Polar Bears in the Beaufort Sea: A 30-Year Mark–Recapture Case History

S. C. Amstrup, T. L. McDonald, and I. Stirling

Knowledge of population size and trend is necessary to manage anthropogenic risks to polar bears (*Ursus maritimus*). Despite capturing over 1,025 females between 1967 and 1998, previously calculated estimates of the size of the southern Beaufort Sea (SBS) population have been unreliable. We improved estimates of numbers of polar bears by modeling heterogeneity in capture probability with covariates. Important covariates referred to the year of the study, age of the bear, capture effort, and geographic location. Our choice of best approximating model was based on the inverse relationship between variance in parameter estimates and likelihood of the fit and suggested a growth from ~500 to over 1,000 females during this study. The mean coefficient of variation on estimates for the last decade of the study was 0.16—the smallest yet derived. A similar model selection approach is recommended for other projects where a best model is not identified by likelihood criteria alone.

Key Words: Capture–recapture; Covariates; Logistic modeling; Population estimation.

1. INTRODUCTION

Polar bears (*Ursus maritimus*) in the southern Beaufort Sea (SBS) area are managed as one population (Treseder and Carpenter 1989). The harvest there is kept below presumed maximum sustained yield (Taylor, DeMaster, Bunnell, and Schweinsburg 1987) by a users’ agreement between the Inupiat of northern Alaska and the Inuvialuit of northwestern Canada. There are, however, no de jure limits on hunting by aboriginal peoples in northern Alaska. Hunting in Russia may be increasing, and oil and gas development in the SBS is expanding (Amstrup, Stirling, and Lentfer 1986; Amstrup, Gardner, Myers, and Oehme 1989; Stirling 1990; Amstrup 2000).

Optimistic population estimates in the 1950s and 1960s resulted in excessive harvest and declines in SBS polar bear numbers (Amstrup et al. 1986). Managers need reliable
estimates of population size and trend to prevent this from recurring. Despite over 30 years of polar bear capture, estimates of population size and trend remain elusive. Failures of past capture-recapture methods to provide reliable estimates apparently resulted from heterogeneity in capture or survival probabilities. Both can bias population estimates (Seber 1982; Hwang and Chao 1995).

In the case of polar bears of the SBS, there are many potential causes of heterogeneity. Polar bears can live 30 years in the wild (DeMaster and Stirling 1981) and are more individualistic than innate in their behaviors. Capture probabilities for individual bears, therefore, could vary greatly. Also, radiotelemetry data show that individual bears may not be uniformly available for capture. Capture effort and success varied among years because of natural factors like weather and sea ice and because of changing directives of funding agencies. Previous mark-recapture (e.g., Jolly–Seber; Pollock, Nichols, Brownie, and Hines 1990) analyses provided estimates of population size that showed no trend, fluctuated wildly among years, and were surrounded by wide confidence intervals (Figure 1).

Here we describe an approach to open population mark-recapture modeling to derive population estimates. We describe how covariates measured over the years helped explain complex capture histories and improve estimates. A key feature of our modeling process was construction of capture probability models to simultaneously account for conventional recapture and radiotelemetry data. Finally, we illustrate a model-selection technique that blended improved model fit with improved prediction variance.
2. METHODS

2.1 FIELD PROCEDURES

We captured polar bears throughout the Beaufort Sea (Figure 2) during the springs of 1971–1979, 1982–1992 (except for 1990), and 1998. Autumn captures occurred in 1981–1986, 1988, 1989, 1994, 1997, and 1998. We also utilized capture data from archives of the U.S. Fish and Wildlife Service for the period 1967–1980 (Lentfer, Hensel, Gilbert, and Sorensen 1980). In the SBS, polar bears achieve their peak weights by autumn, and minimum weights occur in early spring (Durner and Amstrup 1996). Winter is the most difficult time for polar bears, and we believe that mortality among polar bears during summer is minimal. Spring and autumn capture events, therefore, were pooled into annual capture occasions.

We captured and recaptured polar bears by drug immobilization (Stirling, Spencer, and Andriashek 1989). Independent animal care and welfare committees approved capture and marking protocols. Captured polar bears were tattooed and ear tagged. A vestigial premolar tooth was removed for age determination (Calvert and Ramsay 1998). After 1980, we collared a limited number of adult females with radio transmitters. Because male polar bears have necks that are larger in diameter than their heads, they would not wear collars and were not instrumented. Activity and temperature data transmitted from collars and our aerial radio tracking confirmed the bears were alive. Each telemetry position fix, therefore, constituted a remote recapture.
2.2 Model Building

After 1981, the principal focus of our research was radiotelemetry movement studies. Because of the need to deploy all collars, we often chose not to capture an animal that was clearly a male. This sampling bias minimized representation of males in our capture samples. Therefore, we limited modeling to females.

Our treatment of capture history follows that described in Lebreton, Burnham, Colbert, and Anderson (1992), although our model notation is more explicit. At each of $k$ capture occasions, a zero was recorded if an individual was not captured, a one was recorded if an individual was captured and successfully released, and a two was recorded if an individual died upon capture or was harvested. A string of zeros, ones, and two constituted the capture history for each bear.

We let $\phi_j$ represent the probability of surviving from capture occasion $j$ to capture occasion $j + 1$ ($j = 1, \ldots, k - 1$). We let $p_j$ represent the probability of capture at capture occasion $j$ ($j = 1, \ldots, k$). The probability of any capture history occurring is conditional upon successful first marking and release and depends only on $\phi_j$ and $p_j$. For example, if there were six occasions ($k = 6$), the probability of obtaining the capture history 011001 would be

$$P(011001) = \phi_2 p_3 \phi_3 (1 - p_4) \phi_4 (1 - p_5) \phi_5 p_6.$$ 

The probability that an animal is not seen after time $j$ is a function of the survival and capture probabilities for time periods after time $j$ ($\phi_a$ and $p_a$ for $a > j$). This probability, denoted $\chi_j$ (Lebreton et al. 1992), is computed recursively by first setting $\chi_k = 1$ and then, for $j = k - 1, \ldots, 1$, setting

$$\chi_j = 1 - \phi_j (1 - (1 - p_{j+1}) \chi_{j+1}).$$

We let $P(h_i)$ represent the probability of observing capture history $h_i$, the capture history of the $i$th animal, and we let

$$L(\phi, p) = \prod_i P(h_i)$$

be the likelihood of the entire data set, assuming independence of individuals. Because the log likelihood,

$$\ln(L(\phi, p)) = \sum_i \ln(P(h_i)),$$

is monotonic and increasing, parameter values that maximize $\ln(L(\phi, p))$ also maximize $L(\phi, p)$ and the maximum likelihood estimates of $\phi_j$ and $p_j$ produce the largest possible $\ln(L(\phi, p))$. We made no assumptions regarding survival and capture rates because we modeled them as functions of covariates (Lebreton et al. 1992).

We employed covariates (1) that changed through time but were constant among animals, (2) that changed among animals and were constant through time, and (3) that changed through time and among animals. We related covariates to $\phi_j$ and $p_j$ by introducing...
an additional subscript for the individual and then setting
\[
\ln(\phi_{ij} / (1 - \phi_{ij})) = \beta_1 x_{ij1} + \beta_2 x_{ij2} + \cdots + \beta_s x_{ij_s}
\]
and
\[
\ln(p_{ij} / (1 - p_{ij})) = \gamma_1 z_{ij1} + \gamma_2 z_{ij2} + \cdots + \gamma_p z_{ijp}.
\]
Here \(\phi_{ij}\) represents survival of the \(i\)th animal from capture occasion \(j\) to occasion \(j + 1\), \(p_{ij}\) represents probability of capture for the \(i\)th animal during the \(j\)th capture occasion, \(x_{ija}\) is the value of the \(a\)th survival covariate at the \(j\)th trap occasion for the \(i\)th animal \((a = 1, 2, \ldots, s)\), and \(z_{ijb}\) is the value of the \(b\)th capture probability covariate at the \(j\)th trap occasion for the \(i\)th animal \((b = 1, 2, \ldots, p)\). We set \(x_{ij1}\) and \(z_{ij1}\) to one, producing an intercept term in the model.

Logistic equations relate \(\phi_{ij}\) and \(p_{ij}\) to a linear function of study covariates through the coefficients \(\beta_i\) and \(\gamma_i\). Therefore, we change the notation of the log likelihood, \(\ln(L(\phi, p))\), to \(\ln(L(\beta, \gamma))\). Once the coefficients \(\hat{\beta}_i\) and \(\hat{\gamma}_i\) are estimated, we compute estimates of the population parameters as
\[
\hat{\phi}_{ij} = \left(1 + \exp\left(-\left(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + \cdots + \hat{\beta}_s x_{ij_s}\right)\right)\right)^{-1}
\]
and
\[
\hat{p}_{ij} = \left(1 + \exp\left(-\left(\hat{\gamma}_1 z_{ij1} + \hat{\gamma}_2 z_{ij2} + \cdots + \hat{\gamma}_p z_{ijp}\right)\right)\right)^{-1}.
\]
We used the published Fortran optimization function DFPMIN (Press, Flannery, Teukolsky, and Vetterling 1988) to carry out our likelihood maximization of \(\hat{\beta}_i\) and \(\hat{\gamma}_i\). We linked DFPMIN to the statistical package S-PLUS (version 3.3, MathSoft, Inc.) so that DFPMIN could be executed from within S-PLUS. Our S-PLUS and Fortran routines are available from the Western EcoSystems Technology, Inc., web page, http://www.west-inc.com/.

Computations were performed on personal computers running Windows (Microsoft, Inc.).

We estimated \(\hat{N}_j\) by inverting and summing the estimated capture probabilities, \(\hat{p}_{ij}\), for each animal actually captured at occasion \(j\), i.e.,
\[
\hat{N}_j = \sum_{i=1}^{n_j} \frac{I_{ij}}{\hat{p}_{ij}},
\]
where \(n_j\) is the number of observed capture histories and \(I_{ij}\) is one if animal \(i\) was captured or killed at occasion \(j\) and zero otherwise (McDonald and Amstrup 2000).

McDonald and Amstrup (2000) show that the variance of \(\hat{N}_j\) can be estimated by
\[
\hat{V}
(\hat{N}_j) = \sum_{i=1}^{n_j} \left[ \frac{I_{ij}(1 - \hat{p}_{ij})}{\hat{p}_{ij}^2} + \frac{I_{ij}^2 \hat{\sigma}_{p_{ij}}^2}{\hat{p}_{ij}^3} + \frac{I_{ij}(1 - \hat{p}_{ij}) \hat{\sigma}_{p_{ij}}^2}{\hat{p}_{ij}^4} \right].
\]

### 2.3 Covariate Evaluation

Our models for survival and capture probability differed only in their covariates. We developed a list of covariates and combinations of covariates that we hypothesized might
help explain variation in capture histories and thereby contain predictive strength. Significance of each covariate was gauged by a Wald \( t \)-test (dividing the estimates of regression coefficients by their estimated standard errors; Manly 1994). If \( "t" \)-values of coefficients were >2 in absolute value, we afforded those covariates further evaluation.

2.4 Model Selection

Predictive strength of models in their entirety was gauged by the maximized log likelihood. We compared models with three likelihood criteria: (1) drop in deviance (McCullagh and Nelder 1989), (2) Akaike information criteria (AIC) (Akaike 1973), and (3) QAIC, the quasi-likelihood adjustment to AIC (Burnham and Anderson 1998). AIC was defined as \(-2 \ln(L(\beta, \gamma)) + 2(s + p)\), where \( s \) and \( p \) were the number of coefficients in the survival and capture models, respectively; QAIC attempts to overcome shortcomings of the AIC when data are overdispersed. QAIC was defined as \(-2[\ln L(\beta, \gamma)/\hat{c}] + 2(s + p)\), where \( \hat{c} \) was an estimate of the overdispersion in the capture histories (Anderson, Burnham, and White 1994). Overdispersion results when capture histories display more variation than that anticipated by a multinomial statistical model (Anderson et al., 1994). The value of \( \hat{c} \) (1.48) was based on TEST2 and TEST3 of Burnham, Anderson, White, Brownie, and Pollock (1987).

To test the explanatory value of all logical covariates for which we had data, models were ordered according to their maximized log likelihood. We then examined point and interval estimates of population size produced by each model. Patterns in those estimates were evaluated to determine if they were realistic (Burnham and Anderson 1998, p. 25) in relationship to known features of polar bear population dynamics and to empirical observations. We chose our best approximating model (Burnham and Anderson 1998) based on an observed inverse relationship between the maximized log likelihood of our models and coefficients of variation (CVs) associated with \( \hat{N}_j \).

3. RESULTS

We analyzed 1,716 captures of 1,025 female polar bears obtained between 1967 and 1998. Individuals were captured between 1 and 10 times. Of the 1,025 bears, 228 wore radio collars during portions of their capture histories. Telemetry relocations accounted for 433 of the 1,137 captures (38\%) recorded after 1981, when telemetry began. Modeling confirmed that it was rare for an instrumented bear to avoid recapture at some point during the year. All high-ranking models estimated the probability of capture for radiocollared bears to be essentially one.

3.1 Covariate Evaluation

All of our models consisted of an equation for capture probability and one for survival probability. The log likelihood was maximized jointly for \( \beta \) and \( \gamma \). Most covariates that we evaluated fit logically into survival or capture equations of each model but not both. For
example, capture effort (helicopter flight hours) and geographic region of capture (latitude and longitude) seemed unlikely to help in predicting survival probabilities. Both, however, were logical covariates to help explain capture probability.

The presence of a radio, the geographic distribution of capture effort, the year of the study, the size of the group in which the animal was observed, and age were the most consistently important covariates, as gauged by model fit and significance of regression coefficients. Other covariates we considered, despite our hypothesis that they carried important information, were eliminated during model building.

3.2 Model Selection

We created 82 models and ranked them based on their apparent fit as reflected in our likelihood criteria. Values for AIC (QAIC) [deviance] ranged from 2,606 (1,766) [2,582] to 3,031 (2,050) [3,013], depending on which combinations of covariates were included in the models. The transition from poorest to best fit was not linear, however, and many models had similar criteria values. Families or clusters of final models distinguished by small differences in our criteria were separated by larger jumps (Table 1).

An unexpected discovery was that model rankings varied little among model-fitting criteria. AIC and QAIC, which adjust for loss of degrees of freedom (and theoretically strike a balance between fit and parsimony), and simple drop in deviance, which does not, all provided similar model rankings. Figure 3 illustrates how closely QAIC and deviance track each other. Because there were few differences among these procedures, we hereafter simplify presentation by providing QAIC results only unless otherwise specified.

Two models had QAIC values that were much lower than those for all other models. However, models with the lowest values for QAIC provided relatively large variances on estimates of population size as well as large fluctuations in \( \hat{N}_j \). In other words, there was an inverse relationship between likelihood fit and biological usefulness. To make our final model selection, we standardized the QAIC values and the mean CV on \( \hat{N}_j \) for all models tested and plotted them on the same graph (Figure 3). Our best approximating model was near the intersection of the QAIC and CV curves (Fretwell 1972; Burnham and Anderson 1998, fig. 1.2).

This best approximating model was ranked 15th by QAIC. In our best model, the study area and effort were divided into western and eastern components and we included main and two-way interaction effects of those geographic covariates. Hence, the relationship between where bears were known to live and the locations of capture effort (both of which are potential contributors to capture heterogeneity) were included (Table 1).

Despite the compromise between a good likelihood fit and narrow confidence intervals on \( \hat{N}_j \), our best model still suggested considerable variation in \( \hat{N}_j \) among years (Figure 4a). One source of that variation was obvious. In 1990, 1993, 1995, and 1996, we did not perform routine mark-recapture work. In those years, a few bears were captured when they became a safety hazard near developed areas. Also in those years, some bears wearing radiocollars were relocated. Nonetheless, the sums of the reciprocals of the \( p_j \)'s for animals actually captured in those years, and hence \( \hat{N}_j \), were very low.
Table 1. Calculated Model Equations, Likelihood Fit Statistics (Deviance [DEV], AIC, QAIC), and Mean Coefficients of Variation (CV) on $\hat{N}_j$. $\phi_j$ represents the probability of surviving between capture occasions, and $p_j$ represents the probability of capture at each occasion. The top 15 ranking mark–recapture models for polar bears in the Beaufort Sea are presented. Model 15 was the best compromise between increasing CV($\hat{N}_j$) and decreasing maximized likelihood (see Figure 2).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Dev</th>
<th>QAIC</th>
<th>Capture equations&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Survival equations&lt;sup&gt;b&lt;/sup&gt;</th>
<th>d.f.</th>
<th>DEV</th>
<th>AIC</th>
<th>QAIC</th>
<th>CV&lt;sup&gt;0&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td></td>
<td>ln($p_j/(1-p_j)) = \gamma_{1z_{j1}} + \gamma_{2z_{j2}} + \cdots + \gamma_{p_{z_{jP}}}$</td>
<td>ln($\phi_j/(1-\phi_j)) = \beta_1 \tau_{j1} + \beta_2 \tau_{j2} + \cdots + \beta_8 \tau_{j8}$</td>
<td>12</td>
<td>2,582.5</td>
<td>2,606.5</td>
<td>1,766.0</td>
<td>0.209</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td></td>
<td>$-2.58 + 6.38(radio) + 0.001(W.Eff)$</td>
<td>$1.14 + 5.80(SigYr) + 0.330(age2)$</td>
<td>12</td>
<td>2,582.9</td>
<td>2,606.9</td>
<td>1,766.3</td>
<td>0.209</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td></td>
<td>$-2.97 + 6.51(radio) - 0.005(Yr)$</td>
<td>$1.14 + 5.77(SigYr) + 0.331(age2)$</td>
<td>12</td>
<td>2,636.5</td>
<td>2,660.5</td>
<td>1,802.4</td>
<td>0.217</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td></td>
<td>$-2.91 + 6.53(radio) + 0.005(Effect)$</td>
<td>$1.26 + 2.40(SigYr) - 0.153(age2)$</td>
<td>10</td>
<td>2,644.2</td>
<td>2,664.2</td>
<td>1,803.7</td>
<td>0.218</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td></td>
<td>$-2.91 + 6.56(radio) + 0.005(Effect)$</td>
<td>$1.17 + 3.40(SigYr) - 0.018(age2)$</td>
<td>9</td>
<td>2,654.6</td>
<td>2,663.6</td>
<td>1,802.6</td>
<td>0.219</td>
</tr>
<tr>
<td>6</td>
<td>11</td>
<td></td>
<td>$-3.28 + 6.42(radio) + 0.005(Effect)$</td>
<td>$0.781 + 3.67(SigYr) + 0.399(age2)$</td>
<td>10</td>
<td>2,653.5</td>
<td>2,673.5</td>
<td>1,809.9</td>
<td>0.189</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
<td></td>
<td>$-3.45 + 6.40(radio) + 0.004(W.Eff)$</td>
<td>$0.811 + 3.78(SigYr) + 0.354(age2)$</td>
<td>9</td>
<td>2,654.5</td>
<td>2,672.5</td>
<td>1,808.6</td>
<td>0.181</td>
</tr>
<tr>
<td>8</td>
<td>6</td>
<td></td>
<td>$-3.16 + 6.39(radio) + 0.005(Effect)$</td>
<td>$0.824 + 3.68(SigYr) + 0.350(age2)$</td>
<td>8</td>
<td>2,665.2</td>
<td>2,671.2</td>
<td>1,807.1</td>
<td>0.181</td>
</tr>
<tr>
<td>9</td>
<td>9</td>
<td></td>
<td>$-3.38 + 6.39(radio) + 0.004(W.Eff)$</td>
<td>$0.809 + 3.79(SigYr) + 0.354(age2)$</td>
<td>9</td>
<td>2,655.6</td>
<td>2,673.6</td>
<td>1,809.3</td>
<td>0.182</td>
</tr>
<tr>
<td>10</td>
<td>8</td>
<td></td>
<td>$-3.67 + 6.40(radio) + 0.005(Effect)$</td>
<td>$0.766 + 3.98(SigYr) + 0.358(age2)$</td>
<td>8</td>
<td>2,675.4</td>
<td>2,673.4</td>
<td>1,808.6</td>
<td>0.181</td>
</tr>
<tr>
<td>11</td>
<td>12</td>
<td></td>
<td>$-4.34 + 6.54(radio) + 0.005(Effect)$</td>
<td>$-0.664 + 3.61(SigYr) + 2.06(age2)$</td>
<td>11</td>
<td>2,658.2</td>
<td>2,680.2</td>
<td>1,815.1</td>
<td>0.181</td>
</tr>
<tr>
<td>Rank</td>
<td>Dev/QAIC</td>
<td>Capture Equations (^a)</td>
<td>Survival Equations (^a)</td>
<td>d.f.</td>
<td>DEV</td>
<td>AIC</td>
<td>QAIC</td>
<td>Mean CV (^b)</td>
<td></td>
</tr>
<tr>
<td>------</td>
<td>----------</td>
<td>-----------------------------</td>
<td>-----------------------------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>--------------</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>10</td>
<td>(\ln(p_{ij}/(1-p_{ij})) = \gamma_{1z_{ij1}} + \gamma_{2z_{ij2}} + \cdots + \gamma_{pz_{ijp}})</td>
<td>(\ln(\phi_{ij}/(1-\phi_{ij})) = \beta_1x_{ij1} + \beta_2x_{ij2} + \cdots + \beta_xx_{ijx})</td>
<td>8</td>
<td>2659.2</td>
<td>2675.2</td>
<td>1809.8</td>
<td>0.182</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>13</td>
<td>((-3.61) + 6.40(\text{radio}) + 0.005(\text{effort.2}) - 0.051(\text{Yr}) + 1.14(\text{grp2.2}))</td>
<td>((0.793) + 5.41(\text{SigYr}) + 0.472(\text{age2}))</td>
<td>12</td>
<td>2692.2</td>
<td>2716.2</td>
<td>1840.0</td>
<td>0.179</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>14</td>
<td>((-1.44) + 6.45(\text{radio}) + 0.002(\text{W.Eff.2}) + 0.005(\text{E.Eff.2}) - 0.091(\text{Yr}) - 0.186(\text{Gsz}) - 1.36(\text{Reg}) + 0.004(\text{Reg} \times \text{W.Eff.2}) - 0.003(\text{Reg} \times \text{E.Eff.2}))</td>
<td>((0.791) + 5.39(\text{SigYr}) + 0.471(\text{age2}))</td>
<td>12</td>
<td>2692.4</td>
<td>2716.4</td>
<td>1840.2</td>
<td>0.179</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>15</td>
<td>((-1.76) + 6.504(\text{radio}) + 0.002(\text{W.Eff.2}) + 0.005(\text{E.Eff.2}) - 0.004(\text{Yr}) - 1.378(\text{Reg}) + 0.004(\text{Reg} \times \text{W.Eff.2}) - 0.003(\text{Reg} \times \text{E.Eff.2}))</td>
<td>((0.683) + 5.10(\text{SigYr}) + 0.614(\text{age2}))</td>
<td>11</td>
<td>2696.7</td>
<td>2718.7</td>
<td>1841.0</td>
<td>0.176</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Values shown are regression coefficients and (covariate names). Recall that the intercept term in each equation is derived setting \(x_{ij1}\) and \(z_{ij1}\) to 1.

\(^b\)All years included in calculation of mean CV.
The cause of the peaks in $\hat{N}_j$ in 1980, 1984, 1989, and 1994 was less obvious. These peaks varied in absolute size among models but were most pronounced in models that incorporated geographic covariates and were weak or absent in models not including geographic covariates. The relationship of $\hat{N}_j$ peaks to geographic covariates was both a quandary and our first clue to their cause.

A new analysis of radiotelemetry data identified two relatively distinct groups or subpopulations of polar bears adjacent to northern Alaska. Kernel smoothing of polar bear radiolocations allowed us to plot the bounds of each group (Figure 2) and to calculate relative probabilities of encountering bears from each group at any location (S. C. Amstrup, unpublished data). The peaks in $\hat{N}_j$ corresponded with years in which we expended more hunting effort near Barrow or Wainwright (Figure 4b). We now understand that the probability of catching eastern Chukchi Sea bears near those communities ranged from 80 to 90% (S. C. Amstrup, unpublished data). Conversely, the probability of catching Chukchi Sea bears drops off rapidly as effort moves east of Barrow. Hence, the population spikes were explained largely by discovery that we were sampling two groups of polar bears rather than one evenly mixed group, as we had hypothesized.

After partitioning Chukchi Sea and SBS bears, our best approximating model suggested the female population could have been as high as 1,500 during the latter 1990s. This would suggest a total population size in the SBS of $>2,500$. With the years of no mark–recapture
(1990, 1993, 1995–1996) removed, CVs on $\hat{N}_j$ ranged from 0.12 to 0.48 and averaged 0.16 during the last decade of study.

4. DISCUSSION

4.1 COVARIATE EVALUATION

We assumed at the start of this study that the polar bears of the SBS were members of one population extending from approximately Wainwright to Tuktoyaktuk (Treseder and Carpenter 1989; Amstrup, Durner, Stirling, Lunn, and Messier 2000). Geographic covariates and new analyses of movements data were key to understanding fluctuations in $\hat{N}_j$. Recognizing the geographic component of capture heterogeneity allowed us to separate the contribution of capture probabilities in the SBS from those in the adjacent eastern Chukchi Sea stock of bears. These estimates met our likelihood and biological criteria. Confidence intervals on $\hat{N}_j$ were the tightest yet recorded for this population.

Our modeling approach has major ramifications for studies dealing with fixed budgets and multiple objectives. In addition to seeking $\hat{N}_j$, we have been compelled to try to understand movement and distribution patterns of polar bears and to determine where they make their maternal dens. Those objectives required major expenditures for telemetry. More radios applied meant fewer animals marked and less capture effort. Capture–recapture and radiotelemetry efforts coexist in most current large-mammal studies. The ability of our modeling approach to seamlessly meld data from both shows promise to aid in interpretation and to improve population estimates for large animals worldwide.

4.2 MODEL SELECTION

A best approximating model should reflect reality (Burnham and Anderson 1998, p. 25). Fortunately, we had gauges by which to assess the realism of our models. First, we knew that polar bears compensate for a low reproductive rate with the potential for long life (Taylor et al. 1987). Hence, models that predict rapid increases or decreases in population size would not mirror reality. Also, although the magnitude has not been known, empirical evidence suggests a population increase during the term of our studies (Amstrup et al. 1986; Stirling and Andriashek 1992; Amstrup 2000). Our models that incorporated geographic components minimized interannual fluctuations in $\hat{N}_j$ and realistically predicted population increase.

Interval estimates of a best model should instill confidence in its predictions. Our choice of best model based on the inverse relationship between confidence intervals on $\hat{N}_j$ and likelihood fit (Fretwell 1972; Burnham and Anderson 1998, fig. 1.2) incorporated likelihood and real-world criteria and yielded the narrowest interval estimates yet derived for this population. Our CV (0.16) compared favorably with the mean CV on female $\hat{N}_j$ in Hudson Bay (0.145; calculated from Lunn, Stirling, Andriashek, and Kolenoisky 1997), where a much higher and more consistent portion of the population was marked. A similar
approach to final model selection is recommended for other projects where a best model is not obvious from likelihood criteria alone.

CAVEATS

Our best model suggested an increase from around 500 females early in the study to as many as 1,500 at study end. Assuming the increase in numbers of males was comparable with that recorded for females, this could suggest a total population size of over 2,500 animals—many more than previously hypothesized.

Despite the significant improvements in estimates provided by our model, we recommend a conservative approach to management of polar bears in the SBS. A λ of 1.035 is near the maximum that seems possible for a hunted polar bear population (Taylor et al. 1987) and should be viewed cautiously. Likewise, simulation studies (McDonald and Amstrup 2000) suggested there might be a small positive bias in $\hat{N}_j$ when the data set contains significant heterogeneity. This heterogeneity bias could inflate $\hat{N}_j$. Finally, lower 95% confidence bounds on $\hat{N}_j$ were $<1,000$ females, which would translate into $<2,000$ bears. Cautious harvest management, therefore, still is advised and collection of a more intensive SBS mark–recapture data set is recommended.

ACKNOWLEDGMENTS

Principal funding for this project was provided by the Alaska Science Center, Biological Resources Division, U.S. Geological Survey. We are especially thankful for the help of George Durner, Dennis Andriashek, and many others who helped collect data used in this exercise. We thank referees and editors for their many helpful comments.

[Received August 2000. Accepted September 2000.]

REFERENCES


