Using Visual Observations to Compare the Behavior of Previously Immobilized and Non-Immobilized Wild Polar Bears

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ABSTRACT. During 17 field seasons between 1973 and 1999, we conducted a long-term study of the behavior of undisturbed wild polar bears in Radstock Bay, southwest Devon Island, Nunavut. In a subset of 11 seasons (6 spring and 5 summer) between 1975 and 1997, we used three different drug combinations to chemically immobilize a small number of adult and subadult polar bears on an opportunistic basis and applied a temporary dye mark so that individual bears could be visually reidentified. We then used multinomial logistic regression to compare the behavior of 35 previously immobilized bears of five different demographic classes (sex, age, and reproductive status) to the behavior of non-immobilized bears of the same demographic classes in the same years and seasons. During the first two days after immobilization, bears slept significantly more and spent less time hunting than did bears that had not been immobilized. However, previously immobilized bears returned to the same behavioral patterns and proportion of total time spent hunting as non-immobilized bears within two days and no further negative behavioral effects were detected in the following 21 d. We visually confirmed successful hunting by three adult bears within 0.4 to 2.1 d of being immobilized, all of which went on to make additional kills within the following 24 h. The return to normal behavior patterns, including the ability to hunt successfully, within 48 h of immobilization appears consistent with the hypothesis that polar bears do not experience longer-term behavioral effects following brief chemical immobilization for conservation and management purposes.

Key words: activity budget; behavior; chemical immobilization; handling effects; hunting success; diel cycle; lunar cycle; multinomial logistic regression; polar bear; *Ursus maritimus*

RÉSUMÉ. Durant 17 saisons de recherche, entre 1973 et 1999, nous avons effectué l'étude à long terme du comportement d'ours polaires sauvages non perturbés à la baie Radstock, dans le sud-ouest de l'île Devon, au Nunavut. Dans un sous-ensemble de 11 saisons (six printemps et cinq étés) échelonnées de 1975 à 1997, nous avons utilisé trois combinaisons de drogues différentes pour immobiliser chimiquement un petit nombre d'ours polaires adultes et d'ours polaires immatures de manière opportuniste, puis nous avons appliqué une marque de colorant temporaire sur les ours afin de pouvoir les réidentifier individuellement. Ensuite, nous avons recouru à la régression logistique multinomiale pour comparer le comportement de 35 ours précédemment immobilisés faisant partie de cinq catégories démographiques différentes (sexe, âge et état reproducteur) au comportement d'ours non immobilisés faisant partie des mêmes catégories démographiques pour les mêmes années et les mêmes saisons. Au cours des deux premières journées suivant l'immobilisation, les ours dormaient beaucoup plus et consacraient moins de temps à la chasse que les ours qui n'avaient pas été immobilisés. Cependant, les ours qui avaient été immobilisés ont repris les mêmes habitudes de comportement et consacré le même temps à la chasse que les ours non immobilisés en dedans de deux jours, et aucun autre effet négatif sur leur comportement n'a été décelé au cours des 21 jours qui ont suivi. Nous avons eu la confirmation visuelle d'une chasse réussie par trois ours adultes dans la période de 0,4 à 2,1 jours suivant l'immobilisation, tous trois ayant réussi à faire d'autres prises dans les 24 heures qui ont suivi. Le retour aux habitudes de comportement normales, y compris l'aptitude à faire une chasse réussie, dans les 48 heures suivant l'immobilisation semble cadrer avec l'hypothèse selon laquelle les ours polaires ne subissent pas d'effets comportementaux de longue haleine après une brève immobilisation chimique à des fins de conservation et de gestion.

Mots clés : budget des activités; comportement; immobilisation chimique; effets de la manipulation; réussite de la chasse; cycle diel; cycle lunaire; régression logistique multinomiale; ours polaire; *Ursus maritimus*

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INTRODUCTION

Article II of the [International] Agreement on the Conservation of Polar Bears, signed in 1973 by the five Arctic countries responsible for managing polar bears and ratified in 1976, specifically states that, "Each Contracting Party shall take appropriate action to protect the ecosystems of which polar bears are a part, with special attention to habitat components such as denning and feeding sites and migration patterns, and *shall manage polar bear populations in accordance with sound conservation practices based on the best available scientific data* (our emphasis). Throughout their circumpolar range, short-term chemical immobilization of polar bears has been a key method to facilitate the collection of data for estimations of abundance and other biological parameters such as morphological measurements, reproductive success, movements, and habitat use that are important for management and conservation (Vongraven et al., 2012).

Because of the shared concerns of scientists, Indigenous hunters, and others about the possibility of negative effects on polar bears resulting from chemical immobilization (e.g., Wong et al., 2017), several quantitative studies have been undertaken to address the issue. When the results of initial analyses, which assessed factors such as survival, body condition, and reproductive success of individually marked bears at the time of their first capture, were compared to the same data collected during subsequent recaptures, no significant negative effects resulted (Ramsay and Stirling, 1986; Amstrup, 1993; Messier, 2000; Lunn et al., 2004). Although Ramsay and Stirling (1986) found that adult female polar bears with cubs first captured in western Hudson Bay between 1967 and 1984 weighed significantly less when they were recaptured a few years later, subsequent research demonstrated that polar bears in most demographic classes (i.e., representing sex, age, and reproductive status) in western Hudson Bay lost body mass over time because progressively earlier breakup of the sea ice had shortened the critical spring feeding period (Stirling et al., 1999; Stirling and Parkinson, 2006; Regehr et al., 2007). Thus, it became apparent that the female bears' loss of weight was caused by climate warming, not because of having been previously immobilized. Most recently, two studies used satellite collars deployed on immobilized polar bears (predominantly adult females) to determine the time required for bears to return to normal movement patterns. Thiemann et al. (2013) found that 69% of their study animals returned to normal in less than 3 d and the rest shortly thereafter, while Rode et al. (2014) found that bears reached near normal activity levels in 2–3 d and fully normal activity in 5 d.

During an overall total of 17 field seasons (7 spring and 10 summer) between 1973 and 1999, we conducted a long-term study of the behavior of undisturbed wild polar bears in Radstock Bay, southwest Devon Island, Nunavut. In a subset of 11 seasons (six in spring, five in summer) between 1975 and 1997, we immobilized small numbers of polar bears of all demographic classes and applied a temporary dye mark to facilitate identification. In this study, we used visual observations of the behavior and hunting success of previously immobilized polar bears compared to observations of non-immobilized polar bears of the same demographic classes in the same seasons to address the following three objectives: 1) independently evaluate the conclusions of previous immobilization studies that were based on mark-recapture data and movements of satellite-tracked bears rather than on direct visual observations, which provide more detailed behavioral data, 2) document how soon after immobilization bears returned to successful hunting, and 3) evaluate how long after immobilization observations of previously immobilized and non-immobilized bears could be pooled for future behavioral analyses.

METHODS

Study Area

Radstock Bay, on southwest Devon Island, Nunavut, Canada (Fig. 1), was selected for our study because it contains prime polar bear hunting habitat in both spring and summer. Additionally, the south coast of Devon Island and associated bays were known from ongoing population studies to usually have substantial numbers of bears (Stirling et al., 1984). A pilot study conducted in 1973 using visual observations to quantify the behavior of free-ranging polar bears confirmed the validity of the approach and the suitability of Radstock Bay for a long-term observational study of undisturbed wild polar bears that was envisaged at the time (Stirling, 1974). Radstock Bay is approximately 30 km long and 12 km wide at the mouth. From spring through early summer (April–July), both the bay and much of Barrow Strait, immediately south of the coastline of Devon Island, are usually ice-covered. Because the region is a polar desert, the smooth expanses of annual ice in sheltered areas such as deep bays and fjords are covered with only a few centimeters of snow. Thus, few ringed seals (*Pusa hispida*) overwinter deep in the bays because there is insufficient snow to hide breathing holes or facilitate the creation of birth and haul-out lairs. However, winter winds form drifts deep enough to hide abundant ringed seal breathing holes, haul-out lairs, and birth lairs along the pressure ridges that form in the outer few kilometers of the mouths of bays along the southern coast of Devon Island and offshore into Barrow Strait to the south (Calvert and Stirling, 1985; Hammill and Smith, 1989). Thus, during spring and early summer, bears of all demographic classes (except for dependent cubs, Stirling and Latour, 1978) primarily hunt ringed seals and, to a lesser degree, bearded seals (*Erignathus barbatus*) along pressure ridges and associated snowdrifts near the mouth of Radstock Bay and farther into the bay itself along new leads and pools of open water as they form from late spring through to breakup of the sea ice (Stirling and Archibald, 1977; Smith, 1980).

FIG. 1. Map of the study area at Radstock Bay, southwest Devon Island, Nunavut. Circles around camp locations indicate the 5 km radius of optimal viewing distances. The view south from Cape Liddon was obscured by a rising hillside.

Capture and Marking of Polar Bears for Possible Observation

For this project, we defined spring as 15 April to 5 June and summer as 25 June to 20 July. The spring season was chosen to encapsulate the six-week period from birth to weaning of ringed seal pups (approximately between early April and late May; McLaren, 1958; Smith, 1987). During that time, much of the hunting behavior of bears in the land-fast ice is focused on seal subnivean birth lairs and breathing holes primarily occupied by territorial breeding adults and newborn pups (Smith and Stirling, 1975). The summer season was selected to represent the period when snow on the sea ice was largely melted, exposing breathing holes and newly formed cracks in the ice. The ringed seal breeding season is finished so the absence of territorial behavior beneath the ice makes it possible for seals of all ages, including recently weaned and naïve pups and subadults, to move freely while feeding beneath the ice and breathe in the newly formed cracks, pools, and undefended breathing holes.

Prior to or near the beginning of 11 observation periods between 1975 and 1997, small numbers of polar bears (1–7) were immobilized nonselectively for roughly 60 min by firing an immobilization dart from a helicopter as the bear ran on the sea ice in Radstock Bay and up to about 25 km away. The drugs used to immobilize polar bears were, from 1975 to 1977, a mixture of Sernylan® (phenylcyclidine hydrochloride) and Sparine® (tiletamine hydrochloride); in 1980, Rompun® (xylazine hydrochloride) and Ketamine® (ketamine hydrochloride); and from 1990 to 1997, Telazol® (a mixture of tiletamine hydrochloride and zolazepam hydrochloride), which became the most widely used drug for polar bears in 1986 because of its superior overall safety record and reduced side effects (Stirling et al., 1989; Rode et al., 2014). However, inclusion of our visual observations of the responses of polar bears immobilized with drug combinations used prior to the widespread adoption of Telazol in this study, but which are no longer in use for bears or have been discontinued, provides a unique opportunity to independently reassess whether there might have been detectable changes in the bears' behavior that were not identified by the methods available at the time. The number of bears immobilized each year fluctuated due to variable research funding and numbers of bears present in or near Radstock Bay at the time each observation period began. While immobilized, each bear was given a unique but temporary alphanumeric dye mark on its rump, side, or shoulder to facilitate its identification if resighted.

Immobilized bears were assigned ages based on collection of a vestigial premolar and counting the annuli (Calvert and Ramsay, 1998). Although ages of all dependent cubs (0.5–2.5 y) accompanying their mothers were recorded and they were individually marked, their behaviors were not quantified during this study as they are largely ineffectual hunters, and most of their activities are determined by their mothers (Stirling and Latour, 1978). The age of first breeding of polar bears in the Lancaster Sound population is four years; thus, for this study, subadults were defined as independent bears 2.5–3.5 y of age (Stirling et al., 1984). Male and female subadults were pooled for analyses because of small sample sizes.

All capture and tagging of polar bears were approved by the Canadian Wildlife Service Animal Care Committee. Behavioral observations were conducted under research permits from the Government of the Northwest Territories and with the consent of the Hunters and Trappers Association in Resolute, Nunavut (formerly Northwest Territories).

Observing and Recording Behavior

Polar bears were observed from small all-weather huts (Fig. 2) located on the edges of cliffs on Cape Liddon (300 m asl, 74°38′ N, 91° 06′ W) and Caswell Tower (234 m asl, 74°43′ N; 91°11′ W) in Radstock Bay (Fig. 1). Individual bears were located on the ice by semi-continuous searching at 15–30 min intervals with 15–60× zoom Bausch and Lomb telescopes and then observed for as long as they remained visible, using the focal animal approach (Altmann, 1974; Stirling, 1974). There were 2–4 observers in the camp during each observation period.

FIG. 2. Polar bear observation camp at Cape Liddon, Radstock Bay, during a spring observation period.

Twenty-four-hour daylight in both spring and summer facilitated continuous observation except during occasional fog patches, blowing snow, or when the bear disappeared behind an ice ridge or a land feature. A bear's behavior could often be reliably documented at distances of up to 7–8 km, depending on light conditions, although the best viewing tended to be at distances of about 5 km or less as estimated from topographic maps (see 5 km optimal viewing radii from both observation camps, Fig. 1).

Whenever possible, the sex and age class of observed bears that had not been previously immobilized were estimated. Adult males were usually obvious from their larger size, body and head shape and, if not too distant, the presence of penile hairs and long guard hairs on the back of their forelegs (Derocher et al., 2005). Adult females have a smaller and slightly more compact head, often a rounder rump because of fat deposition there, and sometimes a yellowish urine spot on the rump below the base of the tail. It was more difficult to distinguish young adult males from adult females that were not accompanied by dependent cubs. In some cases, the sex of two distant bears together could be inferred from their behavior. For example, if a smaller bear tended to walk first and was followed by a larger bear, it would be an adult female followed by the adult male of a breeding pair (Stirling et al., 2016). However, if the larger bear usually walked ahead, it would be an adult female leading a dependent cub (I. Stirling, unpubl. observ.). If the sex of a bear was uncertain, it was listed as a "U-bear" for unclassified. Records of immobilized, tagged, and individually marked bears were associated with their unique research identification numbers. Non-immobilized (and thus unmarked) bears were assigned sequential "B" numbers (i.e., B1, 2, 3…) during each observation period, but could not be individually reidentified if they returned to the study area between observation periods.

The start and stop times of all behaviors along with descriptive comments were recorded to the nearest minute in handwritten field notes and later compiled in an electronic database. If a focal bear exhibited behaviors that were directed to or in response to other individuals (excluding dependent cubs), such interactions were recorded. The durations of observations of both previously immobilized and non-immobilized bears varied as a function of how long they spent in viewable habitat (Fig. 1), their hunting success, the behavior of other bears, and weather.

Definitions of Behaviors Quantified

Observed polar bear behaviors were tabulated in four categories: hunting, investigative, sleeping, or miscellaneous.

Hunting is the most important behavior because success or failure determines body condition and thus, ultimately, survival and reproductive success (Rode et al., 2020). Spring and early summer prior to sea ice breakup is the most important period for hunting seals, during which a bear's success will largely determine its annual deposition of fat needed for reproduction and sustenance during periods of seasonal fasting (Stirling and Øritsland, 1995). Methods of hunting include the standing still hunt, sitting still hunt, lying still hunt, walking stalk, and aquatic stalk (Stirling, 1974). For the purposes of this paper, we pooled the time spent in all hunting behaviors, as well as feeding on kills, into the single category of hunting.

We use the term *investigative* to include all behaviors a bear may undertake while searching for seals, including walking and stopping to stand (sometimes on hind legs) to look around and smell. Polar bears generally walk on the sea ice at a steady pace of 3–4 km/h during which, despite sometimes appearing disinterested, they constantly assess their surroundings using sight and smell to search for

possible prey. In spring, they may vary their direction of travel to investigate drifted snow ridges which, they have learned from experience, may contain subnivean breathing holes or birth and haul out lairs (Smith and Stirling, 1975). Their state of constant alertness is confirmed by their ability to instantly change speed or direction toward a seal they may smell beneath the windblown snow, hear breathing in a hole or lead in the ice, or recognize as a distant dark spot on the ice.

We defined any period of lying, predominantly motionless, for 60 minutes or more as *sleeping*. Periods of lying for fewer than 60 minutes were allocated to the miscellaneous category. In some cases, when lying still while hunting becomes protracted, it is possible that a bear slept for part of the time although it was still capable of responding to a seal instantly if it surfaced to breathe. Thus, periods of extended motionless lying by a seal breathing hole, in a hunting position, were classified as hunting.

We pooled the following behaviors in the *miscellaneous* category: standing, sitting or lying for less than 60 minutes, drinking, defecating, swimming briefly, rolling in the snow, a female playing with her cubs or nursing, and breeding behavior.

Statistical Methods

To evaluate the behavioral response of polar bears to chemical immobilization, we designed the study so that the total durations of observations of previously immobilized bears in each demographic class and season were matched as closely as possible with the durations of observations of non-immobilized bears of the same demographic class during the same season. This study design controlled for possible variability resulting from unknown ecological fluctuations between years, such as those documented in other areas (Stirling and Lunn, 1997).

We conducted analyses using multinomial logistic regression (Hosmer et al., 2013) where the response variable (BEH_{it}) was the observed behavior of an individual polar bear (*i*) during a one-minute increment (*t*), which could assume one of the four previously defined categories: hunting (H), investigative (I), sleeping (S), and miscellaneous (M). In multinomial logistic regression, the log odds of observing a specific category of the response variable relative to a reference category are modeled as a linear combination of regression coefficients. To facilitate interpretation, we present modeling results by using estimated values of the regression coefficients to predict the probabilities of observing specific behaviors as a function of different combinations of covariates (i.e., independent variables). For example, we used the modeling results to estimate the probabilities of hunting by bears in a certain demographic class that had and had not been recently immobilized. In all models, we specified sleeping (S) as the reference category of the response variable. Thus, the probability of sleeping was calculated as one minus the summed probabilities of observing the other three

categories of the response variable. Computations were performed in the R language (version 4.0.2; R Core Team, 2020) using the package nnet (Venables and Ripley, 2002).

Multinomial logistic regression analyses followed a three-step process. First, we constructed a preliminary model that included individual, group, and environmental covariates that we hypothesized might influence polar bear behavior. The preliminary model did not include covariates related to whether or when a polar bear had been immobilized. The purpose of this step was to identify covariates that, although not the focus of our investigation, explained variation in the data and would allow a more powerful assessment of the effects of immobilization during subsequent steps of analyses.

The preliminary model can be represented as $BEH_{it} = \beta_0 + \beta_1\ season_{it} + \beta_2\ AF_{it} + \beta_3\ AFC12_{it} + \beta_4\ AM_{it} + \beta_5\ Sub_{it} + \beta_6\ season_{it}{:}AF_{it} + \beta_7\ season_{it}{:}AM_{it} + \beta_{8\text{-}10}\ moon_{it} + \beta_{11\text{-}13}\ tod_{it}$, where the β terms are vectors of regression coefficients corresponding to possible categories of the response variable. The binary covariate $season_{it}$ was set to 0 or 1 depending on whether an observation occurred in the spring or summer, respectively (Table 1). Demographic class was coded using the binary covariates AF_{it} (adult female [AF] without dependent young), $AFC12_{it}$ (adult female with yearling [C1] or two-year-old [C2] cubs), AM_{it} (adult male), and Sub_{it} (subadult of either sex). The model did not include a covariate for adult females with cubs-of-the-year (i.e., $AFC0_{it}$, where C0 represents cubs-of-the-year) because they were the reference level for demographic class. Due to sample size limitations, we used the grouped demographic classes $AFC12$ (i.e., instead of separating AFC1s from AFC2s) and Sub (i.e., instead of separating female and male subadults). The preliminary model included the interaction terms $season_{it}{:}AF_{it}$ and $season_{it}{:}AM_{it}$ because the overall patterns of behavior of adult females without dependent young and adult males during the spring may be influenced by mating activity (Molnár et al., 2008; Laidre et al., 2013; Stirling et al., 2016). The covariate $moon_{it}$ is a four-level factor for lunar phase: new (reference level), waxing, full, and waning (Lazaridis, 2022). We hypothesized that lunar phase might affect polar bear behavior based on previous ecological studies documenting its influence on light and tidal action (e.g., Benoit et al., 2010; Mercier et al., 2011; Last et al., 2016), the influence of the moon on vertical migration of zooplankton in the water column (Kim et al., 2016; Petrusevich et al., 2020,), and evidence that feeding patterns of some species of seals and whales are influenced by the lunar cycle (Trillmich and Mohren, 1981; Jansen et al., 2015; Owen et al., 2019). The covariate tod_{it} is a four-level factor for time-of-day, coded as six-hour intervals starting at midnight (i.e., 00:01 – 06:00 [reference level], 06:01 – 12:00, 12:01 – 18:00, 18:01 – 24:00). We included tod_{it} because previous studies have suggested circadian rhythms for polar bears (Stirling, 1974; Ware et al., 2020) and aspects of the haul-out behavior of ice-breeding seals (Finley, 1979; Calvert and Stirling, 1985; Carlens et al., 2006). Including lunar cycle and time of day in the model

TABLE 1. Definitions of terms used in analyses of behavioral data for polar bears.

Term	Definition
AF_{it}	Covariate for demographic class in multinomial logistic regression, indicating that a bear was an adult female without dependent young.
$AFC12_{it}$	Covariate for demographic class in multinomial logistic regression, indicating that a bear was an adult female with dependent yearlings (C1) or two-year-olds (C2).
AM_{it}	Covariate for demographic class in multinomial logistic regression, indicating that a bear was an adult male.
BEH_{it}	Response variable in multinomial logistic regression, defined as the observed behavior of an individual polar bear (i) during a one-minute increment (t), which could assume one of four categories: hunting (H), investigative (I), sleeping (S), and miscellaneous (M).
i	Index for an individual polar bear.
imm_{it}	Covariate for immobilization in multinomial logistic regression, indicating that a bear was known to have been immobilized earlier in the same calendar year.
$moon_{it}$	Covariate for lunar phase in multinomial logistic regression, coded as a four-level factor corresponding to the levels new, waxing, full, and waning.
Sub_{it}	Covariate for demographic class in multinomial logistic regression, indicating that a bear was a subadult of either sex.
$season_{it}$	Covariate for season in multinomial logistic regression, defined as a two-level factor indicating whether an observation occurred in the spring or summer.
tsm	Abbreviation for time-since-marking.
$tsm48h_{it}$	Binary covariate for tsm in multinomial logistic regression, set to 1 if a bear had been immobilized less than 48 hours prior to observation.
$tsm72h_{it}$	Binary covariate for tsm in multinomial logistic regression, set to 1 if a bear had been immobilized less than 72 hours prior to observation.
$tsm120h_{it}$	Binary covariate for tsm in multinomial logistic regression, set to 1 if a bear had been immobilized less than 120 hours prior to observation.
$tsm7d_{it}$	Continuous covariate for tsm in multinomial logistic regression, set to 1 at the time of immobilization and declining to 0 over the next 7 days.
$tsm14d_{it}$	Continuous covariate for tsm in multinomial logistic regression, set to 1 at the time of immobilization and declining to 0 over the next 14 days.
$tsm21d_{it}$	Continuous covariate for tsm in multinomial logistic regression, set to 1 at the time of immobilization and declining to 0 over the next 21 days.
t	Index for a one-minute increment of observation.
tod_{it}	Covariate for time of day in multinomial logistic regression, coded as a four-level factor corresponding to 6-hour increments starting at midnight.

TABLE 2. Multinomial logistic regression models fit to observational data for polar bears. All candidate models included terms from the preliminary model, which are described in the main text and not shown here. Time-since-marking (tsm) covariates are defined in the main text and Table 1. The covariate imm_{it} represents an effect for having been immobilized previously in the same year. A plus sign (+) in the Interaction column indicates that the model included interactions between the tsm covariate and demographic class. Model specifics are reported as degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion (AIC), the difference between AIC of a model and the most supported (i.e., low AIC) model (ΔAIC), and the AIC model weight (w).

Tsm	imm_{it}	Interaction	df	logLik	AIC	ΔAIC	w
$tsm48h_{it}$	+	+	60	−126497	253114	0	1.00
$tsm21d_{it}$	+	+	60	−126533	253186	72	0.00
$tsm21d_{it}$	NA	+	57	−126872	253859	745	0.00
$tsm48h_{it}$	NA	+	57	−126905	253925	811	0.00
$tsm72h_{it}$	+	+	60	−126903	253925	812	0.00
$tsm14d_{it}$	+	+	60	−126905	253930	816	0.00
$tsm120h_{it}$	+	+	60	−127055	254231	1117	0.00
$tsm7d_{it}$	+	+	60	−127085	254290	1177	0.00
$tsm14d_{it}$	NA	+	57	−127265	254643	1530	0.00
$tsm72h_{it}$	NA	+	57	−127308	254730	1616	0.00
$tsm120h_{it}$	NA	+	57	−127438	254990	1876	0.00
$tsm7d_{it}$	NA	+	57	−127495	255103	1990	0.00
$tsm48h_{it}$	+	+	48	−127646	255388	2275	0.00
$tsm48h_{it}$	NA	NA	45	−128117	256323	3210	0.00
$tsm72h_{it}$	+	NA	48	−128189	256473	3360	0.00
$tsm72h_{it}$	NA	NA	45	−128636	257362	4249	0.00
$tsm7d_{it}$	+	NA	48	−128666	257428	4314	0.00
$tsm14d_{it}$	+	NA	48	−128983	258063	4949	0.00
$tsm120h_{it}$	+	NA	48	−129035	258167	5053	0.00
$tsm7d_{it}$	NA	NA	45	−129083	258255	5142	0.00
$tsm21d_{it}$	+	NA	48	−129087	258271	5157	0.00
$tsm14d_{it}$	NA	NA	45	−129308	258706	5592	0.00
$tsm21d_{it}$	NA	NA	45	−129416	258921	5808	0.00
$tsm120h_{it}$	NA	NA	45	−129450	258990	5876	0.00
NA	NA	NA	42	−129659	259401	6288	0.00

served to explain variation in the data resulting from factors we are not primarily interested in, which increased our ability and statistical power to investigate the effects of chemical immobilization. We evaluated support for terms in the preliminary model using likelihood ratio tests. All terms explained significant variation in the data

(i.e., P [LR > $\chi^2_{df=3}$] < 0.001) and were therefore carried forward to the second step of analyses.

In the second step, we tested for a possible influence of immobilization on polar bear behavior by introducing two additional types of covariates. First, we created the covariate imm_{it}, which was set to 1 if a bear was known

to have been immobilized earlier in the same calendar year. Second, we developed six time-since-marking (tsm) covariates representing shorter-term effects. The binary covariates $tsm48h_{it}$, $tsm72h_{it}$, and $tsm120h_{it}$ were set to 1 if a bear had been immobilized less than 48, 72, or 120 h prior to a behavioral observation, respectively, and the continuous covariates $tsm7d_{it}$, $tsm14d_{it}$, and $tsm21d_{it}$ were set to 1 at the time of immobilization and declined linearly to 0 over the next 7, 14, or 21 days, respectively. Each tsm covariate represented a different hypothesis for how polar bear behavior might be affected by immobilization. For example, the covariate $tsm48h_{it}$ represented the hypothesis that polar bears experienced a step change in behavior during the first 48 hours after immobilization (as reported by Thiemann et al., 2013 and Rode et al., 2014), whereas $tsm21d_{it}$ represented the hypothesis that polar bears experienced changes in behavior that persisted for 21 days after immobilization but diminished in magnitude over this period. We evaluated support for the different tsm covariates using model selection techniques, as described below.

We created four models using each tsm covariate. Each model consisted of the terms from the preliminary model and the following additional terms: model 1, the tsm covariate only; model 2, the tsm covariate and imm_{it}; model 3, the tsm covariate and interactions between tsm and demographic class, so that different classes of animals could exhibit different responses to immobilization; and model 4, the tsm covariate, imm_{it}, and interactions between tsm and demographic class. This process resulted in a candidate set of 25 models (i.e., the preliminary [i.e., null] model + 6 tsm covariates × 4 models using each tsm covariate). We evaluated the relative fit of models in the candidate set using Akaike's Information Criterion (AIC), which resulted in the top model $BEH_{it} = \beta_0 + \beta_1\ season_{it} + \beta_2\ AF_{it} + \beta_3\ AFC12_{it} + \beta_4\ AM_{it} + \beta_5\ Sub_{it} + \beta_6\ season_{it}{:}AF_{it} + \beta_7\ season_{it}{:}AM_{it} + \beta_{8\text{-}10}\ moon_{it} + \beta_{11\text{-}13}\ tod_{it} + \beta_{14}\ tsm48h_{it} + \beta_{15}\ tsm48h_{it}{:}AF_{it} + \beta_{16}\ tsm48h_{it}{:}AFC12_{it} + \beta_{17}\ tsm48h_{it}{:}AM_{it} + \beta_{18}\ tsm48h_{it}{:}S_{it} + \beta_{19}\ imm_{it}$. Because this model was strongly supported by the data (i.e., ΔAIC was 72, much lower than the second most supported model; Table 2), we carried it forward to the third step of analyses and did not perform model averaging (Burnham and Anderson, 2002).

In the third step, we drew conclusions about the effects of immobilization and other factors on polar bear behavior by using the top model to compare the predicted probabilities of different outcomes (i.e., H, I, S, M) as a function of different combinations of covariates. We evaluated the performance of the top model using five-fold cross-validation. We estimated uncertainty in model coefficients (and, by extension, in predicted probabilities) by generating 1000 bootstrap datasets via sampling with replacement and refitting the top model to each dataset. For both cross-validation and uncertainty estimation, resampling was performed with bears as the sampling unit (i.e., during resampling, either all or none of the observations known to come from an individual bear were selected; Ferdinandy et al., 2020). We took this approach

because it was not possible to use multilevel models to account for repeat observations of individuals (Koster and McElreath, 2017) without introducing potential bias into the results because our ability to track bears differed between animals that were immobilized, which allowed for individual identification because of the application of a temporary paint marking, vs. animals that were not immobilized (or had lost their paint marking) and could only be individually identified during a single continuous observation bout. Our approach of resampling of bears provided estimates of model performance and precision that partially accounted for potential individual-level variation and serial autocorrelation. To quantify the statistical significance of behavioral differences between two groups of bears (e.g., bears that had been immobilized vs. bears that had not), we calculated relative risk as the probability of the first group exhibiting a specific behavior divided by the probability of the second group exhibiting the behavior. We also report the proportion of bootstrap iterations for which relative risk was less than 1.0 (i.e., the probability of a decline [$Prop_{dec}$]) or greater than 1.0 (i.e., the probability of an increase [$Prop_{inc}$]).

Hunting Success of Previously Immobilized Polar Bears following Immobilization

To complement the multinomial logistic regression, we documented two specific aspects of the return to hunting by previously immobilized polar bears. First, although our top behavioral model (see above) indicated that all demographic classes of polar bears were less likely to hunt within 48 h of immobilization, because we visually observed bears directly (i.e., as opposed to relying on remotely collected movement data; Thiemann et al., 2013; Rode et al., 2014) we were able to confirm that they did not stop hunting completely during that period. Thus, as a measure of how quickly some bears were able to return to successful hunting, we summarized observations of successful hunts by previously immobilized animals during the first 60 h (2.5 d) post immobilization. For additional context, we also report previously unpublished data on the return to hunting post immobilization by four bears in two previous and independent studies. Second, because the number of kills made by each demographic class of previously immobilized and non-immobilized bears in either the spring or summer seasons were too few for statistical comparisons, we pooled the total observation times of all previously immobilized and non-immobilized (i.e., control) bears and present a simple comparison of the number of hours of observation made per kill for each group.

RESULTS

During the 11 observation periods between 1975 and 1997, visual observations of 35 previously immobilized polar bears were made for variable lengths of time

TABLE 3. Durations of observation periods from 1975 to 1997 and the number of marked polar bears documented in each period.

Year	Season	Observation dates	Polar bears previously immobilized (marked)		Polar bears not previously immobilized (unmarked)		Drugs used for immobilization
			Number of records	Minutes	Estimated number	Minutes	
1975	Spring	16 April–6 June	1	319	1	986	Sernylan/Sparine
	Summer	21 June–26 July	4	9623	2	185	Sernylan/Sparine
1976	Spring	20 April–21 May	4	7955	10	3482	Sernylan/Sparine
	Summer	3 July–21 July	8	14,703	6	8170	Sernylan/Sparine
1977	Spring	22 April–16 May	2	2683	10	2354	Sernylan/Sparine
	Summer	25 June–14 July	3	13,877	5	5746	Sernylan/Sparine
1978	Summer	21 June–20 July	4	16,886	6	2730	Sernylan/Sparine
1980	Spring	16 April–12 May	5	4844	10	3170	Ketamine/Rompun
1981	Summer	6 July–21 July	1	1193	1	1149	Sernylan/Sparine
1990	Spring	22 April–17 May	2	1357	4	1503	Telazol
1997	Spring	22 April–15 May	1	53	0	0	Telazol
Total				73,493		29,475	

TABLE 4. Summary of the demographic classes of previously immobilized polar bears and non-immobilized control bears from the same demographic classes observed during the observational periods from 1975 to 1997.

Demographic class	Total number of previously immobilized (marked) polar bears observed	Estimated number of control polar bears (unmarked) observed that had not previously been immobilized
Adult female alone	6	6
Adult female with COY	8	25
Adult female with yearling or 2-year-old cubs	4	7
Subadult (both sexes)	4	0
Adult male	11	19
Total	33	57

TABLE 5. Minutes of observational data for polar bears. Demographic classes are adult females without dependent young (AF), adult females with cubs-of-the-year (AFC0), adult females with yearling or two-year-old cubs (AFC12), and subadults (Sub). The covariate $imm_{it} = 1$ represents observations that were made later in the same calendar year that a bear was known to have been immobilized.

Immobilization status	AF	AFC0	AFC12	AM	Sub	Total
$imm_{it} = 0$	2887	13,653	2706	11,466	0	30,712
$imm_{it} = 1$	11,294	30,796	8725	11,962	9479	72,256
Total	14,181	44,449	11,431	23,428	9479	

(Table 3). In some cases, individuals were observed in more than one season. The demographic classes of previously immobilized polar bears are listed in Table 4.

Multinomial Logistic Regression

The data consisted of 102,968 min of observation with the following distribution across the four categories of the response variable: 32,037 min (H), 27,718 min (I), 27,453 min (S), and 15,760 min (M). Observations were made on 83 polar bears, although the number of unique individuals contributing to the data was likely less than 83 due to the difficulty of tracking non-immobilized individuals over time. All demographic classes except subadults included observations for bears that had been immobilized and those that had not been immobilized earlier in the year (Table 5).

We evaluated the potential effects of immobilization by comparing the fit of models with different tsm covariates. The covariates allowed for changes in the probabilities of exhibiting four categorical behaviors during a period of 48 h (2 d) to 21 d following immobilization. The most supported

(i.e., low AIC) model had 60 parameters and included the covariate $tsm48h_{it}$ as well as interactions between $tsm48h_{it}$ and demographic class (Tables 2 and 6). This finding supports the hypothesis that the primary effects of immobilization on polar bear behavior occur within the first 48 h, compared to the null hypothesis of no effects and the alternative hypotheses of fixed effects lasting 72 or 120 h, or effects with a linearly declining magnitude over 7, 14, or 21 days. The sample size of data supporting this conclusion included 7108 and 95,860 minutes of observation for bears that had, and had not, been immobilized within 48 h, respectively. The overall accuracy of the top model from five-fold cross-validation was 0.40.

The top model indicated that all demographic classes of polar bears were less likely to hunt within 48 h of immobilization, although visual observations confirmed that not all bears stopped hunting completely. Most demographic classes of bears were more likely to sleep and engage in miscellaneous behaviors during this 48 h period (Table 7). Specifically, AFs were 0.54 times as likely to hunt within 48 h of immobilization, compared to AFs that had not been immobilized (95% CI = 0.00–1.64,

TABLE 6. Estimated multinomial logistic regression coefficients for the top (i.e., low AIC) model fit to observational data for polar bears. The reference response category was sleeping (S). Covariates are defined in the main text and in Table 1.

Response category	(Intercept)	$season_{it}$	AF_{it}	$AFC12_{it}$	AM_{it}	S_{it}	$season_{it}{:}AF_{it}$	$season_{it}{:}AM_{it}$	Waxing	Full
Hunting	−0.58	0.01	−1.79	0.86	−1.89	0.52	2.44	2.53	0.30	1.24
Investigative	0.50	−0.92	−1.33	0.10	−0.97	0.63	1.99	1.13	0.45	0.92
Miscellaneous	−0.16	0.05	0.13	−0.13	−1.15	−0.40	−0.43	0.30	−0.09	0.52

Response category	Waning	06:01–12:00	12:01–18:00	18:01–24:00	$tsm48h_{it}$	$tsm48h_{it}{:}AF_{it}$	$tsm48h_{it}{:}AFC12_{it}$	$tsm48h_{it}{:}AM_{it}$	$tsm48h_{it}{:}S_{it}$	imm_{it}
Hunting	0.47	−0.53	−0.33	0.25	−26.56	24.78	39.77	24.96	24.26	0.41
Investigative	0.40	−0.63	−0.11	0.41	−11.28	8.68	29.49	9.34	10.03	−0.13
Miscellaneous	0.16	−0.53	−0.24	0.12	2.38	−3.70	14.85	−3.38	−2.90	−0.18

TABLE 7. Estimated probabilities and standard errors (SE) of polar bears exhibiting four categorical behaviors, derived from the top (i.e., low AIC) model, for bears that had not been immobilized within 48 h (not imm.) and bears that had been immobilized within 48 h (imm. < 48 h). Demographic classes are adult females without dependent young (AF), adult females with cubs-of-the-year (AFC0), adult females with yearling or two-year-old cubs (AFC12), adult males (AM), and subadults (Sub). Predicted probabilities are for the summer and reflect reference levels for the covariates $moon_{it}$ (i.e., new) and tod_{it} (i.e., 00:01–06:00). Covariates are defined in the main text and in Table 1.

	Hunting				Investigative				Miscellaneous				Sleeping			
	not imm.		imm. < 48 h		not imm.		imm. < 48 h		not imm.		imm. < 48 h		not imm.		imm. < 48 h	
Demographic code	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
AF	0.27	0.13	0.18	0.21	0.32	0.10	0.05	0.10	0.17	0.07	0.10	0.36	0.25	0.15	0.66	0.30
AFC0	0.18	0.06	0.00	0.06	0.21	0.03	0.00	0.08	0.29	0.06	0.89	0.22	0.32	0.07	0.11	0.15
AFC12	0.35	0.14	0.02	0.04	0.19	0.05	0.71	0.34	0.20	0.05	0.27	0.28	0.26	0.15	0.00	0.18
AM	0.33	0.10	0.21	0.13	0.24	0.05	0.06	0.04	0.12	0.04	0.08	0.10	0.31	0.10	0.65	0.17
Sub	0.25	0.11	0.08	0.07	0.33	0.11	0.18	0.10	0.16	0.10	0.17	0.34	0.26	0.15	0.57	0.24

proportion of bootstrap iterations for which the probability of hunting declined within 48 hours of immobilization [$Prop_{dec}$] = 0.81). Equivalent statements of relative risk for AFC0s, AFC12s, and AMs were 0.09 (95% CI = 0.00–0.87, $Prop_{dec}$ = 0.99), 0.05 (95% CI = 0.00–0.56, $Prop_{dec}$ = 1.0) and 0.65 (95% CI = 0.00–1.35, $Prop_{dec}$ = 0.92), respectively. We could not make similar inferences for subadults because none were observed that had not been previously immobilized. However, subadults were 0.24 (95% CI = 0.00–0.63, $Prop_{dec}$ = 1.0) times as likely to hunt within the 48 h of immobilization, compared to more than 48 h of immobilization, suggesting that they exhibited a similar response to other demographic classes.

The top model included additional covariates that provided insight into factors influencing polar bear behavior (Table 8). During the spring, non-immobilized AFs and AMs were 0.18 (95% CI = 0.00–0.70, $Prop_{dec}$ = 0.99) and 0.15 (95% CI = 0.05–0.33, $Prop_{dec}$ = 1.0) times as likely to hunt, compared to during the summer. This difference likely reflects a reduction in the amount of time spent hunting during the spring due to the physiological influence of potential and realized mating activity. We also found that polar bears were most likely to hunt under a full moon (even during periods of 24 h sunlight). For example, AFs were 1.68 (95% CI = 0.95–3.40, $Prop_{inc}$ = 0.96) times as likely to hunt under a full moon compared to a new moon. Similarly, polar bears were slightly more likely to hunt during the last quarter of a 24 h day. For example, AFs were 1.24 (95% = 1.01–1.68, $Prop_{inc}$ = 0.98) times as likely to hunt from 18:01–24:00, compared to 12:01–18:00.

Finally, we unexpectedly found that bears that had been immobilized earlier in the same year—but not within 48 h of observation—were on average 1.42 (95% CI = 1.01–2.26, $Prop_{inc}$ = 0.98) times as likely to hunt, compared to bears that had not been previously immobilized (see Discussion). This finding may represent a relatively short-term effect because the median time elapsed between immobilization and subsequent behavioral observations was approximately 10 days.

Comparison of Hunting Success for Immobilized vs. Non-Immobilized Bears

In total, previously immobilized bears were observed for a total of 1224.9 h during which they made a total of 29 kills, for an average of 42.2 h (1.76 d) per kill. In comparison, non-immobilized bears were observed for a total of 491.3 h during which they made 11 kills, for an average of 44.7 h (1.86 d) per kill. Based on a randomization procedure, this result corresponds to a probability of 0.61 that previously immobilized bears exhibited a higher kill rate (kills/h) than non-immobilized bears, which suggests similar hunting success between the two groups.

TABLE 8. Estimated probabilities and standard errors (SE) of polar bears exhibiting four categorical behaviors, derived from the top (i.e., low AIC) model. The column "Fixed predictors" includes a textual description of the baseline conditions for a group of predictions across which one predictor changed as indicated in the "Varying predictor" column. Demographic classes are adult females without dependent young (AF), adult females with cubs-of-the-year (AFC0), adult females with yearling or two-year-old cubs (AFC12), adult males (AM), and subadults (Sub).

Fixed predictors	Varying predictor	Hunting		Investigative		Miscellaneous		Sleeping	
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Not immobilized, spring, new moon, 00:01–06:00	AF	0.04	0.03	0.17	0.08	0.39	0.10	0.40	0.07
	AM	0.04	0.03	0.32	0.09	0.14	0.07	0.50	0.15
Not immobilized, summer, AF, 00:01–06:00	new	0.27	0.13	0.32	0.10	0.17	0.07	0.25	0.15
	waxing	0.29	0.12	0.39	0.10	0.12	0.06	0.20	0.13
	full	0.41	0.12	0.35	0.08	0.12	0.0	0.11	0.08
	waning	0.32	0.1	0.35	0.10	0.14	0.07	0.19	0.12
Not immobilized, summer, AF, new moon	00:01–06:00	0.27	0.13	0.32	0.10	0.17	0.07	0.25	0.15
	06:01–12:00	0.24	0.14	0.25	0.11	0.14	0.06	0.37	0.20
	2:01–18:00	0.23	0.12	0.33	0.12	0.15	0.06	0.29	0.18
	18:01–24:00	0.28	0.12	0.38	0.11	0.15	0.07	0.20	0.14
Immobilized more than 48 hours earlier in the same year, summer, new moon, 00:01–06:00	AF	0.38	0.14	0.26	0.08	0.13	0.06	0.23	0.14
	AFC0	0.27	0.06	0.18	0.03	0.24	0.04	0.32	0.06
	AFC12	0.47	0.14	0.15	0.03	0.15	0.04	0.23	0.15
	AM	0.45	0.1	0.19	0.04	0.09	0.0	0.28	0.09
	Sub	0.35	0.11	0.27	0.10	0.13	0.08	0.25	0.13

In addition, we visually observed successful hunting by three previously immobilized adult bears within 60 h of having been immobilized: 1) an adult female with a C0 immobilized with Sernylan/Sparine made her first kill 2.1 d after immobilization and a second kill 0.9 d later, 2) a lone adult male immobilized with Ketamine/Rompun made his first kill 1.4 d after immobilization and three more kills in the following 0.9 d, and 3) a lone adult female immobilized with Telazol made her first kill 0.4 d after immobilization and two more in the following 0.72 d.

DISCUSSION

For this study, we used a dataset of long-term visual observations designed to evaluate the behaviors of polar bears that had, and had not, been previously immobilized.

Recovery of Normal Overall Behavior Patterns following Immobilization

Previously immobilized bears from all demographic classes spent a greater amount of time sleeping and a reduced amount of time hunting during the first 48 h post immobilization, compared to those observed more than 48 h after immobilization and bears that had not been immobilized. These results are consistent with previous studies on the recovery times of adult female and subadult polar bears based on movement data from satellite collars (Thiemann et al., 2013; Rode et al., 2014), which concluded that most bears recover to near-normal levels in 2–3 days and fully normal levels after about five days. However,

because our analyses were based on visual observation and did not depend upon interpretation of remotely collected data, we were able to accurately document the four key behavioral categories and confirm that recovery from the primary effects of immobilization on polar bear behavior—especially on the return to successful hunting—occurred within 48 h. Furthermore, we did not detect negative behavioral effects in the following three to 21 days, regardless of the immobilizing drugs used.

Multinomial models provide a powerful framework for analysis of behavior (Koster and McElreath, 2017). Specifically, we were able to evaluate relative support in the data for different durations and functional forms (i.e., step change vs. gradual decline) of behavioral response, while controlling for other factors that were not of primary interest but explained variation in the data. In the summer, AFC12s and AMs were the demographic classes with the highest probability of hunting (Table 7), possibly reflecting the energetic demands on females of providing for dependent young and, for males, maintaining a larger structural size (Ryg and Øritsland, 1991; Stirling and Øritsland, 1995; Pagano et al., 2018; Johnson et al., 2021). In the spring, adult females without dependent young (AFs) and AMs were significantly less likely to hunt compared to during the summer, reflecting temporary fasting behavior associated with breeding activity (Cherry et al., 2009; Stirling et al., 2016). Consequently, adult males may also hunt more actively in summer to compensate for a lower proportion of time spent hunting during spring. Our finding that polar bears were slightly more likely to hunt during the last quartile of the day (i.e., 18:00–24:00) appears consistent with the finding based on telemetry data that

polar bear activity levels exhibited an acrophase inversion to approximately 24:00 in the spring associated with increased feeding during the ringed seal pupping season (Ware et al., 2020).

To our knowledge, our analyses provide the first evidence of the influence of lunar phase on polar bear behavior, with increased hunting associated with a full moon (Table 8). Although not well understood, the influence of the lunar cycle on hunting behavior of marine mammals has also been reported for Galapagos fur seal (*Arctocephalus galapagoensis*; Trillmich and Mohren, 1981), northern fur seal (*Callorhinus ursinus*; Lea et al., 2010), and short-finned pilot whale (*Globicephala macrorhynchus*; Owen et al., 2019). These species all had deeper feeding dives during a full moon than during a new moon, which was suggested to be associated with differences in depth of prey species. Last et al. (2016) provided evidence that, even during the dark polar night, vertical migrations of zooplankton are driven by moonlight in synchrony with the altitude and phase of the moon. However, such newly termed lunar vertical migrations (LVMs) occur during winter throughout the Arctic in fjord, shelf, slope, and open-sea ecosystems, which Last et al. (2016) hypothesized might function to reduce the ability of visual predators to use lunar illumination to hunt, although they did not discuss the extent to which the lunar effect continued during summer. In contrast, Naylor (2001) noted the significance of tidal cycles (driven by the lunar cycle) on several species of marine invertebrates. Mercier et al. (2011:82) reported that reproductive patterns of several species of deep-sea invertebrates dwelling well below the euphotic zone also showed a significant relationship to the lunar cycle but concluded that "the exact nature of this lunar period (endogenous or exogenous rhythm) and its adaptive significance in the deep sea remain elusive." At this point, we are unable to explain the ecological circumstances that may result in a lunar cycle in polar bear hunting, but we suggest it remains an interesting topic for future research.

Polar bears are highly intelligent animals and, except for family groups and male-female pairs during breeding behavior in spring, primarily function as solitary individuals that hunt a variety of prey species at different seasons in a wide range of habitats both geographically and seasonally (Stirling and Latour, 1978; Amstrup et al., 2000; Galicia et al., 2021; Pagano, 2021). Although difficulty reidentifying non-immobilized bears precluded fitting multilevel (i.e., hierarchical) models that allowed for individual differences in behavior, it was possible to partially account for such effects during variance estimation by using a non-parametric bootstrap procedure that resampled data with individuals (or observation bouts, for non-immobilized bears) as the sampling unit (Ferdinandy et al., 2020). In our analyses, five-fold cross-validation of the most supported multinomial logistic regression model indicated a limited ability (overall accuracy = 0.40) to predict polar bear behavior on a minute-by-minute basis. This finding is not surprising given that the behavior of individual bears is likely influenced by differences in temperament and health (e.g., nutritional condition), intra- and inter-specific interactions, past experiences, and other external factors that we were not able to quantify, such as environmental conditions. This possible explanation appears supported by Rode et al. (2014), who noted that individual variation among bears made some approaches to estimating recovery and movement rates unreliable. Consequently, they concluded that the poor fit of their modelled estimates could be due to individual-based variation that was not explained by seasonal variation or other factors, which caused the authors to rely more on individual estimates of recovery times compared to modeling results based on pooled data. Similarly, Thiemann et al. (2013) noted that "normal" or pre-capture movement is difficult to characterize because a bear's movements before capture are unknown and both individual and population-level variability in movement patterns are high. They also noted that, although there was variability among individuals, most bears (59%) were moving at least short distances within 12 h of capture. Consequently, Thiemann et al. (2013) concluded that it was inappropriate to define a single recovery threshold for the subpopulation and instead analyzed individual recovery thresholds. Taken together, the non-parametric bootstrap analysis of our visual observations of the behavior of individual bears and the analyses of remotely collected data on the post-immobilization movements of bears with satellite collars confirm that a significant amount of the lack of predictability in the time taken for bears to return to normal behavior is largely a consequence of individual variability.

An unexpected result was that bears that had been immobilized earlier in the same year but not within the first 48 h of observation appeared on average 1.42 (95% CI = 1.01 – 2.26, $Prop_{inc}$ = 0.98) times as likely to hunt as bears that had not been previously immobilized. The median time elapsed between immobilization and these subsequent behavioral observations was approximately 10 d. Therefore, although we do not have an explanation for this result, we speculate that some polar bears may exhibit a short-term increase in hunting behavior for several days post-immobilization, which might represent a "rebound" period during which bears attempt to compensate for hunting opportunities lost during or immediately after immobilization. Regardless, this remains an aspect worthy of future investigation.

Hunting Success of Previously Immobilized Polar Bears following Immobilization

In addition to the times from immobilization to successful hunting reported for three focal bears in this study, four similar observations were made during other field studies but have not been previously published. Two subadult bears immobilized for population assessments in the southern Beaufort Sea, in 1971 with Sernylan/Sparine and in 1986 with Telazol were resighted two days and one day later, by which time they had already killed one and

two seals, respectively (I. Stirling, unpubl. data). Similarly, during an independent physiological study of polar bears in the southern Beaufort Sea from 2014 to 2016, Pagano et al. (2018, pers. comm., 2020) immobilized nine adult and subadult females without dependent cubs with Telazol in April and fitted them with satellite radio collars equipped with a video camera. Despite having been kept immobilized for 2–4 times as long as necessary simply for tagging and attachment of satellite collars because of the need to record other research data, two of the previously immobilized bears were observed killing a seal on video only 0.92 d and 0.97 d after being immobilized.

Pagano (2018, pers. comm., 2020) also documented a total of five seals killed during 328.7 h of recorded video (not quantified by behavioral category) for an average of one kill every 65.7 h (2.7 d). Despite the smaller sample size of total observation and differing methodology, this result is similar to the values for both the previously immobilized and non-immobilized control bears in this study (2.1 and 2.3 d, respectively).

Taken together, this study and those that relied on data from satellite collars, suggest that most bears sleep more and hunt less in the first 48 h following immobilization, although some return to successful hunting within that period. Although our sample sizes were small, the times taken for bears immobilized with all three different drug combinations to be observed hunting successfully, were all less than 50 h. These results reconfirm for Indigenous hunters and others that the conclusions of earlier studies that immobilization of polar bears did not have detectable negative effects on their behavior were correct. Furthermore, the fact that all three bears known to have killed a seal less than 24 h after immobilization had received Telazol also supports the conclusion that bears immobilized with this drug recover more quickly than did those immobilized with the previous drug combinations (Stirling et al., 1989; Rode et al., 2014).

In summary, our unique visual observations of the behavior and hunting ability of polar bears after being briefly immobilized, when compared to non-immobilized bears of the same demographic classes, supported the hypothesis that short-term chemical immobilization did not cause detectable negative effects beyond 48 h post-immobilization. Our results appear consistent with previous studies that used different methodologies (Thiemann et al., 2013; Rode et al., 2014). These findings provide critical insight into the safety of chemical immobilization and, when considered together with costs and benefits of different study methods used for polar bears (e.g., live-capture, biopsy darting, aerial survey), can help wildlife researchers and managers decide how best to collect the scientific data needed for the species' long-term conservation and management.

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