Differential use of salmon by vertebrate consumers: implications for conservation

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Salmon and other anadromous fish are consumed by vertebrates with distinct life history strategies to capitalize on this ephemeral pulse of resource availability. Depending on the timing of salmon arrival, this resource may be in surplus to the needs of vertebrate consumers if, for instance, their populations are limited by food availability during other times of year. However, the life history of some consumers enables more efficient exploitation of these ephemeral resources. Bears can deposit fat and then hibernate to avoid winter food scarcity, and highly mobile consumers such as eagles, gulls, and other birds can migrate to access asynchronous pulses of salmon availability. We used camera traps on pink, chum, and sockeye salmon spawning grounds with various run times and stream morphologies, and on individual salmon carcasses, to determine how different wildlife species use salmon resources. Wildlife use of salmon was highly heterogeneous. Ravens were the only avian consumer that fed heavily on pink salmon in small streams. Eagles and gulls did not feed on early pink salmon runs in creeks, and only moderately at early sockeye runs, but were the dominant consumers at late chum salmon runs, particularly on expansive river flats. Brown bears used all salmon resources far more than other terrestrial vertebrates. Notably, black bears were not observed on salmon spawning grounds despite being the most frequently observed vertebrate on roads and trails. From a conservation and management perspective, all salmon species and stream morphologies are used extensively by bears, but late salmon runs are disproportionately important to eagles and other highly mobile species that are seasonally limited by winter food availability.

1 **Differential use of salmon by vertebrate consumers:**

2 **implications for conservation**

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Abstract

11

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13 strategies to capitalize on this ephemeral pulse of resource availability. Depending on the timing

14 of salmon arrival, this resource may be in surplus to the needs of vertebrate consumers if, for

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17 resources. Bears can deposit fat and then hibernate to avoid winter food scarcity, and highly

18 mobile consumers such as eagles, gulls, and other birds can migrate to access asynchronous

19 pulses of salmon availability. We used camera traps on pink, chum, and sockeye salmon

20 spawning grounds with various run times and stream morphologies, and on individual salmon

21 carcasses, to determine how different wildlife species use salmon resources. Wildlife use of

22 salmon was highly heterogeneous. Ravens were the only avian consumer that fed heavily on pink

23 salmon in small streams. Eagles and gulls did not feed on early pink salmon runs in creeks, and

24 only moderately at early sockeye runs, but were the dominant consumers at late chum salmon

25 runs, particularly on expansive river flats. Brown bears used all salmon resources far more than

26 other terrestrial vertebrates. Notably, black bears were not observed on salmon spawning grounds

27 despite being the most frequently observed vertebrate on roads and trails. From a conservation

28 and management perspective, all salmon species and stream morphologies are used extensively

29 by bears, but late salmon runs are disproportionately important to eagles and other highly mobile

30 species that are seasonally limited by winter food availability.

Introduction

32   The annual return of anadromous salmon contributes pulses of marine nutrients to

33   freshwater and terrestrial systems that propagate through food-webs and influence primary

34   producers, invertebrates, fish and wildlife (Willson & Halupka 1995). Vertebrate consumers of

35   adult wild salmon include bears, wolves, marten, mink, and coyote, and a diverse array of avian

36   scavengers including bald eagles, ravens, jays, mergansers, gulls, and even owls (this study). Life

37   history variation in salmon spawning phenology can extend this resource subsidy through time

38   for more mobile consumers that forage among runs that peak at different times (Schindler et al.

39   2013). Consumers with distinct life histories might also partition the salmon resource based not

40   only on the interaction of consumer life history with salmon phenology but also on the spatial

41   dispersion of spawning aggregations. Moreover, understanding how the spatiotemporal

42   dispersion of salmon can influence multiple vertebrate consumers would increase understanding

43   about how the needs of wildlife can be incorporated into salmon management (Levi et al. 2012).

44   Recent research proposed incorporating brown bear fitness into salmon management

45   decisions (Levi et al. 2012) because their body mass, litter size, and population density are

46   closely linked to salmon consumption (Hilderbrand et al. 1999). Bald eagles (*Haliaeetus*

47   *leucocephalus*) might also be a promising focal taxa for incorporating wildlife needs into salmon

48   management because they (1) are large-bodied birds and thus have higher caloric requirements

49   than smaller bird species, (2) are primarily fish-eaters, (3) are of conservation interest to the

50   public and tourism operators, and (4) reach much higher population densities in salmon-fed

51   systems. However, due to their distinct life histories, bears and eagles may respond differently to

52   spatiotemporal patterns of salmon availability.

53   Bears avoid winter food limitation by storing fat during the pulse of returning adult

54   salmon. Female brown bears (*Ursus arctos*) nearly double their body mass as they deposit fat

55   during the months of salmon availability in preparation for hibernation and lactation (Kingsley et

56   al. 1983). Even with reduced salmon biomass entering rivers due to commercial fishing, salmon

57   represent roughly 60-80% of bear diets in many coastal salmon systems (Mowat & Heard 2006).

58   In contrast, bald eagles capitalize on resource pulses by moving long distances both locally and

59   regionally to track asynchronous resource availability (Elliott et al. 2011). When salmon are

60   regionally abundant in summer and early fall, salmon are in surplus to the energetic needs of

61   eagles. In contrast to bears, eagles cannot hibernate and are limited by food availability in late

62   winter after salmon have disappeared from the landscape (Elliott et al. 2011). This leads eagles to

63   forage over large areas and then to congregations in the thousands on late salmon runs when

64   salmon becomes limiting. Thus the activity of eagles and other migratory avian scavengers is

65   expected to increasingly concentrate on late salmon runs.

66   The spatiotemporal dispersion of salmon resources is in part a consequence of salmon

67   species richness, as salmonid species and/or populations have varying phenologies and prefer

68   different spawning habitats (See *Study System* below). Abiotic factors such as stream morphology

69   and habitat type might also mediate which consumers access particular salmon resources. For

70   example, forest specialists (e.g. martens) might restrict their use of salmon to small and forested

71   streams, while large avian consumers might avoid these small streams in preference for large

72   open areas with better escape terrain.

73   Further, bear activity at spawning grounds can mediate availability of salmon carcasses to

74   other consumers. After capturing salmon in rivers and streams, brown bears move carcasses to

75   land to feed, often feeding selectively on body parts, such as brains and gonads, that provide the

76   most concentrated amount of fat (Gende et al. 2001). Some estimates suggest that bears consume

77   as little as 25% of the salmon they kill (Quinn 2005), leaving partially-consumed carcasses

78   available to a wide range of scavengers.

79   Here we report the findings of a study in which we used remotely-triggered camera traps

80   to quantify how wildlife foraging activity varies at salmon spawning grounds (Shardlow & Hyatt

81   2013), and rates of scavenging on individual salmon carcasses deposited on the forest floor by

82   brown bears. We monitored runs with distinct run timing and variable stream morphologies

83   including small creeks in forested areas, lake shores, pools off of larger rivers, and river flats

84   around braided mainstems of larger rivers. We also used camera traps on roads and trails before

85   spawning to estimate the relative abundance of carnivores as a comparison to carnivore activity

86   on salmon spawning grounds.

Study area

88   Spawning ground monitoring was conducted in the Chilkat and Chilkoot drainages near

89   Haines, Alaska (Fig. 1) from June to November 2011. Monitoring of individual carcasses took

90   place between August and October in both 2012 and 2013. The Chilkoot River flows less than 1

91   km from Chilkoot Lake before reaching the ocean. Chilkoot Lake is a glacially turbid lake,

92   approximately 6 km long and 2 km wide. Primarily sockeye (*Oncorhynchus nerka*), but also coho

93   (*Oncorhynchus kisutch*), spawn on the shores of the lake, and pink salmon (*Oncorhynchus*

94   *gorbuscha*) spawn in the lower river and lake. Sockeye and coho also spawn in the river upstream

95   of the lake.

96   The Chilkat drainage is a larger river system with multiple tributaries. The river is braided

97   through a wide valley and meets the Tsirku and Klehini rivers 21 miles from the ocean at an area

98   known as the Council Grounds. Ground water bubbles up from an alluvial fan at the intersection

99   of these rivers, which prevents the river from freezing. A late chum salmon (*Oncorhynchus keta*)

100   run spawns in the Chilkat River near the council grounds from October-December and in the

101   lower Klehini River earlier in September-October. Pink salmon spawn in creeks 10 miles and 18

102   miles from Haines and in parts of the upper Chilkat River from August to early September.

103   Sockeye salmon spawn in pools in the upper Chilkat River, Mosquito Lake, and in Chilkat Lake

104   with early and late runs spanning June through October. Coho spawn in lakes and streams

105   throughout the watershed but not in dense aggregations. Coho salmon persist in small streams

106   into January. The availability of chum and coho salmon late in the year draws a large

107   congregation of bald eagles to the Chilkat River. Black-billed magpies (*Pica hudsonia*), common

108   ravens (*Corvus corax*), mew gulls (*Larus canus*), and glaucous-winged gulls (*Larus glaucescens*)

109   are also abundant and feed alongside the eagles.

110   **Methods**

111   *Spawning Ground Monitoring*

112   We used twenty motion-activated infrared cameras (Bushnell Trophycam) to monitor wildlife

113   activity on pink, chum, and sockeye spawning grounds from August-November 2011 (Figs. 1-2).

114   We classified stream morphology into creeks, pools, flats, and lakes. Creeks are small streams

115   with forest cover, which includes the pink salmon spawning grounds at 10 mi and 18 mi Creek,

116   and chum salmon spawning grounds at Herman Creek. Pools are slow moving shallow offshoots

117   of the Chilkat River, including Bear Flats and Mule Meadows. Flats are expansive seasonally-

118   flooded areas of braided river with no forest cover on the Chilkat and Klehini Rivers. The lake

119   category included the lakeshore spawners of Chilkoot Lake and Mosquito Lake (Fig. 1). We

120   monitored dirt roads and trails on the Kelsall road system, which parallels the Upper Chilkat

121   River and branches to follow the Kelsall River and Nataga Creek tributaries (Fig. 1). We placed

122   camera traps on roads and trails in early summer to provide an index of relative abundance of

123   terrestrial carnivores such as black bears, brown bears, coyotes, lynx, and wolves. All cameras

124   were set to take three pictures when triggered with a three second delay between successive

125 triggers. To avoid overestimating visitation rates when the same individual or group foraged in

126 front of the camera for an extended period, we post-processed the camera data to identify unique

127 visitations. We defined unique group visitations as visits with a greater than two minute delay

128 between the last photograph from one visit to the first photograph of the next. We weighed each

129 unique group visit by the observed group size to estimate the number of individual encounters

130 (unique visits weighted by group size per camera-day). We chose a short two-minute delay

131 because we often observed one group of animals replace another in quick succession (e.g.,

132 subdominant sow with cubs replaced by another sow).

133 *Salmon Carcass Monitoring*

134 We used motion-activated infrared cameras (Bushnell Trophycam) to monitor wildlife visitations

135 to, and feeding activity on, individual salmon carcasses at two mid-season sockeye runs (Chilkoot

136 Lake and Mule Meadows, August and September) and one late season chum salmon run (Herman

137 Creek, September and October) in both 2012 and 2013. At each site we erected a grid of eight

138 cameras, four cameras 15m from spawning grounds and four cameras 50m from spawning

139 grounds, with 150m lateral spacing between cameras. Each camera was baited with a single

140 salmon carcass staked to the ground. All cameras were set to take three pictures when triggered

141 with a one-minute delay between successive triggers. Cameras were checked weekly and

142 carcasses were replaced if missing or decomposed. We defined unique visitations as visits with a

143 greater than five minute delay between the last photograph from one visit to the first photograph

144 of the next on any one camera at the site.

145 **Results and Discussion**

146 We obtained over 48000 images from salmon spawning grounds during 788 camera-days

147 in 2011, and over 40000 images from individual salmon carcasses during 2012 and 2013. More

148 than 24000 images were recorded in 2012 over 675 camera-days and just over 16000 images

149 were obtained in 2013 across 714 camera-days. There was substantial variation in wildlife

150 activity across spawning grounds with different stream morphologies and run timing (Fig. 3, 6).

151 *Spawning Ground Monitoring, 2011*

152 Brown bears foraged extensively on all salmon runs regardless of species, run timing, and stream

153 morphology (Figs. 2-4). Despite previous research suggesting higher foraging efficiency on small

154 streams (Quinn et al. 2001), brown bears nevertheless frequently utilized lakeshore spawners.

155 Ravens, which are resident forest birds, were the only birds to feed extensively on early runs of

156 pink salmon, which were also consumed by mustelids (mink and marten) and coyotes (Fig. 4A),

157 but ravens were not observed at 10 mile creek despite an abundance of carrion (Fig. 3). Ravens

158 also generally fed more than other avian scavengers on sockeye spawning grounds (Fig. 4A), but

159 they were outnumbered at Chilkoot Lake where eagles were more often observed, and Bear Flats,

160 where magpies were observed slightly more frequently (Fig. 3). We speculate that ravens selected

161 against the relatively coastal spawning areas at Chilkoot Lake and 10 mile creek in favor of

162 concurrent inland spawning areas.

163 Migratory avian scavengers, including eagles, gulls, and magpies did not feed on early

164 pink salmon runs (Fig. 3, Fig. 4A). This was likely due to a combination of early run timing and

165 avoidance of small streams when salmon are available elsewhere at sites with more suitable

166 stream morphology. The absence of birds, other than ravens, at early salmon runs was followed

167 by a high concentration of eagle and gull activity at late salmon runs (Figs. 3-4). However, avian

168 scavengers fed on salmon less often than brown bears at the late chum salmon run at Herman

169 Creek, indicating that stream morphology and run timing both influenced where these consumers

170 preferentially fed on salmon (Figs 3-4).

171   Brown bears were observed disproportionately more on salmon spawning grounds than

172   expected by their abundance. Black bears were the most commonly observed animal on roads and

173   trails during summer 2011, followed by coyotes, brown bears, wolves and lynx (Fig. 5). Black

174   bears, which are dominant salmon consumers in many systems without brown bears, were

175   notably absent on salmon spawning grounds (Fig. 5), which suggests that risk associated with

176   interference competition by brown bears is strong enough to prevent black bear consumption of

177   this energetically profitable resource. Similarly, coyotes were much more abundant than wolves,

178   but wolves were observed as frequently as coyotes on salmon spawning grounds. Lynx were not

179   observed on spawning grounds (Fig. 5).

180   *Salmon Carcass Monitoring, 2012-2013*

181   A wide variety of species were observed both visiting and consuming salmon carcasses in both

182   2012 and 2013 (Fig. 6). Encounter rates of species varied among sites and between years (Fig. 7).

183   We observed no differences between visitations at carcasses near to (15m) and farther from (50m)

184   spawning grounds for any species (all $p > 0.2$). As with spawning ground monitoring in 2011,

185   brown bears were the dominant visitors to all carcasses regardless of run timing. Although avian

186   activity overall was observed to be higher at late runs at Herman Creek than mid-season runs at

187   Chilkoot Lake and Mule Meadows, avian encounters were much lower on individual salmon

188   carcasses in 2012 and 2013 than on spawning grounds in 2011. As salmon carcasses sites were

189   either 15 or 50m from spawning grounds and often under forest cover, this could suggest that

190   avian scavenging on partially-consumed salmon carcasses deposited by bears might be limited to

191   larger, open areas immediately adjacent to spawning grounds or in sparsely or unforested habitats

192   like river flats.

193   Visitation of wildlife to salmon carcasses occurred consistently at each site, but

194   consumption of carcasses was observed less frequently. While small carnivores such as mink and

195   marten and avian scavengers were observed feeding on individual carcasses at all sites

196   throughout the duration of the carcass monitoring, bears rarely fed on carcasses until the end of

197   the late chum salmon run at Herman Creek. Since salmon carcasses were used to bait camera

198   stations rather than live salmon, this could indicate a preference for predation over scavenging, or

199   for consumption of fresher fish until the point at which salmon becomes limiting. The

200   observation that bears frequently return to salmon carcasses after initially high grading on the

201   most calorie-rich portion of the fish suggests that estimates of salmon consumption by bears are

202   likely biased low (Gende et al. 2001).

203   The extensive use of all salmon resources by brown bears suggests that increasing total

204   salmon biomass can be a suitable management strategy to help conserve or maximize brown

205   bears population productivity. Because bears rely on all salmon species, it is plausible to

206   maximize the salmon available to bears by increasing escapements (salmon that escape the

207   fishery and are available to spawn) for low value species, such as pink and chum, and maximize

208   economic value to fishermen by exploiting high-value species, such as sockeye, coho, and king,

209   for maximum sustainable yield. This seems particularly plausible because pink and chum have

210   early and late run times respectively, which extends the temporal availability of salmon biomass,

211   although they do not permeate as far into watersheds as other salmon species, restricting access to

212   more interior salmon predators and scavengers.

213   The complete absence of eagles and other avian scavengers on early pink salmon runs

214   suggests that regional salmon availability far exceeds their energy requirements during this time

215   of year. These avian scavengers congregate in enormous numbers at late chum salmon runs when

216   salmon become a limiting resource (Elliott et al. 2011; ~3500 observed at our field site by aerial

217   counts). The Chilkat River eagle gathering from October to January is the earliest of these

218   congregations and the farthest north. The Squamish and Harrison river systems in southern

219   British Columbia also support large eagle congregations that peak in January. Other much smaller

220   congregations continue in south-coastal British Columbia and Northern Washington State though

221   April. These few late chum salmon runs are disproportionately important resources the the larger

222   panmictic eagle population in the Pacific Northwest, Alaska, and Western Canada (Elliott et al.

223   2011).

224   An obvious question is why other terrestrial vertebrates use salmon so much less than

225   brown bears and avian scavengers. Bears can integrate over the salmon resource pulse by

226   depositing fat and hibernating, and migratory avian scavengers can track asynchronous pulses of

227   salmon on vast spatial scales. Because other salmon consumers do not employ these life history

228   strategies, their populations do not reach the salmon driven numbers reached by bears and mobile

229   avian scavengers. Winter food availability rather than salmon may limit the populations of most

230   terrestrial carnivores, but the importance of salmon to each species is likely to be idiosyncratic.

231   Wolves, for example, are more successful at hunting ungulate prey in winter than during summer,

232   such that salmon can lead to apparent competition by maintaining wolves at high density even

233   when ungulate biomass is low (Adams et al. 2010). Black bears do possess the hibernation

234   strategy to integrate over salmon resources, and do so in many river systems without brown

235   bears, but interference competition with brown bears prevents salmon consumption at our field

236   site. It is unclear to what degree interspecific competition affects salmon consumption by other

237   species, but is plausible that coyotes, which are locally abundant (Fig. 4), were observed

238   infrequently due to interference competition from wolves. For small-bodied scavengers, such as

239   mink and marten, the spatial distribution of salmon, rather than biomass per se, may be a more

240   important driver of population productivity because even relatively small quantities of salmon

241   may support the low population density of resident individuals. However, this depends on the

242   accessibility of salmon carcasses, which can be quickly flushed from systems in the absence of

243   large woody debris (Cederholm et al. 1999), or deposition of partially consumed carcasses by

244   bears (Helfield & Naiman 2006).

245   Understanding how salmon use is influenced by consumer life history, run timing and

246   stream morphology, is an important first step toward integrating wildlife needs into salmon

247   management as part of an ongoing paradigmatic shift toward Ecosystem-based fisheries

248   management (Levin et al. 2009). Our results suggest that is it plausible to combine all salmon

249   biomass irrespective of run timing and stream morphology when managing salmon for productive

250   bear populations (Levi et al. 2012), despite likely differences in the accessibility of salmon

251   biomass in different stream morphologies. In contrast, it is not plausible to combine all salmon

252   biomass when considering the impact of salmon fisheries on eagles, gulls and other migratory

253   avian scavengers. Accounting for the needs of bald eagles in fisheries management might instead

254   focus on increasing escapements at late chum salmon runs where eagles congregate in Southeast

255   Alaska, British Columbia, and Northern Washington. Similarly, resource extraction that threatens

256   late chum salmon runs will have a disproportionately large impact on regional eagle populations.

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304   **Figure Legends**

305   **Figure 1.** (A) Chilkat and Chilkoot river systems near Haines, Alaska and locations of pink,

306   sockeye, and chum spawning sites that we monitored with camera traps. (B) Location of study

307   area in Northern Southeast Alaska at the end of the Lynn Canal.

308   **Figure 2.** Examples of recorded images of wildlife visitation to salmon spawning areas at (A-B)

309   pools, (C-D) river flats, (E-F) small streams, (G-H) and lakeshores.

310   **Figure 3.** Mean individual encounter rate of salmon consumers at nine salmon spawning grounds

311   in 2011. Sites are labeled to indicate early pink salmon runs in creeks, sockeye runs in pools and

312   lakes (that spawn over an extended period from early to late), late chum salmon runs at flats and

313   creeks, and the very late chum salmon run at Chilkat Flats. To account for instances where

314   multiple individuals of the same species were recorded in one frame (e.g. flocks of gulls, sows

315   with cubs) individual encounters are the number of unique group encounters (>2 min apart)

316   weighted by the mean number of individuals in each group. Error bars indicate standard errors of

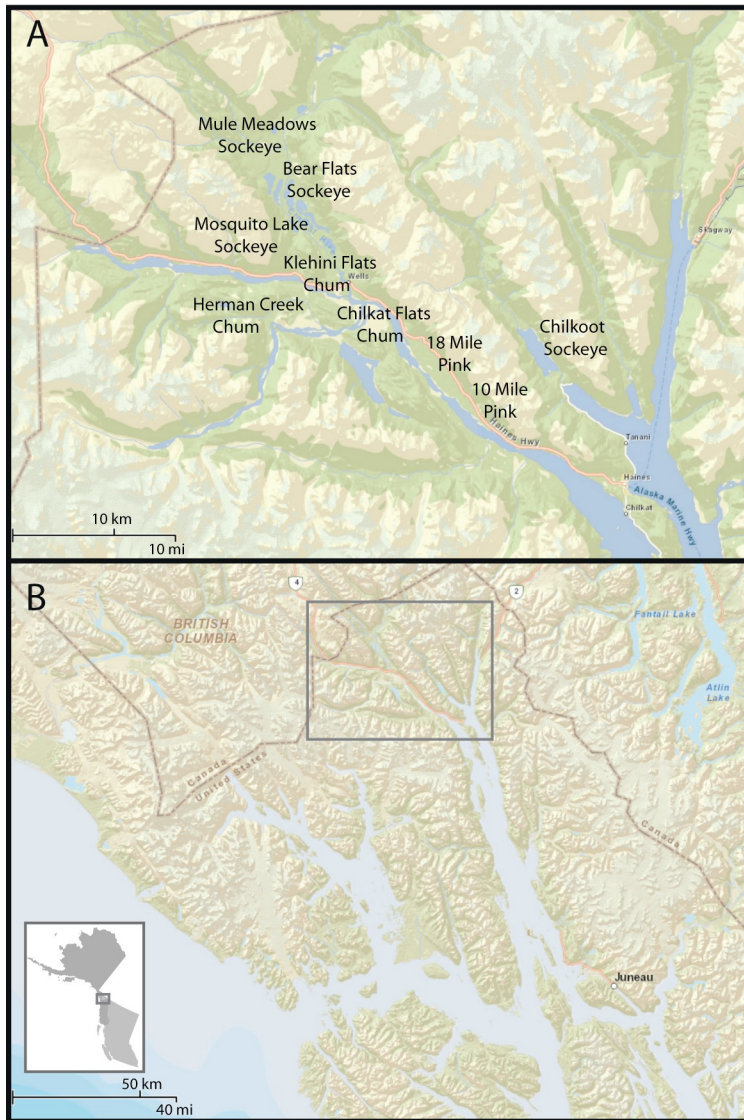317   the mean across cameras within each site.

318   **Figure 4**. Individual encounter rate of salmon consumers on (A) pink, sockeye, and chum salmon

319   spawning grounds, and (B) on spawning grounds at creeks, pools, flats, and lakes during

320   spawning ground monitoring in 2011.

321   **Figure 5.** Relative abundance of terrestrial carnivores as measured by camera trapping rates on

322   dirt roads and trails in the upper Chilkat River watershed from June to August and on salmon

323   spawning grounds from August to October 2011. Black bears were the most commonly observed

324   species on roads and trails but completely avoided spawning areas, which were dominated by

325   brown bears. We encountered 83 unique black bears, 42 coyotes, and 21 brown bears, 4 wolves,

326   and 3 lynx.

327 **Figure 6.** Recorded images of wildlife consumption of individual salmon carcasses at baited

328 camera trap stations during 2012 and 2013. A wide variety of species were observed feeding on

329 salmon carcasses, including brown bears (A, B), eagles, ravens, crows (C), mink, marten (D),

330 coyotes (E), and wolves (F).

331 **Figure 7.** Mean individual encounter rate of salmon consumers visiting individual salmon

332 carcasses at two mid-season (Chilkoot Lake and Mule Meadows) and one late season (Herman

333 Creek) salmon runs in 2012 and 2013. Error bars indicate standard errors of the mean across
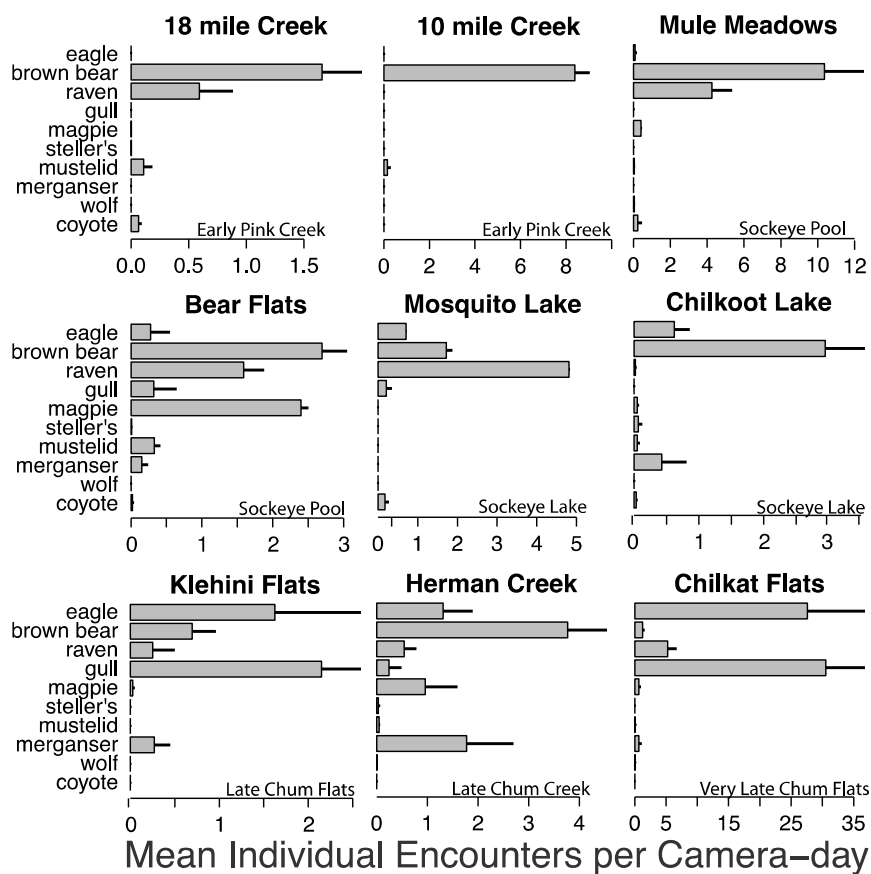
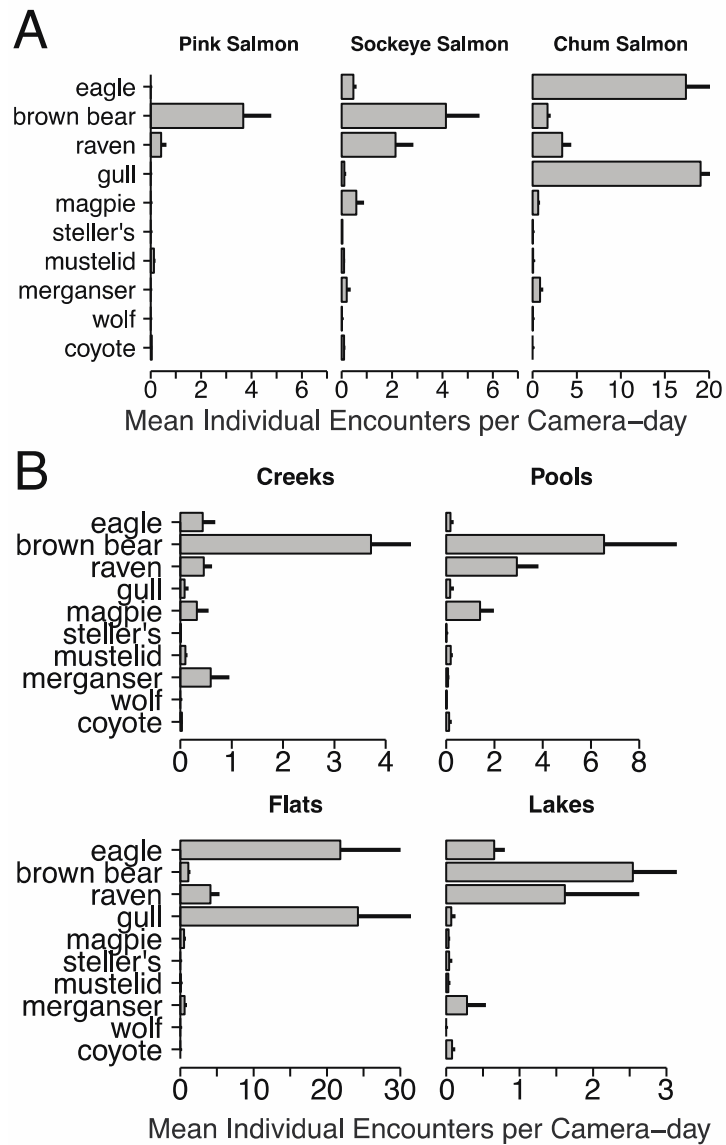334 cameras within each site.

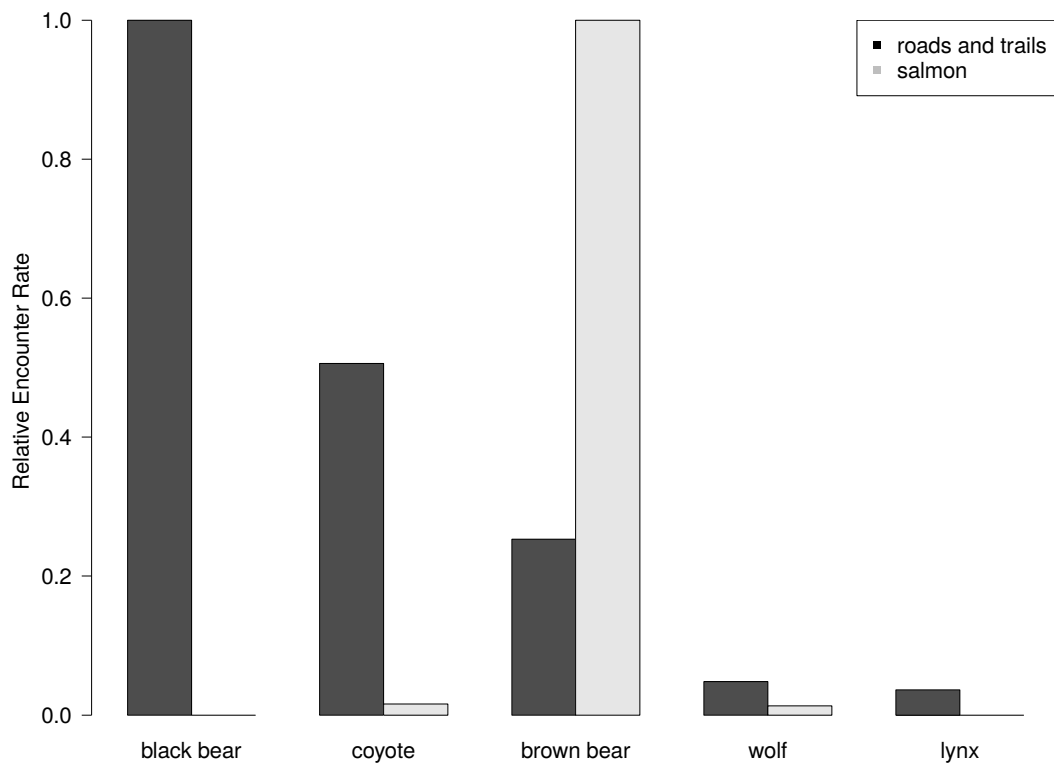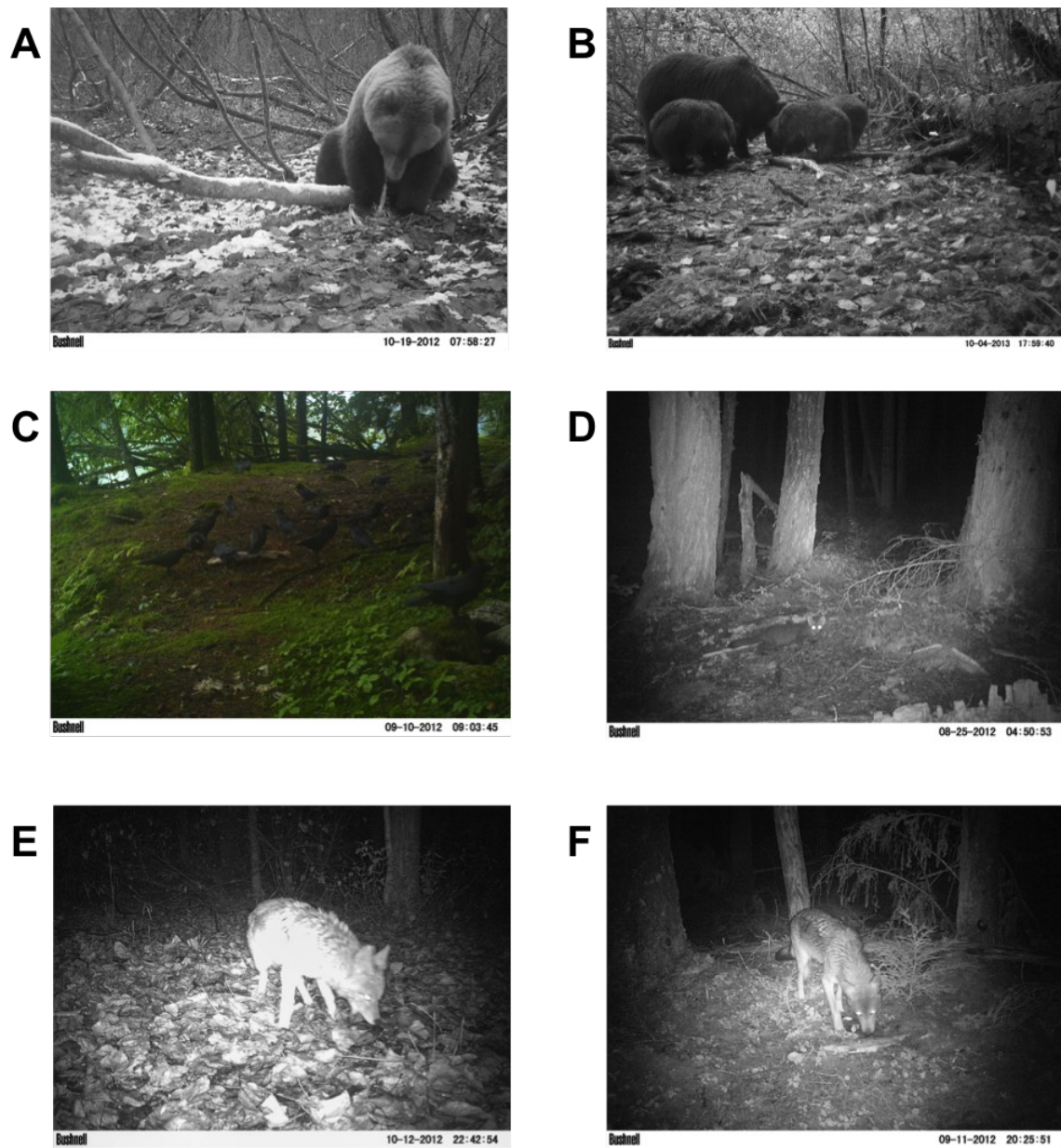335   **Figure 1**

336 **Figure 2**

337   **Figure 3**

Mean Individual Encounters per Camera–day

338   **Figure 4**

339   **Figure 5**

340   **Figure 6**

341   **Figure 7**

Mean Individual Encounters per Camera–day