FEDERAL AID ANNUAL RESEARCH PERFORMANCE REPORT

ALASKA DEPARTMENT OF FISH AND GAME
DIVISION OF WILDLIFE CONSERVATION
PO Box 115526
Juneau, AK 99811-5526

Alaska Department of Fish and Game
Wildlife Restoration Grant

GRANT NUMBER: AKW-20 **SEGMENT NUMBER:** 20

PROJECT NUMBER: 4.43

PROJECT TITLE: Grizzly Literature and Data Project: Literature review and data assimilation of grizzly bear populations to understand sustainable rates of harvest (FY17-FY18)

PROJECT DURATION: 1 July 2016–30 June 2018

REPORT DUE DATE: 1 September 2017

PARTNER: None

PRINCIPAL INVESTIGATORS: Kerry L. Nicholson,

COOPERATORS: John Merickel (Region III Biometrician I/II), Danny Caudill (Region III Wildlife Biologist III)

WORK LOCATION: Region III

I. SUMMARY OF WORK COMPLETED THIS SEGMENT ON JOBS IDENTIFIED IN ANNUAL WORK PLAN

OBJECTIVE 1: Conduct a literature review on 1) grizzly bear population and harvest data worldwide; 2) population and harvest data on grizzly bears in Interior and Arctic Alaska; 3) sustainable harvest for grizzly bears; 4) models of grizzly bear population dynamics.

JOB/ACTIVITY 1A: Compile and collect literature of harvest on grizzly bears.

Federal funds were used to pay salaries associated with collecting this data and it is an ongoing activity.

OBJECTIVE 2: Assess current management needs regarding grizzly bear populations throughout the Interior and Arctic regions of Alaska.

JOB/ACTIVITY 2A: Review survey and inventory reports and management reports to identify gaps in each region regarding grizzly bear population dynamics

Federal funds were used to pay salaries associated with collecting this data and it is an ongoing activity. Management reports have been compiled and individual regions will be summarized. Upon pursuit of this objective, it has highlighted the need for a specific workshop or meeting with the Area Biologists to understand their needs in addition to overall general biological understanding of grizzly bear biology in Northern and Interior Alaska.

JOB/ACTIVITY 2B: Interview area biologists to identify data gaps and understand the current natural mortality, non-reported harvest, the harvestable surplus and the priorities in the region for grizzly bears.

Area biologists have been interviewed on an individual basis. What has become apparent is the need for a larger cohesive meeting in which data gaps are outlined and explained for each biologist to hear and understand. Priorities can then be decided as a group for how the region will move forward with grizzly bear research.

OBJECTIVE 3: Compile and analyze available data on Interior and Arctic grizzly bear populations.

JOB/ACTIVITY 3A: Assess status, composition and abundance of grizzly bear populations relative to harvest and compare with other estimates where data are available.

In spring 2016, it was decided to use aerial survey and Mark-Recapture Distance Sampling (MRDS) as developed by (Becker and Christ 2015) for subunit Game Management Unit (GMU) 20A. The aerial survey was to be the quickest and potentially a cost-effective way to determine population status of grizzly bears. The intent was to conduct a survey during one spring season across the entire GMU that would yield an estimate with relatively acceptable precision that could be improved upon if and when an additional survey was to be conducted. Theoretically, 2 years should have been sufficient to obtain an acceptable estimate of population size.

In 7 days with 5 planes for approximately 8 hours a day flying (208 hrs of flying) we flew 464 of the possible 2018 transects (23%; Table 1). We observed 5 black bear and 10 grizzly bear groups by end of day May 8th (Table 2). We observed 2.18 grizzly bear groups / 1000km flown in the higher elevation and riparian areas, whereas we observed 0.15 groups / 1000 km flown in the flat transects (see attached memo in Appendix 1).

For distance sampling to work successfully, visibility must not be an issue. In Unit 20A, we managed to survey the higher risk areas prior to leaves obstructing visibility. However, there are large portions of the flat landscape with coniferous forests in which visibility will never increase. If a habitat map were to be created, these low visibility areas could be eliminated from the available survey area increasing the confidence in detection, but reducing the abundance estimate if bears were missed in being counted. MRDS is a technique that improves with additional data; therefore future attempts should be constructed within the mountainous area (Zones 2, 4, 7, 12; Figure 1) as the flats (Zone 1&5; Figure 1) were adequately covered. Additionally, we still lack sufficient data on den emergence for bears in the spring. We assumed based upon expert opinion and general ecology of grizzly bears from other regions that all bears had emerged from dens.

Therefore, attempts should be made to ensure we are removing this potential bias from the method.

JOB/ACTIVITY 3B: Estimate population parameters (e.g., reproduction, survival and mortality) for grizzly bears

We have run a cursory analysis on Reynolds and Ver Hoef (2000) 1981-1998 Alaska Range grizzly bear demographic and survival data to calculate survival. We modeled estimates of transitions from every possible state (life stages). No covariates or any time/stage/age structures were considered at this point, so every "estimate" is just the empirical proportion from the data. The specific model used was a multinomial model with a generalized logit link, because the stages are considered to have no order of priority to them. There are several nuisance parameters that are also estimated to satisfy the assumptions of a multinomial model. The nuisance states are "permanently dead" and "censored", which must be included in order for the transitions to contain all possible mutually exclusive outcomes of the data range. The inclusion of the censored state accounts for the fact that detection is not perfect, but the transition probabilities are not directly adjusted for detection. We are continuing to refine the analysis and finalize the results.

JOB/ACTIVITY 3C: Determine feasibility of a harvest viability analysis where appropriate data are available to model growth rates and survival under various scenarios

At the request of Lincoln Parrett, Danny Caudill and John Merickel have worked together to roughly estimate trend in age of harvest for GMU 22 (Appendix 2). The analysis is preliminary and they plan to work with everyone to develop a plan to move forward with this at a larger scale. Right now the most appropriate avenue is to focus on interior and arctic regions (with the possibility of including 13). Creating a single model that evaluates all the data at once (as opposed to a GMU by GMU approach) seems like the most rigorous and best use of the available data. However, this approach also makes for complicated model structures that account for different hypotheses about different GMUs. The primary focus would be looking into the effects of year, season, and sex on age at harvest. Additionally, the effects of GMUs, changes in regulations and hunter residency are also of interest.

JOB/ACTIVITY 3D: Identify gaps in knowledge and data for additional analysis

No work was accomplished on this objective during the report period.

JOB/ACTIVITY 3E: Evaluate monitoring approaches to understand effects of various harvest methods on grizzly bears

Grizzly bears often occur at low densities presenting many challenges for sampling. Capture-mark-resight or CMR (e.g., Miller et al. 1997), DNA mark-recapture (Boulanger et al. 2004), or distance line transect sampling approaches are the most commonly employed methods for assessing grizzly bear populations, although costs often limit the successful application of such field methods in large, remote areas.

Using MRDS to enumerate bears is difficult to accomplish in a short time period (i.e., 1-2 seasons) and inexpensively (<$120K per year). The lack of success we observed in GMU 20A in one sampling season could be due to the method, but more likely the low density of bears in the unit. There are additional concerns that although we may eventually enumerate bears with this technique, the level of precision to the estimate will still be inadequate. Other options should be considered or reconsidered in moving forward and accept that it will be a costly endeavor, will take multiple seasons, and likely the precision of the estimate may be low.

Alternative method to use in such a low density situation could be non-invasive mark re-sight survey approach developed recently by Schmidt et al. (2017). This approach is applied concurrently with site-occupancy and sign surveys, to estimate abundance and site-occupancy rates for a low density grizzly bear population in Interior and Northern Alaska. This approach has particular promise for regions north of the Brooks Range, but would need consideration if used south of the Brooks Range.

In June I participated in a survey which implemented the Schmidt et al. (2017) method on the Upper Noatak river. Though this method is similar to Becker and Christ (2015), there are key differences in which increase the applicability for low density bear populations for multiple locations in Interior and Northern Alaska. The method still depends upon timing bear emergence and leaf-out, utilizes the same number of planes and observers, and the survey would similarly cost 120K. To this end, I am developing a relationship with J. Schmidt with National Park Service to evaluate the feasibility of utilizing this method in alternative locations important to ADF&G.

This objective will continue to be evaluated as alternative options present themselves.

OBJECTIVE 4: Report findings and develop a research protocol proposal.

JOB/ACTIVITY 4A: Provide a summary of efforts and outline possible future directions for grizzly bear research

No work was accomplished on this objective during the report period.

JOB/ACTIVITY 4B: Identify gaps in knowledge relative to management needs and recommend potential research projects within Region III and across Alaska

No work was accomplished on this objective during the report period.

JOB/ACTIVITY 4C: Develop and write a research proposal(s) and operational plan(s) for identified project(s) with possible major field components

No work was accomplished on this objective during the report period.

II. SIGNIFICANT DEVIATIONS AND/OR ADDITIONAL FEDERAL AID-FUNDED WORK NOT DESCRIBED ABOVE THAT WAS ACCOMPLISHED ON THIS PROJECT DURING THIS SEGMENT PERIOD

None.

III. PUBLICATIONS

None.

IV. RECOMMENDATIONS FOR THIS PROJECT

None.

LITERATURE CITED:

Becker, E. F., and A. M. Christ. 2015. A unimodal model for double observer distance sampling surveys. PLoS ONE 10(8):e0136403. 10.1371/journal.pone.0136403

Boulanger, J., S. Himmer, and C. Swan. 2004. Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. Canadian Journal of Zoology 82(8):1267-1277. 10.1139/z04-100

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs (133):5-55.

Reynolds, H. V., and J. M. Ver Hoef. 2000. Effects of harvest on grizzly bear population dynamics in the Northcentral Alaska Range. Alaska Department of Fish and Game, Division of Wildlife Conservation, Final Research Performance Report 1 July 1996-30 June 1999, Federal Aid in Wildlife Restoration W-24 to W-27-2 Study 4.28, Juneau.

Schmidt, J. H., K. L. Rattenbury, H. L. Robison, T. S. Gorn, and B. S. Shults. 2017. Using non-invasive mark-resight and sign occupancy surveys to monitor low-density brown bear populations across large landscapes. Biological Conservation 207:47-54. http://dx.doi.org/10.1016/j.biocon.2017.01.005

PREPARED BY: Kerry L. Nicholson

DATE: -21 August 2017

THE STATE of ALASKA
GOVERNOR BILL WALKER

Department of Fish and Game

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MEMORANDUM

TO:	Scott Brainerd Research Coordinator Doreen Parker McNeill Management Coordinator Tony Hollis Area Biologist 20A	*DATE*:	June 28, 2017
FROM:	Kerry L. Nicholson	*SUBJECT*:	20A Grizzly Bear Survey

Survey Objectives: Distance sampling to estimate abundance of grizzly bears throughout unit 20A May 2-May 10, 2016

Survey Objectives: In spring 2016, it was decided to use aerial survey and Mark-Recapture Distance Sampling (MRDS) as developed by Becker and Christ 2015 for subunit Game Management Unit (GMU) 20A. The aerial survey was to be the quickest and potentially a cost-effective way to determine population status of grizzly bears. The intent was to conduct a survey during one spring season across the entire GMU that would yield an estimate with relatively acceptable precision that could be improved upon if and when an additional survey was to be conducted. Theoretically, 2 years should have been sufficient to obtain an acceptable estimate of population size.

Survey Design: Unit 20A is approximately 17,600 km^2. The survey area was broken into 6 zones. Zones were created for ease of data handling, map creation, and orientation (Figure 1). Based upon elevational criteria the unit was divided up into flat straight line (land with ≤7° slope), riparian (buffer center of stream out by 300 m either direction) and contour transects (≥7° slope; up to 6000 ft in elevation) (Figure 1). We excluded glaciers and anything above 6000ft. Flat transects were divided into North-South and East-West directions with standard intervals of 2km. Riparian transects were designated with a direction to fly, the offset distance to fly from center of river and the direction from the river. Generating the amount of transects to survey are dependent upon multiple factors. We generated more transects than would be expected to be accomplished in 10 days of survey for 5 planes (n = 2018 transects). This was done to avoid running out of pre-designated options and allow for substitutions should one not be able to be flown for some reason. Deciding exactly how many transects is needed is variable (Becker personal communication). The creation and delineation of these transects was an evolving process as the biometrician made changes to accommodate unanticipated situations.

Logistics of Data Collection: We attempted to count bears in Unit 20A during 2 May-10 May 2016. Don Young and Kerry Nicholson were co-PIs from Region III who collaborated with Earl Becker and Rebecca Strauch from Region II to determine if distance sampling would be a feasible method to count bears in the region. An additional bonus to this collaboration allowed the opportunity to pass on the knowledge of this technique from the experts in a different Region. Becker would mentor biometricians and PIs and Strauch would work with Region III GIS personnel. Observers for the method included Young, Nicholson, Becker, John Merickel, Scott Brainerd, Tony Hollis, Bob Hunter, Tod Nichols, Bob Schmidt, and Glenn Stout all ADF&G staff. Pilots included Harley McMahon (PA-18, State Charter), Marty Webb (PA-18, State Charter), Jessie Cummings (PA-18, State Charter), Paul Zackowski (PA-18, State Charter), and Andy Greenblatt (PA-18, State Charter). Lodging and logistics was based out of Fairbanks and Delta. Pilots and Region II staff stayed at Sophie Station in Fairbanks or at the Fish and Game bunkhouse in Delta. Total cost was approximately $65,000 which included all transportation for Region II employees, logistics, 5 aircraft charters, aviation fuel, and food.

On May 2nd we began the surveys starting in the flats of 20A. It took approximately 3 days to complete the straight line transects, though some aircraft started on the contours before finishing the straight lines (Figure 1). On May 4th we decided to have 1 plane initiate flights out of Delta Junction in addition to Fairbanks. We were able to send an observer (Merickel) with Cummings and communicated each evening. The data was downloaded approximately every other day to avoid issues with data loss and keeping up on data management.

Survey Conditions and Assumptions: In April 2016, Don, Kerry and Earl conducted pre-survey flights to view the landscape and determine leaf-out conditions of various locations within 20A. At this time, it was determined the method could be feasible for 20A, but would be extremely difficult for 20B. Unit 20B would not be a good candidate due to the lack of visibility of the ground as the vegetation is dense and consisting of mostly evergreens.

Overall the weather provided for some challenging survey conditions limiting the hours spent in a day flying or limiting the locations we could fly. However, there was never a day that someone was not flying. Initial flights focused on the flats (Zone 1&5; Figure 1) as this area would green up faster than the mountains. This was the case as by the 7th of May, we would have violated assumptions of visibility for many parts of the area.

Visibility is key to obtain valid population estimation with aerial surveys. Bias can occur when a bear is available to be counted but goes unobserved or undetected or when an undetected bear was “unavailable” to be seen, usually due to environmental conditions like thick canopy. This can occur for spring bear surveys if the survey is started too early, and some bears are in their dens during the survey; or if the survey goes too late, in which case leaf-out can cause 100% obstruction of some bears, making them unavailable to be detected. Therefore sampling of bears must occur prior to leaf-out in the spring or after leaf-fall in the autumn. Additionally, all bears must be available to be sampled, which means they must be out of their dens, post or prior to hibernation. These two factors limit the window for the survey to occur.

Results: In 7 days with 5 planes for approximately 8 hours a day flying (208 hrs of flying) we flew 464 of the possible 2018 transects (23%; Table 1). We observed 5 black bear and 10 grizzly bear groups by end of day May 8th (Table 2). We observed 2.18 grizzly bear groups / 1000km flown in the higher elevation and riparian areas, whereas we observed 0.15 groups / 1000 km flown in the flat transects.

On May 8th we decided to assess our progress as it was becoming apparent that another approach would likely be needed to obtain a population estimate and understand factors that can influence the timing and efficiency of surveys. The initial criteria for a successful survey was to fly for 10 days in one year and observe 75 bear groups, though the more ideal sample size would be >100. This sample size is obtainable for GMU20A, but not in one year. We invested 208 hrs of flying and decided that it would be highly unlikely that we would observe 65 more bear groups in 3 more days of flying (120 hrs). We observed 1 bear group every 20.8 hrs and if the trend were to keep up, likely we would have seen 6 more bear groups. Even if we extended the survey length to 14 days, the likelihood of seeing 65 independent bear groups was still extremely low.

Discussion/Recommendations: Despite methodological drawbacks, it is still extremely important in understanding grizzly bear density and distribution as it can provide managers insights into the role of grizzlies as predators on moose (*Alces alces*) or caribou (*Rangifer tarandus*) and could benefit managers in improving bear seasons and bag limits. For wildlife managers to estimate potential harvest effects, it is necessary to understand population demographic parameters. Unfortunately, key demographic parameters such as population abundance, fecundity rate, and mortality are measures that are logistically demanding and expensive in terms of money and personnel resources. Additionally, obtaining each demographic parameter is a task onto itself due to the lack of ubiquitous methodology and imperfections associated with each technique. Often, biologists must obtain these parameters on a site-by-site basis which can rarely be extrapolated region-wide or obtain the parameters periodically as we are constantly improving and evolving the techniques. These issues can lead to strikingly different estimations for the same population through time, or different estimations for the immediate neighboring regions.

For distance sampling to work successfully, visibility must not be an issue. In Unit 20A, we managed to survey the higher risk areas prior to leaves obstructing visibility. However, there are large portions of the flat landscape with coniferous forests in which visibility will never increase. If a habitat map were to be created, these low visibility areas could be eliminated from the available survey area increasing the confidence in detection, but reducing the abundance estimate if bears were missed in being counted. MRDS is a technique that improves with additional data; therefore future attempts should be constructed within the mountainous area (Zones 2, 4, 7, 12; Figure 1) as the flats (Zone 1&5; Figure 1) were adequately covered. Additionally, we still lack sufficient data on den emergence for bears in the spring. We assumed based upon expert opinion and general ecology of grizzly bears from other regions that all bears had emerged from dens. Therefore, attempts should be made to ensure we are removing this potential bias from the method.

Using this version of distance sampling to enumerate bears is difficult to accomplish in a short time period (i.e., 1-2 seasons) and inexpensively (<$120K per year). The lack of success in one sampling season could be due to the method, but more likely the low density of bears in the unit.

There are additional concerns that although we may eventually enumerate bears with this technique, the level of precision to the estimate will still be inadequate. Other options should be considered or reconsidered in moving forward and accept that it will be a costly endeavor, will take multiple seasons, and likely the precision of the estimate may be low.

Post-survey Data Storage: Data has been stored in \\dfg.alaska.local\Builds\Fairbanks_ArcGIS__BearSurvey20A and in Anchorage on \\dfg.alaska.local\gis\Anchorage\GISStaff\wc\Earl__BearSurveys_Unit20a2016 However, a more permanent location should be designated for future reference.

Literature cited:

Becker, E. F., and A. M. Christ. 2015. A Unimodal Model for Double Observer Distance Sampling Surveys. PLoS ONE 10(8):e0136403. 10.1371/journal.pone.0136403

Table 1. Allocation of transects proposed, flown, and number of grizzly bear groups observed for mark-recapture distance methods to estimate grizzly bear abundance based on geographic features for Game Management Unit 20A in Alaska, May 2016

Transect type	Zone Location	Total # transects	Approximate distance (km)	# flown transects	Actual Flown (km)	% completed # transects	% completed distance	# grizzly groups (total # individuals)
Contour		847	16386	192	3864	23%	24%	7 (16)
Riparian		62	873	16	260	26%	30%	2(3)
North-South	Flats 1	79	1245	59	939	75%	75%	0
	Flats 5	177	6043	132	4518	75%	75%	1(3)
East-West	Flats 2	213	2048	33	343	15%	17%	0
	Flats 4	261	2630	8	75	3%	3%	0
	Flats 7	192	3228	10	267	5%	8%	0
	Flats 12	187	2107	14	357	7%	17%	0
Totals		2018	34560	464	10623	23%	31%	

Table 2. Summary of black and grizzly bear observations from distance methods to estimate grizzly bear abundance in Game Management Unit 20A, Alaska May 2016.

Species	Date	Group ID	Observed bear	Group Size	Group Type	Activity	Transect #	Segment	Side	Cover	Snow	Avg MPH	Altitude (m)	Time
Black	2016-05-02	1001	Young	4	F+Y	Feeding	3185	454	Left	50	0	83.6	281.2	1344
	2016-05-04	1003	Young	1	Lg M	Feeding	3088	1592	Right	0	0	81.9	225.2	1454
	2016-05-04	3001	Merickel/ McMahan	1	Lg M	Stand	250	1103	Right	10	0	83.2	822.5	1142
	2015-05-05	3002	McMahan	1	Adult	Bedded	169	1527	Right	10	0	72.8	809.8	1442
	2015-05-05	3003	Nicholson/ McMahan	1	Sub-Adult	Stand	280	1540	Left	10	0	48.1	709.4	1527
Grizzly	2016-05-03	2001	Hollis/ Greenblatt	3	F+2yo	Walking	3057	382	Right	10	0	83	267.8	1036
	2016-05-04	1002	Young/ Webb	1	Adult	Bedded	184	1281	Left	0	100	94.7	1407.5	1025
	2016-05-04	4001	Becker/ Zakowski	4	F+C	Bedded	243	412	Left	0	50	73	1042.8	1542
	2016-05-06	2002	Zakowski	2	Breeding	Stand	257	1288	Left	0	25	69.1	1266.4	1602
	2016-05-06	5001	Cummings	1	Adult	Stand	258	1954	Left	0	0	73.3	1321.2	1745
	2016-05-06	5002	Merickle/ Cummings	2	Breeding	Walking	191	1962	Right	0	0	56.8	1434.5	2020
	2016-05-07	2003	Zakowski	2	F+2yo	Running	227	145	Left	0	0	88.8	1352.7	1826
	2016-05-07	3005	Brainerd/ McMahan	1	Lg M	Walking	309	1662	Right	10	0	61.5	953.5	0930
	2016-05-07	3006	McMahan	2	F+2yo	Walking	400	1729	Right	0	0	79	922.2	1425
	2016-05-08	3007	Becker/ McMahan	4	F+2yo	Standing	416	1773	Left	45	0	70.9	839.7	1320
Groups	Total Animals		Avg Alt. (M)	Min Alt. (M)	Max Alt (M)	Std Alt.								
15	30		910	225.2	1434.5	411								

Appendix 2

Unit 22 (all subunits) grizzly harvest trends in age at harvest 1970–2016.
Preliminary analysis conducted by Danny Caudill.

Table 1: The number of harvested grizzly bears by GMU in Alaska 1970-2016:

GMU	Total Harvest 1970–2016	Mean Annual Harvest per 1,000 mi^2 1970–2016
22A	805	2.622
22B	793	2.271
22C	455	4.720
22D	424	1.130
22E	115	0.553

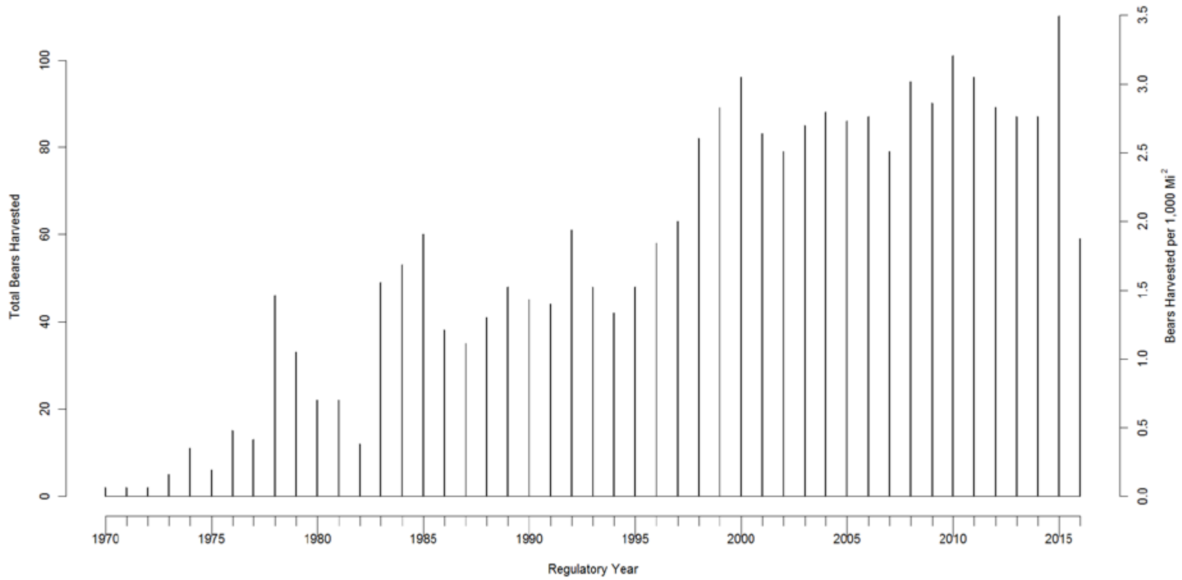


Figure 1. Change in harvest over time for GMU 22 in Alaska 1970-2016.

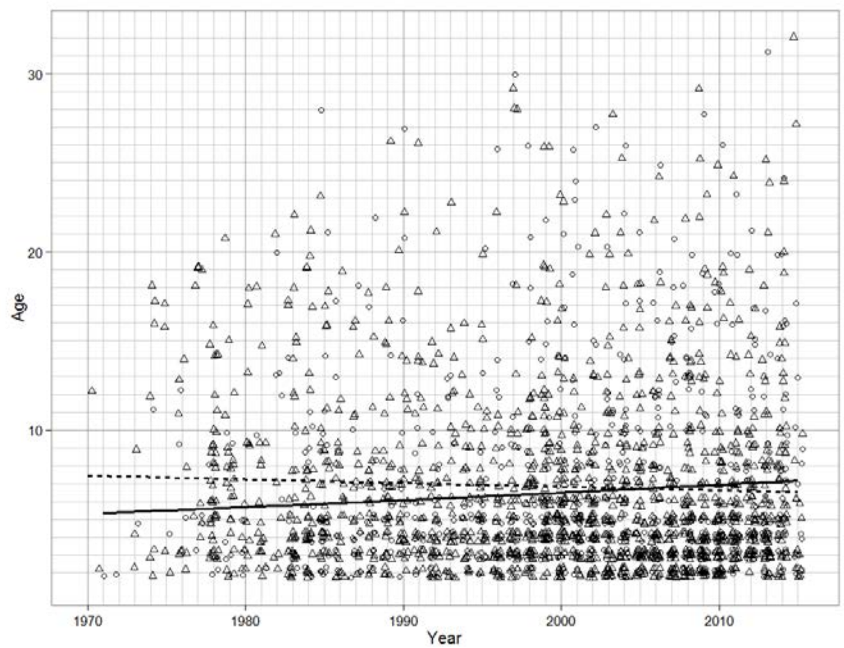
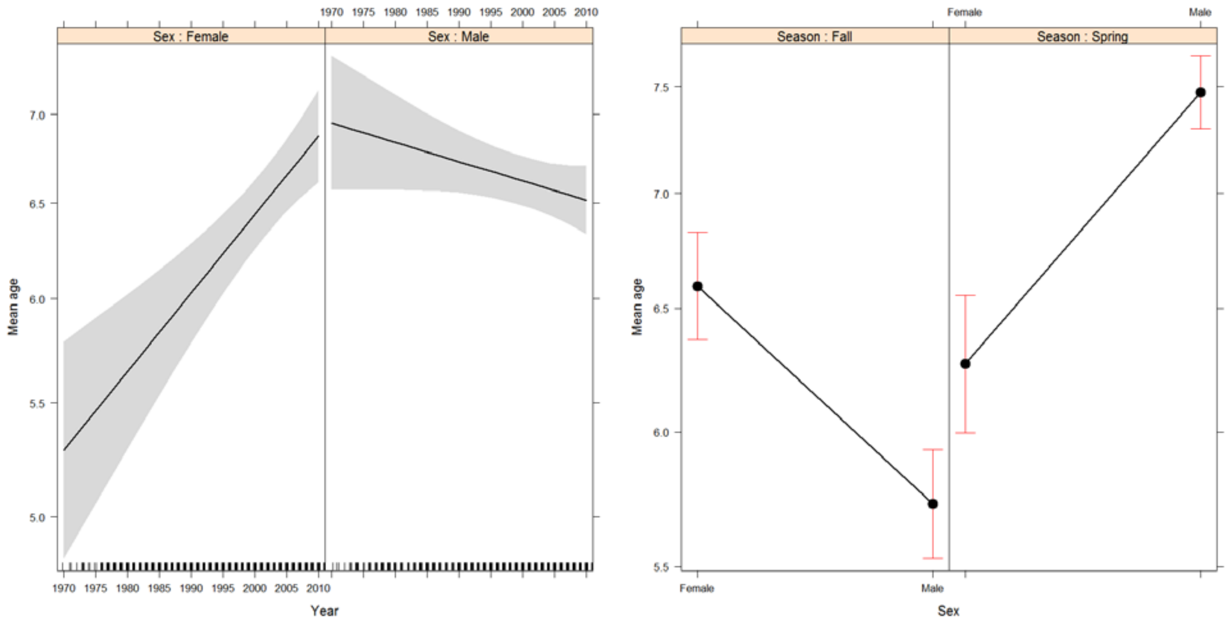
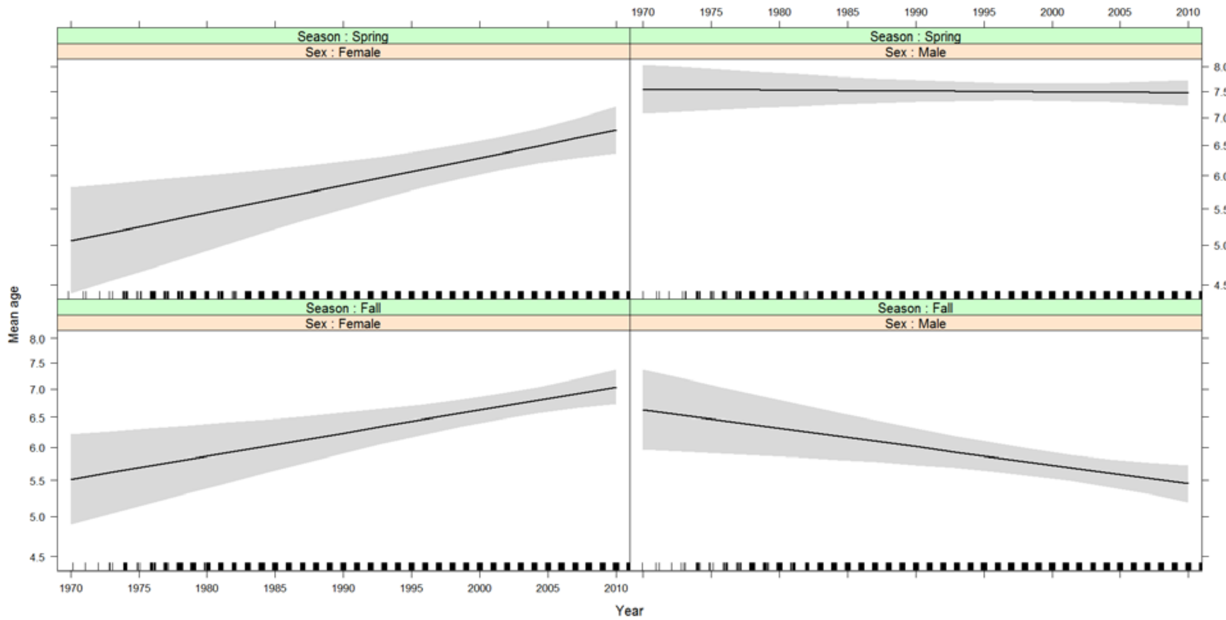


Figure 2. Scatterplot of all grizzly bears harvested by year and age in GMU 22 1970-2016. Females are circles and the solid line. Males are triangles and the dashed line. The two trend lines are significant, see additional plots below.



Effects plots from the Poisson regression model: Age ~ Year*Season + Season*Sex (lower order terms are included). Left panel shows the trends in age at harvest over time, with the expected slight negative trend in males (i.e. due to truncation of the age distribution that harvest by definition causes). However, the increase in female age seems odd and could be a consequence of more prime age females becoming available (i.e. without cubs or yearlings) to harvest. The next panel and plot decompose the female trend further. The right panel shows the seasonality of harvest age. Again for males the expected trend arises where older males are harvested in the spring (presumably from hunters that are specifically targeting bears), whereas younger males are harvested in the fall (presumably from hunters opportunistically taking bears while out for other species). If the trend from the left panel for females is due to infanticide then we would expect older individuals to be harvested in the fall, because they would be with cubs in the spring and thus not available by regulation (need to check the history on that). However there appears to be little difference in age at harvest for females in the spring vs. fall, which is further assessed in the next plot.



Effects plots from Poisson regression model: Age ~ Year*Season*Sex (lower order terms are included, even two way interactions). This model is hyper complicated and many of the terms are not significant, but we present it to show the female trend in spring vs. fall, which is nearly identical (left plots). Hence we do not find evidence to support infanticide as the cause of the increasing trend. This conclusion obviously only applies if females whose cubs are killed by and large are breed and with cubs the following spring (which is also obviously the hypothesis for why it could be advantageous for males to kill cubs). Another potential cause of an increasing trend in female age is that age-at-first reproduction is increasing, but that would seem to imply bear density increased. Longer reproductive pauses between litters could also plausibly lead to an increase in age at harvest, but again would seem to imply higher bear density. If something with resources changed then that could be an alternate explanation to density in the two previous scenarios.