Scent-marking investment and motor patterns are affected by the age and sex of wild brown bears

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Members of the Carnivora employ a wide range of postures and patterns to mark their scent onto objects and thereby communicate with conspecifics. Despite much anecdotal evidence on the marking behaviour of ursids, empirical evidence of scent-marking motor patterns displayed by wild populations is lacking. Analysing the time that different age and sex classes spend at scent-marking trees and the behaviours involved at different times of year could provide further insight into the function of marking. We used camera traps stationed at scent-marking trees to investigate scent-marking behaviour by wild brown bears, *Ursus arctos*. Through image-based data, we found evidence to support the hypothesis that time investment and scent-marking motor patterns are dictated by the age and sex of the bear. Adult males spent more time scent marking and displayed a more complex behavioural sequence of marking than adult females and juveniles. Adult male behaviour at marking trees was consistent throughout the year, indicating a continued benefit of chemical signalling outside of the breeding season. Juvenile bear behaviour at marking trees changed with age. Young dependent cubs were more likely to imitate their mother's behaviour, whereas older dependent cubs were more likely to engage in marking behaviour independently. The marking motor patterns of independent subadults were more simplistic than those of younger dependent cubs, suggesting a change in behaviour with independence. We suggest that these findings further support the hypothesis that scent-marking behaviour by brown bears functions in intrasexual competition between adult males. Cub behaviour at marking trees suggests an influence of social learning.

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Chemical signalling has been proposed as a mechanism by which mammals are able to advertise their own qualities and assess similar qualities in conspecifics (Gosling, 1990; Gosling & Roberts, 2001; Johnston, 2008). The duration of time and energy invested in scent-marking behaviour is likely to be a reflection of the importance of the chemical signal to the signaller. For example, in meerkats, *Suricata suricatta*, dominant males invest significantly more time in scent marking than dominant and subordinate females (Jordan, 2007). Similarly, in banded mongooses, *Mungos mungo*, the time spent investigating scent marks is influenced by the age and sex of both the signaller and receiver, and the type of scent mark influences the duration of inspection (Müller & Manser, 2008). Assessing potential competitors through scent mark investigation may result in receivers regulating their behaviour towards

signallers, particularly if the signaller is of higher competitive ability, to avoid agonistic encounters (Gosling, 1982; Hurst, Thom, Nevison, Humphries, & Beynon, 2005; Roberts & Gosling, 2001). Strategic costs incurred by scent marking can be considered as time and energy expenditure and the risk of increased intraspecific competition (Maynard Smith & Harper, 2003). A higher investment in costly signalling behaviour could indicate a potential net fitness benefit, through increased breeding opportunity and reduced agonistic encounters (Dawkins & Krebs, 1978; Maynard Smith & Harper, 2003). Assessing seasonality in scent-marking behaviour, between breeding and nonbreeding seasons, has previously provided a strategic link between chemical signalling and breeding behaviour (Clapham, Nevin, Ramsey, & Rosell, 2012; Nie et al., 2012) and may therefore provide insight into time and energy investment.

Overt postures have evolved to facilitate the deposition of scent marks as a result of varied marking behaviour. In the Canidae, sex and dominance ranking affect marking postures (Allen, Bekoff, &

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Crabtree, 1999; Gese & Ruff, 1997; Jordan, Golabek, Apps, Gilfillan, & McNutt, 2013; Kleiman, 1966), with males generally performing more elevated postures, such as raised-leg urination, and females exhibiting squat urination (Gese & Ruff, 1997; Jordan et al., 2013). Sillero-Zubiri and Macdonald (1998) found that raised-leg urinations and rolling by Ethiopian wolves, *Canis simensis*, was almost always preceded by investigation of the object/area, whereas investigation before squat urination was rarer. In captivity, giant pandas, *Ailuropoda melanoleuca*, invest more energy in receiving elevated scents (urine and anogenital gland secretion) than those placed lower down, and subadult males display avoidance behaviour of elevated adult male urine (White, Swaisgood, & Zhang, 2002). The function of elevated marks may be to signal competitive ability and possibly aggressive intent between adult males (White et al., 2002), while additionally increasing signal range and persistence (Nie et al., 2012). The performance of overt marking postures can therefore indicate when scent communication is taking place, and provide an insight into function (Jordan et al., 2013).

Little is known about the ontogeny of scent-marking behaviours exhibited by young carnivores; however, mammalian glandular secretions are primarily controlled by reproductive hormones (reviewed in Johnston & delBarco-Trillo, 2009; Müller-Schwarze, 2006). In spotted hyaenas, *Crocuta crocuta*, marking frequency increases significantly with the onset of puberty in both sexes (Woodmansee, Zabel, Glickman, Frank, & Keppel, 1991), and a consistent level of anal gland secretion (paste) is only produced from the anal pouch in hyaenas over 3 years of age (Theis, 2008). Silwa (1996) reported that aardwolf, *Proteles cristata*, cubs learn the motor patterns of marking behaviour by imitating their parents, indicated by increased marking frequency with age and cubs rarely marking when alone. Assessing the development of scent-marking behaviour between juvenile and adult life stages provides additional insight into its function (White, Swaisgood, & Zhang, 2004).

As ursids are predominantly solitary and generally do not defend territories (Stirling & Derocher, 1990), their need to communicate has been somewhat disregarded in the literature. However, Nie et al. (2012) recently documented sex and seasonal differences in the scent-marking behaviour of wild giant pandas, and Clapham et al. (2012) reported that wild adult male brown bears, *Ursus arctos*, communicate their competitive ability to other males by scent marking onto trees year-round, indicating the additional importance of discerning strategic behaviours by studying wild individuals. In captivity, brown bears rub all parts of their body against trees, walls, gates and on the ground, while bipedal, quadrupedal, sitting or lying down. Males are reported to use a wider variety of marking postures than females, although back rubbing while standing upright on the rear legs (bipedal) appears to be the most prevalent (Tschanz, Meyer-Holzapfel, & Bachmann, 1970). Few chemical analyses have been conducted on brown bear glandular secretions. However, Rosell et al. (2010) found that brown bear anal gland secretion (AGS) contains a high number of compounds with the majority having a high molecular weight (>300), indicating its possible use as a long-lasting scent mark. Bears have been observed to sit at the base of trees while scent marking, which could function to deposit AGS (Rosell et al., 2010). Johnston (2005) postulated that multiple marking postures may create a more complex chemical signal in that scent is deposited from multiple locations on the body; the resulting mosaic signals are thought to aid in individual recognition (Johnston, 2005) but could also function in scent matching (Gosling, 1982) by creating signature scent mixtures (Wyatt, 2010). By studying the behaviour of wild bears at scent-marking trees, and comparing this with the behaviour of other species for which more is known concerning the chemical constituents of scent marks, we

may be able to draw parallels and identify a focus for future analyses to test derived hypotheses.

Here, we further investigated the function of tree marking in wild brown bears by assessing the differences in scent-marking behaviour by different age and sex classes. Despite much anecdotal evidence on the marking behaviour of brown bears, we could find no empirical data on marking patterns displayed by wild populations. By examining the time spent at marking trees and the behavioural sequences displayed, we tested the hypotheses that time investment and scent-marking motor patterns are dictated by (1) the sex of the bear, (2) its developmental life stage and (3) the season in which the behaviour is conducted (breeding or nonbreeding). If time investment at marking trees is determined by sex, then adult males are predicted to display longer bouts of scent investigation and marking than adult females. If sex affects scent-marking motor patterns, then adult males are also predicted to display a more complex behavioural sequence than adult females. If developmental life stage affects scent-marking behaviour, breeding adults are predicted to display longer bouts of scent investigation and marking, and a more complex behavioural sequence of marking than juveniles. If the season affects time investment and scent-marking motor patterns, then adult bears are predicted to mark and investigate for longer bouts during the breeding season and with a more complex behavioural sequence.

METHODS

Study Site

Glendale Cove is an estuarine intertidal zone of Knight Inlet, British Columbia, Canada (50°41′N, 125°44′W). The region is situated in the Pacific mid-coast of the province, and is characterized by a mild, hypermaritime climate. In the spring of each year (April–June), approximately 20 brown bears are attracted to tidal marshes in the south of the estuary, to feed in the sedge meadows (*Carex* spp.) and intertidal zone (Clapham et al., 2012). Five species of anadromous Pacific salmonids (*Oncorhynchus* spp.) migrate up rivers and streams along the Pacific coast to spawn and eventual decomposition of these fish releases marine-derived nutrients. Approximately 40–50 brown bears use the Glendale spawning channel as a primary energy resource during the autumn (August–October; Nevin, 2003; Clapham et al., 2012).

Data Collection and Categorization

A subset of data for this paper were originally collected to assess the social function of tree-marking behaviour by brown bears in 2009 and 2010 (see Clapham et al., 2012), with additional data collection in 2011. Seventeen Reconyx (Reconyx Inc., Holmen, WI, U.S.A.; models RC55 & PC85) digital passive still-image infrared camera traps monitored 22 traditionally used scent-marking trees (see Clapham, Nevin, Ramsey, & Rosell, 2013) over a 3-year period. Cameras were armed during the 'breeding season' (1 June to 31 July in 2009/2010 and 15 April to 31 July in 2011) and 'nonbreeding season' (1 August to 5 October in 2010/2011). Each occasion when a brown bear was captured on an image, or set of images, was classified as an 'event' (Kays & Slauson, 2008) and given a unique ID; 401 brown bear events were captured during the breeding season and 1197 during the nonbreeding season. The age–sex class of the individual(s) captured was assessed and their behaviour recorded for each event. Age–sex class was determined from images through the observation of genitals, size, weight, body shape, presence of young or drooping mammary glands (Clapham et al., 2012). Bears were categorized within the following age–sex demographic categories: adult males, adult females (lone, breeding), adult females with