

POPULATION DYNAMICS OF BROWN BEARS ALONG BROOKS RIVER IN KATMAI NATIONAL PARK,  
ALASKA

By

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## ABSTRACT

### POPULATION DYNAMICS OF BROWN BEARS ALONG BROOKS RIVER IN KATMAI NATIONAL PARK, ALASKA

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Measuring wildlife population demographics can be challenging especially in remote areas such as Katmai National Park, Alaska. Here concerns over dramatic changes in number of brown bears (*Ursus arctos*) seen using Brooks River have led to questions about whether the population has changed. Fortunately, individual bears congregating on salmon spawning streams can be identified by unique physical and behavioral features, which has allowed creation of a long-term, non-invasive record of individual brown bears using Brooks River.

We used these bear identification records from 2000–2018 in a mark-recapture framework to estimate age-sex specific survival. We found no changes in survival or relationship between survival and sockeye salmon (*Oncorhynchus nerka*) escapement. We then used the bear records as a time series of counts in a state-space model to estimate abundance and productivity from 2000–2019. Bear abundance was positively related to sockeye salmon escapement in previous years. However, only some age-sex groups exhibited this relationship. Abundance of breeding females and their cubs was positively related to salmon escapement from the same year, which may indicate they were avoiding Brooks River during years when escapement was low and competition among bears was high. The relationship between annual escapement and productivity measures were not significant, although there were signs that a change in productivity may have occurred.

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## INTRODUCTION

Katmai National Park and Preserve, located in the Bristol Bay region of Southwest Alaska, protects over 1.6 million ha of habitat. The Park is mostly roadless and trailless wilderness and is off the road system, only accessible by plane or boat. This remote location, lack of accessibility, harsh weather, and limits to staff and funding make it difficult to measure and monitor wildlife populations, especially species whose ecology is complicated by long lives and multiple life stages.

The Bristol Bay region is home to the largest salmon (*Oncorhynchus spp.*) run in the world and relying on this resource is one of the largest coastal brown bear (*Ursus arctos*) populations in the world. Katmai's enabling legislation declares that the park's purpose is "to protect habitats for, and populations of, fish and wildlife, including... high concentrations of brown/grizzly bears and their denning areas" (ANILCA 1980). Because of the abundance of salmon, bears in this region of Alaska are willing to tolerate each other and people in closer proximity than most other places (Jope 1983). This tolerance creates a unique opportunity to observe and study bears more closely than in other areas (Egbert et al. 1976).

At Katmai, biologists and trained technicians can recognize individual bears congregating on salmon spawning streams season after season and year after year. Identification is accomplished by recognizing unique physical features and behavioral characteristics of individual bears. During the late 1980s biologists at Katmai began developing protocols to study bear behaviors using individual identification of bears congregating along salmon streams. Data collection at Brooks River continued in Katmai over subsequent decades,

and the bear identification process has provided standardized, long-term, non-invasive records of individual brown bears using the Brooks River.

Brooks River attracts many of Katmai's visitors. People come to enjoy world class fishing, photography, and bear viewing. Around 2013, visitors and staff noticed fewer bears congregating along Brooks River than in years past. They began asking "where are all the bears?" Had the number of bears using Brooks River changed, and if so, why? My objectives were to answer these questions by using the Brooks River bear monitoring data set.

Often, the 2 most important processes to influence localized abundance are survival and productivity, the number of births and deaths in a population. In chapter 1 I focused on survival by investigating if and how annual counts of bears along Brooks River changed over time. I compiled the Brooks River bear monitoring data from 2000–2018 and looked for changes in annual number of bears recorded. Results showed a decrease in number of independent bears, individual bears not considered cubs part of a family group, observed along Brooks River from 2009–2016. I found a significant positive relationship between sockeye salmon escapement (salmon escaping commercial harvest) in the Naknek River drainage and counts of independent bears 2–3 years later, indicating escapement was positively associated with individual bears observed.

I also investigated whether a change in survival was linked to changes in counts of bears at Brooks River. I used individual observation records as detection histories in a capture-recapture framework to estimate survival. Because salmon are the major food source for bears in this region and why bears are attracted to Brooks River, I hypothesized that a change in

salmon escapement leads to changes in survival, specifically in younger age groups, that influenced number of bears seen at Brooks River. My results did not show significant changes in annual survival of independent bears, or a relationship to sockeye salmon (*Oncorhynchus nerka*) escapement. Changes in annual cub survival and number of cubs observed suggest some other population process, such as productivity, influenced annual counts of independent bears along Brooks River.

In chapter 2, I estimated true abundance and examined productivity using counts of individual bears in a state-space model. True abundance refers to abundance corrected for imperfect detection. I examined whether change in counts of bears along Brooks River reflected an actual change in abundance, or changes in detection through time. The state-space model provided annual estimates of age and sex specific bear abundance, survival, and productivity from 2000–2019.

I also examined changes in productivity and abundance over time from the state-space model. I hypothesized that changes in salmon escapement led to changes in productivity and bear abundance. Using a post hoc regression to analyze the relationship between state-space model results and sockeye salmon escapement, I found that fluctuating sockeye salmon escapement showed a significant positive relationship with abundance of independent bears 2 years later. This relationship suggests that past events, such as food availability, influence where bears choose to fish for salmon. After years when salmon escapement is low, some bears may choose not to return to Brooks River. When I looked at specific age-sex groups within the Brooks River bear population, only some groups showed significant positive relationships with salmon escapement from 2 years prior. Abundance of breeding females and

their cubs was positively related to salmon escapement from that year which may indicate avoidance of Brooks River during years when escapement was lower and competition among bears was higher. The relationship between annual escapement and productivity measures were not significant, although there were signs of decreased cub abundance and cub survival which could indicate a change in productivity occurred. The state-space model was not able to account for changes in bears' availability to be detected and therefore could not differentiate between changing use patterns and productivity.

The long-term, non-invasive data on over 300 individually identifiable brown bears provided a rare long-term look at a population of brown bears. It enabled me to estimate age and sex specific survival and abundance through time and to evaluate relationships between annual survival, productivity, and salmon escapement. Future work integrating recapture histories and count data may help tease apart the relationship between salmon escapement and bears of Katmai.

Each of these chapters is written for independent publication with coauthors. Therefore, text uses the plural "we" instead of singular "I".

## LITERATURE CITED

## LITURATURE CITED

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## **CHAPTER 1: BROWN BEAR SURVIVAL ALONG BROOKS RIVER IN KATMAI NATIONAL PARK, ALASKA.**

### **Abstract**

Measuring and monitoring wildlife population demographics can be costly, challenging, and invasive. These issues hold true in Katmai National Park in southwest Alaska where the remote location, lack of accessibility, harsh weather, and limits to staff and funding make it difficult to monitor one of the largest populations of brown bears. Yet, abundant food resources of this region (i.e., migrating salmon) provides a unique opportunity to study bears due to their tolerance of each other and people. Individual bears congregating on salmon spawning streams are identified by unique physical and behavioral features, which allowed a standardized, long-term, non-invasive record of individual brown bears using the Brooks River area over time. Concerns over dramatic changes in the number of individual bears seen using Brooks River have led to questions about whether the population of bears has changed.

We used bear identification records from 2000–2018 in a non-invasive mark-recapture framework to estimate age-sex specific survival and explore the impacts of salmon escapement. We estimated average annual survival for spring cubs (0.718, 95% CrI: 0.649–0.787), subadult males (0.840, 95% CrI: 0.694–0.961), subadult females (0.909, 95% CrI: 0.794– 0.983 ), adult males (0.876, 95% CrI: 0.774– 0.968 ), and adult females (0.891, 95% CrI: 0.790– 0.973). We found that annual counts of independent bears using Brooks River decreased from 2009–2016, and that bear counts were positively related to annual sockeye salmon escapement 2–3 years later. Yet, we found no changes in survival or relationship between age-sex specific survival and salmon escapement. These results suggest that sockeye salmon escapement influenced some

non-survival aspect of the population. Several years of low cub counts while annual cub survival was below average suggests that escapement might have influenced productivity.

## **Introduction**

Wildlife have cultural, economic, and ecological values to society. Wildlife management seeks to maintain healthy wildlife populations by measuring and monitoring population demographics such as survival, sex ratios, and reproductive rates (Miller et al. 2001). Yet, monitoring wildlife population demographics can be challenging and often requires costly and invasive techniques such as tagging or collaring. When using these techniques, it can be difficult to obtain a sample size large enough and long enough to develop a robust understanding of the population. These challenges are compounded by a study species whose ecology is complicated by long lives and multiple life stages.

Katmai National Park, in southwest Alaska, hosts a balance of two important resources: brown bears (*Ursus arctos*) and salmon (*Oncorhynchus spp.*). This region is home to the largest salmon run in the world (Elison et al. 2018), and one of the largest coastal brown bear populations in the world rely on the salmon resource. Katmai's enabling legislation declares that the park's purpose is "to protect habitats for, and populations of, fish and wildlife, including ... high concentrations of brown/grizzly bears and their denning areas" (ANILCA 1980). Today the park protects more than 1.6 million ha of brown bear habitat and salmon spawning grounds. Thus, understanding how the brown bear population might be changing is critical to the park maintaining its mission. Yet, the remote location, lack of accessibility, harsh weather, and limits to staff and funding make it difficult to monitor changes in the bear population

without using costly and invasive tagging and collaring techniques. There is a growing concern about the status of the brown bear population in this region and how rapidly shifting environmental conditions might be influencing the population.

Because salmon are abundant, bears in this region of Alaska tolerate each other and people in closer proximity than most other places (Jope 1983). This tolerance creates a unique opportunity to view and study bears more closely than in other areas (Egbert et al. 1976). At Katmai, biologists and trained technicians recognize individual bears congregating on salmon spawning streams season after season and year after year (Olson et al. 1998, Smith 2002, Troyer 1975, 1976, 1977, 1978). Identification is accomplished by recognizing unique physical features and behavioral characteristics of individual bears.

During the 1970s and 80s, biologists at McNeil River State Game Sanctuary (McNeil) on the northern border of Katmai National Park began collecting data on brown bears using this ability to recognize individuals by physical and behavioral features. Sellers and Aumiller (1994) recognized the need to understand trends and population demographics of naturally regulating brown bear populations, so they used the McNeil River brown bear monitoring dataset in a capture-recapture framework to estimate survival according to sex and age groups. Similarly, during the late 1980s biologists at Katmai began developing protocols to study bear behavior using unique physical and behavioral traits of bears congregating along salmon streams (Olson 1993, Olson and Gilbert 1994, Olson et al. 1997, 1998). The monitoring data collection at Brooks River (Figure 1.1) continued in Katmai over the decades, and the bear identification process has allowed standardized, long-term, non-invasive records of individual brown bears using the area.

This bear monitoring dataset could offer a non-invasive way to monitor this environmentally and economically valuable species.

Today, data from the Brooks River bear monitoring program have brought up concerns as the number of individual bears seen has changed dramatically over the past decade leading biologists and visitors to wonder if and how the population of bears was changing. We proposed examining survival of this naturally regulated brown bear population using unique physical and behavioral features to identify individual bears in a non-invasive mark-recapture framework. We built upon Sellers and Aumiller (1994) by incorporating modern analytical tools that helped account for imperfect detection of bears (Lebreton et al. 1992, Gimenez et al. 2007, Royle 2008). Our first objective was to compile the annual counts of uniquely identifiable bears using Brooks River each season and describe male: female sex ratio, family group to single bear ratio, and reproductive rate. Unless the bear population changed over time, we expected our results to align with Sellers and Aumiller (1994). Our second objective was to calculate annual survival of age and sex groups within the bear population. If counts of bears using Brooks River changed over the years, we would investigate whether changes in survival could have influenced these counts. Because salmon are a major food source for bears in this region (Hilderbrand et al. 1999), we also examined the effect of annual sockeye salmon escapement on brown bear survival. We hypothesized a change in salmon escapement may have led to a change in survival that impacted the number of bears seen along Brooks River.

## Study Area

Katmai National Park and Preserve is located along the base of the Alaska Peninsula, with Bristol Bay and the Bering Sea on the western side and the Pacific Ocean on the eastern border (Figure 1.1). The area was established as Katmai National Monument in 1918 to preserve the site of the largest volcanic eruption of the 20<sup>th</sup> century, and then expanded in 1931 to include the Brooks River area for the purpose of protecting brown bears and other wildlife (Norris 1996). In 1980, the monument was significantly expanded again and designated a National Park and Preserve encompassing 1.6 million ha (Figure 1.1). Katmai National Park and Preserve is surrounded by federal, state, and private land. Bear hunting is not allowed within the Park but is allowed in adjacent lands through state and federal hunting seasons and in the 160,000 ha Katmai Preserve.

Data collection for this study occurred along the Brooks River in Katmai, which serves as a spawning stream and major migratory route for sockeye salmon traveling upstream to smaller tributaries for spawning (Hartman et al. 1964). Brooks River is approximately 3.2 km long and flows from Brooks Lake to Naknek Lake (Figure 1.1). It is bisected near its midpoint by a 1.5 m tall waterfall that creates a bottleneck for salmon, which must jump the falls to continue their migration. The river is bordered by a forest cover of alder (*Alnus* spp.), spruce (*Picea* spp.), birch (*Betula* spp.), and willows (*Salix* spp.). The lower end of the river is more open with marshes and wetlands. During July, the temperature around Brooks River averages 13.1 degrees Celsius. Average precipitation is 4.2 cm. During September, the temperature averages 8.7 degrees Celsius with an average of 8.1 cm of precipitation (NOAA 2018).

There are 2 main periods when bears congregate along Brooks River. The first period usually begins in late June and lasts through July as bears gather to fish mainly by the falls and along the lower river. Bears feed on salmon that are backed up trying to jump the falls. This serves as an early season food resource for bears in the area. The second period of bear activity is during September and October as bears congregate in the lower river to feed on spawning and dying salmon that accumulate in the slower moving waters of the lower river. Brooks River attracts visitors during the summer and early autumn months. Visitors come to enjoy sportfishing, bear viewing, and photography while learning about the area's rich cultural and geological history. Peak visitation along Brooks River occurs in July where as many as 600 people visit daily via boat or floatplane.

## **Methods**

### *Data Collection*

Brown bear monitoring began in 1988 and regularly occurred since 2000 at the study site (Olson and Gilbert 1994, Olson et al. 1997, 1998). Scan sampling was conducted during the early monitoring season ("July monitoring") and later monitoring season ("fall monitoring"). The July monitoring season began on the first Monday after June 21<sup>st</sup> and continued for 5, 8-day cycles, usually into the first week of August. The fall monitoring season began on the first Monday after August 26<sup>th</sup> and ended after 5, 8-day cycles into the first week of October. During each day, one observer systematically visited 3 different viewing platforms for the July monitoring season (Figure 1.1: sites 1, 2, and 3), and 2 viewing platforms during the fall monitoring season (Figure 1.1: sites 2 and 3). For both seasons, the complete monitoring cycle

consisted of monitoring 6 consecutive days followed by 2 days off. Most years 1 person conducted all monitoring and bear identification.

Each day of monitoring comprised 2 observation sessions lasting 2–3 hours each. During a session, one observer conducted a scan sample every 10 minutes. A scan sample required identifying and recording each bear present at that instant along that section of the river. Each day the 2 sessions were conducted at 2 different locations. During the July monitoring, sessions cycled through 3 locations during 2 possible times of 14:00–16:00 and 19:00–22:00. During the fall monitoring, the 2 monitoring sessions only occurred at the 2 lower river locations and cycled through 2 of 3 possible times of 8:00–10:00, 14:00–16:00, or 18:00–21:00.

Bears were identified by physical and behavioral features, a method commonly used across a variety of species (Friday et al. 2000, Dawson and Miller 2008, Van Horn et al. 2014, Goswami et al. 2011). Observers identified bears using fur color, shed patterns, ear and muzzle shape, body size, and fishing habits that include styles and locations of catching salmon. Physical feature identification of brown bears has been used in other research at locations such as in Brooks Camp (DeBruyn et al. 2004), McNeil River State Game Sanctuary (Sellers and Aumiller 1994, Egbert and Stokes 1976), coastal British Columbia, Canada (Nevin and Gilbert 2005), and Yellowstone National Park (Knight et al. 1995).

During a bear monitoring season, an individual bear had to be observed during  $\geq 3$  monitoring sessions to be considered a regular user and entered into the official record. Bears deemed a regular user during a season were then assigned a unique 3-digit number that cross-

referenced the bear's sex, age category, reproductive status, and physical and behavioral features.

For calculating survival, we only included bears identified during  $\geq 2$  monitoring seasons according to Sellers and Aumiller (1994). We concentrated on data collected from 2000 to 2018, the longest period of consistent data collection. However, information on some individual bears from before this time was used to estimate age and productivity.

### *Count Data*

The presence of individually recognizable bears was noted each monitoring season. We created a capture history across seasons and years for individual bears, and then grouped these individuals by sex and age class to calculate separate annual survival estimates for adults, subadults, males, and females. For our study we defined independent bears as subadult or adult individuals, this did not include cubs that were part of a family group dependent on a sow

Like other studies in the area (Glenn and Miller 1977, Sellers and Aumiller 1994, Sellers et al. 1999), we defined adult bears as individuals  $\geq 5$  years old. Generally, this is the age when bears of this region become sexually mature. Subadult bears were defined as independent bears, individuals not part of a family group, estimated at 2–4 years old. Unless an observer recognized an adult from when it was a dependent cub, observers estimated age through body size and behavioral characteristics. We did not count bears still in a family group cared for by a sow as independent, individually recognizable bears. Instead, we conducted a separate analysis for dependent cubs based on identifiability of the sow.

Monitoring litters of individual sows allowed us to calculate reproductive statistics including average litter size, average female age with first litter (primiparity), and average number of years between litters. Our calculation for average age of primiparity only included sows that survived to produce their first known litter. We used a Kruskal-Wallis nonparametric test (Kruskal and Wallis 1952) to look for differences in litter size based on number of litters a sow had over time, number of years between litters, and litter size based on a sow's age. If the Kruskal Wallace test was significant, we then used a Scheffe's test (Scheffe 1956) to determine specific differences. We placed sows into age categories defined as young adult (5–7 years old), adult (8–14 years old), and senior adult (15+ years old). These calculations only included sows first identified while they were dependent cubs, subadults (age 2–4) or young adults (age 5–7). These age groups were easier to estimate using body size and behavioral features, so it provided a sample of females with greater certainty of their age.

Annual sockeye salmon escapement estimates for the Naknek River drainage, collected by the Alaska Department of Fish and Game (ADF&G) (Erickson et al. 2018), were used as an index of salmon abundance in Brooks River. Escapement represents the number of salmon escaping commercial harvest and returning to freshwater systems to spawn. We conducted a cross-correlation analysis in the program R (R Core Team 2019) using package *tseries* (Trapletti and Hornik 2019) to look for negative lags when changes in escapement might have led to significant changes in counts of bears. We then applied a Poisson generalized linear model, using the quasipoisson function in package *lme4* (Bates et al. 2015), to estimate the relationship between annual counts of bears and salmon escapement while incorporating lag effects from the cross-correlation analysis.

### *Dependent Cub Survival from First Year to Second Year*

We estimated survival (S) of dependent cubs (spring cub and yearling) by following individual litters of recognizable sows. We first calculated average survival by age group of dependent cubs using Apparent Percent Success (APS; Williams et al. 2002) and combining all litters from 2000–2018.

$$(APS; S_{APS} = 1 - (\# \text{ deaths} / \# \text{ bears at risk}))$$

Censored litters, i.e., when the sow with cubs was not seen in subsequent seasons, were omitted from the APS calculations to prevent bias (Winterstein et al. 2001). We did not calculate survival from yearling to first independent subadult year since many dependent cubs could not be identified across these age groups. We assumed an open population, and that bears were identified correctly and did not change behavior because they were being monitored. We also assumed that individual sows were independent, and that no censoring took place.

### *Annual Spring Cub Survival*

We applied the Mayfield method (Mayfield 1961) to calculate annual summer survival for spring cubs from 2000–2018. The Mayfield method allowed us to calculate annual cub survival instead of pooling survival across years (Sellers and Aumiller 1994) and can accommodate a smaller sample size. The Mayfield method uses exposure days to calculate survival instead of number of individuals at risk (APS and Kaplan-Meier methods). The daily survival rate was calculated as

$$S_{Mayfield} = 1 - (\# \text{ deaths} / \# \text{ exposure days}).$$

This method allowed us to use counts of cubs even if we were unsure of their fate due to censoring in subsequent monitoring seasons. To calculate exposure days, we used the dates when sows with spring cubs were first and last observed during the July monitoring season. We did the same for the following fall monitoring season. If a spring cub was not observed between monitoring seasons, we calculated the midpoint between the date the cub was last seen in July to when it was first seen during the fall monitoring.

Summer period survival from the beginning of July monitoring to the end of fall monitoring was calculated by raising the daily survival rate to the power of  $L$  (Mayfield 1961).  $L$  equals the number of days from the first day of July monitoring to the last day of fall monitoring that year.

$$S_{\text{period}} = (S_{\text{daily}})^L$$

We assumed that identified bears represented a random sample of the Brooks River population, that days were independent, individuals were independent, and survival was constant for summer. We also assumed that bears were identified correctly and that they did not change behavior because they were being observed (Williams et al. 2002). Censoring was assumed to be random and independent of death. Censored family groups were included in the Mayfield analysis up until the point they were last seen (Vangilder and Sheriff 1990).

We combined Mayfield summer period survival estimates with winter APS survival values. Winter APS was calculated by dividing the number of spring cubs not seen the following year, by the number of spring cubs known to be at risk during the corresponding fall monitoring

period. Sows not observed the following year were considered censored; their cubs having an unknown fate. These censored litters were omitted from the calculation.

The combined Mayfield and APS period survival estimates provided an annual survival estimate from the time spring cubs were first seen to the time they were next seen as yearling cubs the following year. After testing for correlation, we used the equation for the product of 2 independent variables (Hogg and Craig 1978) to calculate variance of the combined Mayfield and APS survival.

#### *Cormack-Jolly-Seber Survival Analysis*

We applied a Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) to the subadult male, subadult female, adult male, and adult female capture-recapture data using a Bayesian framework in the program JAGS (Plummer 2003) using package *jagsUI* (Kellner 2016). We chose this model to help account for the imperfect observation process since it calculates both a recapture ( $p$ ) and survival ( $\phi$ ) probability. When an individual bear was no longer seen, the model applied a probability that the bear was alive and not detected and a probability that the bear had died. This provided a less biased estimate of annual survival that could account for undetected bears.

The CJS model used a state-space formula modeling a true state process and an observation process as described by Kery and Schaub (2012). In the true state process, an individual ( $i$ ) alive and identified at time  $t$  could survive to time  $t+1$  with survival probability  $\phi_{g,t}$  based on that individual's age-sex group ( $g$ ). An age-sex group's survival was drawn from a uniform distribution with uninformative priors ( $\phi_{g,t} \sim U(0,1)$ ). In the observation process, an

identified individual alive at time  $t$  could be resighted with probability of detection  $p_g$ . An age-sex group's probability of detection was drawn from a uniform distribution with uninformative priors ( $p_g \sim U(0,1)$ ). The CJS modeled a constant seasonal probability of detection for each age-sex group. Since there were 2 capture periods each year, survival was measured seasonally from July through August and from September through the following June. The 2 seasonal survival estimates combined to make the annual survival estimates. The code for the CJS model is provided in the supplemental material (Appendix III). We ran 3 chains 25,000 iterations long with a burn in of 2,000 iterations and a thinning rate of 5.

We assumed that every identified bear during a monitoring season had the same probability of being re-sighted given that it occupied the area, every identified bear of an age-sex group that was present for one year had the same probability of survival to the next year, individual bears were identified and recorded correctly, sampling periods were instantaneous (short), all emigration from the sampled area was permanent, and the fate of each bear was independent of the fate of any other bear (Williams et al. 2002).

Given our estimates of brown bear survival, we examined the effect of annual sockeye escapement. Because annual survival was a derived model parameter, we ran a post hoc logistic regression in the program JAGS (Plummer 2003) using the ADF&G measure of sockeye salmon escapement and the posterior distributions of the annual survival estimates for each CJS age-sex group.

$$\text{logit}(S_{g,t,n}) = a_g + b_g E_t$$

Where  $S$  is annual survival,  $g$  is the age-sex group,  $t$  is the year,  $n$  is the observation from the posterior distribution of  $S_{gt}$ , and  $E_t$  is annual salmon escapement. Thus, for each value in the posterior of  $S_g$  ( $n=13,800$ ), we ran 3 chains of 1,000 iterations with a burn in of 500 iterations and a thinning rate of 5, producing super posteriors for  $a_g$  and  $b_g$  ( $n=4,140,000$ ).

## Results

### *Brooks River bear count characteristics*

From 2000–2018, 192 independent bears were counted: 44 individuals as subadult males and 102 as adult males. Some of the adult males were first seen as subadults and were counted as both. We counted 52 bears as subadult females and 90 as adult females with some of them first observed as subadult females. Independent bears were seen an average of 8.26 seasons (SD: 7.83). We excluded 129 individuals from the analysis because they were only seen 1 season. Of these 129 single season bears, 93 were male; 48 were subadult males and 45 were adult males. The remaining 36 single season bears were female; 18 were subadult females and 18 were adult females.

The average number of independent bears counted annually between 2000 and 2018 was 67.63 (SE: 22.36). Counts were increasing from 2000–2009, decreasing from 2009–2016, then increasing from 2016–2018. Average adult male to adult female ratio was 29.05 males (SE: 9.65): 24.42 females (SE: 7.16) (119.0 males/100 females). Average proportion of subadults to independent bears each year was 15.42% (SE: 9.48). The ratio of single females to sows with cubs averaged 15.84 single females (SE: 6.27): 8.58 sows with cubs (SE: 3.88) (184.6 single females/100 sows with cubs). Proportion of family groups to independent bears averaged

13.04% (SE: 5.37%). We observed an average of 9.21 spring cubs (SE: 4.30) each year, and 17.79 dependent cubs (SE: 8.17) which included spring cubs, yearlings, and dependent 2+ year old bears.

The cross-correlation analysis showed significant lags between annual sockeye salmon escapement and counts of independent bears (Figure 1.3). When escapement was above average, average counts of bears 2-3 years later were higher (Figure 1.3). The quasipoisson regression showed a 25.99% increase in number of independent bears counted for every standard deviation (571,000 salmon) increase in escapement occurring 2 years prior ( $P < 0.001$ ) (Figure 1.4). The relationship between counts of independent bears and escapement from that year did not meet our significance threshold ( $P = 0.0974$ ).

### *Bear productivity*

We observed 96 litters from 41 individual sows. Average litter size during July was 2.2 cubs (SE: 0.96). Using sows first seen as young adults (age 5–7) or younger, we calculated average age of first litter to be 7.43 years (SE: 2.06 years,  $n = 23$  sows). We observed 63 family groups their yearling year. Of those yearling family groups, 15 of them retained cubs as dependent 2-year-old bears.

On average there were 4.02 years (SE: 1.76) between the time a sow was first seen with a litter of spring cubs to the year she was next seen with a litter of spring cubs. This calculation included sows who had lost their entire litter, so these sows might have returned the following year with a new litter. Since most sows kept their cubs as dependents for 2 years, this would

indicate that there were often 2 years between the time 1 litter was emancipated and the next spring cub litter.

We saw no difference in litter size based on how many litters a sow had (litters 1–4;  $\chi_3^2=4.14$ ;  $P=0.247$ ), and no difference in number of years between litters 1–4 ( $\chi_7^2=6.52$ ,  $P=0.481$ ).

We found a difference in litter size based on a sow's age group ( $\chi_2^2=6.37$ ;  $P=0.0413$ ). The young adult age group had the smallest average litter size of 1.75 cubs ( $n=16$ ) compared to adult (2.39 cubs,  $n=28$ ) and senior (2.00 cubs,  $n=19$ ) litters ( $F_{50}=3.18$ ;  $\alpha=0.05$ ).

#### *Dependent bear survival*

Dependent bear survival from the time first seen as a spring cub to last seen as a yearling dependent cub during fall monitoring was 0.718 (95% CI: 0.649–0.787). The largest decrease in survival occurred over winter for first year cubs (Figure 1.5). The combined Mayfield and APS methods estimated annual survival from the time a spring cub was first seen during the July monitoring to when it was first seen as a yearling cub the following year. Annual spring cub survival varied between 2000–2017 (Figure 1.6), with an average of 0.718 (SE: 0.279)

#### *Adult and subadult survival*

We estimated survival and average seasonal probability of detection for subadult males (survival: 0.840, detection: 0.650), subadult females (survival: 0.909, detection: 0.705), adult males (survival: 0.876, detection: 0.598), and adult females (survival: 0.891, detection: 0.713) (Table 1.1). In general, average annual subadult and adult female survival was higher than male annual survival of the corresponding age group, although credible intervals of each age-sex

group overlapped (Table 1.1). Average seasonal probability of detection of adult females had a significantly higher seasonal probability of detection than adult males (Table 1.1).

Annual survival estimates for each age-sex group did not vary significantly from year to year, however years 2009–2013 showed below average mean annual survival for both adult males and adult females (Figure 1.7). We found no relationship between annual survival and annual sockeye salmon escapement using the post hoc regression (Table 1.2).

## **Discussion**

Due to Katmai's large, protected landscape and an abundant salmon food resource, we expected these Brooks River count data to show a long-lived, self-regulating bear population with high and consistent survival of adult bears, higher male to female ratio, and lower family group to single bear ratios compared to populations of hunted bears (Keay et al. 2017, McLellan 1994, Knight and Eberhardt 1985, Miller 1990). Our results supported these hypotheses with population demographics similar to other protected bear populations that rely on abundant salmon food resources (Sellers and Aumiller 1994, Sellers et al. 1999). We saw evidence of some self-regulating mechanisms such as older age at first reproduction (McLellan 1994, Keay et al. 2017). Yet, with abundant salmon food resources of this area there was evidence that sows had larger litters, shorter reproductive intervals, and higher cub survival than did sows from areas with less abundant food sources (Hilderbrand et al 1999, 2019).

Our long-term data on nearly 200 individually identifiable brown bears enabled us to estimate age and sex specific survival through time and to evaluate relationships between

annual survival, seasonal counts of bears, and salmon escapement. We did not observe significant changes in annual survival of independent bears. Furthermore, we found no significant relationship between sockeye salmon escapement and annual survival of independent bears, however there was a significant relationship between salmon escapement and counts of independent bears 2–3 years after high escapement years. Changes in annual cub survival and number of cubs observed suggest some other population process, such as productivity, might have influenced annual counts of independent bears along Brooks River.

#### *Count Data Characteristics*

Our hypothesis that the Brooks River brown bear population would display similar demographics to the 1994 study at McNeil was supported by our analysis of count data. McNeil shares a northern border with Katmai, and, although McNeil is only about 100,000 ha, still offers a large, protected landscape for bears with abundant salmon food resources. We found identical adult sex ratios and a similar proportion of subadults to adults. The McNeil study reported a greater percentage of family groups (39%) compared to 13% at Brooks River. This may be a density-dependent mechanism indicating the Brooks River population was closer to carrying capacity during the time of this study. At carrying capacity, increased competition for food resources, particularly salmon, could decrease cub survival (Miller et al. 2003) or create a lull in productivity leading to a decrease in bears seen along Brooks River from 2010–2016. Zedrosser et al. (2006) found that body size of female brown bears in Scandanavia was negatively related to population density, while Hilderbrand et al. (2019) found that female body size was the primary driver of productivity. This suggests that during times of greater

population density there is increased competition for food which may decrease female body weight leading to decreased productivity.

Although many of these Brooks River count data and productivity characteristics matched the McNeil report and other similar studies (Sellers et al. 1999), the extent to which the Brooks River population represents the greater regional bear population is unknown. The Brooks River data could be a skewed representation of the regional population because it is a feeding aggregate. The Brooks River ratio of family groups to single independent bears was low which could indicate avoidance of the area by females with cubs. The sex ratio of counts at Brooks River could also be skewed from the actual population because Brooks falls might attract dominant male bears. Sellers et al. (1999) speculated that the 1994 McNeil report had a higher ratio of male bears due to more males having the falls in their larger home ranges compared to females.

### *Productivity Analysis*

The Brooks River bear population may be displaying several different density-dependent mechanisms such as delayed sexual maturation and low proportion of family groups. The Brooks River average age of first reproduction was consistent with values reported in the Katmai Preserve (7.2 years old; Sellers et al. 1999), which supports the theory of delayed age of primiparity (McLellan 1994, Keay et al. 2018). Several studies on density-dependent dispersal patterns of young female brown bears suggest that in high density areas female dispersal patterns promote the formation of matrilineal assemblages which lead to reproductive suppression (Odden et al. 2014, Stoen et al. 2006). Stoen et al. (2006) suggested behavioral

reproductive suppression might develop in female brown bears in these matrilineal assemblages due to a hierarchical system among females or due to inbreeding avoidance. The higher subadult female probability of detection at Brooks River (Table 1.1) compared to subadult male and adult male probability of detections would be consistent with this theory of matrilineal assemblages forming in high density populations. To test this theory, a study of genetic relatedness of Brooks River females would need to be conducted.

We found a significant difference in litter size at Brooks River based on age group of the sow. On average, young adult sows (5–7 years old) were observed with smaller litters than were sows of the adult age group (age 8–14). Younger sows may produce fewer cubs due to their smaller body mass. It may also be that cub survival is lower for younger sows; therefore, fewer cubs lived long enough to be recorded during the Brooks River monitoring in July. Both theories are consistent with Hilderbrand et al. (2019) who found that body mass was positively related to the number of cubs a sow produced, and that age was positively correlated with probability of recruitment. Either way, this relationship between sow age and observed litter size could impact productivity if adult females in the Brooks River population had an uneven age distribution.

#### *Dependent Cub Survival*

Our average survival estimates for spring cubs are difficult to compare to other research because they do not account for survival from den emergence to when the cubs are first seen during June and July. Therefore, our calculations overestimate true spring cub survival. In southcentral Alaska, Miller (1990) reported spring cub survival from May to July at 0.75.

Similarly, at Black Lake, AK, Miller and Sellers (1990) reported cub survival from May to July as 0.60. We might expect early season spring cub survival at Brooks River to be near these values.

The Sellers and Aumiller (1994) McNeil study had a similar bias to ours from not incorporating spring cub survival from den emergence to when first seen during June and July. Average cub survival from when first seen as a spring cub to when last seen as a yearling was lower at McNeil (0.47 from 1980–1991) compared to Brooks River 2000–2017 (0.718). Although these studies are from 2 different locations, this difference could indicate generally higher cub survival from 2000–2017 compared to 1980–1991. Differences in bear density and food availability may be influencing cub survival at these 2 locations.

#### *CJS Survival Analysis*

The CJS model provided survival estimates based on independent bears that were consistent with other brown bear studies (Sellers and Aumiller 1994, McLellan et al. 1999, Haroldson et al. 2006, Sellers et al. 1999, Bled et al. 2017). We found no significant differences in average survival between age-sex groups (Figure 1.7), although females generally had higher survival than males of the corresponding age group. Subadult males had the lowest average annual survival with greatest variance. This difference is likely due to males, particularly subadult males, having higher rates of dispersal outside of their maternal range and being more transient, moving longer distances than females (Glenn and Miller 1977, Stoen et al. 2006). Males also had a lower seasonal probability of detection than did females which further supports this transient hypothesis.

Because we were relying on physical and behavioral features to identify bears, younger and more transient bears might have been less recognizable, leading to potential misidentification across years. This misidentification would be more likely if bears were absent from Brooks River for several years before returning. A bear might be misidentified as 2 different bears creating a violation of our assumption that all bears were identified correctly. This violation would result in a negative bias to our survival estimates (Laake et al. 2014). Future models testing and incorporating the effect of misidentification and overall availability of individual bears in the area would help account for bias.

#### *Annual Trends: Synthesis*

We found no changes in annual survival of independent bears over time, therefore, annual survival was not likely to have caused variation in bear counts along Brooks River. We thought that changes in annual salmon escapement would impact annual survival estimates of Brooks River bears, but we failed to show a significant relationship between survival and escapement. Brown bears are omnivores and K-selected species. Their ability to change food sources when salmon abundance is low means a variety of environmental factors influence overall food availability (Van Daele et al. 2012). Changing food sources based on availability occurs across species. For example, Svanback and Bolnick (2007) used three-spine sticklebacks (*Gasterosteus aculeatus*) to show that reduced prey availability caused individuals to add alternative prey to their diet. In the future, incorporating more covariates into our model such as berry abundance and river level may capture these varying environmental conditions. Also, the Naknek River drainage escapement is managed by the State of Alaska. Although management has potential to impact the bears Katmai is charged with protecting, the annual

management goals of 800,000–2,000,000 sockeye salmon provide some consistency to the number of salmon returning to spawn each year. The Naknek River sockeye escapement has been above 800,000 since 1974 (Erickson et al. 2018). It may be that escapement was not a limiting factor of survival, and the minimum escapement threshold needed to negatively affect independent brown bear survival was not realized from 2000–2018.

Changes in counts of bears along Brooks River do not appear to be caused by changes in survival, yet there are other factors likely affecting the annual number of bears seen. It could be that counts changed because more bears were drawn to Brooks River when salmon escapement was high. Inversely, it could be that some age-sex groups such as adult females with cubs avoided Brooks River during periods of low salmon escapement. In Yellowstone National Park, Stringham (1983) found that litter abundance of grizzly bears was inversely related to postnatal abundance of adult males. Some bears might avoid competition for salmon at Brooks River during years of lower escapement causing a reduction in counts of individual bears. Future research estimating annual abundance and seasonal variation in probability of detection could help answer this question.

There was a significant positive relationship between sockeye salmon escapement in the Naknek River drainage and number of independent bears seen along Brooks River 2-3 years later (Figure 1.3). This relationship would suggest salmon escapement had some effect on bear availability in the area or population dynamics other than survival. This relationship might be caused by changing use patterns where bears are drawn to locations with abundant salmon, such as Brooks River during years with high salmon escapement. If these locations then change and have lower salmon abundance, bears may stop visiting these sites and use other salmon

streams or food sources in the future. There also could have been a change in productivity where declines in salmon abundance caused decreased cub production leading to fewer independent bears in the future.

Annual spring cub survival was below average from 2009–2015, coupled with low cub counts and low numbers of family groups present. This reduction could indicate a period of low cub productivity, which may be the result of shifting food availability or a density-dependent mechanism. The effects of adult male infanticide as a density-dependent factor have been debated. Knowing annual abundance of specific age and sex groups as well as their survival would help clarify whether use patterns or density-dependence might be driving some of the changes along Brooks River. When adult male abundance is high, there could be a risk of lower cub survival through infanticide or competition for resources.

## **Conclusion**

The ability to identify individual bears based off their physical and behavioral features allowed us to estimate survival and demographics of this local bear population. This identification ability provided a less invasive and relatively inexpensive way to complete a capture-recapture analysis compared to tagging or collaring methods. The CJS model allowed us to investigate age and sex specific survival while accounting for imperfect detection. Results suggested that the number of independent bears seen along Brooks River was influenced by salmon escapement, however escapement did not have a significant relationship with independent bear survival. Changes in cub survival and number of cubs observed suggested some other population process, such as productivity, might have influenced annual counts of independent bears. In the future, incorporating more environmental covariates, estimating true

brown bear abundance as it relates to annual counts, and assessing probability of detection that varies across years will allow us to better understand fluctuations in this naturally regulated bear population.

## **APPENDICES**

**APPENDIX I: TABLES**

Table 1.1: Annual survival and seasonal probability of detection for the 4 age-sex groups monitored in the Cormack-Jolly-Seber model.

<b>Age-sex group (sample size)</b>	<b>Average Annual Survival</b>	<b>95% Credible Interval</b>	<b>Average Seasonal Probability of Detection</b>	<b>95% Credible Interval</b>
Subadult male (44)	0.840	0.694– 0.961	0.650	0.561– 0.733
Subadult female (52)	0.909	0.794– 0.983	0.705	0.637– 0.768
Adult male (102)	0.876	0.774– 0.968	0.598	0.565– 0.632
Adult female (90)	0.891	0.790– 0.973	0.713	0.681– 0.744

Table 1.2: Average effect of sockeye salmon escapement on brown bear survival with 95% credible interval (change in survival/1 million sockeye salmon).

<b>Age-sex group</b>	<b>Average effect of escapement on survival</b>	<b>Credible interval</b>
Subadult male	0.0381	-0.27–0.37
Subadult female	-0.0189	-0.39–0.37
Adult male	0.0543	-0.27–0.41
Adult female	0.0735	-0.27–0.45

## APPENDIX II: FIGURES

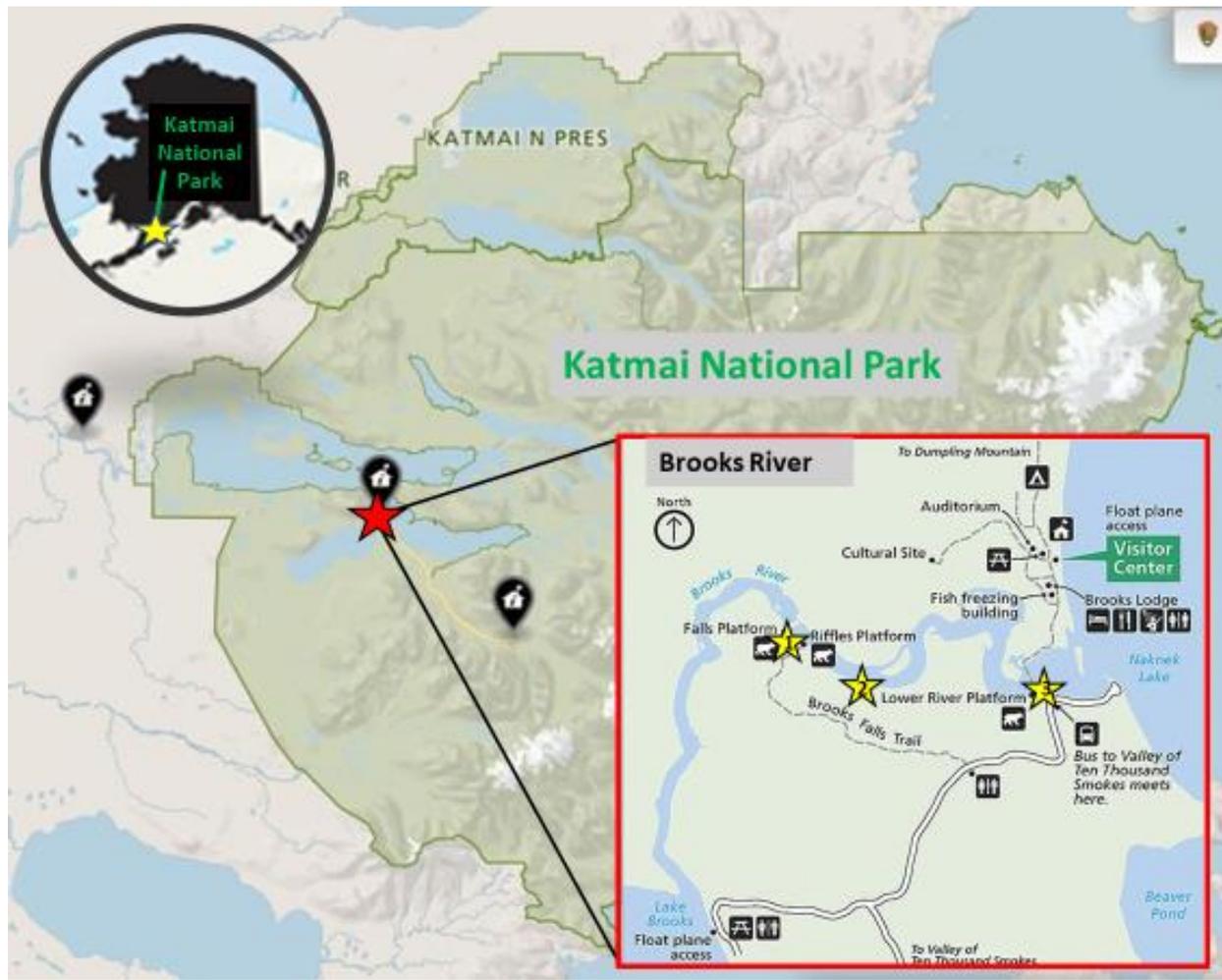


Figure 1.1: Katmai National Park and Preserve located in Alaska with map of Brooks River in the lower right corner. The yellow stars on the Brooks River map indicate 3 observation sites (1: falls platform, 2: cutbank stand, 3: lower river platform) where bear monitoring data was collected (2000–2018).

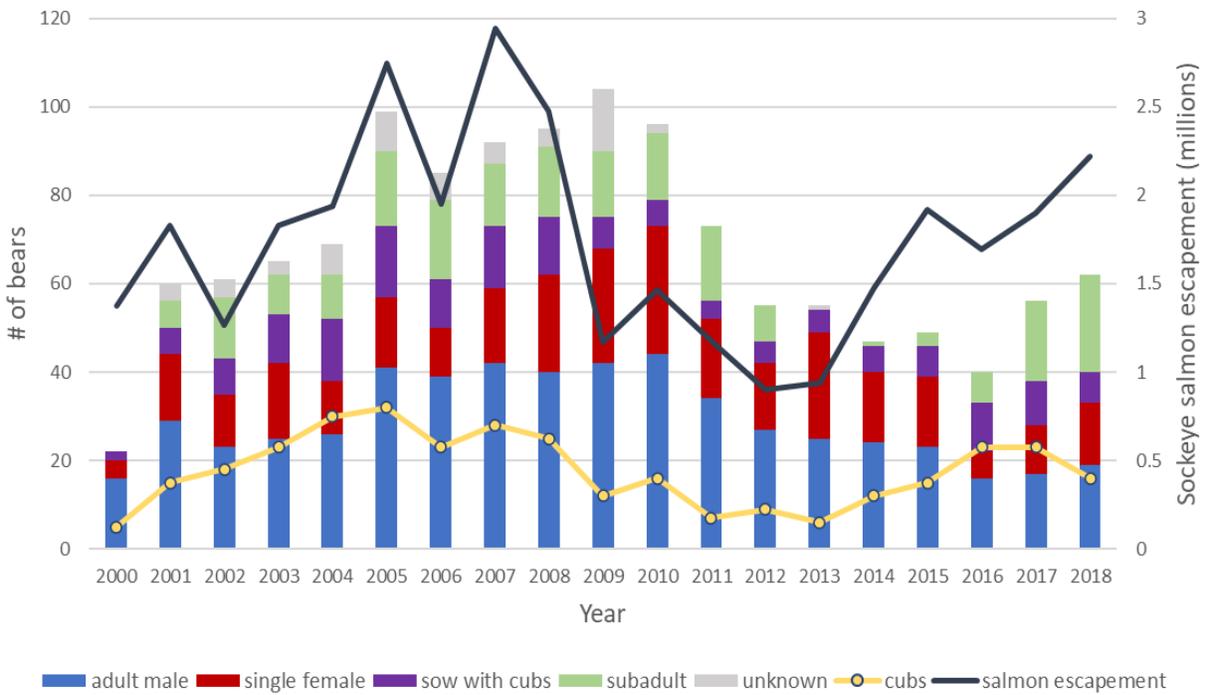


Figure 1.2: Annual bear counts by sex and age grouping, and annual sockeye salmon escapement at Brooks River, AK, 2000–2018.

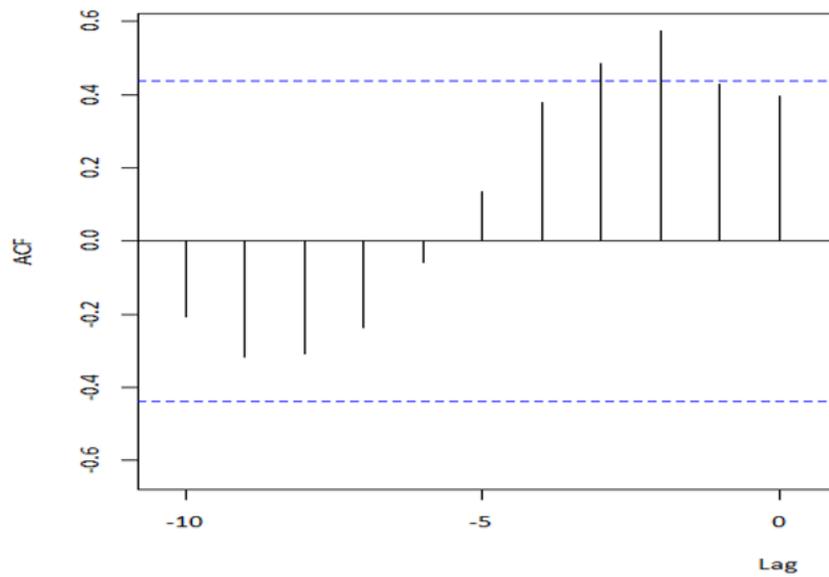


Figure 1.3: Cross-correlation between annual sockeye salmon escapement in the Naknek River drainage and annual counts of independent bears from 2000–2018. The y-axis shows the autocorrelation function. The x-axis shows the lag in years. Bars passing over the dotted blue line show a significant relationship. There is a significant positive relationship between escapement and bear counts lagging 2–3 years.

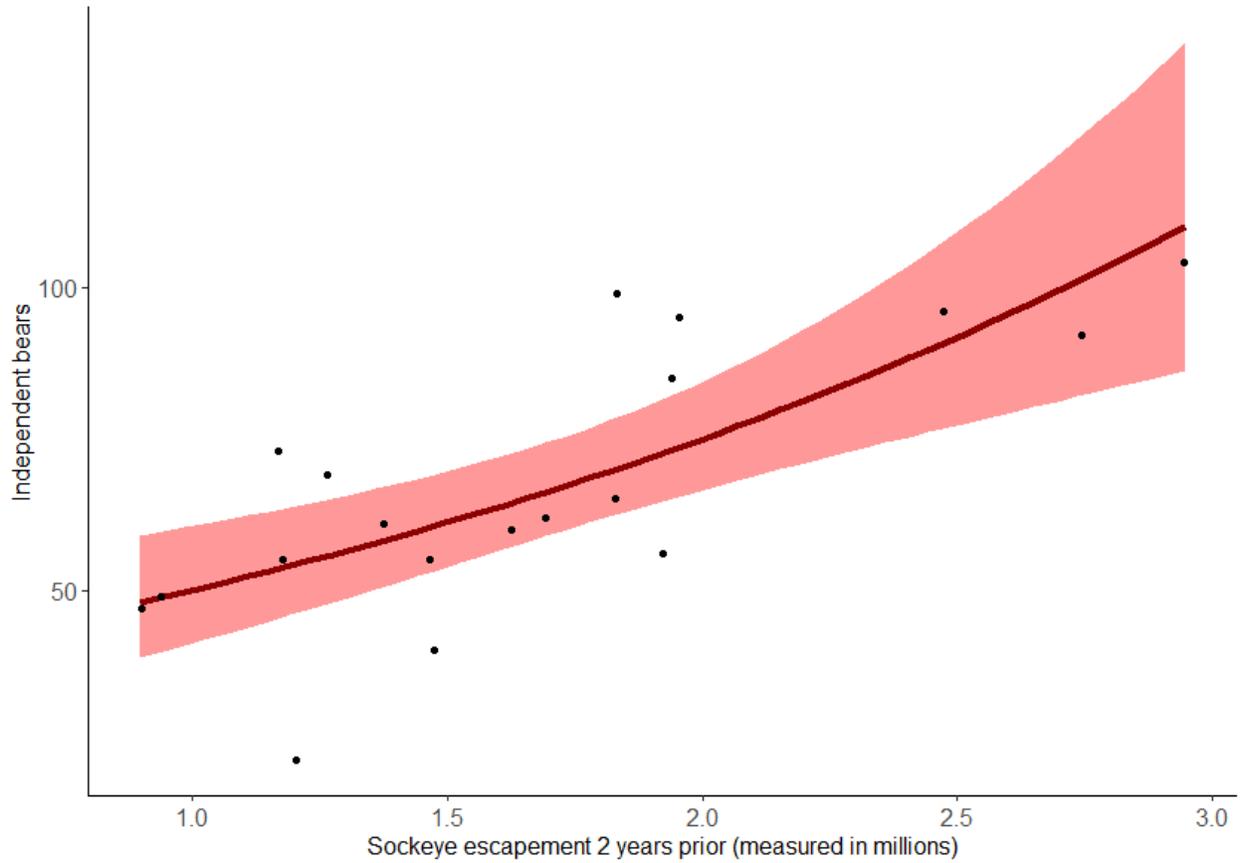


Figure 1.4: Quasipoisson regression with mean (red line) and 95% confidence interval (pink). The regression depicts a significant positive relationship between sockeye salmon escapement in the Naknek River drainage (2000–2018) and the number of bears counted along Brooks River 2 years later.

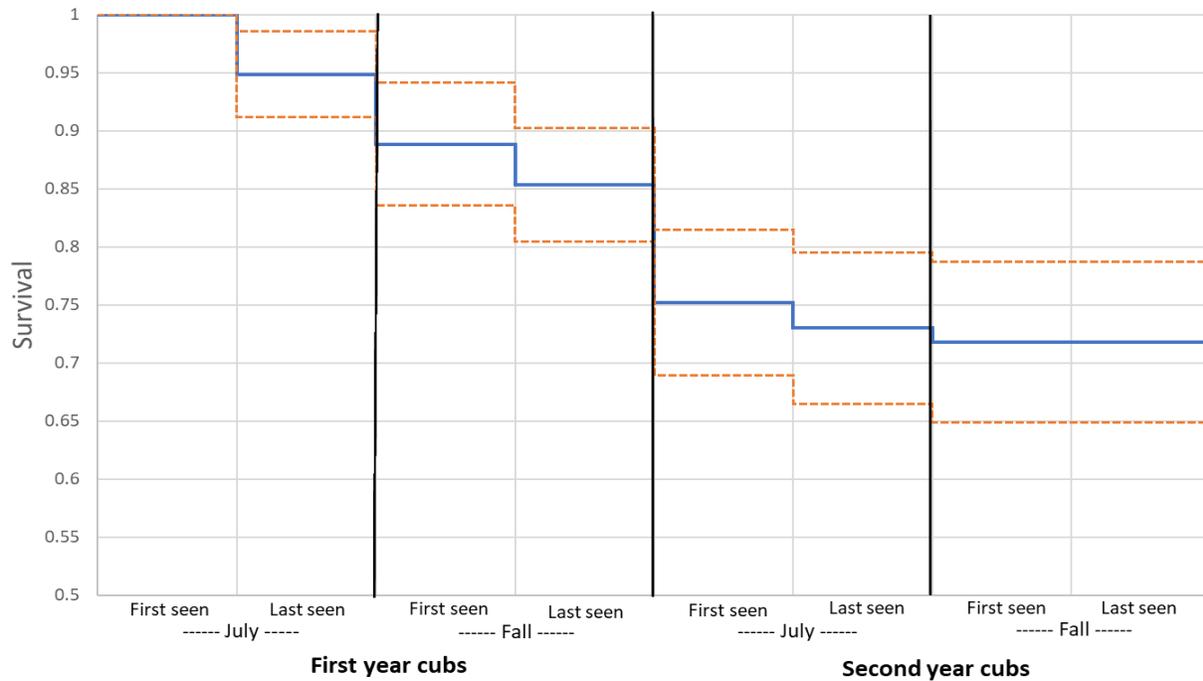


Figure 1.5: Average survival (blue) and 95% confidence interval (orange) of dependent cubs by age class using Apparent Percent Success (APS). Litters from 2000–2018 were used in the calculation.

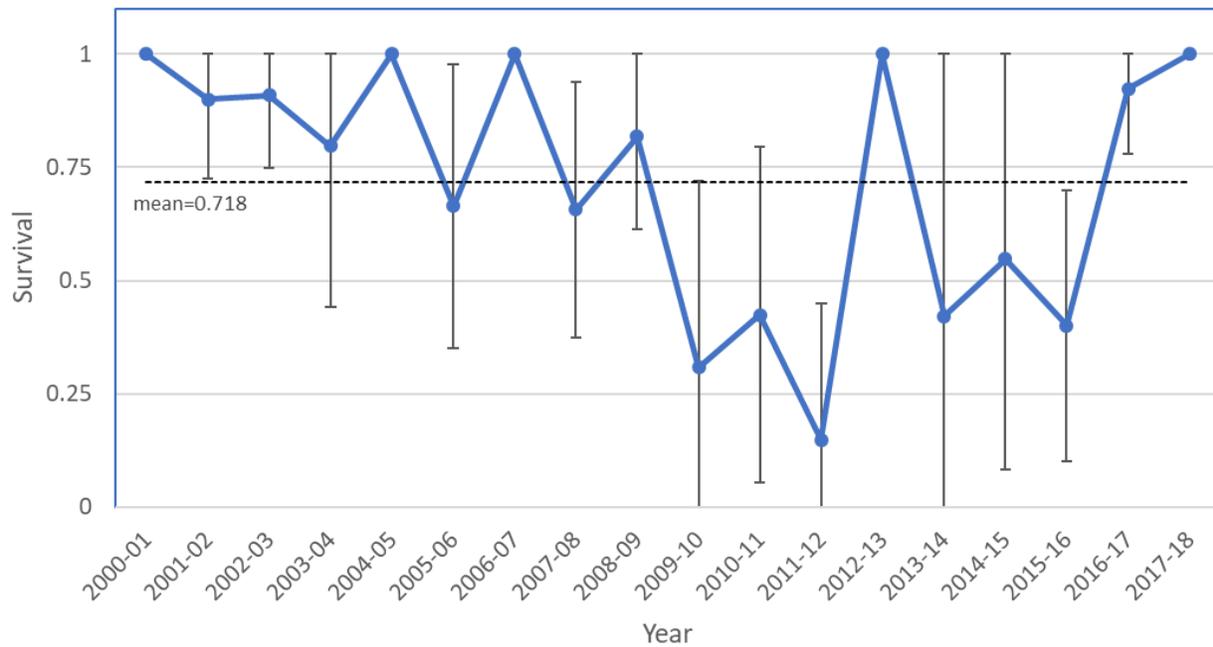


Figure 1.6: Mean survival (dotted line), annual survival (blue), and 95% CI (vertical black bars) for spring cubs based on when they were first counted during July monitoring to when they were next seen during their second year. This model used combined Mayfield and Apparent Percent Success (APS) methods to estimate period survival.

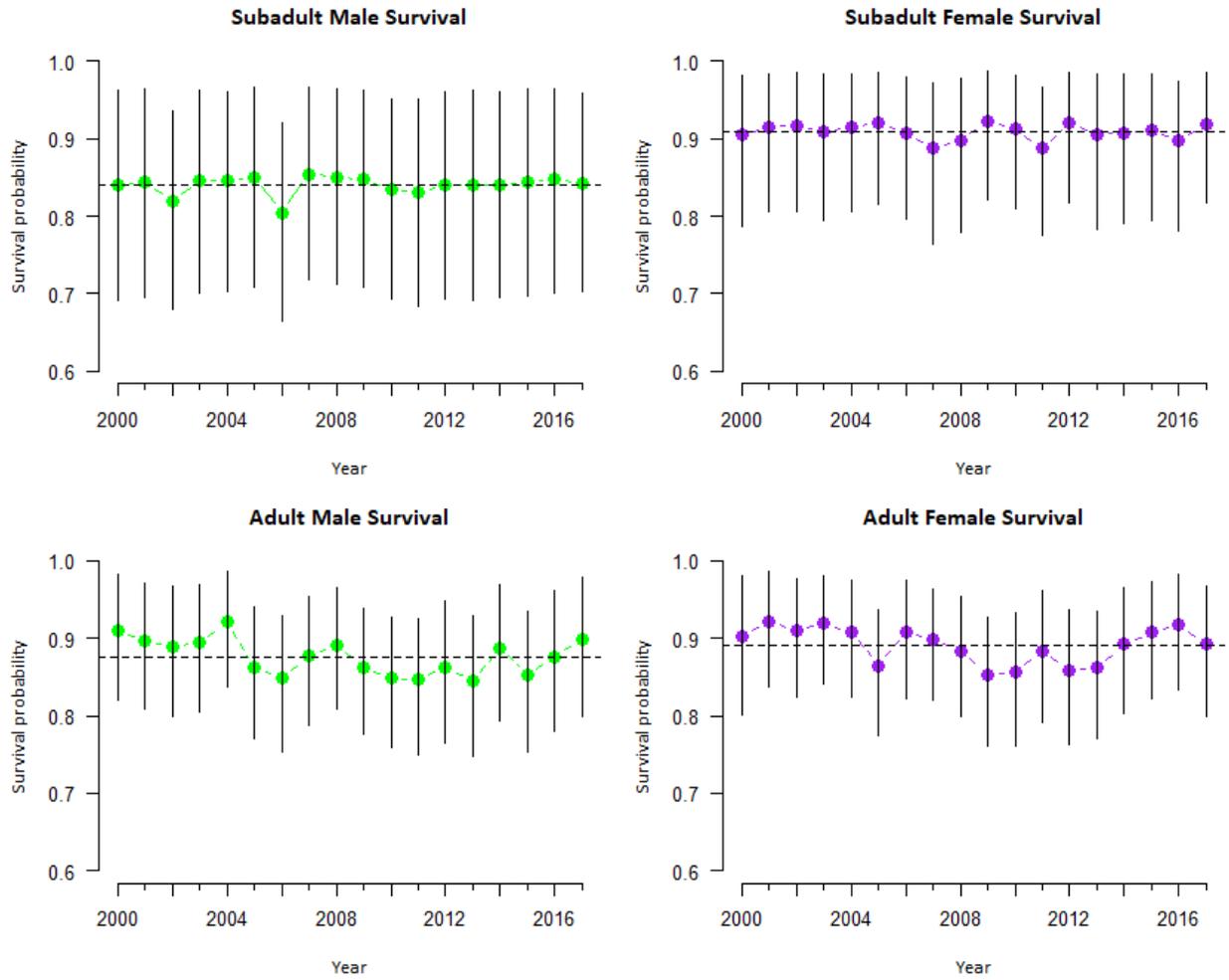


Figure 1.7: CJS model estimating mean and annual survival with 95% credible interval for subadult males (top left), subadult females (top right), adult males (bottom left), and adult females (bottom right).

### APPENDIX III: CORMACK-JOLLY-SEBER MODEL CODE

```
### Cormack-Jolly-Seber (CJS) model estimating survival and probability of detection of Brooks
River bears, 2000–2018
### 4 age-sex groups, probability of detection per group, annual survival per group
### JAGS code based off CJS model from Kery and Schaub (2012)

### JAGS code ###
sink("cjs-age.jags")
cat("
  model {
    # Priors and constraints
    for (i in 1:nind){
      for (t in f[i]:(n.occasions-1)){
        phi[i,t] <- beta[x[i,t],t]
        p[i,t] <- p.g[x[i,t]]
        phi.new[i,conversion[t,2],conversion[t,3]] <- phi[i,t] #formats seasonal survivals
        to annual survival
      } #t
    } #i

    for (u in 1:4){
      p.g[u] ~ dunif(0, 1)      # Priors for group recapture
      mu.beta[u]~dunif(0,1)
      for(t in 1:(n.occasions-1)){
        beta[u,t] ~ dnorm(mu.beta[u],tau) T(0,1)      # Priors for group survival
        beta.new[u,conversion[t,2],conversion[t,3]] <- beta[u,t] #group survivals in
        annual formatting
      } #t
    } #u

    beta.annual[1:4,1:18] <- beta.new[1:4,1,1:18]*beta.new[1:4,2,1:18] #calculates annual
    survival from 2 seasonal survivals

    tau<-pow(sigma,-2)
    sigma~dunif(0,10)

    # Likelihood
    for (i in 1:nind){
      # Define latent state at first capture
      z[i,f[i]] <- 1
      for (t in (f[i]+1):n.occasions){
```

```

        # State process
        z[i,t] ~ dbern(mu1[i,t])
        mu1[i,t] <- phi[i,t-1] * z[i,t-1]
        # Observation process
        y[i,t] ~ dbern(mu2[i,t])
        mu2[i,t] <- p[i,t-1] * z[i,t]
    } #t
} #i
}
",fill = TRUE)
sink()

# Function to create a matrix with information about known latent state z
known.state.cjs <- function(ch){
  state <- ch
  for (i in 1:dim(ch)[1]){
    n1 <- min(which(ch[i,]==1))
    n2 <- max(which(ch[i,]==1))
    state[i,n1:n2] <- 1
    state[i,n1] <- NA
  } #i
state[state==0] <- NA
return(state)
}

# Bundle data
jags.data <- list(y = counts, f = f, nind = dim(counts)[1], n.occasions = dim(counts)[2], conversion
= conversion, z = known.state.cjs(counts), x = x)

# Function to create a matrix of initial values for latent state z
cjs.init.z <- function(ch,f){
  for (i in 1:dim(ch)[1]){
    if (sum(ch[i,])==1) next
    n2 <- max(which(ch[i,]==1))
    ch[i,f[i]:n2] <- NA
  } #i
  for (i in 1:dim(ch)[1]){
    ch[i,1:f[i]] <- NA
  } #i
  return(ch)
}

```

**LITURATURE CITED**

## LITERATURE CITED

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## **CHAPTER 2: TRENDS IN ABUNDANCE OF BROWN BEARS ALONG BROOKS RIVER IN KATMAI NATIONAL PARK, ALASKA.**

### **Abstract**

Estimating abundance can be one of the most challenging tasks for wildlife managers. Species can be wide ranging, elusive, and hard to count, and population estimates can be impacted by a multitude of factors. Along Brooks River, in Katmai National Park, Alaska, biologists and trained technicians can identify individual bears by recognizing unique physical features and behavioral characteristics allowing for long-term, non-invasive monitoring of individual brown bears each year. In 2013, visitors and staff at Katmai noticed a decline in the number of bears using Brooks River. Initial research did not show a significant change in survival of the Brooks River bear population, implying that the change in counts may be driven by other factors such as changing productivity or use patterns.

Our objectives were to estimate abundance and investigate how salmon escapement influenced age-sex group abundance and productivity. Abundance of independent bears was positively related to sockeye salmon escapement in previous years. This relationship suggests that past events influence where bears choose to fish for salmon. However, only some age-sex groups exhibited this relationship. Abundance of breeding females and their cubs was positively related to salmon escapement from the same year, which may indicate they were avoiding Brooks River during years when escapement was low and competition among bears was high. The relationship between annual escapement and productivity measures were not significant, although there were signs that a change in productivity may have occurred (trends in abundance showed an age-based lag)

## Introduction

Estimating wildlife abundance is one of the most common goals in wildlife management and one of the most challenging. Species abundances can vary widely over short time periods and most species are hard to accurately count. Additionally, population estimates based on counts can be impacted by a multitude of factors including weather, habitat conditions, and observer biases. As a result, estimating wildlife abundance can be costly, time consuming, and imprecise.

Southwest Alaska is home to one of the world's largest brown bear (*Ursus arctos*) populations supported by the largest sockeye salmon (*Oncorhynchus nerka*) run in the world (Elison et al. 2018). To protect these resources, millions of hectares of state and federal lands have been set aside to help preserve brown bear habitat and salmon spawning grounds including Katmai National Park and Preserve. Because of the seasonally abundant food source, bears in this region are willing to tolerate each other and people in closer proximity than most other places in the world (Jope 1983). This tolerance creates a unique opportunity to view and study brown bear population dynamics.

In Katmai National Park, biologists and trained technicians can identify individual bears by recognizing unique physical features and behavioral characteristics (Olson et al. 1998, Smith 2002, Troyer 1975, 1976, 1977, 1978). The identification process at Katmai has allowed long-term, non-invasive monitoring of individual brown bears. During the 1980s, protocols were developed to study behavioral characteristics of the bears concentrated on salmon streams, particularly Brooks River (Olson 1993, Olson and Gilbert 1994, Olson et al. 1997, Olson et al.

1998). This data collection at Brooks River has continued for decades and provides counts of individual bears using Brooks River each season.

In 2013, visitors and staff at Katmai National Park noticed a decline in number of bears seen using Brooks River. Further investigation showed a steady decline in number of bears seen starting in 2009. Initial research failed to show a significant change in survival of the Brooks River bear population, implying that the change in counts may be driven by other factors such as changing productivity or use patterns (Skora 2021). Katmai's remote location, coupled with its harsh weather and limits to staff and funding, make it difficult to accurately estimate and monitor brown bear abundance using traditional mark-recapture approaches. There is growing concern about the status of the brown bear population in this region, or how constantly shifting environmental conditions might be influencing the population over time.

The recent use of state-space modeling techniques to portray population dynamics (De Valpine and Hastings, 2002; Buckland et al., 2004; Clark and Bjornstad, 2004) offers a framework for using time series of counts to estimate abundance while accounting for imperfect detection. Our first objective was to use seasonal counts of uniquely identifiable bears along Brooks River to estimate annual abundance of age-sex groups from 2000–2019. We hypothesized that changes in bear counts would reflect changes in abundance and population dynamics. Hilderbrand et al (1999a) found that bear populations with access to large quantities of spawning salmon had higher densities, larger bears, and greater reproductive success. Fall diets high in salmon led to higher body fat gains which are important for cub production (Hilderbrand 1999b, Farley and Robbins 1995). Therefore, our second objective was to investigate how salmon escapement influences age-sex group abundance and productivity. We

hypothesized that annual salmon escapement influences bear abundance at Brooks River by affecting productivity through the annual probability of sows successfully breeding, average annual litter size, or annual survival of younger age groups.

## **Study Area**

Katmai National Park and Preserve is located along the base of the Alaska Peninsula, with Bristol Bay and the Bering Sea on the western side and Pacific Ocean on the eastern border. It was established as Katmai National Monument in 1918 to preserve the site of the largest volcanic eruption of the 20<sup>th</sup> century, and then expanded in 1931 to include the Brooks River area for the purpose of protecting brown bears and other wildlife (Norris 1996). In 1980, the monument was significantly expanded and designated a National Park and Preserve encompassing 1.6 million ha (Figure 2.1). Katmai National Park and Preserve is surrounded by federal, state, and private land. Bear hunting is not allowed within the park but is allowed in the 160,000 ha Preserve under a regulated permit system.

Data collection for this study occurred along the Brooks River in Katmai, which serves as a spawning stream and major migratory route for sockeye salmon traveling upstream to smaller tributaries for spawning (Hartman et al. 1964). Brooks River is approximately 3.2 km long and flows from Brooks Lake to Naknek Lake (Figure 2.1). It is bisected near its midpoint by a 1.5-meter-tall waterfall that creates a bottleneck for salmon, which must jump the falls to continue their migration. The river is bordered by a forest cover of alder (*Alnus* spp.), spruce (*Picea* spp.), birch (*Betula* spp.), and willows (*Salix* spp.). The lower end of the river is more open with marshes and wetlands. During July, temperature around Brooks River averages 13.1 degrees

Celsius. Average precipitation is 4.2 cm. During September, temperature averages 8.7 degrees Celsius with an average of 8.1 cm of precipitation (NOAA 2018).

There are 2 main periods of activity for bears along Brooks River. The first period usually begins late June and lasts until late July as bears congregate to fish mainly by the falls and along the lower river. Bears concentrate to feed on salmon that are backed up trying to jump the falls. This serves as an early season food resources for bears in the area. The second period of bear activity is during September and October as bears congregate in the lower river to feed on spawning and dying salmon that accumulate in the slower moving waters.

## **Methods**

### *Data Collection*

Brown bear monitoring along Brooks River in Katmai National Park, AK, was initiated in 1988 (Olson and Gilbert 1994, Olson et al. 1997, 1998) and has regularly occurred since 2000. Scan samples occurred twice each year during 2 separate monitoring periods: the early monitoring season (“July monitoring”) and later monitoring season (“fall monitoring”). The early monitoring season usually began on the first Monday after June 21<sup>st</sup> and continued for 5, 8-day cycles, usually into the first week of August. The fall monitoring season usually began on the first Monday after August 26<sup>th</sup> and ended after 5, 8-day cycles into the first week of October. During each day, an observer systematically cycled through 3 different viewing platforms for the early monitoring season, and two during the fall monitoring season. For both seasons, a complete cycle consisted of monitoring 6 consecutive days followed by 2 days off.

Bears were identified by physical and behavioral features, a method commonly used across a variety of species (Friday et al. 2000, Dawson and Miller 2008, Van Horn et al. 2014, Goswami et al. 2012). At Brooks River, observers identify bears using fur color, shed patterns, ear and muzzle shape, body size, and behaviors that include styles and locations of catching fish. Physical feature identification of brown bears has been used in other research at locations such as in Brooks Camp (DeBruyn et al. 2004), McNeil River State Game Sanctuary (Sellers and Aumiller 1994, Egbert et al. 1976), coastal British Columbia, Canada (Nevin and Gilbert 2005), and Yellowstone National Park (Knight et al. 1995).

#### *Count Data*

To estimate abundance from 2000–2019, we compiled records of individually recognizable bears for each monitoring season within each year. To be included in the dataset, an individual bear must have been observed during  $\geq 3$  monitoring sessions during each respective season. Individuals were then assigned a 3-digit identifying number that referenced the bear's sex, age category, reproductive status, and physical and behavioral features. We used these individual records to assign 7 age-sex classes: spring cubs, yearling cubs, dependent 2-year-olds, male and female subadults, and male and female adults. We further divided the adult female category into 4 classes according to reproductive status: nonbreeding females, 1<sup>st</sup> year breeding females with spring cubs, 2<sup>nd</sup> year breeding females with yearling cubs, and 3<sup>rd</sup> year breeding females with dependent 2-year-olds. We often could not identify sex of dependent cubs, so we did not assign them a sex. We created 10 age-sex groups.

We used the term independent bears when referring to individual bears that were not cubs in a family group reliant on a sow. Subadult bears were defined as independent bears not yet sexually mature, estimated to be 2–4 years old. Like other studies in the area (Glenn and Miller 1977, Sellers and Aumiller 1994, Sellers et al. 1999), adult bears were defined as individuals at or around the age of sexual maturity, which is typically  $\geq 5$  years of age. Unless we recognized an adult from when it was a dependent cub, we estimated age through body size and behavioral characteristics. Dependent bears still in a family group cared for by a sow were not counted as independent individually recognizable bears. Litter age and size were recorded based on identifiability of the sow.

#### *State-Space Model*

We developed a state-space model in the program R (R Core Team 2019) using a Bayesian framework with the program JAGS (Plummer 2003), package *jagsUI* (Kellner 2016). The model used count data to estimate abundance and accounted for imperfect detection inherent to observational data (Kery and Schaub 2012; Figure 2.2).

To portray trends in age and sex demographics, we built a population model using age and sex groupings (*g*) from the count data (Figure 2.3). Incorporating these specific age and sex categories in the analysis allowed us to monitor annual changes in probability of breeding, probability that sows kept their cubs an extra year, average litter size (fecundity), as well as changes in survival, and abundance.

#### *Spring Cubs (not sex-specific)*

We modeled spring cub abundance as,

$$N_{cubs,t+1} = \rho_t N_{AFNB,t} * S_{AFNB,t} * f_{a,t}$$

$$f_t \sim \text{Normal}(\mu_f, \sigma_f)$$

$$S_{g,t} \sim \text{Normal}(\mu_{S,g}, \sigma_{S,g})$$

$$N_{cubs,t=1} = \text{Poisson}(C_{cubs,t=2000}),$$

where, number of cubs ( $N_{cubs}$ ) at time,  $t+1$ , was a function of the proportion ( $\rho_t$ ) of nonbreeding females ( $N_{AFNB,t}$ ) that successfully bred the previous year ( $t$ ) survived ( $S_{AFNB,t}$ ) and multiplied by average annual fecundity ( $f_{a,t}$ ). We estimated annual fecundity ( $f_{a,t}$ ) using a normal distribution centered on mean  $\mu_f$  with variance  $\sigma_f$ . We assigned a uniform uninformative prior to both  $\mu_f$  and  $\sigma_f$  ( $\sigma_f \sim U(0,1)$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of cubs in July of year 2000. This provided a starting point for the model to estimate abundance in following years.

#### *Yearling Cubs (not sex-specific)*

We modeled dependent yearling cub abundance as,

$$N_{yearlings,t+1} = N_{cubs,t} * S_{cubs,t}$$

$$N_{yearlings,s,t=1} = \text{Poisson}(C_{yearlings,t=2000}),$$

where the number of yearlings ( $N_{yearlings}$ ) at time  $t+1$  was equal to number of spring cubs ( $N_{cubs}$ ) the previous year ( $t$ ) that survived the year ( $S_{cubs,t}$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of yearling cubs in July of year 2000.

#### *Dependent 2-year-old Cubs (not sex-specific)*

We modeled dependent 2-year-old cub abundance as,

$$N_{2yrs,t+1} = \Psi_t N_{yearlings,t} * S_{yearlings,t}$$

$$\Psi_t \sim \text{Normal}(\mu_\Psi, \sigma_\Psi)$$

$$N_{2yrs,,t=1} = \text{Poisson}(C_{2yrs,t=2000}),$$

where  $N_{2yrs,t+1}$  was number of yearling cubs the previous year ( $N_{yearlings,t}$ ) that survived ( $S_{yearlings,t}$ ) and were kept for an extra year with probability  $\Psi_t$ . The probability of retaining cubs was estimated with a mean ( $\mu_\Psi$ ) and variance ( $\sigma_\Psi$ ). We assigned a uniform prior around  $\mu_\Psi$  and  $\sigma_\Psi$  ( $\sigma_\Psi \sim U(0,1)$ ). For the first year, abundance was estimated using a Poisson distribution centered around the count of dependent 2-year-old cubs in July of year 2000. If a 2-year-old was not kept as a dependent, it was emancipated and became a subadult. We used a 50:50 sex ratio (Steyaert et al. 2012, Sellers et al. 1999) to transition dependent cubs into the next state - male and female subadults.

#### *Male and Female Subadults*

We modeled subadult male and female abundance as,

$$N_{Sa(M \text{ or } F),t+1} = ((1-\Psi_t)0.5N_{yearlings,t} * S_{yearlings,t}) + (0.5N_{2yrs,t} * S_{2yrs,t}) + ((1-\omega_{(M \text{ or } F),t})N_{Sa(M \text{ or } F),t} * S_{Sa(M \text{ or } F),t})$$

$$\omega_{sex,t} \sim \text{Normal}(\mu_{\omega,sex}, \sigma_{\omega,sex})$$

$$N_{Sa(M \text{ or } F),,t=1} = \text{Poisson}(C_{Sa(M \text{ or } F),t=2000}),$$

where abundance of subadult male or females each year ( $N_{Sa(M \text{ or } F),t+1}$ ) was defined as the number of yearling cubs of each sex from the previous year ( $N_{yearlings,t}$ ), that survived ( $S_{yearlings,t}$ ), and were emancipated ( $1-\Psi_t$ ). In addition to the surviving yearling cubs, subadults included the dependent 2-year-old cubs ( $N_{2yrs,t}$ ) from the previous year that were assigned as either male or

female, survived ( $S_{2yrs,t}$ ), and were emancipated. We also included subadults that survived and remained subadults not transitioning into adulthood ( $1-\omega_{(M\ or\ F),t}$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of male or female subadults in July of year 2000.

Subadults remained in the male or female age-sex category until they reached sexual maturity, usually around 5 years old. The model estimated probability of subadults transitioning into adults each year.  $\omega_t$  was the probability that a male or female subadult became an adult in a particular year.  $\mu_\omega$  was the mean probability of becoming an adult, and  $\sigma_\omega$  was the annual stochasticity. We assigned a uniform prior around  $\mu_\omega$  and  $\sigma_\omega$  ( $\sigma_\omega \sim U(0,1)$ ). We used a uniform uninformative prior to estimate the probability of becoming an adult during the first year of the model  $t=1$  ( $\omega_{t=1} \sim U(0,1)$ ).

### *Adult Males*

We modeled adult male abundance as,

$$N_{AM,t+1} = (N_{AM,t} * S_{AM,t}) + (\omega_t N_{SaM,t} * S_{SaM,t})$$

$$\omega_t \sim \text{Normal}(\mu_\omega, \sigma_\omega)$$

$$N_{AM,t=1} = \text{Poisson}(C_{AM,t=2000}),$$

where adult male abundance ( $N_{AM,t+1}$ ) was defined as number of adult males the previous year that survived ( $S_{AM,t}$ ) and number of subadult males ( $N_{SaM,t}$ ) that survived ( $S_{SaM,t}$ ) and transitioned to adult males ( $\omega_t$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of adult males in year 2000.

## Adult Females

Adult females can transition between 4 breeding categories: nonbreeding females, 1<sup>st</sup> year breeding females, 2<sup>nd</sup> year breeding females, and potentially go into a 3<sup>rd</sup> year of being a breeding female before returning to the nonbreeding female pool. We modeled nonbreeding female abundance as,

$$N_{AFN,t+1} = ((1-\rho_t)\omega_t N_{SaF,t} * S_{SaF,t}) + ((1-\rho_t)N_{AFN,t} * S_{AFN,t}) + (\phi_t N_{AF1,t} * S_{AF1,t}) + ((1-\psi_t)N_{AF2,t} * S_{AF2,t}) + (N_{AF3,t} * S_{AF3,t})$$

$$\rho_t \sim \text{Normal}(\mu_\rho, \sigma_\rho)$$

$$\phi_t \sim \text{Normal}(\mu_\phi, \sigma_\phi)$$

$$N_{AFN,t=1} = \text{Poisson}(C_{AFN}, t=2000),$$

where total number of nonbreeding females each year  $t+1$  was based on number of subadult females ( $N_{SaF,t}$ ) from the previous year that survived ( $S_{SaF,t}$ ), transitioned to adults ( $\omega_t$ ) and did not breed ( $1-\rho_t$ ). Nonbreeding females also included number of nonbreeding females ( $N_{AFN,t}$ ) from the previous year ( $t$ ) that survived ( $S_{AFN,t}$ ) and did not breed ( $1-\rho_t$ ), plus the number of breeding females from the previous year ( $N_{AF1,t}$ ) that survived ( $S_{AF1,t}$ ) yet lost their entire litter ( $\phi_t$ ). In addition, adult nonbreeding females included number of 2<sup>nd</sup> year breeding females from the previous year ( $N_{AF2,t}$ ) that survived ( $S_{AF2,t}$ ) and did not keep their yearling cubs an extra year ( $1-\psi_t$ ), plus the 3<sup>rd</sup> year breeding females ( $N_{AF3,t}$ ) from the previous year who survived ( $S_{AF3,t}$ ) and then returned to the nonbreeding category. For the first year, abundance was estimated using a Poisson distribution centered on the count of nonbreeding females in July of year 2000.

We modeled 1<sup>st</sup> year breeding female abundance as,

$$N_{AF1,t+1} = (\omega_t \rho_t N_{SaF,t} * S_{SaF,t}) + (\rho_t N_{AFN,t} * S_{AFN,t})$$

$$\Omega_{F,t} \sim \text{Normal}(\mu_{\omega,F}, \sigma_{\omega,F})$$

$$\rho_t \sim \text{Normal}(\mu_{\rho}, \sigma_{\rho})$$

$$N_{AF1,t=1} = \text{Poisson}(C_{AF1,t=2000}),$$

where first year breeding females ( $N_{AFN,t+1}$ ) were defined as number of subadult females the previous year ( $N_{SaF,t}$ ) that survived ( $S_{SaF,t}$ ), became adults ( $\omega_t$ ), and successfully bred ( $\rho_t$ ). In addition, first year breeding females included nonbreeding adult female from the previous year ( $N_{AFN,t}$ ) who survived ( $S_{AFN,t}$ ) and successfully bred ( $\rho_t$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of first year breeding females in July of year 2000.

We modeled 2<sup>nd</sup> year breeding female abundance as,

$$N_{AF2,t+1} = (1-\phi_t) N_{AF1,t} * S_{AF1,t}$$

$$\phi_t \sim \text{Normal}(\mu_{\phi}, \sigma_{\phi})$$

$$N_{AF2,t=1} = \text{Poisson}(C_{AF2,t=2000}),$$

where  $N_{AF1,t+1}$  was the product of the number of 1<sup>st</sup> year breeding females the previous year ( $N_{AFN,t}$ ) that survived ( $S_{AFN,t}$ ) and did not lose their entire litter ( $1-\phi_t$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of 2<sup>nd</sup> year breeding females in July of year 2000.

We modeled 3<sup>rd</sup> year breeding female abundance as,

$$N_{AF3,t} = \Psi_t N_{AF2,t} * S_{AF2,t}$$

$$\Psi_t \sim \text{Normal}(\mu_\psi, \sigma_\psi)$$

$$N_{AF3,t=1} = \text{Poisson}(C_{AF3,t=2000}),$$

where  $N_{AF3,t+1}$  was the product of number of 2<sup>nd</sup> year breeding females from the previous year ( $N_{AF2,t}$ ) that survived ( $S_{AF2,t}$ ) and kept their litter an extra year as dependent 2-year-olds ( $\Psi_t$ ). For the first year, abundance was estimated using a Poisson distribution centered on the count of 3<sup>rd</sup> year breeding females in July of year 2000. On the rare occasion cubs were kept as dependent 3-year-olds, we kept them in the same dependent 2-year-old model category.

Although it was possible that a 1<sup>st</sup>, 2<sup>nd</sup>, or 3<sup>rd</sup> year breeding female slipped back into estrous, mated, and then returned the following year as a successfully bred 1<sup>st</sup> year breeding female, this was rarely observed at Brooks River. To simplify the model, we had all 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> year breeding females return to nonbreeding females the year following litter failure or cub emancipation.

To account for environmental stochasticity, the model estimated abundance of these age and sex groups ( $N_{estg,t}$ ) by drawing from a Poisson distribution ( $\lambda_{g,t} = N_{g-1,t} * S_{g-1,t}$ )

$$N_{estg,t} \sim \text{Poisson}(\lambda_{g,t}).$$

Here  $\lambda_{g,t}$  represented annual growth rate of an age-sex group ( $g$ ). It represented the time period, year  $t$ , and surviving until the July counting period in year  $t+1$ .

This population model (Figure 2.3) provided a map to follow the transition of one age-sex group ( $g$ ) at time  $t$  to the next age group at time  $t+1$ . Abundance of one age group depended on survival of the previous age group the year before. Our population model represented the true underlying state of the sample population as shown in Figure 2.2 in blue. For each time period, the model portrayed abundance of each age-sex group and their transition rate through time (Figure 2.4).

### *Observation Process*

The observation model linked the ecological or state process to the observed data. Since we had 2 separate counts ( $C$ ) of bears along Brooks River from July and fall monitoring, we used a binomial distribution to estimate annual abundance ( $N_t$ ) of each age-sex group ( $g$ ) using these 2 seasonal replicate counts ( $C_s$ ) (Figure 2.5).

$$C_{g,t,s} \sim \text{Binomial}(N_{g,t}, P_g)$$

$P_g$  was the probability of detecting an age-sex group. It was drawn from a uniform uninformative prior ( $P_g \sim U(0,1)$ ). Using the binomial distribution required that the counts occurred over a relatively short period of time so the population could be considered closed. Estimates of Brooks River bear survival showed that changes in adult and subadult survival was minimal between the July and fall monitoring seasons.

The code for the state-space model is provided in the supplemental material (Appendix III). We ran 3 chains 75,000 iterations long with a burn in of 15,000 iterations and a thinning rate of 6. Our model estimated probability of detection for 7 age-sex groups (subadult male, subadult female, adult male, nonbreeding female, b1 female, b2 female, and b3 female).

Breeding females shared a probability of detection with their cubs since cubs were associated with an individual sow. There were also times when we did not know the sex of a subadult bear encountered during a monitoring season. To use these observations, we randomly assigned subadults of unknown sex to a category using a random number generator.

### *Post model analysis*

To investigate the relationship between sockeye salmon escapement and population parameters derived from the state-space model (i.e., brown bear abundance, survival, and probability of breeding), we ran a post hoc logistic regression analysis in the program JAGS. We used estimates of sockeye salmon escapement for the Naknek River drainage collected by the Alaska Department of Fish and Game (Erickson et al. 2018, Sands 2019; Figure 2.6). Previous work (Skora 2021) showed a significant positive relationship between escapement and counts of bears after a lag of 2–3 years. Therefore, we tested the relationship between annual age-sex group abundance and escapement of that year and of 2 years prior. We used posterior distributions of annual abundance, survival, and probability of breeding estimates from the State-space model.

$$\text{Log}(\mu_{g,t,n}) = \alpha_g + \beta_g * E_t + e_t$$

$$\text{Logit}(\mu_{g,t,n}) = \alpha_g + \beta_g * E_t + e_t$$

Where  $\mu$  is annual abundance on the log scale or survival and probability of breeding on the logit scale,  $g$  is the age-sex group,  $t$  is the year,  $n$  is the observation from the posterior distribution of  $\mu_{gt}$ ,  $E_t$  is annual salmon escapement ( $E_{t-2}$  for salmon escapement from 2 years prior), and  $e_t$  is a normally distributed random effect parameter used to correct for

overdispersion. Thus, for each value in the posterior of  $\mu_g$  ( $n=18,000$ ), we ran 3 chains of 1,000 iterations with a burn in of 500 iterations and a thinning rate of 5, producing super posteriors for  $a_g$  and  $b_g$  ( $n=5,400,000$ ).

## Results

We identified over 320 individual bears during the 20-year period from 2000–2019. An average of 68 (SD: 22) independent bears were counted each year with an average of 29 (SD: 9) adult males and 24 (SD: 7) adult females. There was an average of 9 (SD: 4) spring cubs seen each year. The year 2009 had the highest count of ( $n = 104$ ) independent bears, while the year 2000 had the lowest count of 22 independent bears. Mean annual abundance of independent bears was estimated as 106 (95% CrI: 42–157). We estimated an average abundance of 47 (95% CrI: 23–77) adult males, 40 (95% CrI: 15–58) adult females, and 23 (95% CrI: 6–46) spring cubs (Table 2.1). Our model indicated that 2009 had the highest abundance of independent bears (145, 95% CrI: 123–171), while 2000 had the lowest (43, 95% CrI: 35–51).

We found that estimates of independent bear abundance declined from 2009–2016 followed by increasing abundance from 2017–2019 (Figure 2.7). Our model estimates indicated that abundance of adult males declined from 2010–2017 (Figure 2.8). Nonbreeding female abundance was above average (abundance 2009–2014: 33, 29, 31, 28, 33, 24; mean: 21) from 2009–2014 while abundance of first year breeding females was below average (abundance 2009–2014: 4, 8, 3, 6, 5, 10; mean: 10) during this period (Figure 2.8). In general spring cub abundance was low from 2009–2014 (i.e., abundances below average; Figure 2.9). Older age groups experienced similar periods of below average abundance during the following years.

Table 2.1 shows mean estimated abundance for each of the 10 age-sex groups analyzed and mean probability of detection. Mean annual adult male abundance (n=46) was only slightly higher than mean annual adult female abundance (n=41), regardless of female breeding status. Nonbreeding females had higher detection (mean: 0.548) than breeding females (mean: 0.337; Table 2.1). 1<sup>st</sup> year breeding females had a lower probability of detection (mean: 0.301) than 2<sup>nd</sup> year breeding females (mean: 0.460; Table 2.1).

### *Escapement*

For our second objective, we evaluated the impact of escapement on abundance using the post hoc analysis. There seemed to be a positive relationship between total abundance of independent bears and that year's escapement, but the relationship failed to meet our significance threshold ( $\beta$ : 0.103, 95% CrI: -0.04–0.25). Looking at specific age-sex groups within the population, we found a significant positive relationship between escapement and abundance of breeding females and their cubs (B1 female:  $\beta$ : 0.331, 95% CrI: 0.09–0.59; B2 female:  $\beta$ : 0.316, 95% CrI: 0.03–0.61; coy:  $\beta$ : 0.330, 95% CrI: 0.11–0.56; yrlg:  $\beta$ : 0.437, CrI: 0.11–0.79). Except for male subadults, which also had a significant positive relationship with escapement ( $\beta$ : 0.616, 95% CrI: 0.20–1.12), other age-sex groups did not show a significant relationship with that year's escapement.

There was a significant positive relationship between total independent bear abundance and past (2-year) escapement ( $\beta$ : 0.183, 95% CrI: 0.07–0.30; Figure 2.11). Within the population, there was a significant positive relationship between prior escapement and adult males ( $\beta$ : 0.151, 95% CrI: 0.01–0.30) and subadults ( $\beta$ : 0.548, 95% CrI: 0.17–0.97). There were

no significant relationships between prior escapement and adult females, nonbreeding females, breeding females, or their cubs. Limited data on 3<sup>rd</sup> year breeding females and dependent 2-year-old cubs caused high variance in survival and abundance estimates for these groups, so they were omitted from post hoc analysis.

For productivity, we did not observe a significant relationship between annual probability of a sow successfully breeding and salmon escapement ( $\beta$ : 0.307, 95% CrI: -0.30–0.95; Figure 2.10). However, we did identify a positive relationship between annual probability of breeding and escapement from the following year ( $\beta$ : 0.695, 95% CrI: 0.13–1.32). There was no significant relationship between salmon escapement and abundance of spring cubs the following year ( $\beta$ : 0.129, 95% CrI: -0.15–0.41), nor was there a significant relationship between escapement and annual spring cub survival ( $\beta$ : 0.0912, 95% CrI: -0.57–0.79). There was no significant relationship between escapement and the probability of a sow keeping her yearling cubs for an extra 3<sup>rd</sup> year ( $\beta$ : 0.214, 95% CrI: -0.60–1.06).

## **Discussion**

Our analysis provided a rare long-term look at a population of brown bears. We produced estimates of annual Brooks River bear abundance, survival, and productivity from 2000–2019. Annual abundance estimates indicated a decline from 2009–2016 followed by increasing abundance in recent years. Fluctuating sockeye salmon escapement levels showed a significant positive relationship with abundance of independent bears 2 years later, however, when we looked at specific age-sex groups within the bear population, only some groups, adult male and subadults, had significant relationships lagging salmon escapement. There was no

significant relationship shown between escapement and productivity measures, however there was some evidence that a change in productivity may have occurred. It appears that escapement may be influencing both productivity and stream usage by bears.

### *Escapement and abundance*

We failed to identify a significant relationship between annual salmon escapement and corresponding abundance of independent bears for that year, however there was a significant positive relationship between escapement and independent bear abundance 2–3 years later. This relationship was not consistent among specific age-sex groups within the population. Only adult males and subadults showed the significant positive relationship with prior escapement. These relationships seem to be related to changing use patterns and suggest that past events may influence where some demographic classes of bears choose to fish for salmon. The effects of changing resource availability may not always be immediate within the population.

When escapement was low, fewer bears might have come to Brooks River due to increased competition. In southeast Alaska, Gende and Quinn (2004) described a tendency for dominant bears to exclude less dominant bears from preferred salmon foraging sites. They noted social dominance may be more pronounced during seasons when streams have low salmon returns. We would expect less dominant bears such as breeding females trying to protect their cubs to be most vulnerable to increased competition. We see evidence for this competition in the significant positive relationships between annual escapement and that year's abundance of breeding females along Brooks River. Alternatively, abundance of other age-sex groups, such as adult males and subadults, exhibited a time lag in relationship with

escapement. These groups may tolerate decreased escapement and increased competition for a couple years before trying new sites.

Bears choosing to avoid Brooks River might have exploited fewer salmon streams during years with lower escapement, incorporating less salmon in their diet. Along the Pacific coast of Katmai, Erlenbach (2020) noted that proportion of salmon consumed by bears decreased over time with decreasing escapement, while proportion of vegetation in bear diets nearly doubled. Similarly, bears at Brooks River may have shifted their diet to include more plant matter during times of lower salmon escapement.

Conversely, more bears were likely attracted to Brooks River when escapement was high though it may have taken some classes of bears longer to return to Brooks River. During this analysis, we used estimates of sockeye salmon escapement for the entire Naknek River drainage. So, when salmon were abundant in the Naknek River drainage, we assume they were abundant at Brooks River as well as the surrounding streams. Bears would have multiple plentiful salmon streams to choose from. Also, drainages surrounding the Naknek River drainage (Alagnak and Egegik) show similar trends in annual sockeye salmon escapement (Figure 2.6) which would decrease the need for bears to travel long distances seeking Brooks River in particular. These shared escapement trends suggest that changes in bear abundance at Brooks River were not likely due to large amounts of immigration and emigration.

On Kodiak Island, Van Daele et al. (2012) found that brown bears had a 62% increase in salmon intake as salmon escapement increased across the landscape. They also found that the number of fishing sites bears use correlates with number of days that bears exploited salmon.

This suggests that during years with higher escapement, bears eat more salmon. Bears visited more salmon streams and spent more time fishing when salmon were available for longer periods. Other studies have shown seasonal shifts in the distribution of brown bears as they exploit various food resources and spawning populations (Barnes 1990, Schindler et al. 2013). Deacy et al. (2016) showed that bears “surf the salmon red wave” by tracking variations in spawn timing across the landscape. Increased salmon consumption related to increased salmon escapement was attributed to increased duration of foraging (Deacy et al. 2018). Bears spent more time foraging on salmon when there were more salmon. Therefore, if bears are eating more salmon when escapement is high, they are likely dedicating more time to fishing and visiting more salmon streams. Bear abundance along Brooks River may have increased during high escapement years because more bears visited Brooks River to fish for salmon. Bears were willing to tolerate each other in closer proximity due to reduced competition.

Our abundance estimates also showed a change in the proportion of 1<sup>st</sup> year breeding females to nonbreeding females at Brooks River, while total abundance of adult females remained constant (Figure 2.12). This could indicate either a shift in productivity or a change in use patterns by females based on breeding status. If this were a lull in productivity related to salmon escapement, we would expect to see a decreasing proportion of 1<sup>st</sup> year breeding females to nonbreeding females following years of low escapement. We would expect the reduction in salmon escapement to cause a decrease in food availability leading to a decrease in number of females who successfully breed and become 1<sup>st</sup> year breeding females. Instead, we see the change in proportion coinciding with years of lower escapement not following years of low escapement. Therefore, we suspect escapement was impacting use patterns.

Nonbreeding females would likely be better able to compete for fishing locations during low escapement years while breeding females would be more likely to avoid risky competitive areas (Ben-David et al. 2004, Deacy et al. 2016, Gende and Quinn 2004).

Even though our state-space model accounted for imperfect detection, it did not account for changing availability of bears to be detected. Bears who chose not to use Brooks River for multiple years lowered the model's abundance estimate. Trends and changes in climate such as the Pacific Decadal Oscillation create shifts in salmon productivity and abundance across the landscape (Hilborn et al. 2003, Beamish et al. 1999). If these periods of lower or higher salmon abundance led to periods of altered use patterns by bears, the state-space model would not be able to differentiate altered resource use from a change in abundance especially over longer periods of time.

#### *Escapement and productivity*

We did not find a significant relationship between probability of breeding and escapement, but there was a significant change in the number of breeding females and cubs across years. The trend in annual probability of breeding lagged behind the trend in annual escapement. We found a significant positive relationship between probability of breeding and the following year's escapement (Figure 2.10). Since it is unlikely that female bears can predict the following year's escapement to determine their productivity, something else must be influencing probability of breeding estimates. As discussed before, the change in bear abundance could have been driven by changing patterns of use where less dominant bears often in specific age-sex groups tended to avoid Brooks River during times of increased

competition. There has already been a noted trend of 1<sup>st</sup> year breeding females avoiding large salmon streams during their first year with cubs. Sellers and Aumiller (1994) noted it in their analysis of McNeil River bears and thought it could be due to intraspecific strife. Others have noted that increased risk of infanticide and intraspecific competition due to high bear densities at salmon streams could cause some bears to move to less risky areas with less energy dense food sources (Deacy et al. 2016, Gende and Quinn 2004). We see evidence of this trend in the state-space model's low estimate of probability of detection for 1<sup>st</sup> year breeding females compared to 2<sup>nd</sup> year breeding females.

On Admiralty Island, Ben-David et al. (2004) noted about half the females with cubs they followed changed their foraging strategies and consumed less salmon than when they were single. Radio telemetry data found that females with offspring were on average farther away from salmon streams during the spawning season compared to females with no young. If more breeding females avoided Brooks River while escapement was low from 2009–2014, this would explain the significant positive relationship between 1<sup>st</sup> year breeding and 2<sup>nd</sup> year breeding female abundance and escapement. It could also explain why escapement seemed to be leading probability of breeding in the state-space model. The model compensated for the drop in 1<sup>st</sup> year breeding females and spring cubs by reducing productivity and the probability that a sow bred. We suggest the reduction was due to changing use patterns.

Even though we did not find a significant relationship between escapement and probability of breeding, there is other evidence that escapement impacted productivity. If escapement only impacted use patterns and not productivity, we would expect to see less dominant age-sex groups simultaneously following the same trends in annual escapement.

Instead, we see a lag effect based on age starting in 2009 when spring cub abundance and counts decreased, followed by decreased yearling cub abundance and counts the following year, followed by decreased subadult and adult abundance and counts in the years following yearling abundance decline (Figure 2.13). This suggests that there was a decrease in number of cubs produced which coincided with a drop in salmon escapement (Figure 2.14) and led to decreased abundance of yearlings, subadults, and adults in the following years. Similarly, in 2014 we observed an increase in spring cub counts and abundance followed by an increase in yearling abundance and counts the following year, followed by an increase in subadult and adult abundance in the ensuing years. This suggests increasing productivity and coincides with years of increasing sockeye escapement.

These shifts in use patterns at Brooks River violate the state-space model assumptions that the draw to Brooks River is the same each year. The model therefore interprets changes in use as changes in abundance and breeding. However, the model sheds light on how use of Brooks River changed in relation to escapement. Future work could decouple the observation process with an availability parameter. These parameters could help identify shifting patterns of bear use but runs the risk of overparameterizing the model. Integrating individual bear sighting histories into the population model could help better identify changes in availability. Reliably identifying bears that do not use Brooks River for several years can be challenging. Advances in facial recognition software may be able to help with bear identification over longer periods of time without having to resort to tagging.

Increasing the precision of parameter estimates would also help unravel the relationship between escapement and productivity. Productivity is more than just one parameter occurring

over 1 year, it is the probability a sow will successfully breed one year, the number of cubs she produces the following year, and the survival of those cubs in future years. Additionally, the relationship with escapement is tied to so many factors including variation in fishing ability, salmon vulnerability, stream specific salmon abundance, salmon diversity, intraspecific competition, and landscape connectivity (Deacy et al. 2018). Increasing our sample size through continued monitoring at Brooks River or increasing monitoring to other sites could help increase the precision of our estimates and share relationship parameters across sites allowing us to tease out some of the variability.

Future work incorporating density dependent factors into the state-space model and other environmental factors such as annual berry productivity, winter severity, spawn timing, and river levels will help managers continue to understand the dynamics of individual bear populations. Tracking bear movements using GPS collars remains a valuable tool and could help inform managers about the population of bears that Brooks River draws. Long term tracking can provide information on trends in use of salmon streams such as Brooks River but would require following bears from a variety of age-sex groups over a range of years with varying salmon escapement. Our findings showed breeding females to be more sensitive to changing escapement levels compared to other age-sex groups. We suggest focusing collaring efforts on adult females as they transition in breeding status which can help identify the shifting use patterns.

## Conclusion

Bear monitoring along Brooks River remains an important tool for monitoring brown bear abundance, survival, and behavior along the Brooks River in Katmai National Park. The monitoring framework and consistent data collection through time allow for a rare long-term look into brown bear population dynamics. We demonstrated a significant change, both increasing and decreasing, in independent bear abundance across time that was positively related to previous year's sockeye salmon escapement. When looking at specific age-sex groups within the population, the relationships between abundance and salmon escapement were not the same indicating that changes in abundance may be due to changing use patterns and that the effects of changing resource availability might not always be immediate within the population. However, lags in cub abundance patterns suggest escapement may influence both stream use patterns and productivity. Future work will help continue to unravel the relationships between environment and population dynamics.

## **APPENDICES**

**APPENDIX I: TABLES**

Table 2.1: Estimates of mean annual abundance and mean probability of detection for 10 age-sex groups of brown bears monitored along Brooks River from 2000–2019.

Age-sex group	Mean annual abundance	95% credible interval	Mean probability of detection	95% credible interval
Adult male	46	23–77	0.394	0.304–0.490
Nonbreeding female	21	7–37	0.548	0.426–0.669
B1 female	10	2–21	0.301	0.229–0.390
B2 female	7	1–16	0.460	0.357–0.581
B3 female	3	0–10	0.247	0.165–0.372
Subadult male	9	0–21	0.569	0.426–0.713
Subadult female	10	0–23	0.581	0.451–0.705
Spring cub	23	6–46	0.301	0.229–0.390
Yearling cub	14	1–35	0.460	0.357–0.581
Dependent 2-year-old	6	0–19	0.247	0.165–0.372

## APPENDIX II: FIGURES

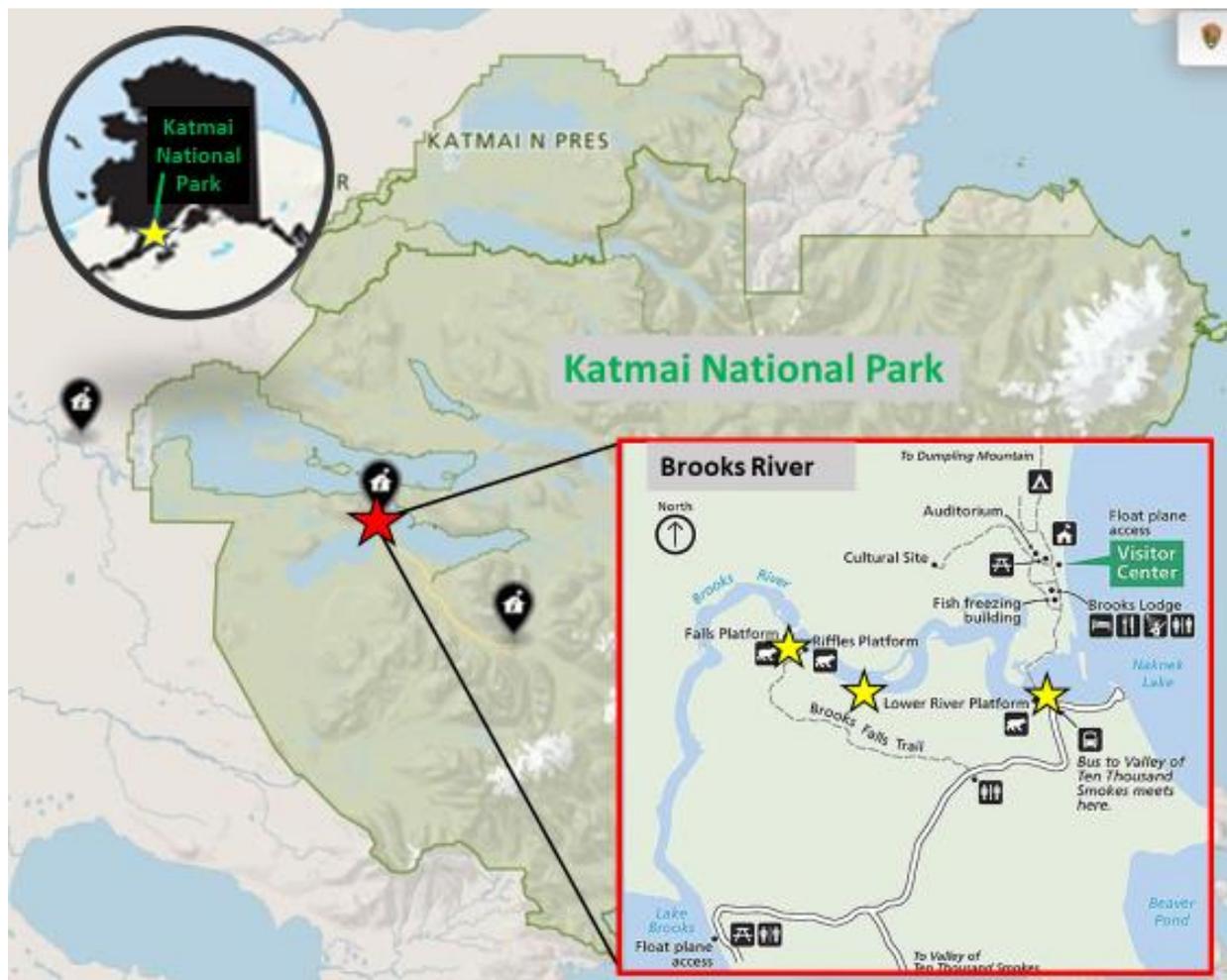


Figure 2.1: Map of Katmai National Park including Brooks Camp and the locations of the 3 bear monitoring sites along Brooks River, Alaska.

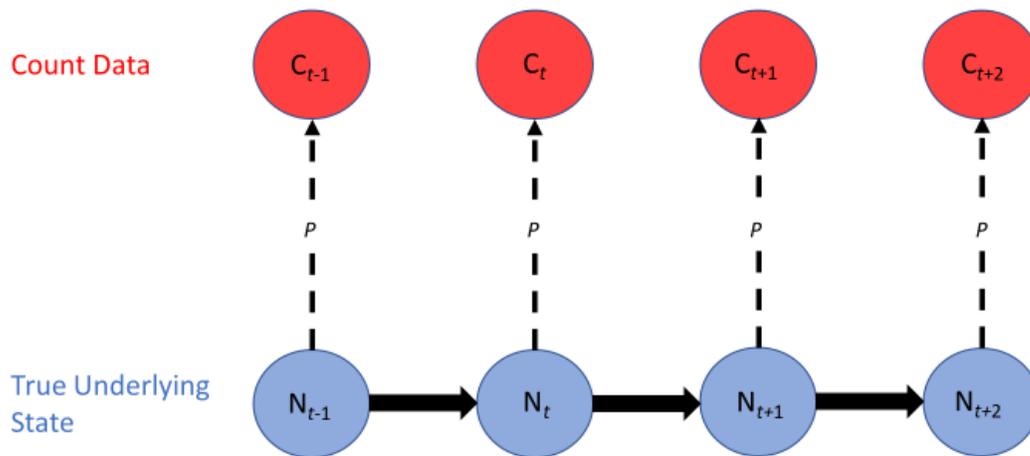


Figure 2.2: The state-space model estimates the true underlying state of a population while accounting for imperfect detection in count data.  $t$  represents units of time, in this case observation years.  $N_t$  is true abundance of the population at time  $t$ .  $C_t$  are counts of bears occurring at time  $t$ . The counts are a function of the true underlying state and a probability of detection  $P$ .

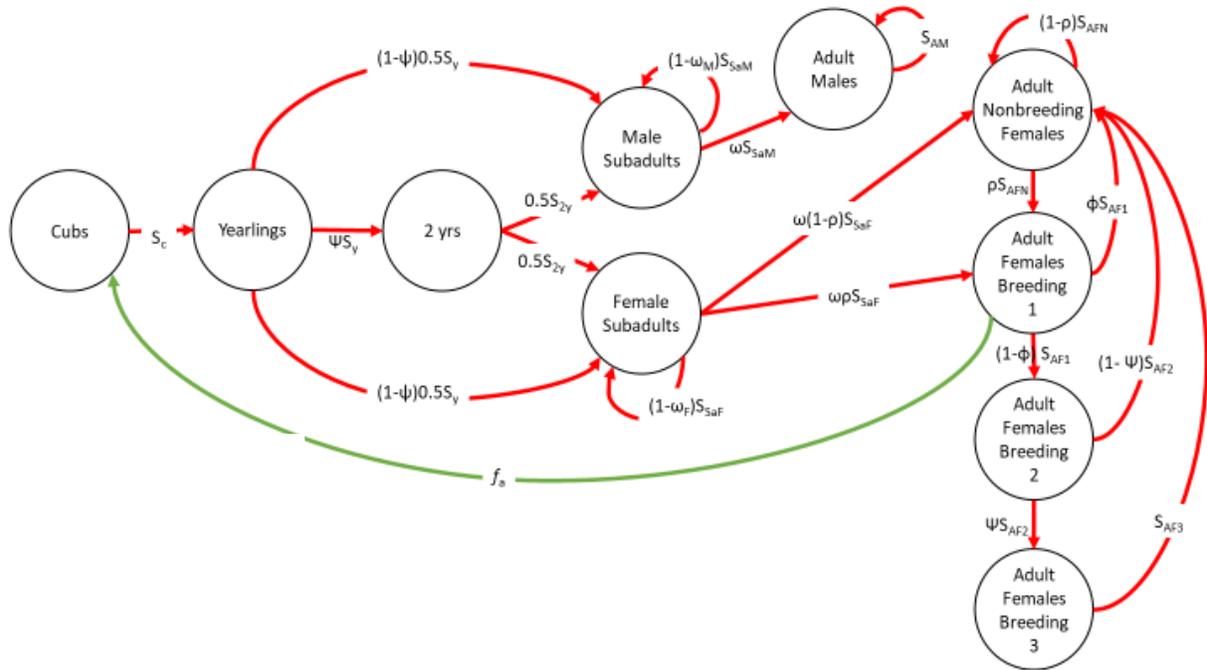


Figure 2.3: Population model of Brooks River bears accounting for 10 different age-sex groups. Here  $S$  is annual survival (0–1),  $f$  is fecundity (cubs/female),  $\omega$  is the probability of transitioning to an adult (0–1),  $\rho$  is the probability of a female successfully breeding and producing a litter of cubs the following year (females; 0–1),  $\phi$  is the probability an entire litter is lost, and  $\psi$  is the probability that a female keeps her yearling cubs an extra year as dependent 2-year-olds. We assumed a 50:50 sex ratio of yearling and dependent 2-year-old cubs.

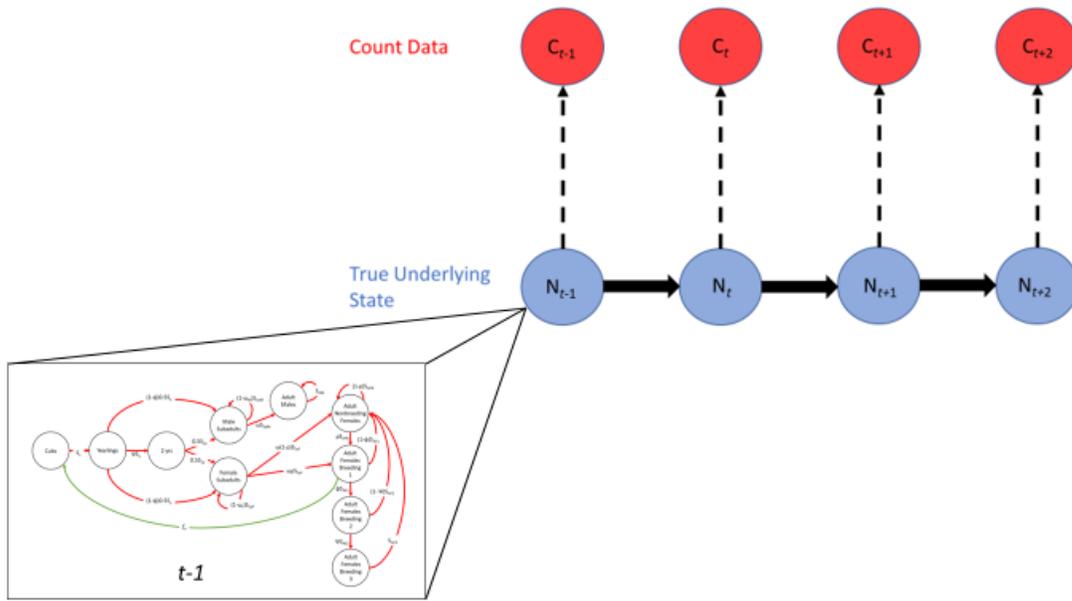


Figure 2.4: The population model represents the true underlying state of the brown bear population. Each time period measures the true state and transition rates of the age and sex groups in the population model.

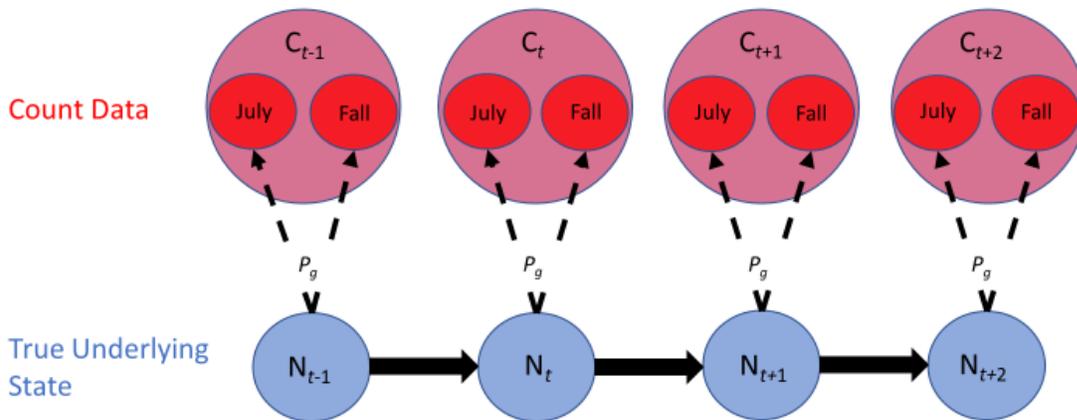


Figure 2.5: Model of count data with 2 replicate counts (July and Fall) each year time= $t$ .

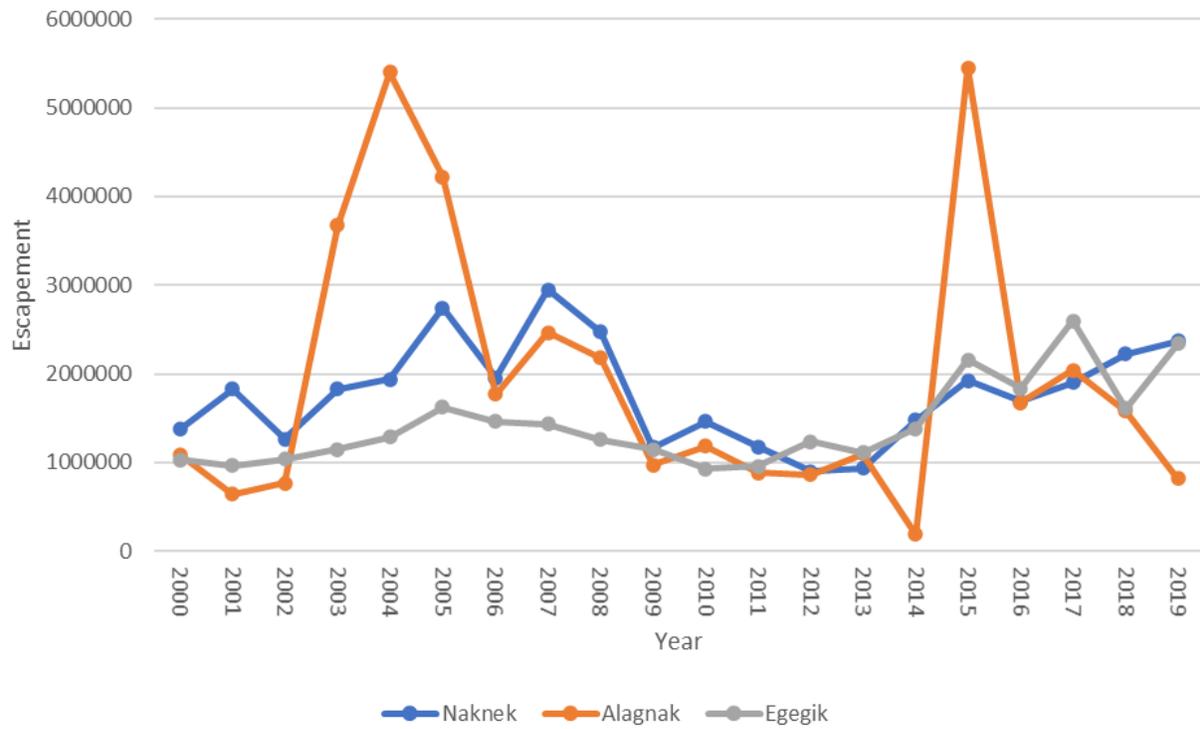


Figure 2.6: Annual sockeye salmon escapement from 2000–2019 for the Nakenek River drainage (blue), drainage to the north, Alagnak (orange), and the drainage to the south, Egegik (gray). These drainages show similar trends in escapement across years.

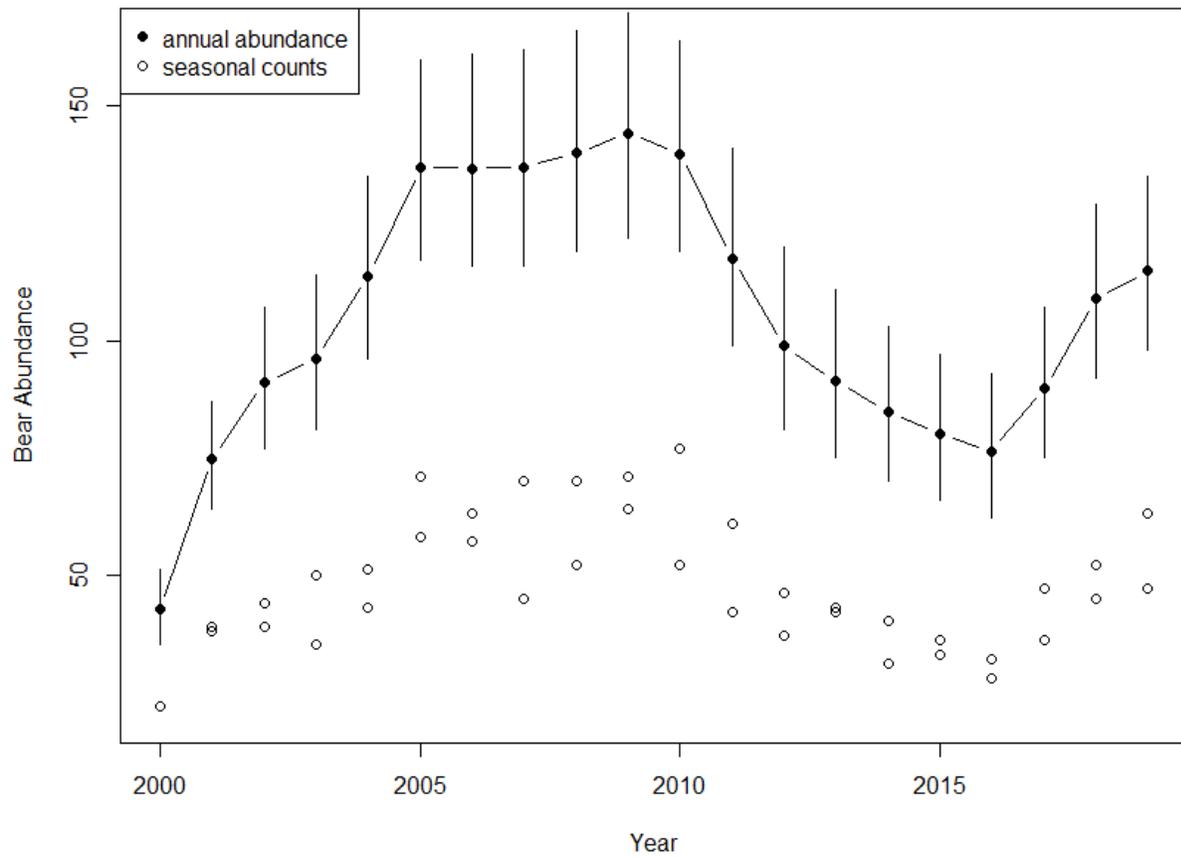


Figure 2.7: Seasonal counts (open circles) and estimates of annual abundance (closed circles) of independent bears along Brooks River from 2000–2019.

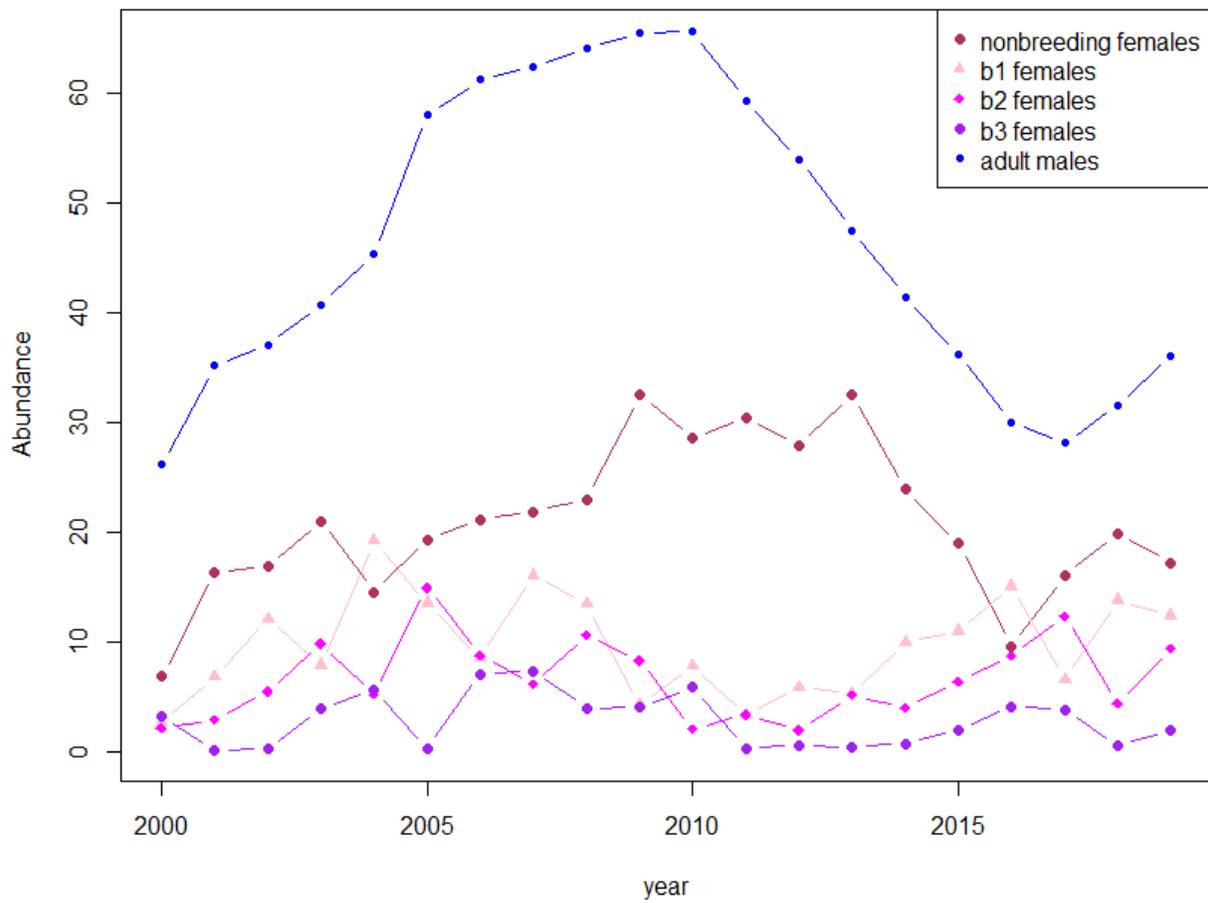


Figure 2.8: Adult male and female abundance by breeding status at Brooks River from 2000–2019. Adult male abundance (blue) declined after 2010 and continued until 2017. Nonbreeding female abundance (red) was above average from 2009–2014 while breeding female abundances (pink, magenta, purple) were below average during this period.

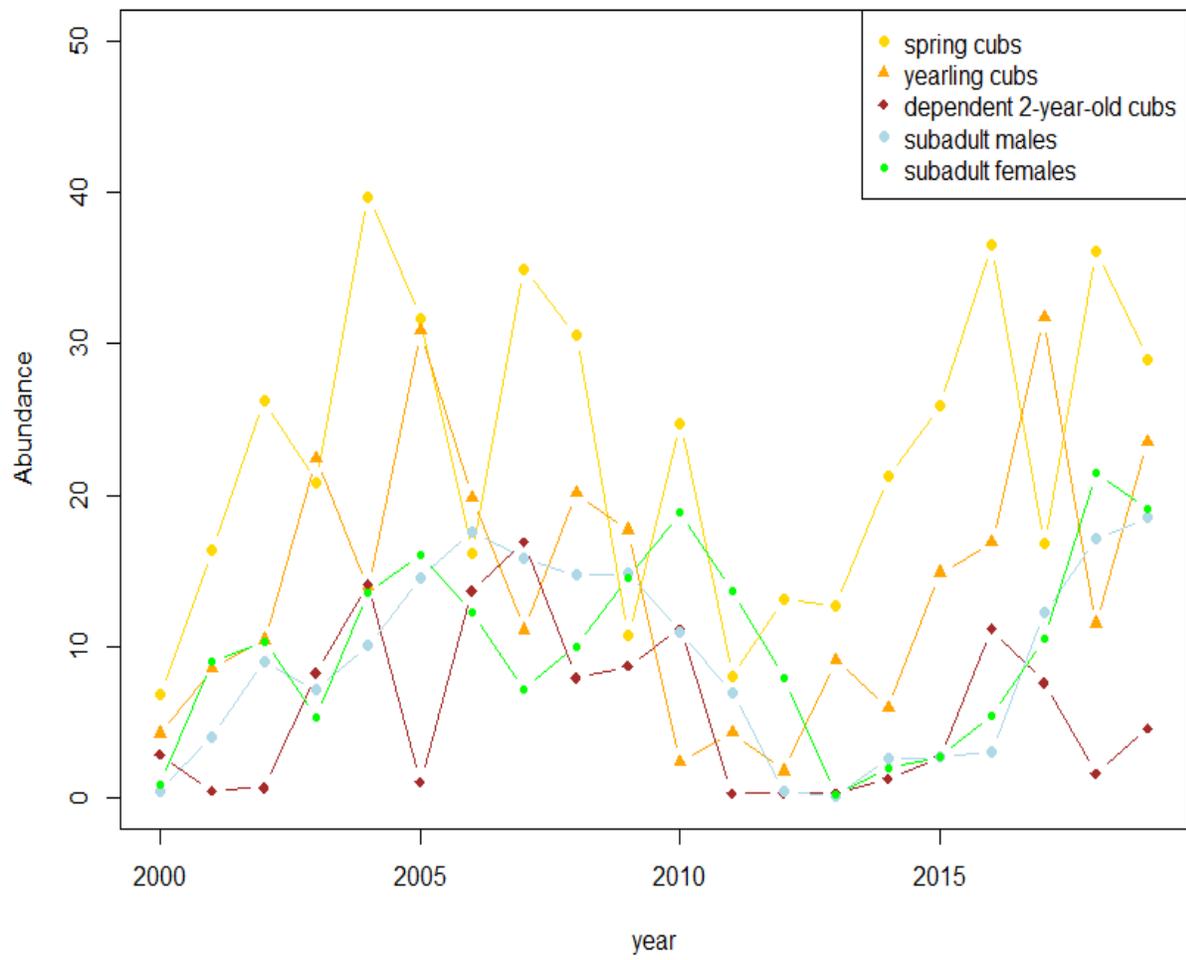


Figure 2.9: Estimates of annual dependent cub abundances (gold, orange, maroon) and subadult abundance (light blue, green) at Brooks River from 2000–2019.

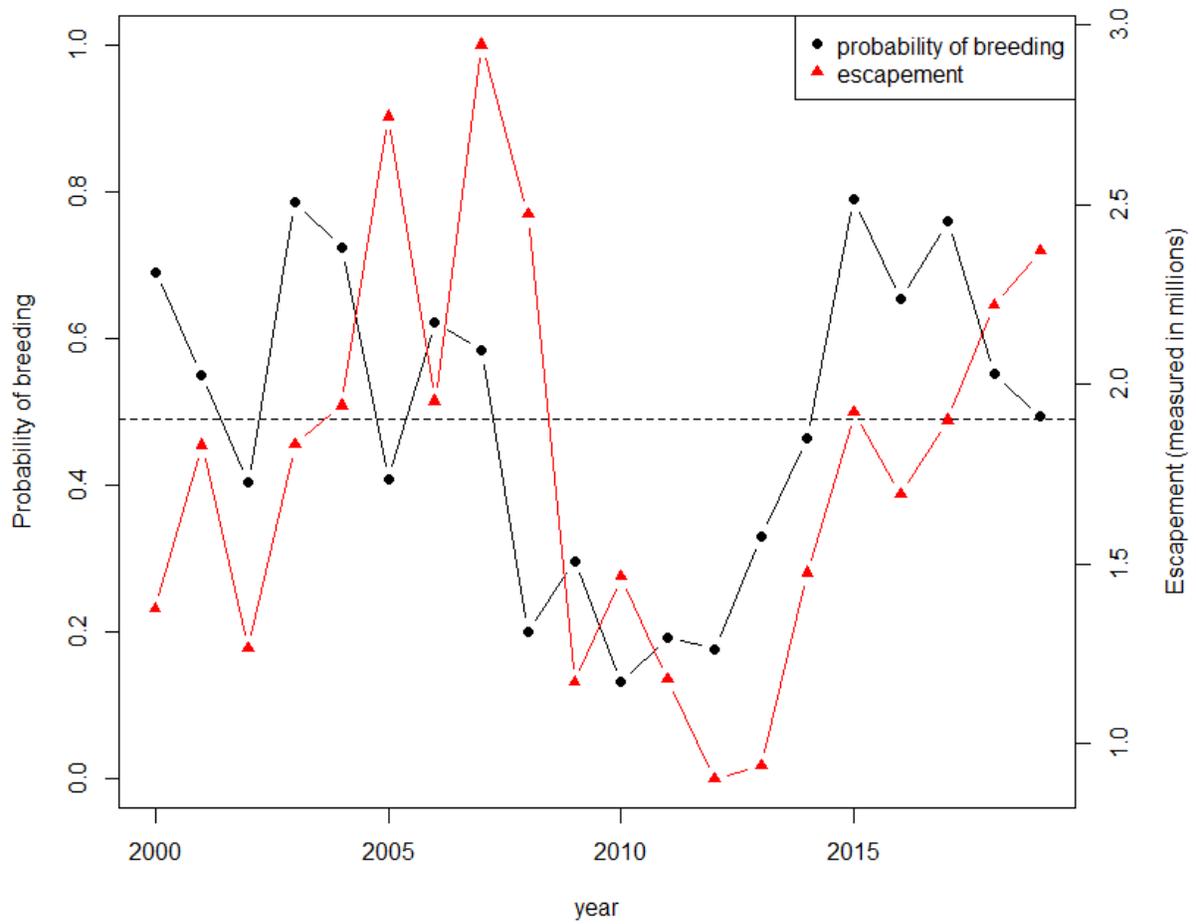


Figure 2.10: Estimates of annual probability of breeding for female bears along Brooks River (black). Annual sockeye salmon escapement estimates for the Naknek River drainage from 2000–2019 (red). The annual probability of breeding seems to lag behind the following year’s escapement.

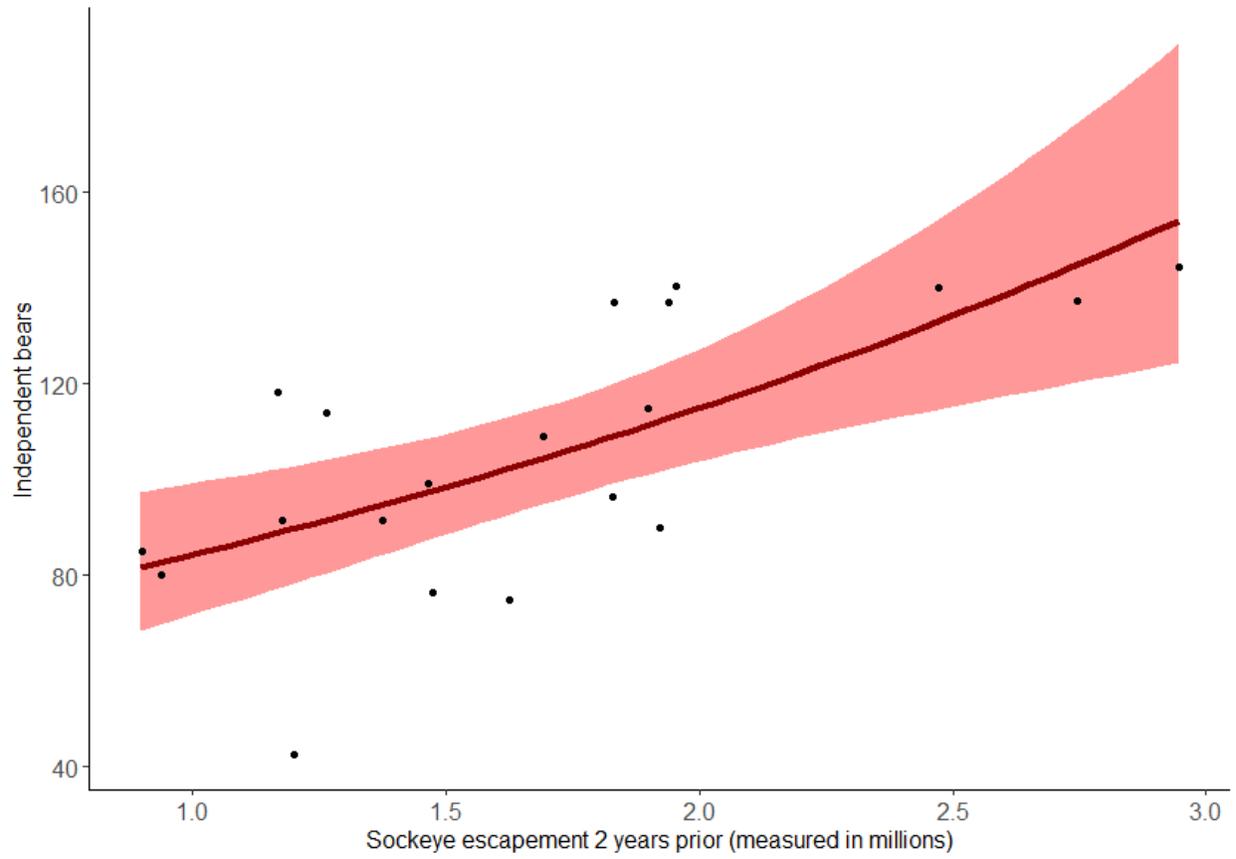


Figure 2.11: 2000–2019 estimates of annual sockeye salmon escapement (measured in millions) from the Naknek River drainage and independent bear abundance 2 years later. Regression shows a significant positive relationship (red), with 95% credible interval (pink), between independent bears and prior sockeye salmon escapement.

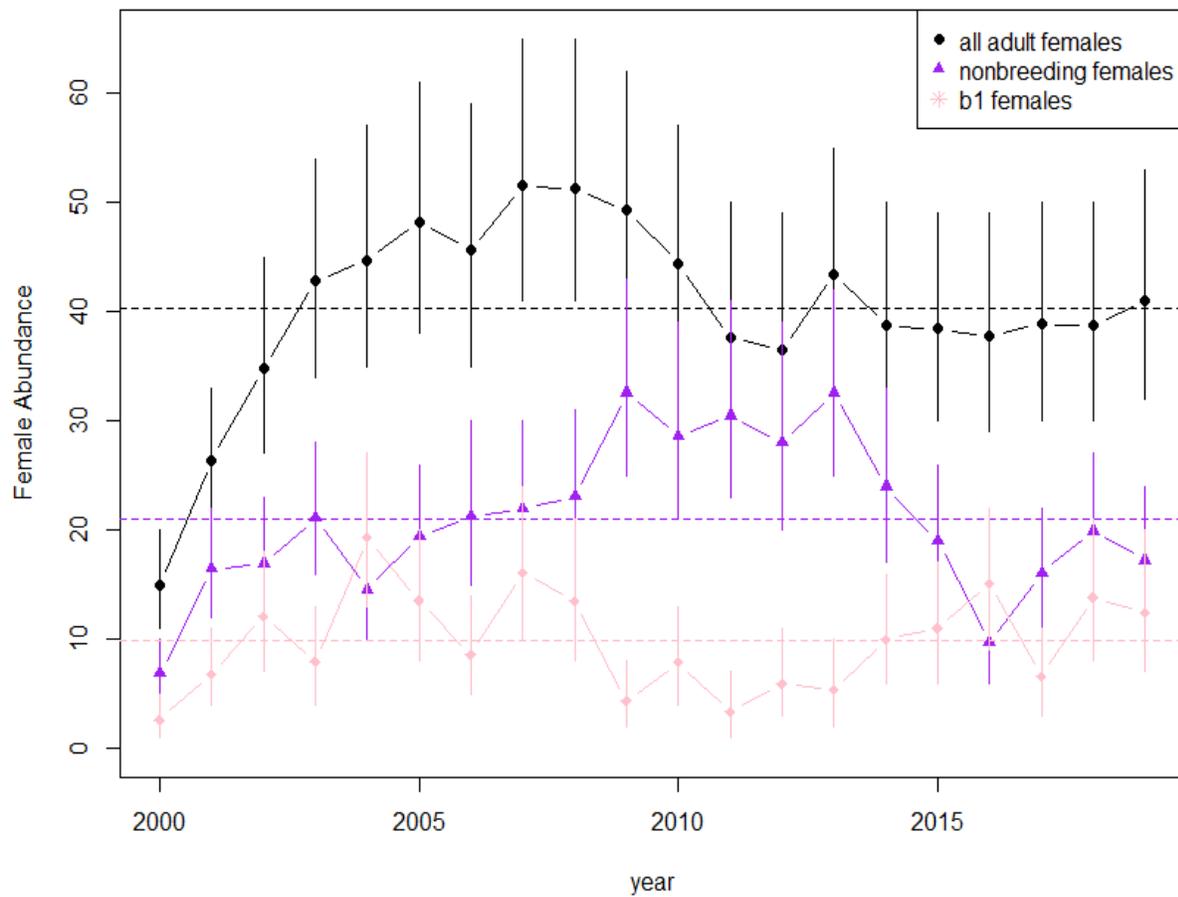


Figure 2.12: Annual abundance of females by breeding status at Brooks River from 2000–2019. Nonbreeding female abundance (purple) is significantly above average for most of 2009–2013 coinciding with years of low sockeye salmon escapement. 1<sup>st</sup> year breeding female abundance (pink) is mostly below average during this same period while total adult female abundance (black) remains fairly constant.

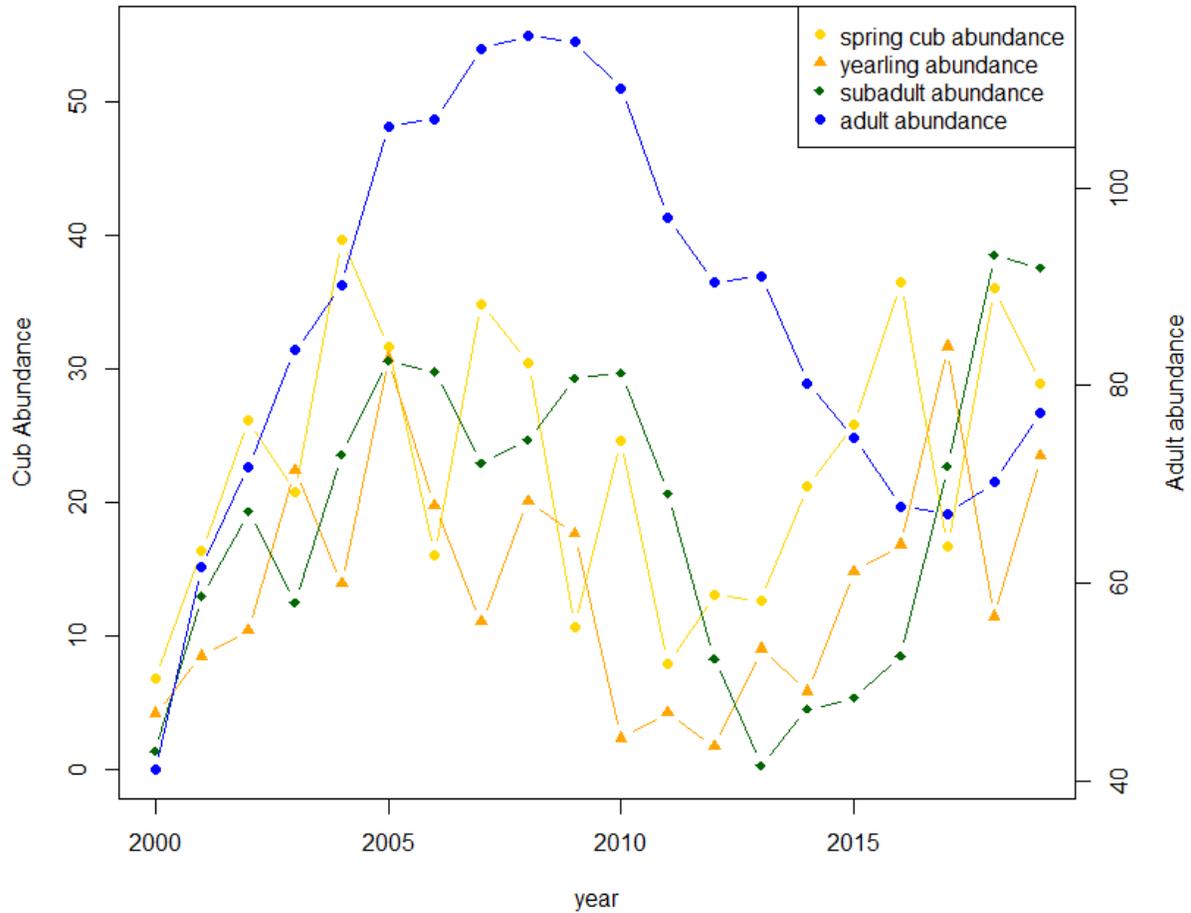


Figure 2.13: State-space model estimates of annual abundance of spring cubs, yearling cubs, subadults (both male and female), and adult bears (both male and female). The lull in abundance for each age group lags after the initial lull by spring cubs. Spring cub abundance (gold) is mostly below average from 2009–2013, yearling abundance (orange) is below average the following years from 2010–2014, subadult abundance (dark green) is below average 1–2 years later from 2012–2016, and adult abundance (blue) is below average from 2014–2019.

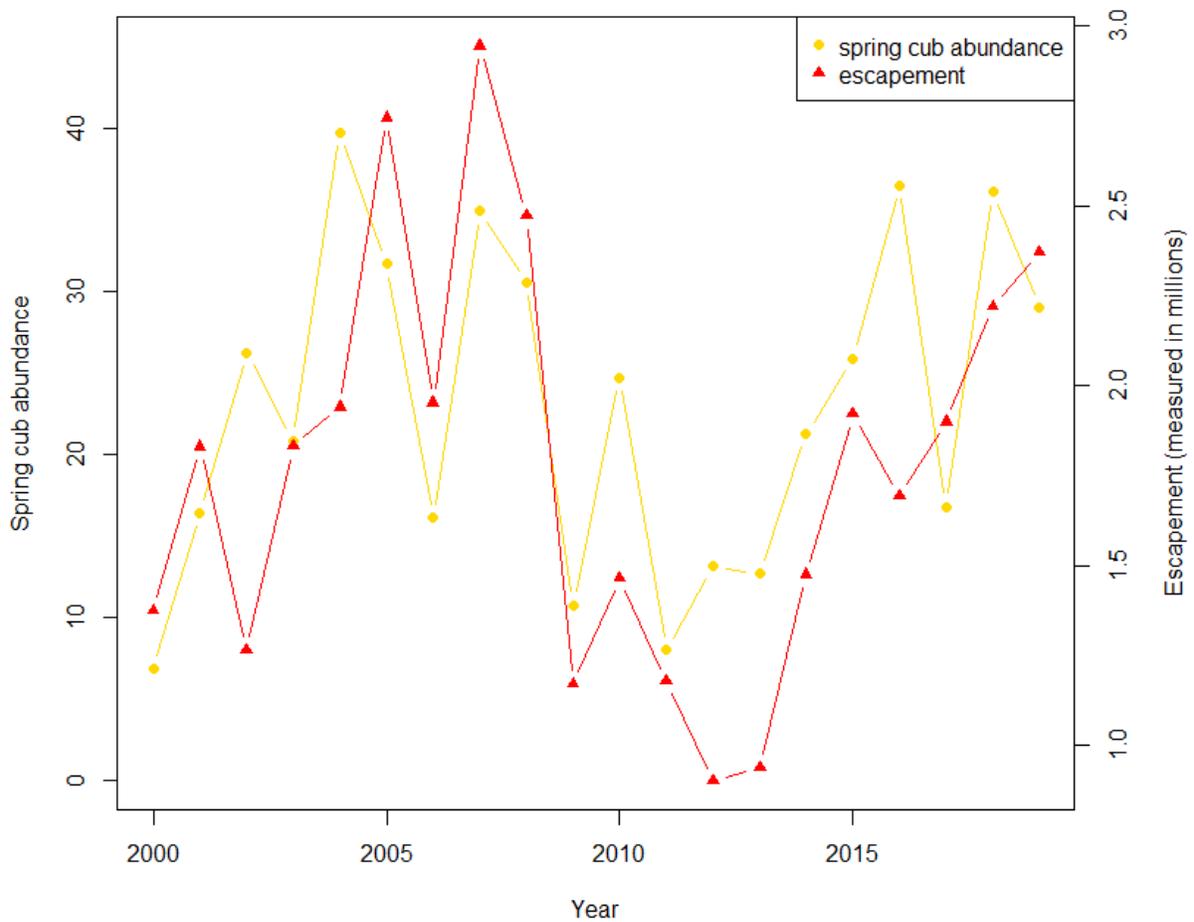


Figure 2.14: State-space model estimates of annual spring cub abundance at Brooks River and sockeye salmon escapement for the Naknek River drainage from 2000–2019. Spring cub abundance (gold) tracks annual escapement (red) and shows a significant positive relationship. This is likely due to changing use patterns by 1<sup>st</sup> year breeding females related to escapement and competition.

### APPENDIX III: STATE-SPACE MODEL CODE

```
### State-space model (SSM) for Brooks River Bears, 2000–2019
### JAGS code based off SSM from Kery and Schaub (2012)

### JAGS model ###
sink("ssm.jags")
cat("
  model {

    # Priors and constraints
    #male
    N.est.male[1]~dpois(16)
    p.male~dunif(0,1)
    mean.survival.male~dunif(0,1)
    sigma.survival.male ~ dunif(0, 10)      # Prior for sd of state process
    tau.survival.male <- pow(sigma.survival.male, -2)

    #nb.female
    N.est.nb.female[1]~dpois(4)
    p.nb.female~dunif(0,1)
    mean.survival.nb.female ~ dunif(0, 1)
    sigma.survival.nb.female ~ dunif(0, 10)  # Prior for sd of state process
    tau.survival.nb.female <- pow(sigma.survival.nb.female, -2)

    #b1.female
    N.est.b1.female[1]~dpois(1)
    p.b1.female~dunif(0,1)
    mean.survival.b.female ~ dunif(0, 1)
    sigma.survival.b.female ~ dunif(0, 10)  # Prior for sd of state process
    tau.survival.b.female <- pow(sigma.survival.b.female, -2)

    #b2.female
    N.est.b2.female[1]~dpois(1)
    p.b2.female~dunif(0,1)

    #b3.female
    N.est.b3.female[1]~dpois(2)
    p.b3.female~dunif(0,1)

    #probability of breeding
```

```

mean.prob.breed ~ dunif(0, 1)
sigma.prob.breed ~ dunif(0, 10)      # Prior for sd of state process
tau.prob.breed <- pow(sigma.prob.breed, -2)

#fecundity
mean.fecundity~dunif(1,4)
sigma.fecundity~dunif(0,10)
tau.fecundity<-pow(sigma.fecundity,-2)

#probability entire coy litter is lost after 1st year
prob.litter.lost~dunif(0,1)

#Subadult
#Male Subadults
N.est.Msubs[1]~dpois(2)
p.Msubs~dunif(0,1)
mean.survival.Msubs~dunif(0,1)
sigma.survival.Msubs ~ dunif(0, 10)      # Prior for sd of state process
tau.survival.Msubs <- pow(sigma.survival.Msubs, -2)
#Female Subadults
N.est.Fsubs[1]~dpois(2)
p.Fsubs~dunif(0,1)
mean.survival.Fsubs~dunif(0,1)
sigma.survival.Fsubs ~ dunif(0, 10)      # Prior for sd of state process
tau.survival.Fsubs <- pow(sigma.survival.Fsubs, -2)

#Becoming Adult
mean.prob.adult~dunif(0,1)
sigma.prob.adult~dunif(0,10)
tau.prob.adult<-pow(sigma.prob.adult,-2)

#Cubs
#Coy
N.est.coy[1]~dpois(3)      # Prior for initial cub population
mean.survival.coy~dunif(0,1)
sigma.survival.coy~dunif(0,10)      # Prior for sd of state process
tau.survival.coy<-pow(sigma.survival.coy,-2)
#Yrlg
N.est.yrlg[1]~dpois(2)      # Prior for initial cub population
mean.survival.yrlg~dunif(0,1)
sigma.survival.yrlg~dunif(0,10)      # Prior for sd of state process

```

```

tau.survival.yrlg<-pow(sigma.survival.yrlg,-2)
#dep2yo
N.est.dep2yo[1]~dpois(2)          # Prior for initial cub population

#probability of keeping 2+ year old
mean.prob.keep~dunif(0,1)
sigma.prob.keep~dunif(0,10)
tau.prob.keep<-pow(sigma.prob.keep,-2)

# Likelihood
# State process
for (t in 1:T){
  lambda.male[t]<-(N.est.male[t]*survival.male[t])+((N.est.Msubs[t]*survival.Msubs[t])*
    prob.adult[t])
  lambda.nb.female[t]<-((N.est.nb.female[t]*survival.nb.female[t])*(1-prob.breed[t]))+
    ((N.est.b1.female[t]*survival.b.female[t])*prob.litter.lost)+
    ((N.est.b2.female[t]*survival.b.female[t])*(1-prob.keep[t]))+
    (N.est.b3.female[t]*survival.b.female[t])+
    (((N.est.Fsubs[t]*survival.Fsubs[t])*prob.adult[t])*(1-prob.breed[t]))
  lambda.b1.female[t]<-((N.est.nb.female[t]*survival.nb.female[t])*prob.breed[t])+
    (((N.est.Fsubs[t]*survival.Fsubs[t])*prob.adult[t])*prob.breed[t])
  lambda.b2.female[t]<-(N.est.b1.female[t]*survival.b.female[t])*(1-prob.litter.lost)
  lambda.b3.female[t]<-(N.est.b2.female[t]*survival.b.female[t])*prob.keep[t]
  lambda.Msubs[t]<-(((0.5*N.est.yrlg[t])*survival.yrlg[t])*(1-prob.keep[t]))+
    ((0.5*N.est.dep2yo[t])*survival.yrlg[t])+((N.est.Msubs[t]*survival.Msubs[t])*
    (1-prob.adult[t]))
  lambda.Fsubs[t]<-(((0.5*N.est.yrlg[t])*survival.yrlg[t])*(1-prob.keep[t]))+
    ((0.5*N.est.dep2yo[t])*survival.yrlg[t])+((N.est.Fsubs[t]*survival.Fsubs[t])*
    (1-prob.adult[t]))
  lambda.coy[t]<-(((N.est.nb.female[t]*survival.nb.female[t])*prob.breed[t])+
    (((N.est.Fsubs[t]*survival.Fsubs[t])*prob.adult[t])*prob.breed[t]))*fecundity[t]
  lambda.yrlg[t]<-(N.est.coy[t]*survival.coy[t])
  lambda.dep2yo[t]<-(N.est.yrlg[t]*survival.yrlg[t])*prob.keep[t]
  prob.keep[t]~dnorm(mean.prob.keep,tau.prob.keep)T(0,1)
  prob.adult[t]~dnorm(mean.prob.adult,tau.prob.adult)T(0,1)
  survival.male[t]~dnorm(mean.survival.male,tau.survival.male)T(0,1)
  survival.nb.female[t]~dnorm(mean.survival.nb.female,tau.survival.nb.female)T(0,1)
  survival.b.female[t]~dnorm(mean.survival.b.female,tau.survival.b.female)T(0,1)
  survival.Msubs[t]~dnorm(mean.survival.Msubs,tau.survival.Msubs)T(0,1)
  survival.Fsubs[t]~dnorm(mean.survival.Fsubs,tau.survival.Fsubs)T(0,1)
  survival.coy[t]~dnorm(mean.survival.coy,tau.survival.coy)T(0,1)
}

```

```

survival.yrlg[t]~dnorm(mean.survival.yrlg,tau.survival.yrlg)T(0,1)
prob.breed[t]~dnorm(mean.prob.breed,tau.prob.breed)T(0,1)
fecundity[t]~dnorm(mean.fecundity,tau.fecundity)T(1,5)
}#t

for (t in 1:(T-1)){
  N.est.male[t+1] ~ dpois(lambda.male[t])
  N.est.nb.female[t+1] ~ dpois(lambda.nb.female[t])
  N.est.b1.female[t+1] ~ dpois(lambda.b1.female[t])
  N.est.b2.female[t+1] ~ dpois(lambda.b2.female[t])
  N.est.b3.female[t+1] ~ dpois(lambda.b3.female[t])
  N.est.Msubs[t+1]~ dpois(lambda.Msubs[t])
  N.est.Fsubs[t+1]~ dpois(lambda.Fsubs[t])
  N.est.coy[t+1]~dpois(lambda.coy[t])
  N.est.yrlg[t+1]~dpois(lambda.yrlg[t])
  N.est.dep2yo[t+1]~dpois(lambda.dep2yo[t])
}#t

# observation process
for (t in 1:T){
  for (j in 1:TR){
    y.male[t,j]~ dbin(p.male,N.est.male[t])
    y.nb.female[t,j]~dbin(p.nb.female,N.est.nb.female[t])
    y.b1.female[t,j]~dbin(p.b1.female,N.est.b1.female[t])
    y.b2.female[t,j]~dbin(p.b2.female,N.est.b2.female[t])
    y.b3.female[t,j]~dbin(p.b3.female,N.est.b3.female[t])
    y.coy[t,j]~dbin(p.b1.female,N.est.coy[t])
    y.yrlg[t,j]~dbin(p.b2.female,N.est.yrlg[t])
    y.dep2yo[t,j]~dbin(p.b3.female,N.est.dep2yo[t])
    y.Msubs[t,j]~dbin(p.Msubs,N.est.Msubs[t])
    y.Fsubs[t,j]~dbin(p.Fsubs,N.est.Fsubs[t])
  }#j
}#t

# Derived parameters
for (t in 1:T){
  N.total[t]<-N.est.male[t]+N.est.nb.female[t]+N.est.b1.female[t]+N.est.b2.female[t]+
  N.est.b3.female[t]+N.est.Msubs[t]+N.est.Fsubs[t]
  N.female[t]<-N.est.nb.female[t]+N.est.b1.female[t]+N.est.b2.female[t]+
  N.est.b3.female[t]
  N.b.female[t]<-N.est.b1.female[t]+N.est.b2.female[t]+N.est.b3.female[t]

```

```
      N.cubs[t]<-N.est.coy[t]+N.est.yrlg[t]+N.est.dep2yo[t]
      N.subs[t]<-N.est.Fsubs[t]+N.est.Msubs[t]
    }#t
  }
  ",fill = TRUE)
sink()
```

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## LITURATURE CITED

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