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Defining pacing quantitatively: A comparison of gait characteristics between pacing and non-repetitive locomotion in zoo-housed polar bears

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ABSTRACT

Pacing is a commonly investigated behavior in zoo animals, however, little data have been published to support a precise definition of pacing. High speed video of pacing behavior in 11 zoo-housed polar bears (*Ursus maritimus*) was compared with goal-oriented locomotion in the same bears. Specifically, step cycle duration and head height ratio were measured, as was the variability of these two dimensions. The median step cycle duration while pacing was found to be 17.0% (±26.7%) shorter than step cycle duration while locomoting ($P < 0.01$). Step cycle duration while pacing also displayed a significantly lower coefficient of variation than step cycle duration while locomoting (9.4 ± 3.5% versus 22.7 ± 10.0%; $P < 0.01$). Median head height was found to be 15.3% (±10.5%) higher while pacing than while locomoting ($P < 0.05$) and was also found to have a significantly reduced coefficient of variation as compared to locomoting (5.6 ± 2.6% versus 16.6 ± 8.7%; $P < 0.05$). The results of this study confirm that pacing is quantifiably different than non-repetitive locomotion and may reflect a state in which animals are disengaged with their environments.

1. Introduction

Pacing is a widespread behavior in captive mammals and is operationally defined as repetitive locomotion in a fixed pattern (Burgener et al., 2008; Mason, 2006; Shyne, 2006). Specifically, the behavior comprises the majority of reported stereotypies among zoo-housed carnivores (Clubb and Mason, 2007; Clubb and Vickery, 2006; Mason et al., 2007). Like other stereotypic behaviors, pacing is a concern for those managing animals in zoos and similar institutions. Visitors may perceive pacing to be a negative behavior and not understanding the complex nature of the behavior, attribute it to inferior care at the current host institution even when it may be a relic of an animal's previous living conditions (Mcphee and Carlstead, 2010; Woods, 2002). Additionally, the occurrence of pacing may compromise the educational value of zoos by supplanting species-typical behavior and by rendering an animal less engaging to the general public (Altman, 1998; Mason, 2006; Miller, 2012). Most importantly, stereotypic behavior is sometimes linked with higher levels of stress, reduced reproductive success, and poorer quality of life in the animals exhibiting the behavior (Carlstead et al., 1999; Liu et al., 2006; Mason, 1991; Shepherdson et al., 2004; Vasconcellos et al., 2009). However, physically preventing the behavior rather than addressing the underlying causes can actually further decrease an animal's welfare (Mason and Latham, 2004). It is therefore essential to continue ongoing research on the causes and significance of pacing and other stereotypic behaviors in captive animals.

Prior research has tied pacing to various direct causes such as lack of novel enrichment, anticipation of husbandry events, or enclosure limitations (Anderson et al., 2010; Jenny and Schmid, 2002; Mountaudouin and Pape, 2004; Papadouka and Matthews, 1995; Ross, 2006; Watters, 2014). Possibly because of the great variety of situations and stimuli that elicit pacing, research differs in conclusions as to the abnormality of the behavior, or whether or not it represents some sort of variation of a species-typical behavior seen in the wild, such as roaming behavior observed in wild polar bears (Amstrup et al., 2000; Ferguson et al., 1999). For example, some research raises the possibility that pacing and other stereotypic behaviors are potentially products of permanent aberrations in neural circuitry within the brain caused by abnormalities in captive environments (Campbell et al., 2013; Dallaire et al., 2011; Lewis et al., 2007). Other research seems to indicate that pacing is

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merely a seasonal behavior and therefore likely tied to routine hormonal and/or environmental fluctuations (Cabib, 2006; Carlstead and Seidensticker, 1991) or that it is an appetitive behavior that occurs in anticipation of specific events (Watters, 2014). So, it is often unclear to zoo professionals whether pacing should be classified as a stereotypic behavior and to what degree its manifestation should be considered a welfare concern (Clubb and Mason, 2007; Cless et al., 2014). More thorough qualitative descriptions of the behavior can aid us in classifying and treating the behavior (Bauer et al., 2013).

Few studies describe in detail the characteristics and form of pacing, and, for the most part, it is simply identified as an animal walking repetitively back and forth along the same path for a minimum of three repetitions (Clubb and Mason, 2007; Swaisgood and Shepherdson, 2005). By closely examining pacing behavior, we can find clues as to what degree the behavior is centrally regulated, i.e. controlled by the spinal cord, the cerebellum, and/or the dorsal striatum of the basal ganglia, which are all important areas for generating automated behavior that is less reliant on higher order systems in the brain (Campbell et al., 2013; Pearson, 2000). A detail that informs us as to whether an animal is actively sensing its environment is the height that it carries its head and the amount of movement that its head makes. Since the head contains the bulk of an animal's sensory apparatuses, its posture likely reflects the alertness and attentiveness of an animal to its environment (Dyck and Baydack, 2004; Mason and Turner, 1993). The step cycle is another component of gait that provides clues as to what degree locomotion is a product of automatic processing versus higher cognitive inputs or reflex adjustments. The step cycle is defined as the sum of movements made by one leg from the time it leaves a surface (lift off) until it returns again (set down) (Goulding, 2009; Hiebert and Pearson, 1999; Mason and Turner, 1993). Step cycles are a product of rhythmical neural output by circuits in the spinal cord known as central pattern generators, or CPGs (Dietz, 2003; McKay-Lyons, 2002) combined with proprioceptive reflexes. Descending activity from the brain can then further modify these local control circuits. Variability in the step cycle therefore indicates a deviation from the rhythmical output that is a product of the CPGs and lower regions of the brain including the cerebellum and striatum. Variability may therefore be indicative of a greater influence of sensory feedback and integrative cortical input in generating a behavior (Kurz et al., 2012; Yakovenko et al., 2005).

Our study seeks to inform a more descriptive and accurate definition of pacing and to determine whether the current criteria for pacing (three repeats of the same route) is actually capturing a distinct behavior from regular locomoting. We collected high speed videotape of locomotion in 11 polar bears and compared head height, step cycle duration, and the variability of these two details between pacing and non-repetitive walking. We hypothesized that if pacing truly reflects a different motivational state in bears than non-repetitive walking, then the two behaviors should differ significantly in regard to the gait components of head height and step cycle duration as well as the variability of these two measurements. Specifically, we would expect pacing to display reduced variability and a shorter step cycle, reflecting a reduction in the role descending input plays in modulating neural output from CPGs in the production of the behavior.

2. Methods

2.1. Subjects

We videoed four male and seven female adult polar bears known to perform pacing between Fall 2012 and Winter 2014. The subjects' ages ranged from 3 to 28 years with a mean of 14.3 years and none were genetically related. All bears in the study were born in captivity and dam-reared. No subjects in the study were known to have any injuries or illnesses during the time of the study. Subjects were housed in seven zoos accredited by the Association of Zoos and Aquariums (AZA) and one non-accredited institution in semi-naturalistic enclosures. Three institutions housed two bears in the study, whereas the other five bears were all housed at separate institutions. Even for bears housed at the same institution, no two bears in the study inhabited the same enclosure at the same time. However, three of the subjects of our study did cohabit an exhibit with a non-subject bear.

2.2. Video recording

Each bear was videoed from visitor viewing areas while performing at least two bouts of pacing and at least two bouts of non-repetitive walking. The videoing of each bear took place over the course of 1 or 2 consecutive days to prevent seasonal variation from being a factor in the comparison between the two types of locomotion. Video was recorded at 120 frames/s of bears moving perpendicularly to the viewer with a single handheld Casio Exilim EX-FC150 camera (512 × 384 pixel resolution, Casio America, Dover, NJ, USA). The videoing of a single bout occurred from a fixed location; however, the camera location was not fixed across separate bouts to accommodate larger changes in the bears' locations. During the period we observed each bear, we took video of all perpendicularly oriented locomotion and pacing behavior that matched the criteria outlined below.

For the purposes of this study, pacing was identified as a bear walking the same route at least three consecutive times. Video of a pacing bout therefore began after the bear crossed the same path for the third time and continued until the bear changed its route or became inactive for more than 3 s (360 frames).

All locomotion was videoed, but locomotion that did not have an obvious goal was culled from the analysis to prevent the inadvertent grouping of any possible non-repetitive/non-obvious pacing behavior with non-repetitive locomotion. Locomotion was identified as goal-oriented if the bear performed a different behavior directly after walking. However, we excluded non-repetitive locomotion that directly preceded pacing bouts because, even if not clearly identifiable as pacing, this locomotion may actually be part of or related to the pacing behavior. Only a very small percentage of observed locomotion was both non-repetitive and not goal-oriented. For the most part, either pacing or goal-oriented locomotion was observed. Examples of goal-oriented locomotion included movement to a novel entity within the environment (even if the ensuing behavior was not visible, e.g. door to holding opened), locomotion followed by interaction with another animal or keeper, or locomotion followed by interaction with the environment on-exhibit such as rolling, scratching, and (or) object manipulation.

2.3. Video analysis

Raw video was first cropped and converted to Microsoft video format using Virtual Dub (GNU General Public License). Video was then analyzed using the Winalayze motion analysis software package (Miromak, Berlin, Germany). For seven of the 11 bears head height was measured every 15 frames (or 124.5 ms) for which the nose of the bear was clearly visible. Head height was calculated as a ratio of the distance of the bear's nose from the ground (Line C, Fig. 1) in a given frame compared with the length of the bear's fully extended front leg from the ground to top of the shoulder (Line B, Fig. 1), which is a consistent measurement within each block of video. The measurement of the bear's fully extended front leg was taken once for a block of video when the leg formed an approximately 90° angle (±3°) with the ground (Line A, Fig. 1). Line C, the