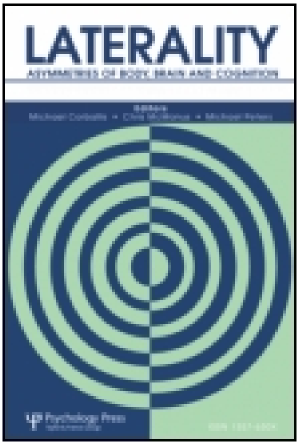

Laterality: Asymmetries of Body, Brain and Cognition
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/plat20

Right paw foraging bias in wild black bear (*Ursus americanus kermodei*)

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To cite this article: T. E. Reimchen & M. A. Spoljaric (2011): Right paw foraging bias in wild black bear (*Ursus americanus kermodei*), Laterality: Asymmetries of Body, Brain and Cognition, 16:4, 471-478

To link to this article: http://dx.doi.org/10.1080/1357650X.2010.485202

LATERALITY, 2011, 16 (4), 471–478

Psychology Press
Taylor & Francis Group

Right paw foraging bias in wild black bear (*Ursus americanus kermodei*)

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Using field observations of ~ 15 wild adult black bear (*Ursus americanus kermodei)* foraging on a salmon stream during two autumns on the central coast of British Columbia, we tested for laterality of forelimb use during lunging and during handling of salmon. Of 288 lunging events observed overall, 53% were non biased, 26% were right-limb biased, and 21% left-limb biased ($p = .53$ between left and right bias). Among six bears in which we could ascertain individual identity (182 lunging events), there was heterogeneity among individuals ($p < .05$) of which two were significantly right biased and one significantly left biased ($p < .005$). Of 186 carcass-handling (pick-up) events, 68% were right-pawed ($p < .005$) and there was no heterogeneity among five individually identifiable bears ($p = .19$). There was no forelimb laterality in adjustment of the prey in the mouth or in securing the prey to the substrate. This is the first report of task-specific behavioural lateralisation of a wild carnivore and is suggestive of a right bias (left-hemisphere dominance) in object manipulation.

Keywords: Carnivore; Foraging; Handedness; Laterality; Ursus.

Laterality in forelimb use has been identified across a broad assemblage of vertebrates, although the directionality varies within and among taxa (Dill, 1977; Lehman, 1981; reviews in Bisazza, Rogers, & Vallortigara, 1998; Rogers, 2002; MacNeilage, Rogers, & Vallortigara, 2009; Vallortigara & Rogers, 2005). Some of the directionality is task specific and probably related to hemispheric dominance. Emerging views suggest that the right hemisphere, which processes spatial cues, might account for the taxonomically broad tendency for

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We thank Dan Klinka for discussion, Marvin Robinson for discussion and logistical assistance, Stan and Karen Hutchings for travel assistance, and the Hartley Bay Band Council for permission to conduct observations in their territory. TER acknowledges the David Suzuki Foundation and the Natural Sciences Engineering Research Council of Canada (operating grant NRC2354) for financial support.

http://www.psypress.com/laterality DOI: 10.1080/1357650X.2010.485202

left-forelimb bias in grasping moving objects and processing ballistic movement (Rogers, 2009). In contrast, right-limb bias occurs in primates during tool use (Rogers, 2002) and also in frogs and domestic dogs when removing objects from the head (Bisazza et al. 1998; Tan, 1987) but for the latter, this may be limited to females (Quaranta, Siniscalchi, Frate, & Vallortigara, 2004; Wells, 2003) and potentially facilitated by human contact (Wells, 2003).

Bears (Ursidae) are the largest and most widely distributed terrestrial carnivores and use their forelimbs for multiple tasks including digging and prey capture. In western North America, bears (*Ursus* spp) congregate on rivers and forage on adult salmon and exhibit reasonably stereotyped capture and manipulation techniques (Frame, 1974; Klinka & Reimchen, 2002; Reimchen, 1998). During pursuit, bears plunge into the water with their forelimbs extended and either pin the salmon to the substrate before seizing it with their jaws or directly grab the salmon with their jaws during the plunge. The bears also scavenge on carcasses during which the carcass remnants are lifted with their paw from the substrate to their jaws. As part of a field study on foraging behaviour of Black bear (*Ursus americanus kermodei*) from coastal British Columbia (Klinka & Reimchen, 2009a, 2009b), we quantify here the relative use of either the left or right forelimb during the lunge and handling phases. Assuming the left bias in limb use in vertebrates is associated with grasping moving objects (Rogers, 2009), we would predict increased left-forelimb bias during food capture and potential right bias during prey handling in the bears.

METHOD

Study area and protocols

Observations were made during studies of black bear foraging behaviour at Riordan Creek, Gribbell Island (56° 26′ N; 128° 58′ W), off the mid-coast of western Canada. The island supports a combination of old growth and second growth coastal western hemlock forest and has several salmon streams containing from 1000 to 2000 spawning pink salmon (*Oncorhynchus gorbuscha*).

Behaviour was recorded from 6 to 12 hours per day in 3-hour intervals (details in Klinka & Reimchen, 2009a, 2009b). There were about 25–30 different bears on the stream over the course of the study (September 2001, 2002, 2003) of which the four were the white Kermode bear, a genetic colour morph of "Black bear" (Ritland, Newton, & Marshall, 2001). Bear activity was visually monitored and videotaped both during daylight and darkness. At night we used a monocular night-viewing scope (ITT mode CSC N16140-DX, 50,000 × amplification, 0.95 cycles per milliradian resolution) and a Sony DCR-TVR 720 camcorder with 880 nm infrared illumination. For the present study we examined videotape coverage from 2000 and 2001 using a Panasonic AG-1960 SVHS with slow-motion capability. Under low light levels or at greater distances, individual identity of bears could not be ascertained and these data were grouped as unidentified (separate for white and black morphs). However, based on unique coat markings and body scars, we were able to accumulate at least 10 observations on each of five black morphs and a single white morph. Those with fewer observations ($N < 10$) were grouped in with the unidentified black or unidentified white.

Quantification of behaviour

In total, 657 foraging events were recorded (40 hours of video tape). Laterality could not be assessed in many of these as the bears were facing away from camera, but we were able to score 288 separate lunging and 186 separate pick-up events. Bear forelimb movement was quantified for active foraging as well as for scavenging. During the lunge for the salmon, the bear has one or both forelimbs extended, and we recorded from stop-frame action three categories: no bias (both limbs equally extended), strong left bias, and strong right bias (lunge leading strongly with left or right forelimb respectively). During scavenging, bears would lift a carcass to their mouth with either their left or right paw, which was recorded (left, -1, right, $+1$). When the bear carried the salmon, we recorded the orientation in the jaws (salmon-head to the right versus head to the left). Bears often adjusted the fish in their mouth with either paw, which was recorded. In subsequent manipulation and ingestion, bears also pressed the salmon against the substrate with a single paw, and this was recorded. We also investigated the possibility that relative forelimb use was related to stream position (left stream edge, centre, right stream edge, facing upstream, facing downstream) but found no statistical effects on laterality (log-linear χ^2 – all p non-significant) and do not discuss it further.

Statistical analyses

We used binomial tests (test proportion of 0.5) and one sample t-tests (test value of 0) to determine any bias in the combined handling movements lunge, pick-up, and press. Kolmogorov-Smirnov tests were used to determine if limb use during lunging behaviour for individual bears departed from normality. Chi-square tests were also used to assess variability among individual bears and to determine if any bias was correlated with bear colour. We used log-linear analysis to determine if either colour morph had a particular paw preference.

RESULTS

We tested for potential lateralisation in forelimb use when bears lunged during pursuit of salmon. Among the 288 separate foraging events videotaped, 53% were unbiased and 47% preferent; 17% and 24% were left biased and right biased respectively, $t(287) = 1.2$, $p = .23$. We obtained repeated observations ($N = 182$) on lunging in six different identifiable bears (Figure 1). Among these bears there were differences among individuals, $\chi^2(10) = 21.1$, $p < .05$, of which three had significant departures from normality with two being right biased ($n = 20$, 53, z-scores $= 1.85$ and 1.94 respectively, $p < .005$) and a single individual being left biased ($n = 61$, z-scores $= 1.97$, $p < .005$). We also compared overall lunging laterality between the two coat colour morphs and this showed an excess of left limb use for the white morph relative to the black morph, partial $\chi^2(1) = 43.1$, $p < .001$, z-score $= 3.63$.

During scavenging, bears used a single forelimb when picking up the salmon carcass for ingestion. Overall, there was a significant right paw bias [Figure 2, $n = 186$, right paw 68%, Binomial: $p < .0005$; mean $= 0.35$,

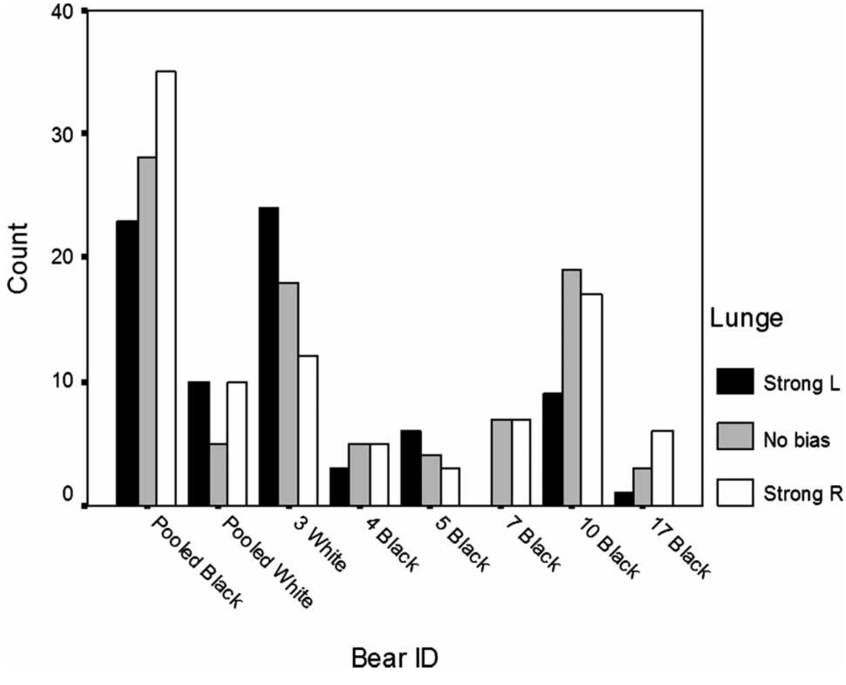

Figure 1. Forelimb use during the lunging behaviour for different bears at Gribbell Island, British Columbia. Pooled black ($N \sim 10$) and pooled white ($N \sim 3$) include bears without identification and one known individual with fewer than 10 observations.

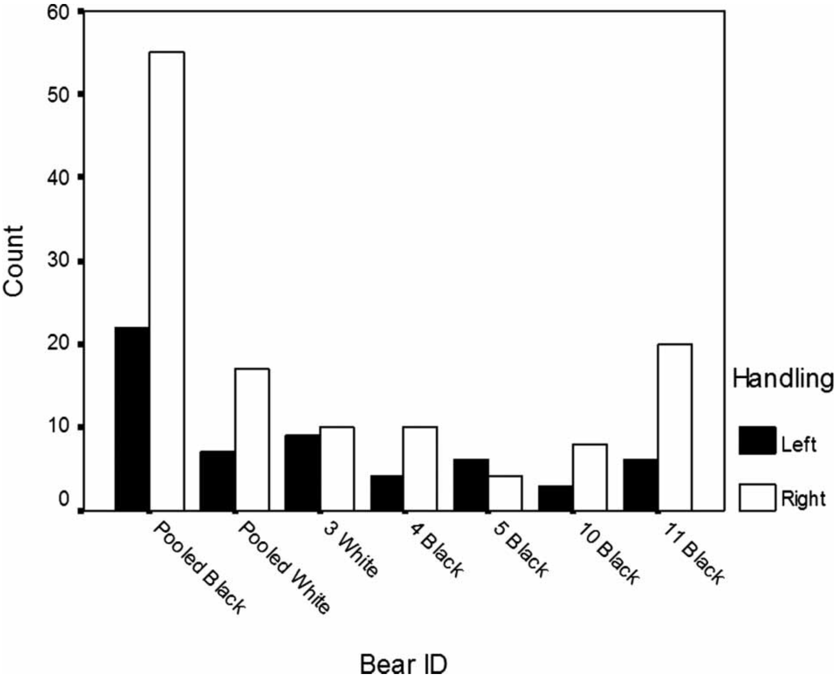

Figure 2. Paw use during handling or "pick-up" of salmon carcass for individual bears at Gribbell Island, British Columbia. Pooled black ($N \sim 10$) and pooled white ($N \sim 3$) include bears without identification and one known black individual with fewer than 10 observations.

$t(185) = 5.2$, $p < .001$]. We obtained 80 observations from five individually identifiable bears and there was no heterogeneity among these, $\chi^2(4) = 6.2$, $p = .19$.

We tested for potential laterality in several additional behaviours. At the time of capture, bears would seize the salmon and hold it crosswise in their jaws with the salmon head positioned either to the left or to the right side of the jaw. Of 194 captures, there were similar proportions for left- and right-orientated salmon (left = 89, right = 105; Binomial $p = .28$) and no heterogeneity among five identifiable bears, $\chi^2(4) = 5.04$, $p = .28$. In addition, bears used either paw to adjust position of the salmon in the mouth, and among 38 separate foraging events there were 17 and 21 with left and right paw adjustment respectively (Binomial: $p = .63$). Following capture, or during scavenging, bears commonly held the salmon in position by a single paw during subsequent ingestion. Among 247 events overall, left and right paw were used with similar frequency (left = 114, right = 133, Binomial: $p = .25$) and trends were similar among the six identifiable bears [left bias = 59, right = 60; Binomial: $p = 1.0$, $\chi^2(5) = 6.4$, $p = .27$].

DISCUSSION

Based on the general left-forelimb bias in vertebrates for grasping moving objects (Rogers, 2009), we predicted this laterality would also occur in lunging and capture of salmon by American black bears. We observed no overall population bias during lunging but significant heterogeneity among individuals comprising both right-biased and left-biased individuals. There was evidence for population laterality in the pick-up or handling of the carcass and this was right biased in the majority of bears. Additional behaviours such as paw use for positional adjustment of the salmon in the jaws as well as securing salmon to the substrate showed no evidence for individual or population laterality.

The island population of bears in this study includes low frequencies of an unusual white coat colour morph (Kermode) that is rare or absent throughout most of the North American distribution of black bear (Cowan & Guiguet, 1956). We were able to obtain replicated data on one of these white bears and it was the only bear in our field study that was significantly left biased during the lunging phases. If this single example is representative, it might comprise a genetic linkage between coat colour and behaviour, possibly associated with stable competitive interactions within populations (for example, Ghirlanda, Frasnelli, & Vallotigara, 2009). However, rather than a morph effect, these data may reflect individual preferences (Rogers, 2009) possibly from copying, which can develop during the extensive parental training that occurs in bears (Hall & Swaissgood, 2009). Whatever the origin of the differences, the potential of an association with laterality is present as the white morph has higher salmon capture efficiency than the black morph in this locality (Klinka & Reimchen, 2009a).

Behavioural lateralisation of forelimb use occurs in a diversity of vertebrates. Among carnivores, domestic cats show a slight left paw bias when reaching towards mobile objects (Cole, 1955; Fabre-Thorpe, Fagot, Lorincz, Levesque, & Vauclair, 1993) and sex-specific paw bias when retrieving food from an empty jar (Wells & Millsopp, 2009). Domestic dogs exhibit a right paw bias when accessing a preferred food (Aydinlioğlu et al., 2000) and a sex-specific limb bias in removing objects from the head (Quaranta et al., 2004; Tan, 1987, Wells 2003). Although lateralisation in dogs is potentially compromised by early human training effects (Wells, 2003), it is more likely that the behaviour is linked to neurochemical and hormonal lateralisation in the canine brain (Quaranta et al., 2004; and see Quaranta et al., 2006, 2007). Some of the data on laterality in captive species have been questioned given the widespread bias for right-handed provisioning by human observers (Palmer, 2003), yet this cannot be relevant in our study as the bears we observed are wild. We assume that the modest right paw bias during pick-up of the salmon may reflect fundamental hemispheric dominance involved in object manipulation (for example, Rogers, 2002, 2009; Vallortigara & Rogers 2005). Right foot preference in pigeons during landing but not during take-off (Davies & Green, 1991) and right limb bias in toads during the removal of an object from the head suggests left-hemisphere dominance (Bisazza, Cantalupo, Robins, Rogers, & Vallortigara, 1997; Rogers, 2009). This might account for our observations that paw bias in bears occurred during the initial lunging and pick-up of the salmon but not when adjusting salmon position in the jaws or holding carcasses to the substrate.

The existence of behavioural lateralisation in different vertebrate groups may reflect shared anatomical asymmetries and parallel evolution to deal with food handling or other life history requirements (Bisazza et al., 1997; Clapham, Leimkuhler, Gray, & Mattila, 1995; Lippolis, Bisazza, Rogers, & Vallortigara, 2002). Our observations on a large solitary wild carnivore showing a general right forelimb bias in picking up prey, and individual left and right biases in lunging and capture of prey but not in other attributes of foraging including adjustment and securing the prey reflects task-specific laterality. Whether these data are representative of other wild carnivores will require a much broader database.

Manuscript received 20 January 2010
Revised manuscript received 19 March 2010
First published online 6 January 2011

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