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In-Air Auditory Psychophysics and the Management of a Threatened Carnivore, the Polar Bear (*Ursus maritimus*)

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Management criteria for preventing biologically-significant noise disturbance in large terrestrial mammals have not been developed based on a sound, empirical understanding of their sensory ecology. Polar bear (Ursus maritimus) maternal denning areas on the coastal plain of Alaska's North Slope hold large petroleum reserves and will be subject to increased development in the future. Anthropogenic noise could adversely affect polar bears by disrupting intra-specific communication, altering habitat use, or causing behavioral and physiological stress. However, little is known about the hearing of any large, carnivorous mammal, including bears; so, management criteria currently in use to protect denning female polar bears may or may not be proportionate and effective. As part of a comprehensive effort to develop efficient, defensible criteria we used behavioral psychoacoustic methods to test in-air hearing sensitivity of five polar bears at frequencies between 125 Hz and 31.5 kHz. Results showed best sensitivity between 8 and 14 kHz. Sensitivity declined sharply between 14 and 25 kHz, suggesting an upper limit of hearing 10-20 kHz below that of small carnivores. Low frequency sensitivity was comparable to that of the domestic dog, and a decline in functional hearing was observed at 125 Hz. Thresholds will be used to develop efficient exposure metrics, which will be needed increasingly as the Arctic is developed and effects of disturbance are intensified by anticipated declines in polar bear health and reproduction associated with climate change driven sea ice losses.

Petroleum extraction and other human activities on Alaska's North Slope overlap spatially and temporally with polar bear maternal denning habitat and the sensitive peri-partum and emergence periods (Durner, Amstrup, & Ambrosius, 2006). Substantial noise is associated with these activities and U.S. wildlife managers have raised concerns regarding the impact of noise disturbance on parturient female bears (Manci, Gladwin, Villella, & Cavendish, 1988; Perham 2005). At present there are no empirically-based, standardized criteria available to protect any large terrestrial mammal from noise.

The suspected effects of anthropogenic noise on wildlife are varied (Larkin, Pater, & Tazik, 1996; Richardson, Greene, Malme, & Thompson, 1995) but can be separated broadly into auditory and non-auditory effects. Under freeranging in-air conditions, exposure to sufficient noise to cause hearing loss has yet to be documented in wildlife habitat. Historically, the major concern for bears has been that noise could stimulate den abandonment (e.g., Manci et al., 1988), which can cause cub mortality (Amstrup, 1993; Linnell, Swenson, Andersen, & Barnes, 2000). However, systematic attempts to measure the rate of abandonment have

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suggested that this response is rare, particularly in the absence of direct intrusion into the den (Amstrup, 1993; Linnell et al., 2000). However, these observations do not rule out behavioral and physiological responses that could act cumulatively to cause biologically-significant effects.

Research to detect biologically-significant, population-level effects of noise is challenging. Only now is evidence of population-level effects mounting for communities of nesting birds exposed to high-duty cycle broadband noise (Francis, Ortega, & Cruz, 2009; Habib, Bayne, & Boutin, 2007). The vulnerability of large terrestrial carnivores to population-level effects is unclear because very little is known of their sensory ecology or responses to noise (Barber, Crooks, & Fristrup, 2009; Bowles, 1995). In particular, the only in-den behaviors of free-ranging polar bears that have been measured in the presence of noisy disturbances are general activity levels (Amstrup, 1993). Details, such as in-den maternal care patterns have yet to be described in the absence of disturbance, let alone in its presence. In addition, acoustic characteristics of disturbance have not been measured simultaneously with behavior in any bear species.

There are limited data on noise effects from another Arctic carnivore that raises its young in a subnivean lair, the ringed seal (*Phoca hispida*). However, although the ringed seal data are a useful point of reference, they can only be generalized to bears after considering contextual and life-history differences. Ringed seals have responded with escape to helicopter overflights in two studies (Blackwell, Lawson, & Williams, 2004; Born, Riget, Dietz, & Andriashek, 1999), but other observations suggest that they can habituate to high-amplitude transient sources (Blackwell, Lawson, et al., 2004). Therefore, exposure type, experience, and context must be considered. The data were collected on ringed seals hauled on ice or swimming in water, where the strategic choices are very different from those of a mother in a lair with a pup. Cummings, Holliday, and Lee (1986) detected sounds produced by ringed seals inside a lair in the presence and absence of seismic exploration noise using a hydrophone array, transmitted primarily through the water or ice. They found no change in acoustic behaviors, but did not expose the seals to helicopter overflights or other vehicular traffic.

These observations suggest that the type of source, experience, and context can alter responses and therefore risks. In addition, life-history and strategic options of ringed seals and polar bears differ substantially. Approximately 25% of ringed seal dens are opened by predators, principally polar bears (Furgal, Innes, & Kovacs, 1996), exerting a strong selective pressure in favor of escape behaviors. Polar bears, on the other hand, are attacked in their dens only rarely (Amstrup, Stirling, Smith, Perham, & Thieman, 2006). Ringed seals can easily escape their dens by diving into the water, whereas polar bears have no convenient exit and rarely come out until spring emergence (Smith, Partridge, Amstrup, & Schliebe, 2007). Amstrup (1993) provided data from activity sensors on radio-collars and documented no long-term increases in activity during exposures to vehicular traffic. However, without information on received sound in the den or polar bear auditory capabilities, it is difficult to interpret these results.

Review of the scientific literature (Barber et al., 2009; Bowles, 1995; Southall et al., 2007) shows that the above summary is typical of efforts to evaluate the risks of noise exposure on a given species. Typically, the research is conducted

without the benefit of standardized procedures (Pater, Grubb, & Delaney, 2006) and for heterogeneous purposes. Broadly, three types of information are needed to make a defensible evaluation of the potential for biologically-significant effects – what stimuli the animal received, the context of the exposure, and the behavioral and physiological strategies the animal uses when threatened (Frid & Dill, 2002). Noise is not only a disturbance, but it is also a source of information. The receiver needs this information to determine which strategy should be adopted from a pool of possible behavioral and physiological responses.

Evidence like that of Blackwell, Lawson, et al. (2004) is common in disturbance studies involving large, intelligent mammals – animals modulate their behavioral responses to minimize the impact to themselves (Ydenberg & Dill, 1986). A denning polar bear has a variety of strategic choices when confronted with a noisy disturbance, which will be based on the acoustic information she receives while in the den, including source proximity, direction of travel, whether or not the source is familiar and predictable, and the likelihood that it will get close enough to invade the den. Noise also has the potential to mask biologically-important sounds within the den. The most basic information needed to evaluate the potential for any of these noise effects is the psychophysical capabilities of the receiver.

Among the potential biologically-significant effects of noise for which there is at least some evidence (Barber et al., 2009; Bowles, 1995) are (1) increased arousal, which has the potential for energetic effects and sleep disruption, (2) masking or modification of biologically-important acoustic signals, (3) distraction or movements that could put the listener at risk (e.g., risk of predation), (4) changes in habitat use and time-activity budgets, and (5) stress exceeding an individual's natural allostatic scope (McEwen & Wingfield, 2003).

Currently, regulatory and natural buffer zones protect denning polar bears. U.S. federal regulations require a 1-mile buffer zone around active polar bear dens (Perham, 2005) and the subnivean construction of maternal dens provides a degree of acoustic isolation (Blix & Lentfer, 1992). Current guidelines are characterized as 'conservative' in National Environmental Policy Act (NEPA) and regulatory documents, but this obscures an absence of evidence – there is no proof that the current guidelines are consistently protective and proportional to the potential for effects. The state-of-the-art method for locating dens, forward-looking infrared (FLIR) technology, is not perfectly efficient and requires well-trained observers and optimal weather conditions (Amstrup, York, McDonald, Nielson, & Simac, 2004). Also, unregulated noisy activities (e.g., hunting from snowmobiles) can occur in the vicinity of dens. As a result, denning females can be exposed to high-amplitude disturbances at close range even in regulated areas.

Noise-producing activities in the Arctic are expected to increase as the climate changes (Prowse et al., 2009). Areas used by polar bears are attractive to industry, recreation, and transportation. Science-based noise exposure criteria will be needed if the impact of these activities is to be mitigated effectively. Metrics of noise exposure that correct for psychophysical characteristics are important elements of criteria used for humans because they are much more efficient than uncorrected metrics (e.g., Leatherwood, Sullivan, Shepherd, McCurdy, & Brown, 2002). Therefore, we have begun to collect the needed psychoacoustic data as part

of a comprehensive effort to develop science-based noise exposure criteria for polar bears. A previous study of polar bear hearing using electrophysiological methods (i.e., auditory evoked potentials [AEP], Nachtigall et al., 2007) highlights the difficulties in getting good, biologically representative thresholds in the absence of comprehensive psychoacoustic data. Here we present behavioral audiograms for the polar bear, a first for any bear species, and discuss the management implications of these data.

Method

We used an adaptive behavioral procedure to measure the auditory thresholds of five polar bears, four females and one male, at two zoological facilities, the San Diego Zoo and Sea World San Diego. All bears were 12 years old at the time data collection was initiated. This age class reflects bears in the prime of their reproductive life (DeMaster & Stirling, 1981). All bears were in good health and had not been treated with high doses of potentially ototoxic drugs or exposed to unusually high noise levels.

An adaptive 'step-down, step-up' presentation protocol (Nachtigall, Lemonds, & Roitblat, 2000) was used to deliver shaped 500 ms tones to the bears at frequencies between 125 Hzand 31.5 kHz (Fig. 1). Recordings were collected during every experiment to ensure that the bears could not detect stimulus onset using spurious cues such as clicks. Bears could not be moved into an isolated acoustic environment for testing and so were tested within their regular, off-exhibit holding environments. Custom-designed sound isolation materials (e.g., lead-lined acoustic curtains) were erected around the test spaces to isolate them from outside noise to the extent practicable and sources such as refrigeration units, air conditioning, and fluorescent lightingwere turned off . The combined noise reduction amounted to over 30 dB across the test range. Calibrated instrumentation microphones and recording systems were used to measure background levels after noise reduction. Experimental trials contaminated by uncontrollable transient noise (e.g., tour buses and airplanes) were repeated or eliminated.

Tone delivery was controlled using a National Instruments system equipped with an NI-PXI-8196 embedded controller and an NI-PXI-5922 two-channel high-speed digitizer (24-bit, 500 kHz sampling rate). We recorded test signals with an ACO-7013 microphone to monitor test stimuli during every trial and during calibrations. Stimuli were generated by an NI-PXI-5421 Arbitrary Waveform Generator (100 MS/s, 16-bit), and a custom program written in NI-LabView. This program controlled sequences of presentations and collected response data. The noise floor of the system was measured in an IAC Sound Isolation Chamber before the start of trials.

Stimuli were delivered simultaneously through two sets of speakers mounted approximately 46 cm from the bears on the mesh of their test cage. They were oriented toward the head of the subject when stationed. They consisted of a pair of Fostex FE-107E 4-in full range drivers (linear range 125 Hz to 5 kHz) and Fostex FT-17H Horn Super Tweeters (linear range 4 kHz - 50 kHz).

All subjects were naïve to the training protocol at the start of experiments, which had to be completed within a set period (8 months in both facilities). Using positive reinforcement (food rewards), bears were trained to lie in a consistent location and place their noses on a marked target. Calibrated measurements of test stimuli were collected from this location weekly for every test stimulus to ensure that levels were delivered as expected and there were no spurious signals (e.g., pops or clicks) to indicate the onset of stimuli). The bears were trained to 'break' this stationing response when they heard a 0.5 s tone (go, no-go response protocol).

Each experimental trial had a 30% chance of being a catch (blank) trial. The bears were prone to distraction, a challenge that grew worse as the probability of a catch trial increased. We used the highest practicable rate. The rate of false positive responses during catch trials determined whether data from a block of trials was usable. False positive rates greater than 20% triggered the cessation of a trial. For the purposes of this discussion, we estimated thresholds by averaging the level of the last correct detection and the first incorrect detection in the downward leg of a step downstep up series. Only the data from the downward leg were used as the bears tended to become distracted during the upward leg.

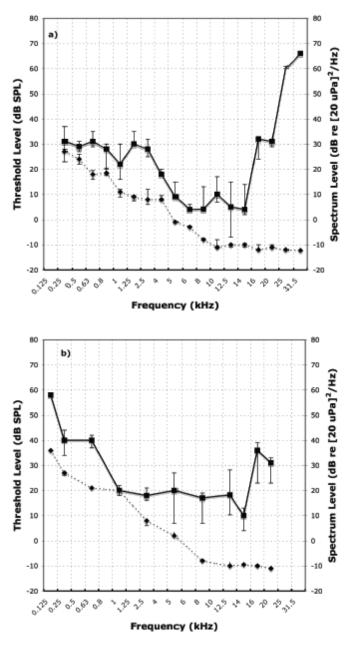


Figure 1. Audiogram (solid line) of mean (error bars = \pm - SEM) hearing thresholds across frequencies for a) 2 polar bears at the San Diego Zoo and b) 3 bears at Sea World San Diego, and median ambient noise levels (dashed line) in the testing facility. (dB SPL = decibels sound pressure level; kHz = kilohertz).

Results

We report results from the two test facilities separately because ambient noise levels and reinforcement protocols in each facility differed somewhat. Measured thresholds at the San Diego Zoo were lowest between 6 and 14 kHz (Fig. 1), and 8 and 14 kHz at SeaWorld San Diego. Background noise approached the limits of the measurement system (averaging spectrum levels of -10 to -13 decibels (dB) above 8 kHz at both facilities. The bear with the best average of reversals at 14 kHz had a threshold of -10 dB SPL. The rapid decline in sensitivity from 14 to 20 kHz, which was consistent among all subjects and well above the noise floor, can be interpreted as species-typical. Thus, our data show that the polar bear's upper limit of hearing is 10-20 kHz lower than that of the small terrestrial carnivores (Fig. 1) that have been tested (Fay, 1988).

Averaged reversal levels at 14 kHz ranged from -10 dB to 8 dB SPL. At 125 Hz, the variability was greater, from 25 dB to 55 dB, consistent with the greater variability of noise at low frequencies (Fig. 1). The limits of performance of the bears were likely noise limited at the low end of the test frequency range, particularly in the noisier test space at SeaWorld. The lowest threshold measured in the quieter San Diego Zoo test space was comparable to measurements of dog absolute thresholds in sound conditioned spaces (e.g., Lippman & Grassi, 1942).

Discussion

Our results are consistent with evidence that the auditory range of terrestrial mammals scales with body size, at least within broad taxonomic groups. Based on the mass of the brown bear's (*Ursus arctos*) middle ear bones (Nummela, 1995), the upper limit of hearing of the polar bear is as expected for its size based on comparative studies of many terrestrial species (Hemilä, Nummela, & Reuter, 1995). No data are available on the auditory anatomy of the polar bear that would permit us to make the estimate directly. Data on pinnipeds, the only large carnivores for which there is adequate information on both anatomical specializations and psychophysics, cannot be generalized to the polar bear because their auditory anatomy, particularly the mass and shape of the ossicles in the middle ear, is specialized for a diving lifestyle (Nummela, 1995).

Polar bears are semiaquatic marine mammals (Nummela, 2008). Therefore, they might be expected to have auditory specializations for underwater hearing. They are strong swimmers that travel long distances in the Arctic Ocean to get to and from hunting and denning habitat (Mauritzen et al., 2003). However, they are not aquatic in the sense of routinely diving for prey or navigating underwater in the manner of pinnipeds, sirenians, or marine mustelids, and they typically swim with their heads above water. Nearly all their prey is captured above water using visual and olfactory cues (Stirling, 1974). They have diverged only recently from an entirely terrestrial congener, the brown bear (*Ursus arctos*), with less than about 200,000 years of divergence (Kuertén, 1964). Thus, the suggestion that they have auditory adaptations for an amphibious lifestyle must await supporting morphological data. Our results certainly indicate that, from a management perspective, dogs and other small mammals should not be treated as

good auditory models for the polar bear at the high end of the range, and possibly at the low end as well.

The shape of the auditory threshold function is of importance for management because noise from industrial sources tends to be concentrated at low frequencies. There are few data on the in-air noise from industrial sources in Arctic habitats, but those that are available (Blackwell, Greene, & Richardson, 2004; MacGillivray, Hanny, & Perham, 2009) are consistent with a large body of data showing that human activities produce noise with greatest energy concentrated at frequencies below 5 kHz.

For polar bears, it will be essential to understand their psychophysical capabilities and at least the basics of their acoustic ecology before the effects of noise can be predicted properly. Outside the den, sound is an important source of information when it is dark, when sources are at a distance, and in areas where vision is obscured. From within a den, sound will be the most immediate and best source of information about events outside. However, nothing is known about how bears use sound in their environment. Masking from continuous human made noise has the potential to compromise important activities of polar bears such as hunting. navigation, communication and defense, and it can render a denning mother "blind" to events outside the den. Transient sounds can also have an effect. Although bears are often characterized as primarily olfactory hunters, their hearing is essential during the latter stages of a hunt because sound propagates more rapidly than scents. Cushing, Cushing, and Jonkel (1988) demonstrated the use of acoustic cues for localizing seals under ice and in sub-nivean lairs. Additionally, female bears must also be able to monitor the continuous 'humming' from cubs (Derocher, Van Parijs, & Wiig, 2010; Peters, Owen, & Rogers, 2007). Data on humming in bear cubs shows that most of the spectral energy is found below 2 kHz and the highest amplitude for this vocalization is found below 500 Hz (Peters et al., 2007). Although the precise communicative significance of this vocalization is unknown, preliminary analyses in other bear species suggest that it may instigate behavioral or physiological facilitation of nursing in the hibernating mother (Peters et al., 2007).

Fischbach, Amstrup, and Douglas (2007) and Perham (2005) have emphasized the increasing potential for anthropogenic disturbance of females in land-based dens. Long-term radio-telemetry data have documented a significant increase over time in the proportion of pregnant females denning on land or landfast ice on the North Slope rather than on sea ice (Fischbach et al., 2007). Concentrations of these dens overlap extensively with active and proposed petroleum extraction activities, which are expected to increase as new petroleum reserves in Arctic Alaska are identified. In addition, recreational, shipping and fishing activities are expected to increase as the Northwest Passage becomes consistently ice-free during the summer. The type and frequency of noisy human disturbances can be expected to increase in association with these activities.

Although it is now recognized that effects of anthropogenic disturbance must be interpreted in the context of an animal's natural defensive adaptations (Ydenberg & Dill, 1986), there are still no data-based assessments of noise effects on large wide-ranging mammals that would make such an analysis possible, e.g., the strategic decision point that would induce a female to abandon her den. Polar

bears may be more vulnerable than other bear species because the reproductive fast can last up to 8 months (Atkinson & Ramsay, 1995; Derocher & Stirling, 1998; Ramsay & Dunbrack, 1986), during which females can lose half their body weight. There is already documented nutritional stress in polar bears due to lost feeding opportunities associated with climate change-driven declines in sea ice cover in Alaska (Rode, Amstrup, & Regehr, 2007) and on the Western Hudson Bay (Stirling, Lunn, Iacozza, Elliot, & Obbard, 2004). Shorter reproductive intervals, fewer cubs surviving into their second year, and reduced juvenile weight (Rode et al., 2007) have been measured and correlated to these losses. If additional stressors are added, reproduction and survival could be further compromised.

Management Implications

Effective mitigation, i.e., bridging the gap between the needs of the polar bear and those of industry, will require better predictive models of effect. The National Research Council has provided a conceptual framework for assessing biologically-significant behavioral effects of noise disturbance (National Research Council, 2000). Data on natural rates of disturbance in the den, the ecology of physiological and behavioral responses, and adequate samples of responses to noise are needed to determine whether bears experience effects such as additional, uncontrollable energetic expenditure or added reproductive stress when exposed to noisy activities.

In light of evidence of the polar bear's threatened status (U.S. Department of the Interior, 2008), growing public concern, and commercial interests in polar bear habitat (Owen & Swaisgood, 2008), it is essential that defensible noise exposure criteria be developed. Future research should be designed to obtain data needed to develop criteria (Pater et al., 2006), including polar bear psychophysics, as described here; acoustic cues that penetrate into dens; the scope, costs, and benefits of defensive behaviors (e.g., arousal in response to noise); mechanisms for coping with noise masking; and natural and anthropogenic noise 'budgets' in the habitat of free-ranging bears.

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