Original Research Paper

Enrichment study in three captive polar bears (Ursus maritimus) at Aalborg Zoo

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Abstract

Polar bears (Ursus maritimus) are vulnerable to environmental changes, which often leads to the development of stereotypical behaviour in captivity. Multiple studies have shown that the usage of enrichment could reduce stereotypical behaviour in captive animals thereby, improving their welfare. When choosing enrichments, it is necessary to examine the individual personalities, since differences in behavioural reaction norms of the medians could lead to different preferences among animals regarding the types of enrichment used. This study investigated the behaviour of three polar bears (one adult female and her two cubs) at Aalborg Zoo and whether different types of enrichment would have an impact on their behaviour and reduce stereotypes. Furthermore, this study also investigated whether the three polar bears differed in their behavioural reaction norms, behavioural instability, and behavioural diversity. No differences were found in behavioural reaction norms between the enrichment days and control days, except for the skewness and kurtosis. The mother bear was observed to have more stereotypical behaviour than her cubs, which correlated well with her low behavioural diversity index. A significant difference in behavioural reaction norms was found between the mother and her cubs although, there was no difference between the cubs’ reaction norms. So, no significant differences in behavioural reaction norms and behavioural instability were found between the two cubs.

Keywords: Polar bears, zoo animals, behavioural diversity, behavioural reaction norms, behavioural instability, animal welfare, zookeeping, stereotypical behaviour.

Introduction

Analysis of welfare in captive carnivores

During the last decade, there had been an increased focus on the welfare of captive animals (Miller et al., 2020). Miller and Coworkers (2020) proposed in their article that “When animals have the inability to engage in certain behaviours that they are motivated to perform, then welfare can be compromised” (Miller et al., 2020, page 3). Large carnivores, especially bears, are often particularly susceptible to engage in a large variety of stereotypical behaviours (Clubb and Mason, 2003; Mason and Latham, 2004; Canino and Powell, 2010). Among bears, it was proposed by Canino and Powell (2010) that polar bears (Ursus maritimus) are the most likely of the Ursids to engage in stereotypical behaviour (Canino and Powell, 2010, page 2). In order to provide the best welfare possible for polar bears and other large carnivores, zoos use enrichment as a method of reducing stereotypical behaviour (Ross, 2006; Kelly et al., 2014).
Stereotypical behaviour is defined as a repetitive motion, which serves no purpose for the animal (Shyne, 2006; Linder et al., 2020). Furthermore, stereotypical behaviour has been linked to stress, because it correlates with corticoids and poor welfare (Clubb and Mason, 2003; Mason and Latham, 2004). A polar bear’s home range in the wild usually spans between 50,000-350,000 km², whereas in captivity they only have an infinitesimal fraction of the available space (Canino and Powell, 2010; SeaWorld Parks and Entertainment, 2020). This has also been proposed as one of the reasons, why polar bears in captivity have a strong tendency to pace (Linder et al., 2020). Shyne (2006) showed that adding a choice for the animal to engage or not to engage in enrichment activities reduces stereotypy.

Different opinions exist about how to measure animal welfare. Some studies used stereotypical behaviour (Mason and Latham, 2004), while others used behavioural diversity measurements (Miller et al., 2020). A high behavioural diversity correlated to good welfare (Miller et al., 2020). Whether there was a correlation between stereotypical behaviour and behavioural diversity varies between studies (Gunn and Morton, 1995; Vickery and Mason, 2004; Goswami et al., 2019; Miller et al., 2020). However, not all studies showed an improvement in welfare after enrichment. This could either be explained by individual animals having different personalities or that the animals were thriving at the time of testing (Wilson et al., 2019). Pertoldi et al., (2016) proposed the concept of behavioural instability, which was used to determine the instability of an individual’s behaviour. Behavioural instability can be measured by observing, what is known as bilateral behavioural traits, which were traits that could have two different occurrences, for example looking to the left versus looking to the right (Linder et al., 2020). Additionally, Bech-Hansen et al. (2019) has introduced behavioural instability of symmetry (BSYM) and behavioural instability of variance (BVAR) as two new variables to this concept. BSYM was defined as the behavioural instability of symmetry, where a deviation from a studied behaviour or trait was indicated by deviations for a symmetric distribution (Bech-Hansen et al., 2019). BVAR was derived from the concept of different genotypes having different stress factors, and when an individual was experiencing a suboptimal environmental change, these factors become more varied among individuals (Pertoldi et al., 2016). Therefore, heterogeneity among stress could be expected under conditions of suboptimal environments, which meant a variation could be used as an indicator of behavioural instability, where a high variance led to less likelihood of predicting behaviours for the individuals (Bech-Hansen et al., 2019; Linder et al., 2020).

Behavioural instability could be used to quantify the behavioural reaction norms in individual animals (Linder et al., 2020). Behavioural reaction norms provide information on how an animal behaved and how it changed in response to different environmental conditions (Dingemanse et al., 2010). Behavioural reaction norms are described by a linear relationship between environmental changes and the behaviour of the animal, which are often illustrated by fitting a regression line with an intercept on the point, where an environmental change happened and a slope, which indicated the behavioural plasticity of the animal (Dingemanse et al., 2010). This indicated that differences in the slope between individuals would indicate a difference in personalities (Dingemanse et al., 2010). With a better understanding of an individual’s behaviour and behavioural reaction norms, it was easier to determine the specific needs of the individual, for example, what type of enrichment would be beneficial for the individual (Mason and Latham, 2004). This method was especially useful for large carnivores since they have a higher risk of having poorer welfare than other animals (Clubb and Mason, 2003; Canino and Powell, 2010).

Aim of the study

The purpose was to examine the behaviour of three polar bears at Aalborg Zoo, Denmark, before and after enrichment. The polar bears were an adult female and her two cubs. It was hypothesized, that there would be a difference in stereotypical behaviour between the three bears, and it was expected, that enrichment would reduce the amount of stereotypical behaviour for each individual polar bear. Furthermore, we expected to find a difference in the bears’ behavioural reaction norms. These hypotheses were investigated using the concepts of behavioural diversity index, behavioural instability, and behavioural reaction norms.
Materials and methods

Participating animals and enclosure

This study includes behavioural observations of an adult polar bear and her two young twin cubs (referred to as water cub and land cub mainly due to the zookeeper’s observations for their preferences) 10 months old at the start of the observation period. The cubs were kept inside with their mother until March. The bears’ diet consisted of various types of meat (e.g., fish, goat), horse fat, fruits, vegetables, dog pills and frozen blocks of blood and was given. The bears were fed at varying times throughout the week in an attempt to prevent the development of stereotypical behaviour. The area of both enclosures spans 768 m². The bears have access to a pool for swimming and the land areas are covered in concrete and gravel as well as having multiple big boulders placed around the enclosure. Apart from this, the bears had access to a den. The inside of the den was not visible to visitors.

Enrichment setup:

The observation period of this study was two weeks where eight observation days were chosen (15th-, 17th-, 18th-, 26th-, 28th-, 30th-, 31st of October and the 1st of November 2020). The polar bears were recorded from 8:00 AM to 1:30/2:00 PM using six action cameras (three Kitvision Escape HD5, two Annox Outdoor Action Camera and one Kitvision Venture 4K), which were placed around the enclosure in order to eliminate as many blind spots as possible. The 15th-, 17th-, 18th-, 31st of October and the 1st of November 2020 were used as a baseline and on the 26th-, 28th-, 30th of October the bears were given stimuli consisting of blood enrichment (horse blood was smeared over the gravel and boulders in the enclosure); unscented boxes, which were left in the enclosure for two days; and then scented boxes, which were infused with stock vinegar for three days). These days were chosen because it was the days with the most amount of footage available.

Video analysis

The recorded behaviour was analysed by four observers and scored using the ethogram in Table 1. To ensure that all the observers scored the behaviours the same way, a concordance test (≥80%) was performed before the video analysis. The footage was analysed using focal sampling of the five and a half to six hours of available footage.

Table 1. The behavioural ethogram used in this study.

| Behavioural categories | Description |
|------------------------|-------------|
| Activity on land       | Physical activity in which an individual is crawling on boulders, walking and running on land. NB: Turning around on the spot without moving a full bears length does not count as being active on land (Dahl et al., 2020). |
| Activity in water      | Physical activity in which an individual is swimming, playing and feeding in water (Dahl et al., 2020). |
| Social play            | Behaviour where an individual is playing with another individual on land or in water. This also includes the manipulation of an object together (Linder et al., 2020). |
| Playing alone (land)   | Behaviour where an individual is playing alone on land including manipulation of an object (Linder et al., 2020). |
| Inactive               | Behaviour where an individual is sitting, lying, standing, or sleeping. NB: see also Activity on land (Dahl et al., 2020). |
| Feeding                | Behaviour in which the individual eats food. This also includes the cubs suckling (Dahl et al., 2020). |
| Stereotypy             | Behaviour that is repeating at least two times in a row, for example pacing between the exact same two spots with the same pattern (Dahl et al., 2020). |
| Out of sight           | Behaviour where the individual cannot be accounted for by the cameras. This includes when the individual is indoors or in the blind spot of the cameras. The behaviour of indoors starting when the individuals head is inside and ends when it is outside (Dahl et al., 2020). |
| Enrichment             | Behaviour in which the individual actively uses energy on the enrichment |
Data collection:

The data analysis was conducted in RStudio version 1.3.1093 and Microsoft Excel version 16.43. As the data were not normally distributed, it was analysed with a non-parametric approach.

To determine if there were enough observations to perform statistical testing, a moving average for each individual and each bear were calculated and plotted (Appendix A). The data for each behaviour was pooled for each category and randomized afterwards. Behaviours that had more than 150 observations were limited to 150 after randomization.

The proportion of time each bear spent on each behaviour for each day was compared to the other bears and between baseline and enrichment periods.

The medians for all the behavioural data sets were calculated to examine the differences between the length of each behaviour and examine whether one individual was more active than another for a given behaviour. The medians for both individuals and enrichments were plotted with a trend line between the median of the pooled control data and each enrichment period. The slope of a trend line portrayed an individual’s reaction norm (Dingemanse et al., 2010). Furthermore, the kurtosis and skewness were calculated and compared with a χ²-test.

Differences between medians were tested with, Kruskal Wallis Tests and with Mann-Whitney U Tests when comparing only two groups. If the Kruskal-Wallis test yielded a significant result, a Nemenyi test (Pohlert, 2014) was utilized to test, which pairwise comparison differed. When testing whether the control period differed from one of the enrichment days, a Wilcoxon signed-rank test was utilized with the median being the value of the enrichment day. Additionally, a χ²-test was utilized to examine, if there was a difference in the median slopes between individuals, to further examine whether their behavioural reaction norms differed.

The behavioural diversity index was calculated for each day (for the enrichment days this was done from the time the enrichments were distributed) by use of Shannon’s Diversity Index (Miller et al., 2020).

Results and discussion

The proportion of time each individual spent on each behaviour

Time spent on each behaviour. All three bears had used more than 5% of their time on the behaviours "activity on land", "inactive" and "out of sight", whereas only the cubs had used more than 5% of their time on "activity in water" during control days.

The data showed a difference in time spent on different behaviours between the three bears, especially between the adult female and the two cubs (Figure 1). There was a significant difference in the amount of time spent for at least one pair of bears under the behaviour "activity on land" (p<0.05) and "inactive" (p<0.01).

Nemenyi test showed a significant difference between the land cub's and the adult female's time spent on being active on land (p<0.05) on the control days. Therefore, the adult female was more active on land than the land cub. Furthermore, the adult female also tended to be more active on land than the water cub, but the difference was not significant (p=0.0612). The adult female was more inactive than both cubs on the control days (p<0.05). By comparing control days and enrichment days, we did not find any significant difference between the time spent on any of the behaviours for neither of the bears.
Figure 1. Proportion of time each polar bear spent on the different behaviours during the control days and enrichment days. If the bear had used less than 5% of its time on that behaviour it was not tested.

By comparing control days and enrichment days, we did not find any significant difference between the time spent on any of the behaviours for neither of the bears (Appendix B).

A1) Activity on land (blood enrichment)

A2) Activity on land (unscented box enrichment)

A3) Activity on land (scented box enrichment)

B1) Activity in water (unscented box enrichment)
**Enrichment (Appendix C.1)**

**Activity in water (scented box enrichment)**

![Graphs showing activity in water](image)

**Behavioural reaction norms**

The median time spent on each behaviour varied when the bears were exposed to the enrichment. Each bear was plotted with the two types of enrichment along the x-axis and the time spent along the y-axis (Figure 2).

The land cub showed a significant difference in median time spent when given blood in the behaviour "inactive" (p<0.01), while the unscented boxes yielded significant differences in the behaviour "activity in water" (p<0.001) and "inactive" (p<0.01). Lastly, the scented boxes yielded significant differences in behaviours "activity on land" (p<0.05) and "social play" (p<0.01) (Figure 1) (Erreur! Source du renvoi introuvable.)

The water cub showed a significant difference in the behaviour "inactive" when given enrichment with blood (p<0.001), while the scented boxes yielded a significant result in the behaviour "social play" (p<0.05), and the unscented boxes yielded significant differences in the behaviour "activity in water" (p<0.001) (Figure 2) (Appendix C.1).

Lastly, the adult female showed a significant difference in median time spent when given enrichment with blood in the behaviours "inactive" (p<0.001). She also showed a significant difference in the behaviour "inactive", when both the unscented boxes (p<0.05) and the scented boxes (p<0.05) were given (Figure 2) (Appendix C.1).

**Figure 1.** Behavioural reaction norms for all individuals showing the median time spent on a behaviour, skewness and kurtosis for the pooled control data and each enrichment together with a trend line. The slope of the trend line for each individual is given next to the bear's name, as well as the difference in slope in percent (D) between the cubs (D_Land/Water), the adult female and the land cub (D_Land/Adult) and the adult female and the water cub (D_Adult/Water). If there were fewer than two observations for a polar bear doing a behaviour, neither the median, skewness or kurtosis were calculated. The medians, skewness and kurtosis between the control period and each enrichment were compared using a χ² test and significant results are indicated with * next to a bear's name. In preparation for the χ² test, the skewness values were multiplied with 100 and the kurtosis values were multiplied with 10. To compare the median, skewness, and kurtosis between the bears for an enrichment, either a Kruskal-Wallis test (if there were more than two groups) or Mann-Whitney U test (if there only were two groups) were utilized.

For enrichment with blood, the Kruskal-Wallis test showed no significant difference between the medians. For enrichment with the unscented boxes, the Kruskal-Wallis test showed a difference between medians for "activity on land" (p<0.01). The Nemenyi test showed a significant difference between the adult female and the water cub (p<0.01). For enrichment with the scented boxes, the Kruskal-Wallis test showed a difference between medians for "activity on land" (p<0.05) and "inactive" (p<0.05). The Nemenyi test then showed a significant difference between the medians of the land cub and the adult female (p<0.05) for "activity on land" and a significant difference between the medians of the adult female and the water cub (p<0.05) for "inactive" (Figure 2) (Appendix C.4).

Both skewness and kurtosis showed significant differences in the slopes for the adult female and her cubs, but less so between the two cubs (Appendix C.2&C.3). When the skewness and the kurtosis of the pooled data for each behaviour for each polar bear were compared a χ² test was utilized. This showed significant differences between enrichment and control days for all behaviours (Appendix C.2&C.3).
Behavioural diversity indices

When a bear's behavioural diversity indices (Appendix D) were examined during the control periods the Kruskal-Wallis test yielded a significant result (p<0.01). The Nemenyi test showed that there was a significant difference between the adult female and the land cub's behavioural diversity indices (p<0.01).
Furthermore, there was a tendency for the adult female and the water cub's behavioural diversity indices were different, but not significantly different (p=0.0855).

Table 2. Behavioural diversity indices for each bear; The control is represented with the median value of the five indices of one bear along with a 95% confidence interval for that sample (based on bootstrap), while each enrichment period is based on one day. The control period was tested against each enrichment with a Wilcoxon signed-rank test. The polar bears' behavioural diversity indices during the control period were tested against each other with a Kruskal-Wallis test and a Nemenyi test. A different letter next to a bear’s name indicates that these were significantly different. The p-value under each enrichment was for the Wilcoxon signed-rank test.

|                  | Control       | Blood         | Unscented box | Scented box |
|------------------|---------------|---------------|---------------|-------------|
| Land cub         | 1.422         | 0.786         | 0.752         | 1.062       |
|                  | [1.385:1.426] | p=0.05906     | p=0.05906     | p=0.05906   |
| Water cub        | 1.381         | 0.890         | 0.796         | 0.950       |
|                  | [1.350:1.416] | p=0.05906     | p=0.05906     | p=0.05906   |
| The adult female | 0.486         | 0.693         | 0.476         | 0.597       |
|                  | [0.457:0.534] | p=0.1041      | p=0.5879      | p=0.5879    |

A Wilcoxon signed-rank test was utilized to determine whether there was a significant difference between a bear's behavioural diversity index during the control period and enrichment period. The results showed no significant difference between a polar bear's indices for the control period and an enrichment day (Table 2).

Discussion

In this study, the adult female was observed to be more stereotypical than her two cubs (Figure 1). She had stereotypical behaviour four out of the eight observation days and her cubs had no stereotypy except for one single observation for the land cub, which lasted for <0.05% of the total time. Factors that are known to influence stereotypy are the size of the enclosure, view out of the enclosure, the amount of access to novel items and feeding method, which correlated to anticipatory behaviour (Greenwald and Dabek, 2003; Montaudouin and Pape, 2004; Shepherdson et al., 2013; Kelly et al., 2014). We found that the adult female was more inactive than the cubs on the control days and spent more time being active on land than the land cub and tended to be more active on land than the water cub. The behavioural diversity indices showed that there were significant differences in behaviour between the adult female and the land cub and no significant difference between the adult female and the water cub’s behaviour (Table 2). The adult female had the lowest values of diversity, which indicated she had lower welfare when compared with the cubs. Concerning this Miller et al., (2020) proposed that “when behavioural diversity is low, an animal is likely stereotyping or lethargic, both of which are potential signs of compromised welfare” (Miller et al., 2020). This corresponds with the behaviour observed for the adult female since she has the lowest behavioural diversity and has the most stereotypical behaviour in our study. However, the only method to be used to determine if stereotypy has a negative effect would be to measure corticoid levels or other stress hormones for the bear in question (Linder et al., 2020).

The data indicated that there was a significant difference in behavioural reaction norms between the adult female and her two cubs. Furthermore, the two cubs had no significant differences between their behavioural reaction norms. Dahl et al. (2020) also observed no significant differences in behavioural reaction norms but some patterns of differences between two 3-year-old polar bears, which was also siblings. The bears in both studies were genetically similar and had been living together entire life. This could influence how their personalities had developed (Wilson et al., 2019).

A possible reason the adult female differed in behavioural reaction norms compared to her cubs could be the fact that the adult female was an aged individual and therefore has had more time to develop an irreversible plasticity due to environmental changes or lack of environmental changes (Wilson et al., 2019). However, the results from our study do not indicate that there was a correlation between age and the development of behavioural reaction norms (Appendix C). When the behavioural reaction norms of the bears from our study were compared with the bears from Linder et al. (2020) we saw that during our enrichment with the unscented boxes there was a higher difference in slopes between all bears during “activity on land” than found by Linder et al. (2020), this was also the case for “activity in water” and for
most of the cases during “inactive”. When these two studies were compared, there did not appear to be any correlation between age and the development of behavioural reaction norms either.

The study found significant differences in the slopes between the adult female and her cubs both for the kurtosis and the skewness (Appendix C). This indicated a variation in the predictability between behaviours when comparing the adult female and her two cubs. However, when the two cubs were compared with each other, this study found no significant differences in the slopes, which indicated higher predictability for future behaviour among those two. This could be explained by the fact that the two cubs spend most of their time together and therefore have similar behaviours when compared with the adult female.

We found that the cubs spend more time on enrichment than the adult female. Furthermore, there was no significant difference in behaviour between the control days and the enrichment days. It is shown in Figure 1 that there was a difference between which bear spend the most time on certain enrichments. For example, the adult female used more time than the cubs on blood enrichment whereas, the cubs used more time than her on the enrichment with the boxes. This could indicate that the bear's personality or age should be considered when deciding which type of enrichment to use in the future. It was proposed by (Linder et al., 2020), that this type of selective choice between individuals could indicate certain individuals might prefer one type of enrichment over others. Since the enrichment for this project only lasted a couple of hours on the enrichment days, there was not enough conclusive evidence to support, whether the results were representative for an entire day of behaviour. To further support this, it would be necessary to film for an entire day for a couple of weeks with alternating days of enrichment.

**Conclusion**

No behavioural changes were observed for the three polar bears when they were given enrichment. The adult female had the lowest behavioural diversity and highest stereotypical behaviour. Furthermore, there was a significant difference between the adult female’s behavioural reaction norms and the behavioural reaction norms of cubs. However, there was no significant difference between the reaction norms of the two cubs, which could be because of genetic similarities although there did not appear to be a correlation between age and the development of behavioural reaction norms.

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**References**

Bech-Hansen M. et al. 2019 ‘Effect of landscape elements on the symmetry and variance of the spatial distribution of individual birds within foraging flocks of geese’, Symmetry, 11(9), p. 1103. doi: 10.3390/sym11091103.

Canino W. and Powell D. 2010 ‘Formal behavioral evaluation of enrichment programs on a zookeeper’s schedule: a case study with a polar bear (Ursus Maritimus) at the Bronx Zoo’, Zoo Biology, 29(4), pp. 503–508. doi: 10.1002/zoo.20247.

Clubb R. and Mason GJ. 2003 ‘Captivity effects on wide-ranging carnivores’, Nature, 425(6957), pp. 473–474. doi: 10.1038/425473a.

Dahl F. M. et al. 2020 ‘Effect of enrichments on behavioural reaction norms of two captive polar bears (Ursus maritimus) in Aalborg Zoo, Denmark’, Genetics and Biodiversity Journal, p. 12. doi: 10.46325/gabj.v0i0.745.

Dingemanse NJ. et al. 2010 ‘Behavioural reaction norms: animal personality meets individual plasticity’, Trends in Ecology & Evolution, 25(2), pp. 81–89. doi: 10.1016/j.tree.2009.07.013.

Goswami S. et al. 2019 Effects of personality and life-history on the welfare of captive Asiatic lions (Panthera leo persica). doi: 10.7287/peerj.preprints.27495.

Greenwald KR. and Dabek L. 2003 ‘Behavioral development of a polar bear cub (Ursus maritimus) in captivity’, Zoo Biology, 22(5), pp. 507–514. doi: 10.1002/zoo.10095.

Gunn D. and Morton DB. 1995 ‘Inventory of the behaviour of New Zealand white rabbits in laboratory cages’, Applied Animal Behaviour Science, 45(3), pp. 277–292. doi: 10.1016/0168-1591(95)00627-5.
Kelly K. et al. 2014 ‘Individual effects of seasonal changes, visitor density, and concurrent bear behavior on stereotypical behaviors in captive polar bears (Ursus maritimus)’, Journal of applied animal welfare science, 18, pp. 1–15. doi: 10.1080/10888705.2014.924832.

Linder A. C. et al. 2020 ‘Using behavioral instability to investigate behavioral reaction norms in captive animals: Theoretical implications and future perspectives’, Symmetry, 12(4), p. 603. doi: 10.3390/sym12040603.

Mason G. J. and Latham N. R. 2004 ‘Can’t stop, won’t stop: is stereotypy a reliable animal welfare indicator?’, Animal Welfare, (13), pp. 57–69.

Miller L. J. et al. 2020 ‘Behavioral diversity as a potential indicator of positive animal welfare’, Animals, 10(7), p. 17. doi: 10.3390/ani10071211.

Montaudouin S. and Pape G. L. 2004 ‘Comparison of the behaviour of European brown bears (Ursus arctos arctos) in six different parks, with particular attention to stereotypies’, Behavioural Processes, 67(2), pp. 235–244. doi: 10.1016/j.beproc.2004.02.008.

Pertold, C. et al. 2016 ‘The novel concept of “behavioural instability” and its potential applications’, Symmetry, 8(11), p. 135. doi: 10.3390/sym8110135.

Pohlert T. 2014 ‘The pairwise multiple comparison of mean ranks package (PMCMR)’, R package, pp. 1–9.

Ross S. R. 2006 ‘Issues of choice and control in the behaviour of a pair of captive polar bears (Ursus maritimus)’, Behavioural Processes, 73(1), pp. 117–120. doi: 10.1016/j.beproc.2006.04.003.

Seaworld Parks and Entertainment 2020 All about polar bears - habitat and distribution | SeaWorld parks & entertainment, SeaWorld Parks and Entertainment. Available at: https://seaworld.org/animals/all-about/polar-bear/habitat/ (Accessed: 3 December 2020).

Shepherdson, D. et al. 2013 ‘Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears’, Applied Animal Behaviour Science, 147(3), pp. 268–277. doi: 10.1016/j.applanim.2013.01.001.

Shyne A. 2006 Meta-analytic review of the effects of enrichment on stereotypic behavior in zoo mammals, Zoo Biology, 25(4), pp. 317–337. doi: https://doi.org/10.1002/zoo.20091.

Vickery S. and Mason G. 2004 ‘Stereotypic behavior in Asiatic black and Malayan sun bear, Zoo Biology, 23, pp. 409–430. doi: 10.1002/zoo.20027.

Wilson, V. et al. 2019. Future directions for personality research: Contributing new insights to the understanding of animal behavior, Animals, 9(5), p. 240. doi: 10.3390/ani9050240.