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Abstract

Salmon provide a key source of marine-derived nutrients to aquatic and surrounding terrestrial habitats in coastal areas of the North Pacific. Bears are a major predator of salmon and provide an important pathway for carcass transfer to riparian zones. We studied selective consumption of salmon (*Oncorhynchus keta* and *O. gorbuscha*) by bears (*Ursus arctos* and *U. americanus*) on 12 streams on the central coast of British Columbia, Canada. We predicted bears would select more energy-rich parts, and eat less of each fish (i.e., selective consumption), in streams with more prey and simpler habitat (i.e., streams that facilitate salmon capture). Bears were 12% more likely to consume fish selectively in narrow, shallow streams with less pool volume, where salmon are easier to catch, than in deep, wide streams. However, bears were also 21% more likely to selectively consume fish in streams with more wood obstacles and undercut banks, where hunting was predicted to be more difficult. This suggests that stream characteristics can have significant indirect effects on riparian nutrient subsidies to ecosystems through selective feeding by bears.

Introduction

Pacific salmon (*Oncorhynchus* spp.) are an important source of cross-boundary, marine-derived nutrient delivery to North Pacific coastal ecosystems. Salmon spend most of their lives growing in the sea, before migrating to their natal freshwater streams to spawn. After spawning, they die and deliver valuable nutrients to surrounding aquatic and terrestrial ecosystems (Schindler et al. 2003; Helfield and Naiman 2006). Foraging bears facilitate salmon nutrient transfer to terrestrial habitats, as they pull live fish out of streams and leave their carcasses on land nearby (Hilderbrand et al. 1999; Quinn et al. 2009). Once a salmon carcass is abandoned by a bear, the remains become available to a suite of other species (e.g., insects and scavenging birds) that transfer nutrients (reviewed in Gende et al. 2002 and Janetski et al. 2009). These nutrients are also incorporated into surrounding plant matter (Hocking and Reynolds 2011; Hocking and Reynolds 2012), and can have impacts on local breeding bird communities (Christie and Reimchen 2008, Field and Reynolds 2011)

Carcasses left in the riparian zone are particularly important to nutrient transfer because they are less likely to be washed downstream into the estuary than the senescent salmon which die in the streams (Cederholm et al. 1989). Even bear-killed salmon abandoned within streams have more value, in nutrient terms, than senescent salmon carcasses, for certain species. For example, caddisfly (Trichoptera) larvae preferentially colonize bear-killed salmon due to increased temporal availability, energetic content and accessibility of tissue (Winder et al. 2005). The amount of salmon biomass abandoned by bears is, therefore, an important component to overall nutrient transfer to both terrestrial and aquatic pathways.

To understand the patterns of salmon consumption by bears, we turn to classical foraging theory to ask: when should bears stop eating a given carcass and invest the additional

time and energy required to catch a new one? A variant on the classical patch model of foraging theory (Charnov 1976) by Sih (1980) treats each prey item as a patch and each bite as a choice. The decision to abandon a partially eaten carcass depends on the diminishing rate of return from continuing to eat a fish after the most energy-rich parts have been consumed versus investing time and energy in catching a new fish. This framework predicts that bears should be more selective for energy-rich parts of salmon in streams where fish are easier to catch. Reimchen (2000) and Gende et al. (2001) demonstrated a preference by bears for high-energy tissues such as the brain and eggs. The ease with which bears can catch salmon should depend on habitat characteristics that offer refuge and escape opportunities for the fish, such as wide, deep streams with large pools, wood obstacles and undercut banks (Gende et al. 2004b, Braun and Reynolds 2011, Andersson and Reynolds, 2017). Furthermore, bears kill more salmon, up to a density-dependent asymptote (Quinn et al. 2003; Quinn et al. 2016), and are more selective for energy-rich parts (Gende et al. 2001) at higher salmon spawning abundances. Though individual behaviour may vary from bear to bear, we predict that these patterns will, generally, be observed across a large number of streams over a full salmon spawning season.

Selective consumption patterns by bears may also differ with the sex and species of prey as well as the date in the salmon spawning season. Because of their eggs, females have a higher caloric value per total mass than males (Hendry and Berg 1999, Gende et al. 2004a), which means bears would need to consume more of each male to acquire similar energetic rewards. Chum are larger than pink salmon, with estimated masses of 3.5 kg and 1.2 kg, respectively (Hocking and Reynolds 2011). Therefore, eating an equal amount of biomass of each, before abandonment of the carcass, would result in a lower proportion of consumption of a chum salmon carcass than of a pink salmon carcass. Furthermore, it may be easier to selectively remove and consume energy-rich parts of larger size-classes of salmon because

their bodies could allow for more handling dexterity, manoeuvrability and precision of brain removal by bears (Reimchen 1994). Selective consumption patterns may also change through the fall because bears enter hyperphagia, a pre-hibernation stage associated with substantially increased appetite leading to daily caloric intake increases from 8 000 kcal to 20 000 kcal, at some point in the salmon spawning season (Nelson 1980; Nelson et al. 1983). Moreover, the energy quality of salmon flesh and quantity of eggs decreases through the season (Hendry and Berg 1999; Reimchen 2000). As the number and quality of salmon decreases toward the end of the spawning period, bears may need to eat more of each kill to acquire similar energy rewards and meet their energetic requirements.

Our objectives were to compare the consumption of salmon carcasses by bears among streams and to quantify relationships with spawning salmon abundance and stream characteristics. We predicted that the proportion of bear-killed salmon that show evidence of selective tissue consumption would be: 1) higher in streams with greater prey abundance, 2) higher in streams with less wood, undercut banks, pools and water volume (i.e. possible refuge for prey), 3) higher on chum salmon than pink, and 4) higher earlier in the salmon spawning season (Table 1). Our prediction of more selective consumption earlier in the season was less confident as there is conflicting evidence for brain preferences based on spawning status of the salmon. Reimchen (2000) demonstrated that bears would more often selectively consume the brains of early-stage spawning salmon, and reject the brains of the more spawned-out fish, whereas Frame (1974) noted a preference for the brains of spawned-out salmon. Therefore, our predictions are based on the preference for eggs (Gende et al. 2001) and presence of more pre-spawned, egg-filled salmon earlier in the spawning season than at the end when the population shifts to more spawned-out salmon showing signs of senescence. Thus, if all else were equal, we predicted higher selective consumption patterns at the start of the season than at the end. Predictions relating to salmon sex are also less clear: bears could be more selective

when eating females if they target eggs and discard the rest of the carcass, or they could be less selective because females are smaller than males. We studied 12 streams in a remote region along the central coast of British Columbia, Canada, where human disturbance to habitats is minimal. The results reveal how patterns in bear consumptive behaviour may be influenced by hunting difficulty caused by physical attributes of the stream, with consequences for the amount of biomass left in the riparian zone, local food webs, and overall nutrient transfer in the ecosystem.

Methods

The 12 streams were located in Heiltsuk First Nation territory in the Great Bear Rainforest on the central coast of British Columbia, Canada (Fig. 1). Stream characteristics were measured in the summer of 2014 and salmon counts and measurements took place during the salmon spawning season in the fall of 2014. We were not able to quantify the number of bears at each stream. Black bears (*Ursus americanus*) are found throughout the region, whereas grizzly bears (*U. arctos*) are usually limited to the 4 mainland streams. Exploratory analyses did not reveal any differences in trends (e.g. number of kills, predation rate and selective consumption) between the mainland and the island streams.

Stream characteristics

Streams were divided into representative study reaches, which were sampled using a stratified random sampling design. Each stream's study reach began where the stream met the estuary. From that point we measured the bankfull width of the stream in 3 equidistant locations and calculated the total reach length as 30 times the average bankfull width (Bain and

Stevenson 1999). Bankfull width is the maximum width that water could reach in the channel before flooding over the banks. Each reach was separated into 4 equidistant sections and 3 transects were assigned randomly per section, totalling 12 transects per reach.

At the reach level, we measured total pool volume per 100 m, total volume of wood per 100 m, and percent of reach with undercut banks according to standard practices (Bain and Stevenson 1999). All qualifying wood (diameter > 0.1 m and length > 1.5 m within the stream banks) was measured and a total volume was calculated per 100 m to normalize for differing reach lengths. These streams had no obvious bottlenecks or ledges caused by large woody debris that may make hunting easier at those locations. Pool dimensions (i.e., width, length, maximum depth and tail depth) were measured for all pools (Fausti et al. 2004). Tail depth (i.e. depth at downstream riffle crest) is the deepest part of the downstream portion of the pool. Residual pool volumes were calculated using maximum depth minus tail depth, to account for differences in water volumes of pools, as water levels will vary by the amount of recent rainfall, and then standardized per 100 m (Lisle 1987). Transect level measurements included bankfull width and channel height which both standardize for fluctuating water levels, with varying rainfall, over the measurement season and represent stream size better than a single water level measurement. There is variability in flow in each stream with rainfall but given the close proximity of the streams we make the assumption that the size of the streams varies together in wet or dry conditions and, thus, the stream rankings for size remains the same. Furthermore, even the largest streams, during highest flows, were accessible and therefore did not completely protect salmon from hunting (as would be the case in a large river where fish could take refuge in the centre). All stream locations and characteristics are presented in Table 2.

147 *Salmon characteristics*

148 Each site was visited 3 times throughout the salmon spawning season (between 11
149 September and 21 October, 2014) to quantify patterns of consumption of salmon. A thorough
150 search of the measured stream reach, as well as a 5-m band of the riparian zone on both
151 banks, was conducted to locate bear-killed salmon. We recorded the sex, species, and
152 consumptive patterns of each fish. Sex was determined by examining the gonads or, if absent,
153 we examined the jaw/snout, teeth, skin colouration and other sexually dimorphic characteristics
154 that readily distinguish the sexes. A categorical spawning status was assigned to each salmon
155 carcass based on a visual inspection of the skin condition, colouration, quantity of eggs, caudal
156 fin damage and other visible decay. The spawning status categories were: 1) pre-spawned, 2)
157 partially spawned, 3) post-spawned, and 4) heavily decomposed. These “decomposed”
158 individuals were not included in the analysis because heavy decay and scavenging or
159 colonization by maggots made it impossible to quantify consumptive choices by bears or
160 categorize spawning status of the fish at the time of consumption. Furthermore, we excluded
161 measurements of wolf-killed salmon, which are distinguished by their clean, surgical removal of
162 the brain case and abandonment of the rest of the carcass (Darimont et al. 2003). These kills
163 were usually in highly localized regions of estuaries at low tide, rather than along the stream in
164 the forest where we were working. Bear-killed salmon with selective consumption of the brain
165 were identified by their less-surgical removal of the brain, which often damaged the snout, eyes
166 and surrounding tissue (Reimchen 1994) and by the consumption patterns on the surrounding
167 salmon carcasses. We marked each measured carcass by cutting off the tip of the lower jaw to
168 avoid re-measurement on the next visits.

169 *Selective consumption scoring systems*

170 Each carcass was assigned binary categorical values based on the amount of
171 consumption (i.e., whether or not the majority of dorsal and trunk musculature was consumed)
172 and type of body parts consumed (i.e., eggs, brain). A carcass was considered selectively
173 consumed if the eggs (in females) and/or brain (both sexes) were consumed and <50% of the
174 overall carcass was consumed (i.e., there was a demonstrated selectivity for the energy-rich
175 parts and abandonment of majority of the catch). Alternatively, if the energy-rich parts had been
176 eaten but more than 50% of the fish was consumed or if the energy-rich parts had not been
177 consumed then no selectivity for energy-rich parts had occurred.

178 To check the robustness of our conclusions to the way in which we scored “selectivity”,
179 we also tried an alternative analysis with a different response variable: 1) <50% of salmon
180 consumed = “selective” consumption, and 2) > 50% of salmon consumed = “non-selective”
181 consumption. That is, we removed the requirement of consumption of an energy-rich part from
182 the response variable and just focused on how much of the carcass was eaten. We used the
183 same statistical methods as for the original models. The results for this model competition are
184 included in the supplementary material and are similar, overall, to the main results. Though
185 salmon may be scavenged days after the initial kill (Quinn and Buck, 2000), we are still
186 confident in our two scoring systems because scavenging rates can be low (Gende et al.
187 2004a), and our observation of the decomposition status of each carcass allowed us to analyse
188 the results with the freshest kills removed (to verify that the results weren’t skewed by bears
189 scavenging these carcasses and removing significantly more flesh after our visits). Furthermore,
190 we are still able to make inferences about how much flesh is left on the banks and to the
191 riparian zone after both initial consumption and scavenging.

Spawning salmon abundance

Counts of pink and chum salmon were made as part of the ongoing annual surveys by members of our research group in conjunction with the Heiltsuk First Nation and personnel from Fisheries and Oceans Canada. We used visual estimation of live spawning salmon as well as counts of all senescent and bear-killed salmon located in the stream and within a 5 meter band on each bank. When 3 counts were achieved, the area-under-the-curve (AUC) estimation method was used to determine the total number of spawning salmon per stream (English et al. 1992). The spawning abundance at streams with fewer than 3 counts was determined using the peak live + dead estimation method. This method is highly correlated with AUC estimation in previous studies that examined streams in this area (Field & Reynolds, 2011; Hocking & Reynolds 2011), and was confirmed to be a close match in the study streams (chum salmon AUC mean= $1\,172.6 \pm 337$, chum peak mean= $1\,423.1 \pm 421.92$, $r = 0.962$, $p < 0.001$, $n = 7$ streams; pink salmon AUC mean= $1\,874.8 \pm 845.17$, pink peak mean= $1\,859.0 \pm 976.26$, $r = 0.996$, $p < 0.001$, $n = 5$ streams). We combined pink and chum salmon, to calculate “total prey abundance”, representing the total number of salmon per stream available to bears. This reduced the number of parameters in our models and accounted for the issue of collinearity between pink and chum salmon abundances. A mismatch in timing of pink and chum salmon runs could complicate analyses especially with respect to the date variable. However, the run timings of both species were relatively equal across most streams and therefore this mismatch is negligible. Out of twelve streams, the proportion of chum salmon to total salmon peaked at our middle count in six streams, decreased in one stream, increased in two streams and could not be calculated for three streams where count occurrences were too low.

214 *Statistics and modelling*

215 Statistical analyses were performed with R (version 3.2.2; R Project for Statistical
216 Computing, Vienna, Austria). We compared generalized linear mixed effects models (GLMMs),
217 with a binomial response and logit link, using Akaike's Information Criterion (AIC_c), corrected for
218 small sample size. The models describe the probability of selective consumption of each bear-
219 killed salmon under varying conditions of prey susceptibility (i.e., stream complexity) and
220 abundance. Mixed-effects models account for a lack of independent samples at the stream
221 level in the study design. We compared 5 models to evaluate the relative support for each
222 hypothesis (Table 3). Care was taken to limit the number of hypotheses to a priori, biologically
223 feasible models in order to avoid spurious findings from testing large "all-subsets" models
224 (Burnham and Anderson 2002).

225 In order to deal with collinearity and reduce the number of parameters in our models, we
226 created reduced sets of linearly uncorrelated variables through principal components analysis
227 (PCA). This method extracts orthogonally-linear sets of "principal components" with minimal
228 loss of information and eliminates co-linearity between variables (Graham 2003). A PC named
229 "cover" was created to combine wood volume/100 m and percentage of bank that is undercut
230 since these features were positively correlated and are both predicted to offer shelter in the form
231 of hiding and escape opportunities for spawning salmon (Deschênes and Rodríguez 2007;
232 Braun and Reynolds 2011). The first principal component explained 77% of the variance with
233 both variables loading >0.71. Another PC named "escape" was created in a separate analysis
234 to combine the positively correlated and hydro-geologically related variables: pool volume/100
235 m, bankfull width, and channel height. These variables represent water quantity, which is
236 associated with escape opportunities for spawning salmon along with lowered visibility for
237 hunting bears (Fukushima & Smoker, 1998; Gende et al., 2004b). The first principal component

for “escape” explained 72.5% of the variance and all variables loaded >0.57.

The response variable was binomially distributed with 0 = “non-selective” and 1 = “selective” consumption. The global model was as follows:

$$(1) \quad Y_i \sim \text{Bin}(1, p_i)$$

$$(2) \quad \text{logit}(p_i) = \beta_0 + \beta_1 \text{sex}_i + \beta_2 \text{species}_i + \beta_3 \text{date}_i + \beta_4 \text{cover}_i + \beta_5 \text{escape}_i + \beta_6 \text{abundance}_i + a_i$$

$$(3) \quad a_i \sim N(0, \sigma_a^2)$$

where logit stands for the logistic link, p_i is the probability that a carcass was selectively consumed for energy-rich parts, β_0 is the intercept and β is a vector that regulates each estimable parameter’s contribution to the probability of selective consumption. Habitat complexity (i.e., cover and escape indices) and salmon abundance are fixed, centered, scaled continuous variables (Schielzeth 2010). Sex, species, and date were included in all models, except the null model, as forced parameters to control for possible differences in predator preferences per type of fish (i.e., due to inherent differences in the amount of flesh and energy-rich parts) or over time in the season. These parameters would also account for differences in sex and species ratios between streams and differences in the sampling date among sites. a_i is included as a random intercept, by stream, to control for variability at the stream level and account for a lack of independent sampling within streams. The random intercept is assumed to be normally distributed with mean 0 and variance σ_a^2 and accounts for the lack of information about bear abundance or other inherent differences in streams that are not accounted for in the model (Zuur et al. 2009). Variance Inflation Factors (VIF) for each of the models were all less

than 2, which confirms that the model parameters did not have a multicollinearity issue (Zuur et al. 2010).

Results

Bears selectively consumed 31% of all carcasses examined across the 12 streams ($n=659$), with a higher proportion of selective consumption of females (38.6%) than males (20%), and more on chum (35.7%) than pink salmon (25.4%). In species by gender subgroups, selective consumption occurred on 31.2% of pink females, 15.3% of pink males, 44.6% of chum females and 23.7% of chum males.

As predicted, selective consumption was higher at narrower, shallower streams with fewer pools (i.e., low escape index) but, contrary to our predictions, selective consumption was higher at streams with more wood obstacles and undercut banks (i.e., high cover index) (Fig. 2). The bivariate plots revealed no obvious trends in selective consumption over time in the season nor with the number of spawning salmon (Fig. 2). The top model in the AIC_c competition was the habitat complexity model which includes the escape index, cover index and the forced parameters of sex, species and date (Table 3).

The probability plots generated from the top model's predictions further confirmed that bears selectively consumed salmon more frequently in narrower, shallower streams with fewer pools, and in streams with more wood and undercut banks (Fig. 3). These plots illustrate the top model's predicted probabilities of selective consumption, holding all other parameters constant at their means. The predicted probability of selective consumption is higher for females than males, and on chum salmon than on pink (Fig. 3). Sex, species and date were included as forced parameters to control for possible differences in patterns with these

variables. There is some uncertainty in the date and escape index parameter estimates, which both have 95% confidence intervals that overlap zero (Fig. 4). This uncertainty is reduced considerably under the alternative scoring system (supplementary material) which is the more relevant measure in terms of implications for nutrient transfer.

The results for the alternative scoring system for selective consumption, based only on the amount of flesh eaten, were similar to the original scoring system, including bivariate plots (Fig. S1), AIC_c competition (Table S1), and probability plots (Fig. S2). The only exceptions were a reversal of the effect of sex, whereby males had a higher probability of being consumed selectively (48%) than females (41%) as well as a stronger effect for date, which has parameter coefficient estimates that do not overlap zero, and escape and cover indices (Fig. S3).

Discussion

These results confirm our prediction that bears would feed more selectively on salmon that they caught on smaller streams (i.e., narrower, shallower and with smaller pool volume), though the estimate of this effect carried some uncertainty. We were surprised to find that the opposite appears to be true of streams with less wood volume and fewer undercut banks, where bears tended to feed less selectively on each catch. We discuss these results in light of both the theory that generated the predictions and also the implications for the role of stream habitats and salmon abundance in mediating transfer of salmon-derived nutrients to riparian zones.

The finding that bears ate more of each salmon that they caught on larger streams is consistent with our prediction, based on the trade-off between continuing to consume a given carcass versus hunting for new fish, when hunting is more difficult. However, contrary to our predictions, bears were more likely to be selective in their feeding in streams with higher cover,

where we assumed that hunting would be more difficult. This may be because bear's hunting technique (e.g., chasing, wading/plunging, standing at waterfalls) may be determined by topographic features (Luque and Stokes 1974; Klinka and Reimchen 2002; Gill and Helfield 2012) and may differ between "high cover" and "low cover" streams. If bears use these stream features to their advantage to trap prey, it is possible that although wood and undercut banks may decrease the visibility of individual prey, they do not necessarily protect them from capture. If so, then the inability to target their desired prey before capture could lead to increased selectivity in consumption after capture, which would explain the results for streams with high cover. This explanation is supported by results in Andersson and Reynolds (2017) where bears were less able to capture preferred larger, higher-quality salmon in streams with higher cover over the same spawning period. In the same high cover streams where size-biased predation was not occurring, bears caught more fish than at low cover streams (with sized-biased predation), and consumed those kills more selectively (Andersson and Reynolds, 2017).

Contrary to our predictions, there was no relationship between selective consumption and the number of spawning salmon (Fig. 2). Furthermore, the number of salmon was included in the 2nd model which was an identical but more complex version of the top model, with little additional explanatory power and, therefore, has no biologically interpretable effect (Arnold, 2010). Furthermore, in a *post hoc* analysis using salmon density instead of abundance, the models were ranked in the same order and with similar weights as our original analysis (i.e., top model: habitat complexity; $AIC_c w_i = 0.46$, second model: habitat complexity + density; $AIC_c w_i = 0.23$). This is inconsistent with our expectations from foraging theory (e.g. Charnov, 1976, Sih, 1980), and the findings of Gende et al. (2001) who demonstrated that bears selected more energy-rich parts and consumed less of each fish in habitats and years with higher salmon density. Abandoning a carcass in pursuit of new prey makes sense when prey are abundant and easy to catch; low-quality parts can be left uneaten when a surplus of high-quality prey with

high-quality parts is still widely accessible (e.g., Goss-Custard 1977). Perhaps the number of spawning salmon was never low enough for bears to compensate in an obvious way by altering their consumption patterns. We found that predation rates were relatively low at these streams, ranging from 2.1% to 21.4% (Andersson and Reynolds, 2017).

We considered sex, species, and time of year because these all may influence selective consumption. Even though they were not directly competed in the model selection process (except with the null model), these forced parameters were generally good predictors of selective consumption. As predicted, bears were less selective in their consumption, and ate more of each catch, as the season progressed. This effect was even clearer in the top model of the analysis that used the alternative scoring system that considered total prey consumption, rather than incorporating energy-rich tissues as part of the score (Fig. S3). Salmon have fewer eggs and lower energy stores after spawning (Hendry and Berg 1999; Reimchen 2000) and bears increase their caloric consumption at the end of the season (Nelson 1980). Salmon that have spawned contain approximately half of the energetic value of pre-spawned salmon (Gilbert and Lanner 1995) due to loss of musculature and gametes (Gende et al. 2004a) and generally are not preferred (Gende et al. 2004b). Increased hunger, coupled with lower energy prey, may cause bears to consume more of each carcass near the end of the season when this is all that is available. We also found a higher probability of selective consumption when bears consumed females rather than males. Eggs can comprise 20% of a female's body mass (Hendry and Berg 1999). We found that 89% of the females that were considered selectively consumed were missing eggs whereas 49% were missing brains (these 2 are not mutually exclusive – many carcasses were missing both). The alternative scoring system, which does not include energy-rich parts, revealed that bears were more likely to eat the majority (>50%) of a female carcass than a male carcass, probably because females are smaller and, therefore, the same number of bites on prey of each sex would result in a higher proportion of the carcasses of females being

consumed. Finally, as predicted, bears were more likely to selectively consume chum than pink salmon. This is also potentially due to the size difference. Additionally, our findings are consistent with Reimchen's (1994) suggestion that it may be easier for bears to select for energy-rich parts on larger fish (e.g., chum) due to the higher dexterity associated with handling the larger prey.

Though we consider initial consumption of the carcass and scavenging to both be important factors in this consumption analysis (with the same consequences to nutrient transfer), it is possible that bears scavenged carcasses directly after our visits and, therefore, caused us to misidentify some carcasses as "selectively consumed" despite them being shortly thereafter scavenged and ending up as non-selectively consumed. To account for this, we ran a *post hoc* analysis using only bear-killed salmon in the later categories of decomposition. We assumed that bears would most likely return to scavenge the freshest kills after our visits so the killed fish with "decomposition level 0" were removed from the *post hoc* analysis. Habitat complexity continued to rank higher than the "density" and "density + habitat complexity models" (by similar weights). Furthermore, in the top model, the directionality of each of the model coefficients was the same as the original top model and the magnitude of their effect was similar.

Size-biased predation (i.e., for larger prey) by bears can have significant impacts on the flux of biomass to terrestrial ecosystems (Carlson et al. 2011) which can have significant impacts on the abilities of scavengers to utilize the biomass (e.g. Meehan et al. 2005). We can illustrate an analogous effect, due to selective consumption per fish, rather than selective predation, by comparing 2 streams at each extreme of the cover index, based on the probabilities of selective consumption (Fig. S2). The alternative scoring system, which considers the amount of flesh eaten, not contingent on energy-rich parts, is more relevant when

investigating terrestrial nutrient inputs. Holding date, escape index, sex and species parameters constant at their means, approximately 60% of carcasses in streams with the highest cover index will be consumed selectively whereas only approximately 30% of carcasses in streams with the lowest cover index will be consumed selectively. In this calculation, we assume that each chum salmon weighs ≈ 3.5 kg, and each pink salmon, ≈ 1.2 kg (Hocking and Reynolds 2011). We further assumed that bears eat 1/4 of each “selectively consumed fish” (i.e., the ones that were $<50\%$ consumed) and ate 3/4 of each “non-selectively consumed” fish, which was a typical observation. Thus, for every 100 chum and 100 pink salmon killed by bears at each stream, the stream with highest cover index is subsidized with 192.5 kg (chum) + 66 kg (pink) = 258.5 kg (total) of abandoned carcass biomass that remains uneaten by bears. The stream with lowest cover is subsidized with 140 kg (chum) + 48 kg (pink) = 188 kg (total) of abandoned carcass biomass. This represents a difference of 70.5 kg of salmon biomass, for every 100 fish of each species killed, based only on the differences between the probabilities of selective consumption in streams with little or a lot of wood and undercut banks. Further multi-year studies in these streams that increase sample size, quantify patterns of carcass distribution, predator waste excretion, and overall nutrient transfer would be valuable for quantifying habitat-mediated nutrient transfer via predation and consumption.

This study contributes to our understanding of cross-boundary, nutrient-transfer pathways and how they can be shaped by characteristics of the stream in conjunction with the foraging behaviour of bears. Consideration of the behavioural ecology of predators thereby helps us understand how nutrient subsidies reach aquatic and terrestrial habitats.

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533 statistical problems. *Methods Ecol. Evol.* **1**:3–14.

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536

537 Table 1 Models, variables, mechanisms and predictions for original scoring and
 538 alternative scoring systems for selective consumption of salmon by bears. A null
 539 model and a model that compared only forced variables (sex, species and date)
 540 are not shown.

			Predicted association with selective consumption	Sources ^a
Model	Variables	Mechanisms		
Prey abundance	Number of salmon	Search times for prey are lower in prey-rich patches	Positive	1,2,3,4
Habitat complexity	Escape index [pool vol/100 m] [bankfull width] [channel height] Cover index [wood vol/100 m] [% undercut banks]	Wider, deeper streams with more pools provide salmon with refuge and lower visibility to bears. Wood in the stream and undercut banks decrease prey visibility and are obstacles for bears.	Negative	5,6,7,8,9,1 0,11,12
Habitat complexity +	All variables combined	All mechanisms above combined	Prey abundance [positive]	1,2,3,4, 5,6,7,8,9,1 0,11,12

prey	Habitat complexity
abundance	[negative]

^a Source: 1) Cunningham et al. 2013, 2) Gende et al. 2001, 3) MacArthur and Pianka 1966, 4) Quinn et al. 2003, 5) Gende et al. 2004b, 6) Quinn and Buck 2001, 7) Quinn and Kinnison 1999, 8) Deschênes and Rodríguez 2007, 9) Fukushima and Smoker 1998, 10) Braun and Reynolds 2011, 11) Floyd et al. 2009, 12) Roni and Quinn 2001

Draft

545 Table 2. Summary of stream features. “Cover index” is a principal component created with the volume of wood
 546 per 100 m and percent of bank that is undercut. “Escape index” is a principal component created with
 547 mean bankfull width, mean channel height and pool volume per 100 m. Salmon abundance, density and
 548 predation rate is calculated at the stream and predation rate is calculated according to the method
 549 described in Quinn et al. (2001).

Stream	Latitude	Longitude	Volume		Cover Index	Mean	Mean	Pool	Escape index	Spawning length (m)	Study Reach	2014 Salmon abundance	Salmon		2014 Chum abundance	2014 Pink abundance
			of wood (m³) per 100 m	Undercut bank (%)		bankfull width (m)	channel height (m)	volume (m³) per 100 m					Density (no. per m²)	Predation Rate (%) for both species		

Ada	52.0553	-128.0507	16.19	23	11.61	8.8	1.05	79.82	50.99	435	360	1 752	0.46	2.1	1 619	133
Beales Left	52.1882	-127.9890	19.67	10	13.98	10.5	1.46	40.64	30.07	300	300	1 302	0.41	5.1	606	696
Beales Right	52.1868	-127.9800	29.09	11	20.65	10.1	1.24	23.32	19.92	200	200	226	0.11	15.0	103	123
Bullock Main	52.4029	-128.0785	66.75	26	47.38	8.6	0.79	45.16	31.13	622	360	6 323	1.18	6.5	3 468	2 855
Clatse	52.3377	-127.8391	22.85	12	16.24	19.6	1.09	31.09	29.85	900	720	8 656	0.49	2.8	865	7 791

Fancy Right	52.0585	-128.0167	32.12	56	23.12	4.3	0.77	22.71	15.86	298	240	290	0.22	12.3	287	3
Fannie Left	52.0426	-128.0668	33.49	31	23.90	10.7	0.79	179.4	108.32	1500	480	14 019	0.97	2.27	8 719	5 300
Goat Bushu	52.2132	-127.8767	25.53	46	18.38	5.9	0.78	59.61	37.66	1000	240	774	0.13	22.4	150	624
Hooknose	52.1249	-127.8370	26.95	35	19.30	11.7	0.99	224.87	134.76	1800	600	2 147	0.10	6.6	522	1 625
Kill Creek	52.4267	-128.0958	62.86	66	44.91	3.4	0.48	1.86	3.33	543	120	1 808	0.98	15.5	1 531	277
Kunsoot	52.1569	-128.0435	52.68	32	37.48	14.3	0.66	36.2	29.34	1280	480	6 910	0.38	5.8	1 851	5 059
Main																
Sagar	52.0959	-127.8388	16.33	14	11.64	15.5	1.39	161.51	101.40	180	180	2 100	0.75	3.7	1 124	976

550

551 Table 3 Comparison of mixed-effects models of selective consumption of salmon
 552 carcasses by bears using Akaike's Information Criterion (AIC_c),
 553 corrected for small sample size. Each model includes a random effect
 554 of site. Sex, species and date are forced fixed effects in each model to
 555 control for possible differences in selective consumption patterns
 556 according to those parameters.

Model	Variables	K^a	AIC _c ^b	Δ AIC _c ^c	w_i^d	ER ^e
Habitat complexity	cover index, escape index, sex, species and date	7	741.18	0	0.458	1.0
Habitat complexity + prey abundance	cover index, escape index number of salmon, sex, species and date	8	741.71	0.53	0.352	1.3
Null with forced parameters	sex, species and date	5	743.78	2.60	0.125	3.66
Prey abundance	number of salmon, sex, species and date	6	745.08	3.90	0.065	7.05
Null	intercept	2	763.90	22.72	0	-

557 ^a Number of parameters ^b Model strength (lower indicates a better fit) ^c Difference of AIC_c value with top
 558 model AIC_c value ^d The Akaike weight; probability that it is the best model ^e Evidence ratio

Figure captions

- Figure 1 Study stream locations ($n=12$) in British Columbia, Canada. Circles represent each stream mouth.
- Figure 2 Relationships between the proportion of selectively consumed salmon and cover index, escape index, date (1 = 11 September 2014) and number of spawning salmon. For cover, escape and # of spawning salmon plots, each point represents the proportion of fish selectively consumed at that stream. Each point in the date plot represents the proportion of fish selectively consumed on that survey date (streams pooled). Selective consumption by bears is defined as eggs and/or brain having been consumed and < 50% of carcass consumed.
- Figure 3 Probability plots for the top model of selective consumption of salmon carcasses by bears. Lines and circles are predicted probabilities of selective consumption against model variables, with other variables set to their mean value. Bands and error bars are 95% confidence intervals.
- Figure 4 Standardized (mean=0, SD=2) coefficient values (circles) with 95% confidence intervals (lines) from the top model of selective consumption of salmon carcasses by bears. The positive coefficient for species indicates more selective consumption of chum than pink salmon and the negative value for sex indicates more selective consumption of females than males.

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