Research Article

Effects of Earlier Sea Ice Breakup on Survival and Population Size of Polar Bears in Western Hudson Bay

ERIC V. REGEHR,[1] *United States Geological Survey, Alaska Science Center, 1011 E. Tudor Road, Anchorage, AK 99503, USA*

NICHOLAS J. LUNN, *Wildlife Research Division, Science and Technology Branch, Environment Canada, 5320 122 Street NW, Edmonton, AB T6H 3S5, Canada*

STEVEN C. AMSTRUP, *United States Geological Survey, Alaska Science Center, 1011 E. Tudor Road, Anchorage, AK 99503, USA*

IAN STIRLING, *Canadian Wildlife Service, 5320 122 Street NW, Edmonton, AB T6H 3S5, Canada*

ABSTRACT Some of the most pronounced ecological responses to climatic warming are expected to occur in polar marine regions, where temperature increases have been the greatest and sea ice provides a sensitive mechanism by which climatic conditions affect sympagic (i.e., with ice) species. Population-level effects of climatic change, however, remain difficult to quantify. We used a flexible extension of Cormack–Jolly–Seber capture–recapture models to estimate population size and survival for polar bears (*Ursus maritimus*), one of the most ice-dependent of Arctic marine mammals. We analyzed data for polar bears captured from 1984 to 2004 along the western coast of Hudson Bay and in the community of Churchill, Manitoba, Canada. The Western Hudson Bay polar bear population declined from 1,194 (95% CI = 1,020–1,368) in 1987 to 935 (95% CI = 794–1,076) in 2004. Total apparent survival of prime-adult polar bears (5–19 yr) was stable for females (0.93; 95% CI = 0.91–0.94) and males (0.90; 95% CI = 0.88–0.91). Survival of juvenile, subadult, and senescent-adult polar bears was correlated with spring sea ice breakup date, which was variable among years and occurred approximately 3 weeks earlier in 2004 than in 1984. We propose that this correlation provides evidence for a causal association between earlier sea ice breakup (due to climatic warming) and decreased polar bear survival. It may also explain why Churchill, like other communities along the western coast of Hudson Bay, has experienced an increase in human–polar bear interactions in recent years. Earlier sea ice breakup may have resulted in a larger number of nutritionally stressed polar bears, which are encroaching on human habitations in search of supplemental food. Because western Hudson Bay is near the southern limit of the species' range, our findings may foreshadow the demographic responses and management challenges that more northerly polar bear populations will experience if climatic warming in the Arctic continues as projected. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2673–2683; 2007)

DOI: 10.2193/2006-180

KEY WORDS capture–recapture, climate change, Cormack–Jolly–Seber, Hudson Bay, polar bear, population size, sea ice, survival, *Ursus maritimus*.

Recent changes in climatic conditions have been associated with changes in physiology, phenology, and distribution for a wide range of species (Stenseth et al. 2002, Walther et al. 2002, Parmesan and Yohe 2003). The effects of climatic change on population size and trend, however, have been difficult to quantify because the robust estimation of demographic parameters requires longitudinal individual-based data (Williams et al. 2002, Amstrup et al. 2005*a*), which are often expensive and difficult to collect. We used long-term data for polar bears (*Ursus maritimus*) collected under 2 sampling protocols to simultaneously evaluate survival in relation to climatic conditions and derive estimates of population size.

Polar bears depend upon sea ice for survival; it is their only predictable substrate for foraging and is also critical to movement and some aspects of reproduction (Amstrup 2003). Polar bears are most common on annual sea ice that occurs over shallow coastal or interisland waters, where biological productivity is high (Amstrup and DeMaster 1988, Stirling and Lunn 1997, Durner et al. 2004). In many parts of the Arctic, warming temperatures and altered atmospheric circulation have resulted in significant changes to the extent, duration, and character of annual sea ice (Vinnikov et al. 1999, Lindsay and Zhang 2005, Stroeve et al. 2005). These changes have raised concerns regarding the long-term conservation of polar bears (Stirling 2002, Derocher et al. 2004, Aars et al. 2006, Regehr et al. 2006).

The Western Hudson Bay (WH) polar bear population occurs near the southern limit of the species' range and is relatively discrete from adjacent populations (Derocher and Stirling 1990, Stirling et al. 2004). In winter and spring, the WH population disperses over the ice-covered bay to hunt seals (*Phoca hispida*, *Erignathus barbatus*, and *P. vitulina*; Iverson et al. 2006). In summer and autumn when Hudson Bay is ice-free, the WH population is confined to a restricted area of the western coast, where polar bears are cut off from their seal prey and must rely on fat reserves for approximately 4 months until freeze-up. Pregnant females are food-deprived for 8 months because they must remain on land in maternal dens, give birth, and nurse until their cubs are large enough to venture onto the sea ice in the early spring (Ramsay and Stirling 1986). In the past 50 years, spring air temperatures in western Hudson Bay have increased by 2–3° C (Skinner et al. 1998, Gagnon and Gough 2005). Consequently, the sea ice now breaks up approximately 3 weeks earlier than it did 30 years ago (Stirling and Parkinson 2006). This forces the WH population off the sea ice earlier, shortening the spring foraging period when seals are most available and reducing polar bears' ability to accumulate the fat reserves needed to survive while stranded onshore.

Previous studies have shown a correlation between rising temperatures, earlier sea ice breakup, and declining recruitment and body condition for polar bears in western Hudson

[1] *E-mail: eregehr@usgs.gov*

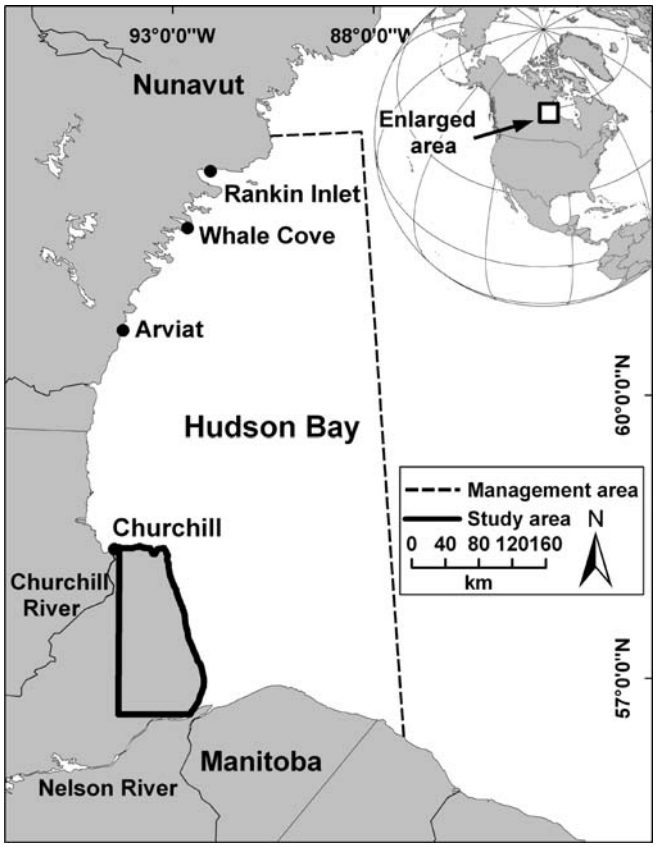

Figure 1. Western Hudson Bay, Canada, showing the management area for the Western Hudson Bay polar bear population and the study area where the Canadian Wildlife Service captured polar bears during the ice-free season, 1984–2004.

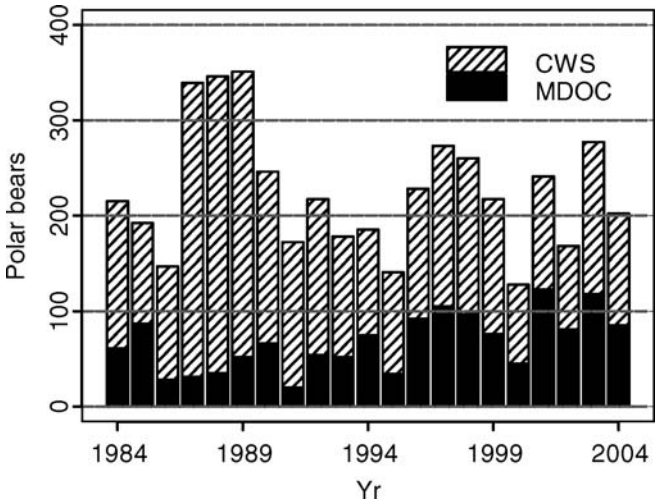

Figure 2. Number of individual polar bears captured in western Hudson Bay, Canada, by the Canadian Wildlife Service (CWS) and the Manitoba Department of Conservation (MDOC), 1984–2004. Bar heights are stacked. For example, in 1994 185 individual polar bears were captured: 110 by the CWS, 75 by the MDOC.

Bay (Derocher and Stirling 1996, Stirling et al. 1999, Stirling and Parkinson 2006). Based on forecasts of continued warming and progressively earlier breakup (Zhang and Walsh 2006), Stirling and Parkinson (2006) predicted that conditions will become increasingly difficult for the WH population. Conversely, in recent years an increasing number of polar bears have been sighted around Churchill, Manitoba, Canada, and around Inuit communities along the Nunavut coast of western Hudson Bay. Some have interpreted the increased sightings as evidence that the WH population is growing, leading to the implementation in 2005 of a 19% increase in the annual harvest quota (Stirling and Parkinson 2006).

We hypothesized that sea ice breakup influences polar bear survival because of its direct effect on the time available for foraging, and that survival rates would reflect both interannual variation in breakup date and the long-term trend toward earlier breakup. We further hypothesized that declines in survival contributed to a decline in population size; increased sightings of polar bears do not reflect a larger population but rather are the result of nutritionally stressed polar bears encroaching upon human settlements in search of food.

STUDY AREA

Historically, Hudson Bay has been covered with annual ice for approximately 8 months of the year and has been ice-free for 4 months (Jul–Nov; Gough et al. 2004). The Canadian Wildlife Service (CWS) captured free-ranging polar bears during the ice-free period, mainly in a 12,000-km^2 study area between the community of Churchill and the Nelson River (Fig. 1). The coastline of the study area was characterized by raised beaches surrounded by mud flats, sedge and grass meadows, and willow (*Salix* spp.); the interior was characterized by wet tundra with stands of scrub spruce (*Picea* spp.) along lake edges, riparian corridors, and areas of discontinuous permafrost (Dredge and Nixon 1992).

During spring breakup, counterclockwise marine currents in Hudson Bay carry the last large ice floes along the Manitoba and Ontario coastline (Saucier et al. 2004), resulting in a high degree of fidelity of the WH population to the CWS study area (Derocher and Stirling 1990, Lunn et al. 2004, Stirling et al. 2004). Although the management boundary for the WH population extended approximately 500 km to the north of Churchill, polar bears were seldom seen along that section of the coast until freeze-up begins in late autumn (Derocher and Stirling 1990; N. J. Lunn and I. Stirling, CWS, unpublished data). While on land, polar bears were greatly concentrated relative to their winter distribution on the sea ice and were easily sighted against a snow-free background (Lunn et al. 2002). Adult males predominated on coastal beaches, whereas single females, females with dependent young, and subadults generally used inland areas (Derocher and Stirling 1990, Lunn et al. 2004, Stirling et al. 2004).

METHODS

From 1984 to 2004, we (the CWS) used helicopters to capture polar bears each year between late August and early October (Stirling et al. 1989). Although sample size varied with project funding (Fig. 2), we attempted to evenly distribute capture effort over the entire study area in every

year after 1986. We captured all observed polar bears regardless of sex, age, or reproductive status, with the exception of some pregnant females that took refuge in dens, which they had excavated in anticipation of maternal denning, and a few individuals that entered water or otherwise could not safely be sedated. We ear-tagged all captured polar bears with a unique identification number and applied permanent tattoos to both sides of the inner surface of the upper lip. We extracted a vestigial premolar from polar bears >1 year old for age determination (Calvert and Ramsay 1998). Cubs-of-the-year (COYs; approx. 8 months old in autumn) were always with their mothers and we could visually age them without error (Ramsay and Stirling 1988). In our analyses, we excluded data for polar bears that we located by radiotelemetry and data for a few previously marked polar bears that we could not individually identify.

The Manitoba Department of Conservation (MDOC) captured problem bears in and around Churchill as part of the community's Polar Bear Alert Program (Lunn et al. 2002). Beginning in 1984, this program followed explicit rules regarding when to haze, capture, or kill polar bears that were considered a threat to human life or property. Therefore, all polar bears that entered the Churchill vicinity were treated similarly. The MDOC immobilized polar bears from the ground and either detained them in a holding facility or transported them out of town. Marking and aging procedures were similar to those used by the CWS. The Animal Care Committee of the CWS (Prairie and Northern Region) and the University of Alberta BioSciences Animal Policy and Welfare Committee approved the immobilization and handling protocol for free-ranging polar bears. The MDOC and Parks Canada issued annual permits under which we conducted our research.

We estimated the date of spring sea ice breakup in the WH management area using the methods of Stirling and Parkinson (2006) and derived the covariate *ice* for use in capture–recapture models by standardizing the Julian date of breakup (Franklin 2001). We used *ice* rather than a large-scale climatic index, such as the Arctic Oscillation, because *ice* directly quantified our hypothesized link between environmental conditions and polar bear survival (Hallett et al. 2004). We used standard regression techniques to describe trends in the sex and age composition of the CWS and MDOC capture samples (e.g., Zar 1996, Hosmer and Lemeshow 2000). Supplemental materials for the analyses in this paper are provided in Regehr et al. (2007).

Goodness-of-Fit

We used program RELEASE (Burnham et al. 1987) to investigate patterns in both the CWS-only and the combined CWS and MDOC data, and to quantify how well the standard Cormack–Jolly–Seber (CJS) model fit various subsets of the data (Regehr et al. 2007). This allowed us to identify homogenous strata (i.e., groups of polar bears with similar survival and recapture probabilities) and to establish a general model that allowed for all detectable sex- and age-based variation. We estimated the variance inflation factor ($\hat{c}$) by applying program RELEASE to each independent stratum in the global model and dividing the summed chi-square statistics by the total degrees of freedom (e.g., Sendor and Simon 2003).

Valid estimation of population size and trend requires a consistent, well-defined study population (Hines and Nichols 2002). If the area exposed to capture effort changes with time, demographic parameters will reflect individuals added to and lost from the study population as the effective boundaries change. We captured free-ranging polar bears in a geographically restricted portion of the study area from 1984 to 1986. From 1987 to 2004, we attempted to search the entire study area each year. We quantified the spatiotemporal distribution of capture effort by overlaying the study area with 25-km^2 grid cells and calculating *t*-like statistics to determine whether the relative distribution of capture locations changed for sequential 3-year periods (Amstrup et al. 2004, 2005*b*).

Capture–Recapture Analysis

The CJS model conditions on first capture and estimates the probabilities of survival (ϕ) and recapture (p) that are most likely to explain the observed capture history data for an open population (Lebreton et al. 1992). We fit CJS models using program MARK (Cooch and White 2005) and R-language software for the general regression approach to capture–recapture (McDonald et al. 2005). The 2 approaches fit identical likelihoods and result in identical parameter estimates, but the latter approach makes it easier to construct complex models with time-dependent individual covariates.

Model selection.—We based model selection on Akaike's Information Criterion (AIC; Akaike 1981), biological realism, and model interpretability. We corrected AIC for small sample size (AIC$_c$) and used $\hat{c} = 1.0$ from the goodness-of-fit analysis (Anderson and Burnham 2002). When appropriate, we based inference regarding important hypotheses on the strength of evidence across multiple models. For pairwise comparisons, we quantified relative support using ΔAIC$_c$, where ΔAIC$_c$ <2 indicated similar support for both models and ΔAIC$_c$ >10 indicated strong support for the lower-AIC$_c$ model (Burnham and Anderson 2002). For each fitted model, we also considered the magnitude and variance of the estimated parameters. This was necessary because AIC attempts to optimize the overall tradeoff between model fit and precision; it does not indicate how many of a model's parameters are estimable, nor does it indicate which of a model's parameters explain appreciable variation in the data (Stephens et al. 2005).

Model fitting.—We estimated survival and population size from the most supported model for the combined CWS and MDOC data, which we developed in several steps. We began by modeling the CWS-only data because they represented a random sample from free-ranging polar bears, whereas the MDOC data were nonrandom in that polar bears effectively sampled themselves by coming into Churchill. This simplified the analysis and allowed us to perform initial investigations of biological hypotheses using

a relatively unbiased data set. Starting with the general model, we evaluated models with restricted parameterizations for p while retaining the general parameterization for ϕ. To reflect interannual variation in sample size, we modeled p as time dependent and as a function of the annual number of helicopter hours flown in capture operations. We fit models with sex- and age-specificity in p to reflect potential differences in sighting probability due to the spatial segregation of polar bears while on land. Throughout the study, the sex ratio in the CWS capture sample remained approximately 1:1 despite observations of field crews that there were fewer large males in the study area since the late 1990s. We hypothesized that as the number of male polar bears declined, a larger proportion of them occupied the limited coastal beaches where they were highly visible. We modeled this change in the relative p of female and male polar bears as an additive sex effect, which differed for the periods 1985–1995 and 1996–2004.

After establishing a parsimonious parameterization for p, we evaluated models with restricted parameterizations for ϕ. We hypothesized a sex effect in survival due to sex-selective harvest (Derocher et al. 1997). Based on the life history of polar bears, we considered 5 age classes: COYs, juveniles (COYs and yearlings combined), subadults (2–4 yr), prime-adults (5–19 yr), and senescent-adults ($\geq$20 yr; Derocher and Stirling 1992, 1996; Amstrup 2003). We first modeled ϕ for prime-adult polar bears while retaining the general parameterization for other age classes, based on the hypothesis that interannual variation in survival was lowest for prime-adults (Bunnell and Tait 1981, Amstrup and Durner 1995, Eberhardt 2002). We then modeled ϕ for the other age classes and evaluated support for combining age classes.

We modeled temporal variation in ϕ using time-constant, time-dependent, and linear trend parameterizations. We investigated the relationship between sea ice and survival by modeling ϕ_j (i.e., survival from the autumn of calendar yr j to the autumn of yr j+1) as a linear function of ice breakup date in the spring of year j (the covariate *ice*). We also modeled ϕ_j using the centered, 3-year running mean of ice breakup date to investigate whether survival was a cumulative function of environmental conditions over several years. Finally, we modeled ϕ_j for COYs using breakup date in the year j–1 to investigate whether COY survival was predominately a function of birth weight, which is related to maternal body condition at the time of den entry the preceding year (Derocher and Stirling 1998). We constructed all CJS models using the logit link function (Cooch and White 2005). After establishing a parsimonious parameterization for ϕ, we revisited the parameterization for p to ensure that it was still valid (Lebreton et al. 1992).

Once we had identified the most supported model for the CWS-only data, we extended the CJS analysis to the combined CWS and MDOC data. Because the CWS often avoided capturing polar bears in the immediate vicinity of Churchill, it is possible that some polar bears were consistently missed by the CWS but were included in the MDOC sample. Also, the nonrandom sex and age composition of the MDOC sample suggested that some strata within the WH population (e.g., subad M) were concentrated around Churchill at the time of sampling. We estimated survival and population size from the combined data to ensure that our analysis represented all possible polar bears. To minimize potential bias associated with differences in sampling protocols, we explicitly allowed CJS model parameters to differ for polar bears that came into Churchill versus polar bears that remained to the south in the CWS study area. For both ϕ and p, we modeled capture-history dependence following capture by the MDOC (e.g., the individual covariate *trap′*) using temporary, permanent, and sex- and age-specific effects (Nichols et al. 1984, Pradel 1993). Age-specific effects in year j were conditional upon age in year j. After identifying a final model that allowed for major sources of variation in the combined data, we revisited the relationship between sea ice and survival and other important hypotheses.

Survival.—The CJS model produces estimates of total apparent survival (ϕ), which is the cumulative probability of remaining alive and available for capture (Lebreton et al. 1992). Because the CJS model right-censors data for animals that were not released following capture, our estimates of ϕ do not reflect the mortality contribution of problem bears that were killed in Churchill. Polar bears from the WH population were harvested as part of an annual, regulated hunt by Inuit from the communities of Arviat, Whale Cove, and Rankin Inlet, located north of Churchill along the Nunavut coast of western Hudson Bay (Fig. 1). We estimated natural apparent survival (ϕ^N) by adjusting the CJS estimates of ϕ using tag-return data from the harvest (Regehr et al. 2007).

Population size.—We estimated population size (N) by applying a Horvitz–Thompson estimator to recapture probabilities using the formula

$$\hat{N}_j = \sum_{i=1}^{n_j} \frac{I_{ij}}{\hat{p}_{ij}},$$

where n_j is the total number of polar bears captured at occasion j, I_{ij} is an indicator variable equal to 1 if the ith polar bear was captured at occasion j and 0 otherwise, and $\hat{p}_{ij}$ is the estimated recapture probability of the ith polar bear at occasion j (McDonald and Amstrup 2001, Williams et al. 2002). This approach is a generalization of the multiple-age Jolly–Seber model (Pollock 1981, Pollock et al. 1990) and has several advantages: 1) it retains the flexibility of the CJS modeling framework, 2) it is straightforward to estimate the size of multiple strata within the population, and 3) it is possible to estimate N from models in which p_{ij} is a function of individual covariates. We estimated the variance of $\hat{N}_j$ using the method of Taylor et al. (2002).

For interpretive purposes, we needed to summarize $\hat{N}_j$ in a way that reduced the variability (and presumably the bias) of the point estimates but preserved biologically meaningful trends. We fit a curve through $\hat{N}_j$ using a variable span

bivariate smoother (S-PLUS 6.2 function supsmu with default parameters; Insightful Corporation 2001) and used a bootstrap procedure to estimate the variance of the smoothed curve (Manly 1997). We resampled the individual capture histories and covariates with replacement to generate 500 new data sets, and fit the most supported model to each. We then reprocessed the resulting $\hat{N}_j$ with the smoother and assumed that the distribution of smoothed values represented the sampling distribution of true population size at each occasion j. We also used $\hat{N}_j$ from the CJS analysis to derive estimates of mean annual population growth rate ($\bar{\lambda}_j$) by fitting a least-squares regression of $\ln(\hat{N}_j)$ versus year, weighted by $1/(\hat{N}_j)$, and exponentiating the slope coefficient (β) from the regression: $\bar{\lambda}_j = e^{\hat{\beta}}$.

RESULTS

The CWS data consisted of 3,306 captures of 1,963 polar bears (Fig. 2), including 19 that were not released. The mean date of capture was 10 September. The MDOC data consisted of 1,417 captures of 963 polar bears, including 95 that were not released (mostly killed as problem bears). The mean date of capture was 31 October. From 1984 to 1990, the number of polar bears captured by the MDOC was variable (annual $\bar{x} = 51$; SD = 22) but did not exhibit a linear trend ($\hat{\beta} = -1.71$ bears/yr, $\widehat{\mathrm{SE}}(\hat{\beta}) = 4.41$, $P = 0.71$). From 1991 to 2004, the number of polar bears captured by the MDOC increased ($\hat{\beta} = 4.7$ bears/yr, $\widehat{\mathrm{SE}}(\hat{\beta}) = 1.66$, $P = 0.02$).

From 1984 to 2003, 792 polar bears were harvested along the Nunavut coast of western Hudson Bay. Most of the harvest occurred toward the end of the ice-free season, as polar bears left the CWS study area and moved northward along the coastline in anticipation of freeze-up (median date of harvest was 5 Nov). The number of polar bears in the harvest that carried research marks deployed by the CWS or MDOC was variable (annual $\bar{x} = 22$; SD = 7) but did not exhibit a linear trend ($\hat{\beta} = 0.14$ bears/yr, $\widehat{\mathrm{SE}}(\hat{\beta}) = 0.29$, $P = 0.64$). The proportions of marked polar bears in the CWS, MDOC, and harvest samples varied with time (5-yr period model vs. time-constant model; $G = 111.6$, df = 3, $P < 0.001$) but were consistently similar for the 3 samples (sample × 5-yr period model vs. 5-yr period model; $G = 14.2$, df = 8, $P = 0.08$). Overall, the marked proportions in the CWS, MDOC, and harvest samples were 0.59 (SE = 0.01), 0.59 (SE = 0.01), and 0.55 (SE = 0.02), respectively. The sex and age composition of the samples is described in Regehr et al. (2007).

The covariate *ice* was based on breakup data for 1984–2003 only (Fig. 3d), because CJS models do not estimate survival following the final sampling occasion. Using linear regression, the mean sea ice breakup date in 2003 (21 Jun) occurred 19.5 days earlier than in 1984 (12 Jul; $\hat{\beta} = -1.03$ d/yr, $\widehat{\mathrm{SE}}(\hat{\beta}) = 0.47$, $P = 0.04$). The trend toward earlier breakup during the current study was consistent with the entire available time series (linear regression from 1971 to 2004; $\hat{\beta} = -0.59$ d/yr, $\widehat{\mathrm{SE}}(\hat{\beta}) = 0.19$, $P < 0.001$). From 1984 to 2003, there was not a statistically significant change in the date of freeze-up in western Hudson Bay (Gagnon and Gough 2005).

Goodness-of-Fit

Program RELEASE indicated that future recapture rates were consistently lower for first-time captures than for recaptures, which suggests lower survival of young polar bears (Cooch and White 2005). We also found evidence for positive capture-history dependence (i.e., increased p following capture) among young males in the combined data (Pradel 1993). The standard CJS model adequately fit the CWS-only and the combined data after partitioning by sex and 2 age classes: prime-adults versus all other ages (Regehr et al. 2007). We began the CJS analysis with a model based on these 4 independent strata, which we further generalized to allow for an additive effect in ϕ between juveniles and an aggregate age class of subadults and senescent-adults. We estimated $\hat{c} = 0.72$ ($\chi^2 = 197.8$, df = 274) for the CWS-only data and 0.81 ($\chi^2 = 251.5$, df = 311) for the combined data, and we used $\hat{c} = 1.0$ for all modeling because the goodness-of-fit analysis did not detect any overdispersion or un-modeled heterogeneity in the WH data after partitioning by sex and age (Burnham and Anderson 2002).

The spatiotemporal analysis of capture locations suggested that we evenly distributed capture effort throughout the CWS study area from 1987 to 2004. Prior to 1987, we were more likely to capture polar bears in the northern part of the study area and along the coast. This was corroborated by the proportion of adult males in the CWS capture sample, which decreased from 0.37 (1984–1986) to 0.25 (1987–1989) as capture operations expanded inland to include more of the habitat typically used by females and family groups. In the last years of the study, more polar bears were again captured along the coast. However, Global Positioning System flight logs (available 2001–2004) indicated that we searched the entire study area in these years and that the shift in capture locations reflected a change in polar bear distribution.

Survival

We estimated survival and population size from the most supported model for the combined CWS and MDOC data. That model included 7 beta coefficients for ϕ and 24 for p, all of which were individually identifiable (Regehr et al. 2007).

Total apparent survival probability ($\hat{\varphi}_j$) was time-constant for prime-adult polar bears, at 0.93 (95% CI = 0.91–0.94) for females and 0.90 (95% CI = 0.88–0.91) for males. Survival of juvenile, subadult, and senescent-adult polar bears varied from year to year as a function of sea ice breakup date ($\hat{\beta}^{ice} = 0.23$, 95% CI = 0.07–0.38; Fig. 3). For these age classes, survival decreased by 2–5% for each week earlier than average that the sea ice broke up. We derived estimates of average $\hat{\varphi}_j$ using the average breakup date for 1984–2003 (Table 1), where the associated confidence intervals represent sampling variance only, not the inter-

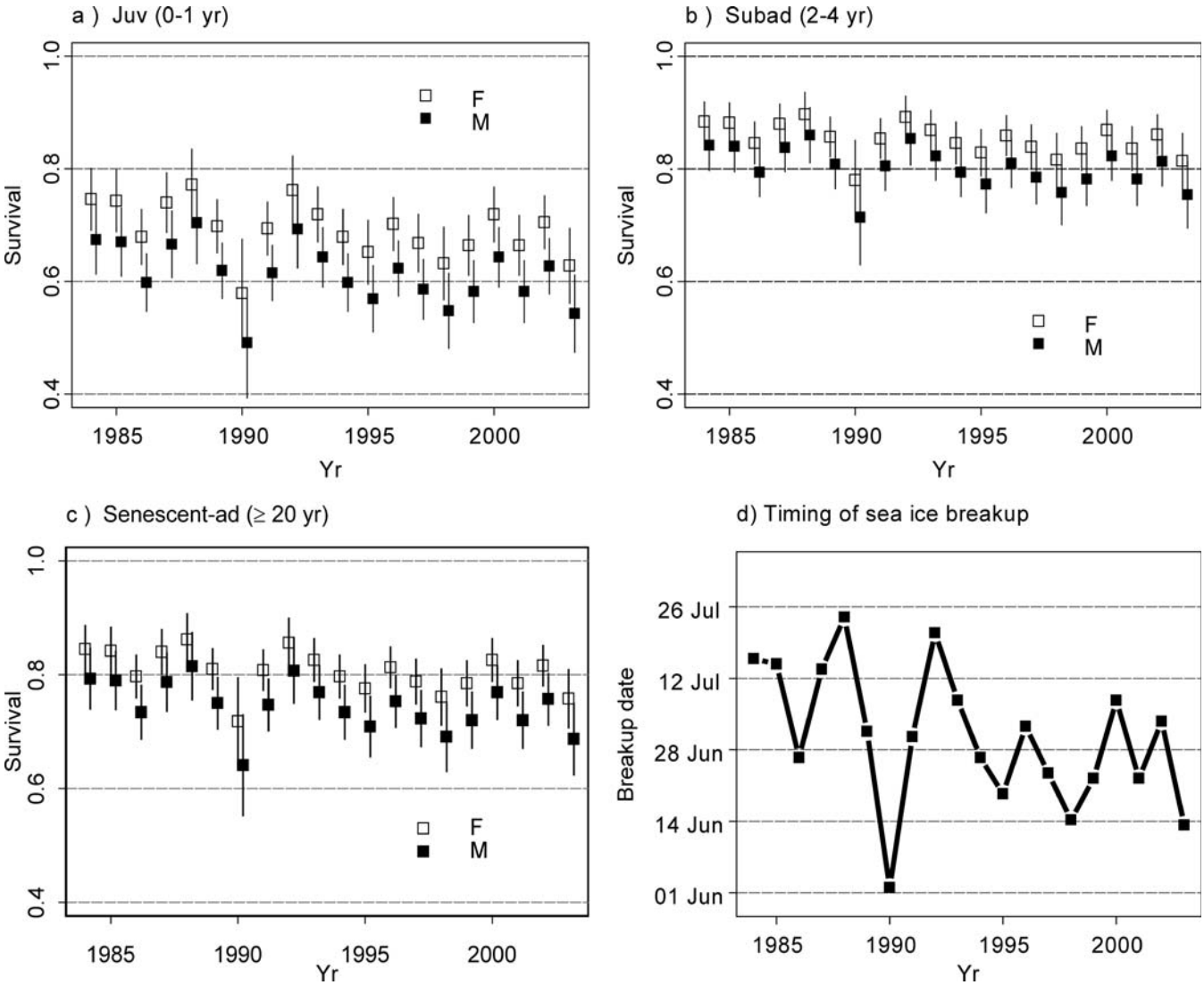

Figure 3. Total apparent survival and 95% confidence intervals for (a) juvenile, (b) subadult, and (c) senescent-adult polar bears in western Hudson Bay, Canada, estimated from the most supported model fit to capture–recapture data collected by the Canadian Wildlife Service and the Manitoba Department of Conservation (MDOC), 1984–2004. Reduced survival rates for subadults and senescent-adults captured around Churchill by the MDOC are not shown. (d) Timing of sea ice breakup in the Western Hudson Bay polar bear management area, which was the best predictor of survival for juvenile, subadult, and senescent-adult polar bears.

Table 1. Average total apparent survival and 95% confidence intervals for polar bears in western Hudson Bay, Canada, estimated from the most supported model fit to capture–recapture data collected by the Canadian Wildlife Service and the Manitoba Department of Conservation (MDOC), 1984–2004.

	F		M	
Age class	Survival	95% CI	Survival	95% CI
Juv (0–1 yr)	0.70	0.65–0.74	0.62	0.57–0.66
Subad (2–4 yr)	0.86	0.82–0.89	0.81	0.76–0.84
Subad (2–4 yr)[a]	0.78	0.74–0.82	0.72	0.68–0.76
Prime-ad (5–19 yr)	0.93	0.91–0.94	0.90	0.88–0.91
Senescent-ad (≥20 yr)	0.81	0.77–0.84	0.75	0.70–0.79
Senescent-ad (≥20 yr)[a]	0.72	0.66–0.78	0.65	0.58–0.71

[a] Reduced survival rates for subad and senescent-ad captured around Churchill by the MDOC.

annual variation in survival due to changing environmental conditions. For subadult and senescent-adult polar bears, capture around Churchill was associated with a permanent decrease of 8–14% in both total survival ($\hat{\beta}^{trap} = -0.49$, 95% CI = −0.21 to −0.77) and natural survival (Table 2).

Population Size

Recapture probabilities (p) were time dependent and differed for females and males by an additive sex effect. The magnitude of the sex effect differed for the periods 1985–1995 and 1996–2004. Polar bears that were captured around Churchill were more likely to be recaptured on subsequent occasions, conditional upon survival. This effect was stronger for juveniles and subadults (odds ratio = 2.68, 95% CI = 2.19–3.28) than for prime-adults and senescent-adults (odds ratio = 2.01, 95% CI = 1.73–2.33).

Table 2. Average natural apparent survival for polar bears in western Hudson Bay, Canada, estimated by adjusting total apparent survival rates from the most supported model fit to capture–recapture data collected by the Canadian Wildlife Service and the Manitoba Department of Conservation (MDOC), 1984–2004, using tag-return data from the harvest.

Age class	F	M
Juv (0–1 yr)	0.73	0.71
Subad (2–4 yr)	0.92	0.94
Subad (2–4 yr)[a]	0.82	0.78
Prime-ad (5–19 yr)	0.93	0.94
Senescent-ad (≥20 yr)	0.82	0.82
Senescent-ad (≥20 yr)[a]	0.72	0.68

[a] Reduced survival rates for subad and senescent-ad captured around Churchill by the MDOC.

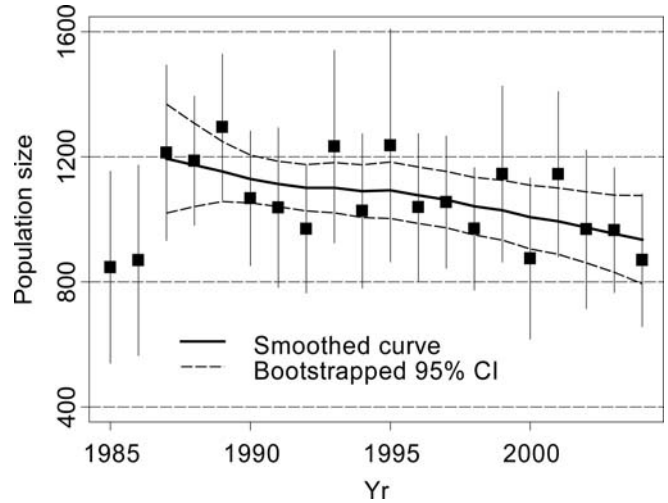

Figure 4. Population size and 95% confidence intervals for polar bears in western Hudson Bay, Canada, estimated from the most supported model fit to capture–recapture data collected by the Canadian Wildlife Service and the Manitoba Department of Conservation, 1984–2004. Smoothed values and bootstrapped 95% confidence intervals are shown for the 1987–2004 point estimates of population size only, because the 1985–1986 point estimates were biased by incomplete sampling of the study area and are not valid.

We derived final estimates of population size by fitting a smoothed curve to the 1987–2004 point estimates of population size ($\hat{N}_j$; Fig. 4). We excluded $\hat{N}_j$ for 1985 and 1986 because incomplete sampling of the CWS study area resulted in a large negative bias for those years. The WH polar bear population declined by approximately 22% from 1,194 (95% CI = 1,020–1,368) in 1987 to 935 (95% CI = 794–1,076) in 2004. For this period, the mean annual population growth rate ($\bar{\lambda}_j$) was 0.986 (95% CI = 0.978–0.995), which indicates that the probability of a stable or increasing population ($\bar{\lambda}_j \geq 1$) was negligible ($P = 0.002$). Ancillary estimates of $\bar{\lambda}_j$ derived from CJS models other than the most supported model indicated that the trend in population size was insensitive to model selection.

DISCUSSION

Western Hudson Bay provides a unique opportunity to quantify the demographic response of a polar bear population to changing environmental conditions, both because of the availability of capture data for both free-ranging polar bears and problem bears that came into Churchill, and because of the long duration and intensity of the study (approx. 80% of ad bore research marks). Several lines of evidence indicate that the relationship between early breakup and decreased survival was a biological phenomenon, common to all WH polar bears. First, although more polar bears generally came into Churchill in years of early breakup ($\hat{\beta} = -0.87$ bears/d, $\widehat{\mathrm{SE}}(\hat{\beta}) = 0.49$, $P = 0.09$), direct human-caused mortality among these bears had no impact on survival estimates. Second, the most supported model allowed for a decrease in survival for subadults and senescent-adults captured around Churchill, in addition to fluctuations in survival associated with breakup date. This decrease was likely due to both an increased probability of 1) natural mortality, because polar bears that came into town in search of food were more likely to be in poor nutritional condition, and 2) anthropogenic mortality, because some polar bears were relocated to the north where they were more likely to encounter Inuit hunters. Third, there was not a significant correlation between breakup date and the number of marked juvenile, subadult, and senescent-adult polar bears killed in the harvest ($\hat{\beta} = -0.10$ bears/d, $\widehat{\mathrm{SE}}(\hat{\beta}) = 0.08$, $P = 0.21$). Finally, CJS models fit to a reduced data set that excluded individual capture histories for polar bears that were either captured or killed by the MDOC, or killed in the Nunavut harvest, corroborated support for breakup date as the best predictor of juvenile, subadult, and senescent-adult survival. A model analogous to the most supported model for the combined CWS and MDOC data estimated $\hat{\beta}^{ice} = 0.39$ (95% CI = 0.14–0.65; likelihood ratio test vs. a null model excluding the covariate *ice*: $\chi^2 = 9.37$, df = 1, $P = 0.002$).

The breakup–survival relationship likely reflects increased starvation associated with entering the winter in poor nutritional condition. Previous studies have suggested that cub survival in the first year of life is related to maternal body condition at the time of birth (Ramsay and Stirling 1988; Derocher and Stirling 1996, 1998). We found that COY survival beyond the age of 8 months (when we first captured them) was predominately a function of environmental conditions in the current year. As the study progressed, the proportion of females in the CWS capture sample remained stable (approx. 0.52) despite an increasing proportion of females in the WH population (to 0.65 in 2004). It is likely that declines in juvenile survival shortened the average inter-birth interval; females produced cubs, lost them, and bred again instead of keeping cubs with them for >2 years until weaned. This pattern, also observed in the southern Beaufort Sea (Regehr et al. 2006), meant that adult females may have been progressively more likely to be pregnant and in dens where they were largely unavailable for capture. Such reproductively based temporary emigration should not have introduced a consistent bias into estimates of female population size because recapture probabilities were time dependent and the most supported model allowed

for a change in female p relative to male p toward the end of the study (Kendall et al. 1997).

Survival of prime-adult polar bears was stable, most likely because prime-adults were in better body condition than other polar bears (E. Richardson, CWS, unpublished data), able to divert resources from reproduction to survival in times of nutritional stress (Bunnell and Tait 1981, Eberhardt 2002), better at catching seals, and more able to take seal kills away from subordinate polar bears. Natural survival of senescent-adult polar bears ($\geq$20 yr), however, was 12–25% lower than for prime-adults and was sensitive to interannual variation in environmental conditions. Although variation in survival has been shown for some animals with long life spans and delayed maturation (e.g., Eberhardt 1985, Jorgenson et al. 1997, Cameron and Siniff 2004), our study is one of the few to have investigated senescence in survival in a statistically rigorous way (Gaillard et al. 1994, Pistorius and Bester 2002).

Evidence from capture–recapture, radiotelemetry, and tag-return studies suggests that exchange between the WH polar bear population and adjacent populations was low (Derocher and Stirling 1990; Stirling et al. 1999, 2004). Thus, it is likely that total apparent survival (ϕ) in this study closely approximated true survival, although the right-censoring of capture histories for polar bears killed in Churchill may have introduced a slight positive bias into our estimates. For prime-adult polar bears, our estimates of ϕ were approximately 5% higher than the estimates reported by Lunn et al. (1997) for all WH polar bears age $\geq$1 year. Our estimates of natural apparent survival (ϕ^N) were similar or slightly lower than those reported for adult polar bears in other populations (Larsen 1986; Taylor et al. 2005, 2006) and were at the lower limit assumed necessary to maintain populations of long-lived mammals (Taylor et al. 1987, Eberhardt 2002). The similarity between female and male ϕ^N for most age classes supports the hypothesis that observed sexual differences in polar bear survival are due to sex-selective harvest (Ramsay and Stirling 1986, Derocher et al. 1997).

Our estimates of population size were robust to minor, unmodeled heterogeneity in recapture probabilities because mean p was relatively high (approx. 0.25; e.g., Pollock et al. 1990, Pledger and Efford 1998). The mean percent relative difference between the point estimates of N from the most supported model and the bootstrapped estimates of N was <1%, suggesting that small-sample bias was minimal. Furthermore, our modeling approach explicitly allowed for heterogeneity associated with differences between the CWS and MDOC sampling protocols, by incorporating time-dependent individual covariates for capture-history dependence. The increase in p following capture around Churchill was likely due to recidivist behavior with respect to the potential food reward at the Churchill dump (Lunn and Stirling 1985) and to the fact that polar bears with fidelity to the northern part of the CWS study area were potentially exposed to sampling by both the CWS and MDOC.

Our point estimate of the size of the WH population in 1995 was 1,236 (SE = 190), similar to the previous estimate of 1,199 (SE = 251; Lunn et al. 1997). Because polar bears are K-selected and populations cannot fluctuate radically among years, we fit a curve through the point estimates using a relatively insensitive smoothing algorithm, which resulted in a lower mean coefficient of variation (9%) compared to the point estimates (12%). We assessed the contribution of the MDOC data to estimates of population size by deriving secondary estimates from the CWS-only data. Whereas estimates of adult population size were similar for the 2 data sets ($\bar{x}$ % relative difference approx. 2%), estimates of total population size were larger for the combined data. This difference increased from 73 polar bears in 1987 to 173 polar bears in 2004 (i.e., in 2004 the smoothed estimate of total population size was 762 for the CWS-only data vs. 935 for the combined data). Apparently, the CWS missed an increasing number of young polar bears as more subadults came into Churchill each year.

We attribute the decline of the WH polar bear population to increased natural mortality associated with earlier sea ice breakup and to the continued harvest of approximately 40 polar bears per year (Lunn et al. 2002), which at some point ceased to be sustainable. We found no support for alternative explanations. Long-term observations suggest that the WH population continues to exhibit a high degree of fidelity to the CWS study area during the early part of the ice-free season (Stirling et al. 1977, 1999, 2004; Taylor and Lee 1995), which precludes permanent emigration as a cause for the decline. Consistently similar proportions of research-marked polar bears in the CWS, MDOC, and harvest samples suggest that the same polar bears were first exposed to capture around the CWS study area and were subsequently exposed to harvest. This refutes the hypothesis that large-scale changes in the onshore distribution of polar bears in western Hudson Bay have created a separate subpopulation that spends the entire ice-free season along the Nunavut coast. Finally, capture–recapture data collected from 2003 to 2005 for the adjacent southern Hudson Bay population included very few polar bears with a previous capture in the WH management area, which suggests that a major distributional shift to the southeast did not occur (M. E. Obbard, Ontario Ministry of Natural Resources, unpublished data).

Polar bears in western Hudson Bay are likely to be among the first to show population-level effects of climatic warming because they occur near the southern limit of the species' range (Lunn et al. 2002) and because recent temperature increases in the region have been among the largest in the Arctic (Ferguson et al. 2005). We propose the following explanation for the concurrent observations of an increasing number of polar bears coming into Churchill and a declining WH population. Sea ice breakup in western Hudson Bay has been occurring progressively earlier due to rising air temperatures (Gagnon and Gough 2005). This shortens the time that polar bears can hunt seals on the sea ice, thereby forcing them ashore in poorer nutritional condition (Stirling et al. 1999) and increasing their risk of

starvation. As polar bears exhaust their fat reserves toward the end of the ice-free period, they are more likely to encroach upon human settlements in search of alternative food sources to sustain themselves until freeze-up (Stirling and Parkinson 2006).

MANAGEMENT IMPLICATIONS

Although climatic warming may initially improve conditions for polar bears in high-latitude regions of heavy ice (Derocher et al. 2004), forecasted declines in the sea ice for most parts of the Arctic are long term and severe (Parkinson 2000, Comiso 2003, Arctic Climate Impact Assessment 2004, Holland et al. 2006). Ultimately, we predict that more northerly polar bear populations will experience declines in demographic parameters similar to those observed in western Hudson Bay, along with changes in distribution and other currently unknown ecological responses (Derocher et al. 2004, Aars et al. 2006). If sea ice loss becomes the limiting factor determining population growth rate, reduced harvest (e.g., Taylor et al. 2006) may be insufficient to slow population declines or impractical due to increasing human–polar bear conflicts. Innovative and flexible management will be necessary to mitigate the negative effects of climatic warming on polar bears in ways that are socially and economically acceptable.

ACKNOWLEDGMENTS

We are grateful to the CWS, the MDOC, and the Natural Sciences and Engineering Research Council for their long-term support of polar bear studies in western Hudson Bay, and to the United States Geological Survey and University of Wyoming for supporting analyses of data resulting from these studies. The Churchill Northern Studies Centre, the Discovery Channel, the National Fish and Wildlife Foundation (Washington, D.C.), Nunavut Wildlife Research Trust, Ontario Ministry of Natural Resources, Parks Canada, Sea World, the World Society for the Protection of Animals, World Wildlife Fund (Canada), and the World Wildlife Fund Arctic Programme provided financial and logistical support. We thank the MDOC, the Nunavut Department of Environment, and the Ontario Ministry of Natural Resources for access to unpublished data. We thank D. Andriashek, W. Calvert, A. E. Derocher, M. Kay, S. Miller, M. A. Ramsay, E. Richardson, and C. Spencer for assistance in the field and laboratory. T. McDonald at WEST, Inc. (Cheyenne, WY) provided advice with the data analysis.

LITERATURE CITED

Aars, J., N. J. Lunn, and A. E. Derocher. 2006. Polar bears. Proceedings of the 14th Working Meeting of the World Conservation Union Species Survival Commission (IUCN/SSC) Polar Bear Specialists Group, 20–24 June 2005, Seattle, Washington, USA. International Union for Conservation of Nature and Natural Resources Species Survival Commission Occasional Paper 32, Gland, Switzerland.

Akaike, H. 1981. Likelihood of a model and information criteria. Journal of Econometrics 16:3–14.

Amstrup, S. C. 2003. Polar bear. Pages 587–610 *in* G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Amstrup, S. C., and D. P. DeMaster. 1988. Polar bear—*Ursus maritimus*. Pages 39–56 *in* J. W. Lentfer, editor. Selected marine mammals of Alaska: species accounts with research and management recommendations. Marine Mammal Commission, Washington, D.C., USA.

Amstrup, S. C., and G. M. Durner. 1995. Survival rates of radio-collared female polar bears and their dependent young. Canadian Journal of Zoology 73:1312–1322.

Amstrup, S. C., G. M. Durner, I. Stirling, and T. L. McDonald. 2005*a*. Allocating harvests among polar bear stocks in the Beaufort Sea. Arctic 58:247–259.

Amstrup, S. C., T. L. McDonald, and G. M. Durner. 2004. Using satellite radiotelemetry data to delineate and manage wildlife populations. Wildlife Society Bulletin 32:661–679.

Amstrup, S. C., T. L. McDonald, and B. F. J. Manly, editors. 2005*b*. Handbook of capture–recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66: 912–918.

Arctic Climate Impact Assessment. 2004. Impacts of a warming Arctic. Cambridge University Press, Cambridge, United Kingdom.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears: implications. Pages 75–98 *in* T. D. Smith and C. Fowler, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5, Bethesda, Maryland, USA.

Calvert, W., and M. A. Ramsay. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. Ursus 10:449–453.

Cameron, M. F., and D. B. Siniff. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Canadian Journal of Zoology 80:601–615.

Comiso, J. C. 2003. Warming trends in the Arctic from clear sky satellite observation. Journal of Climate 16:3498–3510.

Cooch, E., and G. C. White. 2005. Program MARK: a gentle introduction. Fifth edition. <http://www.phidot.org/software/mark/docs/book/>. Accessed 22 Aug 2006.

Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. Integrative and Comparative Biology 44:163–176.

Derocher, A. E., and I. Stirling. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Canadian Journal of Zoology 68:1395–1403.

Derocher, A. E., and I. Stirling. 1992. The population dynamics of polar bears in western Hudson Bay. Pages 1150–1159 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, London, United Kingdom.

Derocher, A. E., and I. Stirling. 1996. Aspects of survival in juvenile polar bears. Canadian Journal of Zoology 74:1246–1252.

Derocher, A. E., and I. Stirling. 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). Journal of Zoology (London) 245:253–260.

Derocher, A. E., I. Stirling, and W. Calvert. 1997. Male-biased harvesting of polar bears in western Hudson Bay. Journal of Wildlife Management 61:1075–1082.

Dredge, L. A., and F. M. Nixon. 1992. Glacial and environmental geology of northeastern Manitoba. Geological Survey of Canada Memoir 432, Ottawa, Ontario, Canada.

Durner, G. M., S. C. Amstrup, R. Neilson, and T. McDonald. 2004. The use of sea ice habitat by female polar bears in the Beaufort Sea. Minerals Management Service Outer Continental Shelf Study MMS 2004–014, Anchorage, Alaska, USA.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Ferguson, S. H., I. Stirling, and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in Western Hudson Bay. Marine Mammal Science 21:121–135.

Franklin, A. B. 2001. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Pages 290–296 *in* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress, The Wildlife Society, 28 June–2 July 1999, Bethesda, Maryland, USA.

Gagnon, A. S., and W. A. Gough. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic 58:370–382.

Gaillard, J.-M., D. Allaine, D. Pontier, N. G. Yoccoz, and D. E. L. Promislow. 1994. Senescence in natural populations of mammals: a re-analysis. Evolution 48:509–516.

Gough, W. A., A. R. Cornwell, and L. J. S. Tsuji. 2004. Trends in seasonal sea ice duration in Southwestern Hudson Bay. Arctic 57:299–305.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale indices seem to predict ecological processes better than local weather. Nature 430:71–75.

Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of lambda using Pradel's (1996) model for capture–recapture data. Journal of Applied Statistics 29:573–587.

Holland, M. M., C. M. Bitz, and B. Tremblay. 2006. Future abrupt reductions in the summer Arctic sea ice. Geophysical Research Letters 33:L23503.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Insightful Corporation. 2001. S-PLUS 6 for Windows guide to statistics. Volume 1. Insightful Corporation, Seattle, Washington, USA.

Iverson, S. J., I. Stirling, and S. L. C. Lang. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. Pages 98–117 *in* I. L. Boyd, S. Wanless, and C. J. Camphuysen, editors. Top predators of marine ecosystems. Cambridge University Press, Cambridge, United Kingdom.

Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78:1019–1032.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Larsen, T. 1986. Population biology of the polar bear (*Ursus maritimus)* in the Svalbard area. Norsk Polarinstitutt Skrifter 184, Oslo, Norway.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lindsay, R. W., and J. Zhang. 2005. The thinning of Arctic sea ice, 1988–2003: have we passed a tipping point? Journal of Climate 18:4879–4894.

Lunn, N. J., S. Schliebe, and E. W. Born, editors. 2002. Polar bears. Proceedings of the Thirteenth Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 23–28 June 2001, Nuuk, Greenland. International Union for Conservation of Nature and Natural Resources Species Survival Commission Occasional Paper 26, Gland, Switzerland.

Lunn, N. J., and I. Stirling. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Canadian Journal of Zoology 63:2291–2297.

Lunn, N. J., I. Stirling, D. Andriashek, and G. B. Kolenosky. 1997. Re-estimating the size of the polar bear population in Western Hudson Bay. Arctic 50:234–240.

Lunn, N. J., I. Stirling, D. Andriashek, and E. Richardson. 2004. Selection of maternity dens by female polar bears in western Hudson Bay, Canada and the effects of human disturbance. Polar Biology 27:350–356.

Manly, B. F. 1997. Randomization, bootstrap, and Monte Carlo methods in biology. Second edition. Chapman and Hall, London, United Kingdom.

McDonald, T. L., and S. C. Amstrup. 2001. Estimation of population size using open capture–recapture models. Journal of Agricultural, Biological, and Environmental Statistics 6:206–220.

McDonald, T. L., S. C. Amstrup, E. V. Regehr, and B. F. J. Manly. 2005. Examples. Pages 196–265 *in* S. C. Amstrup, T. L. McDonald, and B. F. J. Manly, editors. Handbook of capture–recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

Nichols, J. D., J. E. Hines, and K. H. Pollock. 1984. Effects of permanent trap response in capture probability on Jolly–Seber capture–recapture model estimates. Journal of Wildlife Management 48:289–294.

Parkinson, C. L. 2000. Variability of Arctic sea ice: the view from space, an 18-year record. Arctic 53:341–358.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pistorius, P. A., and M. N. Bester. 2002. A longitudinal study of senescence in a pinniped. Canadian Journal of Zoology 80:395–401.

Pledger, S., and M. Efford. 1998. Correction of bias due to heterogeneous capture probability in capture–recapture studies of open populations. Biometrics 54:888–898.

Pollock, K. H. 1981. Capture–recapture models allowing for age-dependent survival and capture rates. Biometrics 37:521–529.

Pollock, K. H., J. D. Nichols, J. E. Hines, and C. Brownie. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107.

Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29–37 *in* J.-D. Lebreton and J. D. Nichols, editors. Marked individuals in the study of bird populations. Birkhauser Verlag, Basel, Switzerland.

Ramsay, M. A., and I. Stirling. 1986. On the mating system of polar bears. Canadian Journal of Zoology 64:2142–2151.

Ramsay, M. A., and I. Stirling. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). Journal of Zoology (London) 214: 601–634.

Regehr, E. V., S. C. Amstrup, and I. Stirling. 2006. Polar bear population status in the southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006–1337, Reston, Virginia, USA.

Regehr, E. V., N J. Lunn, S. C. Amstrup, and I. Stirling. 2007. Supplemental materials for the analysis of capture-recapture data for polar bears in western Hudson Bay, Canada, 1984–2004. U.S. Geological Survey Data Series 304, Reston, Virginia, USA.

Saucier, F. J., S. Senneville, S. Prinsenberg, F. Roy, G. Smith, P. Gachon, D. Caya, and R. Laprise. 2004. Modelling the sea ice–ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. Climate Dynamics 23:303–326.

Sendor, T., and M. Simon. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology 72:308–320.

Skinner, W. R., R. L. Jefferies, T. J. Carleton, R. F. Rockwell, and K. F. Abraham. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology 4:3–16.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297: 1292–1296.

Stephens, P. A., S. S. Buskirk, G. D. Hayward, and C. Martinez del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4–12.

Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. Arctic 55:59–76.

Stirling, I., C. Jonkel, P. Smith, R. Robertson, and D. Cross. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Canadian Wildlife Service Occasional Paper 33, Edmonton, Alberta, Canada.

Stirling, I., and N. J. Lunn. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. Pages 167–181 *in* S. J. Woodin and M. Marquiss, editors. Ecology of arctic environments. Blackwell Scientific, Oxford, United Kingdom.

Stirling, I., N. J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. Arctic 52:294–306.

Stirling, I., N. J. Lunn, J. Iacozza, C. Elliott, and M. Obbard. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast

during open water season, in relation to population trends and annual ice patterns. Arctic 57:15–26.

Stirling, I., and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic 59:261–275.

Stirling, I., C. Spencer, and D. Andriashek. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. Journal of Wildlife Diseases 25:159–168.

Stroeve, J. C., M. C. Serreze, F. Fetterer, T. Arbetter, W. Meier, J. Maslanik, and K. Knowles. 2005. Tracking the Arctic's shrinking ice cover: another extreme September minimum in 2004. Geophysical Research Letters 32:L04501.

Taylor, M., D. P. DeMaster, F. L. Bunnell, and R. E. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51:811–820.

Taylor, M. K., J. Laake, H. D. Cluff, M. Ramsay, and F. Messier. 2002. Managing the risk from hunting for the Viscount Melville Sound polar bear population. Ursus 13:185–202.

Taylor, M. K., J. Laake, P. D. McLoughlin, E. W. Born, H. D. Cluff, S. H. Ferguson, A. Rosing-Asvid, R. Schweinsburg, and F. Messier. 2005. Demography and viability of a hunted population of polar bears. Arctic 58:203–214.

Taylor, M. K., J. Laake, P. D. McLoughlin, and H. D. Cluff. 2006. Demographic parameters and harvest-explicit population viability analysis for polar bears in M'Clintock Channel, Nunavut, Canada. Journal of Wildlife Management 70:1667–1673.

Taylor, M. K., and J. Lee. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. Arctic 48:147–154.

Vinnikov, K. Y., A. Robock, R. J. Stouffer, J. E. Walsh, C. L. Parkinson, D. J. Cavalieri, J. F. B. Mitchell, D. Garrett, and V. F. Zakharov. 1999. Global warming and northern hemisphere sea ice extent. Science 286: 1934–1937.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zhang, X., and J. E. Walsh. 2006. Toward a seasonally ice-covered Arctic Ocean: scenarios from the IPCC AR4 model simulations. Journal of Climate 19:1730–1747.

Associate Editor: Alpizar-Jara.