



Research Article

Brown Bear Density and Estimated Harvest Rates in Northwestern Alaska

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ABSTRACT Human-caused mortality in general, and unregulated hunting in particular, have been implicated in reductions in brown bear (*Ursus arctos*) populations throughout much of their range. In northwestern Alaska, USA, bear densities have not been assessed in 20 years while harvest regulations have been liberalized, raising concerns that broad undetected population declines might occur. We used a modified mark-resight approach to estimate brown bear density during 2005–2018 in 4 subareas throughout the region. We also summarized harvest information for each subarea and used our survey results to estimate harvest rates. We estimated densities for independent bears assuming constant or heterogeneous probabilities of detection and occurrence. We present the results of the constant model for more direct comparison with past work and the heterogeneity model results to provide estimates of density that are less likely to be negatively biased. Using the constant model, we estimated the density of independent bears was 17.0, 49.2, 24.9, and 19.4/1,000 km² on portions of the Seward Peninsula, the lower Noatak River, the upper Noatak River, and Gates of the Arctic National Park and Preserve, respectively. These estimates are broadly similar to those from past work in interior and northwestern Alaska, with the exception of the lower Noatak River subarea where our estimates are the highest reported for a bear population in northern Alaska. We estimated that the harvest rate on the Seward Peninsula was approximately 5.2% or 7.7% on average, depending upon the model used. In the remaining areas, we estimated annual harvest rates were <2.5%, well within sustainability guidelines from past work. Overall, our results suggest that brown bear densities are similar or somewhat higher than in the past in much of northwestern Alaska and that current harvest rates are sustainable in most areas, except perhaps the Seward Peninsula. Ongoing survey work will be useful for further evaluating the assumptions of the modified mark-resight survey approach, assessing population trajectory, and determining the effect of harvest on brown bear populations. © 2021 The Wildlife Society.

KEY WORDS Alaska, brown bear, detection probability, harvest, mark-resight, population density, *Ursus arctos*.

Brown bear (*Ursus arctos*) populations throughout much of their range have been reduced through habitat loss and a history of unregulated harvest and intentional overkill (Mattson and Merrill 2002, Jerina et al. 2003, Schwartz et al. 2003, Huber et al. 2008, Zedrosser et al. 2011). Human-caused mortality remains an important factor in population trajectory range-wide (Wielgus and Bunnell 1994, Wielgus et al. 1994, Mace and Waller 1998), and harvest is an important factor in some areas (Wielgus et al. 2001, Zedrosser et al. 2001, McLoughlin et al. 2003, Swenson et al. 2017, Brockman et al. 2020). Populations in Alaska, USA, and northern Canada are generally considered

to be healthy (Schwartz et al. 2003), although liberalization of harvest regulations since around 1980 has raised concerns that populations could be at risk of decline throughout much of Alaska (Miller et al. 2011, 2017; Morton et al. 2016; Ripple et al. 2019). Most areas, however, lack current information on bear density, and managers must rely on reported harvest and presumptive densities (Miller 1993, Miller et al. 1997), complicating meaningful assessments of harvest management.

One such area lacking consistent information on bear density has been northwestern Alaska, where current population status is relatively unknown, increasingly liberalized hunting regulations have been implemented since the early 1990s, and unreported harvest occurs (Loon and Georgette 1989, Georgette 2001, Westing 2013, Miller et al. 2017). Densities, particularly on the Seward Peninsula, were likely reduced during the early 1900s in association with the extensive gold mining and reindeer herding

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industries (Smith et al. 1990, Georgette 2001, Hughes 2013, Westing 2013) during which brown bears were killed for food and in defense of life and property. Large-scale federal predator control in the mid-1900s, including poisoning, may have had further effects, and as recently as the 1960s hunting was implicated in declines on the north slope of the Brooks Range (Carroll 2013). But as mining and herding diminished and human populations became more concentrated, opportunities for human-caused mortality may have diminished. In addition, after statehood, predator control ended and seasons, bag limits, and sealing requirements (i.e., presentation of the hide and skull to a state representative who collects a tooth, takes skull measurements, and records sex and location of kill) were established, likely allowing populations to recover.

The last attempts to estimate bear densities in portions of northwestern Alaska occurred >20 years ago (Reynolds 1992, Ballard et al. 1993, Miller and Nelson 1993, Miller et al. 1997), but despite the lack of data, the public's general perception is that brown bear populations have increased throughout much of the region (Hughes 2013, Stout 2013, Westing 2013). Perceived increases in bear numbers has led to public support for continued increases in harvest opportunity with the goal of reducing competition between humans and bears for ungulates, particularly moose (*Alces alces*), reducing conflicts around cabins and subsistence camps, and providing for traditional subsistence hunting practices (Hughes 2013, Westing 2013). Understanding the effect of more recent regulatory changes on bear harvest and subsequent effects on bear populations is difficult without estimates of population density.

Although much of the land in northwestern Alaska is managed by the United States National Park Service (NPS), most of these NPS lands (a mixture of National Preserves, National Monuments, and National Parks) allow the harvest of brown bears. Harvest is primarily managed by the Alaska Department of Fish and Game (ADFG), though only federally qualified subsistence users are allowed to harvest bears in some areas. Regardless of differences in mandate, both state and federal regulatory boards must make decisions on the advice of agencies, often in the absence of data on abundance or robust estimates of harvest rate. In an attempt to inform brown bear management in the region, we began an interagency collaboration to begin assessing bear density and harvest in northwest Alaska.

Several approaches have been used to successfully estimate bear density and monitor populations including demographic projection models (Sæther et al. 1998, Garshelis et al. 2005, Gervasi and Ciucci 2018), capture-mark-resight (Miller et al. 1997, McClintock et al. 2006), genetic markers analyzed in a mark-recapture (Mowat and Strobeck 2000; Gervasi et al. 2008; Kendall et al. 2008, 2009; Ciucci et al. 2015) or spatial capture-recapture (Bischof et al. 2016, Murphy et al. 2016, Kendall et al. 2019) framework, line transect distance sampling (Becker and Quang 2009, Walsh et al. 2010, Becker and Christ 2015), and the integration of multiple data types (Gervasi et al. 2012, Popescu et al. 2017). Capture-mark-resight has been used extensively

throughout Alaska but requires physically marking individuals prior to conducting surveys. Although robust, the combination of monetary and logistical costs generally limit spatial coverage and, therefore, spatial inference. Similarly, other alternatives that employ marked individuals (i.e., demographic projection models, genetic markers, integrated approaches) can be cost limiting at large spatial scales in remote areas (Morton et al. 2016). Aerial line transect distance sampling surveys address some of the limitations of approaches requiring physical sampling by eliminating the need for ground access to sampling sites; however, adequate sample sizes are difficult to obtain for low-density populations, and single-pass surveys are more susceptible to bias caused by incomplete availability of bears (Schmidt et al. 2017b). Recently, a modified mark-resight survey design treating spatial, temporal, and individual characteristics as temporary marks was developed specifically for low-density brown bear populations in predominantly non-forested areas (Schmidt et al. 2017a). Like distance sampling approaches, this approach is feasible to implement at large spatial scales, but it is more efficient than distance sampling when encounter rates are low. Despite the stronger assumptions required because of the lack of physical marks in the population and the inability to explicitly address heterogeneity in detection probability among individuals, modified mark-resight surveys are a cost-effective means to estimate bear densities at the landscape scale in remote and undeveloped arctic and subarctic landscapes (Schmidt et al. 2017a).

We present the results of a monitoring program developed by the NPS in cooperation with the ADFG to estimate brown bear density and trend throughout much of northwestern Alaska (Robison et al. 2017). Our survey protocol evolved over time but ultimately resulted in the development of the modified mark-resight survey approach presented by Schmidt et al. (2017a). Our goal was to use the data collected under this program to provide a current assessment of brown bear population density in 4 subareas in the region. In addition, we summarized harvest within each survey subarea and used our population estimates to estimate harvest rates. Our specific objectives were to estimate brown bear density in 4 large subareas of northwestern Alaska and estimate approximate harvest rates within each subarea based on local population size.

STUDY AREA

Our study area consists of 4 distinct subareas covering approximately 85,000 km² of predominantly undeveloped lands in northwest Alaska including portions of the central and western Brooks Range and the Seward Peninsula (Fig. 1; Table 1). Our broad study area covered elevations ranging from sea-level to 2,400 m and was characterized by long cold winters (Nov–Mar; ~0°C to –55°C) and short summers (Jun–Aug; ~0°C to 30°C) with low annual precipitation (~20–45 cm/yr). Our surveys, conducted in mid-May to early June, were largely centered on NPS lands throughout this area but included non-NPS lands based on natural boundaries or areas of particular management

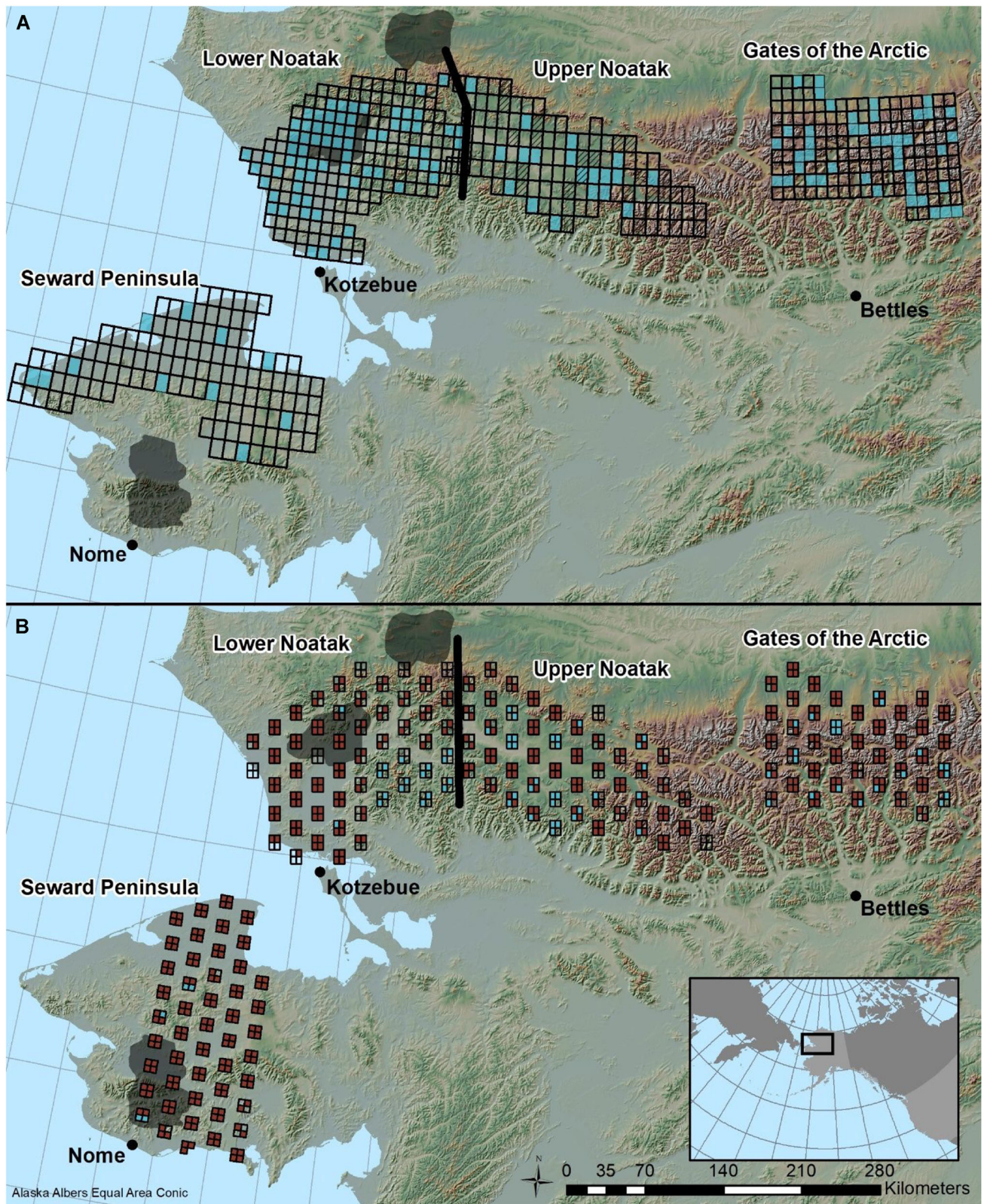


Figure 1. Locations of each of the brown bear survey subareas in northwestern Alaska, USA. Panel A depicts units sampled from 2005–2010, and panel B depicts subunits sampled from 2013–2018. Blue cells were surveyed once, red cells were surveyed twice, and empty cells were not surveyed. The hashed cells in the Upper Noatak in panel A were surveyed in 2005 and the blue cells were surveyed in 2007. Units surveyed during the incomplete 2013 survey of the Seward Peninsula subarea are not shown. The green lines indicate the boundaries of National Park Service units. The gray polygons represent the approximate boundaries of the 3 historical collar-mark-resight projects conducted in the region: the western Brooks Range (northern; Reynolds 1992), the Red Dog Mine area (central; Ballard et al. 1993), and Nome (southern; Miller and Nelson 1993).

Table 1. Sample sizes by year and subarea for brown bear surveys in northwestern Alaska, USA 2005–2018.

Year	Subarea	Units sampled	Subunits sampled	% of subarea surveyed	Bear groups detected	Subarea size (km ²)
2005	Upper Noatak	22		20	13	17,871
2006 ^a	Seward Peninsula	11		9	8	22,463
2007	Upper Noatak	20		18	26	17,871
2008	Lower Noatak	71		38	110	20,772
2010	Gates of the Arctic	45		29	55	16,905
2013 ^a	Seward Peninsula	12	42	7	27	19,998
2015	Seward Peninsula	48	181	28	58	19,998
2016	Lower Noatak	48	131	17	100	23,596
2017	Upper Noatak	46	144	19	59	23,559
2018	Gates of the Arctic	40	140	24	47	18,213

^a Incomplete survey.

interest. The 4 subareas we considered were the central Seward Peninsula, the lower Noatak River drainage, the upper Noatak River drainage, and Gates of the Arctic National Park and Preserve. The specific delineation of each subarea varied between 2 time periods, 2005–2010 and 2013–2018 (Fig. 1), as we developed the survey approach. The orientation of the subareas covering the central and western Brooks Range remained largely unchanged through time, although we made minor modifications to subarea boundaries during the second period. Only the perimeter of the Seward Peninsula subarea changed meaningfully, focusing on Bering Land Bridge National Monument during 2005–2010, and a north-south swath of the Seward Peninsula during 2013–2018 (Fig. 1). Terrain throughout the study area ranges from flat tussock-tundra, to rolling hills, and steep mountains. Specifically, the Seward Peninsula subarea transitions from flat tussock-tundra in the north, to rugged mountains in the central portion, and brushy rolling hills in the south. The lower Noatak subarea is relatively flat and open in the west nearer the coast, becoming more mountainous to the north and east, except along the Noatak River drainage where rolling hills are more common. The Upper Noatak subarea consists predominantly of flat tussock tundra and rolling hills in the Noatak basin, with mountains along the northern, southern, and eastern borders. The Gates of the Arctic subarea contains a primarily mountainous landscape, with some flat and rolling terrain to the north. In these arctic and subarctic ecosystems, woody vegetation is generally limited to patches of willow (*Salix* spp.) and alder (*Alnus* spp.), which are largely concentrated along riparian corridors. Although closed spruce (*Picea* spp.), balsam poplar (*Populus balsamifera*), and Alaska birch (*Betula neoalaskana*) forest does occur in the southern portion of the Seward Peninsula and along the lower Noatak River, we designed our study area boundaries to minimize the inclusion of forests. In addition to brown bears, populations of Dall's sheep (*Ovis dalli dalli*), caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), moose, and black bears (*Ursus americanus*) occur in the region. Detections of black bears were rare within our subarea boundaries.

METHODS

We used 2 similar, but distinct, aerial area-search survey sampling approaches during 2 time periods in our study,

resulting in differences in sampling design and sample unit layout over time (Fig. 1; Table 1). Both survey types consisted of a systematic grid design overlaid on each subarea; we surveyed a subset of each for brown bears. During 2005–2010, we essentially collected single-visit group observation data. During 2013–2018, we used the modified mark-resight approach of Schmidt et al. (2017a) to collect mark-resight data for individual bear groups within each sample unit. We present the details of each approach, and the resulting joint analysis of the data, below.

2005–2010

During the 2005–2010 sampling events, we began by generating a systematic grid across each subarea, with cell size in each subarea based on the expected search intensity required to provide adequate coverage and complete 2 survey units/day. Expected search effort was based on our knowledge of habitat complexity and expected bear densities in each subarea (i.e., smaller cell sizes in areas with more complex habitats or higher expected bear densities). Grid cell sizes were 190 km², 112 km², 160 km², and 108 km² for the Seward Peninsula, Lower Noatak, Upper Noatak, and Gates of the Arctic subareas, respectively. We timed surveys to coincide with the end of den-emergence but prior to leaf-out of woody vegetation, which can obscure bears (i.e., the last 2 weeks of May through the first week of Jun in arctic and subarctic Alaska). For a given survey year, we randomly selected a subset of grid cells (i.e., units) within a given survey subarea (except in 2008 when we selected an additional block of units covering the Ballard et al. [1993] study area within the Lower Noatak subarea; Fig. 1) and assigned each unit to a pilot-observer team. We conducted surveys within 1 subarea each year. We instructed each team to completely search each unit using a tandem fixed-wing aircraft (e.g., Piper Supercub; Piper Aircraft, Vero Beach, FL, USA) with the broad guideline of spending <4 hours in each unit (i.e., 2 units/8-hr day). Pilots varied search intensity and pattern as needed to thoroughly cover the area. When we detected a bear group, we recorded the spatial location and group characteristics (e.g., color, number of cubs, group size). A second team resurveyed a subset of the selected units with the goal of estimating detection probability in a mark-resight framework. The extended resurvey interval (i.e., up to 3 days) likely violated the assumption of population closure between visits and hindered our ability to reconcile potential repeat observations of

individual groups. Therefore, we included data from only the initial survey of each unit, treating the second potential visit as missing data (see below).

2013–2018

For the 2013–2018 survey period, we used the modified mark-resight approach developed by Schmidt et al. (2017a) for the 2013 and 2015 surveys on the Seward Peninsula. The primary difference in survey implementation in comparison with the 2005–2010 work was that we updated and standardized the survey design and protocol to allow us to better meet the assumption of closure between repeated visits, thereby allowing the estimation of the probability of detecting bear groups (Schmidt et al. 2017a). We continued to use a grid-based design but used a uniform unit size (124 km²) across subareas and divided each unit into 4 smaller (31 km²) subunits. We also selected sampling units systematically across each subarea rather than randomly as in our original design (Fig. 1B). Doing so ensured uniform coverage across each subarea and reduced the possibility of bears moving between sample units within a given day.

During each survey, we assigned pairs of pilot-observer teams a list of subunits each day, typically 2 units with 4 subunits each. We instructed them to thoroughly search each subunit with the guideline of spending ≤1 hour in each. We typically searched subunits sequentially, with the second pilot observer team resurveying each subunit covered by the first team within <4 hours (typically within ~1 hr). If subunits could not be resurveyed within approximately 4 hours, we did not attempt a resurvey. We also attempted to survey units in sequence from one end of a subarea to another to minimize the potential for recounting the same bears in different units. Upon detecting a bear group, the observer took multiple high resolution photographs, recorded the spatial location using a global positioning system, counted the number of bears and approximate age classes (e.g., cubs, adults), and noted any other distinguishing features that might aid in identification. We treated these data as temporary, uniquely identifiable marks that could be used to identify individual bear groups over the short resurvey interval. In the evening, each pair of pilot-observer teams compared the information collected on each detected bear group within each subunit and determined whether they had detected the same or different groups. For the low-density populations in our study areas, the combination of spatial location, coloration, group size, and number of cubs appeared sufficient to reliably identify groups (Schmidt et al. 2017a). If it became apparent during a survey within a subarea that we were going to be unable to survey all selected subunits (e.g., a stretch of bad weather), we reallocated our remaining effort so as to cover the remaining portion of the subarea as uniformly as possible to ensure our sample was spatially representative (Fig. 1B).

Abundance Analysis

Because our fundamental search protocol remained the same during both time periods (i.e., aerial area-search of units or subunits with similar effort levels; recording of individual bear groups, group size, approximate age classes), we made the assumption that the probability of detecting a bear group was broadly similar among surveys. A violation of this

assumption could lead to bias in year- or area-specific estimates, but we had no reason to suspect that the basic detection process would vary dramatically over time or space. We included a random effect term at the subunit level for the later surveys to account for heterogeneity in detection, assuming that variation in detection among subunits would encompass differences in habitat-specific detection probabilities (e.g., land cover type), the presence of bears with varying detection probabilities, and observer, weather, and inter-annual heterogeneity. Under this assumption, we included the data from both time periods within a single analysis, treating the 2005–2010 data as if the replicate survey of each unit was not completed (i.e., missing data). We used the mark-resight information from the later surveys to estimate the average probability of detecting a bear group across surveys and used it to adjust the single pass surveys of 2005–2010 for incomplete detection. We acknowledge that the inability to estimate survey-specific detection probability is a limitation to inference; however, our approach allowed us to consider ≥2 recent density estimates for each subarea. Having >1 estimate was useful for 2 reasons: the most recent existing density information was decades old and was limited spatially, and our modified mark-resight method has not been used outside of the initial presentation in Schmidt et al. (2017a). Multiple estimates for each area helped to provide increased confidence in our results and additional context for our findings.

Our analysis closely followed that presented by Schmidt et al. (2017a). We augmented the data (Royle et al. 2007, Royle 2009) from each surveyed subunit (2013–2018) with ≤4 additional 00 capture histories, which was determined to be sufficient based on prior work (Schmidt et al. 2017a). For the 2005–2010 data when we did not use subunits, we scaled our data augmentation to match that of the 2013–2018 period (i.e., 20 capture histories/unit, augmented and observed combined). We then estimated how many of the potential groups were actually present but undetected. The model we used can be written as:

$$y_{jkl} \sim \text{Bernoulli}(z_{kl} \times p_{kjl})$$

$$z_{kl} \sim \text{Bernoulli}(\Psi_{kl})$$

$$\text{logit}(\Psi_{kl}) = \text{int}_{\text{yr}} + e. \text{unit}_k$$

$$\text{logit}(p_{kjl}) = \alpha_0 + e. \text{subunit}_l$$

$$\hat{N}_k = \text{sum}(z_{kl} \times \text{size}_{kl})$$

$$\text{size}_{kl} \sim \text{Poisson}(\text{mean. size}_{kl})$$

$$\log(\text{mean. size}_{kl}) = \text{size. int}$$

$$\hat{D}_k = \hat{N}_k / A_k,$$

where the observed state (y_{jkl}) for each visit (j), survey year (k), and potential group (l) is a function of the true state (z_{kl}) and the probability of detecting a group given it was present (p_{kjl}). We modeled occurrence probability of each

group within each year (Ψ_{kl}) as a function of a year-specific intercept (int_{yr}) and a random effect at the unit-level (*e. unit_k*) to account for spatial variation in group occurrence (*e.g.*, variation in habitat quality). We modeled p_{kl} using an intercept (α_0) and a random effect at the subunit-level (*e. subunit_l*). The subunit-level random effect term helped to address individual heterogeneity that can positively bias estimates of detection probability, thereby negatively biasing estimates of density (Otis et al. 1978). For the 2005–2010 surveys, we excluded the random terms because of the different grid structure and lack of revisits. An estimate of the number of bears ($\hat{N}_k$) is derived by summing the product of the true states (z_{kl}) and average group size ($size_{kl}$). Group size is assumed to be Poisson distributed with a mean of *mean. size_{kl}*, which is modeled using a single intercept term (*size. int*). Estimates of density for each year ($\hat{D}_k$) are simply the estimated total number of bears divided by the area surveyed (A_k). We conducted separate analyses for independent bears (cubs of all ages excluded) and all bears (cubs included) to facilitate comparison with past work (Miller et al. 1997). We also fit a simplified version of the models with no random terms to provide estimates more directly comparable to those of Miller et al. (1997). As in Schmidt et al. (2017a), we included the data from the 2013 partial survey for the purpose of aiding in the estimation of detection probability but did not estimate density for that year because survey coverage was limited owing to poor weather conditions.

We conducted the modified mark-resight analysis in a Bayesian framework, using OpenBUGS (Thomas et al. 2006) for model fitting and R 3.1.0 (R Core Team 2014) as an interface. We used compact priors for intercept terms, $N(0,10)$, and vague priors for the standard deviation of the random effects, $U(0,100)$. We ran 2 independent chains for 100,000 iterations each, discarded the initial 60,000 as burn-in and retained the remainder for inference. We used the Gelman-Rubin diagnostic (Brooks and Gelman 1998) and a visual inspection of the chains to ensure convergence had been reached. We also calculated the Bayesian *P*-value as a measure of model fit, assuming lack of fit to have occurred if values approached 0 or 1 (Gelman et al. 2004). Detailed model code is presented online in Supporting Information.

Harvest Data

During the sealing process for all non-subsistence harvest or defense of life and property (DLP) kills, harvest location is recorded by harvest reporting unit. These units are derived by drainage basin and do not always correspond well to our subarea boundaries. To address this spatial mismatch, we used a spatially proportional approach to estimate harvest within each subarea. We began by determining the average number of bears harvested within each harvest reporting unit that overlapped our subarea boundaries. We used 2 time periods, 1998–2007 and 2008–2017, to provide some context on changes in harvest over time. To calculate harvest within our subareas and a range of harvest rates, we used the 2008–2017 average, corresponding more closely to the time period when our abundance surveys took place. We

calculated the proportion of each harvest reporting unit that overlapped the survey subarea, and attributed that proportion of the harvest from the entire reporting unit to our survey area. For example, if a harvest reporting unit had a mean harvest of 10 bears/year and overlapped our survey subarea by 50%, we assumed 5 of those bears came from our survey subarea annually. We did this for each reporting unit and summed the result to get total average annual harvest for our survey area. We evaluated trends in bear harvest using simple linear regression, with harvest as a function of time across both time periods.

Subsistence harvest was not necessarily captured through the sealing process (*i.e.*, sealing is not required, and harvest is often unreported) but represents an additional source of harvest. For each area, we estimated subsistence harvest that was otherwise unreported by examining patterns documented through household surveys (Westing 2013). We then attempted to cross-reference those bears that had been sealed or reported through subsistence harvest permits and added the number of otherwise unaccounted for bears to the harvest total for each subarea. On the Seward Peninsula, household survey results tended to mirror sealing records (*i.e.*, greater reporting rate), leading us to add no additional unreported harvest. In the remote Upper Noatak, there appeared to be no unreported subsistence harvest and in the Gates of the Arctic study areas it was low, adding an additional 0.5 unreported bears/year to the harvest. In the Lower Noatak, there appeared to be very little overlap between sealing records and subsistence harvest, resulting in the addition of 10 unreported bears/year to the harvest. To estimate potential harvest rate, we divided the average annual harvest (2008–2017) by the total estimated population sizes calculated from the results of the abundance analysis. We did not make the unreported harvest adjustment for trend analyses, only to adjust our estimate of harvest rate. Our measure of harvest does not include bears that were killed for various reasons but not salvaged or otherwise documented through the sealing and reporting system or household surveys. We have no way to estimate how many additional unreported mortalities may occur, so our inference is restricted to reported harvest, estimated subsistence harvest, and documented DLP mortality only. Other studies have suggested that in some circumstances, even in areas without dense human settlement, unreported killing outside of regulated hunting can exceed that of hunting, particularly for females (Liberg et al. 2012, McLellan 2015).

Age and Sex of Harvested Bears

We used data from the state sealing system to estimate average age of male and female bears killed in each study area (1998–2017). Unlike the estimates for overall harvest, which were pared down to be proportional to the amount of area each harvest reporting unit overlapped with the study area, we used all bears harvested in harvest reporting units that overlapped with the study area. Matson's Laboratory (Milltown, MT, USA) aged bears using a tooth extracted as part of the sealing process. We also estimated long-term sex

ratio in the harvest and estimated the proportion of each age class made up of males in each study area for bears aged 3 through 25 (Fraser and Paloheimo 1981, Fraser 1984, McLellan et al. 2017, Brockman et al. 2020). Bears <2 years old were not legal to harvest but were occasionally present in the harvest data as illegal harvest, DLP, or potentially because of mis-aging. We used these data to put our estimates of harvest rate into context and to allow comparisons with other recent studies.

RESULTS

Survey coverage ranged from 7–38% of each subarea in a given year, and the number of bear groups detected during each survey varied from 8–110 (Table 1). Diagnostics indicated that the models converged ($\hat{R} < 1.1$), and measures of goodness of fit showed that the fit of the constant model (Bayesian P -value = 0.81) and the model assuming heterogeneity in detection and occurrence probabilities (Bayesian P -value = 0.63) were adequate. We estimated that mean detection probability was 0.42 (95% CrI = 0.35–0.49) under the constant model, and 0.24 (0.17–0.34) under the heterogeneity model. The single-visit study design of our 2005–2010 study period resulted in less precise estimates as compared to the modified mark-resight design used in 2013–2018 (Table 2). Point estimates of density from the 2013–2018 period were uniformly higher than historical estimates, although the credible intervals from the Seward Peninsula overlapped substantially with the equivalent intervals from historical work (Table 2; Fig. 2). Densities were likely higher in the Lower Noatak drainage during our study period as compared to the early 1990s, under either model (Table 2; Fig. 2). Despite differences in precision, corresponding point estimates from the 2005–2010 versus

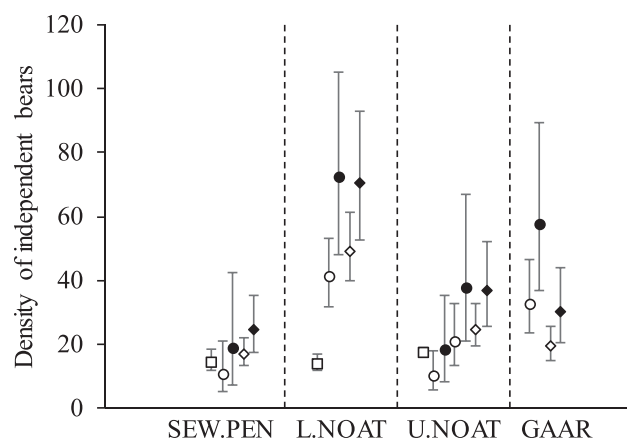


Figure 2. Density estimates (bears/1,000 km²) for independent brown bears from the 4 survey subareas in northwestern Alaska, USA: the central Seward Peninsula (SEW.PEN), the lower Noatak River drainage (L.NOAT), the upper Noatak River drainage (U.NOAT), and Gates of the Arctic National Park and Preserve (GAAR). Squares are estimates taken from Miller et al. (1997). Circles represent estimates based on data collected under the single visit protocol from 2005–2010, and diamonds represent estimates based on data collected under the modified mark-resight protocol from 2015–2018. Open symbols are based on the constant model (i.e., no heterogeneity in detection or occurrence), and closed symbols are based on the model assuming heterogeneity in detection and occurrence. Estimates are for independent bears for all subareas. Vertical dotted lines are included to help visually group estimates by area. Error bars represent 95% confidence intervals for the historical estimates and 95% credible intervals for the estimates from our study.

the 2013–2018 time periods were broadly similar. This consistency provided additional support for the validity of comparisons between current and historical estimates. Estimates for Gates of the Arctic were less consistent and historical information was also unavailable, limiting stronger conclusions for that subarea.

Table 2. Estimated brown bear density (bears/1,000 km²) for each of 4 subareas in northwestern Alaska, USA, for each survey year from 2005–2018 assuming constant probability of detection and occurrence (without heterogeneity) or heterogeneous probability of detection probability and occurrence (with heterogeneity). We do not show estimates for the partial Seward Peninsula survey in 2013 because of poor survey coverage and low sample size. The most comparable historical estimate for each area is also included. Estimates for independent bears exclude dependent cubs. Estimates for all bears include bears of all ages. Estimates from the current study are presented with 95% credible intervals (CrI) and the coefficient of variation (CV). Historical estimates (i.e., pre-2005) are presented with 95% confidence intervals (CI) from Miller et al. (1997).

Subarea and year	Independent bears without heterogeneity			Independent bears with heterogeneity			All bears without heterogeneity			All bears with heterogeneity		
	Density	95% CI or CrI	CV (%)	Density	95% CI or CrI	CV (%)	Density	95% CI or CrI	CV (%)	Density	95% CI or CrI	CV (%)
Seward Peninsula												
1991	14.6	12.1–18.4					29.1	26.1–33.4				
2006	10.7	5.3–21.0	39	19.0	7.2–42.4	48	17.5	9.1–32.2	34	30.8	12.9–61.0	43
2015	17.0	13.5–22.0	13	24.9	17.7–35.2	18	27.1	21.9–34.4	12	39.7	29.3–54.9	17
Lower Noatak												
1987	13.9	11.8–17.2					17.9	15.6–21.0				
2008	41.3	31.8–53.3	14	72.7	47.9–105.2	21	65.6	52.0–84.4	13	115.6	79.1–169.1	20
2016	49.2	40.0–61.6	11	70.5	52.9–93.0	15	70.8	58.6–87.7	11	101.7	77.6–133.1	14
Upper Noatak												
1992	17.8	16.8–19.1					29.5	28.1–31.5				
2005	10.5	5.7–18.2	31	18.4	8.3–35.6	38	18.6	10.8–30.2	27	32.7	16.7–58.6	33
2007	21.4	13.7–33.0	23	37.8	21.1–66.8	32	30.5	20.0–46.5	22	54.0	31.7–92.9	29
2017	24.9	19.4–32.6	14	36.8	25.5–52.1	19	34.1	27.0–44.4	13	50.6	35.9–69.3	18
Gates of the Arctic												
2010	32.8	23.9–46.4	15	57.8	36.8–89.5	24	45.8	33.5–62.5	16	80.7	51.9–122.3	23
2018	19.4	15.0–26.0	14	30.4	20.8–44.1	20	21.3	16.6–28.0	14	33.4	23.0–47.3	19

The average number of bears harvested annually was higher over the last 10 years in comparison to the previous 10 years in all subareas (Table 3), although trends were significant only for the Seward Peninsula ($P = 0.03$) and the Upper Noatak ($P = 0.03$), with increases in reported harvest of 0.7 and 0.3 bears/year, respectively (Fig. 3). Larger harvests came from the Seward Peninsula and Lower Noatak subareas where reported harvest was approximately 30–40 bears/year. Fewer than 10 bears/year were taken from each of the remaining 2 subareas on average (Table 3). Based on the 2008–2017 estimates, potential harvest rates for the Noatak and Gates of the Arctic subareas were <2.5% (Table 3). The Seward Peninsula subarea had a higher potential harvest rate of 5.2% or 7.7% depending upon the model used (Table 3).

The proportion of males in the harvest (1998–2017) was lowest for the Seward Peninsula study area and highest in the Upper Noatak (Table 4). Average age of harvested males and females was also lowest in the Seward Peninsula study area (Table 4). The proportion of the harvest composed of males appeared to be stable or increase with age class except for the Seward Peninsula study area, where the proportion of males appeared to decrease in successive age classes (Fig. 4).

DISCUSSION

We assessed brown bear population status and harvest rates throughout much of northwestern Alaska. Current densities in most subareas are at the upper end of the previously reported range for interior and northwestern coastal Alaska populations (Miller et al. 1997), consistent with stable or slowly growing populations. The primary exception may be the Lower Noatak subarea where densities were higher than previously reported, suggesting densities in this subarea have increased since the 1990s. We caution against drawing strong conclusions regarding population trajectory, although some broad comparisons with past work are appropriate. Based on our best assessment of harvest, estimated harvest rates were low in most areas, with the exception of the Seward Peninsula, in contrast with recently voiced concerns of overharvest (Miller et al. 2011, 2017; Ripple et al. 2019). Although cautious interpretation is warranted because of spatial mismatches between current and past work, and limited data in general, our results represent the only

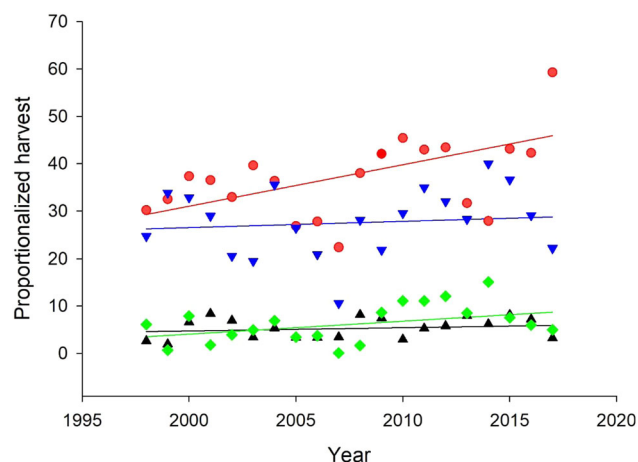


Figure 3. Estimated number of brown bears harvested annually from 4 subareas in northwestern Alaska: Seward Peninsula (red), Lower Noatak (blue), Upper Noatak (green), and Gates of the Arctic (black). Harvest is spatially referenced to specific drainage basins, and proportional overlap between subareas and drainages are used to estimate subarea-specific harvest. These estimates do not include static increases specific to each subarea in an attempt to account for unreported subsistence harvest. Lines are linear estimates of temporal trend; the Seward Peninsula and Upper Noatak had significant positive trends in harvest of 0.7 and 0.3 bears/year, respectively.

contemporary assessment of density and harvest pressure in this large area and will therefore be of interest to managers and researchers alike.

Any survey approach for brown bears must be feasible both monetarily and logistically, and must produce useful population estimates (i.e., estimates that are reasonably precise and unbiased with inference to the population of interest). Schmidt et al. (2017a) demonstrated that the modified mark-resight survey approach performed well in these respects, and we were satisfied that the resulting coefficients of variation ranging between 15–20% for the 2015–2018 estimates (heterogeneity model) would be useful for detecting broad trends in brown bear populations going forward. Survey cost was high (i.e., ~\$125,000/subarea), and pilot and personnel demands were higher than for comparable ungulate surveys, primarily because of the need for rapid repeat visits to the same survey subunit. But the extensive spatial coverage of the surveys enhances overall management utility, and the relative simplicity of field implementation compared to other approaches increases survey

Table 3. Estimated average number of brown bears reported harvested annually from 1998–2007 and 2008–2017 for each of our 4 survey areas in northwestern Alaska, USA. The potential harvest rates and 95% credible intervals (CrI) are based on the 2008–2017 means as a percentage of the estimated total population size from the most recent survey.

Survey area	1998–2007 number harvested		2008–2017 number harvested		Potential harvest rate with heterogeneity (%)		Potential harvest rate without heterogeneity (%)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI
Seward Peninsula	32.2	5.4	41.6	8.4	5.2	3.8–7.2	7.7	6.0–9.5
Lower Noatak ^a	25.4	7.8	30.3	5.8	1.7	1.3–2.2	2.4	2.0–2.9
Upper Noatak	3.9	2.6	8.7	3.9	0.7	0.5–1.0	1.1	0.8–1.4
Gates of the Arctic ^b	4.5	2.1	6.2	1.9	1.1	0.7–1.5	1.7	1.3–2.2

^a Potential harvest rates for Lower Noatak incorporate an annual unreported harvest of 10 bears.

^b Potential harvest rates for Gates of the Arctic incorporate an annual unreported harvest of 0.5 bears.

Table 4. Number and mean age of harvested brown bears by sex in each subarea in northwestern Alaska, 1998–2017. These samples include all bears harvested in reporting units that overlapped each respective subarea. Sample sizes (n) for aged bears are subsets of those bears that were sexed.

Survey area	Number of males harvested	Male age		Number of females harvested	Female age		Percent males
		$\bar{x}$	n		$\bar{x}$	n	
Seward Peninsula	637	6.2	500	430	5.3	346	60
Lower Noatak	543	7.6	499	258	7.1	235	68
Upper Noatak	136	7.9	136	36	5.9	36	79
Gates of the Arctic	187	8.2	187	108	8.3	108	63

completion rates. Overall, the successful completion of surveys in each of the 4 subareas from 2015–2018 and the precision of the resulting estimates supports the idea that this survey protocol may be an effective means for long-term monitoring of brown bear populations in northwestern Alaska (Robison et al. 2017).

Differences in methodology between current and historical projects influence the interpretation of our results. Our heterogeneity model attempted to reduce bias that can occur when heterogeneity remains unmodeled, but our approach was reliant on the assumption that random effects at the unit and subunit levels adequately address heterogeneity in occurrence and detection probability, respectively. Goodness of fit, as measured by the Bayesian P -value, suggested the heterogeneity model fit the data reasonably well, although future incorporation of covariates or physical marks would help to test this conclusion. Historical capture-mark-resight estimates did not account for heterogeneity in

detection probability (Miller et al. 1997); therefore, we also produced estimates with the constant model to provide a more direct comparison to past work, despite the necessary caveats due to differences in survey and analytical methods. Differences in spatial scale may also complicate comparison, and though the spatial extent of the past studies were approximately a tenth the size of our subareas, they were subjectively selected to be representative of populations in the surrounding area (Miller et al. 1997). Obviously, differences in survey methods and spatial extent have implications for meaningful comparisons over time, although the work of Miller et al. (1997) represents the only credible information on bear densities in this part of their range, providing important context.

In general, brown bear densities across our study area were similar to those reported for other interior Alaska populations, with the exception of the Lower Noatak subarea where estimates of 49.2 independent bears/1,000 km²

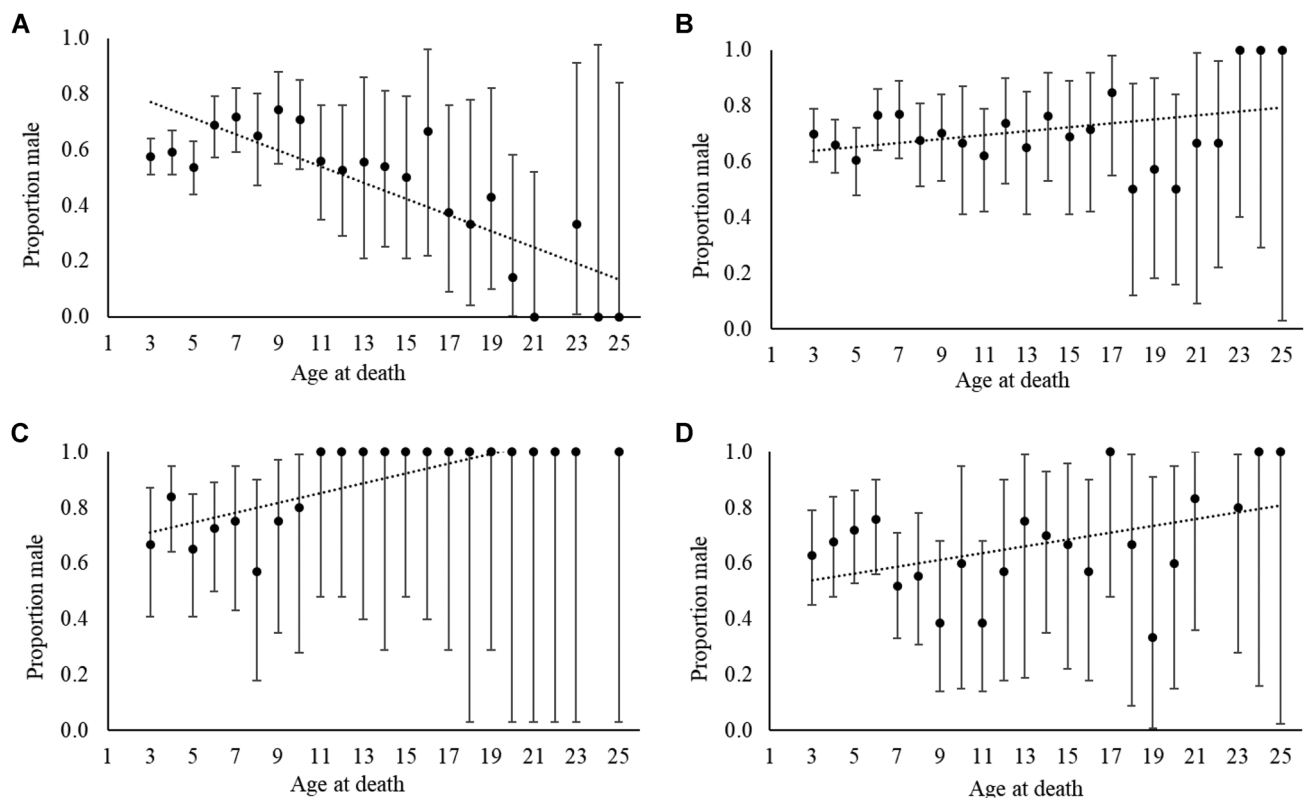


Figure 4. Proportion of brown bears in the harvest that were male for successive age classes, 3–25 years old (harvest of 1–2-yr-olds is prohibited) from 1998–2017 in 4 subareas in northwestern Alaska: Seward Peninsula (A), Lower Noatak (B), Upper Noatak (C), and Gates of the Arctic (D). Age-specific proportions are shown with respective binomial 95% confidence intervals. Dotted lines represent a simple linear regression line, which is included for visual purposes only.

(constant model) and 70.5 independent bears/1,000 km² (heterogeneity model) were the highest reported for interior and northwestern-coastal Alaska (Miller et al. 1997). Bear body size and productivity were generally higher in this subarea as well (Hilderbrand et al. 2019b), suggesting that greater access to food resources (e.g., large spawning concentrations of chum salmon (*Oncorhynchus keta*) in the lower portions of the Noatak River [Menard et al. 2020], beached marine mammals, and a suite of ungulate prey species) may afford a partial explanation. Estimates from the other 3 subareas were similar to those reported for other interior Alaska populations, possibly a function of ≥ 1 factors, including limited food resources (i.e., limited salmon and lower ungulate densities in the Upper Noatak and Gates of the Arctic; Miller et al. 1997, Westing 2012, Rattenbury et al. 2018), limited reproductive output in Gates of the Arctic (Hilderbrand et al. 2019a,b), shorter growing seasons, and higher harvest in the case of the Seward Peninsula.

Recovering brown bear populations can grow at rates of 3–7% (Garshelis et al. 2005; Harris et al. 2006, 2007; Kindberg et al. 2011; Mace et al. 2012), suggesting an increase in density in the Lower Noatak is plausible given varied and abundant food resources. The raw data alone (unadjusted for detection) would have produced density estimates greater than those of Ballard et al. (1993), suggesting current densities are indeed higher than in the past. Although harvest was thought to be a potential limiting factor for this population >30 years ago (Ballard et al. 1993), the current annual harvest rate of <2.5% of the population is within even the most conservative guidelines for productive populations (Sidorowicz and Gilbert 1981, Miller 1990). Similarly, estimated harvest rates of approximately 1% in the Upper Noatak and <2% in Gates of the Arctic suggest current harvest levels do not have a large effect on these populations, despite more limited food resources (Sidorowicz and Gilbert 1981, McLoughlin et al. 2003). Limits to access in the Upper Noatak (predominantly aircraft) and harvest opportunity in Gates of the Arctic (harvest by non-federally qualified hunters is limited to Preserve and adjacent lands) likely act to reduce overall harvest in these areas. The modest increase in reported harvest in the Upper Noatak may be associated with changes in caribou distribution and migration timing that have led to opportunistic harvest of bears by caribou hunters.

The Seward Peninsula subarea differs from the other 3 study areas in that it contains a population center (i.e., Nome; ~3,800 residents) and a road network, likely contributing to the estimated harvest rate of 5.2% or 7.7% (depending upon the model used), which is at or above sustainable rates proposed for other populations in North America (3–5%, McLoughlin et al. 2003; 4–6%, Austin et al. 2004, McLellan et al. 2017; 5.7%, Miller 1990). Harvest rates are similar in Sweden (4.1–5.1%; Bischof et al. 2008) and Russian Karelia (4–6%; Kojola et al. 2003), although harvest of up to 10%/year may be sustainable in some European populations (Zedrosser et al. 2011) such as Slovakia (8.5%; Rigg and Adamec 2007), Finland (11%; Kojola et al. 2003), and Croatia (10%–15%; Huber

et al. 2008). But comparisons with sustainable rates in North American should be made with caution because potential population growth rates are generally higher in Europe (Sæther et al. 1998; Tufto et al. 1999; Zedrosser et al. 2001, 2011). Unlike many areas of Alaska, liberalized regulations appear to have resulted in increases in harvest in the Seward Peninsula subarea (Fig. 3), and reported harvest in the broader area has approximately doubled since the mid-1990s (Hughes 2013, 2015). Food resources for bears on the Seward Peninsula are varied (Gorn and Dunker 2014, 2015; Dau 2015; Menard et al. 2020) and are comparable to those in the Lower Noatak; however, opportunities for ungulate harvest are more limited relative to the other subareas and increased focus on brown bears by hunters may be a consequence. Despite increases in harvest, recent work suggests that reproductive compensation partially mitigates the effects when females with cubs are protected (Brockman et al. 2020), as they are in all subareas in this study. As is the case in Europe (Zedrosser et al. 2011), higher harvest rates (e.g., 8–10%) may be possible in populations with high recruitment (Eberhart 1990, Harris et al. 2006, McLellan et al. 2017), although populations with harvests at the upper end of target ranges should be closely monitored to evaluate recruitment, population trend, and changes in resource abundance (McLellan et al. 2017), which has not been done on the Seward Peninsula.

Although it can be difficult to draw firm conclusions from harvest metrics (Garshelis 1990), and relatively small annual sample sizes, the low average age at harvest (6.2 for males), the sex ratio of harvest (60% male), and the declining proportion of males at successive age classes on the Seward Peninsula do appear to confirm that this population is the most heavily harvested of the 4 we considered. These metrics, with the underlying assumption of constant recruitment, are consistent with a population that is not lightly harvested (Fraser and Paloheimo 1981, Fraser 1984, McLellan et al. 2017, Brockman et al. 2020). Complicating interpretation is that harvest is not evenly distributed throughout the subarea, potentially leading to indicators of high harvest at the local scale (e.g., age at harvest and sex ratio) that may nevertheless be consistent with lower harvest rates at the scale of the subarea. A general lack of data over time limits our ability to determine whether population trajectory has changed appreciably in the last 25 years, although estimated densities were higher in 2015 than in any previous survey in this area (Table 2). If the current harvest rate is unsustainable, we would expect to observe future declines in density, and potentially changes in harvest demographics, absent any compensation through immigration or increases in recruitment.

One potential criticism of our work is that the evolving nature of our surveys complicates inference. Of the 4 subareas, the Seward Peninsula layout was the most substantially modified, from a focus on Bering Land Bridge National Preserve to a north-south swath of the central Seward Peninsula. Regardless, the change in extent had little effect on overall inference because the 2006 survey was incomplete. Survey extent was mainly expanded slightly in

the other 3 subareas for the 2013–2018 period; therefore, we do not suspect evolution in survey layout caused meaningful differences. Variation in survey unit size was less problematic because density is simply a function of the area surveyed and our modified mark-resight analyses were conducted at the level of the individual bear group rather than aggregate counts within units or subunits. The lack of repeat surveys for the 2005–2010 data prevented us from directly estimating detection probability and forced us to make the assumption that it was similar to that of the 2013–2018 surveys, resulting in higher levels of uncertainty surrounding the 2005–2010 estimates. We are comfortable with the assumption regarding the detection process because the search protocols were essentially the same. General agreement between our estimates of detection probability for the modified mark-resight surveys (0.42 under the constant model vs. 0.24 under the heterogeneity model) and the average calculated for capture-mark-resight studies conducted under similar aerial area-search protocols (0.32; Miller et al. 1997) suggests that the detection process was broadly similar between the 2 studies. Our composite estimate of detection across all surveys was also similar to that calculated for the Seward Peninsula data alone (0.33; Schmidt et al. 2017a), suggesting our assumption of a similar detection process was valid. We could have, of course, simply ignored the 2005–2010 data for simplicity; however, including an additional estimate for each subarea provided further context and support for our findings.

Despite the above limitations, our results suggest brown bear densities throughout our study area are similar to those estimated in the past for similar habitats, despite regulatory liberalization in many areas and varying rates of increase in reported harvest over the same time frame. The timelines for regulatory change for each of these subareas were similar, but harvest rates and changes to those rates were inconsistent (Fig. 3), highlighting the fact that liberalized regulations do not inherently result in biologically meaningful increases in harvest. Although there is some evidence that the Seward Peninsula population may be harvest-limited, we found little evidence that liberalized harvest regulations have resulted in unsustainable harvest rates, widespread reductions in brown bear densities in this part of Alaska, or even increases in harvest in some areas (Miller et al. 2017, Ripple et al. 2019). The work we present here is part of an ongoing monitoring program (Robison et al. 2017); therefore, future surveys will help fill data gaps and begin to address concerns over the lack of monitoring data, particularly in areas where harvest occurs (Miller et al. 2017, Ripple et al. 2019). Despite apparently robust populations in our study area, we caution that our tentative conclusions must be tested against future survey data to increase confidence in our findings.

MANAGEMENT IMPLICATIONS

The implications of our work vary across this broad swath of Alaska. It appears that brown bear populations in the Noatak drainage are not currently limited by harvest, although the upper portion of the drainage does have lower

densities and has seen slight increases in harvest. We suspect the Lower Noatak bear population may be partially supported by the chum salmon run, and more focused research might explain some of the apparent growth in this population, and elucidate the role of salmon as a potential factor influencing bear densities in this subarea. In Gates of the Arctic, uncertainty around the reasons few females with cubs were observed and a dearth of historical data preclude strong recommendations until additional data can be collected, although current harvest rates appear to be low. In contrast, relatively high harvest in the Seward Peninsula subarea suggests harvest could be at or approaching levels expected to have effects on population growth. The next survey on the Seward Peninsula is scheduled for 2021, the results of which will help clarify the role of harvest in population trajectory in this subarea. Our ongoing work represents one of the more comprehensive data sets on brown bear abundance in the state, and we encourage agencies to dedicate funds to help increase our understanding of brown bear populations in the region. Continued support for long-term survey protocols will reduce reliance on historical, spatially mismatched studies, refine estimates of density, and increase our understanding of sustainable harvest rates for brown bear populations.

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