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The acute physiological response of polar bears to helicopter capture

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Abstract

Many wildlife species are live captured, sampled, and released; for polar bears (*Ursus maritimus*) capture often requires chemical immobilization via helicopter darting. Polar bears reduce their activity for approximately 4 days after capture, likely reflecting stress recovery. To better understand this stress, we quantified polar bear activity (via collar-mounted accelerometers) and body temperature (via loggers in the body core [T_{abd}] and periphery [T_{per}]) during 2–6 months of natural behavior, and during helicopter recapture and immobilization. Recapture induced bouts of peak activity higher than those that occurred during natural behavior for 2 of 5 bears, greater peak T_{per} for 3 of 6 bears, and greater peak T_{abd} for 1 of 6 bears. High body temperature (>39.0°C) occurred in T_{per} for 3 of 6 individuals during recapture and 6 of 6 individuals during natural behavior, and in T_{abd} for 2 of 6 individuals during recapture and 3 of 6 individuals during natural behavior. Measurements of T_{abd} and T_{per} correlated with rectal temperatures measured after immobilization, supporting the use of rectal temperatures for monitoring bear response to capture. Using a larger dataset ($n = 66$ captures), modeling of blood biochemistry revealed that maximum ambient temperature during recapture was associated with a stress leukogram

(7–26% decline in percent lymphocytes, 12–21% increase in percent neutrophils) and maximum duration of helicopter operations had a similar but smaller effect. We conclude that polar bear activity and body temperature during helicopter capture are similar to that which occurs during the most intense events of natural behavior; high body temperature, especially in warm capture conditions, is a key concern; additional study of stress leukograms in polar bears is needed; and additional data collection regarding capture operations would be useful.

KEYWORDS

blood biochemistry, body temperature, leukograms, polar bears, white blood cells, wildlife capture

Biologists have an ethical and professional obligation to minimize the negative consequences of their research methods on the organisms that they study (Costello et al. 2016, Field et al. 2019). This philosophy has fostered development of non-invasive sampling techniques for free-ranging wildlife (Pauli et al. 2010, Mori 2019); however, some types of data can only be obtained by the physical capture of animals. Physical capture creates unique risks for large-bodied animals that may be pursued before capture (e.g., by helicopter) such as moose (*Alces alces*), brown bears (*Ursus arctos*), and polar bears (*Ursus maritimus*; Arnemo et al. 2006). Polar bears (considered vulnerable by the International Union for Conservation of Nature Red List [Regehr et al. 2016], and threatened to become endangered by the United States [U.S. Fish and Wildlife Service 2008]) are captured for resolving conflict with humans and for collecting important data that would otherwise be inaccessible (Kearney 1989). For example, measurements of body composition and mass provide key predictors of fitness (Rode et al. 2020), blood sampling reveals changes across time and space in the organismal functions (e.g., in nutritional physiology, immune system activity) that drive population trends (Cherry et al. 2009, Whiteman et al. 2018), and markers (e.g., lip tattoos) and tracking devices (e.g., radio-collars) enable population estimates and assessments of habitat use (Amstrup et al. 2004, Durner et al. 2009, Bromaghin et al. 2015). The data provided by these methods are especially valuable in the current era of rapid sea ice loss resulting from anthropogenic climate warming (Derocher et al. 2013).

The choice of field methods in polar bear research is based on overlapping and distinct perspectives from northern Indigenous communities, governmental entities, academic institutions, conservation organizations, and others (Wong et al. 2017). To provide information for this choice, we focus on understanding the behavioral and physiological effects of helicopter darting on polar bears, which is often the only feasible method of chemical immobilization in their remote sea ice and tundra habitats (Figure 1). The sequence of operations during helicopter darting typically includes 1) initial sighting of a bear, at which time it may or may not show a behavioral response to the helicopter; 2) helicopter retreat to reduce disturbance during safety assessment and dart preparation, which typically lasts several minutes; 3) if needed, herding of the animal towards safe habitat for darting (e.g., away from open water); 4) darting run(s) in which the helicopter flies within 10 m of the bear; 5) after a successful darting, helicopter retreat to reduce disturbance while keeping the animal in sight to observe that it exhibits ataxia then lays down; 6) helicopter landing and bear health assessment (e.g., monitoring respiratory rate and rectal temperature); and 7) bear handling, during which samples are collected and tracking devices may be affixed. Biopsy darting (Pagano et al. 2014), for the purpose of collecting tissue samples, also involves low-elevation flight in pursuit of bears. Biopsy darting involves only steps 1–4 and there is less need to herd bears into safer terrain (step 3) because they do not undergo immobilization.

FIGURE 1 Helicopter darting of a polar bear on sea ice, southern Beaufort Sea, 2010. Photo by Mike Lockhart.

Mortalities from helicopter capture are rare. Rode et al. (2014), in a study of 2,517 polar bear captures, calculated a mortality rate of 0.1%, similar to brown bears (*U. arctos*) and other large mammals (Arnemo et al. 2006, Latham et al. 2019, Scasta 2020). Effects other than direct mortality can also be important yet are difficult to assess. A review of decades of polar bear field work on the Southern Beaufort Sea subpopulation reported no long-term effects of helicopter capture on body condition, reproduction, or cub survival (Rode et al. 2014). Earlier reports likewise reported no evidence of long-term effects from helicopter capture on cub and adult body mass (Amstrup 1993, Messier 2000). Two studies of the Western Hudson Bay subpopulation, however, noted small but significant trends of lighter body mass for adult females (Ramsay and Stirling 1986) or their cubs (Lunn et al. 2004) if the females had previously experienced helicopter capture.

After helicopter capture, polar bears return to their typical movement rates in a mean of 4 days (*n* = 74 bears, Thiemann et al. 2013*a*; *n* = 55 bears, Rode et al. 2014). This response likely reflects recovery from immobilization drugs, capture stress, and elevated body temperature (Best 1982, Breed et al. 2019). Polar bears typically regulate their core body temperature at 36.6–37.3°C, and they struggle to dissipate body heat during intense activity (Best 1982, Whiteman et al. 2015). In a captive study (Best 1982), polar bears maintained normothermia when running on a treadmill at speeds up to about twice their typical movement rate (Amstrup et al. 2000). At higher speeds, their body temperature began climbing and did not plateau until their activity ceased; this occurred even with a steep and favorable thermal gradient (e.g., at an ambient temperature of −35°C). In addition, the most commonly used immobilization drug, Telazol (tiletamine hydrochloride and zolazepam hydrochloride), may increase the risk of elevated body temperature (Stirling et al. 1989, Kreeger and Arnemo 2018).

Hyperthermia occurs when body temperature remains above a normal upper threshold, which can vary among animals because of differing temperature tolerances (Hill et al. 2008). Hyperthermia, along with capture stress, can cause complex changes in blood biochemistry. Liver damage may occur, indicated by elevated plasma levels of the enzyme alanine aminotransferase (ALT; Diehl et al. 2000). Impaired liver and kidney function, along with dehydration, can increase plasma sodium and potassium (Hashim 2010). Plasma glutamic acid may rise as a result of activation of the sympathetic nervous system (Jacob et al. 1989, Zlotnik et al. 2010). The overall stress response, coordinated by the autonomic nervous system and the hypothalamic-pituitary-adrenal axis, leads to increased plasma catecholamines, cortisol, and glucose (Hill et al. 2008). Stress can also cause a rapid increase in the white blood cell count (WBC) and in the percentage of neutrophils, and a concomitant decrease in the percentage of lymphocytes, a pattern referred to as a stress leukogram (Cattet et al. 2003).

The acute physiological responses of polar bears to helicopter capture have not been characterized. Our objective was to compare capture responses to natural behavior that potentially includes stressful events of intense

activity such as prey capture or conflict with conspecifics. We used data from free-ranging polar bears in the Southern Beaufort Sea subpopulation that were equipped with high-resolution activity sensors, body temperature loggers, and Global Positioning System (GPS) units. We tested the prediction that activity counts and body temperatures would reach higher levels during helicopter recapture than during natural behavior. We also tested the prediction that rectal temperature, commonly used to monitor bear health during immobilization, would be similar to temperatures recorded by the implanted loggers. In addition, using a larger dataset that also included polar bears without loggers, we tested the prediction that blood biochemical markers of elevated body temperatures and stress would be influenced by the duration of helicopter operations, ambient temperature, and dose of the immobilization drug.

STUDY AREA

We captured polar bears during April–May (spring), August (summer), or October (autumn), in 2008 and 2009, in terrestrial habitat along the northern coast of Alaska, USA, between the city of Utqiagvik and the Alaska-Canada border, on sea ice in the southern portion of the Beaufort Sea, and on sea ice up to 700 km offshore with the aid of an icebreaker in October 2009. The terrestrial environment is a flat coastal plain, dominated by shrub tundra (Barbour and Billings 2000), that lies within the North Slope Borough. Dominant fauna in the region include polar bears and ringed seals (*Pusa hispida*). Sea ice in this region melts and retreats north during June–October but is mostly contiguous with the coast during other months, includes flat pans and large ridges, and generally drifts clockwise following the Beaufort Gyre ocean current (Kwok et al. 2013).

METHODS

We conducted captures via helicopter darting using a Bell-206 (Bell, Fort Worth, TX, USA) or Airbus AS350 (Airbus, Leiden, Netherlands). We located animals by following footprints in the snow or mud or by following a very high frequency signal for individuals wearing radio-collars. Darts contained Telazol (Warner-Lamber, NJ, USA) at doses estimated at 4–10 mg/kg based on visual assessments of body mass (Stirling et al. 1989). During most captures, a second helicopter carrying additional researchers and equipment was within sight or sound of the target bear. We calculated the duration of helicopter operations as the time elapsed between the minute of the initial sighting of the bear and the minute we observed it lying down. These events, recorded on standardized data sheets, included the period during which the bear may have been running away from the helicopter, although such behavior could not be assumed. Bears typically run only during the actual darting, which is often a short component of the helicopter operations. We measured rectal temperature of immobilized bears as soon as possible after they lay down (usually <10 min) with a digital thermometer (Syrvet, Waukee, IA, USA). We weighed bears by suspending them in a net using an electronic load cell and an aluminum tripod. We determined the age at the bear's first capture based on counts of cementum annuli from an extracted vestigial premolar (Calvert and Ramsay 1998), except if we first captured the bear as a dependent cub in which case we aged it based on body size and dentition.

At each capture, we collected blood from the femoral artery (occasionally the vein) in plain (red-top) and ethylenediaminetetraacetic acid (EDTA; anticoagulant; purple-top) vacutainers® (BD, Franklin Lakes, NJ, USA). Within 12 hours we used a hematology diagnostic analyzer (HM5, Abaxis, Union City, CA, USA) to analyze EDTA whole blood for WBC and percentage of neutrophils and lymphocytes. We also centrifuged whole blood from plain vacutainers® (2,000 relative centrifugal force for 10 min), separating serum from red blood cells, and measured serum glucose, ALT, sodium, and potassium with chemistry panels (500-7123; Abaxis) and a veterinary blood analyzer (VS2 VetScan; Abaxis; Whiteman et al. 2018). We then froze serum at −20 to −40°C. To measure serum cortisol, we thawed samples and used an enzyme-linked immunosorbent assay (EA65, Oxford Biomedical Research,

MI, USA; Whiteman et al. 2018). To measure serum glutamic acid, the thawed samples were analyzed with ion-exchange liquid chromatography by the University of Missouri Experiment Station Chemical Laboratories (Columbia, MO, USA; Le Boucher et al. 1997, François 2002).

We fitted 14 bears with accelerometers, temperature loggers, or both, as part of a larger ecophysiological study (Durner et al. 2011; Whiteman et al. 2015, 2017, 2018, 2019). Accelerometers (Actiwatch; Mini-Mitter Respironics, Bend, OR, USA), attached to a GPS radio-collar, were sensitive to motion in all planes and recorded a unitless count every 2 minutes, reflecting acceleration intensity (Van Oort et al. 2004). We recorded body temperature using loggers surgically implanted in the rump (T_{per}; peripheral temperature) or in the abdomen (T_{abd}). We recorded T_{per} with Tidbit V2 loggers (every 5 or 10 min, resolution 0.02°C; Onset Computer Corporation, MA, USA) and recorded T_{abd} with iButton loggers (DS1922L, hourly measurements, resolution 0.0625°C; Maxim Integrated, CA, USA). For T_{per}, we sutured the logger to the surface of the gluteus maximus muscle, beneath the subcutaneous adipose tissue, slightly ventral to the base of the tail; for details see Durner et al. (2011) and Whiteman et al. (2015, 2017). For T_{abd}, we sutured the logger inside the abdominal cavity, adjacent to the peritoneum, on the ventral midline and slightly superior of the umbilicus; for details see Whiteman et al. (2015).

Data analysis

Activity and body temperature from sensors

We analyzed data separately from each sensor deployed on each bear. We first censored the data recorded during the 5 days immediately after the initial capture to exclude the initiation of the healing process and the post-capture period of reduced activity and movement (Thiemann et al. 2013, Rode et al. 2014). In the remaining data, we identified the highest values of activity count, T_{per}, and T_{abd} that were recorded during natural behavior after the initial capture (a period lasting 2–6 months), and helicopter operations and animal handling upon recapture. Then, for the highest value that was recorded during helicopter operations and handling, we calculated its percentile rank among all measurements for that bear and the percent of the overall maximum value that it represented. For example, for bear 20586, there were 40,909 measurements of activity, recorded every 2 minutes during August–October 2008, and their values ranged from 0 to 10,851 (unitless activity counts). The highest activity value recorded during helicopter operations and handling was 7,047, which was in the 99th percentile of all 40,909 measurements and was 65% of the overall maximum value (i.e., 10,851).

We also calculated the number and duration of all events of T_{per} or T_{abd} > 39.0°C. In a previous study, 39.0°C was the highest core and skin temperature measured in resting, captive polar bears in ambient environmental conditions at a site in their natural range (Best 1982). The T_{abd} and T_{per} measurements were instantaneous; however, for calculating duration of elevated body temperature, we defined a single measurement of T_{abd} > 39.0°C as 1 hour because T_{abd} measurements were hourly, and defined a single measurement of T_{per} > 39.0°C as either 5 or 10 minutes, depending on the frequency of sensor measurement. In some occurrences, several hours of consecutive measurements of T_{per} > 39.0°C contained 1–2 measurements ≤39.0°C; these 1–2 measurements represented ≤10 minutes and we ignored these values when calculating duration of elevated temperature. Lastly, we applied linear regression to T_{per} or T_{abd} versus rectal temperature recorded during immobilization.

Blood biochemistry

For each blood biochemistry variable, we constructed 7 linear mixed-effects models (models A–G). All models included the random predictor bear identification (ID) to account for repeated sampling of some individuals and the fixed predictors sex and group. Group was 1 of 6 combinations of capture season, year, and habitat feature

(Apr–May 2009 ice, Aug 2008 shore, Aug 2009 shore, Oct 2008 shore, Oct 2009 shore, Oct 2009 ice). Including group accounted for the potentially confounding differences in blood biochemistry that occur between seasons, years, and habitat features (Whiteman et al. 2018, 2019). Models also included combinations of the fixed predictors duration, temperature, and dose, and the interaction term duration × temperature. Duration was the time elapsed during helicopter operations between steps 1 and 5, as described above. Dose was the amount of Telazol (mg/kg body mass) used to immobilize the bear. Temperature was an interpolated value. We obtained 2-m above-ground air temperature estimates from the European Centre for Medium-Range Weather Forecasts ERA5 global atmospheric reanalysis (Hersbach et al. 2020) using the Env-Data tool (Dodge et al. 2013). We prescribed the Env-Data tool to interpolate temperature values at the location and time of each polar bear capture (scale of 0.25° × 0.25°) by applying spatial and temporal inverse-distance weighting to the surrounding hourly, 31-km resolution gridded ERA5 outputs. Lastly, we considered the interaction term duration × temperature because elevated body temperatures may be more likely during extended helicopter operations in warmer ambient conditions.

We constructed linear mixed-effects models A–G using the R package lmer and evaluated their fit with residual plots, qq plots, and the D'Agostino omnibus test of residual normality. If residuals departed from normality, we log-transformed the response variable and evaluated the impact of potential outliers via residual plots. We then used the R package MuMIn (Bartoń 2021) to estimate model-averaged coefficients for each predictor, weighted by Akaike's Information Criterion scores adjusted for small sample sizes (AIC_c). We considered the full averages, which sets a coefficient to zero if the predictor is not present in a model. This approach reduces biasing a coefficient away from zero when it is absent from models with substantial AIC_c weights (Burnham and Anderson 2002).

We used model-averaged coefficient estimates to predict values of biochemical variables for a polar bear under 3 different scenarios to assess the significance of the predictors duration, temperature, and dose. These 3 scenarios assumed that the bear was a female captured in spring 2009, which was the largest group in our data ($n = 18$ captures). In each of the 3 scenarios, we held 2 of the 3 predictors at their mean values and set the third predictor at its minimum value and then at its maximum value. If the resulting change in a biochemistry variable was greater than half of the standard deviation of the measurements for that variable, we considered the influence of the changed predictor to be significant. This conservative approach focused on effect size and reduced the probability of a type II error (i.e., missing a significant effect), which is appropriate when analyzing potential negative consequences of capture. In addition to modeling the 3 scenarios described above, we used model-averaged coefficients to estimate optimal helicopter operations as the longest duration, warmest temperature, and highest dose that would not result in any significant changes in biochemical variables.

RESULTS

Activity and body temperature during helicopter capture

We collected activity and body temperature data for 13 female and 1 male independent subadults or adults (age [$\bar{x} \pm SD$] = 9 ± 6 yr; range = 2–22 yr; Figure 2; Figures S1–S3, available in Supporting Information). Sample sizes were unequal across sensor types because logistics prevented deploying all sensors on all bears and because some sensors failed during deployment. For 2 of 5 individuals, peak activity occurred during helicopter recapture operations, rather than during natural behavior (Table 1; Figure 2). For these 2 individuals, the helicopter operations had short durations (6 min and 16 min) relative to the other 3 recaptures. For 3 of 6 individuals with T_{per} measurements, peak T_{per} occurred during recapture rather than natural behavior (Table 1; Figure 2). These 3 individuals were also the only bears to exhibit body temperatures >39.0°C during recapture (Table 2). In contrast, all 6 bears exhibited T_{per} > 39.0°C at least once during natural behavior. For 1 of the 6 individuals with T_{abd} measurements, peak T_{abd} occurred during recapture rather than natural behavior (Table 1; Figure 2). This individual
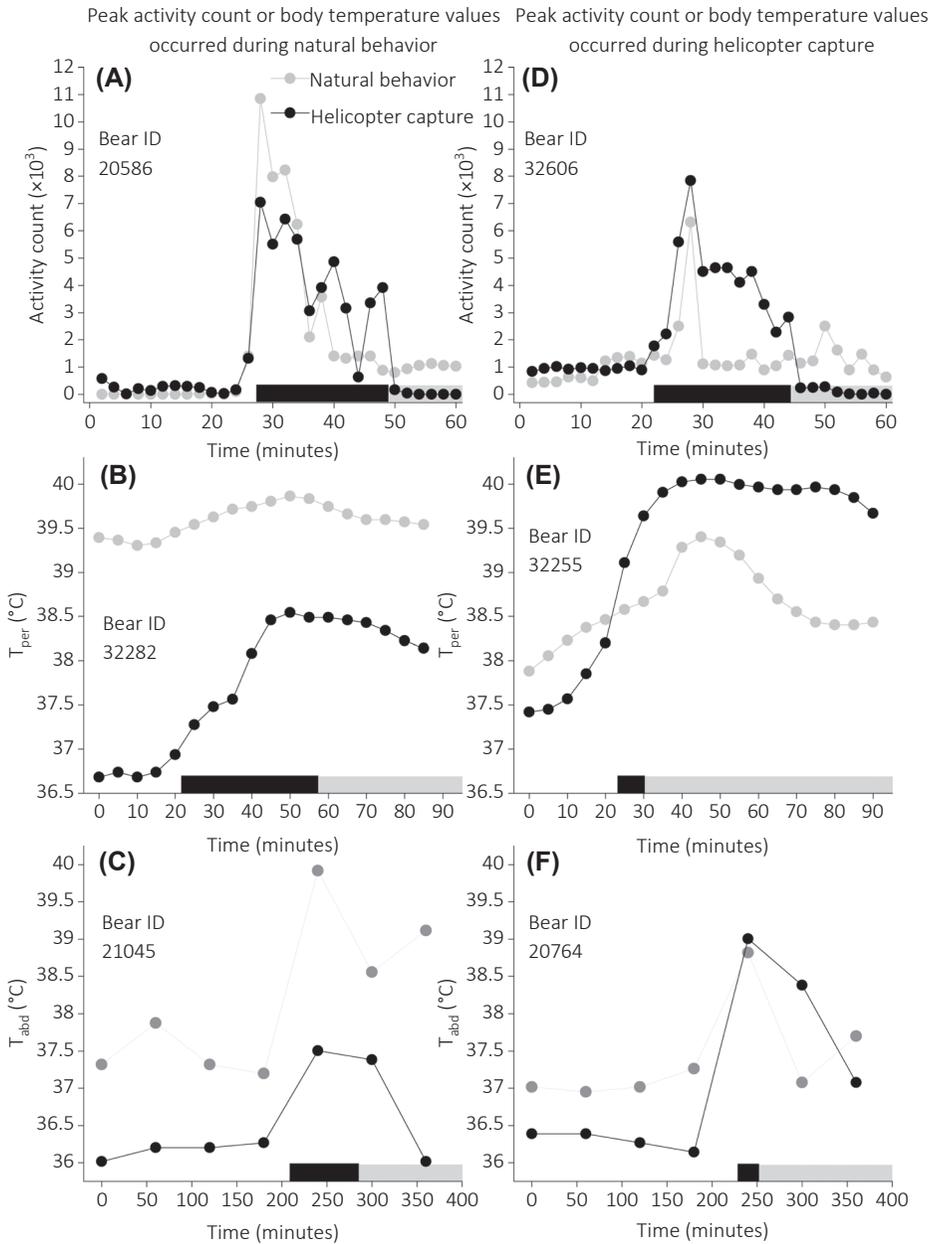
FIGURE 2 Six examples of activity count and body temperature (peripheral [T_{per}], abdomen [T_{abd}]) in free-ranging polar bears (bear identification [ID] provided) in the southern Beaufort Sea, 2008–2009. We measured these variables during several months of natural behavior and during helicopter recapture and handling. For the 3 bears in the left column (A–C), peak values of activity count, T_{per}, and T_{abd} occurred during natural behavior (gray lines); for comparison, values during helicopter recapture and handling are also shown (black lines). For the 3 bears in the right column (D–F), peak values of activity count, T_{per}, and T_{abd} occurred during helicopter recapture and handling (black lines); for comparison, highest values during natural behavior are also shown (gray lines). Bars on the x-axes refer to the data recorded during helicopter recapture: the black bars represent the helicopter operations (from initial sighting of the bear until the minute we observed it to be down) and the gray bars represent the handling time of the immobilized bear until we removed the sensor. We estimated the alignment of these events because internal clocks on the sensors drifted by several minutes during deployment.

TABLE 1 Summary of activity counts and body temperature measurements of free-ranging, female polar bears (1 exception: bear 20947 was male) in the southern Beaufort Sea, 2008–2009. Activity counts (Act), a unitless index of acceleration, were recorded by a collar-borne sensor. Peripheral (T_{per}) and abdominal (T_{abd}) temperatures were recorded by implanted loggers. Recordings included several months of natural behavior (period); a brief period of helicopter operations for darting and recapture (described here by duration, ambient temp, and dose of immobilization drug); and a brief period of handling for sensor retrieval. Captures were on shore unless otherwise noted. Asterisks indicate identifications (IDs) of bears for which peak values of activity count, T_{per}, or T_{abd} occurred during helicopter operations or handling. For bears without asterisks, peak values of activity count, T_{per}, or T_{abd} occurred during natural behavior.

						During recapture				
						Highest sensor value (relative to all values)		Characteristics of helicopter operation		
			Recordings by sensors deployed on bear							
Bear ID	Age (yr)	Period	Type	Frequency (min)	*n*	% of peak	Percentile rank	Duration (min)	Temp (°C)	Dose (mg/kg)
20586	8	Aug–Oct	Act	2	40,909	65	99	22	−9	12.4
20966	10	Aug–Oct		2	50,306	78	99	32	−11	7.6
32282	6	Aug–Oct		2	32,374	78	99	39	−3	11.7
32255*	4	Aug–Oct		2	30,174	100	100	6	−6	10.7
32606*	11	Aug–Oct		2	47,540	100	100	16	−13	7.1
32282	6	Aug–Oct	T_{per}	5	12,970	92	99	39	−3	11.7
21024	6	Apr–Oct		10	23,022	93	97	30[a]	−5	15.1
6810	19	Aug–Oct		5	14,059	93	98	22	−9	6.9
20586*	8	Aug–Oct		5	16,389	100	100	22	−9	12.4
20741*	7	Aug–Oct		5	18,142	100	100	10	−16	11.3
32255*	4	Aug–Oct		5	12,080	100	100	6	−6	10.7
21045	8	May–Oct	T_{abd}	60	3,382	42	92	81[a]	−1	20.1
20947	5	Aug–Oct		60	1,358	82	63	11	−2	4.2
21150	2	Aug–Oct		60	1,533	87	55	26	−5	12.5
20414	12	Aug–Oct		60	1,461	87	98	12	1	5.6
20562	22	Aug–Oct		60	1,413	99	99	23	−4	6.4
20764*	9	May–Oct		60	3,601	100	100	24[a]	−10	9.5

[a]Helicopter recapture operations occurred 50–700 km offshore on sea ice.

experienced a helicopter operation that was similar to the other individuals, and was 1 of 2 bears to exhibit T_{abd} > 39.0°C during recapture (Table 2). Three bears exhibited T_{abd} > 39.0°C during natural behavior. When T_{per} or T_{abd} exceeded 39.0°C during recapture, temperature declined after the bear became inactive and immobilized (Figures 3 and 2E, F).

Measurements of T_{abd} and T_{per} closely correlated with rectal temperatures, differing from the latter by ≤1.0°C (Figure 4). On average, we measured rectal temperature within 13 minutes of the associated T_{abd} recording (range = 1–30 min, *n* = 6) and within 2 minutes of the associated T_{per} recording (range = 0–3 min, *n* = 4), although this alignment included unknown imprecision because the clock within T_{abd} and T_{per} loggers drifted by several minutes during deployment.

TABLE 2 Maximum body temperatures, and summaries of occurrences of body temperatures >39.0°C, in 11 free-ranging female polar bears and 1 male (identification [ID] 20947) in the southern Beaufort Sea, 2008–2009. Peripheral (T_{per}) and abdominal (T_{abd}) temperatures were recorded by implanted loggers. Recordings included several months of natural behavior, a brief period of helicopter operations for darting and recapture, and a brief period of handling for sensor retrieval.

	T_{per} or T_{abd} > 39.0°C					
	During recapture			During natural behavior		
Bear ID	Occurrences	Length (min)	Max. temp (°C)	Occurrences	Length (min)	Max. temp (°C)
T_{per}						
32282	0		38.6	5	5–200	39.9
21024	0		38.4	12	10–70	39.4
6810	0		38.6	3	5–260	39.5
20586	1	25	39.7	1	65	39.6
20741	1	55	40.8	7	10–130	40.0
32255	2	20–40	40.1	1	20	39.4
T_{abd}						
20414	0		37.6	0		38.3
20562	1	60	39.8	1	240	39.8
20764	1	60	39.0	0		38.8
20947	0		37.0	0		38.6
21045	0		37.5	3	60	39.9
21150	0		37.2	3	60–120	39.7

## Blood biochemistry in relation to helicopter operations

We analyzed polar bear blood samples collected from 66 capture events. These events included 50 unique polar bears (35 females, 15 males); 36 individuals were captured once and 14 were captured multiple times. Capture events occurred in April–May 2009 ($n = 30$), August 2008 ($n = 9$), August 2009 ($n = 6$), October 2008 ($n = 9$), and October 2009 ($n = 12$). Mean age at capture was 11 ± 4 years (SD; range = 5–22 yr). The mean duration of helicopter operations for these captures was 19 ± 9 minutes (range = 7–45 min). Mean ambient temperature during captures was $-2.8 \pm 5.8°C$ (−16–14°C), and we administered a mean dose of Telazol of 7.6 ± 2.3 mg/kg (4.1–15.1 mg/kg).

Percent lymphocytes declined with longer duration and warmer temperature but showed no response to dose (Table 3). These results reflect whether the predicted values of percent lymphocytes differed by ≥4.5% when based on minimum and maximum values of duration, temperature, or dose, in a mixed-effects model using model-averaged coefficients (Table S1, available in Supporting Information). We defined the threshold (4.5%) as half of the standard deviation of observed percent lymphocyte values. The models that included predictors of duration and temperature (E, F, G; Table 4) had the highest AIC_c weights (sum = 0.87). The influences of bear ID, group, and sex on percent lymphocytes and all biochemical variables were variable (Table S1). Residuals in models B, E, F, and G departed from normality ($P < 0.05$, D'Agostino omnibus test) although residual plots did not show strong patterns. We identified 2 potential outliers; their removal improved normality but had no effect on the results. For all blood biochemical variables, including percent lymphocytes, results include all data (i.e., no outlier removal).
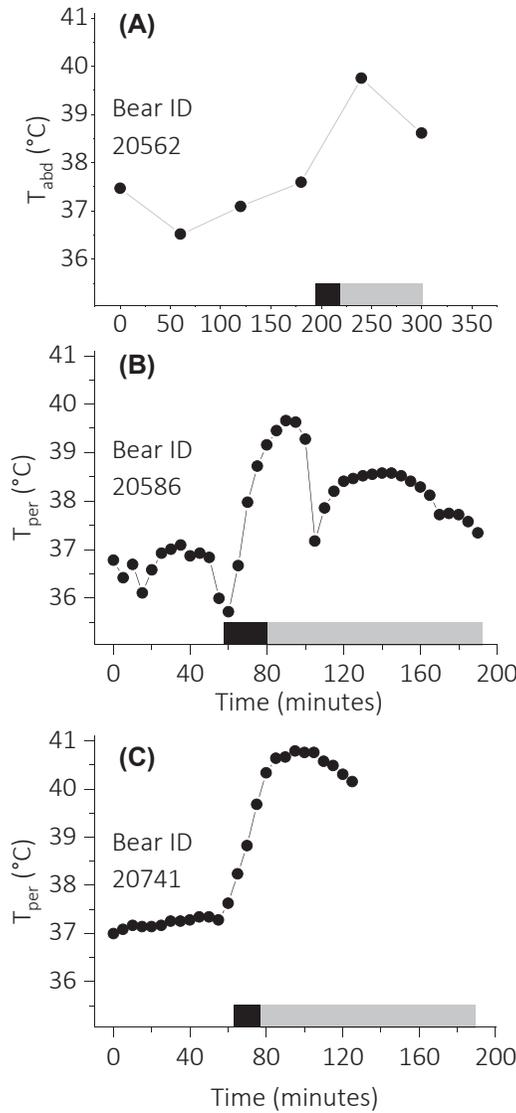
FIGURE 3 Occurrences of polar bear body temperatures >39.0°C during helicopter recapture and handling, southern Beaufort Sea, 2008–2009, as measured by abdominal (A; T_{abd}) and peripheral loggers (B–C; T_{per}). On the x-axes, black bars represent helicopter operations from initial sighting of the bear to the minute we observed it to be down, and gray bars represent the subsequent handling time of the immobilized bear until we removed the sensor. We estimated the alignment of these events because internal clocks on the temperature loggers drifted by several minutes during deployment. ID = identification.

Percent neutrophils increased with longer duration and warmer temperature, and did not respond to changes in dose (Table 3). The percent neutrophil model that included these 2 predictors (model E) had the highest AIC_c weight (0.57; Table 4). Residuals in percent neutrophil model D departed from normality (P = 0.01, D'Agostino omnibus test) although they passed an alternative test (Cramer-von Mises; P = 0.34) and residual plots did not show a strong pattern. Sodium declined with longer duration, increased with warmer temperature, and did not respond to changes in dose (Table 3). The sodium model that included duration and temperature as predictors (E) accounted for the highest AIC_c weight (0.41; Table 4). Residuals in sodium models A–D departed from normality
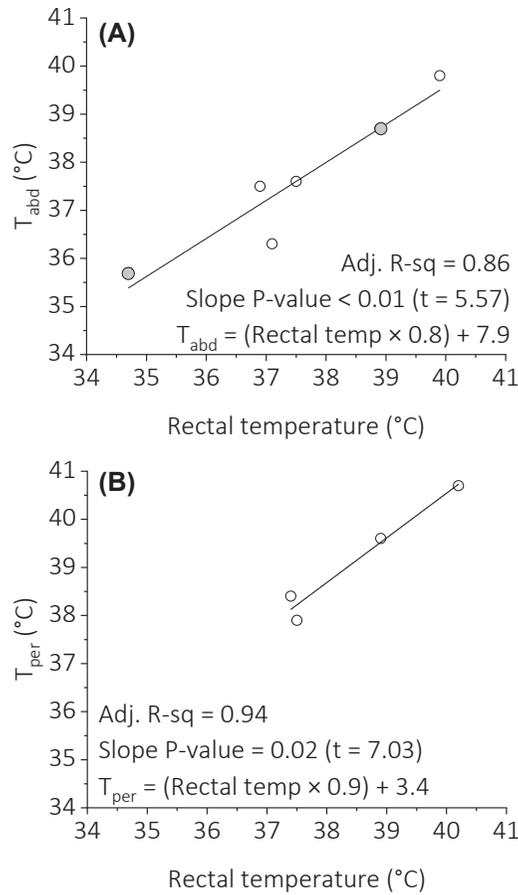
FIGURE 4 Linear regressions using polar bear rectal temperature, measured during immobilization after helicopter capture in the southern Beaufort, 2008–2009, to predict A) abdominal (T_{abd}) and B) peripheral (T_{per}) body temperatures. In A each gray circle is the mean of 2 T_{abd} measurements (rather than single measurements) that were recorded 30 minutes before and after the rectal temperature measurement.

($P < 0.05$, D'Agostino omnibus test) although residual plots did not show strong patterns. We identified 2 potential outliers in sodium models; removal of these potential outliers improved normality, did not change the negative influence of duration, and eliminated the positive influence of temperature. For models of cortisol, glucose, WBC, potassium, ALT, and glutamic acid, all changes resulting from altering predictors between minimum and maximum values were not significant (Table 3) and the highest AIC_c weight occurred for model A, which lacked the predictors of duration, temperature, and dose (Table 4).

Based on model-averaged coefficients (Table S1), the optimal helicopter operations for capturing a female in spring 2009 included duration ≤23 minutes and temperature ≤ −14°C. Because dose did not influence any biochemical variables, we did not consider it here. Captures below these thresholds did not cause significant changes in biochemical variables when compared to captures modeled with the shortest duration (7 min) and coldest temperature (−16°C). Notably, there was only a single capture at −16°C; after removing this capture and re-running models, the optimal temperature threshold was −10°C. Applying the same modeling process but assuming capture of a male instead of a female resulted in an optimal duration ≤21 minutes and temperature ≤ −12°C.

TABLE 3   Measured values of blood biochemical variables for adult female polar bears sampled in spring 2009 in the southern Beaufort Sea, and modeled values for this group under different capture scenarios. Scenarios were based on 3 predictors: duration of helicopter operations, ambient temperature conditions during capture, and dose of immobilization drug. In each scenario, we held 2 predictors constant while we varied the third predictor from the minimum to the maximum observed value. The resulting change in the biochemical variable was significant if the difference between scenarios was greater than half of the standard deviation of the mean of the measured values (indicated with an asterisk).

		Modeled values under different scenarios					
	Measured values	**Duration of helicopter operations**		**Temp**		**Dose of drug**	
Variable (units)	**$\bar{x}$ (SD)**	**7 min**	**45 min**	**−16°C**	**14°C**	**4.1 mg/kg**	**15.1 mg/kg**
Lymphocytes (%)	19 (9)	17*	10*	31*	5*	15	14
Neutrophils (%)	70 (10)	70*	82*	65*	86*	73	76
Sodium (mmol/L)	139 (3)	140*	138*	138*	141*	139	139
Cortisol (ng/ml)	52 (29)	45	46	43	50	45	47
Glucose (mg/dl)	126 (20)	132	133	136	128	133	132
WBC (10^3/μl)[a]	7.4 (2.3)	6.1	6.2	5.9	6.4	6.2	6.0
Potassium (mmol/L)	4.3 (0.2)	4.4	4.3	4.3	4.3	4.3	4.4
ALT (units/L)[b]	40 (22)	38	42	40	39	40	40
GA (μg/ml)[c]	23 (15)	20	21	20	20	21	18

[a]White blood cells.
[b]Alanine aminotransferase.
[c]Glutamic acid.

DISCUSSION

We found only limited support for our prediction that helicopter recapture, rather than natural behavior, would induce higher peak values in activity and body temperature in polar bears. Helicopter recapture, rather than natural behavior, accounted for higher peak activity in 2 of 5 instrumented bears, higher peak T_{per} in 3 of 6, and higher peak T_{abd} in 1 of 6. These results indicate that the very high levels of activity and body temperature during helicopter recapture are often within range of the most intense natural events experienced by free-ranging bears. In addition, the ambient temperature during recapture had a stronger influence on blood biochemical variables than the duration of helicopter operations. The dose of immobilization drugs was not related to any change in biochemistry. The most consistent responses to capture conditions were declines in percent lymphocytes and increases in percent neutrophils, which represents a stress leukogram, similar to capture of brown bears (Cattet et al. 2003). Overall, our results reinforce that elevated body temperatures are a risk during captures and identify stress leukograms as a potential metric of the effects of capture, meriting further study.

Activity and body temperature during helicopter capture

Polar bears often moved away from the helicopter by running, jumping or climbing over obstacles, swimming, and diving. Our data indicate that these actions were similar to the most intense events of natural behavior, potentially including prey capture (Stirling 1974, Iles et al. 2013), conflict with conspecifics (Miller et al. 2015), or traversing rough sea ice and rugged terrestrial terrain. Our datasets of natural behavior did not cover May–June, the most

TABLE 4 Akaike's Information Criterion scores adjusted for small sample sizes (AIC_c) weights (highest in each row has an asterisk) of mixed-effects models used to predict the response of blood biochemical variables to helicopter capture in polar bears, 2009. All models included the predictors of bear identification (ID), sex, and group (defined by season and location of capture). Models B–G also included combinations of additional predictors: duration of helicopter operations (duration), ambient temperature during capture (temp), a duration and temperature interaction term, and dose of the immobilization drug.

Response variable	Models A–G predictors (in addition to bear ID, sex, group) AIC_c weights						
	A	B Duration	C Temp	D Dose	E Duration + temp	F Duration + temp + duration × temp	G Duration + temp + dose + duration × temp
Lymphocytes	0.01	0.01	0.10	0.00	0.61*	0.16	0.10
Neutrophils	0.00	0.05	0.00	0.01	0.57*	0.14	0.23
Sodium	0.07	0.20	0.12	0.02	0.41*	0.13	0.05
Cortisol	0.46*	0.12	0.20	0.15	0.05	0.01	0.00
Glucose	0.42*	0.12	0.24	0.13	0.06	0.02	0.01
WBC[a]	0.43*	0.14	0.17	0.16	0.05	0.03	0.01
Potassium	0.42*	0.23	0.11	0.16	0.05	0.02	0.02
ALT[b]	0.37*	0.21	0.11	0.10	0.05	0.13	0.04
GA[c]	0.40*	0.10	0.10	0.35	0.03	0.01	0.02

[a]White blood cells.
[b]Alanine aminotransferase.
[c]Glutamic acid.

active period of the year, which includes peak hunting opportunities, courtship, and mating (Ferguson et al. 2001, Laidre et al. 2012, Whiteman et al. 2015). The lack of data in these months could bias our interpretation of natural behaviors towards lower activity. Although the probability of intense activity during natural behavior is highest during May–June, it remains possible at any point during the year outside of the time spent in maternal dens.

Body temperatures >39.0°C occurred during some recaptures, emphasizing the importance of monitoring body temperature during immobilization. These occurrences were generally similar in peak temperature and duration to those that occurred during natural behavior, and body temperatures gradually declined during immobilization. Our results support that rectal temperature, commonly measured in the field, provides a reliable proxy for both T_{abd} and T_{per}. Similarly, in humans, rectal temperature closely tracked rising core body temperature during intense exercise (Teunissen et al. 2012). One polar bear also exhibited a rectal temperature and T_{abd} < 36°C. The cause of this mild hypothermia is unknown, although it is possible that the animal swam in cold water shortly before or during capture. Although the immobilization drug Telazol can interfere with thermoregulation, the potential risk is expected to be hyperthermia rather than hypothermia; in addition, Telazol typically does not impair respiration rate and thus would not influence respiratory heat loss (Stirling et al. 1989, Kreeger and Arnemo 2018).

Only 1 polar bear exhibited peak T_{abd} during helicopter recapture. We may have missed brief temperature spikes because we only measured T_{abd} hourly, although such non-detection of substantial spikes is unlikely for 2 reasons. First, in a previous study of captive polar bears, although T_{abd} increased quickly after the initiation of intense exercise, T_{abd} required 70–190 minutes to reach new, elevated equilibrium values (Best 1982). This time lag, due to thermal inertia, suggests that an induced rise in T_{abd} would have been apparent even in our T_{abd} measurements recorded up to an hour after the initiation of helicopter operations. Second, the relatively low ratio of surface area to volume of polar bears (because of their large body size) and their thick fur insulation render it

difficult for them to quickly dissipate an exercise-induced heat load (Scholander et al. 1950, Guppy 1986). This phenomenon makes it unlikely that T_{abd} could have spiked substantially and returned to lower values in less than an hour. The monthly mean T_{abd} in this subpopulation declines from May to September because of reduced food availability (Whiteman et al. 2015); this decline is approximately 0.7°C and is apparent only in long-term, smoothed data, leaving it possible for polar bears to experience brief periods of high T_{abd} during natural behavior even during late summer.

We derived activity and body temperature data from recaptures in October and polar bears may respond differently to helicopter operations and immobilization during other seasons. For example, polar bears are typically in reduced body condition during April–May when spring captures are performed (Whiteman et al. 2018, Galicia et al. 2019), which could help prevent elevated body temperatures because they are displacing less body mass when running. Alternatively, their fur is likely denser during April–May than during late summer (Frisch et al. 1974), which could increase the likelihood of high body temperatures. Similarly, the consequences of 4 days of reduced activity immediately post-capture (Thiemann et al. 2013, Rode et al. 2014) may be more profound during the hyperphagia of April–May. In general, seasonal changes in physiology could also affect how polar bears respond to intense events of natural behavior, suggesting that our inferences may apply across seasons.

Blood biochemistry in relation to helicopter operations

Among predictors describing helicopter operations, warmer ambient temperature during capture had the most pronounced effects on blood biochemical variables. These results were based on data from captures across seasons (Apr–May, Aug, and Oct). This effect of warm ambient temperature highlights that polar bears are poorly adapted for dissipating heat. In our modeling of females captured in spring, increasing ambient temperature from the minimum to the maximum value led to a stress leukogram. This pattern suggests that in response to capture, lymphocytes were sequestered into lymph nodes for secondary immune surveillance and neutrophils were released from bone marrow and tissue reservoirs to attack pathogens (Evans et al. 2001, Van Engen et al. 2014). Stress leukograms are also often associated with an increase in the white blood cell count; it is unclear why we did not observe this trend.

Stress leukograms have been used as a metric of capture response. Brown bears exhibited a greater stress leukogram when captured via leg-hold snares than via helicopter capture, likely because individuals in leg-hold snares were restrained for long periods before immobilization (Cattet et al. 2003). In that study, the differences in percent neutrophils and in percent lymphocytes between bears captured via the 2 methods was similar to the differences in our study caused by increasing ambient temperature from the minimum to the maximum value. Other large carnivores such as wolves (*Canis lupus*) also exhibit stress leukograms in response to long periods of restraint in leg-hold snares (Santos et al. 2017).

The consequences of capture-induced stress leukograms are unclear and have not been studied in bears. In a study of a different large-bodied mammal (ponies; *Equus ferus caballus*), stress leukograms were experimentally induced by dexamethasome injections (a steroid that is analogous to hormones involved with stress responses; Targowski 1975). The resulting decline in lymphocytes did not hinder the ability of lymphocytes to respond to foreign substances (assessed *in vitro* by phytohemagglutinin-induced activation). But the ability of WBC to aggregate at the site of an injury may have been reduced (assessed *in vivo* by tissue swelling after antigen injection; Targowski 1975). The latter result suggests a transient increase in infection susceptibility, although additional study is needed. In the ponies and in humans (Suzuki et al. 1999, Peake et al. 2016), only several hours to several days were needed to return to typical levels of percent lymphocytes and neutrophils. This potential for a quick recovery, combined with the fact that helicopter capture is a single, discrete event, suggests that the stress leukograms we observed were an acute stress response.

In comparison to warm ambient temperatures, long durations of helicopter operations caused smaller changes in percent lymphocytes and percent neutrophils. The maximum duration of helicopter operations was also associated with a decline in blood sodium. The mechanism for this sodium decline is unclear because stress and high body temperatures are expected to cause an increase. Indeed, the maximum ambient temperature was associated with an increase in sodium, potentially reflecting dehydration and reduced kidney function (Hashim 2010). This temperature-induced increase in sodium and the duration-induced decrease in sodium were of small magnitude.

Factors outside of our analysis may have obscured relationships between capture conditions and biochemical variables. For example, cortisol and glucose were not influenced by helicopter operations, despite capture stress generally causing their increase (Malisch et al. 2018). This may reflect that the hypothalamic-pituitary-adrenal stress response is not graded during helicopter captures (i.e., it is more of an off or on response) or that cortisol can be regulated by other mechanisms such as altering concentration of the binding protein (Chow et al. 2010, 2011; Boonstra et al. 2020). In addition, our assessment of peak values of activity and body temperatures did not consider the effect of different durations between initial captures and recaptures, as 15 of 17 datasets encompassed the same duration (i.e., Aug–Oct). Polar bears could react more strongly if a previous capture was more recent. Other potential limitations of our study include the small sample size of bears with activity and temperature loggers, and that we relied on minimum and maximum values of duration, temperature, and dose to evaluate significance in our blood biochemistry models; however, these values are consistent with our field experience.

RESEARCH IMPLICATIONS

When deciding on field methods, biologists should consider that helicopter capture is similar to the most intense events that occur during natural behavior of polar bears. When helicopter capture is used, 2 datasets should be collected to support future analyses. First, detailed narratives describing the helicopter pursuit could give a more nuanced understanding of stressors (e.g., terrain, timing and duration of herding bears or swimming). Second, capture site weather conditions (e.g., ambient temperature, wind, cloud cover) and timing of blood sample collection could potentially help to explain variation in body temperature and biochemical variables. Lastly, future research should investigate the mechanisms and consequences of capture-induced stress leukograms, and account for their influence in ecoimmunological studies.

CONFLICTS OF INTEREST
The authors have no conflicts of interest.

ETHICS STATEMENT

Procedures for capturing, sampling, and instrumenting polar bears were approved by the Institutional Animal Care and Use Committees of the University of Wyoming (Project NSF 44341) and the USGS Alaska Science Center (assurance number. 2010-3), and permitted by the United States Fish and Wildlife Service (permit MA690038).

DATA AVAILABILITY STATEMENT

Data are available at https://doi.org/10.5066/P9OKOCN1.

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REFERENCES

Amstrup, S. C. 1993. Human disturbances of denning polar bears in Alaska. Arctic 46:246–250.

Amstrup, S. C., G. M. Durner, I. Stirling, N. J. Lunn, and F. Messier. 2000. Movements and distribution of polar bears in the Beaufort Sea. Canadian Journal of Zoology 78:948–966.

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

Arnemo, J. M., P. Ahlqvist, R. Andersen, F. Berntsen, G. Ericsson, J. Odden, S. Brunberg, P. Segerström, and J. E. Swenson. 2006. Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. Wildlife Biology 12:109–113.

Barbour, M. G., and W. D. Billings. 2000. North American Terrestrial Vegetation. Cambridge University Press, Cambridge, United Kingdom.

Bartoń, K. 2021. MuMIn: multi-model inference. https://CRAN.R-project.org/package=MuMIn

Best, R. C. 1982. Thermoregulation in resting and active polar bears. Journal of Comparative Physiology B 146:63–73.

Boonstra, R., K. Bodner, C. Bosson, B. Delehanty, E. S. Richardson, N. J. Lunn, A. E. Derocher, and P. K. Molnár. 2020. The stress of Arctic warming on polar bears. Global Change Biology 26:4197–4214.

Breed, D., L. C. R. Meyer, J. C. A. Steyl, A. Goddard, R. Burroughs, and T. A. Kohn. 2019. Conserving wildlife in a changing world: understanding capture myopathy—a malignant outcome of stress during capture and translocation. Conservation Physiology 7:coz027.

Bromaghin, J. F., T. L. McDonald, I. Stirling, A. E. Derocher, E. S. Richardson, E. V. Regehr, D. C. Douglas, G. M. Durner, T. Atwood, and S. C. Amstrup. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. Ecological Applications 25:634–651.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

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

Cattet, M. R. L., K. Christison, N. A. Caulkett, and G. B. Stenhouse. 2003. Physiologic responses of grizzly bears to different methods of captures. Journal of Wildlife Diseases 39:649–654.

Cherry, S. G., A. E. Derocher, I. Stirling, and E. S. Richardson. 2009. Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea. Polar Biology 32:383–391.

Chow, B. A., J. Hamilton, D. Alsop, M. R. L. Cattet, G. Stenhouse, and M. M. Vijayan. 2010. Grizzly bear corticosteroid binding globulin: cloning and serum protein expression. General and Comparative Endocrinology 167:317–325.

Chow, B. A., J. Hamilton, M. R. L. Cattet, G. Stenhouse, M. E. Obbard, and M. M. Vijayan. 2011. Serum corticosteroid binding globulin expression is modulated by fasting in polar bears (Ursus maritimus). Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology 158:111–115.

Costello, M. J., K. H. Beard, R. T. Corlett, G. S. Cumming, V. Devictor, R. Loyola, B. Maas, A. J. Miller-Rushing, R. Pakeman, and R. B. Primack. 2016. Field work ethics in biological research. Biological Conservation 203:268–271.

Derocher, A. E., J. Aars, S. C. Amstrup, A. Cutting, N. J. Lunn, P. K. Molnár, M. E. Obbard, I. Stirling, G. W. Thiemann, D. Vongraven, Ø. Wiig, and G. S. York. 2013. Rapid ecosystem change and polar bear conservation. Conservation Letters 6:368–375.

Diehl, K. A., E. Crawford, P. D. Shinko, R. D. Tallman, and M. J. Oglesbee. 2000. Alterations in hemostasis associated with hyperthermia in a canine model. American Journal of Hematology 64:262–270.

Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Movement Ecology 1:3.

Durner, G. M., D. C. Douglas, R. M. Nielson, S. C. Amstrup, T. L. McDonald, I. Stirling, M. Mauritzen, E. W. Born, Ø. Wiig, E. DeWeaver, et al. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. Ecological Monographs 79:25–58.

Durner, G. M., J. P. Whiteman, H. J. Harlow, S. C. Amstrup, E. V. Regehr, and M. Ben-David. 2011. Consequences of long-distance swimming and travel over deep-water pack for a female polar bear during a year of extreme sea ice retreat. Polar Biology 34:975–984.

Evans, S. S., W.-C. Wang, M. D. Bain, R. Burd, J. R. Ostberg, and E. A. Repasky. 2001. Fever-range hyperthermia dynamically regulates lymphocyte delivery to high endothelial venules. Blood 97:2727–2733.

Ferguson, S. H., M. K. Taylor, E. W. Born, A. Rosing-Asvid, and F. Messier. 2001. Activity and movement patterns of polar bears inhabiting consolidated versus active pack ice. Arctic 54:49–54.

Field, K. A., P. C. Paquet, K. Artelle, G. Proulx, R. K. Brook, and C. T. Darimont. 2019. Publication reform to safeguard wildlife from researcher harm. PLOS Biology 17:e3000193.

François, B. 2002. Recommendations to improve the quality of diagnostic quantitative analysis of amino acids in plasma and urine using cation-exchange liquid chromatography with post column ninhydrin reaction and detection. European Research Network for Evaluation and Improvement of Screening, Diagnosis, and Treatment of Inherited Disorders of Metabolism, Manchester, United Kingdom.

Frisch, J., N. Oritsland, and J. Krog. 1974. Insulation of furs in water. Comparative Biochemistry and Physiology 47:403–410.

Galicia, M. P., G. W. Thiemann, and M. G. Dyck. 2019. Correlates of seasonal change in the body condition of an Arctic top predator. Global Change Biology 26:840–850.

Guppy, M. 1986. The hibernating bear: why is it so hot, and why does it cycle urea through the gut? Trends in Biochemical Sciences 11:274–276.

Hashim, I. A. 2010. Clinical biochemistry of hyperthermia. Annals of Clinical Biochemistry 47:516–523.

Hersbach, H., B. Bell, P. Berrisford, S. Hirahara, A. Horányi, J. Muñoz-Sabater, J. Nicolas, C. Peubey, R. Radu, D. Schepers, et al. 2020. The ERA5 global reanalysis. Quarterly Journal of the Royal Meteorological Society 146:1999–2049.

Hill, R. W., G. A. Wyse, and M. Anderson. 2008. Animal Physiology. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Iles, D. T., S. L. Peterson, L. J. Gormezano, D. N. Koons, and R. F. Rockwell. 2013. Terrestrial predation by polar bears: not just a wild goose chase. Polar Biology 36:1373–1379.

Jacob, S., E. Holm, and B. Fischer. 1989. Effects of hyperthermia on the peripheral metabolism of ammonia and glutamine. Metabolism 38:43–46.

Kearney, S. R. 1989. The polar bear alert program at Churchill, Manitoba. Pages 83–92 in M. Bromley, editor. Bear-people conflict: proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Canada.

Kreeger, T. J., and J. M. Arnemo. 2018. Handbook of wildlife chemical immobilization. Fifth edition. Published by the authors.

Kwok, R., G. Spreen, and S. Pang. 2013. Arctic sea ice circulation and drift speed: decadal trends and ocean currents. Journal of Geophysical Research: Oceans 118:2408–2425.

Laidre, K. L., E. W. Born, E. Gurarie, Ø. Wiig, R. Dietz, and H. Stern. 2012. Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (Ursus maritimus). Proceedings of the Royal Society B 280: 20122371.

Latham, A. D. M., B. Davidson, B. Warburton, I. Yockney, and J. O. Hampton. 2019. Efficacy and animal welfare impacts of novel capture methods for two species of invasive wild mammals in New Zealand. Animals 10:44.

Le Boucher, J., C. Charret, C. Coudray-Lucas, J. Giboudeau, and L. Cynober. 1997. Amino acid determination in biological fluids by automated ion-exchange chromatography: performance of Hitachi L-8500A. Clinical Chemistry 43: 1421–1428.

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

Malisch, J. L., D. J. Bennett, B. A. Davidson, E. E. Wenker, R. N. Suzich, and E. E. Johnson. 2018. Stress-induced hyperglycemia in white-throated and white-crowned sparrows: a new technique for rapid glucose measurement in the field. Physiological and Biochemical Zoology 91:943–949.

Messier, F. 2000. Effects of capturing, tagging, and radio-collaring polar bears for research and management purposes in Nunavut and Northwest Territories. Government of Nunavut, Iqaluit, Northwest Territories, Canada.

Miller, S., J. Wilder, and R. R. Wilson. 2015. Polar bear–grizzly bear interactions during the autumn open-water period in Alaska. Journal of Mammalogy 96:1317–1325.

Mori, B. D. 2019. Animal testing: the ethical principle of the 3Rs from laboratories to "field" research with wild animals. Etica & Politica XXI:553–570.

Pagano, A. M., E. Peacock, and M. A. McKinney. 2014. Remote biopsy darting and marking of polar bears. Marine Mammal Science 30:169–183.

Pauli, J. N., J. P. Whiteman, M. D. Riley, and A. D. Middleton. 2010. Defining noninvasive approaches for sampling of vertebrates. Conservation Biology 24:349–352.

Peake, J. M., O. Neubauer, N. P. Walsh, and R. J. Simpson. 2016. Recovery of the immune system after exercise. Journal of Applied Physiology 122:1077–1087.

Ramsay, M. A., and I. Stirling. 1986. Long-term effects of drugging and handling free-ranging polar bears. Journal of Wildlife Management 50:619–626.

Regehr, E. V., K. L. Laidre, H. R. Akçakaya, S. C. Amstrup, T. C. Atwood, N. J. Lunn, M. Obbard, H. Stern, G. W. Thiemann, and Ø. Wiig. 2016. Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. Biology Letters 12:20160556.

Rode, K. D., T. C. Atwood, G. W. Thiemann, M. St. Martin, R. R. Wilson, G. M. Durner, E. V. Regehr, S. L. Talbot, G. K. Sage, A. M. Pagano, and K. S. Simac. 2020. Identifying reliable indicators of fitness in polar bears. PLoS ONE 15:0237444.

Rode, K. D., A. M. Pagano, J. F. Bromaghin, T. C. Atwood, G. M. Durner, K. S. Simac, and S. C. Amstrup. 2014. Effects of capturing and collaring on polar bears: findings from long-term research on the southern Beaufort Sea population. Wildlife Research 41:311–322.

Santos, N., H. Rio-Maior, M. Nakamura, S. Roque, R. Brandão, and F. Álvares. 2017. Characterization and minimization of the stress response to trapping in free-ranging wolves (*Canis lupus*): insights from physiology and behavior. Stress 20: 513–522.

Scasta, J. D. 2020. Mortality and operational attributes relative to feral horse and burro capture techniques based on publicly available data from 2010–2019. Journal of Equine Veterinary Science 86:102893.

Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some Arctic and tropical mammals and birds. Biological Bulletin 99:225–236.

Stirling, I. 1974. Midsummer observations on behavior of wild polar bears (*Ursus maritimus*). Canadian Journal of Zoology 52:1191–1198.

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

Suzuki, K., M. Totsuka, S. Nakaji, M. Yamada, S. Kudoh, Q. Liu, K. Sugawara, K. Yamaya, and K. Sato. 1999. Endurance exercise causes interaction among stress hormones, cytokines, neutrophil dynamics, and muscle damage. Journal of Applied Physiology 87:1360–1367.

Targowski, S. P. 1975. Effect of prednisolone on the leukocyte counts of ponies and on the reactivity of lymphocytes in vitro and in vivo. Infection and Immunity 11:252–256.

Teunissen, L. P. J., A. de Haan, J. J. de Koning, and H. A. M. Daanen. 2012. Telemetry pill versus rectal and esophageal temperature during extreme rates of exercise-induced core temperature change. Physiological Measurement 33: 915–924.

Thiemann, G. W., A. E. Derocher, S. G. Cherry, N. J. Lunn, E. Peacock, and V. Sahanatien. 2013. Effects of chemical immobilization on the movement rates of free-ranging polar bears. Journal of Mammalogy 94:386–397.

U.S. Fish and Wildlife Service. 2008. Determination of threatened status for the polar bear (*Ursus maritimus*) throughout its range. Federal Register 73:28211–28303.

Van Engen, N. K., M. L. Stock, T. Engelken, R. C. Vann, L. W. Wulf, L. A. Karriker, W. D. Busby, J. Lakritz, A. J. Carpenter, B. J. Bradford, et al. 2014. Impact of oral meloxicam on circulating physiological biomarkers of stress and inflammation in beef steers after long-distance transportation. Journal of Animal Science 92:498–510.

Van Oort, B. E. H., N. J. C. Tyler, P. V. Storeheier, and K.-A. Stokkan. 2004. The performance and validation of a data logger for long-term determination of activity in free-ranging reindeer, *Rangifer tarandus L*. Applied Animal Behaviour Science 89:299–308.

Whiteman, J. P., H. J. Harlow, G. M. Durner, R. Anderson-Sprecher, S. E. Albeke, E. V. Regehr, S. C. Amstrup, and M. Ben-David. 2015. Summer declines in activity and body temperature offer polar bears limited energy savings. Science 349: 295–298.

Whiteman, J. P., H. J. Harlow, G. M. Durner, E. V. Regehr, S. C. Amstrup, and M. Ben-David. 2018. Phenotypic plasticity and climate change: can polar bears respond to longer Arctic summers with an adaptive fast? Oecologia 186:369–381.

Whiteman, J. P., H. J. Harlow, G. M. Durner, E. V. Regehr, S. C. Amstrup, and M. Ben-David. 2019. Heightened immune system function in polar bears using terrestrial habitats. Physiological and Biochemical Zoology 92:1–11.

Whiteman, J. P., B. C. Rourke, M. Robles, H. J. Harlow, G. M. Durner, S. C. Amstrup, E. V. Regehr, and M. Ben-David. 2017. Polar bears experience skeletal muscle atrophy in response to food deprivation and reduced activity in winter and summer. Conservation Physiology 5:cox049.

Wong, P. B. Y., M. G. Dyck, Arviat Hunters and Trappers, Ikajutit Hunters and Trappers, Mayukalik Hunters and Trappers, and R. W. Murphy. 2017. Inuit perspectives of polar bear research: lessons for community-based collaborations. Polar Record 53:257–270.

Zlotnik, A., B. Gurevich, A. A. Artru, S. E. Gruenbaum, M. Dubilet, A. Leibowitz, G. Shaked, S. Ohayon, Y. Shapira, and V. I. Teichberg. 2010. The effect of hyperthermia on blood glutamate levels. Anesthesia & Analgesia 111:1497–1504.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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