

Annotated Bibliography

These were ordered to start with the studies that gave an overview, followed by observational studies quantifying the behaviour, and then experimental studies that tried to affect the behaviour. The last study was different from the rest as it was the only one that involved studying physical samples from the participants, and thus was added to the end.

Citation

Szokalski, M. S., Litchfield, C. A., & Foster, W. K. (2012). Enrichment for captive tigers (*Panthera tigris*): Current knowledge and future directions. *Applied Animal Behaviour Science*, 139(1-2), 1-9. <https://doi.org/10.1016/j.applanim.2012.02.021>

Summary

It was previously known that suboptimal conditions in captivity can lead to stereotypical behaviours, such as pacing. This was previously hypothesized to result from the inability for large carnivores to roam vast territories and actively hunt prey. Szokalski et al. (2012) focused on identifying specific enrichment practices to help reduce pacing and finding areas that may need further research. To do so, they found research articles addressing tiger feeding/hunting, olfactory, social, and enclosure enrichment, and overviewed the effects each form of enrichment had on stereotypical behaviours. Overall, most forms of enrichment seemed to have some sort of effect on reducing pacing behaviours, however, many studies struggled to show any statistical significance due to very small sample sizes. Thus, a need for supporting research for existing articles was identified. In addition, there appears to be a lack of research on the effects of social housing and human interactions on tiger behavior. This raised the question as to how social housing affects tiger behaviour, especially considering how many captive tigers are housed in close quarters or in pairs/trios. The possibility for keepers to provide enrichment was also explored and prompts the questions of whether human interactions may count as enrichment and reduce pacing behaviour. However, the value of these interactions is yet to be validated, and thus further research in these two categories in particular would prove useful.

Contribution

This article gives an overview of current enrichment strategies used to reduce pacing behaviour, with differing levels of success. It also highlights the issue of small sample sizes in many of the studies conducted on tiger behaviour. In addition, the article addresses the need for future research to focus on the effects of human interactions and social housing on tiger behaviour. As a relatively specific review article, this also provides an overview of major research conducted in the field, allowing for further research into how different forms of enrichment affect pacing behaviour in different ways.

Citation

Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrensclager, A., & Mason, G. (2016). Stereotypic route tracing in captive Carnivora is predicted by species – typical home range sizes and hunting styles. *Animal Behaviour*, *117*, 197-209.
<https://doi.org/10.1016/j.anbehav.2016.05.010>

Summary

Previous comparative research suggested that body mass, territoriality/home range size (HRS), and average distance travelled daily by a species in the wild predicted infant mortality and susceptibility to stereotypic behaviours in captivity. In this study, researchers looked at the average percentage of time that an animal exhibited stereotypic behaviour during observation by collecting data from studies from 1960-2010 (Kroshko et al. 2016). This added 10 years' worth of more recent data to the previously studied database. This resulted in coverage of more than 1300 individuals over a total of 23 species. In addition, this study screened out studies with sample sizes less than 5 to decrease the likelihood of the addition of anecdotes, and only used studies involving observations to prevent experimental techniques from influencing results. In addition, the identity code of each animal was used to screen for duplicates and the mean stereotypic behaviour value was used. Captive infant mortality rate was also collected from the International Zoo yearbook for species corresponding to the stereotypic behaviour study. Contrary to previous research, when data regarding stereotypic behaviour was analyzed against daily travel distance, it was not a significant predictor of susceptibility to stereotypic behaviour when HRS was controlled for ($P=0.065$). However, when the opposite was tested, a significant predictor effect was found for HRS when daily travel distance was controlled for ($P=0.032$). Predictability was further increased when HRS was combined with body mass ($P<0.0001$), however, body mass alone was not a significant predictor of stereotypical behaviour ($P>0.1$). Additionally, nothing except body mass predicted captive infant mortality ($P=0.006$). This shows that current research has led to drastically different results in comparison to what was previously available. In addition, further research is needed to determine what aspect of a large HRS makes stereotypical behaviour more likely in captive Carnivora.

Contribution

This article advances knowledge in the field by providing updated information about predictors from wild individuals that may indicate the susceptibility of an animal to stereotypic behaviour in captivity. In addition, it contradicts previous research that attributed daily travel distance in the wild to stereotypical behaviour in captivity, and thus introduces new ideas in the field. Lastly, although this study looks at multiple species and stereotypic behaviours in general, it is biased in favour of Felidae and pacing is the most common stereotypical behaviour observed, and thus it is an ideal representative of research in this field.

Citation

Lyons, J., Young, R. J., & Deag, J. M. (1997) The effects of physical characteristics of the environment and feeding regime on the behaviour of captive felids. *Zoo Biology*, 16, 71-83. [https://doi.org/10.1002/\(SICI\)1098-2361\(1997\)16:1<71::AID-ZOO8>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1098-2361(1997)16:1<71::AID-ZOO8>3.0.CO;2-8)

Summary

Restricted environments and a lack of control over feeding have been known to cause pacing, or repetitive walking in carnivores. In this article, researchers focused on determining how feeding regimes and cage size influences pacing, along with highlighting how habitat space is used by felids (Lyons et al. 1997). To do so, 9 species, or a total of 19 felids were studied at the Edinburgh Zoo through instantaneous scan sampling during 4 1-hour sessions every day over the course of February and March. This resulted in a total of 560 scans per enclosure that divided observations into 6 behavioural categories. To study the effect of feeding regimes, pre-existing routines of either daily feeding or feeding every 3rd day were observed and recorded for differences in pacing behaviour. Results showed that animals that were fasted paced significantly more on fasting days than feeding days ($P < 0.002$). However, felids that were fed daily exhibited greater amounts of pacing an hour prior to feeding, but this result was statistically insignificant ($P > 0.05$). The results did, however, show a significant positive relationship between the enclosure size and overall movement ($P < 0.01$). Smaller cage sizes indicated possible increases in pacing, but the results were not significant. There was, however, a significant positive correlation between the percent of scans spent pacing and the percent of scans spent near the edge of the enclosure ($P < 0.01$). These results are significant as they bring up issues with attempts to mimic natural events such as irregular meals, which seem to increase stress. In addition, the correlation between time spent near the edge of an enclosure and pacing may hint towards a new definition of pacing, and could indicate possible solutions, such as enriching the edge of the enclosure to provide stimulation. However, further research into this relationship is required.

Contribution

This article is significant as it covers multiple possible causes of pacing, such as feeding regime, and enclosure size. Additionally, the article covers the relationship between edge utilization and pacing, which is not a commonly researched aspect of pacing. It is also interesting that this study ultimately concluded cage size did not affect pacing, as contradictory evidence is found in more recent studies. As such, this article is important to provide a historical basis to research in this field and is a gateway to further research, which is evident through the large number times this article has been cited.

Citation

Bashaw, M. J., Kelling, A. S., Bloomsmith, M. A., & Maple T. L. (2007). Environmental effects on the behaviour of zoo-housed lions and tigers, with a case study of the effects of a visual barrier on pacing. *Journal of Applied Animal Welfare Science*, 10(2), 95-109.
<https://doi.org/10.1080/10888700701313116>

Summary

It was previously known that different environments can influence how much felids exhibit pacing behaviours, with factors such as visual barriers, hiding spots, visitor presence, and usable surface area playing a role. In this article, researchers aimed to determine how large felids would behave in different environments, in addition to tracking how temporal factors may influence behaviour by studying 3 lions (1 male, 2 females) and 2 tigers (1 male, 1 female) (Bashaw et al. 2007). The lions were observed in a large exhibit or a smaller area off display while the tigers were housed in a large exhibit with visual barriers, or a smaller exhibit with no visual barriers. Data was collected through timed observations classified into behavioural categories either in the morning, midday, or afternoon. Results showed that the large felids rested significantly less in the morning ($P=0.046$) in comparison to midday or afternoon. Similarly, nonstereotypic activity was higher in the morning ($P=0.058$) than the other two times. This supported the hypothesis researchers initially had that the tigers would be more active closer to dawn as they are naturally nocturnal animals. Regarding environmental conditions, the larger exhibit with more visual barriers did correlate with decreased pacing, but the result was not statistically significant ($P=0.121$). However, in a case study with 1 tigress comparing behaviour before, during and after the placement of a visual barrier from social stimulants, the presence of the barrier actually increased the frequency of pacing. This may suggest that visual barriers from conspecifics may not be as significant in decreasing pacing as seen in studies with smaller felids. In addition, there was no olfactory barrier so the tigress was not completely isolated, and this may have affected results. Thus, further research involving more effective barriers between conspecifics are necessary.

Contribution

This article advanced knowledge in the field by providing evidence for a potential difference between pacing in small and large felids, particularly through the supposed ineffectiveness of a visual barrier decreasing pacing in a tigress. In addition, this article highlights how the time observations are taken can drastically change results as tigers are more active in the morning in comparison to midday and afternoon and thus the likelihood of pacing is also different regardless of experimental factors. This article has also been cited 67 times, forming the base of research in this field.

Citation

Mohapatra, R. K., Panda, S., & Acharya U. R. (2014). Study on activity pattern and incidence of stereotypic behaviour in captive tigers. *Journal of Veterinary Behavior – Clinical Applications and Research*, 9(4), 172-176. <https://doi.org/10.1016/j.jveb.2014.04.003>

Summary

It was previously known that animals in suboptimal environmental conditions may exhibit stereotypical pacing, or repetitive movement without an apparent goal. In this study, researchers attempted to determine if stereotypical behaviour in tigers differed based on age, sex, enclosure size, or the time of day (Mohapatra et al. 2014). The study collected a total of 1254 hours of data through instantaneous observations at 1-minute intervals between 7:00-18:00 of 10 adults, 4 subadults, 3 cubs, and 2 older tigers (a total of 13 females and 6 males). Behaviour observed was condensed into 3 categories: active, resting, and stereotypic. It was found that stereotypic behaviour peaked between 10:00-11:00 and 15:00-16:00, the latter of which is thought to be because of the tiger waiting for food. This hypothesis is supported by previous studies, and by observations of aggression towards the feeding keeper. No significant difference in pacing was observed between males and females ($P=0.1$). However, there was a significant difference in pacing based on age-group ($P=0.007$), as cubs were observed to not pace at all. This raises the question as to when tigers start pacing as tigers under 1.5 years of age were not seen to pace in previous studies either, thus a closer estimate of what age at which pacing begins remains to be found. In addition, this study suggests that pacing is not significantly different based on sex, which contradicts findings in previous studies. As such, further research into why this study was different or looking at possible confounding factors for studies on this topic is needed.

Contribution

This article contributed to the field of pacing in tigers as it quantified specific temporal associations with pacing, confirming previous studies suggesting an association. In addition, it supported previous research regarding minimal pacing in cubs while suggesting an approximate age after which pacing becomes more common. Lastly, this article contradicts previous findings indicating a difference between pacing behaviour in males and females, and thus prompts further research into the topic, and encourages further attention to be paid to confounding variables. Ultimately, this article contributes a lot of new information and is one of the more recent articles in the field.

Citation

Breton, G., & Barrot, S. (2014). Influence of enclosure size on the distances covered and paced by captive tigers (*Panthera tigris*). *Applied Animal Behaviour Science*, 154, 66–75.
<https://doi.org/10.1016/j.applanim.2014.02.007>

Summary

The amount of pacing, or repetitive locomotory behaviour exhibited by a carnivore is known to be correlated with distance normally travelled in the wild. In this article, researchers quantified how pacing and locomotion linked back to distances travelled in the wild and how enclosure size limited or enabled either of these behaviours (Breton & Barrot, 2014). A sample of 38 tigers in 14 enclosures was observed, encompassing 7 different zoos in France. Data was collected for 10 minutes every hour for the first and last three hours in the outdoor habitats, resulting in a total of 60 minutes of observation everyday. Each tiger was observed over 7 days, with the first day being counted as a pre-observation phase to confirm the periods of the most activity, and the next 6 days being the official observation phase where data was collected by recording distance paced and total distance covered. In addition, information about enclosure size (small, medium, and large), age (adult or young), and sex was also collected. Significantly more distance was covered in larger enclosures ($P=0.001$) for both males and females. In addition, enclosure size had a significant negative correlation to distance paced ($P=0.00008$), however, this was largely due to data from female tigers ($P=0.0001$), as the correlation was not significant in male tigers ($P=0.24$). Additionally, adults paced significantly more than cubs ($P=0.006$), but when data was divided based on enclosure size, the significance only remained in small enclosures ($P=0.003$), with the difference being insignificant in medium/large enclosures. This study was significant as it contrasted previous studies that found enclosure size did not effect pacing. In addition, the difference between males and females in regards to distance paced and distance covered was highlighted, indicating the sex of a tiger may result in different environmental needs to minimize pacing.

Contribution

This article is significant as it supports the hypothesis that pacing can be reduced through larger enclosures. This contradicts previous studies that suggest pacing is not significantly linked to enclosure size. In addition, the article is one of the few in the field that has a large sample size as it looked at multiple subjects in different zoos. This makes the study more reliable and less anecdotal as the large sample is more likely to represent the population. Lastly, this is one of the more recent studies in the field, yielding more up to date information.

Citation

Nevill, C. H., & Friend, T. H. (2003). The behaviour of circus tigers during transport. *Applied Animal Behaviour Science*, 82(4), 329-337. [https://doi.org/10.1016/S0168-1591\(03\)00066-2](https://doi.org/10.1016/S0168-1591(03)00066-2)

Summary

It was previously known that spatial restrictions can encourage the development of stereotypies such as pacing in tigers. However, there was little knowledge of how tigers behaved when confined in small spaces during transport, which prompted researchers to investigate the topic (Nevill & Friend, 2003). This study looked at a pair of tigers moving from San Antonio to Houston, and a quartet of tigers moving from Ft. Worth to Houston, and then from College Station to Dallas for a total of three trips, each of which was just over 4 hours long. Behaviour was video recorded via cameras throughout the trips and then divided into three classifications, Pacing, lying, and standing/walking. The temperature of the tiger was also monitored at 5-minute intervals through a datalogger fed to the tiger that was later retrieved through the feces. Results indicated that the pair of tigers that had performed just before transportation exhibited the least amount of pacing, mostly lying until the end of the trip. The quartet of tigers exhibited the opposite pattern on their first trip, with the tigers pacing the most during the first portion of the trip and the least amount of pacing during the last 1.5 hours. However, majority of this pacing consisted of one tiger, and thus the results may be skewed. For the trip to Dallas, the quartet exhibited even more pacing, although it too decreased as the trip continued. Temperature did not seem to correlate strongly with pacing behaviour. This study is significant as it shows potential in decreasing pacing through activities such as performances. In addition, it was the first study to look at tiger behaviour during transport. However, further research is needed to confirm if body temperature has anything to do with pacing, and to test how non-circus tigers behave during transport.

Contribution

This article advanced knowledge in the field by piloting research into tiger behaviour during transport. In addition, they measured body temperature alongside pacing, providing evidence that increases in the former may not be due to pacing. Additionally, the pair of tigers displayed minimal pacing despite the small transport wagon, indicating possible solutions for pacing when larger enclosures are not an option. As the first study on the topic, this article provides a baseline for future research and provides unique insight into how there may be minimal pacing even within extremely small enclosures.

Citation

Jenny, S., & Schmid, H. (2002). Effect of feeding boxes on the behaviour of stereotyping amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology*, 21(6), 573-584. <https://doi.org/10.1002/zoo.10061>

Summary

This article studied stereotypies, which were previously known to be caused by suboptimal environments. Researchers focused on pacing behaviour in tigers (*Panthera tigris altaica*) and attempted to determine if this is caused by permanently unsuccessful appetitive foraging behaviour, or if it is an active waiting strategy (Jenny & Schmid, 2002). In addition, an attempt was made to determine if there was a social cause to this behaviour. Two tigers (a male and female) were kept in solitary confinement for 4 months and fed using conventional or box-feeding. Through direct observation, they found the proportion of the day spent pacing was significantly reduced for the female ($P = 0.02$) while the male was unaffected after box-feeding. After being paired, both tigers experienced a significant decrease in pacing with box feeding in comparison to conventional feeding ($P = 0.01$). However, the male also experienced more than a three-fold increase in pacing at 10% during conventional feeding when paired, in comparison to pacing just 3% of the time with conventional feeding in solitary confinement. The results of this experiment are significant as they support the hypothesis of pacing being mainly caused by permanently unsuccessful foraging behaviour. However, the increase in pacing after being paired with the female during conventional feeding contrasts with the decrease experienced by the female in the same conditions, prompting further research into why that occurred. This keeps the social impact on pacing ambiguous but it has an effect nonetheless. In addition, it still needs to be investigated whether the multiple small feeding sessions that are significant in reducing pacing, or if it is the act of opening of the feeding boxes. Additionally, temporal randomness may also play a huge role, in which case it needs to be studied if zookeepers feeding at random times may have similar affects.

Contribution

This article significantly advances knowledge of pacing in tigers as it helps pinpoint permanently frustrated appetitive foraging behaviour a possible cause for the stereotypical behaviour. This supports previous ideas of stereotypies resulting from suboptimal environments but contradicts ideas of pacing being an active waiting strategy. This article also highlights how different tigers behave differently in similar situations, and how pacing may result from a variety of stressors. Being one of the few articles on box-feeding, this is one of the most cited articles in the topic, and thus fairly important to understand when conducting research in this field.

Citation

Skibiél, A. L., Trevino, H. S., & Naugher, K. (2007) Comparison of several types of enrichment for captive felids. *Zoo Biology*, 26, 371-381. <https://doi.org/10.1002/zoo.20147>

Summary

Prior to this study, it was known that enrichment could reduce stereotypic pacing in felids. In this article, researchers quantified the effects of 3 specific forms of enrichment on active behaviour and pacing (Skibiél et al. 2007). They also looked into whether behavioural changes would last once the enrichment was removed. To do so, researchers subjected 6 species at the Montgomery Zoo, or a total of 14 felids to a baseline period with no enrichment for 4 weeks prior to testing an enrichment item. The felids were then exposed to a treatment of fish frozen in ice, 30 mL of spices (chili powder, cumin, or cinnamon), or bone (a horse knuckle or shank bone) for 4 or more consecutive days. Instantaneous scan sample observations (two 30-minute sessions with 1-minute intervals on eligible days) were taken during the baseline period, the first, second and last days of the treatment period, and 7 days after the enrichment was removed for a total of 300 baseline, 180 treatment, and 28 post-treatment observations per species. Behaviours observed were divided into active, inactive, or stereotypic. 2 weeks of no enrichment were given to the felids between treatments to prevent accumulating effects. All the species experienced an increase in activity after all the treatments, except for the lions after the spice treatment. The spices and frozen fish also resulted in a significant decrease in pacing ($P = 0.01$), however, only the frozen fish had results that lasted for more than 7 days ($P=0.02$). This is significant as it suggests enrichment does not have to be costly or complicated to result in significant changes in felid behaviour. However, further research is necessary to determine how combining enrichment could affect results, and if felids may eventually become habituated to what was initially novel enrichment.

Contribution

This article supported previous research indicating the effectiveness of enrichment items in reducing pacing. However, this article quantified the effects of specific enrichment items, and most importantly, investigated the long-term effects of each item. This emphasized the importance of finding enrichment that leaves a lingering effect, as this indicates change in behaviour instead of simple temporary interactions with the enriching items. As such, this is an important article to review when studying the topic as it suggests possible forms of enrichment that can work long term and accumulate beneficial effects.

Citation

Sajjad, S., Farooq, U., Anwar, M., Khurshid, A., & Bukhari, S. A. (2011). Effect of captive environment on plasma cortisol level and behavioural pattern of Bengal tigers (*Panthera tigris tigris*). *Pakistan Veterinary Journal*, 31(3), 195-198. ISSN: 0253-8318

Summary

It was previously known that smaller and less naturalized enclosures could result in more pacing than larger, naturalized environments. It was also known that stereotypic pacing could indicate stress, which in turn could be quantified by measuring plasma cortisol levels. In this study, researchers attempted to determine if there was a link between these chemical and behavioural indicators of stress for tigers (Sajjad et al. 2011). To measure behavioural pacing, 4 tigers in the Lahore Zoo (smaller/less naturalized) and 6 tigers in the Lahore Wildlife park (larger/more naturalized) were observed through focal sampling, dividing behaviour as stereotypic pacing, resting, or other. This was done at 10-minute intervals for an hour every day for 2 months. To measure blood cortisol levels, tigers were corralled into squeeze cages for restraint and blood was collected directly from the tail without anaesthesia. This was done at the same time with the same personnel every collection to minimize external stress to the animal. The sample was then centrifuged for plasma and plasma cortisol levels were measured. Results revealed the animals in the zoo paced 7 times more than the group in the Wildlife Park, which supported results from previous studies. However, there was no significant difference between the plasma cortisol levels for the Zoo and Wildlife Park groups, although both were higher than those reported in previous studies. In addition, the mean plasma cortisol level was greater in the Wildlife Park group, which was unexpected but hypothesized to be due to more stress induced during capture and restraint of each animal. It raises questions as to whether less stressful blood collection methods may result in different results, and if the high overall plasma cortisol levels were due to the season.

Contribution

This article is significant as it has unexpected results showing that plasma cortisol levels are not related to environment size or time spent pacing. The increased pacing in smaller environment supports previous literature that depended on observation, but the results of the chemical analysis contradict previous beliefs. This raises the question of whether pacing is truly an indicator of stress. As one of the few articles that use a sampling method other than just observation, this study is important in determining the proximate causes of pacing.