, that brown bears would be selective in the trees used for scent marking, was supported; the trees chosen were located in regularly visited areas, where the defence of a resource is needed. The criteria of a marking tree appear to be primarily location and then about properties that facilitate their use as a conspicuous object; bears selected rarer species and trees of larger size than the average available. Other features, such as aromatic properties of the species, bark texture and the ability of the bark to hold scent, may act additionally to determine a tree's marking potential. The energetic investment in manufacturing pungent volatile odours could be reduced if signallers utilize tree properties to attract receivers. Across mammalian taxa, whether a tree is selected for marking appears to vary based on environmental context; the principal function is to limit the energetic costs of producing scent marks by placing marks strategically to increase the likelihood of attracting potential receivers.


Chemical signalling is believed to have evolved throughout the animal kingdom because it allows a signaller to manipulate successfully the behaviour of receiving individuals to its own reproductive advantage (Dawkins & Krebs 1978). Individuals benefit from selecting scent-marking strategies that increase their likelihood of detection, yet reduce the potential fitness cost to the signaller by mitigating time and energy investment (Gosling & Roberts 2001). Scent marking on conspicuous trees and plants may function to supplement the olfactory signal, visually and/or chemically (Gorman & Mills 1984; Bowyer et al. 1994; Rachlow 2001; Hayward & Hayward 2010). Patterns of scent marking are seemingly related to the social dynamics of a species (Macdonald 1980). The marking patterns of nonterritorial mammals are less clear than those of territorial ones, and may display temporal and spatial variation, particularly in reference to defending mates and food resources (Gosling 1990). Artiodactyla and Carnivora select trees for marking depending on: the size and species of the tree; the slope of its trunk (henceforth referred to as 'the lean'); its bark texture; its aromatic properties; and its conspicuousness in the environment (Kile & Marchinton 1977; Benner & Bowyer 1988; Smith et al. 1989; Bowyer et al. 1994; Bothma & le Riche 1995; Massei & Bowyer 1999; Ramos et al. 2006; Barja 2009; Nie et al. 2012; Piñeiro & Barja 2012). Placing scent marks on trees may increase the visibility and dispersal of scent by increasing the elevation of the mark (Gorman & Mills 1984; Alberts 1992), irrespective of the properties of the trees. The height of the scent mark on a tree could communicate size and therefore status of the animal (Alberts 1992). In addition, marking on the underside of a leaning tree may protect the scent mark from rainwater: a strategy selected by tigers, *Panthera tigris* (Smith et al. 1989). Marking trees are probably chosen on the basis that they not only hold and disperse scent, but also act as an additional attractant (Kile & Marchinton 1977; Bowyer et al. 1994); for example, marking trees are often located along major travel routes, where their likelihood of encounter by receivers is increased (Macdonald 1980). Variation in habitat could be used to explain intraspecific variation in spatial marking patterns (Smith et al. 1989). To bridge the gap between speculation and empirical data, we must begin to assess behaviours based on the social and spatial organization of species. Strategic tree selectivity for scent marking is likely to be influenced by a species' social behaviour, spatial structure and environment.

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Ursids mark trees in a similar way to other carnivores. Marking behaviours include rubbing various parts of the body against trees (to deposit scent from sebaceous and apocrine glands; reviewed in Müller-Schwarze 2006), clawing (possibly to deposit scent from pedal glands; reviewed in Sunquist & Sunquist 2002), biting (possibly to deposit scent from salivary glands; as in Patterson 1968) and urinating and depositing anal gland secretions (AGS; Burst & Pelton 1983; Schaller et al. 1985; Green & Mattson 2003). Tree marking with modified cutaneous glands is reported to function in scent marking through the production of pheromones, with secretions under hormonal control (reviewed in Müller-Schwarze 2006; Johnston & delBarco-Trillo 2009). Traditionally used trees are repeatedly marked over generations (Schaller et al. 1985), which indicates that scent marking functions as intraspecific communication in bears (Green & Mattson 2003), rather than occurring in response to external environmental stimuli. However, the function behind the selection of these trees remains unclear. A limited number of authors have attempted to determine tree selectivity in ursids (see Burst & Pelton 1983; Green & Mattson 2003; Puchkovskiy 2009; Nie et al. 2012), yet there is currently no consensus in the literature across the family Ursidae or the order Carnivora. Within the Ursidae, tree species (Puchkovskiy 2009), size (Green & Mattson 2003) and bark texture (Nie et al. 2012) have each been reported to dictate selectivity. As ursids display highly adaptive social behaviour, predominantly exhibiting solitary living (Stirling & Derocher 1990) but tolerating dense aggregations (Craighead et al. 1995), behavioural plasticity may explain variation within the literature on tree selectivity. However, the positioning of scent-marked trees appears to be consistent, being located on human-made/game trails, ridge tops and/or valley bottoms (Burst & Pelton 1983; Schaller et al. 1985; Green & Mattson 2003). Few studies analysing tree selectivity for marking within the Ursidae have considered it strategically, as a potential way to mitigate fitness costs to signallers.

In an attempt to decipher the principal function of tree selectivity for scent marking in large mammals, we took an evolutionary perspective; taking such a perspective may allow us to understand the inconsistent pattern of results across species reported in the literature, and may produce new indications of strategic decision making in a natural context. Using an ursid species as a case study, we investigated the selection and spatial distribution of marking trees in the brown bear, *Ursus arctos*. Assessing the selectivity of marking trees is paramount to understanding whether ursids could mitigate the potential fitness costs of chemical signalling by placing scents strategically. Other studies concerned with tree selection for marking by brown bears failed to construct hypotheses relating to the potential fitness costs/benefits of tree selectivity (Green & Mattson 2003; Puchkovskiy 2009). Taking into account previous literature on ursids and other mammals (principally Artiodactyla), we hypothesized that brown bears would be selective in the trees used for marking; these should be located in regularly visited areas where the need to defend a resource is elevated. We predicted that brown bears would select trees that, through their properties, act as an additional attractant to receivers. If bears select trees based on species, we predicted that coniferous trees would be selected over broadleaved trees. If the size of the tree is important, we predicted that bears would select trees with a larger diameter than others in the area. These trees would probably have properties that facilitated their use as a conspicuous object on which to mark through their rarity.

## METHODS

### *Study Site*

Glendale Cove is an estuarine intertidal zone of Knight Inlet, British Columbia, Canada. The region is situated in the pacific mid-coast of the Province, and has a mild, hypermaritime climate because of its geographical location. The Pacific coast annually receives contributions of marine-derived nutrients from the remnants of five anadromous salmonid species (*Oncorhynchus* spp.), through their migration upstream, spawning and eventual decomposition. Approximately 40–50 brown bears utilize the Glendale spawning channel as a primary energy resource during the autumn (Nevin 2003; Clapham et al. 2012).

Western hemlock, *Tsuga heterophylla*, is the dominant tree species in the area, interspersed with Western red cedar, *Thuja plicata*, amabilis fir, *Abies amabilis*, and Sitka spruce, *Picea sitchensis* (Alaback 1991). Deciduous species include red alder, *Alnus rubra*, and Pacific crabapple, *Malus fusca*, although these species are mainly concentrated at forest edges bordering the estuary. In the spring, approximately 20 brown bears are attracted to tidal marshes in the south of the estuary, to feed in the sedge meadows (*Carex* spp.; Clapham et al. 2012). This coincides with the breeding season, when adult males, lone adult females and courting pairs can often be seen in this area.

Data were collected from May to October 2009–2011. A combination of 13 fixed-distance tree transects, 16 game-trail tree transects and unsystematic random searches were conducted to assess how brown bears utilize their environment for chemical signalling. Methods used for identifying marking trees are outlined below, and were confirmed using 17 Reconyx (Reconyx Inc., Wisconsin, U.S.A.; models RC55 & PC85) digital passive still-image infrared camera traps, which provided data for Clapham et al. (2012). Camera traps monitored 22 different brown bear marking trees throughout the study period, and were armed during the 'breeding season' (1 June–31 July in 2009/2010 and 15 April–31 July in 2011) and 'nonbreeding season' (1 August–5 October in 2010/2011; see Clapham et al. 2012 for camera trapping procedures).

### *Analysis of Marking Trees and Tree Surveys*

#### *Identifying brown bear marking trees*

To distinguish a traditional marking tree from a tree that has merely been scratched or rubbed on a single occasion, we used the description of a black bear, *U. americanus*, marking tree set out by Burst & Pelton (1983): one that has been bitten, clawed, and possibly rubbed, at the approximate height of a standing animal. This was confirmed for brown bear marking trees with camera traps and daily inspections of marking trees during the initial week of the study period. Trees must have displayed evidence of rubbing such as hair remnants, and visible claw and bite marks indicated through wounds on the tree. Scars caused by clawing and biting and the texture change of the bark caused by rubbing indicated that the tree was traditionally used. Only trees fitting this description were included in the analysis. Trees were not required to display evidence of recent marking to be included, as long as the features described above were visible. Fresh marks were identified by resin oozing from wounds, lacerated bark that left fragments exposed, the colour of exposed wood, and any remnants of hair loosely attached. Trees that showed the initial characteristics of a traditional marking tree but did not yet have the necessary evidence to be included were noted for further monitoring in following years, but not included in primary analysis. Camera traps provided corroborative evidence that marks left on trees were from brown bears and not black bears.

If a tree was identified as a marking tree, the species was recorded along with the diameter at breast height (dbh) using a dbh tape. The lean of the tree from 0° was also recorded, using a clinometer. Features of the marks were recorded, including: height of the tallest visible mark from the base of the tree (unattainable in