Selective consumption of sockeye salmon by brown bears: patterns of partial
consumption, scavenging, and implications for fisheries management

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Abstract

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Animal foraging requires a series of complex decisions that ultimately end with consumption of resources. The extent of consumption varies among consumers, including predator-prey systems; some predators always completely consume their prey but others may partially consume prey that are too large to be completely consumed, or consume only parts of smaller prey and discard the remains. Partial consumption of prey may allow predators to maximize energy intake through selectively feeding on energy-rich tissue, as is observed in bears (*Ursus* spp.) selectively feeding on Pacific salmon (*Oncorhynchus* spp.). Here, we examined selective and partial consumption of sockeye salmon (*O. nerka*) by brown bears (*U. arctos*) in western Alaska. First, we tested a series of hypotheses to determine what factors best explain why some salmon are killed and abandoned without tissue consumption, and what tissues are consumed from the salmon that are fed upon. We found that a foraging strategy consistent with energy maximization best explained patterns of selective prey discard and partial consumption, as traits of the fish itself (size, sex, and condition) and the broader foraging opportunities (availability of salmon as prey) were

important. Second, we documented empirical relationships between salmon availability and consumption by bears to evaluate whether current salmon management in Bristol Bay, Alaska limits salmon intake by bears foraging in small streams. Bears reached maximum salmon consumption every 2-4 years in the systems studied, and management scenarios revealed comparatively small increases in salmon consumption by bears in response to large increases in salmon availability, suggesting that current management does not severely limit salmon intake in these populations. Finally, we conducted a field prey choice experiment to explore scavenging as another mechanism of prey consumption. Limited data revealed lower rates of scavenging compared to previous years, and we observed similar patterns of selectivity and partial tissue consumption in scavenged carcasses as were seen in freshly killed salmon. Through exploring the intricacies of selective and partial consumption of salmon by bears, this work aims to increase understanding of the bear-salmon predator-prey relationship, and to add to knowledge about the flow of salmon-derived nutrients through aquatic and terrestrial ecosystems.

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GENERAL INTRODUCTION

Foraging animals make a series of complex decisions when exploiting food resources, including habitat selection, patch exploitation, and prey choice. Predators must also detect, pursue, capture, and kill prey before making consumption decisions, and consumption behavior varies widely across predator-prey systems. In some systems, consumption of prey is always complete (e.g., baleen whales and krill), whereas in others prey is only partially consumed and remains are discarded (e.g., wolves [*Canis lupus*] consuming moose [*Alces alces*], antlions [*Myrmeleon mobilis*] consuming flies [*Drosophila melanogaster*]; Lucas 1985; Vucetich et al. 2012), either because the prey item is too large to be consumed entirely, or because of predator choice. This selective prey consumption is often attributed to predator limitations (gut limitation or satiation) or as part of an energy-maximizing (i.e., optimal) foraging strategy. Moreover, consumption following predation is commonly recognized as the primary mechanism of prey intake for carnivores, but scavenging may also comprise a substantial portion of prey intake for facultative scavengers that both kill prey and consume carrion.

Brown and black bear (*Ursus arctos* and *U. americanus*) predation on Pacific salmon (*Oncorhynchus* spp.) is a well-documented example of a predator-prey system exhibiting both partial consumption of killed prey and scavenging of carcasses. Salmon represent an important prey source for coastal brown bear populations (Hilderbrand et al. 1999b). Though only seasonally available, meat (primarily salmon in coastal regions) consumption is positively correlated with bear body size, population density, survival, and reproductive success (Rogers 1987; Samson and Huot 1995; Hilderbrand et al. 1999b; McLellan 2011). As such, bears may be motivated to eat a large quantity of high quality (i.e., high energy) salmon when possible to increase weight gain and benefit from the resulting reproductive and survival advantages.

However, the motivation behind selective consumption and scavenging decisions is less clear, as are the implications of these foraging choices.

Across and within bear populations and salmon streams, the extent of partial and selective consumption of salmon varies greatly. Bears may consume nearly the entire biomass of a fish in some circumstances but may consume little or nothing in others. This behavior may be attributed to multiple factors that work in concert, particularly those related to ease of fish capture and fish quality such as salmon abundance (Gende et al. 2001), habitat characteristics (Gende et al. 2004; Andersson and Reynolds 2018), timing within the season (Gende et al. 2001), and prey characteristics like fish sex, size, and energetic condition (Reimchen 2000; Gende et al. 2001). In particular, bears foraging in shallow habitats with high salmon abundances exhibit partial and selective consumption, often consuming lipid-rich portions of the fish (i.e., brain in males, gonads in females) and discarding less energetic portions (Reimchen 2000; Gende et al. 2001). This behavior apparently allows bears to maximize energy intake when foraging conditions facilitate fish capture.

In addition to selective consumption, salmon are frequently bitten and killed but left unconsumed by bears (Frame 1974; Reimchen 2000), though the reasons for this behavior are unclear. Discard without consumption may be expected under classical optimal foraging theory (Charnov 1976) if the benefits offered by the fish are low and the costs of obtaining another fish are low enough to encourage rejection of an entire carcass. However, if these captured and discarded fish are of comparatively high energetic quality, and/or capture of additional fish is difficult, then surplus killing may provide an alternative explanation for such apparently wasteful behavior. Surplus killing occurs when a predator kills far more prey than it could possibly consume or cache, and is hypothesized to be triggered by a superabundance of prey (Kruuk

1972; Oksanen et al. 1985; Wiesel 2010) or exceptional prey vulnerability (Delgiudice 1998; Short et al. 2002). This behavior has been documented in many mammalian species, however current knowledge surrounding the phenomenon is largely anecdotal. Empirical data documenting salmon killed and discarded by bears, presented in the first chapter of this thesis[1], provide an opportunity to determine whether discarded prey are the result of surplus killing behavior or arise as part of an energy-maximizing strategy.

The variability in partial and selective consumption of salmon by bears adds complexity in evaluating salmon management for ecosystem-wide needs. Several studies have proposed increasing salmon abundance to feed wildlife populations in response to a perceived limitation in prey (Darimont et al. 2010; Chasco et al. 2017), including bears (Boulanger et al. 2004; Hilderbrand et al. 2004; Levi et al. 2012; Van Daele et al. 2013). Estimates of consumption in these studies are frequently based on bioenergetics models or metabolic demands, and may assume complete consumption of prey when generating target numbers of prey increases. However, for predators that exhibit partial prey consumption, like bears, empirical data are needed to determine how consumption rates would respond to increases in prey availability. Integrating these more complex relationships between prey abundance and prey consumption may alter conclusions about whether or not human use of resources such as salmon limit consumption by wildlife. As such, the second chapter of this thesis explores empirical relationships between salmon consumption by bears and salmon availability, and the management implications that arise from these relationships.

In addition to killing and consuming salmon, bears may scavenge salmon carcasses, particularly in habitats where fishing is difficult. However, scavenging is not limited to these locations, and salmon scavenging has been documented even in shallow systems with dense

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salmon where 20-50% of the annual salmon run may be killed by bears (Quinn and Buck 2000; Quinn et al. 2003). These systems in which prey capture costs are very low provide bears with a choice between killing fish or scavenging carcasses, and thus prey selectivity and selective consumption may manifest themselves among both freshly killed salmon as well as salmon carcasses. Investigation of scavenging rates across varying daily salmon abundances over the course of the salmon run may reveal factors influential in the decision to choose one foraging strategy over the other, and observation of scavenged carcasses can determine whether selectivity and partial consumption of carcasses mirrors that of freshly killed salmon. Bears may consume scavenged carcasses differently than killed salmon if carcasses are of lower quality (e.g., spawned out), however bears provided with carcasses of high quality (e.g., ripe) in isolation of capture costs may make partial consumption decisions in line with true prey preferences. Thus, the third chapter of this thesis focuses on a carcass choice experiment using high quality carcasses to reveal drivers of scavenging behavior and patterns of selectivity in scavenging.

The relevance of patterns of partial and selective consumption of salmon extend beyond bear nutrition and ecosystem-based salmon management to include nutrient cycling. In leaving behind remnants of salmon carcasses, bears play a key role in transferring salmon nutrients into terrestrial systems (Hilderbrand et al. 1999a; Reimchen 2000) where they may be utilized by secondary scavengers (Meehan et al. 2005; Pereira et al. 2014) or incorporated into tissues of surrounding riparian vegetation (Hilderbrand et al. 1999a; Quinn et al. 2018). The distribution of nitrogen via discard of partially-consumed carcasses is substantially greater than that passed in bear urine and feces (66 kg N yr^{-1} versus 0.7 kg N yr^{-1} in average years; Helfield and Naiman

2006), and so identifying the drivers of discarding and partial consumption behavior has broader implications for ecosystem health.

The overall purpose of this thesis is to test hypotheses related to partial consumption of salmon by brown bears as a result of predation and scavenging, and to explore the implications of partial consumption behavior on managing salmon for wildlife. The first chapter explores whether the tendency of brown bears to discard sockeye salmon (*O. nerka*) carcasses without consumption is best explained as an example of surplus killing behavior or an energy-maximizing strategy consistent with optimal foraging theory. In the second chapter, the implications of selectivity and partial consumption behavior are explored by empirically defining the relationship between salmon availability and salmon consumption by bears, and then considering scenarios of altered salmon availability as might occur if fishery management was modified to increase the numbers of adult salmon available to bears. The third chapter explores scavenging as a different mechanism of salmon consumption, and describes an experimental approach to determine drivers of selectivity in scavenging decisions. By empirically identifying relationships between foraging conditions and prey consumption or discard in this body of work, I aim to add to a growing knowledge base about the complexities within the bear-salmon predator-prey relationship, as well as ecosystem-based management of salmon fisheries.

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CHAPTER ONE

Optimal foraging or surplus killing: selective consumption and discarding of salmon by

brown bears

ABSTRACT

Selective consumption of prey by predators, observed in many animals, is often attributed to optimal foraging. Consistent with this idea, brown bears (*Ursus arctos*) often exhibit partial consumption, feeding exclusively on lipid-rich tissues of Pacific salmon (*Oncorhynchus* spp.), and discarding remains. However, bears also kill and abandon salmon without consuming any tissue. These discarded fish may be consistent with optimal foraging choices if they are of poor quality and if bears have easy access to better prey, or may reveal non-adaptive surplus killing behavior if fish are killed and discarded at random or solely based on prey abundance. Using 21 consecutive years of data from sockeye salmon (*O. nerka*) carcass surveys in Alaska, we found that foraging to maximize energy intake best explained prey discarding behavior. Specifically, discarding was more common under high prey abundance, late in the salmon run, and with low quality prey. Patterns of tissue consumption were consistent with these findings; bears were less likely to consume belly, body, and brain tissue when prey condition decreased. Other factors not quantified here (e.g., bear demography, alternative food resources) almost certainly influence prey discard and partial consumption, though the salmon-related factors explored here strongly influenced bear foraging decisions that were consistent with optimal foraging theory. We did not find clear evidence of surplus killing behavior in brown bears foraging on salmon, but prey selectivity manifested itself through both discarding and partial consumption, which contributes to our ability to predict transport of salmon nutrients by bears across ecosystem boundaries.

INTRODUCTION

Foraging animals make decisions at multiple spatial and temporal scales to optimize the balance between energy intake, expenditure, and risk (Stephens and Krebs 1986). For apex predators, with little or no risk (Brown and Kotler 2007; Sergio et al. 2014), decisions are expected to be dominated by optimal exploitation of prey patches. Under this paradigm, resources are distributed in patches that range in quality such as prey density (Charnov and Orians 1973; Charnov 1976). Consumers should forage to maximize the rate of energy intake, using patches and abandoning them in favor of more profitable ones based on the costs of moving between patches and the reward in each patch. By foraging within a patch, the consumer depletes the food source, diminishing the rate of energetic gain (Charnov 1976; Hohberg and Traunspurger 2009), thus there is an optimal time spent foraging in each patch before moving to a new one.

Patches may be small in scale, and a single prey item is often considered a patch (Cook and Cockrell 1978; Formanowicz 1984; Hohberg and Traunspurger 2009). Partial consumption of prey, whereby portions of a carcass are discarded and other body parts are eaten, may result from optimal foraging (Sih 1980; Formanowicz 1984), particularly in situations where the prey item is so large that the predator need not or cannot consume it entirely. Consistent with expectations based on optimal foraging theory, in both vertebrate and invertebrate predators, the extent of partial consumption depends on prey search time (Lucas 1985; Hohberg and Traunspurger 2009), which arises from prey density and availability (Cook and Cockrell 1978; Zong et al. 2012). The quality of a patch or prey item may also influence prey choice and the optimal time spent eating a prey item; predators tend to select and spend more time in patches of high quality (Charnov and Orians 1973; Charnov 1976). Finally, handling time can affect

optimality as well (e.g., Rovero et al. 2000; Cooper and Anderson 2006; Gooding and Harley 2015).

In addition to partial consumption, some predators kill and discard carcasses without consuming any tissue. Thus, selective consumption may be more than merely deciding which tissues to consume, and may instead be thought of as two sequential decisions. After capture, the predator decides first whether to consume or discard the prey, and second, what tissues should be consumed if the prey is not discarded. The reasons for discard without consumption are unclear. This behavior may be adaptive and thus expected under optimal foraging theory if the benefits offered by the captured prey and the costs of obtaining another prey were both so low that obtaining another prey item of higher quality would be more efficient. In such cases a predator might discard the entire carcass. However, in some cases predators capture and discard high quality prey repeatedly, in apparent contradiction to an adaptive foraging strategy that would maximize energy intake. This behavior, termed surplus killing, occurs when a predator kills far more prey than it could possibly consume, and makes no use of the kills (Mueller and Hastings 1975). This is distinguished from caching behavior, where multiple prey items are killed and stored for later consumption. Surplus killing is thought to be triggered by a superabundance of prey (Kruuk 1972; Oksanen et al. 1985; Wiesel 2010) or exceptional prey vulnerability (Delgiudice 1998; Short et al. 2002), and is typically observed in mammals (Kruuk 1972; Andelt et al. 1980; Duffy 1995; Delgiudice 1998; Reimchen 2000; Odden et al. 2002; Short et al. 2002; Gaydos et al. 2005; Wiesel 2010; Zimmermann et al. 2015), though it has also been noted in predatory birds (Nunn et al. 1976) and insects (Lounibos et al. 2008). Though surplus killing is apparently widespread, studies on this behavior pattern are largely anecdotal. As such, the unplanned, uncontrolled, and poorly replicated nature of these findings make it difficult to test

specific hypotheses related to the mechanisms behind surplus killing, or to test if prey discarding

arises from non-adaptive surplus killing behavior or from alternative hypotheses such as energy

maximization.

Brown bears (*Ursus arctos*) and black bears *(U. americanus)* foraging on Pacific salmon

(*Oncorhynchus* spp.) provide an ideal system to test questions about mechanisms behind prey

discarding. Though a single salmon is typically small enough that a bear could consume it

entirely, it is also large enough that just a portion may comprise a meal. Bears selectively

consume energy-rich portions of salmon and discard the rest of the carcass (Reimchen 2000;

Gende et al. 2001; Andersson and Reynolds 2018), but also bite and then discard whole salmon

without any consumption at all (Gard 1971; Frame 1974; Gende et al. 2001). The appearance of

both foraging to maximize energy intake and apparent surplus killing behavior in the same

predator-prey system suggests that these foraging behaviors may not be mutually exclusive, and

that bear foraging may lie somewhere on a continuum between the two.

Several aspects of salmon life history patterns provide additional important sources of

variation in their availability as prey for bears. Salmon abundance changes rapidly on a daily

scale, as the salmon run starts, rises, peaks, and ends over a period of only a month or two. Prey

availability also varies from year to year, as salmon populations commonly fluctuate in

abundance by a factor of ten or more (Quinn 2018). Prey availability can also be considered at a

broader spatial scale than a single focal stream, as proposed by Quinn et al. (2017), including a

wider "neighborhood" of streams among which bears routinely forage. In addition to variation in

prey availability, the quality of salmon as prey is highly variable. Male and female salmon

commonly differ in body size, and female gonads are also markedly larger and more energy-

dense than those of males. Also, because these salmon are semelparous, energetic condition of

individuals declines rapidly with increasing time spent on the spawning grounds (Hendry and

Berg 1999; Gende et al. 2004). Thus, partial consumption behavior and prey discarding might be

influenced by extrinsic factors related to prey availability, and by intrinsic factors related to the

fish itself. Thus, the bear-salmon predator-prey system lends itself to testing predictions from

optimal foraging and surplus killing theories.

However, patterns of selectivity in salmon consumption may also be complicated by

factors outside of salmon themselves, as salmon are not the sole food source available to bears,

nor are individual bears identical in foraging tendencies. Though salmon can represent a

significant fraction of bear diet when available (Hilderbrand et al. 1999b), bears also forage on

vegetation (e.g., berries, sedges; Mowat and Heard 2006; Deacy et al. 2017), as well as other

terrestrial meat sources (e.g., ungulates; Mowat and Heard 2006). The availability and ease of

obtaining these alternative food sources may impact decisions on whether to consume or discard

captured salmon, as a bear may weigh the benefits of consuming a salmon with the benefits and

costs of foraging on alternative foods. Additionally, there is some degree of individuality in bear

foraging, both in technique of salmon capture (Gill and Helfield 2012) and in time spent foraging

on salmon (Gende and Quinn 2004; Gill and Helfield 2012), which may also extend to

differences between individuals in the propensity to discard prey. Dominant bears that spend

more time on salmon streams may be more selective in which salmon they choose to eat and

which to discard. Subordinate bears and females with cubs may abandon prey if interrupted by

large dominant males that can be infanticidal (Swenson et al. 2001; Ben-David et al. 2004), so

prey may be discarded if bears avoid conflict with other aggressive bears. The density of bears

utilizing a given foraging habitat may vary inter-annually by a substantial degree on small

salmon streams (Wirsing et al. 2018), and thus the number of bears present may influence the

frequency of intra-specific encounters and therefore foraging behavior. Competition between bears may also drive prey discard as a strategy to reduce prey availability for competitors. Finally, discards could also be an outcome of fishing practice by less experienced bears, a mother teaching her offspring to fish, or a result of play. Thus, there are many factors beyond the availability and quality of salmon which may also affect prey discarding, and these factors may contribute to variability in observed patterns of salmon discarding and partial consumption behavior.

Our goal was to explore whether bear foraging is best explained by an adaptive energy-maximizing foraging strategy, surplus killing, or a combination of the two behaviors, using data from 21 consecutive years of salmon carcass surveys. Given the possibility for variation in patterns of salmon discarding and partial consumption due to factors unrelated to salmon abundance and condition such as those mentioned above, and the limitation of our dataset to salmon carcasses, we did not expect to explain all of the observed variation in bear foraging. Rather, we sought to determine which behavior was best supported by the data. Following our framework of consumption as a set of two decisions, we first considered whether a fish was consumed or discarded without any consumption, and then considered which tissues were consumed if the fish was not discarded.

Under an adaptive prey discarding strategy, we expected that prey discard and selective consumption would be explained by prey availability, prey attributes (sex, size, condition), and date. An energy-maximizing bear might kill and discard prey when availability is high and many prey options are available, or when the captured prey is low in quality. Prey quality varies by fish sex; muscle tissue is similar in energy content between males and females (Ando et al. 1985; Hendry and Berg 1999), but male salmon are typically larger than females and thus a male fish

may contain more total energy than a female. However, ovaries are much larger and more energy-dense than testes (Brett 1995; Hendry and Berg 1999) so in addition to the effects of body size, differential consumption of body parts is expected between sexes. Individual salmon lose energy very rapidly during their few weeks on the spawning grounds (Hendry and Berg 1999; Gende et al. 2004), and the decline is especially precipitous in females because they spawn their eggs within a few days of arrival (McPhee and Quinn 1998), such that males and females are similar in energy density at senescence (Hendry and Berg 1999). A fish in poor condition with low energetic content may be more likely to be discarded by an energy-maximizing bear than a fish with more fat and protein.

In addition, discard and consumption patterns might vary with date within the salmon breeding season. Fish captured at the beginning of the salmon run may be less likely to be discarded if bears are hungry and are under pressure to accumulate fat before hibernation (Nelson 1980), whereas those captured at the end of the season may be more frequently discarded as bears gain mass and become satiated. Similarly, bears may be more likely to selectively consume brains or bellies rather than the full body of a fish when experiencing some combination of high prey availability and lateness in the season, and in addition, the specific tissues consumed may differ between fish of contrasting sex, size, and condition. These patterns would suggest foraging to maximize energy intake, and we anticipated that if these factors were significant predictors of discarding and selective consumption behavior, then bear foraging behavior may be best explained as adaptive discarding (Table 1.1).

Predictions from a surplus killing perspective were simpler than those under an adaptive discarding scenario. If surplus killing is driven by a superabundance of prey, then prey attributes and timing would not be important and local prey availability alone would predict (and be

positively correlated with) prey discarding (Table 1.1). Alternately, if surplus killing occurs at random, we anticipated that a null model (constant probability of non-consumption) would adequately predict discarding behavior. If surplus killing is both random and also triggered by prey availability, we expected that there would be no difference in model performance between the null model and a surplus killing model (with daily prey availability as the sole variable), but that both would outperform an adaptive discard model (with prey availability, prey attributes, and date as explanatory variables). It is also possible that both surplus killing and adaptive discarding occur, which would be more difficult to distinguish. In this case, we expected an adaptive discard model to outperform a surplus killing model under low prey availability, but we expected the reverse under high prey availability (Table 1.1). This would indicate that surplus killing is prevalent in high but not low prey availability. Alternately, if bears showed both adaptive discard and surplus killing at random, we predicted that an adaptive discard foraging model would significantly predict discarding and selective consumption behavior, but would not outperform a null model, indicating that both random choice and energy maximization drive the decision to discard.

METHODS

Site Description

Hansen Creek is a small (mean depth = 10 cm, mean width = 4 m) tributary of Lake Aleknagik, part of the Wood River Lakes system in southwestern Alaska. It is spring-fed with only minor changes in discharge, even after precipitation events, and so habitat remains similar throughout the salmon run and largely unchanged among years. Two ponds provide water input to the creek, one of which is at the headwaters. Sockeye salmon regularly spawn in both of these

ponds, though access to the pond at the headwaters was prevented by a beaver dam in some survey years (1997–2004). Sockeye are the only species of salmon that use Hansen Creek for spawning (Pess et al. 2014), and the spawning run typically extends from late July to mid-late August. While the ranges of brown and black bears overlap in southwestern Alaska, Hansen Creek is apparently used exclusively by brown bears for foraging. Recent work using hair snares as a non-invasive genetic mark-recapture technique estimated that 18-33 different brown bears forage along Hansen Creek annually over the course of the salmon run, many of which forage on nearby streams as well (Wirsing et al. 2018). However, not a single specimen representing a black bear has been obtained (Wirsing et al. 2018). Hansen Creek is just 2 km in length, and so bears can readily forage along the entire stream in a single day. Two neighboring streams, Eagle Creek and Happy Creek (within 1 km on each side), also support sockeye salmon runs and thus provide additional foraging opportunities. Bear predation rates on salmon are relatively high (20-80% per year) in these streams because their small size facilitates capture of salmon (Quinn et al. 2017).

Survey Methods

We conducted surveys daily at Hansen Creek throughout the sockeye salmon run from 1997–2017, enumerating all live fish daily as a measure of prey availability. It was possible to count every fish in the creek visually because the habitat is shallow, narrow and has few undercut banks. Annual sockeye salmon availability was calculated as the sum of the number of live fish encountered on the last survey date of the season and the cumulative count of dead fish. On the day of these final surveys, typically >90% of salmon had already died and no more were arriving so these were adequate estimates of total salmon abundance in that year. Annual sockeye availability at Eagle and Happy Creeks was calculated by summing the live and dead

count at the peak of the run, determined from three surveys conducted per year. While these counts fail to include late-arriving fish, as well as fish captured by bears and transported away from the stream (Gende et al. 2004; Quinn et al. 2009), they still represent the majority of the run and thus function as an index of annual run size. Annual run sizes at Eagle, Happy, and Hansen creeks were combined to represent prey availability in the "stream neighborhood" (see Quinn et al. 2017). Therefore, we have three measures of prey availability: daily local (at Hansen Creek), annual local (at Hansen Creek), and annual neighborhood (at Eagle, Happy, and Hansen creeks).

In addition to counting live fish, all sockeye carcasses encountered in the stream and visible along the banks (ca. 3 m into the riparian zone) were identified to sex and assessed for cause of death (bear kill or other). Bear kills were distinguished by severe and conspicuous wounds whereas the other fish died of senescence, were killed by glaucous-winged gulls or bald eagles, or were stranded and died in shallow water. All bear-killed fish were inspected for consumption, and any body parts consumed were recorded (brain, body, belly, and/or hump; see Gende et al. 2001 for descriptions of consumption patterns). Body length (mid-eye to hypural plate) was recorded for a subset of the carcasses. In addition, in 1999-2017 some fish (mean = 176 fish, range = 87-278) were measured for length and tagged at the mouth (prior to stream entry), and their presence in the stream was recorded until they died. Consequently, for these individuals we could assess the patterns of consumption with respect to the number of days the fish had been alive in the stream prior to being killed by a bear. Sockeye salmon lose 90-95% of lipid content and 40-80% of total energy from freshwater entry to death (Hendry and Berg 1999), and so in-stream life may be used as a proxy for the energetic condition of these fish. After assessment, carcasses were thrown far into the woods to prevent double counting the next day.

These efforts in the field yielded three nested subsets of data, each containing fewer fish but with more complete data. In total, 225,260 salmon carcasses were examined, 80,064 of which were killed by bears. Most carcasses were encountered in and along stream habitat, however some were found at one of the two ponds along Hansen Creek. We included only carcasses encountered in or along the stream itself in our analyses, as salmon were unable to access the pond at the headwaters due to a beaver dam in some years, and only a small number were killed in the spring-fed pond tributary. Additionally, physical habitat affects the percentage of salmon killed by bears (Quinn and Kinnison 1999) and patterns of consumption (Gende et al. 2001), so exclusion of fish killed in the pond effectively removed habitat as a variable. An unprecedented number of sockeye salmon returned in 2014 (three times the previous maximum run), such that tagged fish were greatly outnumbered by untagged fish and no tagged fish were killed by bears. Additionally, there was an unusually large pre-spawning mortality event at Hansen Creek in this year, when 55% of the fish died prematurely due to high density conditions (Tillotson and Quinn 2017). Though the number of fish killed by bears was consistent with other high prey availability years, the proportion of fish discarded in 2014 (9.6%) was low compared to other high prey availability years. This could be a result of elevated bear scavenging in this year; if an abundance of high quality pre-spawning mortality carcasses were available, bears may have scavenged carcasses of high quality (i.e., ripe) rather than capture and kill a fish of unknown quality that may later be discarded. Thus, to keep the range of annual prey availabilities comparable between the three datasets and to account for this unusual pre-spawning mortality event, we excluded all observations from that year (n = 1,555) from analyses. For reference, we included analyses incorporating observations from 2014 in supplementary materials (Table 1.4).

Statistical Methods

All analyses were run using R Version 3.4.0 (R Core Development Team 2017). To address whether an energetically adaptive foraging strategy or surplus killing better explained the data, we predicted whether bears decided to consume or discard salmon carcasses using generalized linear mixed effects models with a binary response and logit link. Models were built to reflect adaptive discard behavior or surplus killing behavior, based on the inclusion of covariates predicted to be of importance *a priori*. Our data structure naturally divides itself into three subsets (the complete dataset including prey availability, date of death, and fish sex: n = 65,679; a second subset with the addition of fish length: n = 20,515; and a third subset with the addition of in-stream life: n = 985), and creates a tradeoff between sample size and completeness in covariates of interest. As such, we conducted three model comparisons: one for each subset of data (Table 1.2).

In each model comparison, two surplus killing models were built, one with daily local fish availability as the sole fixed covariate, and a null model. In the first model comparison, these surplus killing models were compared using Akaike's Information Criterion (AIC) with the "base" adaptive discard model, which included covariates predicted to be important under optimal foraging theory (Table 1.1). Prey availability was included on three different scales – daily local, annual local, and annual neighborhood. Date of death and fish sex were also included in this model. A second- and third-order term was included for date of death in the base adaptive discard model. In the second model comparison, the two surplus killing models were compared with a "base plus length" adaptive discard model, which contained the same covariates as the base adaptive discard model as well as fish length. The third model comparison compared the two surplus killing models with a "full" adaptive discard model, which also included in-

stream life. In both the base plus length adaptive discard model and the full adaptive discard

model, the interaction between length and sex was included because bears may mistake smaller

males for females during predation (Gende et al. 2001), which could influence rates of discarding

of male and female fish. Additionally, the full adaptive discard model included the interaction

between in-stream life and sex because female energy content declines more abruptly over time

than that of males. Thus, the relationship between fish condition (in-stream life) and discarding

behavior might vary with sex. Other interactions that were not expected *a priori* were explored,

but were not significant, and so were left out of our models. We included all other covariates and

interactions expected *a priori* in adaptive discard models for model comparisons, regardless of

statistical significance, as they were predicted to indicate energetically adaptive foraging

behavior. Year was included as a random factor in all models, allowing for random intercepts to

account for interannual variability and the lack of information about alternative prey availability

and annual bear abundance in most years. Continuous variables were centered and scaled to aid

model convergence, and variance inflation factors were checked to ensure that multicollinearity

of predictors was not present. Pearson residuals were used to assess model adequacy. Only

twelve carcasses were recovered after >12 days alive in the stream, and so these carcasses were

assigned in-stream lifespans of 12 days for analysis purposes. AIC was used to compare models,

and marginal pseudo-R^2 and conditional pseudo-R^2 values were calculated to evaluate model

performance using the "MuMIn" package (Nakagawa and Schielzeth 2013; Barton 2018).

Marginal pseudo-R^2 values represent the amount of variability explained by fixed factors our

mixed-models, while conditional pseudo-R^2 values represent the variability explained by the

entire model (i.e., fixed and random factors). Covariates were evaluated for statistical

significance *post hoc* using a last-entry *Z*–test with the "summary" function (Table 1.3).

To determine which covariates most affected patterns of the consumption of specific salmon tissues, we built a classification tree using the "partykit" package (Hothorn et al. 2006; Zeileis and Hothorn 2014). Classification trees allow for analysis of data that contain independent variables that may interact in a hierarchical manner. The analysis recursively partitions the data by univariate splits into binary nodes that are as homogenous as possible in the categorical response variable. Whereas classification trees constructed from other packages must be trimmed to prevent overfitting, the "partykit" package utilizes permutation tests to determine statistically significant associations between covariates and the response, and prevents overfitting by stopping the recursion when no significant associations exist (Hothorn et al. 2006). We did not measure in-stream life for most fish, so we constructed our tree using only data with observed values of in-stream life. We divided the data into a training dataset with 805 observations and a testing dataset with 202 observations, then constructed a tree using the training dataset with multiple binary responses (body, belly, brain, and hump consumption), predicted by all covariates measured (daily local prey availability, annual local prey availability, and annual neighborhood prey availability, date of death, fish sex, fish length, and in-stream life). A misclassification rate was determined by using the testing dataset to compare predicted to observed outcomes, and then calculating the proportion of predicted outcomes incorrectly classified by the tree.

Variable importance in predicting selective tissue consumption was derived from the decrease in tree performance observed after randomly permuting each covariate, based on the area under the curve (AUC) method used in similarly-structured multiple class classification problems (Hand and Till 2001). Since four response variables were involved (binary indicators for body, belly, brain, and hump consumption), overall AUC was determined by averaging over

the four values. Information loss was defined by the difference between the AUC calculated from tree performance on the testing dataset and the AUC calculated after permuting a covariate, and may be interpreted as a measure of variable importance. Five hundred iterations of variable permutations were conducted to get an average value for information loss.

RESULTS

Over the 21 years of data collection and 67,234 bear-killed salmon examined, 21% were discarded with no consumption and the remaining 79% had varying levels of tissue consumed. Adaptive discard models fit the data substantially better than either the surplus killing or null model for all three sets of data (Table 1.2). In each comparison, the ΔAIC of surplus killing and null models were substantially larger than seven, indicating that these models were not at all supported by the data (Burnham et al. 2011). To ensure that neither the surplus killing nor null models outperformed adaptive discard models in overabundant prey availability conditions, as might be the case if a threshold prey abundance triggered surplus killing, models were re-run using observations with daily prey availabilities > 1500 fish (> 0.2 fish/m^2). Dividing the data in this manner indicated that the ΔAIC between the full optimal consumption model and the surplus killing model was reduced to 7.6 at high densities, but overall the conclusions remained the same, as the Akaike weight (probability of being the correct model) for the adaptive discard model was 0.97 and prey condition, availability, and date were still significant predictors of discard behavior. Re-running the three adaptive discard models on the full dataset (n = 985) revealed that the full adaptive discard model outperformed the base adaptive discard model (ΔAIC = 30.4) and the base plus length adaptive discard model (ΔAIC = 33.5).

Greater prey availability on a daily local scale was associated with a higher frequency of discarding behavior in all three adaptive discard models (base model $Z = 8.00$, $p < 0.001$; base plus length model $Z = 4.74$, $p < 0.001$; full model $Z = 4.35$, $p < 0.001$), but salmon density at a neighborhood scale was not ($Z = -0.15$, $p = 0.88$; $Z = -0.89$, $p = 0.38$; $Z = 0.63$, $p = 0.53$; Table 1.3, Figure 1.1C-D). Increased discarding tended to be associated with increased annual local prey availability but the effect was not statistically significant in any of the three adaptive discard models ($Z = 0.56$, $p = 0.56$; $Z = 0.75$, $p = 0.46$; $Z = -1.15$, $p = 0.25$; Figure 1.1B). The base adaptive discard model indicated that the probability of discarding increased by about 1.5 times for each additional 5,000 live fish available on that day (Figure 1.1C). With all other variables held constant, as daily prey availability reached a maximum of 7,572 fish the probability of discard reached about 30% for both males and females.

Date was a significant predictor of discard behavior in both the base adaptive discard model and the base plus length adaptive discard model (i.e., more prevalent later in the season; Table 1.3, Figure 1.1A). Date was not statistically significant in the full adaptive discard model ($Z = -1.63$, $p = 0.10$), possibly due to the truncated range of values for this covariate in this subset of data. Regardless, trends were maintained across the three adaptive discard models; occurrence of discards increased throughout most of the salmon run but was less common at the very end of the run than in the middle (Figure 1.1A). Holding all other variables constant in the base model, the probability of discarding female and male fish increased by 7.4% and 8.2%, respectively from July 19 to Aug 18.

Prey attributes also significantly predicted discarding behavior (Table 1.3). Males were more often discarded than females in all three adaptive discard models ($Z = 7.82$, $p < 0.001$; $Z = 18.85$, $p < 0.001$; $Z = 5.24$, $p < 0.001$; Table 1.3). In addition, in the base plus length adaptive

discard model, larger fish were less often discarded than smaller fish (Z = -6.64, $p < 0.001$), but larger females were less likely to be discarded than larger males (Figure 1.1E). This pattern was not detected in the full adaptive discard model (Z = 0.11, p = 0.91), possibly due to overrepresentation of larger individuals in the subset of data used for this model. We typically tagged fish at the creek mouth on just one day at the beginning of the season, so this subset was somewhat biased towards early entering salmon that tend to be larger than those arriving later (Doctor and Quinn 2009; Quinn 2018). In-stream life was particularly influential in driving patterns of discard (Z = 5.77, $p < 0.001$). Females that had recently entered the stream had a very low probability of discard, but this probability increased after 2-3 days in the stream (Figure 1.1F).

Classification tree analysis revealed two factors that drove consumption of specific salmon tissues: primarily the fish's sex ($p < 0.001$), and secondarily its in-stream life for both sexes ($p < 0.001$; Figure 1.2). Testing tree performance on new data resulted in a misclassification rate of 20.8%. Randomly permuting fish sex and in-stream life resulted in 15.3% and 3.4% information losses, respectively. Bears were most likely to consume belly tissue from females within the first two days in the stream, but the probability of belly consumption in females decreased from 0.51 to 0.18 after 2 days (Figure 1.2). Bears were much more likely to consume belly tissue in females rather than males, and hump tissue was more likely to be consumed in males than females. Consumption of brain and body tissues of males was more likely in recently arrived fish ($\leq$ 4 days) than those in the stream > 4 days.

DISCUSSION

The patterns of sockeye salmon discarded by brown bears without consumption of tissue were most consistent with adaptive discard models rather than surplus killing or null models. This data-driven conclusion is consistent with observations by Frame (1974), who reported that bears appeared to decide whether to keep or discard a fish by simply holding the fish in its mouth. By implication, a bear may be able to quickly detect prey quality from taste, smell, or other sense. Presumably, bears can also visually distinguish the condition of salmon to some degree, as fish that are very near senescence often have frayed fins, a loss of pigmentation, and fungus covering the body. In fast, deep stream systems where bears may not be able to visually evaluate the condition of a fish, killing the fish prior to the decision of whether to consume or reject a fish is almost certainly required. However, in the shallow waters of Hansen Creek, such an assessment is likely to be possible without capture. Thus, though more easily captured due to low energy reserves (Gende et al. 2004), very low quality fish may be rejected prior to capture based on visual cues. In contrast, the condition of fish that have more recently arrived in the stream and their spawning status may be more difficult for bears to discern, as coloration can remain robust just after spawning and while salmon guard redds from other fish, and this lack of visual information may require a bear to capture and kill a fish to determine its quality before deciding to eat or discard the fish. Through a combination of selection prior to capture, and discarding of captured fish of low quality or missing preferred body tissues, bears may thus search for the best fish to consume. Choice fish may be those that are not only of high energetic value, but also require a short handling time (i.e., are most profitable).

Following expectations from optimal foraging theory and energy-maximizing foraging strategies, prey discarding increased with daily prey availability. This mirrors observed negative

relationships between biomass consumed and prey density in previous work (Gende et al. 2001), and indicates that bears are choosier under high prey abundance. No trend in discarding behavior was observed with neighborhood prey availability (Figure 1.1D), but this may be a product of differences in run timing within the stream neighborhood. Salmon runs to Happy Creek are slightly but significantly earlier than those in Hansen Creek, which in turn are earlier than runs returning to Eagle Creek (Lin et al. 2008).

Timing within the salmon run was a strong predictor of discarding in two of the three optimal consumption models, likely representing bear hunger as Andersson and Reynolds (2018) suggested to explain patterns of selective consumption over time elsewhere. Bears may be hungriest at the beginning of the season with the onset of hyperphagia and an associated increase in appetite (Nelson 1980; Nelson et al. 1983); in our data this may correspond with the low proportion of discards observed in the first quarter of the season except for the first two days (Figure 1.1A). As bears begin meeting required nutritional thresholds and satiation increases as the run progresses, the energy provided per unit of handling time associated with each fish (i.e., its profitability) may change such that bears are more selective, and so the proportion of discarded fish rises over time. At the very end of the season, when again very few salmon are available, we observed less selectivity and fewer discarded fish. The unexpectedly high probability of discard in the first two days of the season may be a product of unavoidable sampling error. Occasionally bears consume close to an entire carcass, including the jaw but leaving behind only pyloric caeca, an apparently distasteful part of the digestive system. In 1998 and 2015, we counted these pieces of tissue daily and found more pyloric caeca remnants along the banks during this early period as well as late in the season (TP Quinn, unpublished data), suggesting that bears may completely consume fish early on, and may only start leaving salmon

jaws and tissues that we could observe at a later date. Thus, our data likely overestimate the probability of discard at the beginning of the season. Even so, these patterns may also reflect a response to perceived prey availability in addition to actual prey availability, since at the beginning of the run when peak salmon abundance has yet to come, future prey availability may be perceived as high. Bears may have learned the phenology of salmon runs in each stream, which is very regular from year to year, and may be more selective at the very beginning of the run.

In addition to the extrinsic factors of prey availability and date, intrinsic prey attributes also influenced the decision to discard. More frequent discard of smaller male and female fish may be a product of the smaller energetic yields offered by smaller fish, combined with increased effort and handling time required to extract tissue. The costs of tissue extraction in relation to prey size may be particularly relevant in brain consumption, as the ratio of brain tissue to cartilage may be positively correlated with fish body size (Gende et al. 2001). Bears selectively kill larger fish (Quinn and Kinnison 1999; Ruggerone et al. 2000; Quinn et al. 2001; Andersson and Reynolds 2017), which may be a product of increased visibility, accessibility, or ease of capture, or this pattern may reflect preferences for larger fish, as the current results suggest. The probability of discard in females drops off more dramatically as size increases than in males, probably because number and volume of eggs are positively correlated with female body size (Quinn et al. 1995). By implication, bears may seek female fish with the most eggs and place high value on salmon eggs compared to other tissues.

The lower probability of discarding newly-arrived females than males (Figure 1.1F), as well as the increased probability of belly consumption in newly arrived females compared to females that had been in the stream longer (Figure 1.2), also suggests that bears may seek ripe

females. Similarly, Reimchen (2000) and Gende et al. (2001) observed that bears occasionally released spawned-out females after capture, but never ripe females, and that ripe fish were consumed to a greater extent than spawned-out fish. Further, Andersson and Reynolds (2018) also observed a greater degree of consumption of female carcasses than male carcasses. In some systems, bears have been observed transporting newly arrived fish into the forest for consumption (Reimchen 1994; Reimchen 2000), and preferentially killing salmon that have spent fewer days in the stream when conditions allow (Gende et al. 2004), indicating that newly-arrived fish are especially valuable. The high value placed on newly-arrived fish is particularly apparent when we consider that these fish are more vigorous, and may evade capture more readily than those nearer to senescence, and so bears presumably expend more time and effort in capturing high-energy fish rather than pursuing easily captured senescing fish. Females in the stream > 6 days were more likely to be discarded than males of the same in-stream life, suggesting that the energetic benefits offered by female fish drop off more dramatically for females than males, as would be expected if females spawn within a few days of arriving in the stream. Thus, the increased probability of discard with increasing in-stream life is likely due to a combination of gonad presence or absence in females and the deterioration of body tissues and decline in energetic content as both male and female fish reach senescence (Ando et al. 1985; Hendry and Berg 1999).

Only prey-specific attributes (i.e., sex and condition) influenced which tissues were consumed, of the fish that were not discarded (Figure 1.2), and fish sex was about four times as important as in-stream life in determining tissue-specific consumption. This suggests that prey quality and nutrition offered by each tissue type were of primary importance in foraging decisions made on a per-bite basis. The decreased probability of belly consumption in females

and brain consumption in males of longer in-stream lives likely reflects decreases in lipid content with increasing time spent on the spawning grounds (Figure 1.2). This is most obvious in female belly tissue, where lipid content declines precipitously with loss of eggs at spawning 3-4 days after entering a stream (McPhee and Quinn 1998). Thus, when targeting brain or belly tissue, it seems likely that bears are foraging primarily for lipids. Harbor seals foraging on salmon in Iliamna Lake, Alaska follow similar patterns of partial consumption of female belly tissue (Hauser et al. 2008), indicating that selective consumption of energy-rich body tissues may be common across salmon predators.

In contrast to the patterns in females, bear consumption of male hump tissue did not decline substantially with increasing in-stream life (Figure 1.2), despite the decrease in muscle lipid content observed as fish approach senescence (Ando et al. 1985; Hatano et al. 1995; Hendry and Berg 1999), perhaps because bears may bite male fish by the hump to capture it and begin consumption from this point. Additionally, protein content of muscle tissue remains comparable over spawning (Ando et al. 1985; Hatano et al. 1995; Hendry and Berg 1999), suggesting that bears may forage for protein, rather than lipid, when targeting hump tissue. Maintenance energy metabolism in captive bears is minimized at intermediate values of dietary protein (i.e., 35% dietary protein; Rode and Robbins 2000; Rode et al. 2001, Robbins et al. 2007), and so diet mixing by selecting various salmon body tissues as well as consuming non-salmon foods is likely to be energetically favorable. Differences in macronutrient content (e.g., lipid, protein) in fish tissues appear to explain some of these patterns, but differences in micronutrient content (e.g., amino acids, vitamins) of fish tissues may also provide an alternative or additional explanation. For example, the muscle tissue of both male and female sockeye salmon decreases

in histidine concentration and female tissue increases in creatine concentration over the course of the spawning migration (Wood 1958).

Despite the wide range of alternative factors that may contribute to variability in bear foraging decisions, the most parsimonious adaptive discard model still explained 24.4% of the variation in observations of discarded versus consumed carcasses. Though not the majority of the overall variability, our analysis excluded factors that may amount to major considerations for foragers, namely nutritional requirements dictated by the age and size of bears as well as individuality in bear behavior. That the present analysis explained nearly a quarter of discarding decisions suggests that salmon-related factors alone play a substantial role in bear foraging, and supports the hypothesis that bear foraging decisions integrate considerations from optimal foraging theory. Importantly, the random effect of year explained a sizeable portion of variability, accounting for the difference between the marginal and conditional pseudo-R^2 values (Table 1.2), indicating that non-salmon factors that vary annually are also influential. Including the effect of year in evaluating overall model performance is appropriate given the natural variation in bear abundance and alternative prey that occurs on an annual scale. Evaluating patterns of partial consumption with a classification tree revealed a misclassification rate of 20.8%, indicating that the majority of partial consumption decisions (79.2%) could be adequately predicted by our adaptive foraging covariates, and further supporting bear consumption of salmon as a product of optimal foraging.

In coastal systems where bears and salmon are present, understanding the mechanisms that drive prey discard and the extent of carcass consumption is important for predictions of bear-mediated nutrient transport. The nutrients delivered to terrestrial ecosystems through the discard of entire salmon carcasses and remnants of partially consumed fish are highly influential

(Gende et al. 2002; Helfield and Naiman 2006), and increasing attention has been given to quantifying the biomass of salmon transported by bears and the ecological effects of this activity (Hilderbrand et al. 1999a; Gende et al. 2002; Gende et al. 2004; Holtgrieve et al. 2009; Quinn et al. 2009). The strong support for discard and partial consumption decisions based on optimal foraging theory shown in the present study suggests that predicting consumption patterns, and thus the remains delivered to the broader ecosystem, can be approached using these relationships predicted from an optimal foraging theory framework.

Our findings add to our knowledge of the selectivity of bear foraging, and suggest that selectivity may manifest itself through both discarding behavior and partial prey consumption. To our knowledge, no other field studies have specifically addressed optimal foraging strategies in bears, and few field studies have demonstrated optimal foraging of other large carnivores (but see Scheel 1993; Hernández et al. 2002; Holmes and Laundré 2006; Vucetich et al. 2012; Elbroch et al. 2015). Furthermore, this study addresses and directly tests for the presence of non-adaptive surplus killing behavior, which until this point has remained a phenomenon documented largely through anecdotal observations. Though not observed here, surplus killing remains a widespread but poorly understood phenomenon, and additional data-driven studies are needed to uncover motivation for this behavior in other systems.

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Table 1.1 Expected results of sockeye salmon consumption by brown bears under hypothesized adaptive discard (AD) and surplus killing (SK) scenarios. If adaptive discard is occurring, we expected an adaptive discard model containing prey availability, prey quality, and date as covariates to be the most parsimonious model compared to a surplus killing or null model. If surplus killing triggered by prey superabundance or at random is occurring, we expected that a surplus killing model with prey availability as the sole covariate or a null model would be the most parsimonious model. If both adaptive discard and surplus killing triggered by prey superabundance is occurring, the most parsimonious model should depend on prey availability conditions. If both adaptive discard and surplus killing at random is occurring, the adaptive discard and null models should be equally parsimonious and will outperform the surplus killing model with prey availability as a covariate.

Bear Behavior	Most Parsimonious Model	Important Covariates[a]
AD	Adaptive Discard Model	Prey Availability, Prey Quality, Date
SK (triggered by prey abundance)	Surplus Killing Model	Prey Availability
SK (at random)	Null Model	None
SK (both triggered by prey abundance and at random)	Surplus Killing and Null Models	Prey Availability
AD **and** SK (triggered by prey abundance)	Adaptive Discard Model (in low prey avail.); Surplus Killing Model (in high prey avail.)	Prey Availability, Prey Quality, Date (in low prey avail.); Prey Availability (in high prey avail.)
AD **and** SK (at random)	Adaptive Discard and Null Models	Prey Availability, Prey Quality, Date

[a] Prey availability may include availability on a daily local, annual local, and annual neighborhood scale. Prey quality may include attributes such as sex, size, and condition.

Table 1.2 Comparisons of adaptive discard and surplus killing generalized linear mixed models.

	k[a]	ΔAIC[b]	Marginal R^{2} [c]	Conditional R^{2} [d]
MODEL COMPARISON 1 (n=65,679)				
Adaptive Discard (Base) (*Date + Date² + Date³ + Annual availability + Daily availability + Neighborhood availability + Sex*)	9	0.0	3.3%	18.0%
Surplus Killing (*Daily availability*)	3	433.1	1.0%	15.8%
Null (*Constant*)	2	649.4	0.0%	16.7%
MODEL COMPARISON 2 (n=20,515)				
Adaptive Discard (Base plus Length) (*Date + Date² + Date³ + Annual availability + Daily availability + Neighborhood availability + Sex + Length + Sex:Length*)	11	0.0	7.3%	23.2%
Surplus Killing (*Daily availability*)	3	831.4	0.7%	17.6%
Null (*Constant*)	2	900.5	0.0%	18.9%
MODEL COMPARISON 3 (n=985)				
Adaptive Discard (Full) (*Date + Annual availability + Daily availability + Neighborhood availability + Sex + Length + In-stream Life + Sex:Length + Sex:In-stream Life*)	11	0.0	16.5%	24.7%
Surplus Killing (*Daily availability*)	3	46.7	5.0%	16.7%
Null (*Constant*)	2	62.9	0.0%	17.0%

Fixed factors included in each model are listed in italics. Date² and Date³ indicate higher order terms for this covariate. All models included year as a random variable.

[a] Number of model parameters, including intercept and year as a random effect.

[b] The model with the lowest Akaike's Information Criterion (AIC) is considered the most parsimonious fit to the data; ΔAIC is the difference in AIC value compared to the top model. Models with a ΔAIC > 7 are considered to have essentially no support.

[c] Amount of variation explained by fixed effects.

[d] Amount of variation explained by both fixed and random effects.

Table 1.3 Estimated coefficients and odds ratios for each adaptive discard model using data from 1997-2017 (2014 omitted).

	Regression coefficient	Odds ratio ± standard error[a]	Z-statistic[b]	p-value
Base Model (n=65,679)				
Intercept	-1.73	0.17 ± 0.04	-8.32	**<0.001**
Date	-1.45	0.24 ± 0.07	-4.61	**<0.001**
Date^2	2.94	18.84 ± 6.88	8.05	**<0.001**
Date^3	-1.19	0.31 ± 0.04	-8.73	**<0.001**
Daily Prey Availability	0.15	1.17 ± 0.02	8.00	**<0.001**
Annual Prey Availability	0.23	1.26 ± 0.53	0.56	0.56
Neighborhood Prey Availability	-0.05	0.95 ± 0.31	-0.15	0.88
Sex = Male	0.16	1.17 ± 0.02	7.82	**<0.001**
Base Plus Length Model (n=20,515)				
Intercept	-1.44	0.24 ± 0.10	-3.56	**0.004**
Date	-0.66	0.52 ± 0.25	-1.39	0.17
Date^2	1.19	3.27 ± 1.74	2.23	**0.03**
Date^3	-0.23	0.80 ± 0.15	-1.24	0.21
Daily Prey Availability	0.16	1.17 ± 0.04	4.74	**<0.001**
Annual Prey Availability	0.42	1.53 ± 0.87	0.75	0.46
Neighborhood Prey Availability	-0.50	0.61 ± 0.34	-0.89	0.38
Sex = Male	0.61	1.83 ± 0.06	18.85	**<0.001**
Length	-0.18	0.84 ± 0.02	-6.64	**<0.001**
Sex:Length	0.09	1.10 ± 0.04	2.85	**0.004**
Full Model (n=985)				
Intercept	-2.44	0.09 ± 0.02	-8.83	**<0.001**
Date	-0.19	0.83 ± 0.10	-1.63	0.10
Daily Prey Availability	0.55	1.73 ± 0.22	4.35	**<0.001**
Annual Prey Availability	-0.25	0.78 ± 0.17	-1.15	0.25
Neighborhood Prey Availability	0.13	1.14 ± 0.23	0.63	0.53
Sex = Male	1.43	4.17 ± 1.14	5.24	**<0.001**
Length	0.02	1.02 ± 0.15	0.11	0.91
In-stream Life	1.32	3.75 ± 0.86	5.77	**<0.001**
Sex:Length	-0.12	0.89 ± 0.15	-0.71	0.48
Sex:In-stream Life	-0.93	0.40 ± 0.10	-3.62	**<0.001**

[a] Continuous variables were centered and scaled by standard deviation, so interpretation of the odds ratio is the difference in odds of being discarded with an increase in 1 standard deviation.
[b] Z-statistics consider the statistical significance of each variable last-entry.

Table 1.4 Estimated coefficients and odds ratios for each adaptive discard model using data from 1997-2017 (2014 included).

	Regression coefficient	Odds ratio ± standard error[a]	Z-statistic[b]	p-value
Base Model (n=67,234)				
Intercept	-1.86	0.16 ± 0.03	-9.51	**<0.001**
Date	-1.59	0.20 ± 0.06	-5.09	**<0.001**
$Date^2$	3.30	27.07 ± 10.02	8.91	**<0.001**
$Date^3$	-1.36	0.26 ± 0.04	-9.89	**<0.001**
Daily Prey Availability	0.07	1.07 ± 0.02	3.90	**<0.001**
Annual Prey Availability	-0.09	0.91 ± 0.30	-0.28	0.78
Neighborhood Prey Availability	0.03	1.04 ± 0.35	0.10	0.92
Sex = Male	0.15	1.16 ± 0.02	7.51	**<0.001**
Base Plus Length Model (n=20,679)				
Intercept	-1.42	0.24 ± 0.06	-5.99	**<0.001**
Date	-0.75	0.47 ± 0.22	-1.60	0.11
$Date^2$	1.29	3.64 ± 1.89	2.50	**0.01**
$Date^3$	-0.27	0.76 ± 0.14	-1.51	0.13
Daily Prey Availability	0.11	1.11 ± 0.03	4.32	**<0.001**
Annual Prey Availability	0.11	1.12 ± 0.30	0.42	0.68
Neighborhood Prey Availability	-0.20	0.82 ± 0.23	-0.73	0.47
Sex = Male	0.60	1.82 ± 0.06	18.70	**<0.001**
Length	-0.18	0.84 ± 0.02	-6.73	**<0.001**
Sex:Length	0.09	1.10 ± 0.03	2.93	**0.003**

[a] Continuous variables were centered and scaled by standard deviation, so interpretation of the odds ratio is the difference in odds of being discarded with an increase in 1 standard deviation.
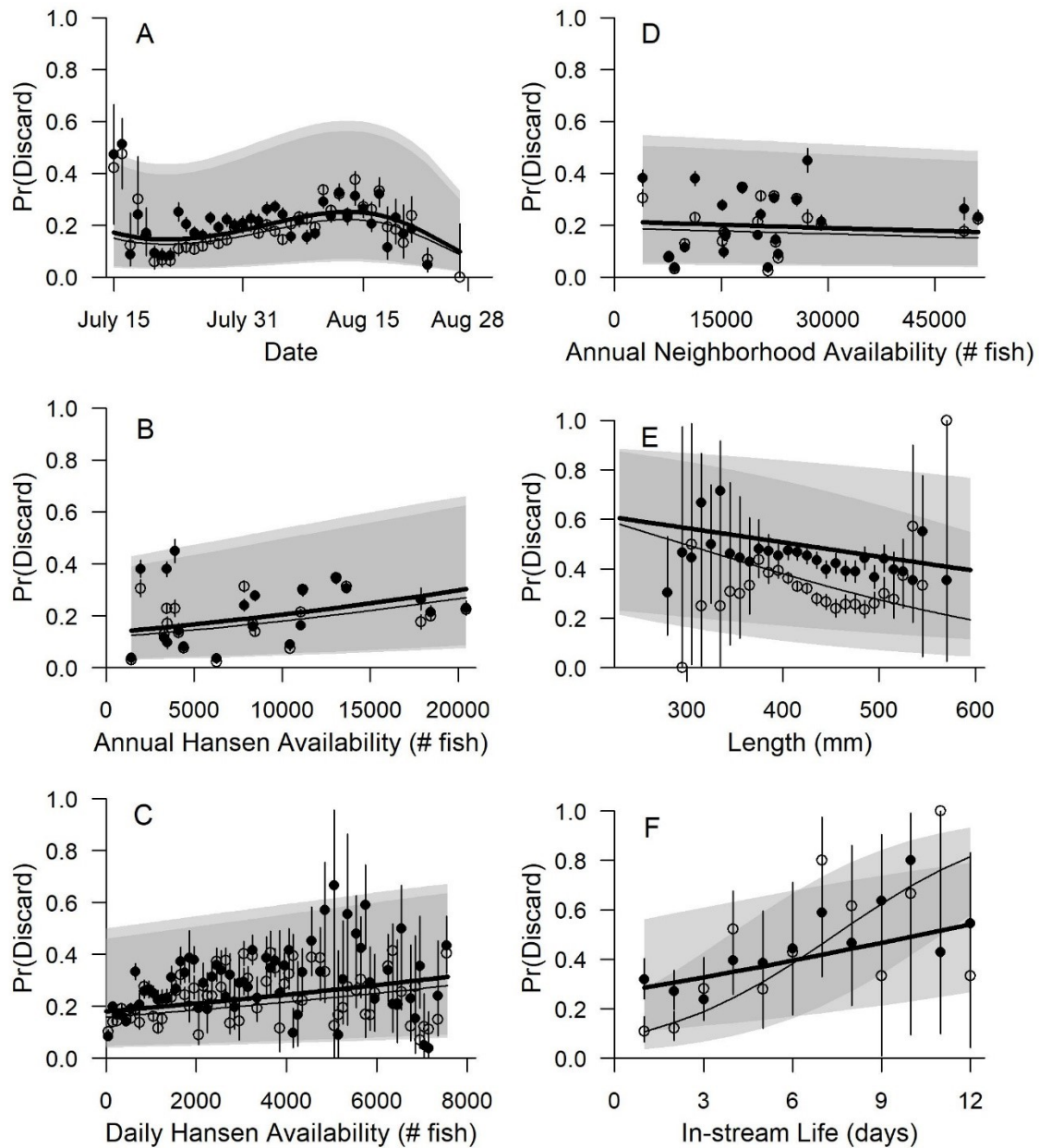[b] Z-statistics consider the statistical significance of each variable last-entry.

Figure 1.1 Relationships between probability of prey discard and each parameter explored. To show the most robust results, the date (A), annual prey availability (B), daily prey availability (C), and neighborhood prey availability (D) plots were derived from the base adaptive discard model (n = 65,679), whereas the fish length (E) plot was derived from the base plus length adaptive discard model (n = 20,515) and the in-stream life (F) plot was derived from the full adaptive discard model (n = 985). Dots indicate the observed proportion of discards for male (solid) and female (open) fish, calculated by binning observations by each unique x-value in the case of date, annual prey availability, neighborhood prey availability, and in-stream life, and binning daily prey availability into bins of 100 fish and fish length into bins of 10 millimeters. Vertical segments display 95% confidence intervals for the data. Thick and thin lines indicate the weighted probability of discard for male and female fish respectively. Predicted probabilities for each variable were calculated by holding all other variables at their average value, and may be interpreted as the predicted probability in an average year. Shaded regions indicate the 95% confidence interval range based on annual variability.
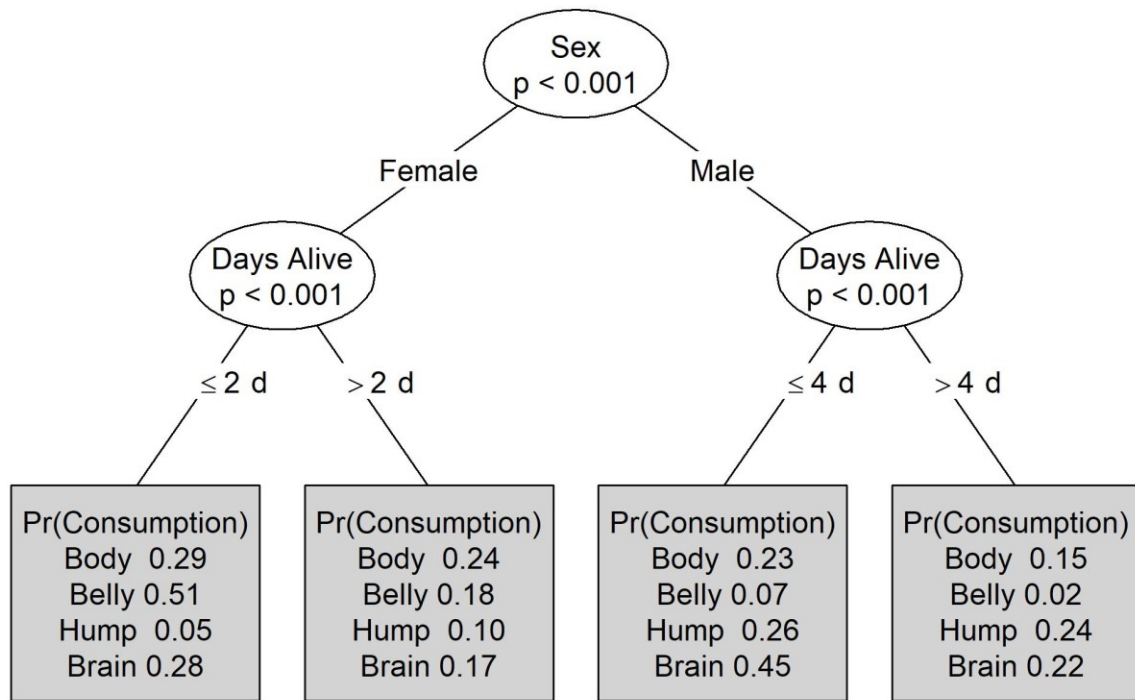
Figure 1.2 Classification tree predicting the probability of consuming body, belly, hump, and brain tissue for 1,007 fish at Hansen Creek, Alaska. Ovals represent variables creating significant splits in the data, with the *p*-value for the split listed below the variable name. Splitting rules are found on each branch of the tree, and grey boxes at the terminal nodes list the predicted probabilities of consumption, which are not mutually exclusive.

CHAPTER TWO

Managing salmon for wildlife: do fisheries limit salmon consumption by bears in small streams?

ABSTRACT

Ecosystem-based management requires consideration of overlapping resource use between humans and other consumers. Pacific salmon are an important resource for both fisheries and coastal brown bears (*Ursus arctos*), as salmon consumption has been positively linked to bear density, size, and reproductive rate. Using 16 to 22 years of empirical data in 4 different small salmon-bearing systems in southwestern Alaska, we explored the relationship between sockeye salmon (*Oncorhynchus nerka*) availability and consumption by bears. We found a negative relationship between the annual biomass of salmon available to bears and the fraction of biomass consumed per fish, and a saturating relationship between salmon availability and the total annual biomass of salmon consumed by bears. Under modeled scenarios, bear consumption of salmon was predicted to increase only with dramatic (on the order of 50% – 100%) increases in prey availability. Even such large increases in salmon abundance were estimated to produce relatively modest increases in *per capita* salmon consumption by bears (2.4 – 4.5 kg/bear/day, 15 – 59% of the estimated daily maximum *per capita* intake), in part because bears did not consume salmon entirely, especially when salmon were most available. Thus, while bears catching salmon in small streams may be limited by salmon harvest in some years, current management of the systems we studied is sufficient for bear populations to reach maximum salmon consumption every 2-4 years. Consequently, allocating more salmon for brown bear conservation would be unlikely to result in an ecologically significant response in these systems.

INTRODUCTION

Ecosystem-based management has received increased attention in recent decades, particularly where human activity competes with other organisms for resources such as in fisheries management (Pikitch et al. 2004; Arkema et al. 2006; Piccolo et al. 2009). The harvest of fishes is often of substantial economic and nutritional value to humans, and many fisheries are managed for sustainable long-term yield of the target species. Effort has been made to reduce the direct effects of harvest on non-target species (e.g., bycatch reduction), but harvest may also indirectly affect both predators and prey of the organism being captured. This problem has been recognized in studies evaluating competition between harvest of fishes and marine mammals (e.g., Trites et al. 1997) and between krill and seabirds (e.g., Karpouzi et al. 2007; Sydeman et al. 2017). Consequently, a multi-species ecosystem-based approach is needed to fully evaluate the effects of fisheries.

Ecosystem-based management is especially relevant to Pacific salmon (*Oncorhynchus spp.*), given the economic, social, and cultural importance of salmon to humans, and also the ecological importance of salmon to marine, freshwater, and terrestrial ecosystems (Cederholm et al. 1999; Naiman et al. 2002). In the ocean, salmon dominate the diet of protected southern resident killer whales (*Orcinus orca*; Ford & Ellis 2006; Ford et al. 2010), and after returning from the ocean to reproduce in fresh water, salmon also provide food for freshwater and terrestrial consumers (e.g., fishes, bears, eagles: Schindler et al. 2003; Levi et al. 2015). Salmon that avoid predation senesce and die after spawning, releasing nutrients to freshwater and terrestrial habitats (Cederholm et al. 1999; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Recognizing the importance of salmon across ecosystems, there have been calls for

managing salmon fisheries to meet these needs (Michael, 1998; Hilderbrand et al. 2004; Piccolo et al. 2009; Darimont et al. 2010; Williams et al. 2011; Peirce et al. 2013).

Among terrestrial predators of salmon, brown (*Ursus arctos*) and black (*U. americanus*) bears rely heavily on salmon in coastal regions (Reimchen 2000, 2017; Hilderbrand et al. 2004). The majority of annual bear diet can be composed of salmon (Hilderbrand et al. 1999a, 1999b; Mowat & Heard 2006), and salmon consumption is positively correlated with body size and population productivity (Hilderbrand et al. 1999b). Fisheries capture salmon before they reach streams for spawning, thereby reducing prey for bears, other predators, and scavengers. Fisheries are managed so that the number of salmon reaching the spawning grounds is far below levels in the absence of harvest, resulting in long term maximum sustainable yield (Ricker 1958). Great effort is devoted to determine the optimal levels of escapement for sustainable fisheries (i.e., number of salmon escaping fisheries to spawn), but it is unclear how to integrate ecosystem benefits into this calculation.

Given the positive relationship between salmon consumption and bear population density, studies have suggested that low salmon availability may limit bear populations (Boulanger et al. 2004), and increasing salmon spawning abundance would increase consumption by bears (Van Daele et al. 2013) and thus bear abundance (Levi et al. 2012). These conclusions may be reasonable if salmon are limiting and bears completely consume all fish they capture, but bears often eat only a fraction of each salmon killed (Reimchen 2000; Gende et al. 2001; Andersson & Reynolds 2018), suggesting that salmon may not always be limiting. Furthermore, bears consume less biomass from each fish when many are available, and may even discard entire carcasses uneaten (Gende et al. 2001; Lincoln & Quinn 2019). Thus, increasing salmon availability by decreasing harvest may not substantially increase the overall salmon

biomass consumed, but instead may result in more fish killed but less tissue consumed per fish. To date, however, no study has evaluated this possibility using empirical data.

Our objective was to use ca. 2 decades of detailed records on salmon abundance and predation by brown bears to explore the relationship between salmon availability and consumption by bears in 4 small systems in southwestern Alaska. Given the prevalence of partially consumed salmon carcasses in our study systems (Gende et al. 2001; Lincoln & Quinn 2019), we hypothesized that in some years, bears may already be consuming close to some maximum amount, making these systems "saturated" with fish. Accordingly, we predicted that the average proportion of each fish consumed would decrease with increasing annual salmon abundance, and that salmon consumption by bears over the entire salmon run would saturate with salmon availability. We also expected that *per capita* consumption of salmon by bears would increase and then plateau with salmon availability. Having determined these empirical relationships between salmon abundance and consumption, we then considered the extent to which hypothetical increases in prey availability would influence salmon consumption by bears. Using data on the relationship between salmon consumption and availability, we tested the null hypothesis that an increase in fish abundance (i.e., from a reduction in fishing) would not significantly affect salmon consumption.

METHODS

Study Sites

For 16 to 22 years between 1997 and 2018 we collected data from four sites in southwestern Alaska where shallow water and high salmon densities facilitate predation by bears. Sockeye salmon (*O. nerka*) are the only species of Pacific salmon or other large fish at

these sites. Three sites are in the Wood River watershed and one in the Lake Iliamna watershed. The Wood River sites are: Hansen Creek (tributary to Lake Aleknagik), and A and C creeks (tributaries to Little Togiak Lake). Hansen Creek is a small, shallow stream (2.1 km long, 3.8 m wide, 9.8 cm mean depth) supporting an average salmon run of 9,567 fish after removals by the fishery over the period of record. A and C creeks are similar in depth to Hansen Creek but substantially shorter (A Creek: 300 m; C Creek: 600 m) and narrower (1.4 and 2.1 m wide, respectively). Consequently, they support fewer salmon each year on average (A Creek: 457 fish; C Creek: 438 fish). A and C creeks are < 1 km from each other but the nearest other stream is several km away so they comprise a somewhat isolated foraging neighborhood. The Iliamna Lake site comprises a series of 8 shallow, spring-fed ponds and six small creeks near the village of Pedro Bay. These ponds range in area from 165 to 1820 m^2 and in average depth from 13.5 to 41.6 cm, and the creeks are 60 to 188 m^2 in area and 10.3 to 23.0 cm deep (Quinn & Kinnison 1999). Other ponds nearby also support sockeye salmon but data collection was inconsistent over the study period. Fish abundances are correlated between ponds within years (Quinn et al. 2012) and the data presented here represent a large and consistent fraction of the total abundance and consumption from the entire pond complex.

Carcass Surveys

We surveyed Hansen Creek daily over the sockeye salmon run from 1997-2018, A and C creeks daily from 2003-2018, and the Pedro Bay ponds every 3-4 days from 1999-2018. We examined every carcass encountered, and evaluated bear-killed fish for consumption. At A and C creeks, the fish's sex, body length (mid-eye to hypural plate), and percentage consumed or the body parts consumed by bears (classified as body, brain, belly, hump, and/or skin tissue) were recorded. At Hansen Creek and the Pedro Bay ponds, we recorded sex and the body parts

consumed by bears for every bear-killed fish, and body length for a subset (Quinn & Kinnison 1999; Lincoln & Quinn 2019). We then tossed carcasses into the woods to prevent double counting on subsequent surveys. In total, we examined 251,448 fish from Hansen Creek, 61,470 fish from the Pedro Bay ponds, 5,757 fish from A Creek, and 6,510 fish from C Creek. In 2014, the annual abundance of fish at Hansen Creek was three times higher than in any other year, and an unusual, large-scale pre-spawning mortality event occurred (Tillotson & Quinn 2017). The many high quality (i.e., ripe) carcasses available for scavenging after being thrown off-site likely influenced bear consumption of salmon observable to us along the creek, so we excluded this year from our analyses.

Salmon Biomass Consumption and Availability

We used site- and sex-specific relationships between fish length and mass to determine each fish's mass prior to bear consumption. We assigned unmeasured carcasses a random length from site- and sex-specific length distributions, and estimated weight accordingly. At A and C creeks, percentage consumed was observed, but for Hansen Creek and the Pedro Bay ponds we estimated the percentage of tissue consumed from each fish using previous observations of the average percentage of biomass eaten under each consumption pattern at these sites: body (67%), belly (28%), brain (2%), hump (4.8%), or skin (2%; Gende et al. 2001). We summed across all body parts consumed (e.g., brain and belly consumed = 2% + 28%) and multiplied the percentage consumed by the estimated mass to get the biomass consumed from each fish.

In addition to salmon that we find partially consumed in the water and along the bank, bears transport some into the forest beyond our survey range (Quinn et al. 2009). To account for these carcasses in our consumption estimates, we used stream-specific average carcass transport rates determined from tagging experiments (Quinn et al. 2009); transport rates were 28.7% of all

fish at Hansen Creek, 32.9% at the Pedro Bay ponds, 42.6% at A Creek, and 46.5% at C Creek. Additionally, on the last survey date of each year at Hansen Creek and the Pedro Bay ponds some live fish remained, and so we used an index of bear predation, detailed and validated in Quinn et al. (2001), to estimate how many would have been killed by bears in the final days.

The total salmon biomass consumed by bears each season was the sum over all fish in that year. We calculated the biomass available each year by summing the estimated mass of all dead fish and also those alive on the last survey date, which were assigned a random length to estimate weight, as outlined above. To determine the relationship between salmon biomass availability and consumption by bears, we competed linear, saturating, and sigmoidal models fit to the data at each site. The model with the lowest Akaike Information Criterion score corrected for small sample size (AICc) was considered to be the best fitting model, though models within 2 units of AICc were considered to fit equally well (Burnham & Anderson 2004). Bear consumption of salmon must be zero when salmon are absent, so we set intercepts at zero for all models. We conducted all analyses in R version 3.4.1 (R Core Development Team 2017).

Bear Abundance and *Per Capita* Salmon Consumption

In 2013-2017, we deployed hair snares at two locations along Hansen Creek; strands of barbed wire spanned the creek at a height from substrate of 50-55 cm, snagging hair from passing bears (Quinn et al. 2014). We checked hair snares every other day from mid-July through late August each year, and distinguished the bears using DNA microsatellites (Wirsing et al. 2018). For each year we generated a genetic capture-mark-recapture population estimate (Wirsing et al. 2018), and then estimated salmon consumption per bear by dividing the biomass consumed by the estimated number of bears.

Fishery Management Scenarios

The Bristol Bay sockeye salmon fishery in Alaska is managed through escapement goals, whereby managers attempt to allow a specific number of fish to escape the fishery (Erickson et al. 2015). Considering this approach, we evaluated three scenarios that altered escapement, increasing the number of salmon available by 10%, 50%, or 100%, using the observed annual salmon returns. For example, in 2017, we estimated that the observed escapement of 14,928 kg of salmon in Hansen Creek would have become 16,421 kg with a 10% increase in escapement (observed * 1.1), 22,392 kg with a 50% increase (observed * 1.5), and 29,855 kg with a 100% increase (observed * 2.0). Fisheries are managed with great complexity, including the Bristol Bay sockeye salmon fishery where escapement goals are set as a range for each river. These goals are typically met and even exceeded (Cunningham et al. 2018); from 2005–2014 the average Wood River escapement was 1.7 million, above the 0.7–1.5 million escapement goal range. Since 2015, when the upper escapement goal was raised to 1.8 million, the average escapement has exceeded even this revised limit, and averaged 3.7 million. Given the uncertainty in salmon management, we present these scenarios as hypothetical thought experiments rather than specific management alternatives.

RESULTS

Effects of Salmon Abundance on Consumption

Bears killed an observed 1,048–9,286 salmon per year at Hansen Creek and, after accounting for salmon estimated to have been killed and transported off-site and those killed after surveys ended, we calculated that 1,585–13,364 were killed annually (mean: 7,892), representing 40–98% of the annual salmon run. Bear predation was numerically lower but

proportionally similar at the Pedro Bay ponds, where an observed 10–7,103 and estimated 12–8,230 fish were killed (mean: 2,157; 0.5–95% of the run). Predation was substantially lower at A and C creeks in terms of numbers of fish killed (45–544 and 93–815, mean: 265 and 309, respectively) but comparable in terms of percentage killed (31–99% and 45–96%).

The average proportion of each fish eaten tended to decrease as the biomass of fish available in that year increased at all 4 sites (Fig. 2.1A-D), although the relationship was statistically significant only at the Pedro Bay ponds ($p = 0.01$). The intercept of these linear relationships was smallest at Hansen Creek ($\beta_0 = 0.41$), revealing that at low salmon abundance, the proportion of each fish consumed was lower than at the 3 other sites. The relationship between per-fish consumption and fish availability varied more at A and C creeks than that at the other 2 systems (A Creek CV= 44.0, C Creek CV = 42.6, Hansen CV = 21.2, Pedro Bay ponds CV = 27.7).

Assessing the relationship between annual salmon biomass available and consumption by bears, model selection revealed that the best fits to the data were a sigmoidal relationship at Hansen Creek, and a linear relationship at the Pedro Bay ponds and A and C creeks (Table 2.1, Fig. 2.1E-H). However, there was also support for a saturating curve at Hansen Creek (ΔAICc = 1.6), the Pedro Bay ponds (ΔAICc = 0.1), and C Creek (ΔAICc = 1.8). Variability in the response tended to increase as available biomass increased, particularly at Hansen Creek and the Pedro Bay ponds. The consumption curves plateaued at 7,732 kg of salmon at Hansen Creek, 2,526 kg at the Pedro Bay ponds, and 940 kg at C Creek. At A Creek, no saturation point was reached, as the relationship was best described as linear. Using these plateaus as estimates of saturation, we calculated the biomass available at which predicted consumption would be $\geq$ 80% of the saturation value, and classified years below that threshold as salmon-limited. By this definition,

61.9% of the years were salmon limited at Hansen Creek (< 24,248 kg available), 75.0% were limited at the Pedro Bay ponds (< 10,236 kg available), and all 16 years were limited at A and C creeks (< 3,863 kg available at C Creek). However, in recent years, enough salmon returned to reach 80% of saturation under current management every 2-4 years at both Hansen Creek and the Pedro Bay ponds (Fig. 2.2).

Salmon biomass consumed *per capita* at Hansen Creek, estimated by dividing the total biomass consumed by the estimated number of bears present each year, tended to increase with the biomass of salmon available in 2013 and 2015-2017 (Fig. 2.3), but low statistical power (n = 4 years of data) was likely responsible for the lack of a significant relationship ($p = 0.10$). Consumption estimates ranged from 132 kg/bear in the 2013 salmon season to 1,747 kg/bear in 2017.

Estimated Effects of Increased Salmon Availability

We assessed how salmon consumption might vary with different management scenarios using our population-wide consumption responses at the 4 sites, during the years when salmon were apparently limiting. The sigmoidal relationship at Hansen Creek and saturating relationships at the Pedro Bay ponds and C Creek were used to predict consumption because they were either the best or equivalent to the best fitting model, and biologically the relationship cannot be linear. At A Creek, we used the best fitting linear relationship to predict consumption because the saturation point was unclear. Under a scenario of a 10% increase in escapement (i.e., modeled escapement = actual escapement *1.1), the average predicted change in salmon biomass consumed was not significantly different from zero at any of the four sites (Fig. 2.4). A 50% or 100% increase in escapement yielded a significant increase in consumption by bears at Hansen Creek (average = 1,500.9 kg or 2,289.9 kg), A Creek (average = 78.8 kg or 167.9 kg), and C

Creek (average = 78.3 kg or 149.8 kg), but not the Pedro Bay ponds (average = 333.3 kg with

100% increase; $p = 0.10$). When expressed as a percent increase rather than in biomass, it is clear

that increases in prey availability do not translate to an equivalent increase in consumption

(68.0% increase at Hansen Creek, 29.5% at Pedro Bay ponds, 89.1% at A Creek, and 61.3% at C

Creek when salmon are increased by 100%). Partial consumption reduces the benefits of

increased escapement; doubling the number of salmon would not double the biomass consumed.

DISCUSSION

Understanding the relationship between predators and a harvested prey species is needed

to predict how management strategies may affect predators of conservation concern such as

brown bears, and thus central in ecosystem-based management. Our results revealed that salmon

consumption by bear populations saturated at high salmon availability from a combination of

decreased consumption per fish (Fig. 2.1; Gende et al. 2001), and a plateau in the number of fish

killed (Quinn et al. 2003, 2017). In some years at Hansen Creek and the Pedro Bay ponds, bears

were estimated to have consumed a biomass of salmon that was near (within 20%) the maximum

biomass consumed, indicating that salmon were sufficiently available under current fishery

management in those years. We also observed partial consumption of salmon even when salmon

were scarce (Fig. 2.1A-D), indicating that salmon consumption in these systems was not severely

limited by fisheries, given that food-limited bears would be expected to completely consume all

prey captured.

While some years appeared to be salmon-limited at Hansen Creek and the Pedro Bay

ponds, as consumption was below the saturation value, salmon numbers deemed sufficient to

reach maximum consumption occurred every 2-4 years (Fig. 2.2). Female bears typically

reproduce every 2-3 years and may forgo embryo implantation if food is limited (Bunnell & Tait 1981), thus the cyclical pattern in salmon availability at Hansen Creek and the Pedro Bay ponds may allow bears foraging there to reproduce at close to their maximum rate. If so, then bear reproduction is not limited by salmon abundances in these systems. Furthermore, bears detected at Hansen Creek routinely moved between salmon-bearing streams within a season (Wirsing et al. 2018), and given the lack of complete synchrony in run size among streams (Rogers & Schindler 2008), salmon limitation at one stream does not imply salmon limitation in all neighboring streams. However, increasing salmon consumption in limiting years may have benefits beyond reproduction, including increased growth and survival (Hilderbrand et al. 1999b). Therefore, independent of influencing reproductive rates, reducing take by salmon fisheries to promote growth or survival might benefit bears.

Observed salmon abundances appeared to be much more limiting at the smaller A and C creeks, where bears always consumed < 80% of their maximum consumption value. However, the ecological importance of this limitation is likely insignificant; there are so few salmon in these streams that they are unlikely to ever feed bears in substantial amounts, even under extreme increases in escapement. The relationship between the proportion of each fish consumed and salmon availability at A and C creeks was more variable than elsewhere (Fig. 2.1C-D), perhaps because bears forage there irregularly while moving between streams with more salmon.

To significantly increase salmon consumption in years of scarcity, large increases in salmon escapement were required (≥ 50%), which would cause substantial losses to the fishery. Smaller, more socioeconomically realistic increases in escapement yielded only modest benefits in our scenarios. We estimated that there were 17-34 bears at Hansen Creek each year from 2013-2016 (Wirsing et al. 2018), so a bear population consuming a maximum of 7,732 kg of

salmon at Hansen Creek would consume 227-455 kg *per capita* annually, corresponding to an estimated maximum daily intake rate of 8-15 kg/bear/day over the 30-day season. Actual daily intake depends on bear size, sex, age, and social status (Van Daele et al. 2013), and so this value is likely to vary even more than we estimate. A 10% increase in Hansen Creek escapement yielded an annual average increase in consumption of 547 kg, which would increase *per capita* consumption by 16-32 kg/season or 0.5 – 1.1 kg/bear/day (< 0.5 fish/bear/day). This change in consumption represents a small fraction of estimated maximum daily intake (3-14%). By contrast, a 100% increase in escapement (doubled run size) increased consumption by 2,290 kg on average at Hansen Creek, which would increase *per capita* consumption by 67-135 kg/season or 2.2 – 4.5 kg/bear/day (1-2 fish/bear/day). This increase would correspond to a larger fraction of maximum daily intake (15-59%), but is still relatively small compared with the magnitude of the increase in salmon availability. We are hesitant to speculate about how these small increases in consumption might change the overall composition of bear diet, and thus its eventual effect on bear densities, because the dietary contribution of salmon in this system is unknown.

Harvest did not appear to limit bear consumption of salmon at the sites studied here, but our results are likely specific to small systems with dense salmon. All 4 sites have clear, shallow water and high salmon densities, and so fish capture is presumably easier than in larger systems with fewer salmon (Quinn et al. 2017). Indeed, Hansen Creek, with a combination of small size and high density, provides more salmon to bears than any other stream surveyed in the system under current fisheries management and salmon abundance, as determined by the number of bear kills (Quinn et al. 2003). While other streams may have larger abundances of salmon under current management (Rogers & Schindler 2003), predation rates are limited by stream habitat in addition to salmon abundance (Quinn et al. 2017). However, the relative importance of Hansen

Creek, and our conclusion that additional salmon would not substantially increase salmon consumption, might change if salmon abundances increased across all stream systems in the Wood River watershed, as predation rates may increase more substantially in response to higher salmon density in larger systems where deeper habitats may limit predation when salmon density is low. Nonetheless, small streams often comprise a large proportion of salmon habitat available for bear foraging, so relationships uncovered here should be considered when evaluating the potential effects of altering salmon management for wildlife.

Additionally, the abundance of salmon in neighboring streams likely influences the nature of predation and consumption relationships between bears and salmon. At the Pedro Bay ponds, a higher proportion of each fish was consumed at near-zero salmon availability than at Hansen Creek, perhaps reflecting the absence of neighboring systems with abundant salmon around Pedro Bay and the presence of other salmon streams near Hansen Creek. Because bears may forage along many streams over the course of the season (Barnes, Jr. 1990; Deacy et al. 2016; Wirsing et al. 2018), small increases in consumption resulting from increased escapements, if realized across multiple foraging streams, could provide an ecologically meaningful increase in salmon consumption. This scenario is plausible, but we were unable to investigate it in the current study.

Beyond alternative sources of the same species found in neighboring systems, the availability of alternative prey species should also be considered when applying these results to other systems. Recent work has found that salmon consumption by bears may be influenced more by salmonid diversity than prey abundance (Service et al. 2019), presumably due to increased duration of prey availability when multiple salmonid species are present within a system. As sockeye-dominated systems, the streams in the current study allowed for an isolated

investigation of how bears may respond to a single salmon population. In systems with returns of multiple salmon species, however, the management implications may differ. Additionally, the availability of terrestrial prey sources (e.g., ungulates) and plant-derived nutrition (e.g., berries, sedges) may also influence dependency on salmon and thus relationships between salmon abundance and consumption (Deacy et al. 2017). Consequently, both habitat and alternative food sources may determine whether current salmon management is sufficient for wildlife needs in other systems.

As complex issues in wildlife conservation become increasingly apparent, so does the importance of evaluating how wildlife and human needs can be balanced through ecosystem-based management. Some studies have evaluated or proposed decreases in harvest to enhance wildlife populations, such as decreasing salmon harvest for killer whale (Williams et al. 2011, Chasco et al. 2017) or brown bear conservation (Levi et al. 2012), managing forage fish landings to ameliorate competition with seabirds (Sydeman et al. 2017), reducing human consumption of wild meat to promote terrestrial carnivores (Ripple et al. 2015; Foster et al. 2016), and limiting krill harvest for ecological concerns (Nicol & Endo 1999). Direct observation of prey intake is often difficult. Thus, many of these studies use estimates of consumption based on bioenergetics models and metabolic demands rather than empirical relationships between predators and prey (Croll & Tershy 1998; Williams et al. 2011; Chasco et al. 2017), highlighting the value of documenting observed relationships between prey abundance and consumption by predators.

The importance of utilizing empirical data to convert the number of prey killed into biomass consumed is further emphasized when considering the prevalence and variability of partial consumption across predator-prey systems. In some cases, consumption is always complete (e.g., baleen whales and krill), but partial consumption is common in many large

aquatic and terrestrial predators including harbor seals (*Phoca vitulina*; Hauser et al. 2008), killer whales (Ford & Ellis 2006), wolves (*Canis lupus*; Vucetich et al. 2012), and cheetahs (*Acinonyx jubatus*; Marker et al. 2003). Despite their utility for assessing harvest-wildlife tradeoffs, studies incorporating partial consumption and directly observed relationships between prey abundance and consumption are rare. Based on an unprecedented empirical analysis of the relationship between salmon abundance and consumption by bears, and in contrast with studies in other systems that propose harvest decreases to alleviate prey limitation, our findings suggest that current management is sufficient for wildlife needs in these systems and demonstrate that balancing wildlife and human needs is attainable.

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Table 2.1 Total consumption of salmon by all bears over the entire salmon run as a function of salmon biomass availability in the Wood River and Iliamna Lake watersheds of southwestern Alaska.

Model name	Model form[a]	Parameters (k)	AICc	ΔAICc
Hansen Creek				
Sigmoidal	$y = \dfrac{7732 * x^2}{12122^2 + x^2}$	2	379.3	0.0
Saturating	$y = 7855 - \left(7855 * 0.94^{x/1000}\right)$	2	380.9	1.6
Linear	$y = 0.21x$	1	388.4	9.1
Pedro Bay ponds				
Linear	$y = 0.17x$	1	345.6	0.0
Saturating	$y = 2526 - \left(2526 * 0.85^{x/1000}\right)$	2	345.6	0.1
Sigmoidal	$y = \dfrac{2301 * x^2}{3590^2 + x^2}$	2	346.0	0.4
A Creek				
Linear	$y = 0.28x$	1	182.5	0.0
Saturating	$y = 343 - (343 * 0.99^x)$	2	189.3	6.7
Sigmoidal	$y = \dfrac{416 * x^2}{650^2 + x^2}$	2	190.3	7.8
C Creek				
Linear	$y = 0.30x$	1	197.9	0.0
Saturating	$y = 940 - (940 * 0.99^x)$	2	199.8	1.8
Sigmoidal	$y = \dfrac{509 * x^2}{687^2 + x^2}$	2	204.1	6.1

[a] Variable x represents annual salmon biomass available (kg), variable y represents annual salmon biomass consumed by bears (kg)
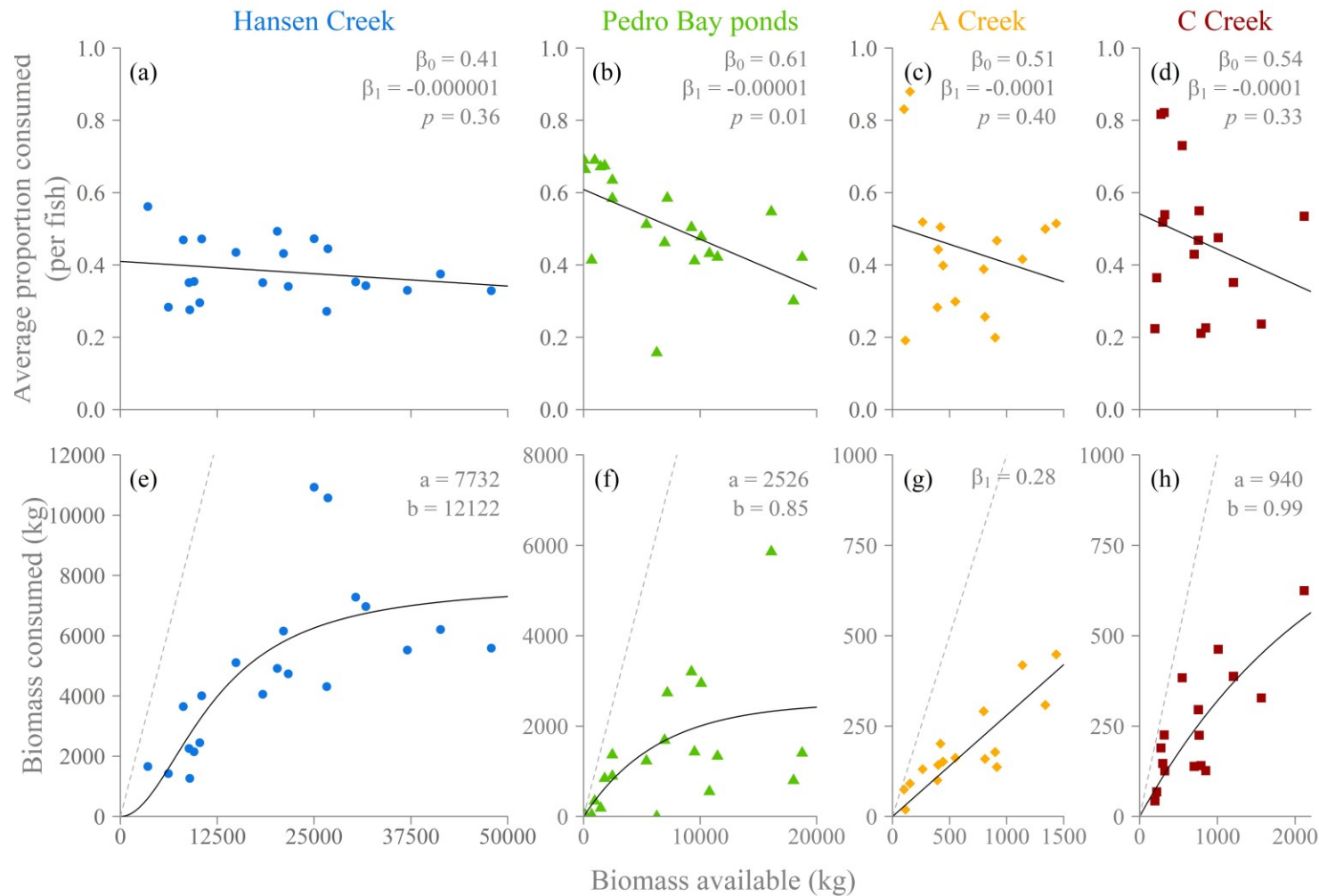
Figure 2.1 Relationships between annual average proportion of each fish consumed by bears (A-D), or annual biomass of salmon consumed by brown bears (E-H), and the annual biomass of sockeye salmon available (note variation among sites). All 4 sites are small, shallow stream systems in southwestern Alaska; Hansen, A, and C creeks are in the Wood River watershed and the Pedro Bay ponds are in the Iliamna Lake watershed. Linear relationships ($y = x\beta_1$) in A-D and G are shown with solid lines, a sigmoidal curve ($y = \frac{a*x^2}{b^2 + x^2}$) is shown in E, and saturating curves ($y = a - (a * b^{x/1000})$) are shown in F and H. Dashed lines are 1:1 to help visualize relationships.
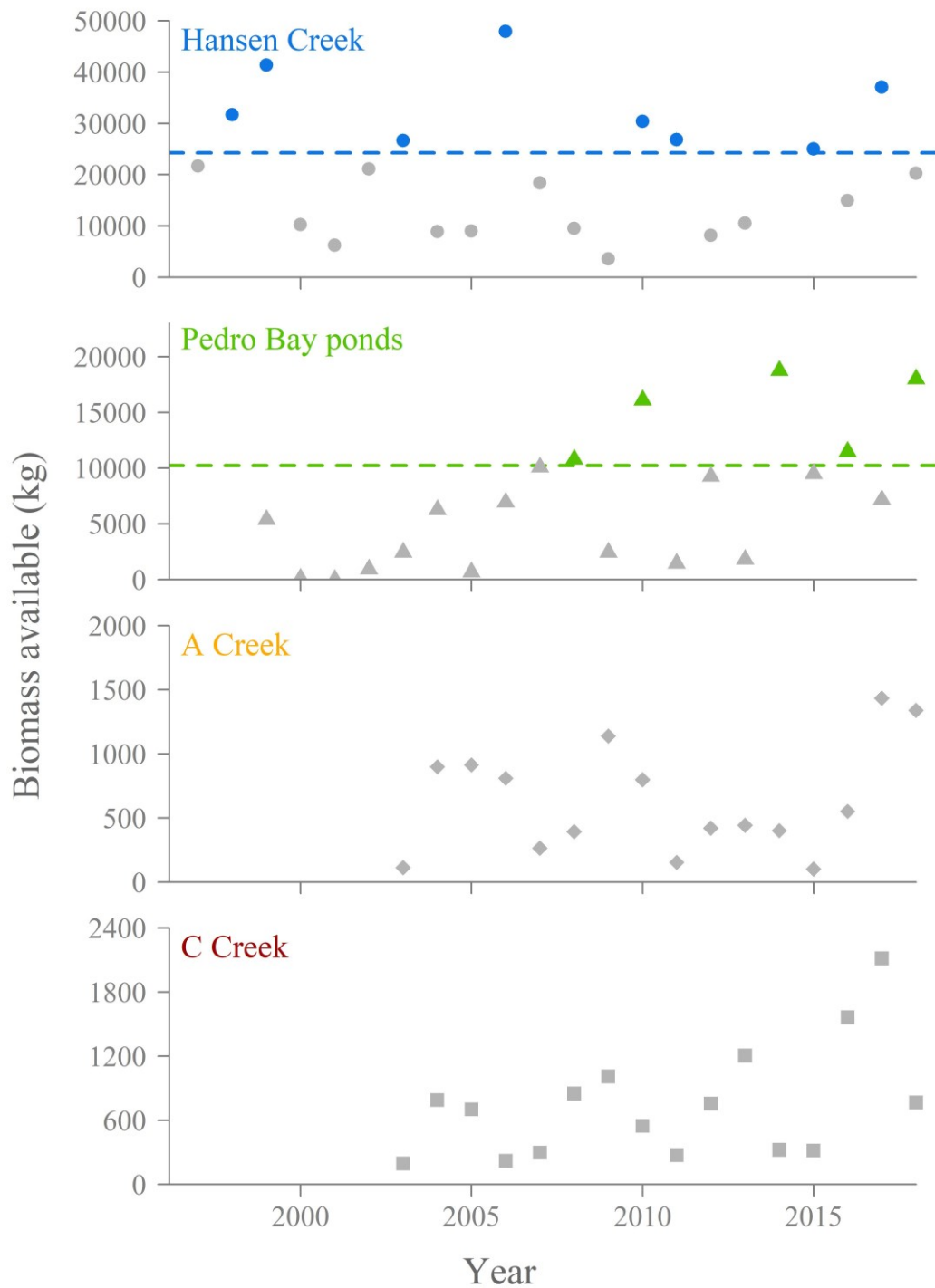
Figure 2.2 Biomass of salmon available among years at 4 sites. Dashed lines indicate availabilities at which bear consumption of salmon was predicted to be at 80% of the saturation point observed in Fig. 2.1. Points above these lines represent years when salmon availability exceeded these values, which were not reached in any year at A or C creeks.
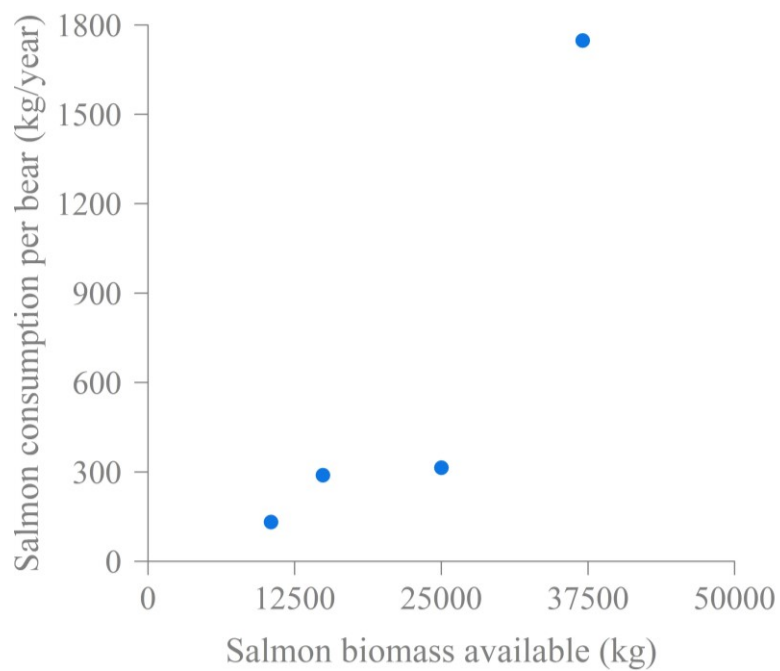
Figure 2.3 Biomass of salmon consumed per bear versus salmon availability, calculated as the total observed biomass consumed divided by the estimated number of bears present that year in Hansen Creek. Data shown is from 2013 and 2015-2017.
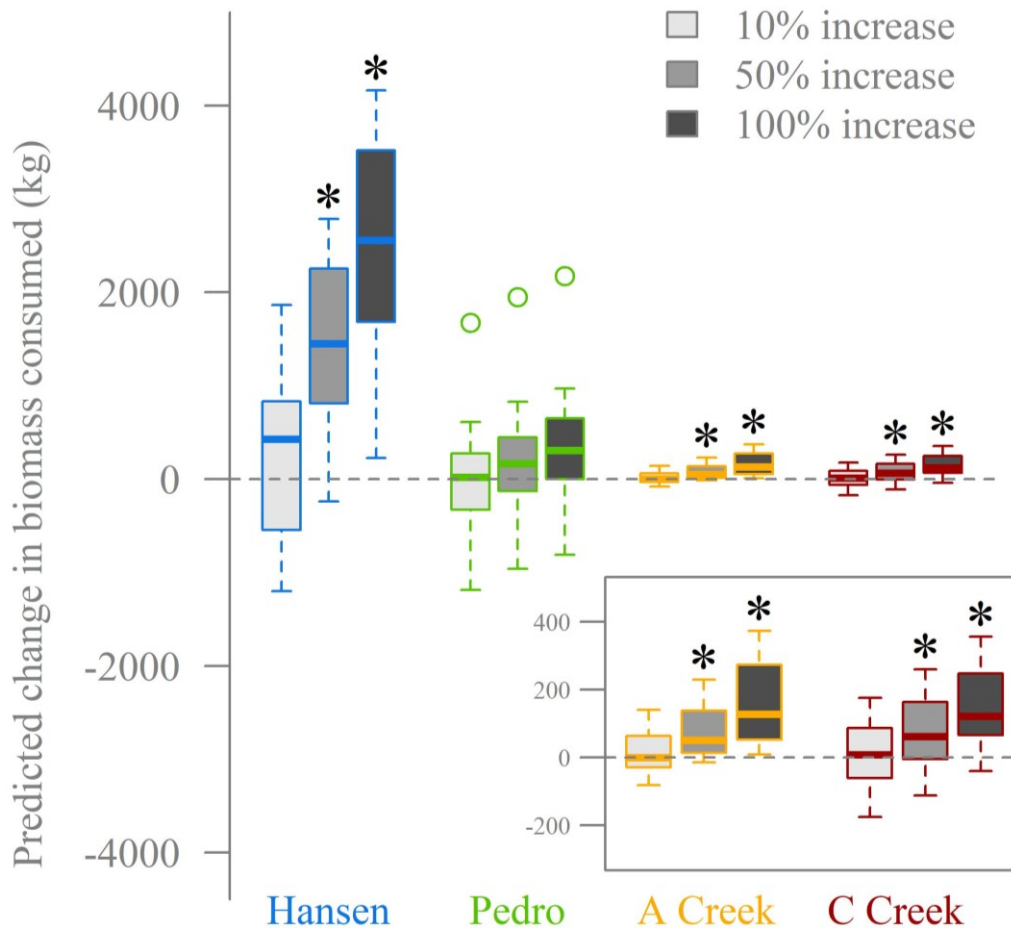
Figure 2.4 Predicted change in biomass of salmon consumed by bears across 3 scenarios of increased escapement (e.g., 10% increase = increasing escapement from 10,000 to 11,000 fish). Only years when salmon were considered to be limiting are included (i.e., when salmon availability was less than the value predicted to result in bear consumption at or above 80% of the saturated value). Boxplots show the distribution of changes in biomass consumed, calculated as the difference in observed consumption and consumption predicted from best-fitting relationships, across all limited years. No change in consumption is marked with a dashed line, and asterisks indicate scenarios in which the average change in consumption was significantly different from zero. Inset repeats boxplots for A and C creeks; note smaller y-axis.

CHAPTER THREE

Scavenging behavior in brown bears: choice and selective consumption of salmon carcasses

ABSTRACT

Scavenging is an underappreciated mechanism of prey consumption for many predators, though it may account for a substantial amount of nutritional intake. Facultative scavengers such as brown bears (*Ursus arctos*) may both prey on and scavenge Pacific salmon (*Oncorhynchus* spp.), though the extent to which bears rely on freshly killed salmon versus salmon carcasses, and whether bears are selective in the carcasses they choose to scavenge, is unclear. We placed pairs of ripe sockeye salmon (*O. nerka*) carcasses differing in sex or size along gravel bars in a small stream (Hansen Creek) in southwestern Alaska, and observed bear responses to the carcasses using camera traps at each gravel bar. We found very low rates of scavenging over two years of study; bears consumed tissue from only 4% of carcasses in 2017 (8 of 194 carcasses), and did not scavenge any carcasses presented in 2018 (0 of 62 carcasses). Scavenging choices did not always mirror those observed in selective salmon predation at Hansen Creek, as bears chose female over male carcasses in 2 of 3 pairs and smaller males over larger males in 2 of 3 pairs. Bears consumed brain and body tissue from male fish (0.13 – 1.17 kg, 8 – 71% of tissue consumed) and brain and belly tissue from female fish (0.22 – 0.46 kg, 11 – 28%). Date, fish availability, and bear predation were not significantly associated with scavenging activity, although sample sizes were small. While limited, these results reveal true prey and tissue preferences of bears foraging on salmon in isolation of prey capture costs, and have implications for both bear nutrition and the flux of salmon biomass and nutrients throughout the greater ecosystem.

INTRODUCTION

Predation is widely recognized as the primary mechanism of foraging by carnivores, but scavenging may contribute substantially to overall food intake in some species. Scavenging has been understudied compared to predation (DeVault et al. 2003; Moleón et al. 2014; Pereira et al. 2014), though more energy is transferred between trophic levels per scavenging link than per predation link (Wilson and Wolkovich 2011). Foraging may fall along a continuum between near obligate predators that exclusively consume killed prey (e.g., cheetahs [*Acinonyx jubatus*]), facultative scavengers (foragers balance killing prey with consumption of carrion; e.g., hyenas [*Hyaena* spp.]), and obligate scavengers that rely solely on carrion (e.g., vultures [*Cathartes* spp.]). Facultative scavenging is ubiquitous, occurring across phylogenetically diverse groups (mammals, birds, insects, reptiles, fish; DeVault and Krochmal 2002; Foltan et al. 2005; Wilson and Wolkovich 2011; Mateo-Tomás et al. 2015), and this strategy allows animals to take advantage of fluctuations in the availability of both live prey and carrion.

The diet of omnivorous brown bears (*Ursus arctos*) may range from primarily plant material to primarily meat (Hilderbrand et al. 1999b; Mowat and Heard 2006), and meat may be obtained either by killing prey or by opportunistic use of carrion (Wilmers et al. 2003). Bears foraging on ungulates in Alaska have been estimated to kill four times more biomass than they scavenge (Boertje et al. 1988), though bears have also been observed scavenging over 50% of experimentally placed mammal carcasses (Magoun 1976). Capturing live prey can be costly for large predators (Carbone et al. 2007); consequently, depending on the temporal and spatial availability of both live prey and carcasses, the ease of prey capture, and intra-specific competition for prey and carrion, the tendency for a bear to scavenge or capture prey may vary (Pereira et al. 2014).

Pacific salmon (*Oncorhynchus spp.*) represent an important seasonal prey source for coastal brown bear populations (Hilderbrand et al. 1999b). Brown bears kill and also scavenge large numbers of salmon (Quinn and Buck 2000; Quinn et al. 2014), but the extent to which salmon nutrition is derived from freshly killed fish versus scavenged fish is unknown. In some habitats such as lakes or large rivers, scavenging may be the only option due to difficulty of fish capture, but in smaller systems bears may have a choice between scavenging or killing salmon. Salmon returns are remarkably similar in space and time among years, creating a predictable pulse of both live prey and carrion, as these semelparous fish species die after spawning in streams. This pattern makes scavenging on salmon somewhat unusual, since the availability of most carrion sources are much less predictable (DeVault et al. 2003). Possibly due to the reliability and ease with which carcasses are encountered, brown bears have been found to scavenge 73% of salmon carcasses in small streams in Alaska (Quinn and Buck 2000).

Notwithstanding the consistency among years in the spatial distribution and timing of salmon breeding, abundance can vary greatly among years, and from day to day during the spawning season (Quinn 2018). Thus, salmon streams provide an ideal system to study how prey and carrion availability may influence the decision to scavenge. Though live prey availability and carcass availability are inversely related in semelparous salmonids, over the course of a salmon run there are a variety of combinations of prey and carrion availability that a bear may experience. At the beginning of the season, both live salmon and carcasses will be scarce, but at the peak run live salmon will become abundant whereas there will be comparatively few carcasses. Then, as fewer salmon arrive than are dying of senescence, carcasses will be increasingly available until the end of the season when no live salmon and only very decomposed carcasses will remain. Capture of live fish and scavenging carcasses both involve

energetic tradeoffs; a live fish may provide higher quality tissue than a carcass because of tissue decay, but depending on the habitat and density of prey, it may require more energy to capture a live fish (Gende et al. 2004). Scavenging does not have a capture cost, as the prey is already dead, although carcasses may still be difficult to find if only available in low numbers. Beyond intra-seasonal changes in prey densities, the quality of live salmon varies within a single season as well, since energetic content of salmon declines with increasing time spent in stream (Hendry and Berg 1999). Thus, salmon still alive towards the end of the run are often of lower quality than those at the beginning, and the benefit of capturing a fish over consuming a carcass may be reduced. Therefore, we may expect rates of scavenging to change with time as well as with prey and carcass availability, reflecting the changing energetic tradeoffs associated with capturing live fish versus scavenging.

The decision to scavenge a given carcass may also rely on characteristics of the carcass itself. Brown bear predation on sockeye salmon is size-, sex-, and energy-selective, with bears targeting larger, male, and high-energy fish (Gende et al. 2001; Quinn and Buck 2001), although high-energy males are discarded more frequently than high-energy females, suggesting that bears may prefer ripe females (Lincoln and Quinn 2019). Bears also show partial and selective consumption of salmon, choosing to eat energy-rich tissues like the brain and eggs in females, and discarding the remains (Reimchen 2000; Gende et al. 2001; Andersson and Reynolds 2018; Lincoln and Quinn 2019). If these tissues are present in carcasses, partial consumption of carcasses is likely similar, although whether initiation of tissue deterioration influences these decisions has not been determined.

Our goal was to uncover the relationships between scavenging rate, prey and carcass availability, and timing within the salmon run. Additionally, by providing bears with a choice

between two carcasses, we sought to reveal whether carcass sex or size influenced the decision

of which carcasses to scavenge, and to explore whether patterns of partial consumption of

scavenged prey mirror those observed in freshly killed prey. Given that scavenging removes the

costs of prey capture, consumption decisions made while scavenging should reveal true prey

preferences in isolation of capture costs. We predicted that we would observe more scavenged

carcasses under low prey availability and high carcass availability, when it is costly to capture a

fish and carcasses are easily encountered, and at the end of the salmon run when live fish are of

poor quality and scarce. We also expected that ripe female carcasses would be preferred over

ripe males, and that larger males would be favored over smaller males. Following partial

consumption patterns observed in brown bear foraging on live fish (Gende et al. 2001; Lincoln

and Quinn 2019), we anticipated that bears would consume the belly and brain tissue of females,

and the brain and body tissue of males.

METHODS

Pairs of sockeye salmon carcasses were made available to bears in the field over the

course of the sockeye salmon run (3-4 weeks) in 2017 and 2018 at Hansen Creek, in the Wood

River Lakes system of Alaska. To standardize for carcass condition and decay rate, in 2017, we

collected carcasses of fish that stranded at the mouth of Hansen Creek as they were ascending

(hence prior to spawning). These carcasses were collected daily and so were within 24 h of death

and thus of approximately equal energetic content and state of decay. In 2018, we collected

carcasses that died from stranding (prior to spawning) at the headwaters of Hansen Creek, in an

extremely shallow section of a beaver pond where a large proportion of the Hansen Creek

sockeye run has spawned in recent years (T. Quinn, unpublished data). We tagged the jaw of

each carcass with a numbered metal band for identification on subsequent surveys, and weighed each carcass. Carcasses were paired either by size (i.e., two males ≥ 10 mm difference in body length, measured mid-eye to hypural plate), or sex (i.e., male and female ≤ 10 mm in body length), and placed on one of five gravel bars in the lowest 0.3 km of the stream in 2017 and at one of five locations along the bank in the upper 0.4 km of the stream in 2018. Camera traps (Bushnell Trophy Cam HD) were set to capture 60-second 1080p HD video of scavenging activity to reveal the initial choice if a bear scavenged both carcasses in one day, and also to reveal if bears were present but did not scavenge, and/or if bears inspected carcasses when present. Carcasses were revisited the next day to assess consumption, and were replaced with fresh carcass pairs. In a few instances when replacement carcasses were not available due to a lack of available fish, pairs were left at each site until fresh carcass pairs could be obtained (1-2 extra days). Scavenged carcasses were weighed and compared to starting weight to determine the biomass consumed. Salmon availability was determined by visual counts during daily stream surveys. Hansen Creek is very shallow (averaging 10 cm deep) and narrow, which allowed us to count nearly every live and dead fish present in the stream on a given day. Bear-killed fish were distinguished from fish dying of senescence by severe wounds. Senescent carcasses were recorded separately to assess the overall availability of salmon for bears.

To identify factors influencing the decision to scavenge, we analyzed both the probability of scavenging and the probability of inspecting a carcass (regardless of whether the carcass was scavenged) using binomial generalized linear models. Only instances in which bear presence was detected by camera trap footage were included in analyses. We included daily salmon availability, day of the year, and the number of bear-killed fish in our models. Bear preference for one carcass over the other within an experimental pair was analyzed using a Fisher's exact

test. Here, we define preference for a carcass as the first carcass consumed. The probability of partially consuming brain, belly, body, and hump tissue was analyzed with additional binomial generalized linear models, with daily salmon availability, day of the year, and carcass length or carcass sex as the predictor variable.

RESULTS

In 2017, 97 carcass pairs were placed between 22 July and 13 August. Bears were detected by the cameras at 48 of these 97 presentations. Bears investigated carcass pairs in 29 instances (Table 3.1), but only made a scavenging choice at 8 carcass pairs (4 sex pairs and 4 size pairs; Table 3.2). Bears made contact with 11 carcasses, but 3 of these carcasses were only bitten, and thus were not considered to be scavenging because no tissue was consumed. In 2018, 31 carcass pairs were presented from 25 July through 5 August. The upper reaches of Hansen Creek typically have more bear activity, as indicated by higher occurrences of bear killed fish (T. Quinn, unpublished data). Nevertheless, there was only one instance in 2018 in which a bear was detected at one of our study sites over the 11-day period, as indicated by camera trap data. This lack of bear activity and a dwindling number of stranded carcasses available for use led us to truncate study efforts on 5 August. Thus, the rest of the analyses presented here were run on 2017 data alone.

In analyzing the 48 instances in which a bear was detected by cameras, we observed positive but not statistically significant relationships between the probability of scavenging and date (i.e., more scavenging late in the season: $F=2.16$, $p=0.15$), number of fish available in the lower section of Hansen Creek (more scavenging with greater prey: $F=3.27$, $p=0.08$), and number of bear kills on that day ($F=3.38$, $p=0.07$). The probability of investigating carcass pairs

was not significantly associated with our variables of interest (date: $F=0.34$, $p=0.56$; prey availability: $F=0.05$, $p=0.83$; bear kills: $F=0.07$, $p=0.79$). Considering the probability of scavenging using only the 29 instances in which bears actively investigated a carcass, we found no significant associations with date ($F=2.64$, $p=0.12$), or prey availability in the lower section of the creek ($F=3.15$, $p=0.09$), but the number of bear kills that day over the whole stream was positively associated with scavenging behavior ($F=4.22$, $p=0.05$).

Tissue was consumed from 8 of the 11 carcasses contacted by bears. The three other fish were bitten and dropped without any consumption. In one of these three cases the male carcass was bitten and dropped and the female carcass was left untouched, and in the other two cases both males within a size pair were bitten and dropped in sequence. Camera images in all three cases suggested that the bear did not attempt to eat the fish. Instead, each carcass was bitten and shaken as if in play. In the remaining carcasses with tissue consumed, bears fed on female carcasses rather than males in two instances, and the male carcass rather than the female in the other instance (Table 3.2). Bears fed on the smaller male rather than the larger male twice and the larger male once. A Fisher's exact test did not reveal statistically significant results for either sex or size preferences.

Both brain and body tissue were consumed from male fish, whereas bears ate the brain and belly tissue from female fish. The amount of biomass consumed ranged from 0.13 kg (brain consumption) to 1.17 kg (brain and body consumption), averaging 0.48 kg per fish (Table 3.3). This represented 8-71% of each fish consumed. Scavenging did not differ between carcasses that had been recently placed and those that had been present at study sites for multiple days; carcasses that had been present at sites for up to three days were still scavenged. Two carcasses were scavenged after being stationed at study sites for two days, and four carcasses were

scavenged after three days. In one of these instances, a bear consumed the brain of a male carcass over the female carcass pairing on the second day, and on the following (third) day a bear consumed the brain and belly of the female fish rather than consume any additional tissue from the male carcass.

DISCUSSION

We observed a much lower scavenging rate than in previous studies of scavenging in the same system (Table 3.1; Quinn and Buck 2000). This is likely attributable to low bear abundance in 2017; concurrent genetic mark-recapture bear occupancy estimates revealed that only about 3 female bears were using Hansen Creek in this year, and data collection from male bears were too low to generate an estimate (A. Wirsing and T. Quinn, unpublished data). This is substantially lower than other years, when around 20-30 bears may forage along Hansen Creek throughout the ca. 1-month season of salmon spawning (Wirsing et al. 2018). In addition to low bear presence, relatively high annual prey availability in 2017 and 2018 may be responsible for the substantially lower proportion of fish scavenged, since under high live prey availability we may expect bears to scavenge less frequently and instead target live fish that may be of higher nutritional quality. However, we did not observe more scavenging under lower prey availability conditions when analyzing within-season trends, as was expected, or at the beginning of the season when most salmon have yet to arrive in the stream and prey availability is typically low. Instead, the limited number of scavenging events observed tended to occur under higher prey availabilities and later in the season. Other studies have also found increased rates of scavenging with increasing prey availability (Mattson 1997), which may be a product of an increased number of bears foraging on the stream when prey availability is high; the resulting decrease in prey abundance per bear may

drive increased scavenging rates. This possibility is supported by our finding that the probability of scavenging was significantly associated with the number of bear kills.

Few choices between carcass pairs were observed, but those that observed did not entirely follow patterns of selectivity observed in bears killing live salmon. Rather than scavenging males over females, as has been seen in selective predation (Quinn and Buck 2001), bears chose female carcasses over male carcasses in 2 of 3 instances. Choices observed during scavenging eliminate the capture costs that may dictate selective predation, and thus may reflect true prey preference, and so the tendency to scavenge female over male carcasses may indicate that bears may prefer tissues present in ripe female carcasses. This supports the line of thinking that bears may search for ripe females in foraging efforts, as seen in patterns of selective prey discarding behavior (Lincoln and Quinn 2019), but may capture males more often because their greater length and deeper bodies may increase visibility or ease of capture. Against our prediction that larger males would be chosen over smaller males, as seen in selective predation (Quinn et al. 2001), bears selected smaller male carcasses in 2 of 3 instances. Though larger males may offer a greater volume of preferred tissues, such as the brain, the head of smaller males may be easier to break into and begin eating. This would contrast with previous speculations that larger fish may be preferentially killed because the extraction of tissues such as the brain, encased in cartilage, may be easier in large fish with a high brain to cartilage ratio (Reimchen 2000; Gende et al. 2001). However, with limited support from small sample sizes, these conclusions are largely speculation.

Patterns of tissue consumption while scavenging largely followed patterns of consumption observed in consuming live fish. Belly tissue was only consumed when scavenging female carcasses, while body tissue was targeted in male carcasses only. Brain tissue was

consumed from both male and female carcasses. We did not observe any consumption of hump tissue in male fish, although this tissue is commonly consumed in fresh fish (Gende et al. 2001; Lincoln and Quinn 2019). This finding may support the idea that bears eat hump tissue out of convenience, as bears may capture fish by biting the hump and so begin eating the fish from this point. Again, isolating prey and tissue preferences from capture costs through observing scavenging behavior in this manner suggests that these patterns of partial consumption represent true tissue preferences. Anecdotally, we did not observe a decrease in amount of a carcass consumed compared to those freshly killed, as observed in brown bears scavenging and preying on ungulates (Mattson 1997), suggesting that the energetic costs of capture in this system are not enough to warrant increased prey intake to offset predation costs. Indeed, some carcasses with brain and body consumption were >70% consumed, as is frequently observed in consumption of freshly killed salmon (Gende et al. 2001).

Interestingly, we observed carcasses that were bitten and dropped without any consumption, as is also observed in predation on salmon (Lincoln and Quinn 2019). In the absence of camera trap data, this behavior would lead us to believe that bears may not be able to obtain all the information about prey quality that they need to make a consumption decision based on sight or smell alone, and that taste may be an important sensory input to consumption decisions. However, camera trap footage showed that in these three cases of bitten and unconsumed carcasses, a bear picked up each carcass using its mouth and shook it in back and forth briefly before releasing the carcass and continuing to travel down the stream. This behavior appeared to be more reflective of "play" than of intentional foraging. These two episodes (one in which two carcasses were handled in this matter, and the other in which one carcass was

similarly handled) occurred over a single 12-hour period, suggesting that perhaps a single bear was responsible for this behavior, however without marked bears we cannot be certain.

The investigation of scavenging behavior presented here complements the exploration of consumption decisions in bears preying on live fish, and together with studies of bear predation, exploration of scavenging behavior provides a more complete understanding of how bears utilize salmon as a resource. Salmon are recognized as an important prey source for bears; salmon consumption is correlated with bear growth, population density, and reproductive success (Hilderbrand et al. 1999b). Thus, consumption patterns of both fresh and scavenged salmon are of interest given the role of salmon in bear nutrition and conservation. Furthermore, bears play a substantial role in nutrient cycling and moving marine-derive nutrients from salmon carcasses into terrestrial systems (Hilderbrand et al. 1999a; Helfield and Naiman 2006), and so the fate of salmon carcasses and their remnants is relevant in considerations of the flux of salmon biomass and nutrients throughout aquatic and terrestrial ecosystems. Knowledge about how carrion exploitation interacts with the broader food-web is at its infancy, although there is growing recognition of the importance of scavenging. Here, we provided a preliminary exploration of how salmon carcasses are exploited by brown bears, though given the small sample sizes and reliance on a single year of data for our analyses, the drivers and patterns of scavenging behavior should be revisited with additional data in order to begin to fill some of these knowledge gaps.

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Table 3.1 Numbers of carcass pairs available, investigated by bears, and scavenged by bears in 2017 and 2018, compared to scavenging rates reported by Quinn and Buck (2000) in the same system.

		# Available	# Investigated	# Scavenged[1]	Annual Scavenging Rate[2]
1997[3]		45	--	11	24.4%
1998[3]		83	--	28	33.7%
2017	Sex pairs	36	10	4	4.1%
	Size pairs	61	19	4	
2018	Sex pairs	22	1	0	0%
	Size pairs	10	0	0	

[1] Includes carcasses bitten and unconsumed in 2017 and 2018 data.
[2] Calculated as number of carcasses scavenged in either pair type (consumed carcasses only) divided by total number of carcasses available.
[3] Reported by Quinn and Buck (2000).

Table 3.2 Scavenging choices made by bears presented with carcasses paired either by sex or size, reported as number of times a carcass was chosen. Only carcasses from pairs where a scavenging choice was made are presented here. Carcasses "chosen" by bears had tissue consumed and "bitten" carcasses had bite marks but no tissue consumed.

		Chosen	Bitten
Sex	Male over female	1	1
	Female over male	2	0
Size	Small over large	2	1
	Large over small	1	1

Table 3.3 Tissue types and biomass consumed from scavenged carcasses at Hansen Creek in 2017. Percent eaten was calculated as the proportion of biomass eaten to total starting body weight.

		Tissues consumed	Biomass eaten (kg)	Percent eaten
Sex pairs[1]	Male	None	0	0%
	Male[3]	Brain	0.22	14%
	Male[4,5]	Brain	0.13	8%
	Female[4,6]	Brain, Belly	0.46	28%
	Female[4,5]	Brain, Belly	0.40	24%
	Female[3]	Belly	0.22	11%
Size pairs[2]	Small	Brain, Body	0.78	45%
	Small[4]	Brain, Body	1.17	71%
	Small[5]	None	0	0%
	Large[5]	None	0	0%
	Large	Brain	--[7]	--[7]

[1]Carcass originated from a male-female pair of carcasses
[2]Carcass originated from a small-large pair of carcasses
[3]Occurred on the second day after placement
[4]Occurred on the third day after placement
[5]Consumed in the same foraging bout
[6]Chosen over a male with brain consumption
[7]Weight not recorded