

Use of Subsistence-Harvested Whale Carcasses by Polar Bears in the Southern Beaufort Sea

Kate M. Lillie,^{1,2} Eric M. Gese,³ Todd C. Atwood⁴ and Mary M. Conner¹

(Received 10 December 2018; accepted in revised form 9 May 2019)

ABSTRACT. The availability of a food subsidy has the potential to influence the condition, behavior, fitness, and population dynamics of a species. Since the early 2000s, monitoring efforts along the coast of northern Alaska have indicated a higher proportion of polar bears (*Ursus maritimus*) of the southern Beaufort Sea (SB) subpopulation coming onshore to feed on subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses during the fall and early winter seasons. Concurrently, Indigenous communities annually hunt bowhead whale and deposit the unused remains at localized “bone piles,” creating the potential for human-bear interactions. Our objective was to determine the annual number of polar bears feeding at the bone pile near Kaktovik, Alaska. Using a hair snag surrounding the bone pile, we collected hair samples to identify individual bears via microsatellite genotypes during 2011–14. We used capture-mark-recapture data in the POPAN open-population model to estimate the number of bears visiting the bone pile. We estimated that as many as 72 (SE = 9) and 76 (SE = 10) male and female polar bears, respectively, used the bone pile located at Kaktovik, Alaska, in 2012, which represents approximately 16% of the SB polar bear subpopulation. It will be important to monitor the number of bears using the bone pile and subsequent human-bear interactions and conflicts along the northern coast of Alaska, if sea ice continues to recede.

Key words: bone pile; onshore behavior; polar bear; southern Beaufort Sea; *Ursus maritimus*; whale carcass

RÉSUMÉ. L'existence de subventions alimentaires a la possibilité d'influencer l'état, le comportement, la condition physique et la dynamique de la population d'une espèce. Depuis le début des années 2000, les efforts de surveillance déployés sur la côte nord de l'Alaska ont laissé entrevoir une plus grande proportion d'ours polaires (*Ursus maritimus*) de la sous-population du sud de la mer de Beaufort venant sur le littoral pour manger les carcasses des baleines boréales (*Balaena mysticetus*) pêchées à des fins de subsistance pendant les saisons de l'automne et du début de l'hiver. En même temps, les collectivités autochtones chassent les baleines boréales tous les ans et déposent leurs restes dans des « tas d'ossements », ce qui crée la possibilité d'interactions entre les humains et les ours. Notre objectif consistait à déterminer le nombre annuel d'ours polaires qui s'alimentent au tas d'ossements situé près de Kaktovik, en Alaska. De 2011 à 2014, à l'aide d'un piège à poils placé près du tas d'ossements, nous avons recueilli des échantillons de poils afin d'identifier les ours individuels au moyen de génotypes microsatellites. Nous avons employé les données de capture-marquage-recapture du modèle de population ouverte POPAN pour estimer le nombre d'ours se rendant au tas d'ossements. Nous avons estimé que jusqu'à 72 (ET = 9) et 76 (ET = 10) ours polaires mâles et femelles, respectivement, ont utilisé le tas d'ossements de Kaktovik, en Alaska, en 2012, ce qui représente environ 16 % de la sous-population d'ours polaires du sud de la mer de Beaufort. Il sera important de surveiller le nombre d'ours qui utilisent le tas d'ossements de même que les interactions et les conflits entre les humains et les ours qui s'ensuivront sur la côte nord de l'Alaska si la glace de mer continue de reculer.

Mots clés : tas d'ossements; comportement côtier; sud de la mer de Beaufort; *Ursus maritimus*; carcasse de baleine

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

The ability of a species to utilize a food subsidy can greatly influence individual behavior, foraging ecology, fitness, and population dynamics (Craighead et al., 1995; Roth, 2003; Herreman and Peacock, 2013; Lyons et al., 2017). Because of climate change, polar bears (*Ursus maritimus*)

are experiencing rapid changes to their environment (Stirling and Derocher, 2012). As a result of decreasing sea ice extent, an increasing proportion of polar bears from the southern Beaufort Sea (SB) subpopulation are being observed onshore during the late summer and fall in Alaska (Schliebe et al., 2008; Gleason and Rode, 2009; Atwood et al., 2016; Pongracz and Derocher, 2017). One of the main

¹ Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, Utah 84322, USA

² Corresponding author: katemlillie@gmail.com

³ U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, Utah 84322, USA

⁴ U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

food resources for bears onshore is the availability of subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses (Schliebe et al., 2008; Herreman and Peacock, 2013; Atwood et al., 2016; Wilson et al., 2017). Indigenous communities along the coast of northern Alaska annually harvest bowhead whales and deposit unused remains onshore at local bone piles, which are composed of unused trimmed blubber, meat, and bones (Ashjian et al., 2010). Bowhead whale bone piles are located in Alaska near Cross Island (~147° W; north of the Prudhoe Bay and Kuparuk oil and gas fields), the community of Kaktovik (~143° W), and at Utqiagvik (~157° W) until 2012. Bone piles constitute a persistent and reliable marine food subsidy for polar bears since they are available each year at the same locations. Analyses suggest that scavenged bowhead whale remains could constitute a large proportion (e.g., 50%–70% of adult female fall diet) of some SB polar bear diets (Rogers et al., 2015; McKinney et al., 2017), which can affect population dynamics if the behavior is widespread. Therefore, it is important to understand the annual usage of this marine food subsidy for conservation and management purposes.

Summer sea ice conditions in the Arctic have progressively changed in recent decades (Serreze and Stroeve, 2015). From 1979 to 2014, the spatial extent of Arctic sea ice in September (when sea ice reaches its annual minimum) has declined by 13.3% per decade because of warming temperatures (Serreze and Stroeve, 2015). Over the same period, the duration of the open-water season (i.e., the period of time when sea ice is mostly absent from continental shelf waters) has increased at rates of 14.8 and 15.5 days per decade Arctic-wide and for the SB, respectively, which indicates the SB subpopulation is experiencing one of the most rapid rates of sea ice loss across the species' range (Stern and Laidre, 2016). Polar bears in the SB subpopulation have historically spent the majority of the year on the sea ice (Amstrup et al., 2000), which they rely on for access to their primary prey (ringed [*Pusa hispida*] and bearded [*Erignathus barbatus*] seals), long-distance movements, mating, and some maternal denning (Amstrup, 2003). However, recent research in the SB found that the estimated proportion of bears observed onshore increased from 5.8% during 1986–99 to 20.0% during 2000–14 (Atwood et al., 2016). Atwood et al. (2016) found trends of earlier arrival onshore, increased length of stay while onshore, and later departure back to the sea ice, all of which were associated with declines in the availability of sea ice habitat over the continental shelf and changes to sea ice phenology. Furthermore, research suggests that onshore behavior appears to be transmitted via social learning from mothers to their offspring, indicating that seasonal land use and scavenging of bowhead whale remains by SB bears may be behavioral modifications in response to environmental change (Lillie et al., 2018).

The bone piles in Alaska are near settlements and oil exploration and extraction infrastructure, which increases the risk of human-bear interactions and conflict. Human-wildlife conflicts can have broad consequences, such as

negatively impacting wildlife populations, altering the structure of ecosystems (Woodroffe et al., 2005), and endangering public safety (Thirgood et al., 2005). Towns et al. (2009) found that an increase in human-polar bear interactions in Churchill, Manitoba, was associated with an increase in the length of the ice-free season and declines in bear body condition. As of the most recent population assessment, the SB subpopulation is considered to be in decline (Bromaghin et al., 2015). Polar bear land use and anthropogenic activities along Alaska's Beaufort Sea coast (including industrial development and tourism) are both likely to increase (Gautier et al., 2009; Reynolds et al., 2014; Rode et al., 2018) and will exacerbate conservation and management challenges, as well as escalate the risk for human-polar bear conflict in this region. In light of these management concerns, it will be important to better understand the potential for fitness benefits of supplemental feeding. For example, a recent study found that consumption of bowhead whale remains in fall was associated with improved body condition in spring (McKinney et al., 2017). However, land use may also increase the probability of exposure to certain pathogens (Atwood et al., 2017), as polar bears feeding at bone piles overlap in space and time with species associated with terrestrial and near-shore habitats, such as Arctic fox (*Vulpes lagopus*), grizzly bear (*Ursus arctos*), glaucous gull (*Larus hyperboreus*), and raven (*Corvus corax*). Whether bears derive a fitness benefit from feeding on bowhead whale remains will likely be an important consideration for informing management decisions regarding the efficacy and safety of future supplemental feeding.

Our objective was to use genetic mark-recapture techniques to determine the number of SB polar bears using the bone pile near Kaktovik, Alaska, over a four-year period (2011–14). We collected hair samples using a hair snag surrounding the bowhead whale carcasses to identify individual bears. We used the open-population model POPAN (Schwarz and Arnason, 1996) to estimate the number of bears that visited the bone pile.

STUDY AREA

The SB subpopulation extends from Icy Cape, Alaska, USA, (70.3° N, 161.9° W) in the west, to Tuktoyaktuk, Northwest Territories, Canada, (69.4° N, 133.0° W) in the east. We collected data in Kaktovik, Alaska (Fig. 1), which is a community of approximately 300 inhabitants along the coast of the southern Beaufort Sea. Indigenous people annually harvest bowhead whales during the fall and deposit any unused whale remains on a spit, approximately 2 km northeast of the village. The bone pile is located in the same geographic region each year. Published accounts of polar bears observed feeding at the bone pile date back to 1986 (Amstrup et al., 1986). Since the beginning of documented bowhead whale harvesting in Alaska (1964), two to four whales have been harvested annually

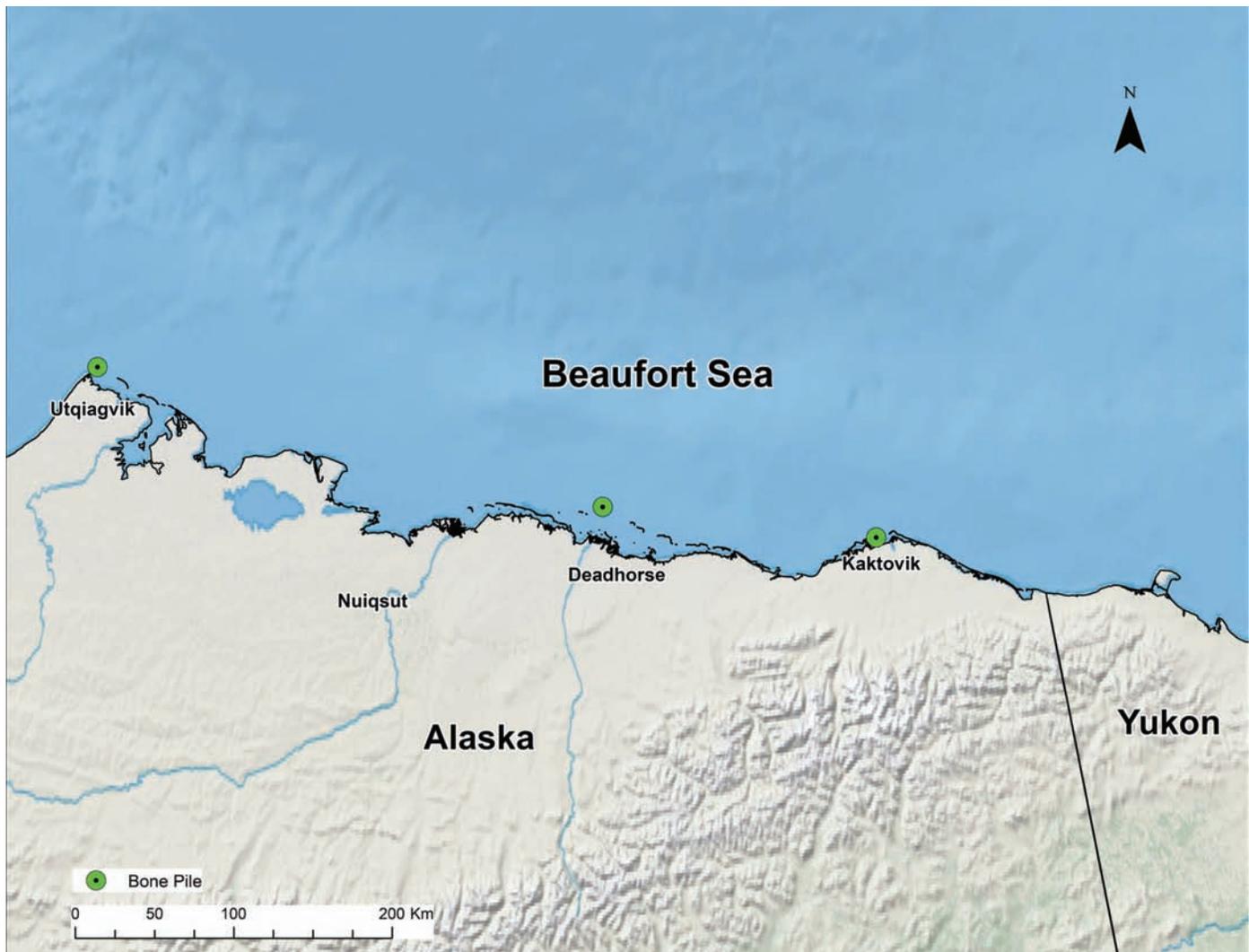


FIG. 1. Map of the study area, showing the approximate locations of the bowhead whale bone piles on the northern coast of Alaska, USA.

at Kaktovik, with few exceptions, since 1989 (Koski et al., 2005). Each year of the study, whalers harvested three bowhead whales in the fall (Suydam et al., 2012, 2013, 2014, 2015). Harvested whales ranged in length from 6.6 m in 2011 (Suydam et al., 2012), to 14.3 m in 2012 (Suydam et al., 2013), with an average length of 10.1 m (Suydam et al., 2012, 2013, 2014, 2015).

METHODS

Data Collection

A hair snag was deployed in Kaktovik, Alaska (e.g., Herreman and Peacock, 2013) each fall of the study (2011–14), to collect hair samples for genetic identification. Collection of hair samples continued through the fall and winter each year during the following periods: 15 September 2011 to 9 December 2011 (85 days); 13 October 2012 to 27 February 2013 (137 days); 8 October 2013 to 20 January 2014 (104 days); and 13 September 2014 to 17

November 2014 (65 days). The hair snag was a barbed wire corral consisting of a single, continuous strand of four-point, 12-gauge barbed wire, attached by bailing wire or fence clips to metal t-posts at a height of 0.65 m. Each post was spaced approximately 10 m apart and pounded into the gravel at a minimum depth of 40 cm. The corral was erected around the bowhead whale carcasses, enclosing an area of approximately 300 m². The hair snag was checked daily for the first four days of sampling. After the first four days, the snag was checked at least weekly to maintain the wire's integrity. We collected samples by plucking hairs from a single barb and putting them inside a small paper envelope. Samples were not collected if a single barb had large quantities of hair since it could have come from more than one individual. We collected only one sample within a 0.75 m section of fence to avoid collecting multiple samples from a single crossing event. All remaining, uncollected hairs were removed via plucking or burning with a gas torch. The samples were air-dried and stored at room temperature until DNA extraction.

Genetic Identification

Hair samples were genotyped at 20 microsatellite loci and a ZFX/ZFY sex identification marker by Wildlife Genetics International (Nelson, British Columbia, Canada) using methods and primers described in detail by Paetkau (2003) and Kendall et al. (2008). The DNA was extracted using a Qiagen DNeasy kit (QIAGEN Inc., Valencia, California, USA) per the manufacturer's instructions. Initially, the DNA extracts were amplified at 11 hypervariable microsatellite markers to identify individual polar bears: G1A, G10B, G10C, CX110, G1D, G10L, G10M, MU59, G10P (Paetkau and Strobeck, 1994; Taberlet et al., 1997; Proctor et al., 2002), and G10H and G10J (GenBank accession numbers U22086.1 and U22087.1, respectively). A minimum of 10 guard hair roots were used to extract DNA if available, or up to 30 whole underfur hairs if needed to supplement guard hairs. DNA extracts that were amplified at < 11 loci were considered unsuccessful and excluded from further analyses. After individual polar bears were identified, each individual was amplified at an additional nine markers including a sex-linked locus: MSUT-2, CPH9, CXX20, MU50, MU51, G10X, CXX173 (Ostrander et al., 1993; Paetkau et al., 1995; Taberlet et al., 1997; Kitahara et al., 2000; Proctor et al., 2002; An et al., 2010), and 14RENPO7 and G10U (GenBank accession numbers AJ411284, and U22092.1, respectively). Samples were amplified at an additional nine markers to enable other types of analyses (not included in this study) as part of the ongoing genetic data collection of the SB subpopulation.

Capture-Recapture Analysis

We estimated the number of SB polar bears that annually visited the Kaktovik bone pile using a capture-recapture analysis in Program MARK 8.1 (White and Burnham, 1999; Cooch and White, 2017). A preliminary analysis conducted with Program CloseTest revealed that bears visiting the Kaktovik bone pile did not represent a closed population (Stanley and Burnham, 1999), so we used the open-population model POPAN (Schwarz and Arnason, 1996) in subsequent analyses. The POPAN model is a parameterization of the Jolly-Seber model that assumes the individuals sampled represent a portion of a larger super-population (Kendall, 1999), which is consistent with a similar modeling effort for the same subpopulation of polar bears conducted by Herreman and Peacock (2013). Inadequate data prevented us from using an open robust design (i.e., the multi-state open robust design model constrained to have a single state).

We conducted separate analyses for each year of our study: 2011, 2012, 2013, and 2014. Thus, we produced individual capture histories for each polar bear identified in the sample set, each year. The sampling occasions were biweekly or monthly depending on changes in the frequency of use of the bone pile by bears. The POPAN model estimates abundance several ways; we used N^* , which

is labeled total gross abundance, survival probability of marked and unmarked animals between sampling occasions (ϕ), detection probability (p), and probability of entry (p_{ent}). N^* can be thought of as either the total number of animals available for capture at any time during the study, or as the total number of animals ever in the sampled area between the first and last occasion of the study. For our study, we interpreted N^* as the total annual number of individual bears that visited the bone pile. Furthermore, we interpreted the value of ϕ from the POPAN model as polar bear site fidelity to the bone pile from one sampling occasion to the next during the sampling period for each year. In other words, for a long-lived animal, ϕ in the POPAN model can be interpreted as the probability an animal remains on the study area (site fidelity), as the sampling period is short relative to lifespan. This interpretation fits for our study because the probability an individual polar bear would die over the course of the sampling period (e.g., two to five months) is low. We constructed a series of models and fit them to the capture data for each year. We used every possible combination of models in which p , p_{ent} , and ϕ were held constant (.) or were allowed to vary by sex (s) and time (t), and N^* was estimated separately by sex (s). We ran all possible combinations of models because we did not know a priori which models would be biologically reasonable for the system. This approach follows the all-combinations strategy and model averaging generally recommended by Doherty et al. (2012). We had 64 a priori models total for all years. For each year, we estimated over-dispersion (\hat{c}) to determine goodness-of-fit of the global POPAN model that converged well $\{\phi(s^*t)p(s^*t)p_{ent}(\cdot)\}$ by using Program RELEASE. Program RELEASE performs a series of chi-square tests to evaluate model fit, with \hat{c} estimated as χ^2/df , where χ^2 is the sum over all chi-squared tests and df is the sum of the degrees of freedom.

We used Akaike's information criterion corrected for small sample size (AIC_c) to rank the models and assign model weight (Burnham and Anderson, 2002). When \hat{c} was above 1, we used quasi- AIC_c ($QAIC_c$) for model selection and \hat{c} to inflate variances of parameter estimates (Burnham and Anderson, 2002). Lastly, to properly account for model uncertainty, the annual N^* estimates of bears visiting the bone pile were obtained by model averaging, in which each model contributed to the final estimate according to its AIC_c or $QAIC_c$ model weight (Burnham and Anderson, 2002). However, because our model set contained models wherein ϕ and p or p_{ent} and p , and potentially ϕ and p_{ent} were confounded [e.g., $\phi(t)p(t)p_{ent}(\cdot)$ or $\phi(\cdot)p(t)p_{ent}(t)$], and this confounding could result in biased estimates of N^* , we deleted all models with confounding from the model set we used for model averaging.

RESULTS

We collected 1477 hair samples over the four-year study, of which 1032 were successfully genotyped. We genetically

identified 158 individual polar bears across the study (77 males and 81 females). We identified 74 bears (42 males and 32 females) in 2011, 105 bears (51 males and 54 females) in 2012, 23 bears (15 males and 8 females) in 2013, and 41 bears (22 males and 19 females) in 2014. Estimates of \hat{c} were less than 1.0 for all years, suggesting no over-dispersion and no lack of fit (range 0.60–0.84). Therefore, we used AIC_c model selection for POPAN models. We estimated all parameters from the POPAN model with model averaging (Table 1). Low sample size prevented us from obtaining parameter estimates (N , ϕ , p , p_{ent}) for 2013. Based on the capture-recapture analysis, we estimated that as many as 72 (SE = 9) and 76 (SE = 10) male and female polar bears, respectively, used the bone pile located at Kaktovik, Alaska, in 2012. We estimated a low of 26 (SE = 3) males and 26 (SE = 6) females used the bone pile in 2014 (Table 2). We found that p , ϕ , and p_{ent} were similar across all years for males and females (Table 2), which indicated similar usage of the bone pile by both sexes.

DISCUSSION

Our estimates (Table 2) indicated that a range of approximately 6%–16% of the subpopulation visited the bone pile using the most recent subpopulation estimate of ~900 bears in 2010 (Bromaghin et al., 2015). We obtained similar estimates for the proportion of males and females visiting the bone pile across all years. As well, we found that males and females had moderate site fidelity to the bone pile, while the probability of a bear entering the study site during a given sampling occasion was low (Table 2). Collectively, our estimates of ϕ suggested that approximately 50%–70% of individual polar bears remained at the bone pile throughout the fall and early winter, and the low p_{ent} suggests most bears were present on the bone pile at the start of the sampling period. Our estimated proportion of SB bears that used the bone pile in 2012 is similar to a previous estimate of bears that used a different bone pile—near Utqiagvik (formerly Barrow, Fig. 1), Alaska—during the winter of 2010–11 (Herreman and Peacock, 2013). Herreman and Peacock (2013) estimated that approximately 15% of the SB subpopulation used the Utqiagvik bone pile using the subpopulation estimate of 1526 bears from 2006 (Regehr et al., 2006). The number of bears onshore appears to be related to sea ice conditions (Atwood et al., 2016). Hence, we suspect that the number of polar bears visiting the bone pile likely fluctuated among years because of other factors (e.g., sea ice conditions and quantity of subsistence-harvested whale remains).

The capture-recapture assumption that individuals are independent may have been violated because we were unable to identify and eliminate dependent cubs from the dataset. This violation would result in variance estimates that were biased low (i.e., the precision of N^* may be overestimated; Boulanger et al., 2004). In addition, our N^* estimates may be biased low because some bears in

the population might be excluded from the bone pile by dominant bears and some might have visited the bone pile outside of the sampling period. Another way N^* could be biased low is if there were heterogeneity in capture probabilities, but we did not detect over-dispersion in the datasets (i.e., \hat{c} was < 1). Lastly, there was a possibility that some bears fed on bowhead remains outside of the hair snag perimeter. Shares of the whale are left in the open for a short amount of time (a day or two) near the butchering site before they are delivered to residences. There is also some diversionary feeding of bears by whalers that occurs during the butchering process. So, in short, there are opportunities for bears to feed on small amounts of whale remains outside of the hair snag. However, we assumed the majority of these bears also visited the bone pile.

Hair snags have the potential to be important tools for monitoring the occurrence of SB polar bears on land and have the benefit of being less costly and invasive than live-capture procedures. Although live-capturing of polar bears provides meaningful and necessary information for conservation and management purposes (Bromaghin et al., 2015; Atwood et al., 2016; Pagano et al., 2018), sampling polar bears using hair snags can be readily used to enhance our knowledge and supplement sample sizes (i.e., genetic marks), as demonstrated by this and previous studies (Herreman and Peacock, 2013; Lillie et al., 2018). We recommend that data continue to be collected at the Kaktovik bone pile for additional years with the goal of using other genetic capture-recapture models (e.g., multi-state open robust design), which can accurately separate estimates of true annual survival from fidelity.

We found that a maximum estimate of 16% of the SB polar bear subpopulation visited the bone pile near Kaktovik, Alaska. Collectively, this and the Utqiagvik study (Herreman and Peacock, 2013) indicate the importance of whale remains across the North Slope of Alaska as a large proportion of the SB subpopulation made use of the bone piles.

Polar bears that feed at the Kaktovik bone pile are close to a human settlement, which creates the potential for human-bear interactions and conflicts. A second bone pile location available to SB polar bears at Cross Island, Alaska, is also close to human settlements (i.e., the Prudhoe Bay and Kuparuk River oil fields). It is widely understood that the chronic consumption of human-provisioned food and resultant food conditioning of consumers enhance the risk of human-wildlife conflict (Hopkins et al., 2012; Herrero, 2018). The Arctic is expected to continue to warm (Larsen et al., 2014), thus we expect polar bears will become more reliant on subsistence-harvested bowhead whale carcasses, which will then likely result in more food-conditioned bears. If human-bear conflicts increase and are found to be associated with polar bears using bone piles, we suggest evaluating the advantages and disadvantages of providing polar bears with access to bone piles, or dispersing whale remains over a broader area away from communities (e.g., Wilson et al., 2017).

TABLE 1. Model selection results from capture-mark-recapture POPAN model for polar bears that used the Kaktovik, Alaska, bone pile for 2011, 2012, and 2014. Models with model weights (w_i) equal to or greater than 0.001 are shown.

Model ¹	K	AIC _c	Δ AIC _c	w_i
2011:				
$\phi(.)p(t)pent(.)$	10	269.847	0.000	0.396
$\phi p(.)pent(t)$	12	271.828	1.981	0.147
$\phi(.)p(t)pent(s)$	11	272.203	2.356	0.122
$\phi(s)p(t)pent(.)$	11	272.238	2.391	0.120
$\phi(t)p(s)pent(t)$	13	274.309	4.462	0.043
$\phi(.)p(.)pent(t)$	8	274.574	4.727	0.037
$\phi(s)p(t)pent(s)$	12	274.631	4.784	0.036
$\phi(.)p(t)pent(t)^2$	13	275.015	5.168	0.030
$\phi(.)p(s)pent(t)$	9	276.748	6.900	0.013
$\phi(s)p(.)pent(t)$	9	276.892	7.045	0.012
$\phi(t)p(t)pent(s)^2$	15	277.063	7.216	0.011
$\phi(s)p(t)pent(t)^2$	14	277.525	7.678	0.009
$\phi(t)p(.)pent(.)$	9	277.733	7.886	0.008
$\phi(s)p(s)pent(t)$	10	279.101	9.254	0.004
$\phi(t)p(.)pent(s^*t)$	16	279.718	9.871	0.003
$\phi(t)p(.)pent(s)$	10	280.062	10.215	0.002
$\phi(t)p(s)pent(.)$	10	280.082	10.235	0.002
$\phi(t)p(t)pent(t)^2$	17	281.256	11.409	0.001
$\phi(s^*t)p(.)pent(t)^2$	17	281.684	11.837	0.001
2012:				
$\phi(.)p(t)pent(t)^2$	13	279.125	0.000	0.501
$\phi(.)p(t)pent(.)$	10	281.147	2.021	0.182
$\phi(s)p(t)pent(t)^2$	14	281.514	2.389	0.152
$\phi(.)p(t)pent(s)$	11	283.425	4.300	0.058
$\phi(s)p(t)pent(.)$	11	283.437	4.312	0.058
$\phi(s)p(t)pent(s)$	12	285.750	6.625	0.018
$\phi(.)p(t)pent(s^*t)^2$	17	286.025	6.900	0.016
$\phi(.)p(s^*t)pent(t)^2$	19	288.136	9.011	0.006
$\phi(t)p(t)pent(.)^2$	14	288.723	9.598	0.004
$\phi(.)p(s^*t)pent(.)$	16	290.020	10.894	0.002
$\phi(t)p(t)pent(s)^2$	15	291.149	12.024	0.001
2014:				
$\phi(t)p(.)pent(s)$	9	154.222	0.000	0.510
$\phi(t)p(s)pent(s)$	10	156.774	2.552	0.142
$\phi(t)p(.)pent(.)$	8	157.903	3.681	0.081
$\phi(.)p(t)pent(s)$	10	158.568	4.346	0.058
$\phi(.)p(.)pent(s)$	6	158.645	4.423	0.056
$\phi(t)p(s)pent(.)$	9	160.432	6.210	0.023
$\phi(s)p(.)pent(s)$	7	160.979	6.757	0.017
$\phi(.)p(s)pent(s)$	7	161.104	6.882	0.016
$\phi(s)p(t)pent(s)$	11	161.361	7.139	0.014
$\phi(.)p(t)pent(.)$	9	162.139	7.917	0.010
$\phi(.)p(.)pent(.)$	5	162.360	8.138	0.009
$\phi(t)p(t)pent(s)$	13	162.482	8.260	0.008
$\phi(t)p(.)pent(t)$	10	162.663	8.441	0.007
$\phi(t)p(t)pent(t)^2$	12	162.982	8.760	0.006
$\phi(s^*t)p(.)pent(s)$	13	163.270	9.048	0.006
$\phi(s)p(s)pent(s)$	8	163.521	9.299	0.005
$\phi(.)p(t)pent(s^*t)^2$	13	163.951	9.729	0.004
$\phi(.)p(s)pent(.)$	6	163.976	9.754	0.004
$\phi(s)p(.)pent(.)$	6	164.746	10.524	0.003
$\phi(s)p(t)pent(.)$	10	164.796	10.574	0.003
$\phi(s)p(s^*t)pent(t)^2$	12	164.862	10.640	0.003
$\phi(t)p(.)pent(s^*t)$	13	165.143	10.921	0.002
$\phi(t)p(s)pent(t)$	11	165.270	11.048	0.002
$\phi(t)p(t)pent(.)^2$	12	165.713	11.491	0.002
$\phi(.)p(t)pent(t)^2$	11	166.178	11.956	0.001
$\phi(s^*t)p(s)pent(s)$	14	166.211	11.989	0.001
$\phi(s)p(s)pent(.)$	7	166.322	12.100	0.001
$\phi(.)p(.)pent(t)$	7	166.335	12.113	0.001
$\phi(s^*t)p(.)pent(.)$	12	166.546	12.324	0.001
$\phi(.)p(s)pent(t)$	8	167.998	13.776	0.001

¹ Key to model notation: K = Number of parameters; AIC_c = Akaike Information Criterion corrected; Δ AIC = difference between the model listed and the AIC_c of the best model; w_i = model weights based on model AIC_c compared to all other model AIC_c values; ϕ = site fidelity between sampling occasions; p = detection probability; p_{ent} = probability of entry between sampling occasions; t = sampling occasion as a categorical variable; s = sex as a group; “.” = constant across encounter occasion and sex.

² Model was not used in model averaging because of potential confounded estimate of N and N^* .

TABLE 2. Model-averaged estimates from the POPAN model of the annual number of female and male polar bears (N) using the bone pile near Kaktovik, Alaska, detection probability (p), entry probability (p_{ent}), site fidelity (ϕ), and standard errors (SE) for 2011, 2012, and 2014. We averaged across the sampling occasions for each year for p , p_{ent} , and ϕ . Only models without any confounding parameters were used for model averaging.

Parameter	Sex	Estimate	SE
2011:			
N	Male	66	8
	Female	51	7
ϕ	Male	0.67	0.09
	Female	0.67	0.09
p	Male	0.47	0.14
	Female	0.47	0.14
p_{ent}	Male	0.09	0.04
	Female	0.09	0.04
2012:			
N	Male	72	9
	Female	76	10
ϕ	Male	0.64	0.08
	Female	0.64	0.08
p	Male	0.42	0.08
	Female	0.42	0.08
p_{ent}	Male	0.08	0.02
	Female	0.08	0.02
2014:			
N	Male	26	3
	Female	26	6
ϕ	Male	0.52	0.17
	Female	0.51	0.17
p	Male	0.70	0.11
	Female	0.71	0.13
p_{ent}	Male	0.01	0.02
	Female	0.08	0.04

Previous studies on grizzly and black bears (*Ursus americanus*) found that human-bear conflicts markedly decreased when bear access to anthropogenic food sources (e.g., garbage) was essentially eliminated, though loss of access to an important food subsidy can adversely affect population dynamics (Gunther, 1994). Onshore behavior appears to develop through social learning from mother to offspring (Lillie et al., 2018). Thus, properly managing polar bears (mother and cubs in particular) that visit the bone pile will be necessary if human-polar bear conflict arises. Managing the risk of human-polar bear conflict resulting from bears visiting the bone pile may require collaboration between resource managers and the community, along with regular monitoring for the potential of adverse population-level effects.

ACKNOWLEDGEMENTS

This work was supported by the Graduate Research Fellowship Program from the National Science Foundation (Grant No. 1147384 to K.M. Lillie), the U.S. Geological Survey's Alaska Science Center, Utah State University, and the U.S. Department of Agriculture, Wildlife Services' National Wildlife Research Center. Funding to the U.S. Geological Survey's Alaska Science Center was provided through the Changing Arctic Ecosystems

Initiative and the Wildlife Program of the Ecosystems Mission Area, and the Bureau of Land Management. We thank C. Simms, A. Smith III, and J. Smith for maintaining the sampling effort at Kaktovik. We appreciate the logistical support provided by the Arctic National Wildlife Refuge and U.S. Air Force. We wish to express our gratitude to the residents of Kaktovik for allowing us to work in their community. This research was approved under the Marine Mammal Protection Act and Endangered Species Act with U.S. Fish and Wildlife Service (USFWS) permit number MA690038. Capture protocols were approved by the U.S. Geological Survey (USGS) Institutional Animal Care and Use Committee. Any use of trade names is for descriptive purposes only and does not reflect endorsement by the U.S. government. Any opinion, findings, conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. The findings and conclusions in this publication have not been formally disseminated by the U.S. Department of Agriculture and should not be construed to represent any agency determination or policy.

REFERENCES

- Amstrup, S.C. 2003. Polar bear, *Ursus maritimus*. In: Feldhamer, G.A., Thompson, B.C., and Chapman, J.A., eds. Wild mammals of North America: Biology, management, and conservation, 2nd ed. Baltimore: Johns Hopkins University Press. 587–610.
- Amstrup, S.C., Stirling, I., and Lentfer, J.W. 1986. Past and present status of polar bears in Alaska. *Wildlife Society Bulletin* 14(3):241–254.
- Amstrup, S.C., Durner, G.M., Stirling, I., Lunn, N.J., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Canadian Journal of Zoology* 78(6):948–966. <https://doi.org/10.1139/z00-016>
- An, J., Bechet, A., Berggren, Å., Brown, S.K., Bruford, M.W., Cai, Q., Cassel-Lundhagen, A., et al. 2010. Permanent genetic resources added to molecular ecology resources Database 1 October 2009–30 November 2009. *Molecular Ecology Resources* 10(2):404–408. <https://doi.org/10.1111/j.1755-0998.2009.02827.x>
- Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., et al. 2010. Climate variability, oceanography, bowhead whale distribution, and Iñupiat subsistence whaling near Barrow, Alaska. *Arctic* 63(2):179–194. <https://doi.org/10.14430/arctic973>
- Atwood, T.C., Peacock, E., McKinney, M.A., Lillie, K., Wilson, R., Douglas, D.C., Miller, S., and Terletzky, P. 2016. Rapid environmental change drives increased land use by an Arctic marine predator. *PLoS ONE* 11: e0155932. <https://doi.org/10.1371/journal.pone.0155932>
- Atwood, T.C., Duncan, C., Patyk, K.A., Nol, P., Rhyan, J., McCollum, M., McKinney, M.A., et al. 2017. Environmental and behavioral changes may influence the exposure of an Arctic apex predator to pathogens and contaminants. *Scientific Reports* 7: 13193. <https://doi.org/10.1038/s41598-017-13496-9>

- Bromaghin, J.F., McDonald, T.L., Stirling, I., Derocher, A.E., Richardson, E.S., Regehr, E.V., Douglas, D.C., Durner, G.M., Atwood, T., and Amstrup, S.C. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications* 25(3):634–651.
<https://doi.org/10.1890/14-1129.1>
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer-Verlag.
- Cooch, E.G., and White, G.C. 2017. Program MARK: A gentle introduction, 17th ed.
<http://www.phidot.org/software/mark/docs/book/>
- Craighead, J.J., Summer, J.S., and Mitchell, J.A. 1995. The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem. Washington, D.C.: Island Press.
- Doherty, P.F., White, G.C., and Burnham, K.P. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152(Suppl. 2):317–323.
<https://doi.org/10.1007/s10336-010-0598-5>
- Gautier, D.L., Bird, K.J., Charpentier, R.R., Grantz, A., Houseknecht, D.W., Klett, T.R., Moore, T.E., et al. 2009. Assessment of undiscovered oil and gas in the Arctic. *Science* 324(5931):1175–1179.
<https://doi.org/10.1126/science.1169467>
- Gleason, J.S., and Rode, K.D. 2009. Polar bear distribution and habitat association reflect long-term changes in fall sea ice conditions in the Alaskan Beaufort Sea. *Arctic* 62(4):405–417.
<https://doi.org/10.14430/arctic172>
- Gunther, K.A. 1994. Bear management in Yellowstone National Park, 1960-93. *Bears: Their Biology and Management* 9 (Part 1):549–560.
<https://doi.org/10.2307/3872743>
- Herreman, J., and Peacock, E. 2013. Polar bear use of a persistent food subsidy: Insights from non-invasive genetic sampling in Alaska. *Ursus* 24(2):148–163.
<https://doi.org/10.2192/URSUS-D-12-00030.1>
- Herrero, S. 2018. Bear attacks: Their causes and avoidance, 3rd ed. Lanham, Maryland: Rowan & Littlefield.
- Hopkins, J.B., III, Koch, P.L., Schwartz, C.C., Ferguson, J.M., Greenleaf, S.S., and Kalinowski, S.T. 2012. Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *Journal of Wildlife Management* 76(4):703–713.
<https://doi.org/10.1002/jwmg.318>
- Kendall, K.C., Stetz, J.B., Roon, D.A., Waits, L.P., Boulanger, J.B., and Paetkau, D. 2008. Grizzly bear density in Glacier National Park, Montana. *Journal of Wildlife Management* 72(8):1693–1705.
<https://doi.org/10.2193/2008-007>
- Kendall, W.L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80(8):2517–2525.
[https://doi.org/10.1890/0012-9658\(1999\)080\[2517:ROCCRM\]2.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2517:ROCCRM]2.CO;2)
- Kitahara, E., Isagi, Y., Ishibashi, Y., and Saitoh, T. 2000. Polymorphic microsatellite DNA markers in the Asiatic black bear *Ursus thibetanus*. *Molecular Ecology* 9(10):1661–1662.
<https://doi.org/10.1046/j.1365-294x.2000.01030.x>
- Koski, W.R., George, J.C., Sheffield, G., and Galginaitis, M.S. 2005. Subsistence harvests of bowhead whales (*Balaena mysticetus*) at Kaktovik, Alaska (1973–2000). *Journal of Cetacean Research and Management* 7(1):33–37.
- Larsen, J.N., Anisimov, O.A., Constable, A., Hollowed, A.B., Maynard, N., Prestrud, P., Prowse, T.D., and Stone, J.M.R. 2014. Polar regions. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., et al., eds. *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press. 1567–1612.
- Lillie, K.M., Gese, E.M., Atwood, T.C., and Sonsthagen, S.A. 2018. Development of on-shore behavior among polar bears (*Ursus maritimus*) in the southern Beaufort Sea: Inherited or learned? *Ecology and Evolution* 8(16):7790–7799.
<https://doi.org/10.1002/ece3.4233>
- Lyons, J., Mastro Monaco, G., Edwards, D.B., and Schulte-Hostedde, A.I. 2017. Fat and happy in the city: Eastern chipmunks in urban environments. *Behavioral Ecology* 28(6):1464–1471.
<https://doi.org/10.1093/beheco/arx109>
- McKinney, M.A., Atwood, T.C., Iverson, S.J., and Peacock, E. 2017. Temporal complexity of southern Beaufort Sea polar bear diets during a period of increasing land use. *Ecosphere* 8(1): e01633.
<https://doi.org/10.1002/ecs2.1633>
- Ostrander, E.A., Sprague, G.F., Jr., and Rine, J. 1993. Identification and characterization of dinucleotide repeat (CA)_n markers for genetic mapping in dog. *Genomics* 16(1):207–213.
<https://doi.org/10.1006/geno.1993.1160>
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12(6):1375–1387.
<https://doi.org/10.1046/j.1365-294X.2003.01820.x>
- Paetkau, D., and Strobeck, C. 1994. Microsatellite analysis of genetic variation in black bear populations. *Molecular Ecology* 3(5):489–495.
<https://doi.org/10.1111/j.1365-294X.1994.tb00127.x>
- Paetkau, D., Calvert, W., Stirling, I., and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4(3):347–354.
<https://doi.org/10.1111/j.1365-294X.1995.tb00227.x>
- Pagano, A.M., Durner, G.M., Rode, K.D., Atwood, T.C., Atkinson, S.N., Peacock, E., Costa, D.P., Owen, M.A., and Williams, T.M. 2018. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science* 359(6375):568–572.
<https://doi.org/10.1126/science.aan8677>
- Pongracz, J.D., and Derocher, A.E. 2017. Summer refugia of polar bears (*Ursus maritimus*) in the southern Beaufort Sea. *Polar Biology* 40(4):753–763.
<https://doi.org/10.1007/s00300-016-1997-8>
- Proctor, M.F., McLellan, B.N., and Strobeck, C. 2002. Population fragmentation of grizzly bears in southeastern British Columbia, Canada. *Ursus* 13:153–160.

- Raynolds, M.K., Walker, D.A., Ambrosius, K.J., Brown, J., Everett, K.R., Kanevskiy, M., Kofinas, G.P., Romanovsky, V.E., Shur, Y., and Webber, P.J. 2014. Cumulative geoeological effects of 62 years of infrastructure and climate change in ice-rich permafrost landscapes, Prudhoe Bay Oilfield, Alaska. *Global Change Biology* 20(4):1211–1224.
<https://doi.org/10.1111/gcb.12500>
- Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. Polar bear population status in the southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006-1337. Anchorage: Alaska Science Center, U.S. Geological Survey. 20 p.
<https://doi.org/10.3133/ofr20061337>
- Rode, K.D., Fortin-Noreus, J.K., Garshelis, D., Dyck, M., Sahanatien, V., Atwood, T., Belikov, S., et al. 2018. Survey-based assessment of the frequency and potential impacts of recreation on polar bears. *Biological Conservation* 227:121–132.
<https://doi.org/10.1016/j.biocon.2018.09.008>
- Rogers, M.C., Peacock, E., Simac, K., O'Dell, M.B., and Welker, J.M. 2015. Diet of female polar bears in the southern Beaufort Sea of Alaska: Evidence for an emerging alternative foraging strategy in response to environmental change. *Polar Biology* 38(7):1035–1047.
<https://doi.org/10.1007/s00300-015-1665-4>
- Roth, J.D. 2003. Variability in marine resources affects Arctic fox population dynamics. *Journal of Animal Ecology* 72(4):668–676.
<https://doi.org/10.1046/j.1365-2656.2003.00739.x>
- Schliebe, S., Rode, K.D., Gleason, J.S., Wilder, J., Proffitt, K., Evans, T.J., and Miller, S. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the southern Beaufort Sea. *Polar Biology* 31(8):999–1010.
<https://doi.org/10.1007/s00300-008-0439-7>
- Schwarz, C.J., and Arnason, A.N. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52(3):860–873.
<https://doi.org/10.2307/2533048>
- Serreze, M.C., and Stroeve, J. 2015. Arctic sea ice trends, variability and implications for seasonal ice forecasting. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 373: 20140159.
- Stanley, T.R., and Burnham, K.P. 1999. A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6(2):197–209.
<https://doi.org/10.1023/A:1009674322348>
- Stern, H.L., and Laidre, K.L. 2016. Sea-ice indicators of polar bear habitat. *The Cryosphere* 10(5):2027–2041.
<https://doi.org/10.5194/tc-10-2027-2016>
- Stirling, I., and Derocher, A.E. 2012. Effects of climate warming on polar bears: A review of the evidence. *Global Change Biology* 18(9):2694–2706.
<https://doi.org/10.1111/j.1365-2486.2012.02753.x>
- Suydam, R., George, J.C., Person, B., Hanns, C., Stimmelmayer, R., Pierce, L., and Sheffield, G. 2012. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2011. SC/64/BRG2. Presented to the 64th International Whaling Commission. Barrow, Alaska: Department of Wildlife Management, North Slope Borough.
- . 2013. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2012. SC/65a/BRG19. Presented to the 65th International Whaling Commission. Barrow, Alaska: Department of Wildlife Management, North Slope Borough.
- . 2014. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2013. SC/65b/BRG08. Presented to the 65th International Whaling Commission. Barrow, Alaska: Department of Wildlife Management, North Slope Borough.
- Suydam, R., George, J.C., Person, B., Ramey, D., Hanns, C., Stimmelmayer, R., Pierce, L., and Sheffield, G. 2015. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2014. SC/66/BRG06. Presented to the 66th International Whaling Commission. Barrow, Alaska: Department of Wildlife Management, North Slope Borough.
- Taberlet, P., Camarra, J.-J., Griffin, S., Uhrès, E., Hanotte, O., Waits, L.P., Dubois-Paganon, C., Burke, T., and Bouvet, J. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Molecular Ecology* 6(9):869–876.
<https://doi.org/10.1111/j.1365-294X.1997.tb00141.x>
- Thirgood, S., Woodroffe, R., and Rabinowitz, A. 2005. The impact of human-wildlife conflict on human lives and livelihoods. In: Woodroffe, R., Thirgood, S., and Rabinowitz, A., eds. *People and wildlife: Conflict or co-existence?* New York: Cambridge University Press. 13–26.
<https://doi.org/10.1017/CBO9780511614774.003>
- Towns, L., Derocher, A.E., Stirling, I., Lunn, N.J., and Hedman, D. 2009. Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biology* 32(10):1529–1537.
<https://doi.org/10.1007/s00300-009-0653-y>
- White, G.C., and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46(Suppl. 1):S120–S139.
<https://doi.org/10.1080/00063659909477239>
- Wilson, R.R., Regehr, E.V., St. Martin, M., Atwood, T.C., Peacock, E., Miller, S., and Divoky, G. 2017. Relative influences of climate change and human activity on the onshore distribution of polar bears. *Biological Conservation* 214:288–294.
<https://doi.org/10.1016/j.biocon.2017.08.005>
- Woodroffe, R., Thirgood, S., and Rabinowitz, A. 2005. The impact of human-wildlife conflict on natural systems. In: Woodroffe, R., Thirgood, S., and Rabinowitz, A., eds. *People and wildlife: Conflict or co-existence?* New York: Cambridge University Press. 1–12.
<https://doi.org/10.1017/CBO9780511614774.002>