DO SPAWNING SALMON INDIRECTLY INFLUENCE UNGULATE SPACE USE IN THE COPPER RIVER DELTA, ALASKA BY ATTRACTING BEARS?

by

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ABSTRACT

One of the key challenges in ecology is understanding the drivers of animal movements and distributions. Here, I used remote camera photography to examine whether the timing of spawning salmon altered ungulate space use due to the presence of bears. Using observational data collection methods, I quantified ungulate and bear presence at individual salmon spawning sites. I then analyzed relationships between bear and ungulate detection data to test for indirect effects between salmon and ungulates by applying linear regression models. A zero-inflated negative binomial model suggested that increases in bear detections are associated with decreases in ungulate detections. Results did reveal little overlap in the timing of ungulate and bear use of stream habitat during salmon spawning times, however, rigorous testing of my hypothesis may be limited by low rates of ungulate detection. Research dedicated to understanding the indirect effects of the timing of salmon spawning in the Copper River Delta can help evaluate the evidence for trophic interactions at various ecosystem levels. It may also offer insights into the potential magnitude the impact salmon has on the prey of large predators, other herbivore densities, plant communities, riparian area morphology, and essential ecosystem functions.

BACKGROUND AND OBJECTIVES

Background

Pacific salmon (*Oncorhynchus* spp.*)* and brown bears (*Ursus arctos*) have been characterized as keystone species in coastal Alaskan ecosystems, including in the Copper River Delta, because they regulate the flows of energy and nutrients in coastal Alaskan ecosystems (Helfield & Naiman, 2006). Salmon are the most important food for coastal bears, composing up to 80% of some bears' diets (Mowat & Heard, 2006). Salmon spawn in different places at different times of year because of complex patterns of water temperature (Hilborn, Quinn, Schindler, & Rogers, 2003). As bears spend much of the summer months seeking, catching, and eating salmon, they move from waterbody to waterbody to maximize their nutritional intake (Deacy, Leacock, Stanford, & Armstrong, 2019). In general, wherever salmon are spawning, one will find bears attempting to eat them.

Large ungulates such as moose (*Alces alces*) and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are also known to forage in the riparian areas where salmon spawn. Although they do not directly consume salmon, salmon fertilize vegetation when they die from natural senescence, predation, or scavengers. This makes riparian vegetation particularly productive and riparian areas a valuable foraging location for ungulates (Helfield & Naiman, 2001). Although not as important a food as salmon, bears deliberately and opportunistically kill ungulates when they can. In other ecosystems, ungulates have been observed changing their space use to avoid locations where they are more likely to encounter predators (Laundre, Hernandez, & Ripple, 2010).

This “landscape of fear” hypothesis suggests a behavioral response wherein prey are responding to the threat of predation rather than the actual presence of predators.

Bears killing salmon or ungulates are two examples of direct ecological effects- food web interactions where one species directly interacts with another. Indirect effects are another important type of food web interaction, where a species affects another through an intermediate player. Riparian areas, which salmon, bears, and ungulates all use, may play host to an indirect effect between salmon and ungulates.

Despite a wealth of research on large-scale predator-prey ecosystem dynamics, the extent to which these concepts are important in less studied ecosystems is poorly understood (Kauffman, Brodie, & Jules, 2010; Laundre, et al., 2010; Schmitz, Beckerman, & O’Brien, 1997; Wilmers & Schmitz, 2016; Winnie, 2012; Winnie & Creel, 2017). For example, it remains unknown whether the landscape of fear influences interactions between bears and ungulates in salmon-rich ecosystems. If this does occur, it would indirectly link salmon and ungulates; the timing of salmon runs would indirectly influence ungulate use of productive riparian habitat through bear avoidance. An indirect link between salmon and moose would have implications for moose conservation and management; anticipated changes in future salmon run timing and abundance would likely change the seasonal dynamics of moose space use (Kovach, Ellison, Pyare, & Tallmon, 2015). Broadly, an understanding of how the spatio-temporal distribution of salmon impacts a wide variety of vertebrate consumers could lead to an increased understanding of how these indirect effects might be incorporated into the management of salmon (Levi et al., 2012).

Goals and Objectives

The goal of this study was to examine if, by attracting bears, the timing of salmon spawning had an indirect effect on ungulate use of riparian areas. The objectives of this study were to:

1. Quantify ungulate and bear presence at salmon spawning sites in the Copper River Delta region.
2. Analyze relationships between bear and ungulate detection data in relation to salmon spawning timing to assess the strength of evidence for indirect effects between salmon and ungulates.

INTRODUCTION

Food Web Dynamics

Trophic levels are a way to categorize ecosystem members based on where they are situated in a food web (Hairston & Hairston, 1993). Idealized food webs usually have four or five trophic levels. The first trophic level consists of producers, species that photosynthesize, harnessing sunlight to produce energy-rich carbon molecules. The second trophic level is primary consumers, those that consume producers. The third trophic level includes secondary consumers which in turn consume primary consumers. Tertiary consumers comprise the fourth trophic level of a food web, and they eat secondary consumers. Finally, occasionally a fifth trophic level will be present and consist of quaternary consumers that consume tertiary consumers. Omnivores and generalist species add complexity to food webs because they can consume species at multiple trophic levels (Hairston & Hairston, 1993).

Keystone species disproportionately influence trophic interactions within ecosystem food webs through their activities, abundance, productivity, and diversity (Paine, 1966, 1969). Loss of these species affects terrestrial plants, scavengers, decomposers, browsers, and stream dwelling fishes. They are of high importance to their communities, and their impact is large relative to their abundance because their function within their communities is unique. Keystone species regulate food web interactions at different trophic levels (Helfield & Naiman, 2006). A classic example of a keystone species is the North American beaver (*Castor canidensis)* whose continued presence and activity in ecosystems helps maintain a healthy ecological community (Naiman, Melillo,

& Hobbie, 1986). Beaver have a positive impact on the types and numbers of terrestrial and aquatic plant and animal species in addition to beneficially influencing channel morphology and the hydrology of entire watersheds. In addition, beaver increase the retention of organic matter, create and maintain wetlands, support nutrient cycling, and modify habitat to promote the biodiversity of vegetation, aquatic invertebrates, fish, amphibians, reptiles, and birds (Naiman et al., 1986). In all of these ways, beavers have a larger effect than one would expect from their abundance alone.

Ecological interactions among ecosystem members are often described as either direct or indirect. Direct ecological effects happen due to a physical interaction between species, such as when one species eats another (Wootton, 1994). When two species have a direct interaction, they can indirectly affect the abundance of a third species (Menge, 1995; Wootton, 1994). An interaction chain occurs when the varying abundance of one species can affect the abundance of another species by changing the abundance of a third species that interacts with both (Wootton, 1994). Broadly, if species A reduces the abundance of species B, and species B reduces the abundance of species C, species A indirectly increases the abundance of species C (Wootton, 1994). The presence of predators in ecosystems can have a direct effect on prey due to their consumption of prey. In addition to exerting direct effects, predators can also have indirect effects on ecosystem resources, such as plant communities, by influencing the space use of prey (Schmitz et al., 1997).

Bear-Salmon Ecosystems

Pacific salmon begin their lives in freshwater rivers and streams, migrate to the ocean, and after spending two to seven years in the ocean, migrate in the late summer and fall back to freshwater spawning sites near where they were born (Quinn, 2005). These spawning sites can be thousands of kilometers away from their ocean habitat. This migration from freshwater to saltwater and back categorizes Pacific salmon as anadromous (Bentley et al., 2014; Gende, Edwards, Willson, & Wipfli, 2002; Hodgson & Quinn, 2002; Quinn, Hodgson, Flynn, Hilborn, & Rogers, 2007). Each of the five species of Pacific salmon have different spawning habitat requirements, including mainstem rivers, off-channel habitat, streams, and lake beaches. Variations in thermal regimes, bed substrate, and streamflow create diversity in the timing of spawning among salmon species, populations within species, and even among individuals within populations (Hilborn et al., 2003). This variation in timing is mostly due to the effect of water temperature regimes on salmon embryo development rates during incubation (Quinn et al., 2007). Among different species and populations, there is variation in the duration of time between a salmon's upstream migration and spawning (Hodgson & Quinn, 2002; Quinn et al., 2007).

The life cycle of Pacific salmon is such that it also provides annual marine-derived subsidies across ecosystem boundaries by way of excretion, gametes, and their mortality (Cederholm, Kunze, Murota, & Sibatani, 1999). Pacific salmon are large and reach high population densities, resulting in a 'conveyer belt' of nutrients and energy to coastal freshwater systems (Gresh, Lichatowich, & Schoonmaker, 2000). Salmon consume most of their nutrients from the ocean and then transport these nutrients with them to freshwater systems when they migrate. One feature of salmon life history that makes them particularly important members of their ecosystems is that they die after successfully spawning. Thus, when these types of fish have a healthy spawning run, carcasses remain that can provide food for a wide variety of terrestrial and aquatic scavengers (Cederholm et al., 1999). These salmon behaviors provide a unique way of moving nutrients upstream and allows marine-derived nutrients to be supplied to both aquatic and terrestrial ecosystems further inland (Cederholm et al., 1999). The movement of salmon nutrients from marine to freshwater to terrestrial ecosystems is an iconic example of a cross-boundary energy and nutrient subsidy (Helfield & Naiman, 2006).

In a 2001 study by Nakano and Murakami, the authors concluded that although food webs can be linked through nutrient transfers across habitats, generally energy flows from the more productive ecosystem to the less productive ecosystem, and in doing so, the more productive system provides significant subsidies to the receiving systems. In addition, they suggest that productivity across habitats might fluctuate seasonally, especially in northern temperate latitudes, due to extreme variations in temperature and light throughout the year (Nakano & Murakami, 2001). Nakano and Murakami (2001) conducted a study of reciprocal subsidies to forest birds and stream fishes by fluctuations in aquatic and terrestrial invertebrate insects across riparian and terrestrial ecosystems. The study found that both forest birds and stream fishes were reciprocally subsidized by the invertebrate prey across the ecosystems, indicating that both fish and bird populations may benefit from and be sustained by the flux of nutrient subsidies that are supplementing their resource budgets (Nakano & Murakami, 2001).

Annual pulses of salmon nutrients propagate through food webs, subsidizing primary producers, invertebrates, fish, and wildlife (Levi et al., 2012, Willson & Halupka, 1995). In a study on Pacific salmon and the ecology of coastal ecosystems, Schindler et al. (2003) noted "terrestrial organisms at nearly every trophic level use salmon-derived nutrients when they are available" (p. 34). The ways in which salmon nutrients are incorporated into an ecosystem fall into five categories: a) flying aquatic insects dispersing nutrients into riparian forests, b) subsurface water flows transporting nutrients to riparian zones, c) floods depositing salmon carcasses on floodplains and nutrients leaching into the soil by invertebrate excretion and microbial decomposition, d) partial consumption by vertebrate scavengers after being removed from the stream by terrestrial predators, and e) consumption by terrestrial predators (Schindler et al., 2003). The variety of vertebrates that consume salmon energy and nutrients have been called the "predator scavenger complex" (Shardlow & Hyatt, 2013). Upwards of 50 wildlife species in coastal southeast Alaska are known or expected to feed on salmon (Willson & Halupka, 1995). Only a few predators (e.g. bears, eagles, wolves), are large or powerful enough to remove live or dead salmon from spawning grounds. The remaining scavengers depend on the large predators, or on abiotic forces (e.g. floods), to make salmon available for scavenging. Once these large predators eat and discard salmon carcasses, these carcasses are then consumed by many different vertebrate scavengers and terrestrial invertebrates that consume and colonize the carcasses (Schindler et al., 2003).

Nutrients derived from salmon also filter into soils via excretion and microbial decomposition during this time to then be taken up by vegetation. The nutrients might also pass up the food chain in the form of biomass when insectivorous species eat the invertebrates that are consuming the salmon (Schindler et al., 2003).

Where bears are abundant, they play a crucial role in transporting salmon nutrients across ecosystem boundaries to riparian and terrestrial ecosystems (Helfield & Naiman, 2006). The interaction between bears and salmon has been called a "keystone interaction" because the subsidy of energy and nutrients is increased in the presence of both species, but not when only one species is present (Helfield & Naiman, 2006). The transfer of these marine-derived nutrients from spawning streams to riparian ecosystems is mediated by bears through partially eaten carcasses and salmon-enriched wastes. An example of bears aiding in the dispersal of salmon-derived nutrients is provided by Schindler et al. (2003). Bears kill a large percentage of salmon populations and carry these carcasses into riparian forests. Coastal Alaskan brown bears will kill live salmon or retrieve the carcasses from river pools and transport them to the bank to be consumed. These salmon are an important seasonal food source for bears, and some bears obtain virtually all of their carbon and nitrogen from salmon (Van Daele et al., 2013). Salmon also contribute to the successful hibernation of bears because they are one of the most nutrient dense foods available to bears in their ecosystem (Hilderbrand et al., 1996).

Ungulates are another group of consumers that likely benefit from salmon's presence in the food web due to the large nutrient subsidy that salmon provide to enhance the growth rate and production of trees and shrubs in terrestrial riparian areas (Helfield &

Naiman, 2001). Moose are the largest member of the Cervidae family and were introduced to the Copper River Delta in 1949. They thrive in the expanding shrub habitat of the Copper River Delta, and they feed on the high quality riparian shrubs that benefit from salmon nutrient subsidies throughout the spring and summer. Moose diets in the Copper River Delta shift seasonally and are comprised of sweetgale and alder in the winter, willows, herbs, grasses, and pond vegetation throughout the spring and early summer, and are primarily composed of willows in the late summer and fall. Moose also use tall alder-willow habitats as calving locations and as cover to prevent predator interactions. (MacCracken, Van Ballenberghe, & Peek, 1997; Tape, Gustine, Ruess, Adams, & Clark, 2016).

The Sitka black-tailed deer, a second ungulate species found in the Copper River system, was transplanted to the Copper River Delta region in 1916 (Kruger & Tyler, 1995). They feed on similar plants to the moose that occupy this region, including a variety of grasses, shrubs, forbs, woody twigs, leaves, and lichens. They tend to inhabit mature spruce forests with a variety of high quality vegetation growing in the understory of these forests, and their ranges vary from season to season depending on snowpack (Hanley, 1984). Similar to the way in which brown bears follow asynchronous salmon resource waves, migrating ungulates also take advantage of vegetation growth waves allowing them to consume high quality forage for the greatest period of time (Deacy, Leacock, Armstrong, & Stanford, 2016; Merkle et al., 2016).

Bear Predation of Ungulates

Both black and brown bears are important opportunistic predators of elk, moose, caribou, and deer (Mattson, 1997; Zager & Beecham, 2006). Their role as opportunistic predators varies due to the availability of prey, alternate foods, and habitat quality (Zager & Beecham, 2006). When ungulate densities are low, predation by bears is additive, in that the mortality of ungulates due to bears causes an immediate reduction in ungulate survival rates. When the density of the ungulate prey approaches the carrying capacity of the system, bear predation may be compensatory, meaning it causes no reduction in overall mortality rates because the mortality from predation reduces mortality from other causes such as starvation (Zager & Beecham, 2006).

Brown bears consume meat when it is available. In addition to their efficiency at catching spawning salmon, they are also effective terrestrial scavengers and predators (Hilderbrand, Hanley, Robbins, & Schwartz, 1999). In a study of Yellowstone bears, Mattson (1997) found that brown bears scavenge and kill 5.5-13.8 ungulates every year, suggesting that ungulates are an important component of the brown bear diet. In a review of elk and moose calf mortality in North America, researchers found that the largest individual source of mortality for these ungulates was predation by bears (Zager & Beecham, 2006). Additionally, predation on ungulates is tied closely to spring weather patterns. Areas without snow see more widespread ungulate space use, and in these times, ungulates are less vulnerable to predation. During high snow years, green-up of vegetation is later and ungulates are spatially restricted due to delayed snow melt, so they may be more likely to have encounters with predators (Zager & Beecham, 2006).

A review of predator-prey dynamics in moose-bear-wolf systems throughout interior and southcentral Alaska found that in nine out of ten multi-year telemetry studies, predation was the most important factor affecting moose population dynamics when compared with other factors such as harvest, malnutrition, disease, and adverse weather (Boertje, Keech, & Paragi, 2010). In these studies, harvest and winterkill were also factors in moose population dynamics, but predation remained the primary factor keeping moose densities low. In low-density post-calving moose populations experiencing bear predation, predators killed up to 41% of moose populations annually. This analysis showed that predators such as brown bears can limit moose populations by killing juvenile moose. In the eight studies used by the authors to determine mortality of moose, black bears (*Ursus americanus*) and brown bears were the most significant predators of moose calves. The combined predation by black bears and brown bears was determined to be the "major cause of mortality among moose calves" (Boertje, et al., 2010, p. 920). This same study also addressed whether brown bears were scavenging or killing adult moose. Results showed that brown bears were effective predators in killing adult moose and they also scavenge on wolf kills of adult moose (Boertje et al., 2010).

Landscapes of Fear

The term "landscape of fear" describes the indirect effect of spatial variation in the predation risk perceived by prey (Laundre et al., 2010). For example, a 2005 study by Creel, Winnie, Maxwell, Hamlin, and Creel provided evidence that ungulates may alter their behavior and use of space and based on the threat of predation. This study detailed the ways in which elk foraging behavior was altered due to the presence of wolves. When there were no wolves present, elk foraged in their preferred, open, grassy habitats. Elk moved into less profitable, forested habitat when wolves were present in the elk's preferred habitat, which also shifted the elk's diet from their preferred grasses to more woody plants. This resulted in a decrease in the quality of food elk were eating (Creel et al., 2005). Meta-analyses of putative landscape of fear effects found that these changes in prey behavior can negatively impact prey populations (Preisser, Bolnick, & Bernard, 2005; Winnie & Creel, 2017).

If prey are encouraged to move to other locations as they respond to the risk of predator presence, this indirect effect may encourage growth of local plant communities (Schmitz et al., 1997). In addition to indirect effects on ecosystem resources, top predators may also have widespread indirect effects on land-based, terrestrial ecosystem functions, such as aiding in carbon cycling. These large-scale ecosystem functions provide important environmental services such as greenhouse gas regulation and ecosystem carbon storage (Wilmers & Schmitz, 2016).

Study Area

Flanked by the Alaska Range and the Wrangell St. Elias, Chugach, and Talkeetna mountains, the Copper River Delta is Alaska's sixth largest catchment area, encompassing 62,960 square kilometers, including 80 linear kilometers of Gulf of Alaska coastline in southeast Alaska (Figure 1) (Adelfio, 2016; MacCracken et al., 1997). It is adjacent to the southern foothills of the Chugach Mountains and the town of Cordova (population: 2,500) located to the west. Human developments within the study region are sparse. The headwaters of the Copper River drain from Copper Glacier in the Wrangell

Mountains. Five valley glaciers terminate on the Copper River Delta, and hundreds of tributaries, lakes, and smaller rivers feed into larger rivers within this ecosystem. The Copper River Delta is characterized by woody wetlands, shrub and scrub, and evergreen forests (Adelfio, 2016). The braided floodplains and lands in this area that are adjacent to running freshwater, including the vegetation and animals who use the vegetation, are often characterized as riparian areas. These areas provide vital ecosystem functions such as filtering pollution, trapping sediments to help keep streams clear, protecting stream banks from erosion, and regulating water temperature due to shade-providing vegetation (Brinson, Swift, Plantico, & Barclay, 1981).

The climate of the Copper River Delta is characterized as transitional between continental and maritime. This region is cool and wet, and the area receives measurable precipitation in the form of rain and snow, on average 220 days per year. The study area also encounters cold and dry continental air masses in the late fall, winter, and early spring months, and snow can occur anytime between October to April (Adelfio, 2016; MacCracken, 1997). The Copper River Delta is protected as critical habitat for fish and wildlife species such as bears, caribou, moose, mountain goats, sheep, wolves, and various birds. This area is also critical spawning habitat for two species of wild salmon that are important to the economy, culture, and ecology of the area: coho (*Oncorhynchus kisutch*) and sockeye (*Oncorhynchus nerka*) (Christensen, Mastratonio, Gordon, & Bormann, 2000).

Figure 1. The Copper River Delta, Adelfio, 2016.

Hypothesis & Prediction

To better understand the relationship among salmon, bears, and ungulates in riparian areas in the Copper River Delta, I tested one of the predictions of the landscape of fear hypothesis. Given the well documented relationships among bears and salmon and bears and ungulates, I sought to understand whether an indirect effect caused by a behavioral response to the "landscape of fear" influenced ungulate space use in my study area. I hypothesized that ungulate occupancy at salmon spawning sites would be less frequent when salmon were present due to the attraction of bears and the threat of predation. I predicted that the number of ungulate detections would diminish with increased numbers of bear detections, and therefore there would be a negative relationship between bear and ungulate presence in riparian areas. I predicted that the number of ungulate detections would decrease as the number of bear detections increased across all sites.

METHODOLOGY

Field Collection

Field technicians mounted remote cameras beginning in 2013 throughout the Copper River Delta at various site locations (Figure 2). The field sites were originally chosen to capture the breadth of thermal and hydrological variation in the study area and with consideration for the logistical challenges of working in remote areas. Because of logistical constraints, there has been some variation in number of cameras set up among sites from year to year, most recently with nine cameras set up in 2019. The study sites were each in a unique catchment area in the Copper River Delta and were known spawning and rearing habitats for coho and sockeye salmon (Adelfio, 2016). The images from these cameras have since been used to study mammals, birds, and fish in these locations. The photographs from these field cameras were downloaded periodically throughout each season by field technicians and uploaded to an external hard drive to house the data from each year.

Figure 2. Sampling of remote camera monitoring sites, Cordova Ranger District, 2018.

Image Coding

In the fall of 2019 and winter of 2020, I viewed and labeled, or tagged, the photographs from each monitoring site with keywords to note the consumers observed at each site. These keywords were designed to note the types and numbers of species at these remote camera locations. Some examples of descriptive keywords for photo organization included, but were not limited to: moose, deer, brown bear, black bear, and salmon. The tagging process included tagging any carnivore or ungulate partially or wholly within the frame of the photo. Ungulates with calves were treated as a single, independent ungulate, and bears with cubs were also treated as a single, independent bear for tagging purposes. There were instances when it was difficult to identify the animal in the frame due to poor lighting and there were also cases when the body was not wholly within the frame. In these cases, experts were consulted. When there was no consensus, the record was disregarded.

Data Handling

After the photographs for each site were reviewed, tagged, and organized within the hard drive, custom scripts written for the R programming environment were used to process the tagged photographs (R Development Core Team, 2018). This process extracted tags from the photographs for later analysis. The resulting Microsoft Excel spreadsheets of tagged photographs were then organized in the hard drive by site name and year. These site files were then combined into a larger, master file for later analysis.

Due to technological issues, occasionally there were errors in date and time associated with some groups of photographs. Date and time errors were corrected using information provided by the technicians who checked the camera sites periodically throughout the season. Species names, keywords, and group numbers were also adjusted and corrected during this process for consistency and clarity. This master file was then exported for additional analysis.

Data Analysis

For the main analysis, I compared five models in R to determine if ungulate detections differed with variation in bear detections. Relationships between salmon presence and bear and moose detection data were analyzed using generalized linear modeling techniques. To exclude sites without enough data for statistical tests, only sites with ten or more ungulate detections were used in analysis. All analyses were performed using the open access statistical program R version 3.5.0 (R Development Core Team, 2018). The error distributions of the models used were chosen because they were appropriate for handling count data as well as potential over-dispersion. The models used were the negative binomial, Poisson, zero-inflated Poisson, zero-inflated negative binomial one, and zero-inflated negative binomial two. The Poisson model and negative binomial models were the first models used in this suite of models because the data for this analysis was count data. These models proved inappropriate because the data was over-dispersed, meaning there was greater variability than expected, or the data was zero-inflated, meaning that there were more zero values than one would expect. Due to these reasons, I then included the other models that accounted for over-dispersion and zero-inflation. Among the suite of models which did not violate generalized linear model assumptions (determined with quantile-quantile plots to test for normal distribution of errors), I selected the model with the lowest small sample size-corrected Akaike Information Criterion (AICc), an information-theoretic criterion, as the single best model (Akaike, 1974). It is important to note that the assumption of independence is slightly violated with these models because of the time series data I was working with. The nature of the time-series data used should not affect the results, and I did not want to fit time-series models because I did not want them to be intractably complicated. Results from this single top model were then used to evaluate the evidence for a relationship between ungulate and bear detections at all site locations and all dates of monitoring. I was not able to fit models with a random effect for site because there was not enough data to allow the model-fitting algorithm to converge. The results of this analysis were graphed and examined for patterns and trends.

Further analysis was done by site to examine overlap in ungulate and bear detection data. Only sites that had 10 or more ungulate detections were used for further analysis. The sites that had less than 10 ungulate detections and were not used for further analysis were 20 Mile (zero ungulate detections), 25 Mile (two ungulate detections), Bering Lake (one ungulate detection), and Martin Lake (two ungulate detections). When graphs displayed overlap in ungulate and bear detection by week, these detections were only analyzed further if they occurred during core salmon spawning runs. Detections outside of runs were not submitted to further analysis. Distributions of bear and ungulate detections as well as salmon spawning durations at these locations were graphed and inspected, and the observed patterns were qualitatively analyzed.

RESULTS

Modeling Ungulate Detections

I collected total detections from 12 sites across 7 years, and I coded 100,645 pictures (Table 1).

Table 1. Ungulate and Bear Detection Totals at Monitoring Sites in the Copper River Delta, 2013-2019.

Site	Moose	Deer	Black Bear	Brown Bear	Total Ungulates	Total Bears
18 Mile	44	0	33	22	44	55
20 Mile	0	0	24	80	0	104
25 Mile	2	0	23	42	2	65
Bering Lake	1	0	7	64	1	71
Black Hole Creek	9	2	31	72	11	103
Ibeck Creek	11	0	1	41	11	42
MA Eyak Lake	0	13	212	522	13	734
Martin Lake	2	0	0	15	2	15
Martin River	12	0	2	237	12	239
McKinley Lake	2	15	1773	100	17	1873
Power Creek	1	9	9	147	10	156
Salmon Creek	14	1	235	198	15	433
All Site Locations	98	40	2350	1540	138	3890

I then analyzed all 12 site locations for combined ungulate detections and combined bear detections. Both bears and ungulates were detected at 11 of the 12 study sites, but only bears were detected at the 20 Mile location (Figure 3).

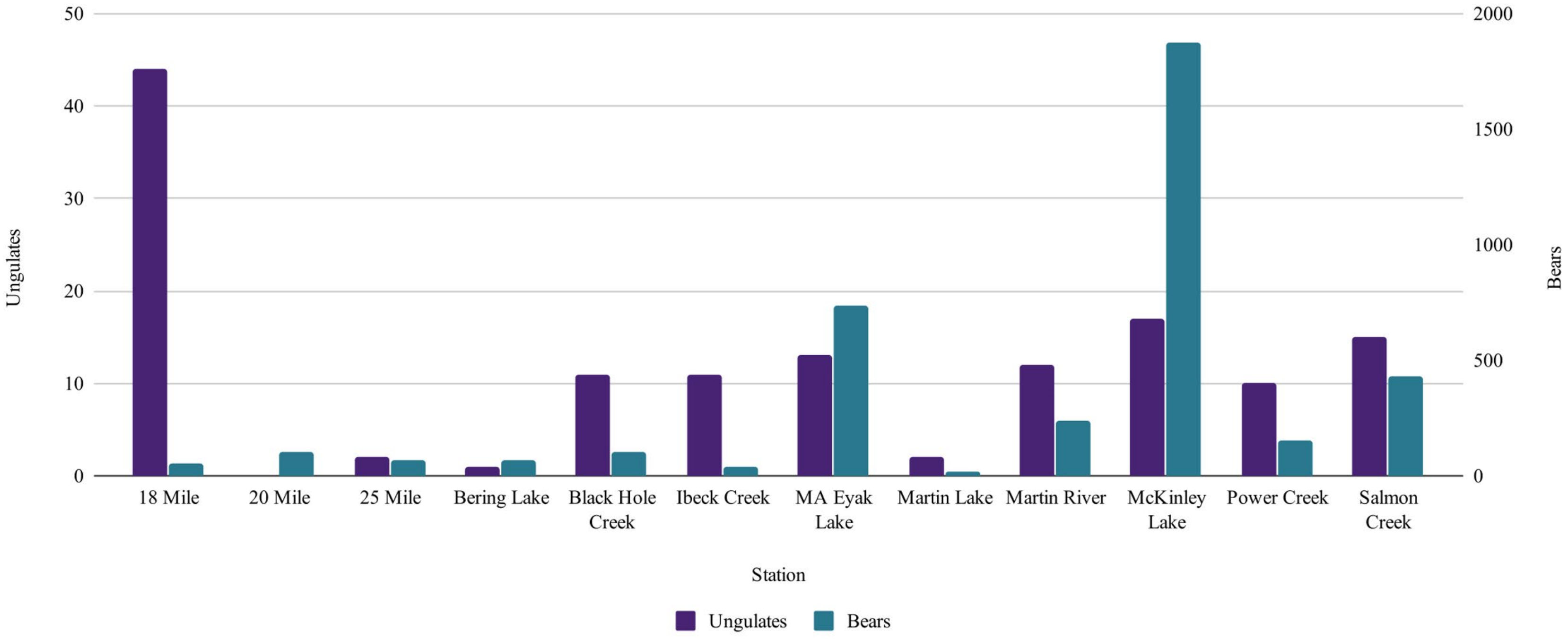

Figure 3. Detections of ungulates and bears across all study sites, (*n*=12).

I further analyzed all sites for individual moose, Sitka black-tailed deer, black bear, and brown bear detections (Figure 4).

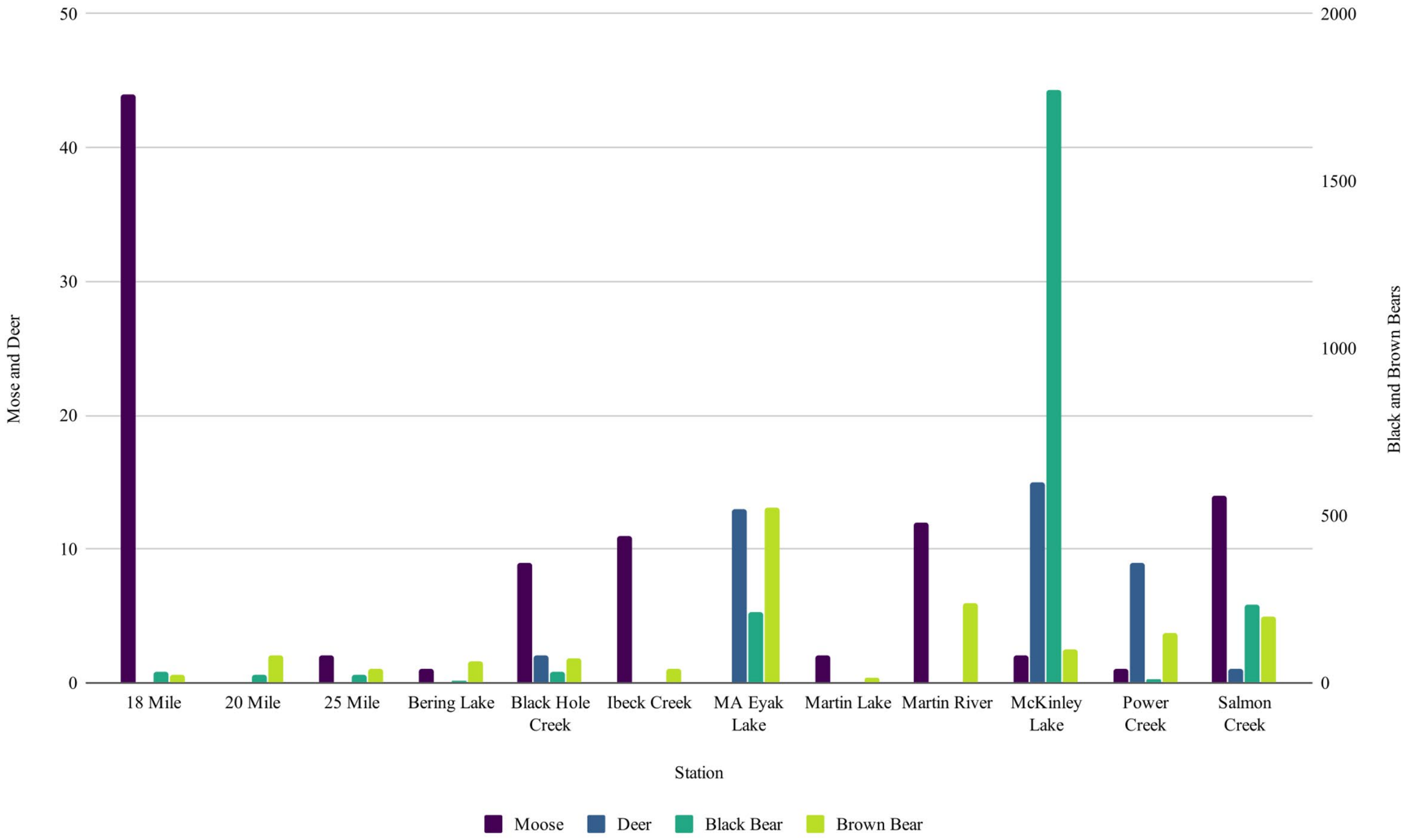

Figure 4. Detections of moose, Sitka black-tailed deer, black bears, and brown bears across study sites, (*n*=12).

Analysis of seven years of bear and ungulate detections by week across all 12 sites and 7 years of monitoring provides an overall picture of the detections, but it does not account for interannual variation with detection abundance (Figure 5). During this time period, there were a total of 138 ungulate detections and 3,890 bear detections. The mean core sockeye salmon spawning period was between weeks 25 and 34. The mean core coho salmon run duration was between weeks 36 and 44. During the sockeye salmon spawning time, there was overlap in ungulate and bear detections from weeks 25 to 33. Week 34 was the only week during the average sockeye spawning run that did not have overlap in ungulate and bear detections. During the coho salmon spawning times there was ungulate and bear detection overlap in weeks 37, 39, 41, 42, and 44.

Figure 5. Ungulate and bear detections by week across all monitoring years and across all monitoring sites. The average sockeye salmon spawning timing is noted in light green shading and the average coho salmon spawning timing is noted in dark green shading.

Detection count data for the main model was summed across years and site by week, and weeks one through fifteen were removed from analysis because bears typically hibernate at this time. This resulted in a sample size of 38 weeks (*N*=38). Results from the zero-inflated negative binomial two model, analyzing eight sites that had ungulate detections of 10 or more, indicated that increased bear detections were associated with decreased ungulate detections at salmon spawning site locations, and predictions suggest that ungulates avoid known salmon spawning riparian areas when bears are present (Figure 6). The zero-inflated negative binomial with quadratic parameterization of the variance did not violate assumptions and had the best fit according to AICc (Hardin & Hilbe, 2007).

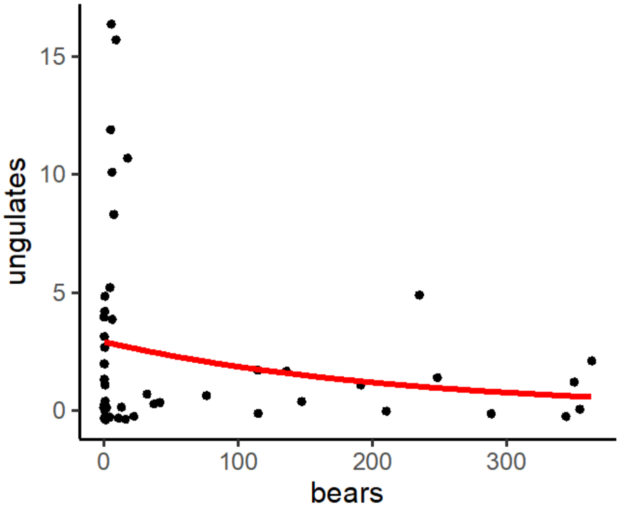

Figure 6. Number of ungulate detections as a function of bear detections at monitoring sites, (*N*=38). The red line shows the estimated relationship between ungulate counts and bear counts from a zero-inflated negative binomial model (estimated slope on the link scale = -0.004497, *z*= -2.212, *P*=0.027). Points are jittered to avoid over-plotting.

Detections Among Individual Monitoring Locations

Further individual site analysis was done for sites with ten or more total ungulate detections (*n*=8).

18 Mile

Ungulate and bear detections were collected at the 18 Mile site over three years from 2013 to 2015, and coding occurred among 5,434 pictures. There were 44 ungulate detections and 55 bear detections during this time (Figure 7). Coho salmon spawning was detected at this site between calendar weeks 37 and 45. The figure shows that during this spawning timeframe for the years 2013 through 2015, there were no ungulates detected, and there were bear detections. An overlap of ungulate and bear detections was observed only in week 25, which was outside of the core salmon spawning time, for the years that data was being collected.

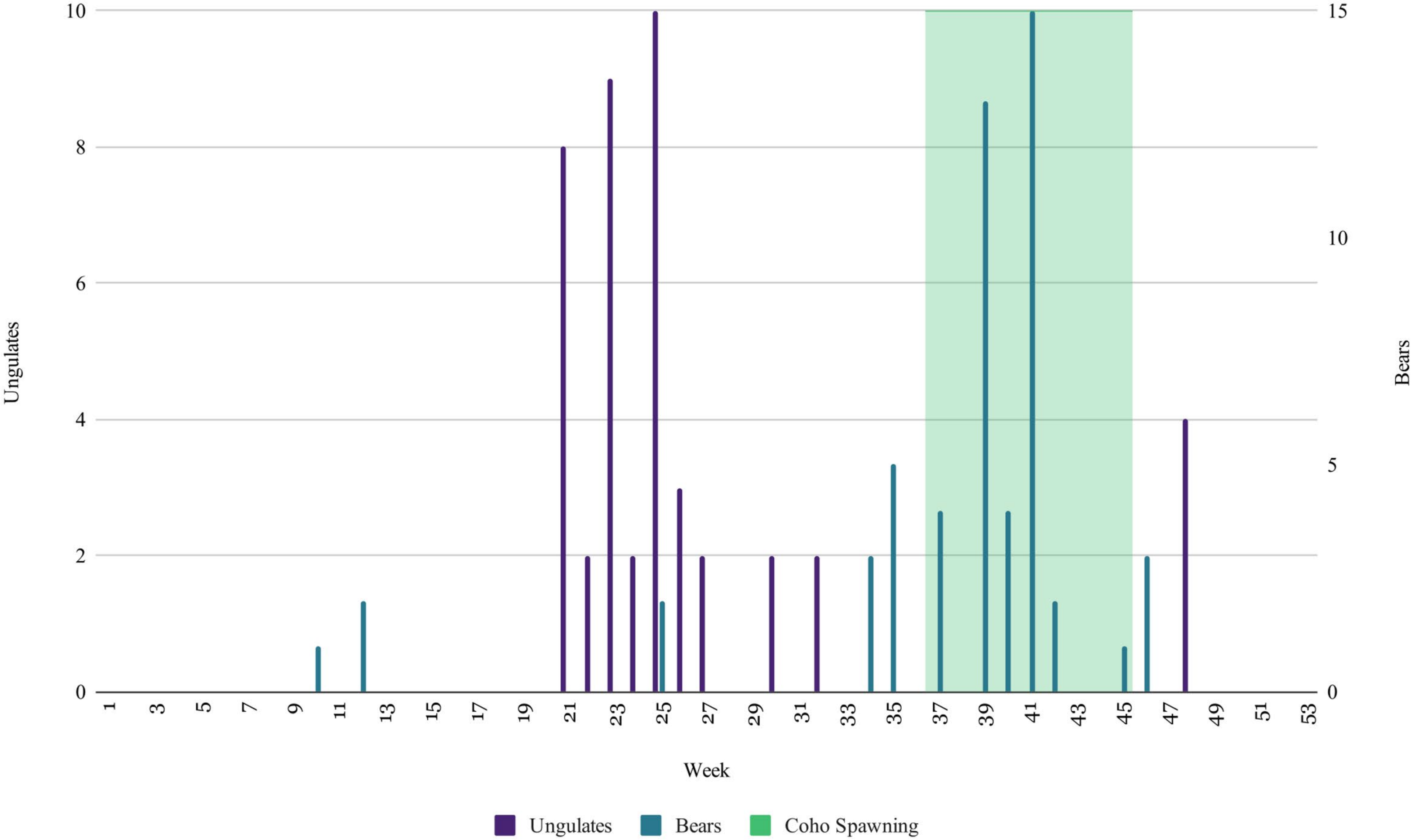

Figure 7. Combined ungulate and bear detections by week at the 18 Mile monitoring site. Coho salmon spawning duration is noted in dark green shading, taking place from calendar week 37 to week 45.

Black Hole Creek

Ungulate and bear detections were coded in 2,501 photographs, collected over seven years at Black Hole Creek from 2013 through 2019. There were 11 ungulate detections and 103 bear detections during this time frame (Figure 8). Coho salmon spawning has been detected at this site from calendar weeks 36 to 44. Throughout the monitoring timeframe at this location, there was an overlap in ungulate and bear detections during weeks 26 and 38. There was one ungulate detection that overlapped with bear detections during salmon spawning, week 38, and upon further analysis, it was determined that this overlap is only due to combining detections across multiple years, and not indicative of detection overlap in the same week of the same year.

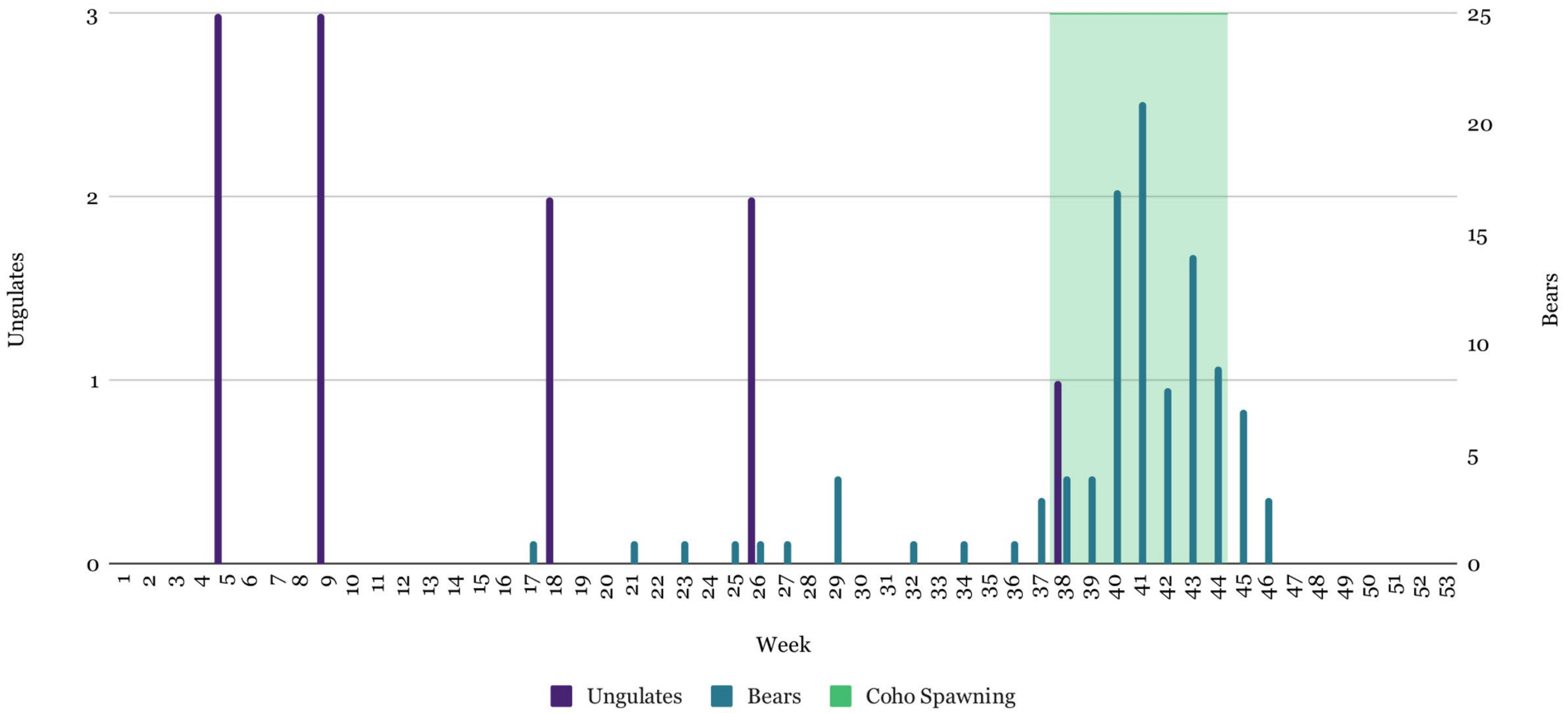

Figure 8. Combined ungulate and bear detections at the Black Hole Creek monitoring site. Coho salmon spawning duration is noted in dark green shading, taking place between calendar weeks 38 and 44.

Ibeck Creek

Ungulate and bear detections were coded in 11,976 photographs, collected over three years at Ibeck Creek from 2013 through 2015. There were 11 ungulates and 42 bear detections during this time period (Figure 9). Coho salmon spawning was detected at this site from calendar weeks 34 to 42. There were no ungulate detections during salmon spawning times over this time frame, and there was no overlap in ungulate and bear detections by week at this field site.

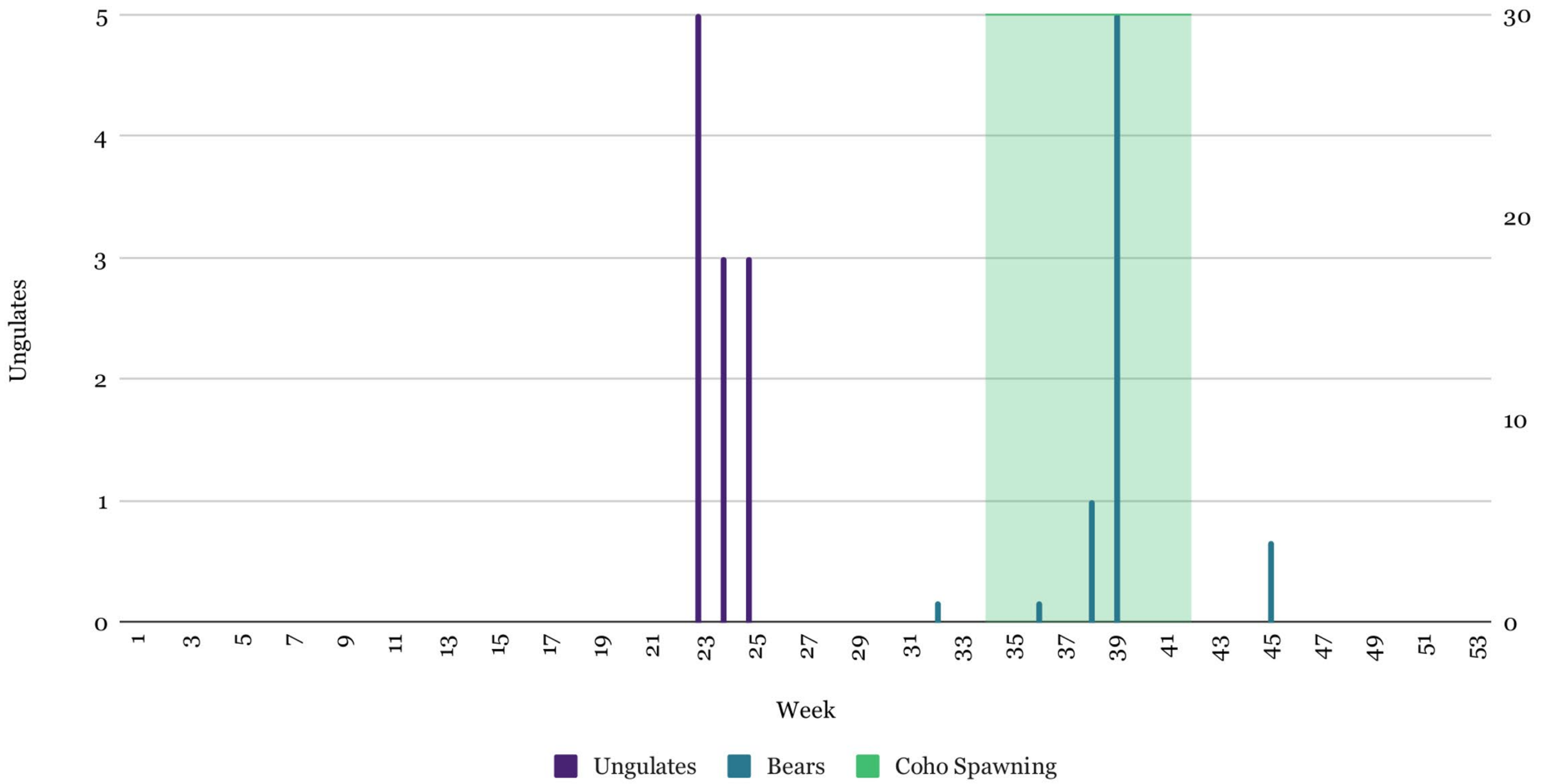

Figure 9. Combined ungulate and bear detections at the Ibeck Creek monitoring site. Coho salmon spawning duration is noted in dark green shading, taking place between calendar weeks 34 and 42.

Middle Arm Eyak Lake

Ungulate and bear detections were coded in 8,413 photographs, collected for five years at the Middle Arm Eyak Lake site from 2013-2015, and 2018-2019. Throughout this time frame, there were 13 ungulate detections and 734 bear detections (Figure 10). Sockeye salmon spawning was detected at this site from calendar weeks 18 to 32, and coho salmon spawning was detected at this site from calendar weeks 37 to 44. This figure shows that there was ungulate and bear detection overlap during sockeye salmon spawning in weeks 19 and 21. Upon further analysis, there was once instance of overlap of ungulate and bear detections in week 19 on May 7, 2019. Six ungulates (Sitka black-tailed deer) and one brown bear were detected that day. Detection overlap in the other weeks was due to detections being summed by week across the years of monitoring. Upon further analysis, there were no other overlap detections among ungulates and bears during the weeks previously mentioned. Additionally, there was no ungulate and bear detection overlap during coho spawning. Week 34, after sockeye spawning and before coho spawning, did experience overlap in ungulate and bear detections, but was not analyzed.

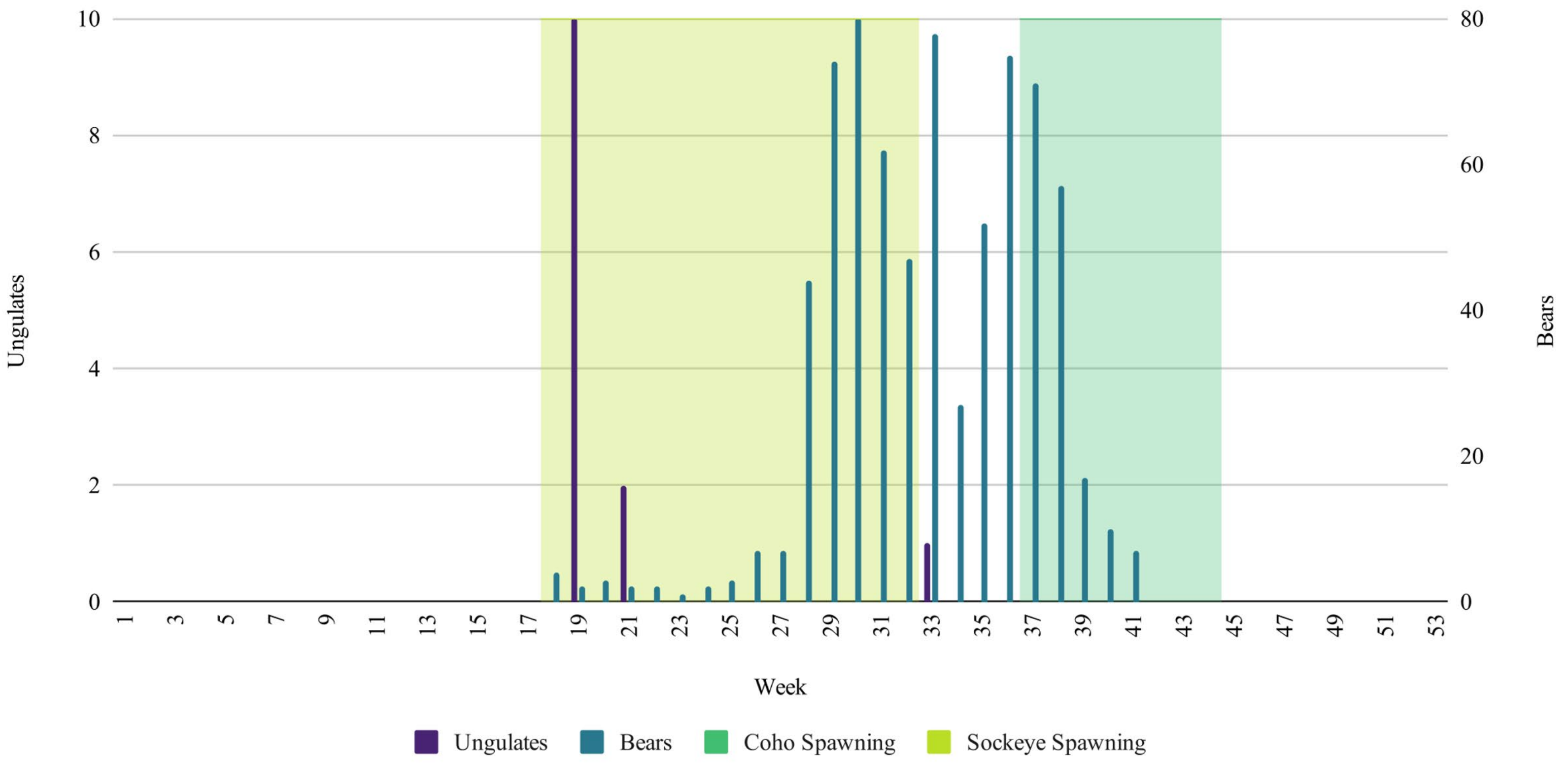

Figure 10. Combined ungulate and bear detections at the MA Eyak Lake monitoring site. Sockeye salmon spawning duration is noted in light green shading from weeks 18 to 33, and coho salmon spawning duration is noted in dark green shading from weeks 37 to 44.

Martin River

Ungulate and bear detections were coded in 2,247 photographs, collected for three years at Martin River from 2013 through 2015. During this time frame, there were 12 ungulate detections and 239 bear detections (Figure 11). Sockeye salmon spawning was detected at this site from calendar weeks 26 to 32, and coho salmon spawning was detected at this site from calendar weeks 34 to 42. There was no overlap in ungulate and bear detections during salmon spawning times, but there was an overlap in ungulate and bear detections in week 45, which was outside of core salmon spawning timing and was not analyzed.

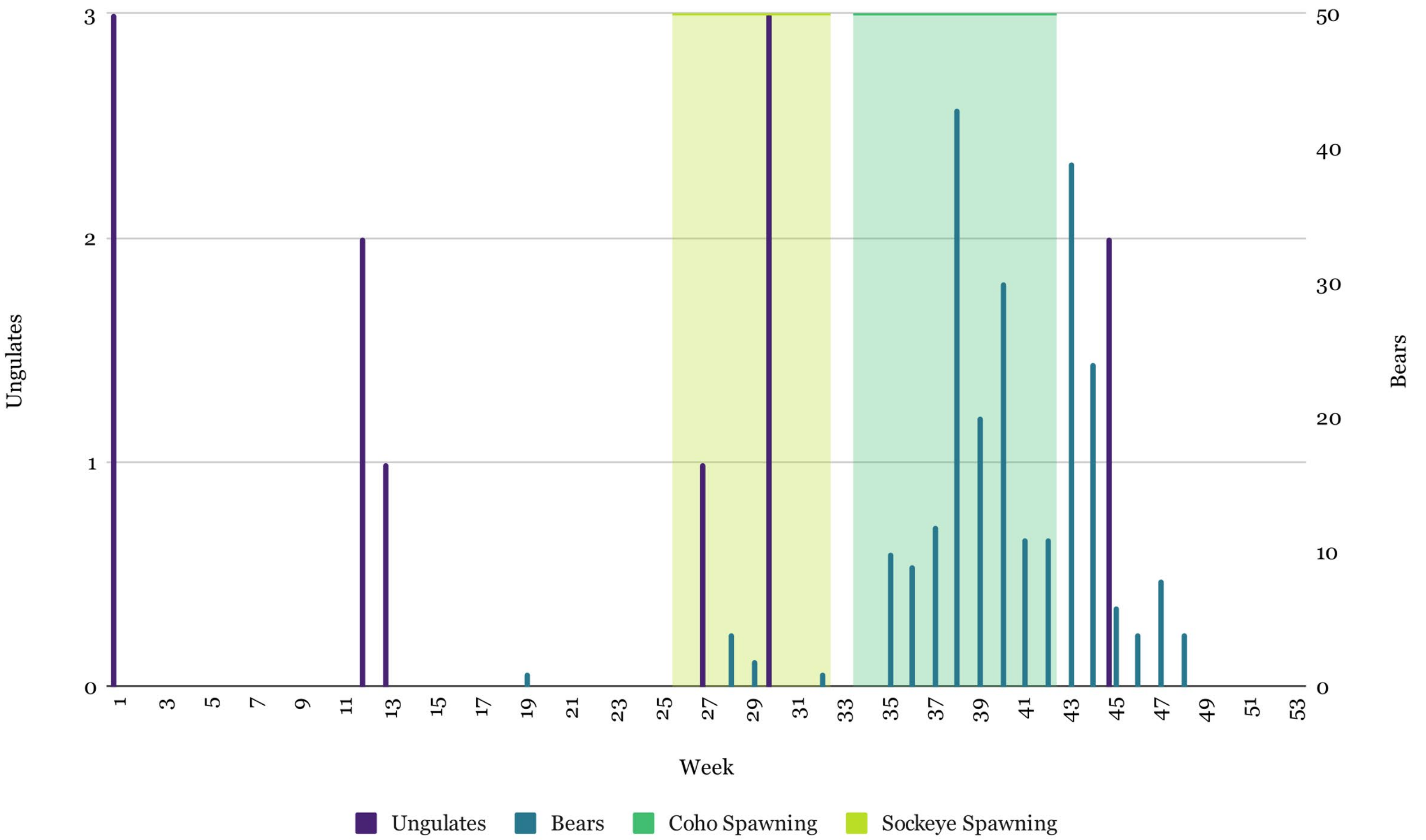

Figure 11. Combined ungulate and bear detections at the Martin River monitoring site. Sockeye salmon spawning timing is noted in light green shading, between weeks 26 and 32. Coho salmon spawning timing is noted in dark green shading, between weeks 34 and 42.

McKinley Lake

Ungulate and bear detections were coded in 22,849 photographs, collected over six years at McKinley Lake from 2013 through 2018. During this time frame, there were 17 ungulate detections, and 1,873 bear detections (Figure 12). This site had the highest number of bear detections of all the monitoring sites. Sockeye salmon were observed spawning at this site between calendar weeks 26 and 34. During the sockeye salmon spawning duration, there was an overlap in ungulate and bear detections during week 26. Upon further analysis, although there were ungulate and bear detections during week 26 when summed across the years of monitoring, there was no overlap of ungulate and bear detections during week 26 of a single year. Other overlaps in ungulate and bear detections were in weeks 24 and 25, and these were not analyzed because they were prior to the time that sockeye salmon typically spawn at this site.

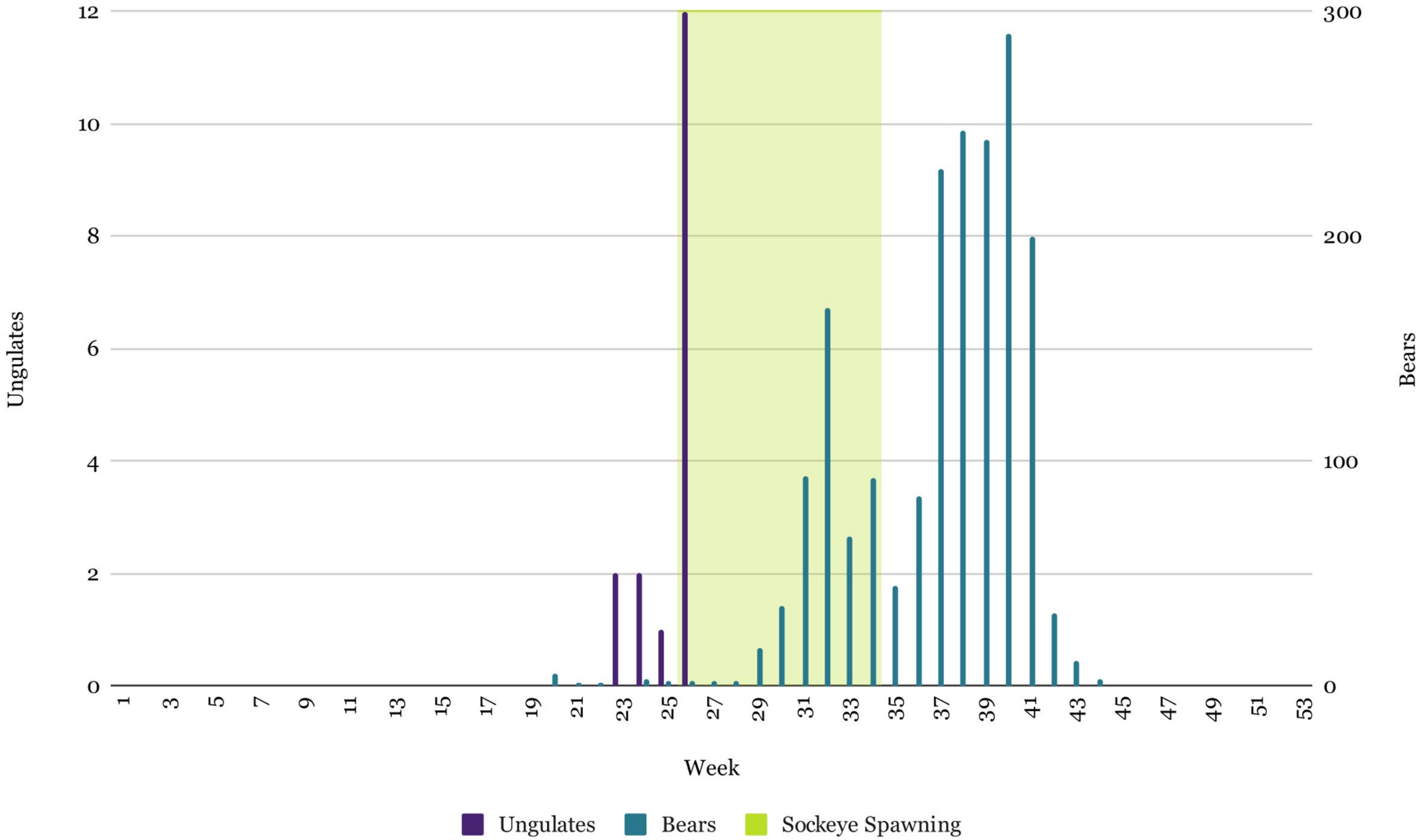

Figure 12. Combined ungulate and bear detections at the McKinley Lake monitoring site. Sockeye salmon spawning timing is noted in light green shading between weeks 26 and 34.

Power Creek

Ungulate and bear detections were coded in 858 photographs, collected over six years at Power Creek from 2014 through 2019. During this time, there were 10 ungulate detections and 156 bear detections (Figure 13). Sockeye salmon were observed spawning between weeks 26 and 35 at this location, and coho salmon spawning was observed between weeks 38 and 47 at this site. During the sockeye salmon spawning time, there was overlap in ungulate and bear detections in weeks 26, 28, 30, and 31. Upon further analysis, despite overlap in ungulate and bear detections summed by week across all years, there was no detection overlap of ungulates and bears by week when broken down from year to year. During the coho salmon spawning time, there was overlap in ungulate and bear detections during week 43. Upon further analysis, in week 43 of 2017, on October 23, there was one ungulate detection, a Sitka black-tailed deer, and two brown bear detections.

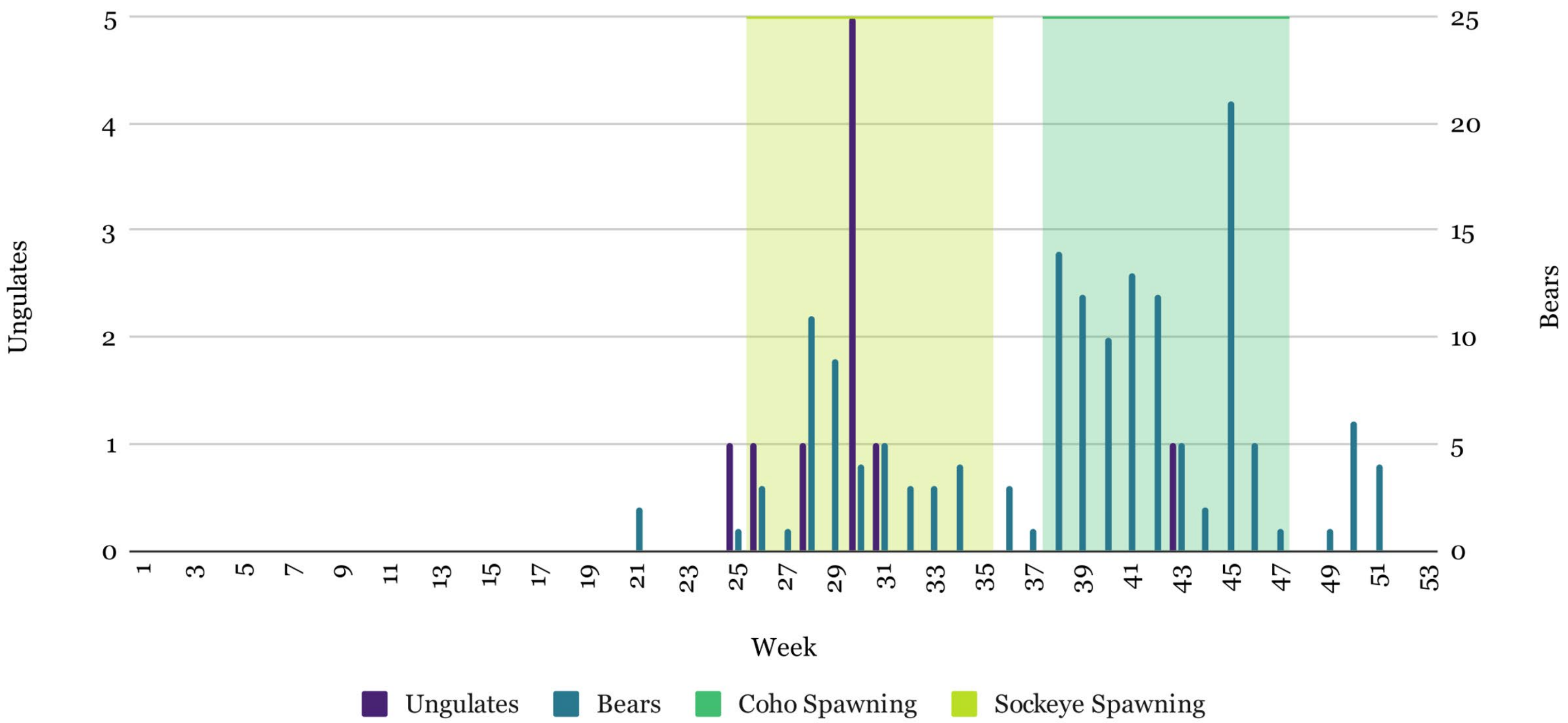

Figure 13. Ungulate and bear detections at Power Creek monitoring site. Sockeye salmon spawning timing is noted in light green shading between weeks 26 and 35, and coho salmon spawning timing is noted in dark green shading between weeks 38 and 47.

Salmon Creek

Ungulate and bear detections were coded in 23,119 photographs, collected for seven years at Salmon Creek from 2013 through 2019. Over this time period, there were 15 ungulate detections and 433 bear detections (Figure 14). Sockeye salmon were observed spawning at this location between calendar weeks 28 and 35, and coho salmon were observed spawning at this location between calendar weeks 37 and 44. During times of salmon spawning, there was no overlap in weekly ungulate and bear detections. There were times of ungulate and bear detection overlap in calendar weeks 23 and 25, which was not analyzed because it was outside of core salmon spawning timing.

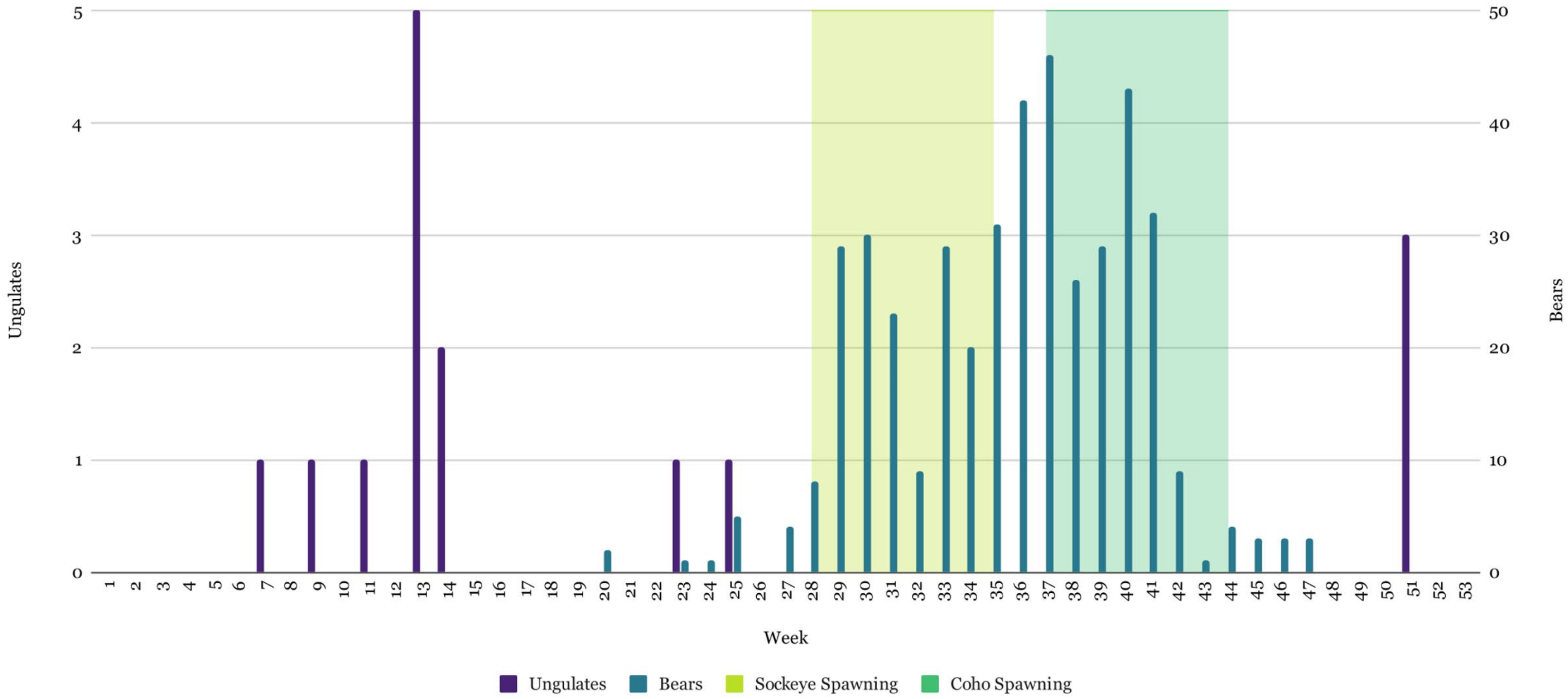

Figure 14. Ungulate and bear detections at the Salmon Creek monitoring site. Sockeye salmon spawning timing is noted in light green shading between weeks 28 and 35, and coho salmon spawning timing is noted in dark green shading between weeks 37 and 44.

DISCUSSION AND CONCLUSION

The results of this study suggest that increases in bear detections are associated with decreases in ungulate detections (estimated slope on the link scale=-0.004497, z= -2.212, P=0.027), indicating that in times when bears are frequenting riparian areas, ungulates tend to be elsewhere. These results provide observational evidence consistent with the hypothesis that salmon can indirectly influence ungulate space use by attracting bears. Generally, ungulates are likely to occupy riparian habitat of known salmon spawning locations in the winter and spring, but they shift away from these locations as bears populate them in the summer and fall. Previous studies and meta-analysis on the landscape of fear concept have identified that due to predators' exertion of pressure on their prey populations, prey behavior may be influenced and changed, and this study on ungulate and bear interactions in the Copper River Delta supports this body of work (Creel et al., 2005; Laundre, Hernandez, Medina, et al., 2014; Laundre, Hernandez, & Ripple, 2010; Preisser et al., 2005; Winnie & Creel, 2017). Through these effects on prey species, predators may indirectly influence the structure of plant communities, thus causing a trophic cascade, or changes throughout an ecosystem due to a disruption at any trophic level (Winnie & Creel, 2017). The costs of the defensive strategies used by prey in these predator-prey landscape-wide interactions include lower energy income, greater energy input for defense mechanisms, lower mating success, increased vulnerability to other predators, and emigration (Preisser et al., 2005). This model sheds light on how ungulates respond to predation risk from bears, and it supports a central prediction from the hypothesis that ungulate detections should decrease as bear detections increase, but further studies are needed to identify ways in which moose and Sitka black-tailed deer alter their space use in response to the risk of predation by bears when bears are occupying known salmon spawning locations.

Further studies are also needed to identify whether or not this shift in space use is due to the timing of spawning salmon. It is well documented that salmon is an important component of the diet of coastal bears, and bears will move across landscapes in order to take advantage and prolong their access to salmon populations (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Deacy et al., 2019; Fortin, Farley, Rode, & Robbins, 2007). Analysis of individual site locations indicates that there was one instance of ungulate and bear detection overlap during core salmon spawning runs on May 7, 2019 at the Middle Arm Eyak Lake monitoring site, and one ungulate and bear detection overlap at the Power Creek monitoring site on October 23, 2017. These two occurrences are rare within the parameters of our data, and although they may suggest very little overlap of ungulates and bears at salmon spawning sites during core salmon runs, I did not have enough data to fit the models to individual site locations because of inflation. Although there is a shift in ungulate space use when bears are present, I was unable to establish a causative link between whether the timing of spawning salmon had an effect on overall ungulate space use due to the space use of bears.

This study was conducted using photographs from remote cameras initially chosen to capture the breadth of thermal and hydrological variation in the study area. Site locations and camera locations at those sites were not set up with the initial purpose to test ungulate and bear detections. To better test ungulate and bear detections, this study design could be improved in a number of ways. First, setting up remote cameras at a reference site without salmon, such as above a waterfall, would provide a control in which to monitor detections of ungulates and bears and compare to sites that do have core salmon runs. Although challenging, another improvement to the study design would be monitoring a reference site without bears- this would provide insight into ungulate space use in the absence of predators. In addition, setting up multiple cameras at all study sites would provide a better overall picture of the site and the animal movements within it. Multiple angles could potentially help identify those animals that were obscured or only partially within the frame of our existing data set. Furthermore, identifying new site locations with both core salmon runs and higher populations of ungulates and bears may provide more ungulate detections and a greater collection of data to analyze. With these improvements to the study design, additional information about climate, topography, vegetation, and other animal space use might provide greater insight to the effect that core salmon runs have on ungulate space use due to the space use of bears.

Due to our limited collection of data and time constraints, there are additional hypotheses and predictions that I was unable to test. Research has shown that bears are important predators of ungulates, although the intensity of predation pressure and the demographics of killed ungulates can vary greatly among locations (Mattson, 1997; Zager & Beecham, 2006). With increased data collection methods, one could test to see if there was a difference in the presence of black bears or brown bears on ungulate space use. One could go even further to test whether the space use of moose is significantly altered by either black or brown bears, or whether the space use of Sitka black-tailed deer is significantly altered by either black or brown bears. Ungulate demography could also be analyzed, looking for patterns and trends in predation by black and brown bears of both moose and Sitka black-tailed deer calves and adults. Studies in Yellowstone National Park, southcentral Alaska, and throughout North America have shown that predation by bears is a primary source of ungulate mortality, but especially in calves (Boertje et al., 2010; Mattson, 1997; Zager & Beecham, 2006). For example, bull moose are larger and somewhat less vulnerable to predation than cows and calves, so their behavior and space use may differ. A broader view of predator-prey relationships could allow for testing a hypothesis about how predators in general might affect the space use of ungulates. Remote cameras recorded 162 coyote detections, 25 wolf detections, and 9 wolverine detections across the various study sites. With increased monitoring at existing sites, or increased site locations, these predator-prey dynamics could be explored by site as well as overall in the Copper River Delta. Exploring these dynamics could have implications for ungulate and bear conservation and management throughout this region. In this study, hypotheses about vegetation quality impacting ungulate movement were not able to be tested, but studies of this nature might provide greater insight into the spatial variability of ungulate movement patterns. With improvements in study design and increased monitoring, testing these additional hypotheses would provide greater insight into these bear-salmon-ungulate ecosystems.

In conclusion, my study highlighted an intriguing pattern in ungulate space use and posited a plausible explanatory mechanism: salmon, by controlling where and when bears collect on the landscape, create a dynamic landscape of fear to which ungulates respond. Although it was determined that ungulate detections do decrease as bear detections increase, I was not able to say with certainty that this is due to the presence of spawning salmon throughout the study area. This study only scratches the surface of what could be a deep dive into landscape level ecosystem studies to determine the influence that bears and salmon have on ungulate space use and populations in the Copper River Delta. These studies may also offer insights into the potential magnitude the impact salmon has on the prey of large predators, other herbivore densities, plant communities, riparian area morphology, and essential ecosystem functions.

VALUE

Implications for Personal Practice & Teaching Science

I am eager to use the skills and knowledge that I gained throughout this project to inform my teaching practice in the future. I believe students learn best when they are interested and invested in the questions they are seeking to answer. The idea for this project was generated after I participated in a wildlife ecology class through the Master of Science in Science Education program in the summer of 2019. In this class we explored wildlife communities of Yellowstone National Park and emphasis was placed on learning about hypotheses of trophic cascades related to Gray Wolves (*Canis lupus*) and their associated habitats in the park. When I returned from this immersive learning experience, I spoke excitedly with anyone who listened. When I approached Dr. William Deacy about doing a scientific research project for my MSSE capstone project, he was able to help me identify questions and develop a study that related to topics I had learned about previously. He encouraged me to use what I had learned about in Yellowstone National Park, apply it to another landscape, and engage in the scientific process with his support.

I am so fortunate to have had the opportunity to engage in this research project and broaden my understanding of ecology and scientific research. As an educator, I strive to provide hands-on, relevant learning experiences in the field of science. Through an inquiry approach, I encourage my students to ask authentic questions and use critical thinking and problem solving as conduits to becoming active and caring participants in their local and global communities. Engaging in this authentic scientific research provided an opportunity for me to become a student again. I was able to put myself in the place of my students and challenge myself to think critically, just as I ask them to do. I needed to ask relevant questions, evaluate complex material, develop ingenuity, and seek alternative perspectives in order to complete my project, and because of this, I have a better understanding of how to encourage my students to do the same. I hope that by sharing my process and research with my students, they can see that we can all be scientists as well as lifelong learners.

By exposing students to and helping them engage in developmentally appropriate content that is relevant to them and their local communities, I can encourage them to ask good questions that have broader implications beyond their backyards. For example, we have riparian and terrestrial habitats within a short distance from our school. I can imagine taking students to these places and asking them to observe interactions among abiotic and biotic factors and generate questions. Then, I can encourage students to seek answers to these questions, through applicable scientific research that they have designed to address their question of interest. Ultimately, I hope that engaging in relevant scientific research experiences will inspire my students to strive toward a more sustainable world.

Implications for Science Education

As a science teacher at a small, progressive school, I try to weave the tenants of progressive education into my curriculum and classroom. Science education is easily housed within a progressive education. Participation in scientific inquiry encourages student voice and choice in curriculum and topics as well as active participation in learning, fosters a curiosity and desire to learn, and helps students discover passion and purpose that hopefully will remain with them through adulthood. This project and process, although a part of a more traditional university program, exemplified progressive education from the beginning. I was able to follow my interests and choose a project that dovetailed with them. From developing a question and a research plan, to collecting and analyzing data, and collaborating with others throughout this, I was an active participant and learner throughout this project. The process itself fueled my curiosity and desire to learn more. Perhaps most importantly, because of this experience, I am even more passionate about science education and its importance than I was before I entered this program. Working through each part of this project while teaching fifth through eighth grade science full time both gave me confidence in my own scientific abilities and knowledge, and it also helped me understand more deeply how each step of this process is beneficial to a student's educational growth and how science education fits within a progressive education.

This project and process helped me grow both personally and professionally. I feel fortunate to work as a member of a small teaching team who encourage one another to grow in their field and in their profession. I am empowered to share both my research and the research process with my team and other colleagues at my school, so that they might be inspired to do their own research that will grow their practice and benefit our students. I also hope that I can use my experience of collaborating with professionals who span multiple disciplines to encourage and foster collaboration among my colleagues. I am optimistic that my students might have the opportunity to further integrate their science education in an interdisciplinary way among many other subject areas at school. This project required drawing on many content areas in addition to science such as writing, technology, math, history, and geography. This project and experience, although rooted in scientific concepts and research, also required comprehensive knowledge and demonstrated ability in many subjects. Indeed, in our world we so rarely work in isolation from one another, and I would like to empower students to integrate and apply their learning and knowledge across disciplines so that they may become well-rounded, knowledgeable, and collaborative citizens.

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