



Classifying the effects of human disturbance on denning polar bears

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ABSTRACT: Climate change is resulting in decreased sea ice extent and increased industrial activity in Arctic regions. In northern Alaska, USA, sea ice loss has increased the frequency of land-based polar bear *Ursus maritimus* maternal dens, leading to greater potential for overlap between industrial activities and denning bears. Responses of denning bears to human disturbance could result in costly reproductive outcomes, although observation of these responses is logistically challenging and expensive. We developed a method to standardize the process of classifying the response of denning polar bears to disturbance using decision rules based on polar bear biology and denning chronology. We applied this method to 46 maternal polar bear dens exposed to human activity (e.g. vehicle traffic, ground-based monitoring). Because the timing of disturbance influences the response and subsequent fitness consequences, we determined outcomes specific to 4 denning periods: (1) den establishment (excavation to cub birth); (2) early denning (cub birth to 60 d old); (3) late denning (60 d old to emergence); and (4) post-emergence (emergence to den site departure). We classified the outcomes of 79 exposures as 37 having 'no documented effect' (no observed response), 7 as 'behavioral' (observed behavioral disruption), 17 as 'early emergence' (den emergence occurring earlier than an undisturbed emergence), 14 as 'early departure' (den site abandonment post-emergence earlier than if undisturbed), and 4 as 'cub mortality' (death or abandonment of ≥ 1 cub). Outcomes with potential fitness consequences occurred in every denning period. Our classification method facilitated a standardized approach that can be used to classify the outcome of den disturbance. Determining outcomes in relation to a specific denning period may facilitate improved implementation of mitigation strategies to reduce disturbance to denning bears.

KEY WORDS: Denning · Human disturbance · Industrial development · Polar bear · Reproduction · *Ursus maritimus*

1. INTRODUCTION

Understanding how mechanisms that affect reproductive success contribute to biologically meaningful population changes is crucial for effective wildlife management (Gill et al. 2001), particularly in populations expected to decline due to changes in environmental conditions. Reproductive success is affected by factors including nutritional condition (Atkinson &

Ramsay 1995, Festa-Bianchet et al. 1998, Cook et al. 2013), habitat quality (Van Horne 1983), population density (Festa-Bianchet et al. 1998), and disturbance (Linnell et al. 2000, Gill et al. 2001). Wildlife populations are exposed to increasing levels of disturbance as our anthropogenic footprint expands through activities such as industrial development (Klein & Magomedova 2002, Wilson et al. 2014) and recreation (Ellenberg et al. 2006, Watson et al. 2014, Rode

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et al. 2018a). Changes in wildlife behavior and habitat use in response to human disturbance are well-documented for a variety of taxa (see reviews in Stankowich 2008, Fahrig & Rytwinski 2009).

An individual's response to human activity and the subsequent biological consequences are the result of interacting factors including the timing, duration, frequency, and intensity of the activity (Frid & Dill 2002, Larson et al. 2020). Individuals differ in whether the activity is perceived as a disturbance and also in their degree of tolerance to the activity (e.g. individuals with greater 'human experience' may be more tolerant; Smith & Van Daele 1990, Holmes et al. 1993, Mech et al. 1998, Thiel et al. 1998, Smith et al. 2007). Some individuals may tolerate disturbance when resources are scarce or the option of avoiding the disturbance has higher consequences (e.g. abandoning young or increased risk of predation; Blumstein 2016). Linking an individual's response directly to fitness consequences can be difficult (Gill et al. 2001). Whereas observations of the immediate behavioral response to a disturbance may be documented, knowledge of the mechanistic links to long-term implications of disturbance is often lacking (Williams et al. 2006, Christiansen & Lusseau 2015).

Altering behavior in response to disturbance (by e.g. fleeing or decreased foraging) incurs energetic costs (Bélanger & Bédard 1990, Lusseau et al. 2006, Williams et al. 2006, Czapanskiy et al. 2021), often leading to declines in body condition, which is particularly consequential for reproductive females (Guinet et al. 1998, Christiansen & Lusseau 2015). Individuals in better body condition may be better equipped to cope with disturbance (Bieber et al. 2014, Evans et al. 2016, Molnár et al. 2020) and have subsequently higher reproductive success (Atkinson & Ramsay 1995) than those in poorer body condition. This relationship may be more pronounced for animals that are dormant for a portion of the year, including many ursid species, given the often prolonged period of fasting. In northern regions, most black bears *Ursus americanus* and brown bears *U. arctos* of all ages and sexes spend several winter months inside a den in a state of metabolic dormancy to conserve energy; however, among polar bears *U. maritimus*, only pregnant females over-winter in dens (Ramsay & Stirling 1988). For bears in northern regions, cub production, size, and survival are strongly linked to maternal mass and condition (Atkinson & Ramsay 1995, Derocher & Stirling 1996, 1998, Robbins et al. 2012, Rode et al. 2020) and a successful winter denning period (Friebe et al. 2001, Seryodkin et al. 2003, Rode et al. 2018b). Successful denning requires den charac-

teristics adequate for protection from environmental conditions and predators (Durner et al. 2003, Liston et al. 2016), a sufficient duration inside the den (Johnson & Pelton 1981, Rode et al. 2018b), and minimal disturbance (Linnell et al. 2000). Because some pregnant polar bears transition directly from a prolonged open-water fasting period to denning, they can go through a period of up to 8 mo without food (Watts & Hansen 1987, Ramsay & Stirling 1988).

Denning inherently limits the ability of bears to move when disturbed. Although short-term, low-intensity disturbance may have small fitness costs (Craighead et al. 1976, Linnell et al. 2000), once individual thresholds of disturbance are surpassed, the probability of negative consequences increases (Linnell et al. 2000, Lunn et al. 2004). Arousals during denning can incur energetic costs (Geiser 2013), including increases in body temperature (Craighead et al. 1976, Laske et al. 2011, Evans et al. 2016) and heart rate (Reynolds et al. 1986, Evans et al. 2016), which have been linked to decreased reproductive success (Ramsay & Dunbrack 1986, Amstrup & Gardner 1994, Swenson et al. 1997, Linnell et al. 2000).

As an ice-dependent species (Amstrup 2003), polar bears are inherently impacted by changes in sea ice quantity, distribution, and the timing of sea ice advance and retreat. In some Arctic regions, a delay in the formation of autumn sea ice has resulted in a 67% decrease in available maternal denning habitat (Merkel & Aars 2022). In other regions, as a result of declining sea ice, polar bears have been forced to modify habitat use patterns and are spending more time on land (Kochnev 2006, Schliebe et al. 2008, Gleason & Rode 2009, Rode et al. 2015, Atwood et al. 2016), which includes denning (Derocher et al. 2011, Olson et al. 2017). For example, in the Southern Beaufort Sea (SBS) subpopulation, the frequency of land-based denning increased from ~34% in 1985–1995 to ~55% in 1996–2013 (Amstrup & Gardner 1994, Fischbach et al. 2007, Olson et al. 2017). Similarly, land-based industrial activity is also anticipated to increase in the Arctic, and these activities generally occur during winter months to minimize impacts to sensitive tundra habitats. Consequently, concomitant increases in land-based denning and industrial expansion in the Arctic will increase the potential for disturbance to maternal dens (Atwood et al. 2017, Durner et al. 2018, Wilson & Durner 2020).

In the USA, polar bears are managed by the US Fish and Wildlife Service (USFWS), protected under the Marine Mammal Protection Act (MMPA), and listed as threatened under the Endangered Species Act. Activities within the range of polar bears in the

USA are evaluated and regulated (see USFWS 2019, 2021), and mitigation measures are implemented to reduce impacts to polar bears, including implementation of a 1.6 km buffer with limited human activity around known dens. Dens, however, often go undetected until a polar bear emerges, potentially as a result of the disturbance (Amstrup 1993, this study). Thus, effective mitigation measures often require intensive monitoring of known or suspected den sites or den detection surveys (e.g. aerial infrared surveys; Amstrup et al. 2004, Wilson & Durner 2020). Den site monitoring, however, also has the potential for disturbance (Belikov 1976, Smith et al. 2007, 2013), and given the low detection rate of aerial infrared surveys (i.e. <45%), detection of most dens is unlikely with this method (Woodruff et al. 2022).

Under the MMPA, take of polar bears (i.e. harassing, feeding, capturing, or killing) is prohibited, except under limited conditions (e.g. subsistence harvest by coastal Alaskan Natives). The MMPA also establishes a legal framework under which incidental take (i.e. unintentional take due to activity not related to the species; NOAA, <https://www.fisheries.noaa.gov/insight/understanding-permits-and-authorizations-protected-species>) may be authorized, and the USFWS receives multiple requests annually for take authorizations including for oil and gas activities and military exercises. Processing these requests requires estimating the number of polar bear takes that may occur because of the proposed activities ‘... on the basis of the best scientific evidence available’ and promulgating regulations that may include mitigation to reduce take. We recognize that this need to make management decisions within a pre-determined timeframe often requires the use of imperfect information (e.g. limited sample sizes).

Generally, we have no knowledge of a bear from den entrance to den emergence (e.g. date of cub birth, likely emergence date, etc.), yet all disturbance has the potential to negatively impact denning females and cubs. Our objective was to develop a framework to assess whether a disturbance to denning polar bears occurred and to determine the outcome for the bear(s) (e.g. behavioral effect, early emergence; described in Section 2.1). Our geographic focus was northern Alaska, which is within the range of the SBS polar bear subpopulation (PBSG 2021).

We reviewed cases involving polar bear dens known to have been exposed to human activities, developed and applied a set of decision rules based on polar bear biology and denning chronology to characterize the response of denning polar bears to the exposures, and classified the outcome relative to 4 denning periods (see Section 2). Our goal was not solely to summarize bears’ responses to human activity (e.g. Robinson 2014, Smith et al. 2010, 2013, Larson et al. 2020), but instead to use the outcomes to develop a standardized method that can then be used by decision makers to inform whether exposure to human activity impacts denning bears during each denning period.

2. MATERIALS AND METHODS

We compiled case studies of maternal polar bear dens that may have been exposed to human activities from published literature and reports submitted to the USFWS by the oil and gas industry and researchers between 1971 and 2018 (Fig. 1 and Table S1 in the Supplement at www.int-res.com/articles/suppl/n049/p043_supp.xlsx). Because industrial activity has been restricted historically within 1.6 km of known polar bear dens (USFWS 2021), we used this distance as a threshold to identify dens exposed to human activity (hereafter, an ‘exposure’) and excluded records where human activity occurred outside this threshold.

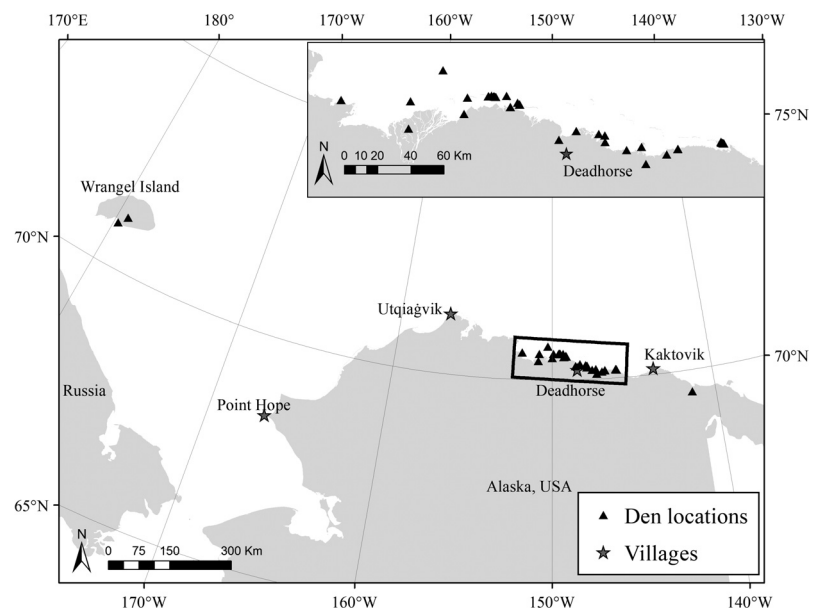


Fig. 1. Locations of maternal polar bear dens that were exposed to human activities based on published literature and reports submitted to the US Fish and Wildlife Service by the oil and gas industry and researchers between 1971 and 2018. Inset: dens on the North Slope in proximity to Prudhoe Bay, Alaska, USA

Although our motivation was to understand and estimate the influence of industrial activities on denning bears, we included records of both industry and research activities because many research activities have correlates in industry (e.g. aircraft and land-based vehicle traffic or inadvertently approaching a den at close distance). We excluded bear capture activities, however, because they are not direct correlates to industry-caused disturbances.

For denning polar bears, the timing of an exposure is a critical factor influencing the response and subsequent fitness consequences (Swenson et al. 1997, Linnell et al. 2000). Therefore, we divided the denning period into 4 stages based on the stages of cub development (described in Section 2.1). For each period, we determined whether sufficient information existed in each case study to determine (1) whether an exposure occurred, (2) whether a response occurred, and (3) if the outcome could be classified according to the period-specific decision rules (described in Section 2.1; see Fig. 2). When known, we recorded the closest distance of the exposure to the den, a narrative of the exposure and exposure type (e.g. vehicle, aircraft), the date of exposure, emergence, and departure, and the outcome (Table S1). Due to our sample size, we did not evaluate different exposure types separately but used the response of the bear to classify the outcome to each exposure.

If a bear was exposed to human activity, we classified outcomes as (1) 'no documented effect' (hereafter, 'no effect'); (2) 'behavioral' (i.e. an observed disruption of a behavioral pattern, e.g. nursing, breeding, feeding, sheltering); (3) 'early emergence' from the den (see below and Table 1); (4) 'early departure' from the den site (see below and Table 1); or (5) 'cub mortality' when ≥ 1 cub died or a female abandoned all or part of her litter, either in the den or on the surface. A case where a female left her cubs due to human disturbance but was later captured and reunited with her cubs was also classified as 'cub mortality' because of the likelihood of a lethal outcome without human intervention. Under most circumstances to which our analysis applied (i.e. analysis of take by industry), capturing and reuniting bears would not be identified and/or possible. In cases where there was ambiguity about the outcome, we were required to make informed decisions, and we deferred to the potential for disturbance to be the cause of the outcome given our motivation was to reduce negative impacts to denning bears. Some dens were associated with multiple exposures within a denning period but we did not have enough information to assess the outcome for these

differently than for dens with a single exposure. However, because we considered exposures in different denning periods separately, some dens were associated with multiple instances of exposure (i.e. in different denning periods in the same denning season) and associated outcomes. For these dens, we did not analyze the periods that followed outcomes of early emergence, early departure, or cub mortality.

2.1. Denning periods

2.1.1. Den establishment

We defined den establishment as the period between the start of maternal den excavation and the birth of cubs (or 15 December for unknown birth date; see Table 1). We are not aware of any studies directly documenting birth dates of polar bear cubs in the wild; however, estimated date of parturition varies from mid-November through early January (Derocher et al. 1992, Van de Velde et al. 2003, Curry et al. 2015). We also assumed all dens excavated by adult females were maternal dens. Two outcomes were possible following an exposure during this period (see Fig. 2). Because cubs are not yet born during this period, the outcome applied only to the adult female. If the exposure did not elicit disruption of a behavioral pattern, we classified the outcome as no effect; alternatively, the exposure could result in a behavioral outcome, such as emerging from the den or temporary or permanent den abandonment.

2.1.2. Early denning

We separated the time when cubs are present in dens into 2 periods, early and late denning, based on cub development and potential differences in the severity of consequences if disturbed (see Table 1). We delineated early denning as the period from cub birth (15 December if birth date was unknown) until cubs reach 60 d old (13 February on average), with 2 outcomes possible following an exposure (see Fig. 2). If all bears remained in the den, we classified the outcome as no effect. If cubs or females without cubs emerged from the den following the exposure, however, we classified the outcome as cub mortality because cubs that emerge from the den before they reach 60 d of age typically cannot survive outside of the den, and bears that emerge from dens earlier than 13 February are rarely observed with cubs (7 of 9 land-based denning females that emerged prior to

13 February in the SBS were subsequently observed without cubs; Rode et al. 2018b, USGS 2018).

2.1.3. Late denning

We defined late denning as the period from when cubs were 60 d old until den emergence, and we defined emergence as the initial act of opening a den and exposing the bears to external conditions (see Table 1). When analyzing case studies, we used emergence dates that were directly observed at continuously monitored dens or estimated from temperature sensors on collared bears (Rode et al. 2018b, USGS 2018). For dens where these data were not available but the den was located near regularly occurring human activity, we considered the first day a bear was observed on the surface as the emergence date. Three outcomes were possible following an exposure during the late denning period (see Fig. 2). We classified the outcome as cub mortality if a dead cub was observed or if a female emerged and departed without cubs; we assumed cubs were present in the latter scenario because an adult female is unlikely to remain in a den without cubs given the length of time she has fasted by late denning. We classified the other 2 outcomes based on when emergence occurred because the duration of denning influences cub survival (Rode et al. 2018b), and emergences caused by disturbance can decrease this duration. However, unless a bear emerged from a den concurrent with an exposure, it was impossible to determine if the emergence occurred earlier than it would have under undisturbed conditions. Consequently, we used 15 March, the median estimated date of den emergence for land-based denning bears in the SBS later seen with cubs (Rode et al. 2018b, USGS 2018), as the threshold for delineating early emergences with potential costs to cub survival from those that were less likely to incur fitness costs. Specifically, we categorized dens exposed to human activities as early emergence if they occurred before 15 March or after 15 March and concurrent with the exposure (e.g. bear observed emerging when activity initiated near the den) and categorized those that occurred on or after 15 March but were not directly linked to an exposure as no effect (see Section 4 and Table 1).

2.1.4. Post-emergence

We defined post-emergence as the period from den emergence until departure from the den site (see

Table 1). Although the relationship between duration of this period and cub survival has not been formally evaluated, it is likely an important period for cub development, given that females delay returning to sea ice to hunt despite having undergone an extended fasting period. Three outcomes were possible following an exposure during this period (see Fig. 2). Cub mortality (as defined for previous periods) and 2 other outcomes classified according to the duration of this period. As with den emergence, it was not possible to determine whether an exposure led to departing the den site earlier than would have occurred under undisturbed conditions. Therefore, we assumed that all exposures influenced the bears' responses and used a threshold duration to categorize the level of impact on cub survival. Departures that occurred <8.0 d after emergence were classified as early departure, while those ≥ 8.0 d after emergence were classified as behavioral. This 8.0 ± 1.1 d period represents the mean (\pm SE) duration bears that were directly observed in the SBS remained at dens post-emergence (see Table 1) (Smith et al. 2007, 2013, Robinson 2014). If bears left the den site after an exposure but later returned, we considered the initial movement to be the departure date.

3. RESULTS

We evaluated 79 period-specific events from 46 dens that included (1) human activity within 1.6 km of the den (i.e. an exposure) and (2) sufficient information to permit classification of outcomes based on polar bear responses to the exposure in accordance with our decision rules (Tables 1 & S1, Fig. 2). The majority ($n = 41$) of the dens were on the North Slope of Alaska, while the remainder were from Wrangel Island, Russia ($n = 2$), Canada ($n = 1$), and unknown locations within the SBS subpopulation ($n = 2$; Fig. 1, Table S1). A total of 24 dens were disturbed in 1 denning period, 12 in 2 periods, 9 in 3 periods, and 1 in all 4 periods. Exposure types included ground-based den monitoring (51%, $n = 40$), vehicle traffic (35%, $n = 28$), aircraft (20%, $n = 16$), heavy equipment (10%, $n = 8$), drill site or ice road construction (10%, $n = 8$), remediation activities (e.g. removal of equipment, cleaning up contaminants; 10%, $n = 8$), snow-machines (6%, $n = 5$), seismic survey activity (4%, $n = 3$), den detection dogs (3%, $n = 2$), or den intrusion by humans (3%, $n = 2$) (Tables 2 & S1). Total percentage exceeds 100% because some dens were exposed to multiple exposure types within a denning period. For exposures with detailed descriptions of

Table 1. Four chronological periods of polar bear maternal denning used to classify outcomes of bears exposed to human activities. We delineated the timing by stage of cub development. When cub age was unknown, we used dates (in parentheses) corresponding to those documented for polar bears in the Southern Beaufort Sea subpopulation. We defined outcomes as no effect; 2) behavioral: disruption of a behavioral pattern); 3) early emergence: emergence from the den that occurred earlier than an undisturbed emergence date as the result of an exposure; 4) early departure: abandonment of the den site post-emergence as the result of an exposure; or 5) cub mortality: death of ≥ 1 cub or a female abandoned all or part of her litter

Period	Timing	Description	Reference	Outcome
Den establishment	Excavation to cub birth (<15 Dec)	Excavate dens in snowdrifts formed where wind-blown snow accumulates on features such as bluffs and riverbanks Enter from Sep–Dec Timing influenced by body condition, snow accumulation, weather	Amstrup & Gardner (1994), Durner et al. (2001, 2003, 2006), Liston et al. (2016) Wiig (1998), Laidre et al. (2015), Escajeda et al. (2018), Rode et al. (2018b) Amstrup (2003), Rode et al. (2018b)	Behavioral No effect
Early denning	Cub birth to 60 d old (15 Dec–13 Feb)	Cubs born early Nov–early Jan; average cub birth 15 Dec Cubs immobile during first ~60 d of life ~60 d old, achieve musculoskeletal development to walk and thermoregulate to survive outside of den	Derocher et al. (1992), Messier et al. (1994), Van de Velde et al. (2003), Curry et al. (2015) Blix & Lentfer (1979), Derocher et al. (2010) Harrington (1968), (Amstrup 1993), Amstrup & Gardner (1994), Kenny & Bickel (2005), Rode et al. (2018b)	No effect Cub mortality
Late denning	60 d old to emergence (>14 Feb to emergence)	Adult presence signified cub presence because female unlikely to be in den this late given lengthy fasting period Established link between denning duration and subsequent cub survival. 15 Mar: Mean estimated emergence date for land-denning bears with cubs that survived ≥ 40 d in the Southern Beaufort Sea <15 Mar considered early emergence; ≥ 15 Mar considered natural date of emergence	Watts & Hansen (1987), Ramsay & Stirling (1988) Rode et al. (2018b) Rode et al. (2018b), USGS (2018) Smith et al. (2007, 2010, 2013), Rode et al. (2018b), USGS (2018)	No effect Early emergence Cub mortality
Post-emergence	Den emergence to den site departure	Bears in and out of den, cubs acclimate to surface conditions and gain strength Period varies geographically and among individuals (0–30 d) Mean (\pm SE) duration: 8.0 ± 1.1 d (range = 2–23 d, n = 25) after emergence	Hansson & Thomassen (1983), Messier et al. (1994) Harrington (1968), Jonkel et al. (1972), Ovsyanikov (1998), Smith et al. (2007, 2010, 2013), Robinson (2014) Smith et al. (2007, 2013), Robinson (2014)	No effect Early departure Cub mortality

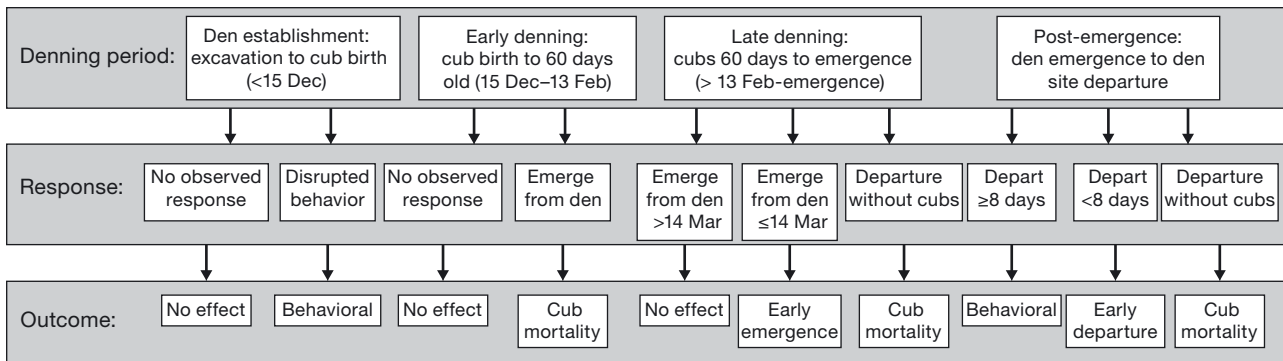


Fig. 2. Decision tree used to classify responses and outcomes of polar bear dens exposed to human activities during 4 denning periods. Denning periods were delineated by bear activity or cub age; when cub age was unknown, we used dates (in parentheses) corresponding to those documented for bears in the Southern Beaufort Sea subpopulation

Table 2. Exposure types during 4 chronological periods of polar bear maternal denning. Some dens were exposed to multiple exposure types within a denning period (e.g. vehicle traffic and ground-based monitoring). (–) exposure types did not occur in a specific period

Exposure type	Denning period				Total
	Den establishment	Early denning	Late denning	Post-emergence	
Ground-based monitoring	1	2	25 ^a	13	40
Vehicle traffic	3	8	11	6	28
Aircraft	4	5	3	4	16
Heavy equipment	–	3	3	2	8
Drill site or ice road construction	–	3	4	1	8
Remediation activities ^b	–	1	6	1	8
Seismic survey activity	–	–	2	1	3
Detection dogs	–	–	2	–	2
Snowmachines	–	–	4	1	5
Den intrusion by humans	–	–	–	2	2

^aIncludes 1 instance of monitoring of unknown distance and mode
^bIncludes removing old equipment, storage containers, gravel from old pads, plugging old wells, and cleaning up contaminants

the distance to the den ($n = 66$), the average distance from the source of the exposure to a den was 223 ± 29 m (range: 0–1000 m), and 39% ($n = 26$) of known-distance exposures were within 100 m of a den. We classified 37 outcomes to exposures as no effect, 7 as behavioral, 17 as early emergence, 14 as early departure, and 4 as cub mortality (Tables 3 & S1).

3.1. Den establishment

We evaluated polar bear responses to exposures during den establishment for females at 8 dens. We classified 5 outcomes as no effect, with exposures including ground-based monitoring ($n = 1$), vehicle traffic ($n = 3$), and aircraft ($n = 4$) (Tables 2, 3, & S1). We classified 3 outcomes as behavioral. One be-

havioral outcome occurred during an aerial infrared den detection survey at 610 m during which the bear emerged from the den; the second occurred when a helicopter hovered 60 m above the den and a bear emerged; the third occurred when a vehicle drove within 30 m of a previously unknown den causing the bear to emerge and leave the area.

3.2. Early denning

We evaluated the outcome of exposures during early denning at 14 dens, including 4 dens that were also exposed during den establishment. We classified 13 outcomes as no effect, with exposures including ground-based monitoring ($n = 2$), vehicle traffic ($n = 8$), aircraft ($n = 4$), drill site or ice road construction

Table 3. Potential responses of maternal denning polar bears exposed to human activities during 4 chronological denning periods. Denning periods were delineated by bear activity or cub age; when cub age was unknown, we used dates corresponding to those documented for bears in the Southern Beaufort Sea subpopulation. (–) responses that were not possible in a specific period

Response	Den establishment	Early denning	Late denning	Post-emergence
No documented effect	5	13	19	–
Behavioral response	3	–	–	4
Early emergence (before 15 March or concurrent with exposure)	–	–	17	–
Early departure post-emergence (duration <8 d)	–	–	–	14
Cub(s) mortality (number of litters)	–	1	2	1

(n = 3), heavy equipment (n = 2), and remediation activities (n = 1) (Tables 2, 3, & S1). We classified one outcome as cub mortality when a radio-collared bear (also exposed during den establishment) was in her den in December during 2 separate aerial surveys but was subsequently relocated alone >300 km from the den in February. Tracks of a heavy vehicle (i.e. a truck with large, low-pressure tires made for tundra and snow travel) were found within 250 m of her den and an established heavy equipment route passed <500 m from the den.

3.3. Late denning

We evaluated the outcome of exposures during late denning at 38 dens, 13 of which were exposed during at least one prior denning period. We classified 19 outcomes as no effect because emergence occurred on or after 15 March and was not concurrent with an exposure (Tables 3 & S1). These exposures included ground-based monitoring (n = 9), vehicle traffic (n = 8), aircraft (n = 2), heavy equipment (n = 2), drill site or ice road construction (n = 3), remediation activities (n = 2), snowmachines (n = 2), den detection dogs (n = 1), or seismic survey activity (n = 1) (Tables 2 & S1). We classified 17 outcomes as early emergence because they occurred either prior to 15 March or on or after 15 March but concurrent with an exposure (e.g. case number 17, Table S1). These included exposure to ground-based monitoring (n = 14), vehicle traffic (n = 2), aircraft (n = 1), heavy equipment (n = 1), ice road construction (n = 1), remediation activities (n = 4), snowmachines (n = 2), den detection dogs (n = 1), and seismic survey activity (n = 1) (Tables 2 & S1). We classified 2 outcomes as cub mortality. In one case, a den located ~100 m from a heavily trafficked road adjacent to a landfill was exposed to daily traffic and heavy equipment from den establishment until early March, when the female was observed abandoning

the den alone. Although cubs were not observed, we classified this as cub mortality because the bear was not likely to have stayed in the den until early March unless cubs were present. The second cub mortality case was documented by a camera monitoring the den that showed a female carrying a dead cub from the den. A necropsy determined the cub died from malnourishment, and subsequent capture of this female and her 2 remaining cubs indicated the cubs had body mass lower than expected (Robinson 2014). Ground-based monitoring had occurred repeatedly over several days, including camera deployment and subsequent camera servicing (e.g. battery and camera card replacement). The repeated disturbance may have caused the female to nurse the cubs less, leading to malnourishment and subsequent mortality.

3.4. Post-emergence

During the post-emergence period, we evaluated the outcome of exposures to 19 dens, 16 of which were also exposed in earlier denning periods (Table S1). We classified 4 outcomes as behavioral, 14 as early departure, and 1 as cub mortality (Table 3). The behavioral outcomes were a result of ground-based monitoring (n = 2), vehicle traffic (n = 1), aircraft (n = 1), and snowmachine (n = 1) (Table 2). The early departures included exposures to ground-based monitoring (n = 11), vehicle traffic (n = 5), aircraft (n = 3), remediation activities (n = 1), heavy equipment (n = 2), ice road construction (n = 1), and seismic survey activity (n = 1) (Tables 2 & S1). In the cub mortality case, a researcher fell into an occupied den, causing the female to flee the den without the cubs. Although the female was subsequently captured and returned to the den, the cubs would have died without human intervention, which would not be possible under most circumstances involving human disturbance.

4. DISCUSSION

As climate-mediated sea ice decline opens the Arctic to more industrial activity (Prowse et al. 2009, Post et al. 2013), maternal denning polar bears will be increasingly impacted (Atwood et al. 2017, Durner et al. 2018, Wilson & Durner 2020), particularly if the proportion of bears denning on land continues to increase (Derocher et al. 2011, Rode et al. 2015, Olson et al. 2017). We developed decision rules based on polar bear biology and denning chronology and applied these rules to a comprehensive collection of records of potential disturbances to polar bear dens with the objective of creating a framework to standardize classification of the potential outcomes for denning polar bears exposed to human disturbance. Our framework facilitates proactive identification of project-specific mitigation measures that may reduce both the likelihood and severity of potential human disturbance. Our review of case studies suggests that tolerance to disturbance varies among individual bears, and we found large variation in the distances and types of exposures that elicited reactions as well as the severity of those reactions. Differences in den (e.g. snow ceiling thickness; Owen et al. 2021) and snow characteristics (e.g. density, snow water equivalent; Ishida 1965, Blix & Lentfer 1992) affect propagation of sound and vibration and likely also contribute to bear responses to human activity.

Outcomes with potential fitness consequences occurred in every denning period. In total, 67% of dens had outcomes (i.e. early emergence, early departure) with potentially critical consequences, and 9% resulted in cub mortality. During den establishment, bears may be more likely to abandon dens when disturbed compared to later in the denning season (Belikov 1976, Amstrup 1993, Amstrup & Gardner 1994, Swenson et al. 1997, Larson et al. 2020). Disturbances during this stage may be less consequential to reproductive success relative to other denning periods because females have invested less in the reproductive effort and can usually re-establish a den that is abandoned during this period (Reynolds et al. 1976, Amstrup 1993, Linnell et al. 2000, Friebe et al. 2001). High-intensity disturbances prior to parturition, however, could potentially have reproductive consequences (e.g. Lunn et al. 2004). For example, brown bears that moved prior to birthing cubs were more likely to lose cubs than bears that did not move, with human activity the suggested cause of the den abandonments (Swenson et al. 1997). Because we delineated the den establishment period as ending at cub birth, any outcome during den establishment per-

tained to only the adult female, so the most consequential outcome during this period was behavioral. In our analysis, however, there was a known reproductive failure in early denning that followed a den establishment exposure, and for 67% of dens initially exposed during den establishment, the reproductive outcome was unknown or not reported. We thus could not definitively conclude that impacts to denning bears during den establishment were less severe than those that occurred during other denning periods as posited in other research (e.g. Reynolds et al. 1976, Amstrup 1993, Linnell et al. 2000, Friebe et al. 2001).

As soon as young are born (i.e. early denning for this study), the consequences of disturbance are potentially more severe because den emergence during the early denning period is likely to be lethal to cubs. The maternal instinct to stay and defend young usually prevails as opposed to fleeing without young (Frid & Dill 2002). Alternatively, the decision to stay or flee could also be based on residual reproductive value (Frid & Dill 2002) or the increased likelihood for females of iteroparous species to abandon their offspring to maximize their long-term reproductive potential when exposed to an apparent significant threat (Clutton-Brock 1984, Magnhagen 1991). Unknown ages of female bears in our analysis, however, precluded us from evaluating this possibility.

One challenge with classifying outcomes during the late denning and post-emergence periods was that dates of emergence or den departure under undisturbed conditions are unknowable. Because premature den emergence or departure can potentially influence cub survival (e.g. Rode et al. 2018b), it was vital to account for the possibility of a proposed activity influencing denning phenology during these times. Consequently, we identified temporal thresholds based on denning phenology in the SBS to classify responses to disturbance as early vs. typical, with the assumption that early responses (i.e. early emergence or departure) are likely to incur fitness consequences to cubs. Specifically, we used the mean estimated date of emergence in the SBS (15 March; Rode et al. 2018b, USGS 2018) and the mean duration bears remained at dens post-emergence that were directly observed in the SBS (8 d; Smith et al. 2007, 2010, 2013, Larson et al. 2020) as thresholds for processing case studies. Our post-emergence threshold (8 d) is less than reported from other regions: Hudson Bay, Canada: 8–9 d (Lunn et al. 2004); Herald Island, Russia: 15–16 d (Ovsyanikov 1998); Viscount Melville Sound/McClure Strait, Canada: 13 d (Messier et al. 1994); Svalbard, Norway: 14 d (Hansson & Thomassen 1983) and may represent a lower bound of the normal

post-emergence duration. We recognize that the uncertainty and individual variation in the timing of denning and parturition could result in a misclassification of denning periods and subsequent outcomes at some dens. On average, however, our approach of identifying emergence and departure thresholds based on median or mean values should minimize bias associated with individual variation. Additionally, whereas Rode et al. (2018b) did not find trends in denning phenology for polar bears in the SBS, there is evidence of change in den phenology in some subpopulations. In later (compared to earlier) years, bears in Baffin Bay exhibited later den entry with no change in emergence dates (Escajeda et al. 2018), bears in East Greenland had earlier den entry dates with similar emergence dates (Laidre et al. 2015), and bears in Svalbard had the same entry dates but earlier emergence (Sulich 2019). This highlights both the differences between subpopulations and the need for further research on potential changes in denning phenology and the subsequent effects on bears (Escajeda et al. 2018).

Although we based our analysis on the best available information, our process relied on several assumptions. Rarely do we have direct knowledge of events or conditions inside a wild bear den, and given the difficulty in conducting research on a wide-ranging species in an extremely harsh environment (Durner et al. 2018), responses of polar bears to disturbance are often difficult to observe, and documentation typically is lacking sufficient detail. A key factor in the ability to classify the outcome of an exposure to a disturbance is consistent, accurate, and complete collection of data. Notably, in many cases in this study, short- or long-term survival of females or cubs was unknown or undocumented, and in 9 instances we had insufficient information to determine if an exposure had occurred. Additionally, the absence of an observable response to disturbance does not mean the animal was unaffected (Frid & Dill 2002, Bejder et al. 2006, Laske et al. 2011, Watson et al. 2014). Responses documented as no effect may alter the bear's normal physiological function (e.g. change in stress hormone levels: Keay et al. 2006, Piñeiro et al. 2012 or increased heart rate: Ditmer et al. 2015). These effects have the potential to be equally consequential to reproduction as behavioral responses (Carney & Sydesman 1999, Ellenberg et al. 2006, Rode et al. 2018b) and can lead to population-level declines (Carney & Sydesman 1999, Ellenberg et al. 2006, Lusseau et al. 2006, Wikelski & Cooke 2006, Currey et al. 2009), even in species thought to be relatively tolerant of human presence given their lack of observed response when disturbed (Yorio & Boersma 1992).

5. CONCLUSIONS

As suitable environmental conditions for polar bears decline, the continued implementation of mitigation measures that limit disturbance to denning polar bears is necessary. This is particularly important for bears such as those in the SBS subpopulation that have experienced both a long-term decline in abundance (Bromaghin et al. 2015, 2021) and increased overlap with industrial activity. Conducting research on cub survival and the physiological effects of disturbance on denning bears is warranted, although determining the appropriate detection and monitoring methods is critical given that research itself may introduce or contribute to disturbance (Cattet et al. 2003, 2008, Wilson & McMahon 2006, Smith et al. 2007, 2013, Thiemann et al. 2013), particularly if bears are physically captured or more substantial physiological research is conducted (e.g. heart rate monitor implants; Ditmer et al. 2015, Stoen et al. 2015). Additionally, companies whose activities overlap with polar bear denning habitat should implement additional measures to reduce den disturbance, such as changing the timing or location of activities (Wilson & Durner 2020) or improving den detection methods (Woodruff et al. 2022). Model-based frameworks for estimating disturbance to polar bears (e.g. Wilson & Durner 2020) enhance our ability to predict outcomes and understand impacts on polar bears and will be most effective when wildlife managers and industry stakeholders work collectively to reduce the level of uncertainty through comprehensive data collection and collaborative research. For example, similar to Larson et al. (2020), we recommend obtaining observations of denning polar bear responses to specific types of activity (e.g. aircraft overflights, seismic operations) in different denning periods to help identify which activities are the most harmful and ascertain the least consequential time for conducting these activities. Additionally, this information could be used to evaluate whether the current 1600 m minimized disturbance area surrounding known dens is sufficient. Indeed, our decision rule and outcome classification approach facilitates an objective and transparent regulatory process to evaluate effects of disturbance on denning polar bears, which is critical given the importance of the public review process in regulating industrial activities in the Arctic. Determining outcomes in relation to a specific denning period may facilitate improved implementation of mitigation strategies to reduce disturbance to denning bears. In the future, we will continue to review incidents of den disturbance in

order to update the framework and provide the most accurate information on disturbance to denning bears and subsequent consequences.

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