Factors influencing pacing in the South China tiger (*P.t. amoyensis*)

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Abstract

In zoos, stereotypic behaviours such as pacing are considered a cause for concern; visitors often interpret pacing as an indicator of stress or boredom and, therefore, compromised welfare. Indeed, factors postulated to influence pacing include stress, and limited enclosure size or lack of access to social partners. The aim of this study was to identify factors that influence pacing behaviour in South China tigers (P.t.amoyensis). Behavioural observations were performed twice daily from 12th January to 21st March and 30th October to 22nd December 2012.

To identify factors affecting pacing behaviour a logistic regression with random tiger effects and several factors as fixed effects was used. A backward stepwise method using Akaike's Information Citerium (AIC) was used to reduce the number of factors in the final model.

To decrease the amount of pacing in the South China tiger in a reserve or a zoo, you must make the camp as big as possible, feed them as regularly as possible, buy young tigers and try to find the right equilibrium in temperature to have active tigers that pace as less as possible. Furthermore, it isn't advisable to get the tigers used to people feeding them. They can be fed if the tigers are not able to see the people, for example, when they are in their shelter. If this is not possible, let one person feed the tigers. This to prevent the tigers to show pacing behaviour to people in general, because they associate them with food.

Besides this, pacing is also used to scent mark the tigers' territory. Information to visitors can be given to make them more aware of this natural behaviour. To prevent more pacing minimize human activity in the camp. Switching between camps also increases exploratory behaviour and decreases pacing behaviour caused by boredom. However it increases pacing behaviour by scent marking their new territory.

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1. Introduction

In zoos, stereotypic behaviours such as weaving or habitual pacing among large mammals are considered a cause for concern. Visitors interpret pacing as a sign of boredom, stress[26] and compromised wellbeing [21]. Zoos try to decrease the amount of pacing by using natural environments, cage enrichment, visual barriers and hiding places. However, combined with the natural camouflage of the animals, these visual barriers make it difficult for visitors to see the subjects[26]. This study aimed to identify factors influencing pacing behaviour in the South China tiger (P.t.amoyensis), and ultimately give advice on how to decrease the amount of pacing.

Stereotypic behaviour is one way to cope with a stressful environment. Wechsler (1995) found that animals that cope with a stressful environment by developing stereotypic behaviour have lower stress hormone levels then animals that do nothing[30]. Burgener et al (2012) observed snow leopards and concluded that not being able to perform appetitive foraging behaviour is the most likely cause for stereotypic pacing in captive carnivores[30]. They also found that captive carnivores that are fed at regular intervals do not display appetitive foraging behaviour. However, the motivation to forage remains high, and stereotypic behaviour may develop as a means of coping with the associated frustration.

In the wild, tigers pace to scent mark their territory and warn off other tigers[22]. Allen (1960) reported a tiger making a circuit of its territory every 10 days, Anderson (1956) suggested a circuit every three to four months[22]. Forest roads were favoured by the animals because they can be covered easily, silently and rapidly, compared to long grass[22]. Some ranges in the Kanha park were so small that tigers used the roads several times a week[22].

In captivity, pacing is considered a form of stereotypic behaviour, like weaving or head-bobbing which have also been observed in tigers[24]. Carlstead (1996) described stereotypic behaviour as ‘a pattern of movement that is performed repeatedly, is relatively invariant in form and has no apparent function or goal’[24]. There are a variety of causes of stereotypic behaviour:

- When an animal is unable to reach a goal, for example reach another conspecific or perform natural feeding behaviour[24].
- When an animal is physically restrained from going to a desired place[24]
- Boredom[24]
- Frustration[24]
- Fear[24]
- Density of animals[21,26]
- The amount of area that is useful to the subject[21,24]
- The number of hiding places, retreat spaces and visual barriers[21, 26]
- Presence of visitors[21, 26]
- Indoor or outdoor housing[21, 26]
- Low stimulus diversity[24]
- Compromised wellbeing[21]
- Lack of sensory access to social partners[22]
- The presence of objects compared to substrate[26]

Carlstead (1996) found that an animal held in a poorly stimulating environment can adapt in two ways: 1) being lethargic, i.e. no longer even looking for the stimuli and 2) develop stereotypic behaviour to satisfy the stimulus for the desired behaviour[24]. Stereotypic behaviour can be prevented by keeping tigers in their natural environment[24].

Moreira (2007) investigated the pacing behaviour of 2 Sumatran tigers and 3 African lions in different housing systems[21]. They found that the tigers paced more in off-exhibit housing compared to on-exhibit housing[21]. More pacing was seen in a small space compared to a large space[21]. Lyons (2007) found another correlation, namely that the total length of edges rather than the size of an enclosure *per se* affects the amount of pacing. Boundariess are specifically used for pacing[27]. Furthermore, raised areas were preferred pacing locations, probably because they offer a better view [27].

Carnivores also pace in response to inadequate sensory access to social partners[21]. Broom (1991) suggested that stereotypic behaviour, including pacing, is a sign of compromised wellbeing[21].

Stevenson (1983), Carlstead (1998) and Erwin and Deni (1979) have suggested that stereotypic behaviour is a result of abnormal organism-environment interactions[21]. Tigers are nocturnal animals and their activity peaks between 19:00 and 5:00. Under captive conditions we want them to be active during the day, and feed and interact with them accordingly. Shepherdson et al (1993) found that increasing the frequency of feeding also increased the behavioural diversity and exploratory behaviour of small felids and reduced the duration and frequency of stereotypic behaviour[21]. Lyons (2007) found that captive felids fed on a 3-day cycle paced more on days that they were not fed [27]. Six out of seven of these tigers also paced more in the hours immediately after feeding[27]. Tigers fed daily paced more in the hour before feeding[27]. Altman (2005) found similar correlations among lions[29]. Lions fed on a set schedule paced half as frequently on a non-feeding day as on a feeding day[29].

2. Research question

The aim of this study was to identify factors that influence pacing behaviour. The following factors were taken into account:

- Camp size
- Feeding frequency
- Alone or together in a camp
- Age
- Weather conditions
- Pacing as a social behaviour
- Enrichment of camp
- Gender
- Time during the day
- Pacing to scent mark a territory
- Pacing during the day
- With or without cubs
- Location of pacing in the camp

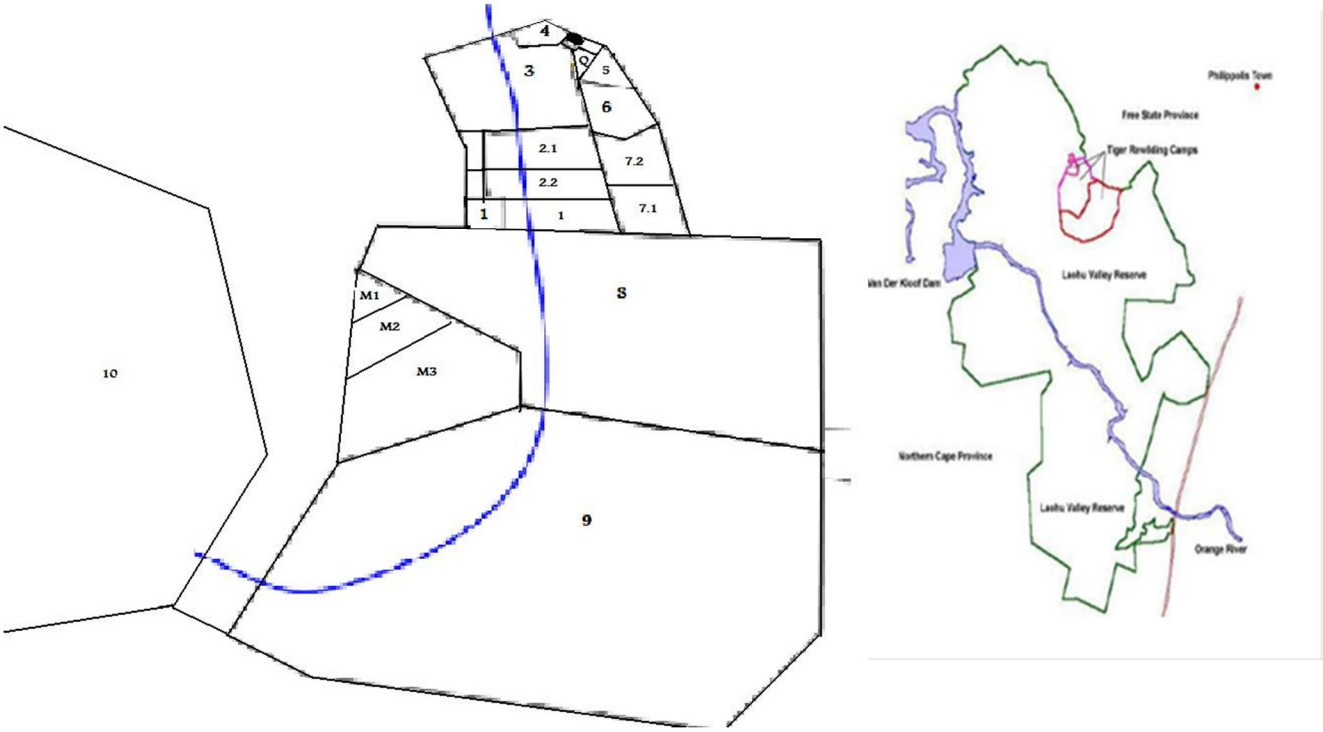
3. Material and Methods

Behavioural observations were performed twice a day from 12th January to 21st March and 30th October to 22nd December 2012.

3.1 Observation sites and camps

The study was carried out in the Laohu Valley Reserve in Phillippolis, Free State, South Africa. The total surface of the reserve is 33 000 hectares, of which 500 hectare is used for the tigers. The remaining 32 500 hectares is used for breeding live prey that are shot and fed to the tigers.

The 400 hectares used for the tigers is divided into several camps (see picture 3.1A). The three largest camps are 40 hectares and two camps of 100 hectares and are used as hunting camps. The other camps vary from less than one half to seven hectares. Some camps have a stream running through them.



Picture 3.1A: Diagram to show the location of the tiger camps in Loahu Valley Reserve.
1. Mini camp (0.5 hectare)
2. Ravene camp 1 and 2 (together 2 hectares)
3. Catkens camp (7 hectares)
4. Tree camp (less than 0.5 hectare)
Q. Quarantine camp (0.5 hectare)
5. Hopes' corner camp (less than 0.5 hectare)

6. Ripples camp (1 hectare)
7. Grass camp 1 and 2 (together 3 hectares)
8. Tigers' roars camp (40 hectares)
9. Hunters' palace camp (100 hectares)
10. New 100 hectare (100 hectares)
M1. Management 1 (less than 0.5 hectare)
M2. Management 2 (less than 0.5 hectare)
M3. Management 3 (less than 0.5 hectare)

There is a fence around the camps to ensure that the tigers do not escape. The electric fences are driven by solar power. During daytime, the batteries are loaded so that they can power the fences during the night and ensure that the fences still work when the sun is not shining. There are two fences, the first is around 50 cm high, while the outer fence is three meters. The fences are around 40 cm apart. The electricity in the fences runs at around 6-8 kilovolts, depending on the amount of grass and bush growing against them.

The camps can be entered through the gates. The tigers can be moved from one camp to another using a road outside the camp. The gates are three meters high and five meters wide, and run on a rail.

All the camps have a water trough, which can be filled by tap. They are checked in the morning and afternoon, so that the tigers are never without water.

3.2 Animals

There are 14 South China tigers in the Laohu Valley Reserve. In 2003, the first two tigers were brought to Laohu Valley from Shanghai Zoo: Cathay and Hope. They were born on 21st January 2003. Next, Tiger Woods and Madonna were brought to the reserve. Tiger Woods was born on the 9th March 2004, Madonna on 20th April 2004.

	Descendants	Born	Extra information
Cathay	Hulooo	23 November 2007	Hand reared
	Jen B and Coco	30 March 2008	
	Huwaa	27 January 2011	Hand reared
	Alpha and Beta	20 July 2011	
Madonna	2 cubs	12 April 2008	Died
	Princess and King Henry	18 August 2008	
	3 cubs (3 females: Xa, Yoya, Zeta)	9 October 2011	

Table 3.2A: This table shows the known genetic relationships between some of the tigers.

3.3 Behavioural observations

During the current study, all 14 resident tigers were observed: Cathay, Hulooo, Tiger Woods, King Henry, Princess, Coco, Jen B, Alpha, Beta, Huwaa, Xa, Yoya and Zeta. The tigers were observed for two to three hours in the morning, just after sunrise, and two to three hours in the afternoon, just before sunset. These times were chosen because the tigers are more active during these hours[23].

In the first half of my research, an ethogram made by E.M.E. Groot (2011) was used (see Appendix A). In this ethogram, behaviours were divided into different subgroups 'Exploring/ hunting behaviour', 'Resting/ common behaviour', 'Homeostatis-related behaviour', 'Communication behaviour', 'Mating behaviour', 'Parental behaviour' and 'Stereotypic or other behaviour'. To avoid observer subjectivity, a detailed description of how to categorize the behavious was made by E.M.E. Groot, [23] (see Appendix B). In the ethogram, the duration for which a certain behaviour was observed, was noted. When a tiger was engaged in several activities in a short period, numbers were placed behind the time (7:40(1), 7:40(2) and so on).

All of the tigers were observed for anything from half an hour to an hour, depending on how many tigers were visible during the observation. Each tiger was observed in the morning and in the afternoon. Coco and Jen B were in the 100 hectare camp from the 3rd of February until the end of the first study period (23rd March). They were observed once every two days.

Coco and Jen B were observed from a tower in the middle of the 100 hectare camp. When Cathay was in the 100 hectare camp (starting 5th March) she was observed from outside the camp, or by driving in with a car to search and observe her. The other tigers were observed from outside the camp.

Some behaviours were examined for their duration, others for their frequency. The behaviours that were examined for duration were 'chew/lick/claw object', 'dig', 'walk', 'stalk', 'slow chase', 'fast chase', 'kill', 'swim', 'rest on belly', 'rest on side', 'rest on back', 'lay in water', 'grooming', 'sit', 'drink', 'eating grass', 'eating food', 'plucking food', 'defecate', 'urinate', 'play', 'play-fight', 'fight', 'flee', 'mount', 'be mounted', 'mate', 'dragging nest material', 'feeding cubs', 'grooming cubs', 'move cubs', 'ignore cubs', 'pacing', 'lethargic' and 'cannot see'. These behaviours added up for the total observation time. Other behaviours were analyzed for frequency. These included 'alert', 'smell', 'chase prey', 'catch prey', 'jump', 'roll over', 'stretch', 'yawn', 'stand', 'body-scratch object', 'head-rub object', 'head-rub tiger', 'scraping ground', 'scratching object', 'spraying', 'vocalization', 'chuffing', 'prusten', 'snarl', 'growl', 'roar', 'flehmen', 'investigation', 'seduction', 'snarling at cubs' and 'kill cubs'.

If there were multiple actions during a single minute, the minute was divided by the number of actions performed during that minute. Because the observation times differed from half an hour to more than one hour (depending on how many tigers were visible) the duration and frequency of the behaviours were normalised from 'minutes per observation' and 'frequency per observation' to 'minutes per hour' and 'times per hour'.

Special events during the observation were noted under 'Happenings information'. The start and end of the event was noted, as well as which tiger was involved; and the happening was described. For example, when a car drove up to a camp, or when an eland came along next to a camp.

During the second half of the research (October - December) an ethogram specific for pacing behaviour was used (see Appendix C). This included additional categories 'proximity' and 'pacing together with' to examine whether pacing is a social behaviour. The definition of proximity was 'being within 4 m of another tiger'. Further the pacing was split into the categories pacing at 'fence', 'corner' and 'gate', to determine whether there

were preferred places to pace. To check if pacing is a natural behaviour used to mark territory, the amount of spraying during pacing was added.

3.4 Statistical analysis

A logistic regression with random tiger effects and with group (young or old), gender, camp number, fed (days ago), time (morning or afternoon), temperature, rain, wind, clouds, river, size of the camps and if the tigers are alone or together in a camp as fixed effects was performed. A backward stepwise method using Akaike's Information Citerium (AIC) was used to reduce the number of factors in the final model.

4. Results

A logistic regression was done with the following results: pacing was influenced by:

4.1 Size of the camp

The amount of pacing in small camps was compared with the amount of pacing in large camps. All camps bigger than 1 hectare were considered ‘big’, all camps smaller than 1 hectare were considered ‘small’.

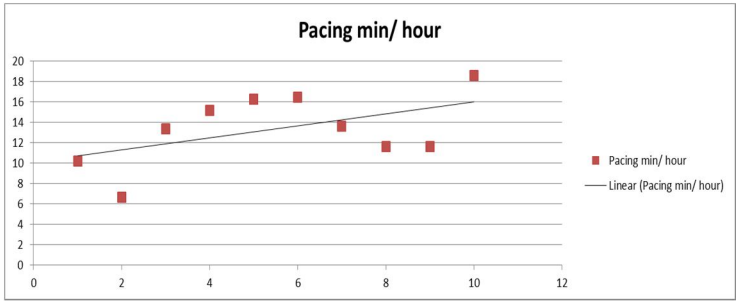
Camp	Camp size	Pacing (mean min/ hour)	Number of observations	SD
Big camp		12.86274998	261	17.61900948
Small camp		11.5043949	517	17.47531875
Camp 1 (0.5 hect)	Small	7.114351852	40	8.795314085
Camp 2 (2 hect)	Big	8.614285714	7	13.0999273
Camp 2.1 (1 hect)	Small	2.700716846	31	10.28036682
Camp 2.2 (1 hect)	Small	7.708986723	53	11.4014161
Camp 3 (7 hect)	Big	17.301875	32	20.25057187
Camp 4 (< 0.5 hect)	Small	14.61773805	145	19.67027618
Camp 5 (< 0.5 hect)	Small	10.290625	16	18.72752145
Camp 6 (1 hect)	Small	11.06495122	82	15.9270613
Camp 7 (3 hect)	Big	10.91383929	112	16.05146735
Camp 8 (40 hect)	Big	16.76886364	44	20.1797889
Camp 9 (100 hect)	Big	12.8177769	37	17.22682427
Camp 10 (100 hect)	Big	5.46875	8	7.61159536
Camp 11 (Q, 0.5 hect)	Small	13.4778816	122	18.19718724

Table 4.1A: Total amount of pacing for all the tigers

The logistic regression indicated that tigers paced less (0.47 times as much) in a big camp compared to a small camp (log odds = -0.75820, SE = 0.37203)

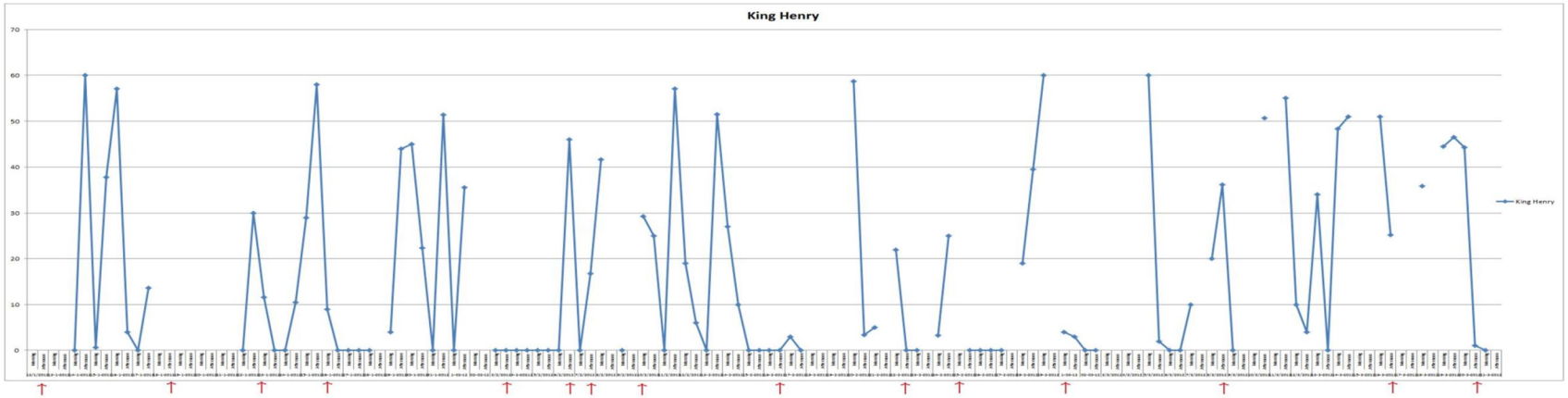
4.2 Feeding

There was an overall impression that the amount of pacing increased with time since the last feed. A significant difference was found: the longer the time since the last feed, the more a tiger paced. With every extra day since the last feed, tigers paced 1.36 times more (log odd = 0.30679 and SE = 0.04973).

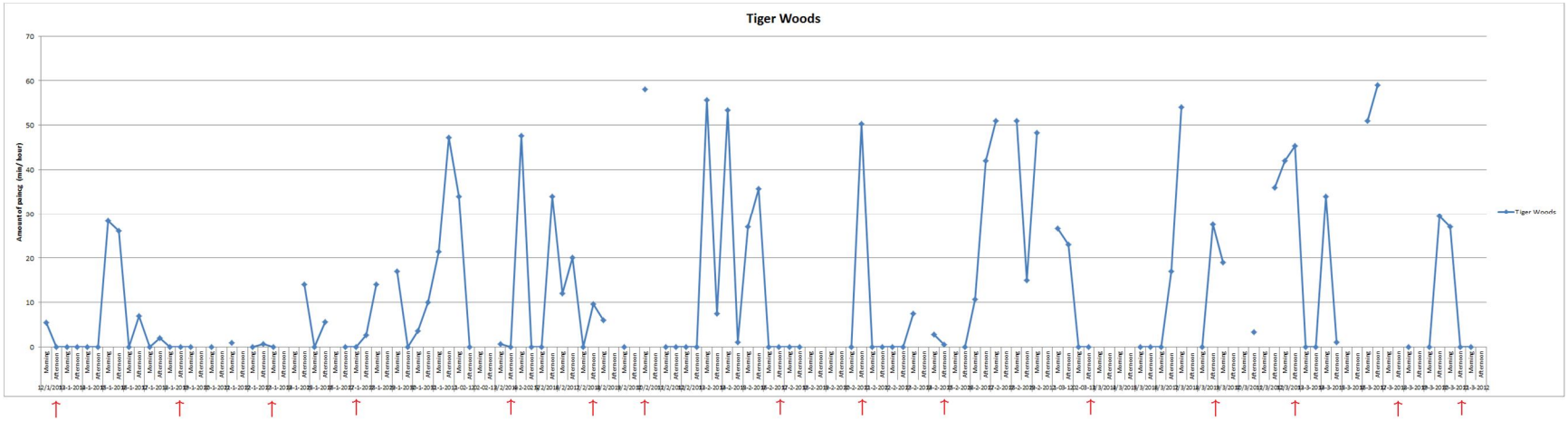


Graph 4.2A: The amount of pacing shown in relation to the days after feeding.

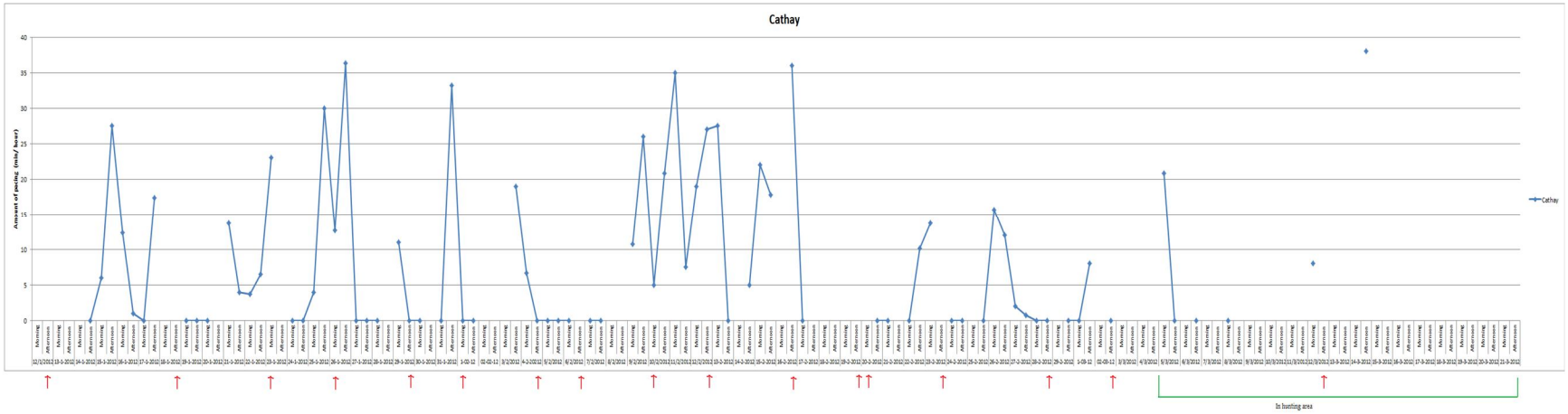
In graphs 4.2B-E the amount of pacing is plotted for each tiger. The arrows mark the times at which they were fed.



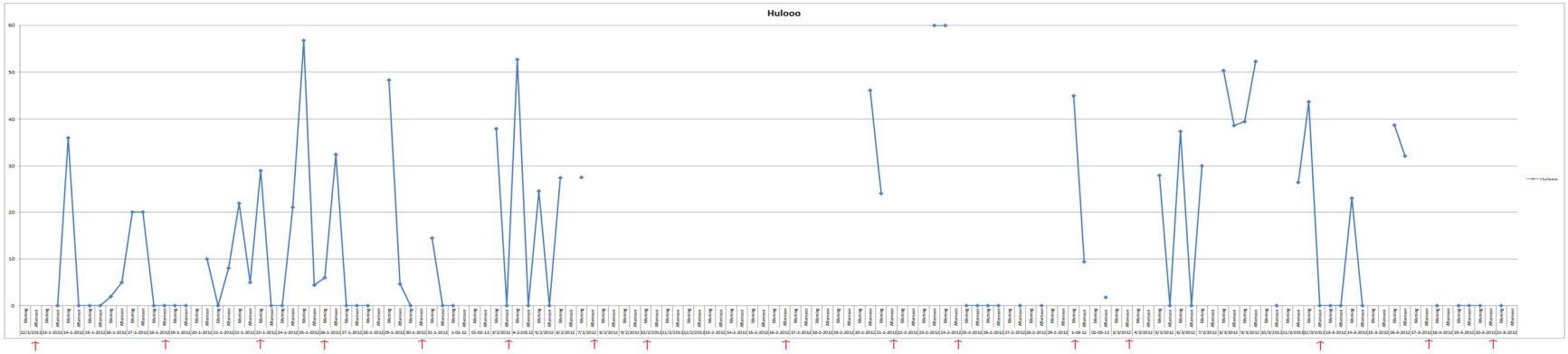
Graph 4.2B: Pacing activity of King Henry. The y-axis shows pacing per hour (in minutes), the x-axis indicates time (date). The arrows indicate the times of feeding. If no observations were performed no dots were placed on the graph.



Graph 4.2C: Pacing activity of Tiger Woods. The y-axis shows pacing per hour (in minutes), the x-axis indicates time (date). The arrows indicate the times of feeding. If no observations were performed no dots were placed on the graph.



Graph 4.2D: Pacing activity of Cathay. The y-axis shows pacing per hour (in minutes), the x-axis indicates time (date). The arrows indicate the times of feeding. If no observations were performed no dots were placed on the graph.From the 5th of Marc,h Cathay was in the 40 hectare camp, where she could hunted blesbock (green block). She was fed once, because she did not catch a blesbock for a couple of days.



Graph 4.2E: Pacing activity of Hulooo. The y-axis shows pacing per hour (in minutes), the x-axis indicates time (date). The arrows indicate the times of feeding. If no observations were performed no dots were placed on the graph.

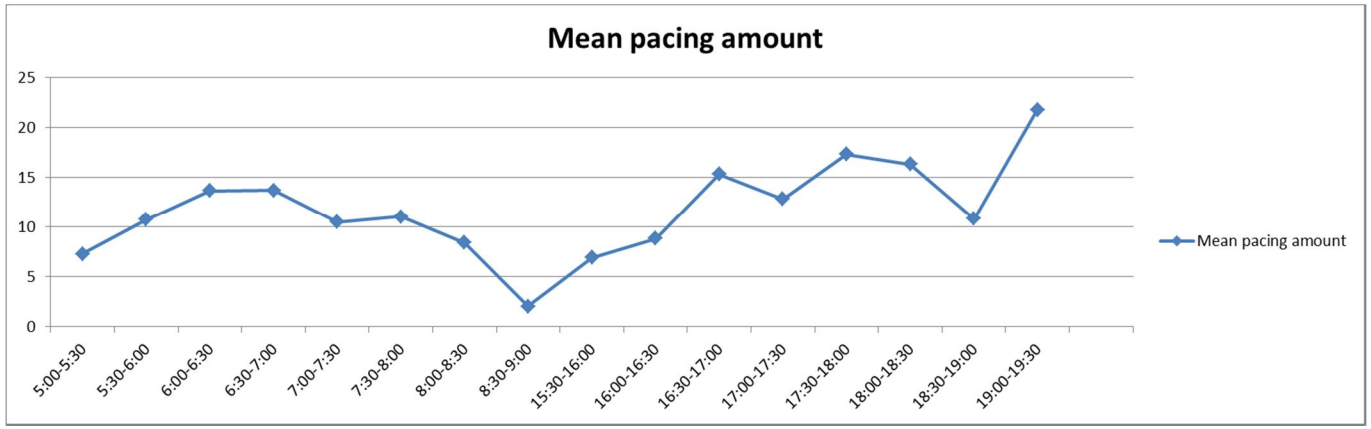
4.3 Time

Tigers paced 8.57 times more in the afternoon than in the morning (log odds = 2.14799 and SE = 0.44074).

	Mean pacing (min/ hour)	N	SD
Pacing morning:	10.98944125	417	16.91978
Pacing afternoon:	13.18306138	357	17.29822

Table 4.3A: The total amount of pacing for all tigers in the morning and the afternoon.

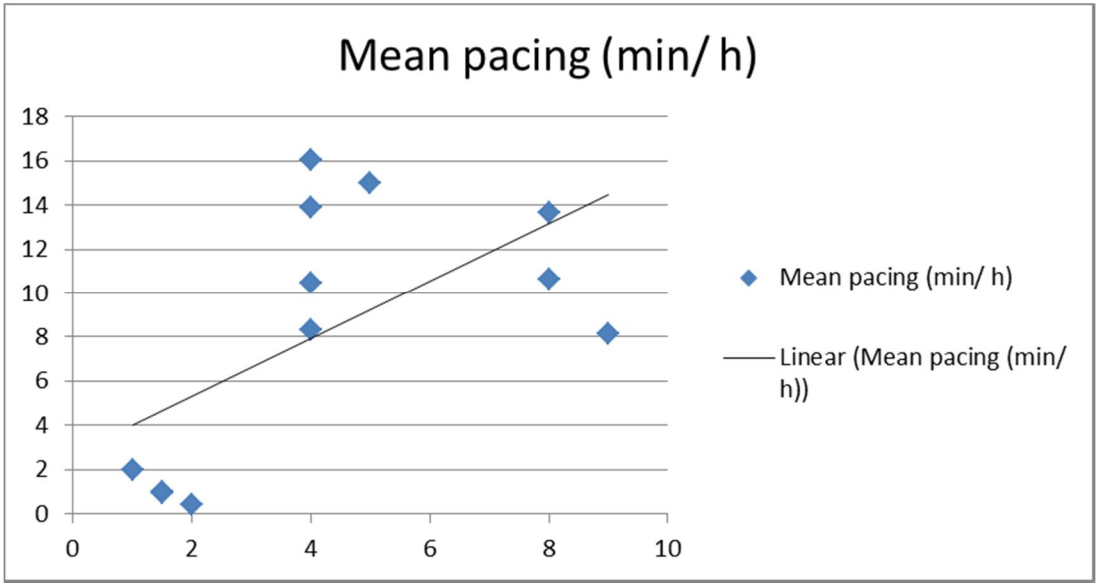
A graph was made of the amount of pacing for all tigers during the observation periods, divided into slots of half an hour.



Graph 4.3C: The mean total pacing activity by all tigers at different times during the day (min/ hour).

4.4 Age

The regression analysis indicated that adult tigers paced 8.4 times more than young tigers (log odds 2.12877 and SE = 0.49147). Huwaaa, Alpha, Beta, Xa, Yoya and Zeta were counted as young tigers. The amount of spraying was taken as an indication of whether a tiger was adult/sexually mature. Tigers start spraying during puberty and it is assumed that spraying is related to maturity.



Graph 4.4A: The mean amount of pacing (min/ hour) in relation to the age (years) of the tigers.

4.5 Temperature

The amount of pacing decreased by 9 percent for every 1 degree centigrade increase in the ambient temperature (factor 0.91). The log odds ratio was -0.09778 and the SE was 0.02266.

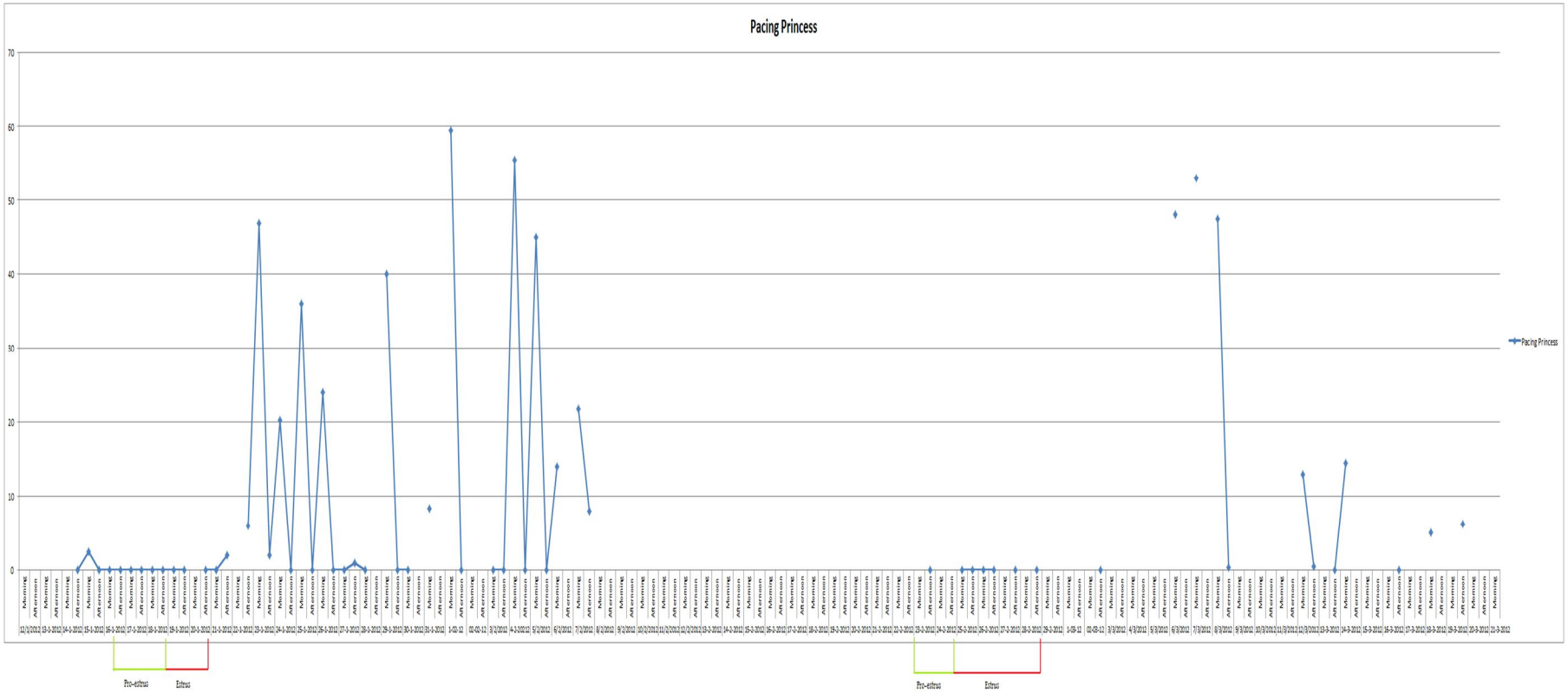
4.6 Pacing during estrus

The only tiger that was in estrus during the study period was Princess. Table 4.6A shows the amount of pacing during pro-estrus and estrus versus other stages of the cycle.

Activity	**Mean during pro-estrus**	**Standard Deviation during pro-estrus**	**n**	**Mean during estrus**	**Standard deviation during estrus**	**N**	**Mean normal**	**Standard deviation normal**	**n**	**95% confidence interval**
Pacing (min./ hour)	0	0	6	0	0	9	12.9045	19.0058	45	(7.1945, 18.614)

Table 4.6A: the amount of pacing during pro-estrus, estrus and at other stages of the reproductive cycle ('normally'). The mean amounts of pacing during pro-estrus and estrus were compared to the normal mean using a one sample T-test. A significant difference was found (P<0.05).

During estrus and pro-estrus Princess paced significantly less (0 minutes per hour), in fact she hardly paced at all during these periods. Graph 4.6A shows the amount of pacing during the study period. Observations are drawn as dots and connected with lines. If no observation was performed no dots is placed in the graph. The graph of the pacing frequency shows that pacing was markedly reduced during estrus and pro-estrus.



Graph 4.6B: This graph shows the pacing activity of Princess during the study period (12th January until 21th March). Significantly less pacing was seen during pro-estrus (green block) and estrus (red block).

4.7 Pacing to scent mark a territory

One known function of pacing by tigers is to enable them to scent mark their territory. To examine the contribution of territorial behaviour to pacing, the amount of spraying associated with pacing was compared to the amount of spraying that was not associated with pacing.

First we wanted to know if spraying was performed to scent mark the boundaries of a territory, or was indiscriminate throughout the territory. Three areas were distinguished:

1. Spraying at the fence / boundary of a territory
2. Spraying on the ground within 4 meter from the fence / boundary of a territory
3. Spraying in another place within the camp / territory

The spraying frequency of all tigers was combined and the mean spraying frequency is shown in table 4.9A.

	Mean	**Standard deviation**	**Total hours of observation**	**P-value**
Total spraying in area 1	0.750477956	2.348383739	776	0.9899 (1-2)
Total spraying in area 2	0.74936412	2.301999382	776	0.006 (1-3)
Total spraying in area 3	0.477026816	1.529164084	776	0.006 (2-3)

Table 4.7A: The mean spraying frequency of all tigers in the different areas described above. An ANOVA test indicated a significant difference in spraying within the different parts of a camp (p= 0.011). Two sample T tests were performed to examine where the differences arose. Spraying in area 3 was found to be significantly less than in either 1 or 2 (p=0.006).

An ANOVA test was performed to determine whether spraying behaviour differed in different parts of a camp. A significant difference in spraying behaviour (p= 0.011) was found between the different areas. Two sample T tests were then performed to further determine where the differences arose. This revealed that tigers spray significantly more in areas one and two: i.e. near the boundaries of their territory.

	Spraying during pacing (times/h)	SD	Spraying not during pacing (times/ hour)	SD	Total n observations
All tigers	1.395860213	3.804048958	0.703430985	2.087944397	776

Table 4.7B: The amount of spraying during pacing compared to the amount of spraying during other activities. A Two sample T test yielded a p-value of < 0.000001.

A further two sample T test was performed to determine whether the amount of that was performed in association with pacing differed to the frequency of spraying without pacing. The tigers were found to spray significantly more during pacing.

4.8 Preferred pacing sites

Lyons (2007) found that it was not the size of an enclosure that affected the amount of pacing, but the total length of boundaries/edges in the enclosure. Edges are specifically used for pacing[27]. Raised areas were also found to be preferred pacing sites, probably because they offer a good vantage point[27]. Earlier observations suggested that tigers paced predominantly along the fence, but not in the corners. In table 4.8A the mean amount of pacing for all tigers at the different areas of a camp is shown.

	Pacing total (min/h)	Pacing fence (min/h)	Pacing gate (min/h)	Pacing corner (min/h)	N observations second period
Min/ hour	9.457588559	8.343438286	0.828970575	0.05	270
Percentage (%)	100	88.21951002	8.765136794	0.528675991	

Table 4.7A: The mean pacing activity for all the tigers in minutes/ hour. The cumulative percentage for pacing site is not 100% because sometimes no pacing site was noted.

As shown in table 4.7A tigers predominantly pace along the fence / boundary. The second most popular pacing location was the gate, with only 0.5% of pacing taking place in the corners of a camp.

5. Conclusion and discussion

Pacing behaviour was influenced by:

Factor	Significant	Result
Size of the camp	✓	The bigger the camp, the less pacing was observed
Feeding	✓	Pacing increased with time since the last feed
Time	✓	More pacing in the afternoon than the morning
Age	✓	Adult tigers pace more than juveniles
Temperature	✓	The higher the temperature the less pacing observed
Pro-estrus and estrus	✓	During pro-estrus and estrus pacing is reduced (n=1)
Scent marking	✓	Tigers pace to scent mark their territory
Place	✓	Tigers pace predominantly along the fences

Table 5A: Factors influencing pacing in the South China tiger (P.t.amoyensis).

5.1 Size of the camp

There was a significant influence of camp size on pacing behaviour. Tigers pace significant less in a larger camp. In a large camp, tigers can behave more naturally and, in some of the big camps (the 40 and both 100 hectare camps), natural prey are present, which also allows them to hunt for their own food. This allows tigers to influence their feeding activity and perform foraging behaviour: as a result less stereotypic behaviour is seen as displacement activity while waiting for the next feed.

There is some discussion about the size of the camps that a captive tiger requires. Baldwin (1991), Lyons (1997) and Pitsko (2003) found that tigers in zoos rest for approximately 75% of the day and use only one-third of available space [24]. This study is used to suggest that tigers do not need much space. By contrast, Moreira (2007) investigated the pacing behaviour of two Sumatran tigers[21] and found that they paced more in small than in a larger enclosure[21]. In the current study, a similar relationship was found even though the mean enclosure spaces were considerably larger than the small exhibition spaces examined by Moreira. While a larger enclosure seems to be preferable to reduce pacing behaviour, it is not yet clear whether there is an optimal or minimum requirement.

5.2 Feeding

In the literature, there is some discussion about the influence of feeding on pacing activity. Shepherdson et al. (1993) found that increasing the frequency of feeding of small felids increased the behavioural diversity and exploratory behaviour and reduced the duration and frequency of stereotypic behaviour[21]. Lyons (2007) found that captive felids fed on a 3-day cycle paced more on the days that they were fasted then on the days that they were fed[27]. Six out of seven of these tigers paced more in the hours after feeding[27]. The tigers that were fed daily, paced more in the hour before feeding[27].

In the current study, we observed an increase in pacing behaviour with increasing time since the last feed. Pacing activity increase by a factor of 1.36 for every additional day since the last feed. This presumably reflects frustration or displacement activity as a result of the inability to influence their own feeding activity. The pacing may represent a means of coping with this stress.

5.3 Time

The South China tigers paced more in the afternoon than in the morning (by a factor of 8.57 times per hour). This might be explained by the fact that some of the tigers (Cathay and KH) were always fed after the afternoon observation, and have started to pace in anticipation. Alternatively, it may represent an overall increase in activity in the afternoon.

5.4 Age

Adult tigers paced more than young tigers. As shown in graph 4.4A, the amount of pacing increased with the age of the tiger. Tigers learn pacing behaviour from their mother. However, pacing behaviour is an element of scent marking and territorial behaviour and, therefore, increases after puberty / sexual maturity.

5.5 Temperature

Ambient temperature was negatively correlated with pacing. The higher the temperature, the less pacing was observed. It is assumed that tigers rest during the hotter parts of the day.

5.6 Pacing during estrus

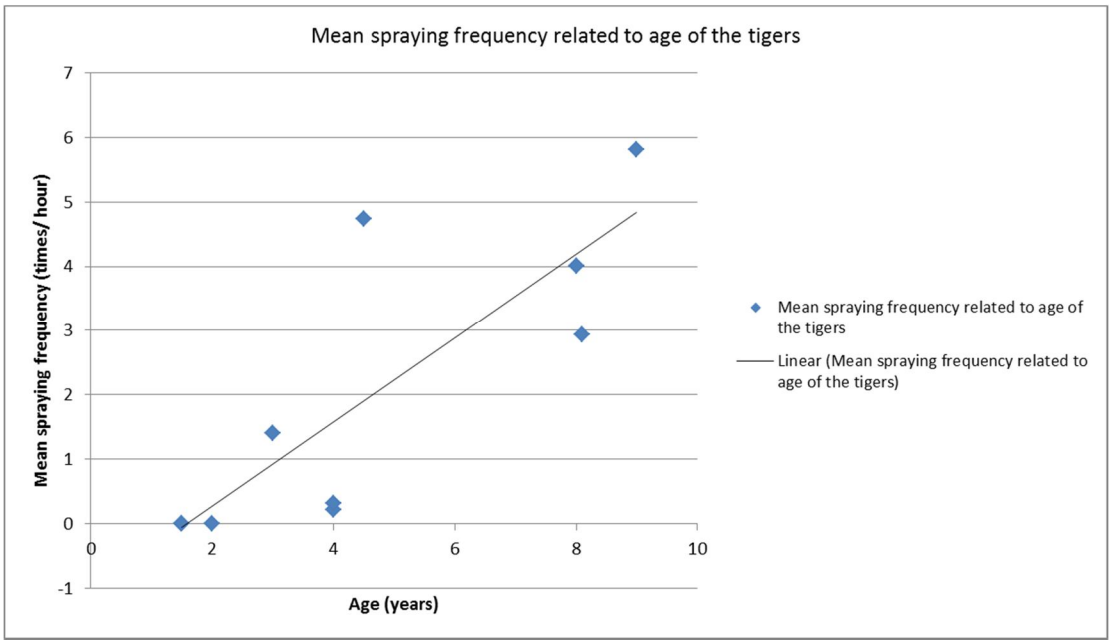
For the Laohu Valley breeding programme, it is important to develop tools to help recognize when female tigers are in estrus. The reported behavioural signs of estrus in tigers include rolling, rubbing, lordosis[11], vocalization[13,15], pacing[13] and purring[11]. However, Princess was found to pacing significant less, or hardly at all, during estrus. Because these observations were based on only one tiger,however, it cannot be assumed that the same applies to all female tigers. Previous observations of another tigress in the reserve (Cathay) found that she rested 36% less during pro-estrus and paced 42% more[23]. However during estrus, Cathay also rested more (60%) and showed much less pacing activity (a 72% reduction)[23].

During the observation period, Princess had a social partner since she shared a camp with Hulooo. One possible explanation for the reduced pacing activity during pro-estrus and estrus was that during these periods she was more focussed on consorting with Hulooo. Outside the sexually receptive periods Princess often paces alongside her mother, Madonna. This may be a response to the restricted physical access[24]. During estrus, Princesses focus may switch from concentrating on social access to a closely enclosed relative to reproductive behaviour.

5.7 Pacing to scent mark a territory

Tigers spray most at the boundaries of their territories. They also spray predominantly during pacing and much less frequently during other activities. It can be concluded that tigers use pacing to assist the scent marking of their territory.

Spraying frequency is also influenced by tiger age. Young tigers don’t spray, and spraying generally starts after puberty. Graph 5.7A depicts the relationship between spraying and age. It is assumed that the frequency of spraying is primarily a function of sexual maturity in tigers.



Graph 5.7A: The mean frequency of spraying as a function of tiger age. A regression analysis yielded an R^2 of 0.68 and a *p-value of 0.0034.*

A regression analysis indicated a significant correlation between tiger age and the frequency of spraying ($R^2 = 0.68$; $p = 0.0034$). It is assumed that tigers start spraying when they reach sexual maturity. In the current study, spraying appeared to be predominantly an activity of animals above 4 years of age.

5.8 Pacing preference sites

As shown in table 4.7A, tigers mostly pace along the fences i.e. boundaries of a territory. This is similar to Lyons (2008) observation that tigers predominantly pace along the edges of an enclosure, although in this case it refers to much larger enclosures.

5.9 Overall conclusion

The overall conclusions that can be drawn from the current study is that if you want to decrease the amount of pacing amount of South China tigers in a reserve or a zoo, it is preferable to make the camps or enclosures as large as possible, and to either feed them frequently or allow them to hunt for their own food. Young, sexually immature tigers will pace less and tigers will pace less in a warmer environment.. Other studies indicate that it isn't advisable to get tigers accustomed to being fed by people or, in any case, aware that people are providing their feed. It is preferable if the tigers are out of site when the feed is placed, for example within a shelter. If this is not possible, it is preferable that the same person always feeds the tigers to prevent them showing pacing behaviour in anticipation of feeding to people in general.

It is also important to appreciate that pacing is a normal element of a tigers' territorial behaviour, often accompanied by scent marking. Making visitors more aware of this natural side to such behaviour can help to destigmatize it. Minimize human activity in and around a camp can also help to reduce pacing, while moving tigers to new camps

also increases exploratory behaviour and decreases pacing behaviour caused by boredom, although it may result in increased pacing to scent mark their new territory.

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Appendix A

Used ethogram; designed by E.M.E. Groot[23]

Ethogram: Captive Tiger Behavior

Observer:		Tiger:		Date:		Arrive morning:		Departure:	
General Information and Circumstances during Observation						Arrive afternoon:		Departure:	
						Arrive evening:		Departure:	

	Camp	Cloud (8)	Wind(11)	Temp. (°C)	Rainfallen (mm)	Other tigers same camp	Tigers in adjacent camps	Amount of prey in camp	Human influences
Morning									
Afternoon									
Evening									

Ethogram

1. Exploring/hunting behavior																											
Alert																											
Smell																											
Chew / lick / claw object																											
Dig																											
Walk																											
Stalk																											
Slow chase																											
Fast chase																											
Change prey																											
Catch																											
Kill																											
Swim																											
Jump																											

2. Resting/common behavior																											
Rest on belly																											
Rest on side																											
Rest on back																											
Roll over																											
Lay in water																											
Stretch																											
Yawn																											

Grooming																											
Sit																											
Stand																											

3. Homeostatic-related behavior																											
Drink																											
Eating grass																											
Eating food																											
Plucking food																											
Defecate																											
Urinate																											

4. Communication behavior																											
Body scratch against object																											
Head rub object																											
Head rub tiger																											
Scraping ground																											
Scratching object																											
Spraying																											
Vocalization																											
Chuffing																											
Prusten																											
Snarl																											
Growl																											
Roar																											
Play																											
Play-fight																											
Fight																											
Flee																											

5. Mating behavior																											
Flehmen																											
Investigate																											
Seduction (f)																											
Mount (m)																											
Be mount (f)																											
Mate																											

6. Parental behavior																											
Dragging																											

nest / den-material																												
Feeding cubs																												
Grooming cubs																												
Move cubs																												
Ignore cubs																												
Snarling at cubs																												
Kill cubs																												

7. Stereotype or other behavior																												
Pacing																												
Lethargic																												
Cannot see																												

Happenings information

Start	End	Whom involved	Description of happening

Appendix B

Used behavioural descriptions: designed by E.M.E. de Groot[23].

Behavioural descriptions	
Alert	Individual is being watchful for possible danger or being prepared for action. Lifting up of the head, eyes focused on subject of intention and head turned that way. Usually interrupting the performed activity at that moment.
Smell	Investigating object/ ground/ air by sniffing it.
Chew/ lick/ claw object	Investigating object by chewing, licking or clawing it. Holding it in mouth can also be observed.
Dig	Digging the ground with the front paws
Walk	Directional moving from one place to another.
Stalk	Moving, slightly crouching, towards individual. Holding crouched position can be part of the stalk. Intention can be serious hunting or playful. If observed, note circumstances as 'happening' and the individual being stalked.
Slow chase	Decreasing distance towards individual at draff. Intention can be serious hunting or playful. If observed, note circumstances of situation as 'happening' and/or the individual being chased.
Fast chase	Decreasing distance towards individual at gallop. Intention can be serious hunting or playful. If observed, note circumstances of situation as 'happening' and/or the individual being chased.
Change prey	Changing from one prey to another during stalk or chase.
Catch	(Attempt to) catch individual or object, sometimes followed by holding it in its grasp. Intention can be serious hunting or playful. If observed, note circumstances of situation as 'happening' and/or the individual or object being caught.
Kill	Bite and subsequent killing of individual.
Swim	Moving around in deep water.
Jump	This can be noted as jumping in the air, or onto something/someone. Standing upright to object is also noted as 'jump'.
Rest on belly	Eyes are closed or open, ears and head are sometimes moved. Hind legs can be underneath the body or laying flat, front legs are underneath the body.
Rest on side	Eyes are closed or open, ears and head are sometimes moved. Laying on lateral side, both hind and front legs on lateral side, shoulder touches the ground.
Rest on back	Eyes are closed or open, ears and head are sometimes moved towards objects of attention. Laying on dorsal side. Cranial part of the body is sometimes in a more lateral position.
Roll over	Rolling over dorsal side, from one lateral side to the other lateral side.
Lay in water	Laying in the water, not moving around.
Stretch	Stretching its legs and neck.
Yawn	-
Grooming	Licking or scratching of own body, more than 3 times (not a simple reaction to flies).
Sit	Caudal part of the body touches the ground. Hind legs are bend is sitting position, front legs stretched under torso, not bend.
Stand	Not to confuse with temporary interruption of activity due to an 'alert'.
Drink	-
Eating grass	-
Eating food	-
Plucking food	Removing the hairs/feather/skin of food without really eating.
Defecate	-
Urinate	Not to confuse with spraying
Bodyscratch	Rubbing the body against an object.

against object	
Headrub object	Rubbing the head against an object.
Headrub tiger	Rubbing the head against another tiger. Note to which tiger this gesture is done.
Scraping ground	Scraping the ground with the hind feet.
Scratching object	Repeated clawing of object with both front paws. Scratching the nails over it.
Spraying	Not to confuse with urinating.
Vocalization	A soft friendly sound, mouth barely opened (huh-huh). Can be short, but also a long moaning sound.
Chuffing	A soft friendly sound, sounding nasal, but is actually created in the throat (thrtrtrtr). Note to which individual this gesture is done.
Prusten	A soft friendly sound, created in the nose, sort sneeze, sounds very alike chuffing (gththt). Note to which individual this gesture is done.
Snarl	Threatening hissing sound (hsss) or vocal bite. If observed, note circumstances of situation as 'happening' and/or the individual who is snarled at.
Growl	Soft threatening rumbling sound, created in throat (grrrr). If observed, note circumstances of situations as 'happening' and/or the individual who is being growled at.
Roar	Loud threatening rumbling sound, created in throat (graurgr). If observed, note circumstances of situation as 'happening' and/or the individual who is being roared at.
Play	Can be with object or other tiger or on its own. If observed, note circumstances of situation as 'happening' and/or individual who is played with.
Play-fight	Biting and/or clawing softly, without damaging each other. If observed, note circumstances of situation as 'happening' and/or individual who is interacted with.
Fight	Biting and/or clawing ferocious, possibly damaging each other. If observed, note circumstances of situation as 'happening' and/or the individual fought with.
Flee	Increasing distance between itself and object of fear, backing off or showing submission (ears flat, body in low position and occasionally looking behind).
Flehmen	Opening the mouth, lips raised, to take in pheromones. Small part of the tongue is usually hanging out of the mouth.
Investigate	Male sniffs underneath the tail of the female. Or the female is being investigated by the male.
Seduction (f)	Female rolls over on back and shows herself to the male, inviting him.
Mount (m)	Male mounts the female to mate.
Be mount (f)	Female being mounted by the male to mate.
Mate	Accepting mounting and subsequent mating. Characterized by the male biting the neck of the female, moaning and roaring, and the female growling.
Dragging nest/ den-material	Dragging materials to make a den or nest to give birth in.
Feeding	Bringing food to the cubs.

cubs	
Grooming cubs	Licking the cub. If observed, note circumstances of situation as 'happening' and/or the cub being groomed.
Move cubs	Moving cubs (in mouth or walking along) towards other place. If observed, note circumstances of situation as 'happening' and/or cub being moved.
Ignore cubs	No interest in cubs, and ignoring their attempts for attention. If observed, note circumstances of situation as 'happening' and/or the cub being ignored.
Snarling at cubs	Snarling at the cubs. If observed, note circumstances of situation as 'happening' and/or the cub being snarled at.
Kill cubs	Bite and subsequent killing of cubs. If observed, note circumstances of situation as 'happening' and/or the cub being killed.
Pacing	Walking up and down same path continuously, intention less.
Lethargic	No reaction on surrounding stimuli, only to pain stimuli.
Cannot see	Tiger is out of vision of the observer.

Appendix C

Tiger	Date	Time	Pacing where	Pacing (1/2 min/ uur)	Pacing together with:	Proximity = within 4 meter	Can not see (1/2 min/ hour)
			Fence				
Temperature (Celsius)	Rain fallen	Wind (1/11)	Gate				Sleeping/ resting (1/2 min/ hour)
			Corner				
Clouds (1/8)			Spraying where	Spraying times	Spraying during pacing	Spraying times:	Other (1/2 min/ hour)
			1 (fence)		Pacing		
Camp (big >1 h/ small)	Together in a camp with:	When fed	2 (4 meter)		Non pacing		Playing (1/2 min/ hour)
			3 (rest)				

Appendix D

Number and Description	Features	Air Speed (km / h)
0 calm	smoke rises vertically; water smooth	0–2
1 light air	smoke shows wind direction; water ruffled	2–5
2 light breeze	leaves rustle; wind felt on face	6–11
3 gentle breeze	loose paper blows around	12–19
4 moderate breeze	branches sway	20–29
5 fresh breeze	small trees sway, leaves blown off	30–39
6 strong breeze	whistling in phone wires; sea spray from waves	40–50
7 near gale	large trees sway	51–61
8 gale	twigs break from trees	62–74
9 strong gale	branches break from trees	75–87
10 storm	trees uprooted; weak buildings collapse	88–101
11 violent storm	widespread damage	102–117
12 hurricane	widespread structural damage	above 118

Source: Laohu Valley Reserve