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Evidence-based practice

Behaviour change in Amur tigers *Panthera tigris altaica* after an enclosure move

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Abstract

It can be challenging for zoological collections to provide captive animals with a habitat that meets all of their needs. The study of enclosures is therefore of paramount importance, with evaluation ensuring animals are housed in enclosures that meet the necessary welfare standards and provide adequate levels of enrichment. Here, the behaviour of socially housed Amur tigers *Panthera tigris altaica* was studied before and after a move into a large, novel and topographically diverse enclosure to assess the impact of the enclosure change. Significant differences in behaviour were observed, in particular a decrease in frequency of locomotion but an increase in diversity of locomotion, alongside an increase in resting and a decrease in stereotypical pacing. These results indicate moving to a more complex enclosure with more environmental enrichment has positive implications for tiger welfare in captivity.

Background

There are countless challenges when attempting to recreate natural habitat for many species in captivity, so appropriate environmental enrichment and enclosure design is crucial for providing a high welfare environment (Morgan and Tromborg 2007; Young 2013). Enclosures must provide for social and behavioural needs; being sufficient in both space and complexity to provide inhabitants with the challenges they would navigate whilst in the wild (Wilson 1982; Mellen 1991). A complex enclosure can aid in the exhibition of natural behaviours as well as increase exploratory behaviours, therefore complexity is often thought to be more important than size (Wilson 1982; Mellen 1991; Pitsko 2003; Biolatti et al. 2016). Consequences of failing to provide suitably large and complex enclosures can have undesirable effects resulting in exhibition of stress-related responses including increases in stereotypic behaviours, such as pacing, overgrooming and periods of prolonged inactivity (Clubb and Mason 2007; Morgan and Tromborg 2007; McPhee and Carlstead 2010).

It is particularly challenging to provide tigers *Panthera tigris* with a sufficient captive environment, given the extreme differences in their wild habitat and the captive provision the majority of zoological collections are realistically able to provide (Biolatti et al. 2016). Tigers have huge home ranges and, as with many carnivore species, hunting, eating and territorial behaviours take up much of their activity budget (Shepherdson et al. 1993; Lyons et al. 1997; Clubb and Mason 2007). As a result, significant research has focused on enrichment devices and techniques to promote a diversity of these behaviours in captivity and to reduce stereotypical behaviours often associated with tigers, such as pacing (Clubb and Mason 2007; Szokalski et al. 2012). The drivers of pacing have been widely hypothesised: from frustration linked to a lack of the appetitive phase of hunting, to restriction of natural ranging and related behaviours (Clubb and Mason 2007). Exhibition in abnormal social groups without enough space or environmental enrichment may also induce pacing (Mason et al. 2007; Szokalski et al. 2012), although in contrast other research has found housing captive tigers with conspecifics reduced cortisol levels and stereotypic behaviours and led to the display of a wider diversity of natural behaviours than in solitary housed counterparts (Pitsko 2003; Narayan et al. 2017; Vaz et al. 2017).

This study focuses on the effect of an enclosure move on the behaviour of a pair of socially housed female Amur tigers *Panthera tigris altaica*. The pair were moved from a small, simple enclosure to a large, complex enclosure in an attempt to improve their welfare and encourage the exhibition of more diverse behavioural repertoire. Alterations to enclosures can be viewed as a form of enrichment (Szokalski et al. 2012), but effective evaluation of changes to captive environments such as the present study allow thorough assessment of success and help inform future practice. Therefore, this study aimed to assess the impact of the enclosure move on the behaviour of the two Amur tigers by recording behaviour before and after the move, identifying changes and their specific drivers.

Action

Study subjects

Two female Amur tigers housed at Knowsley Safari (Merseyside, UK) were the focal individuals in this study, henceforth referred to as ‘the tigers’. Siblings from the same litter, they were born on 1 April 2008 at Port Lympne Wild Animal Park and arrived at Knowsley Safari on 25 November 2009.

Study site

Both enclosures referred to throughout were situated at Knowsley Safari, a large privately-owned zoological collection in Merseyside, UK.

Enclosure A

Enclosure A (Figure 1) was located within the safari drive. Cars passed by one side of the enclosure on a road on the outside of a chain link fence. The enclosure consisted of a 20 m^2 house with a wooden floor and a small outdoor flat grass paddock (2,850 m^2), which was often a quagmire due to poor drainage. Vegetative cover was limited to a small stand of birch *Betula pendula* and scattered bushes. Other features included a felled tree and a three-sided outdoor shelter. The water sources were two drinking troughs, and a feeding hatch was built into the fence. The tigers had views of the following species: African lions *Panthera leo*, capybara *Hydrochoerus hydrochaeris*, vicuña *Vicugna vicugna*, Bactrian camel *Camelus bactrianus*, Père David deer *Elaphurus davidianus*, eastern kiang *Equus kiang* and fallow deer *Dama dama*. An outdoor paintballing centre was located approximately 50 m from the enclosure, out of the line of vision but within hearing range. The tigers were housed in this enclosure from their arrival at Knowsley Safari (25 November 2009) until the move (16 April 2018).

Enclosure B

The tigers moved into Enclosure B (Figure 2) on 16 April 2018. Located in a zoo setting, visitors pass by on foot on all sides of the enclosure outside of a mixed materials fence line (chain link, glass etc.). The enclosure consisted of a house made up five pens (3×13 m^2 and 2×35 m^2) with a 2-m deep sand substrate floor and a 10,000 m^2 outdoor paddock which can be split into two. There was extensive vegetative cover, with scattered bushes, long grass and large oak *Quercus* sp., sycamore *Acer pseudoplatanus* and birch trees throughout. Other features included boulders, felled trees, large mounds and channels. Extensive water sources were

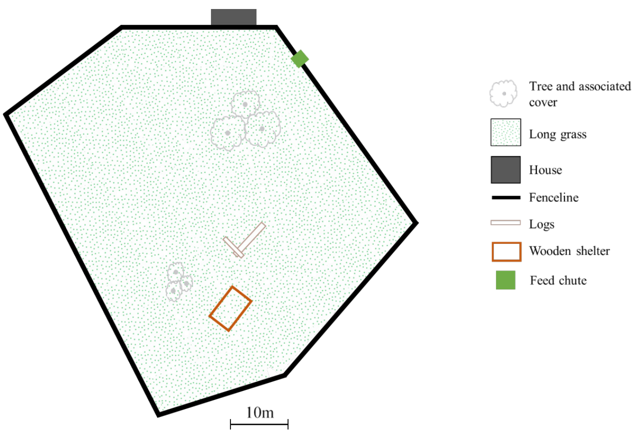

Figure 1. Schematic of Enclosure A with various features defined in the key.

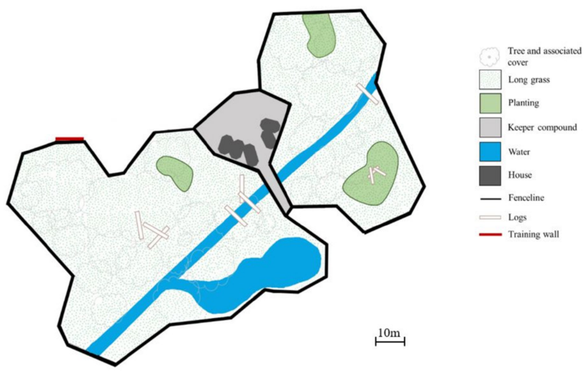

Figure 2. Schematic of Enclosure B with various features defined in a key.

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available including self-filling troughs and an outdoor flowing pool fed by a large stream. There was no feeding hatch, but a training wall was present. Additional visitor infrastructure was in place around the enclosure in sight and sound of the tigers, for example signage, outdoor classrooms and speakers. The tigers had views of giraffes *Giraffa camelopardalis rothschildi.*

Tiger behaviour

The ethogram used (Table 1) was developed from initial observations of the tigers alongside existing literature (Stanton et al. 2015). Behaviours were recorded using continuous focal sampling (Martin and Bateson 2007). The two tigers could be individually identified through differences in stripe pattern.

Table 1. Ethogram of captive tiger behaviour observed in the study. Derived from Stanton et al. (2015).

Category	Behaviour name	Behaviour definition	initial
Foraging	Grass consumption	Tiger ingests grass	GR
	Consumption	Tiger consumes food	C
	Drink	Tiger ingests water	DR
Other	Dig	Tiger uses forepaws to move dirt	DG
	Destroy	Tiger uses paws to destroy inanimate object	D
	Yawn	Behaviour which signals a change in alertness, opens mouth sticks out tongue pulls back lips and inhales	Y
	Sniff	Tiger pushes nose against object and inhales rapidly	SN
	Tail twitch	Tiger’s tail moves back/forth in a jerky manner	TT
	Stretch	Tiger contracts and relaxes muscles with hind quarters in the air with front legs stretched out	STR
	Arch	Tiger’s back arches into air with all feet on the ground	A
	Scuff	Tiger pushes dirt away with hind paws	SC
	Startle	Tiger jumps or flinches in response to event	STA
	Toss	Tiger uses forepaws to throw object into air	T
	Fence test	Tiger pushes nose towards electric wire as if to sniff then pulls head away without being shocked	FT
	Lick lips	Tiger runs tongue over lips and nose	LL
	Other	Tiger exhibits unspecified behaviour	O
Rest	Rest	Tiger lies on stomach/side/back	RT
	Sit	Tiger’s hindquarters are on the ground but forelimbs are not	SI
	Immersion	Tiger rests in water but does not swim	I
	Crouch	Tiger lies down on stomach with all 4 paws on the ground so tiger can stand quickly	CR
Maintenance	Grooming	Tiger runs tongue over paws/fur to remove dirt	G
	Fur shake	Tiger shakes fur to remove water/dirt	SH
	Paw shake	Tiger shakes paw to remove dirt	PS
	Excretion	Tiger defecates or urinates (in squatting position or when walking)	M
	Fight	Aggressive action of physical combat which lasts over 5 sec	FHT
	Claw	Tiger rakes over an object repeatedly with claws	CL
	Chuff	Vocalisation (low huffing noise)	CF
	Hiss	Tiger pulls back lips scrunches nose and bares teeth whilst hissing	H
	Cheek mark	Tiger marks object/ landmark with cheek glands	CM
	Scent mark	Tiger marks object with spray	SM
	Nuzzle	Tiger rubs face against other tiger	N
	Flehmen response	Tiger tastes urine of other tiger and peels lips back across teeth	FLM
	Bat	Tiger taps another tiger with paws (no claws)	BT
	Rar	Vocalisation not full roar	RA
	Roar	Loud vocalisation	RR
	Submit	Tiger submits to another tiger by rolling on back and displaying stomach	SB
	Defensive crouch	Tiger’s ears are flat against head legs tucked under body with head low towards ground teeth bared against threat	CRD

Table 1 (continued). Ethogram of captive tiger behaviour observed in the study. Derived from Stanton et al. (2015).

Category	Behaviour name	Behaviour definition	initial
Locomotion	Walk	Slow movements forward	W
	Stalk	Low to the ground creeping but not crawling	ST
	Climb	Movement up a tree or tall object	CLB
	Crawl	Low movement with stomach on the ground	CRL
	Run	Quick movements forward	R
	Backwards movement	Movement out of an area slowly hindquarters first	BA
	Carry	Tiger holds inanimate object in mouth and transports it to different area	CAR
	Chase	Pursuing of another object	CH
	Leap up	Tiger jumps to higher level	LU
	Leap down	Tiger jumps to lower level	L
	Leap	Tiger leaps forward over gap but remains at the same height level	LD
	Trot	Tiger moves forward at quick pace but not full run	TRT
	Swim	Tiger moves through water	SW
	Rear	Tiger rears up on hind legs	RE
	Pounce	Tiger jumps and lands on object holding it down with front paws	PO
Out of sight	In house	Tiger is not visible but is in house	IH
	Time out	Tiger is not visible but outside of house	TO
Vigilance	Vigilance	Tiger has head up with ears facing same way as eyes focused on an object	V
Pacing	Pacing	Tiger moves back and forth across short area in stereotypic fashion	P

One tiger was identified, and the frequency and duration of all behaviours observed in a 10-min period was recorded. This protocol was repeated for the second tiger, and then observations were alternated between tigers for an hours' worth of data collection at a randomised hour each day. Eleven days were randomly selected over a 2-month period between December 2017 and February 2018 in Enclosure A, and the same in Enclosure B between June and July 2018. The tigers were given a 1-month settling in period in Enclosure B before data collection started to reduce the recording of novelty effects or neophobia (Little and Sommer 2002). Once recorded, observed behaviours were grouped into the following categories: foraging, other, rest, maintenance, social interaction, locomotion, out of sight, vigilance and pacing (Table 1).

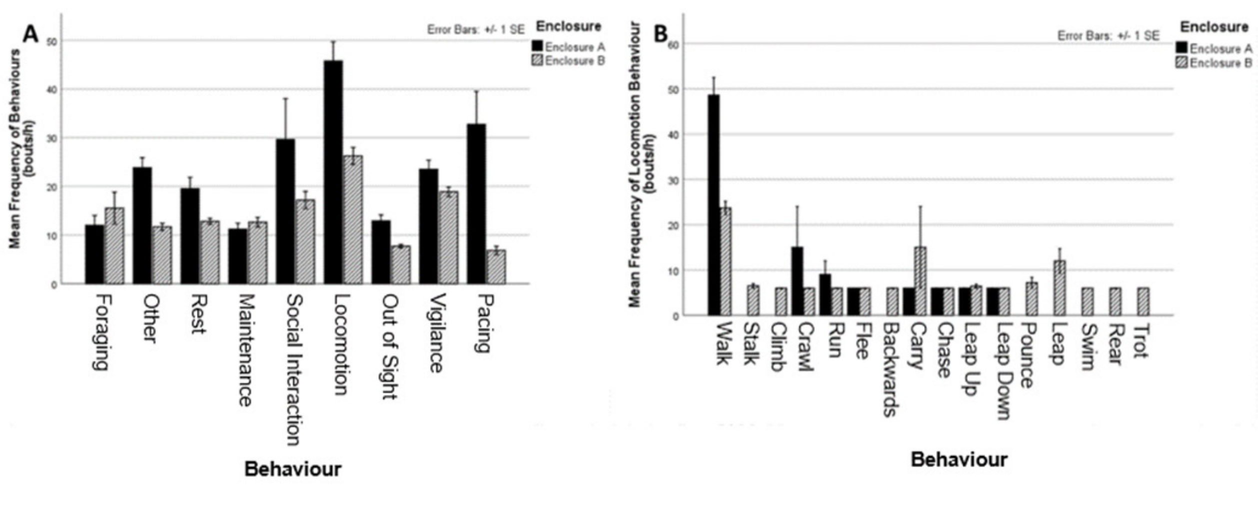

Figure 3. (A) Mean (±SE) frequency of behaviour (bouts/hr) and (B) Mean (±SE) frequency of locomotion behaviour (bouts/hr) of tigers in Enclosure A and Enclosure B at Knowsley Safari.

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Table 2. Results of generalised linear model (GLM) for changes in frequency and duration of behaviour, after relocation from Enclosure A into Enclosure B.

	Mean (±SE) frequency of behaviour (bouts/hr)			Mean (±SE) duration of behaviour (sec)		
Behaviour	Enclosure A	Enclosure B	P-value	Enclosure A	Enclosure B	P-value
Foraging	12 (2.22)	15.54 (2.04)	0.238	31.93 (9.488)	184.14 (29.15)	<0.001
Other	83.82 (1.5)	11.7 (1.5)	<0.001	55.05 (6.86)	11.38 (1.66)	<0.001
Rest	19.56 (1.74)	12.84 (1.74)	<0.001	211.36 (24.28)	356.13 (16.67)	<0.001
Maintenance	11.22 (1.5)	12.66 (1.5)	0.433	55.50 (10.16)	80.98 (9.16)	0.062
Social interaction	29.64 (2.34)	17.16 (2.34)	<0.001	33.03 (6.56)	33.06 (4.64)	0.997
Locomotion	45.72 (1.98)	26.28 (1.98)	<0.001	284.48 (22.81)	217.84 (14.04)	0.013
Out of sight	12.9 (0.84)	7.74 (0.84)	<0.001	354.67 (21.22)	401.92 (21.71)	0.120
Vigilance	23.52 (1.38)	18.9 (1.38)	0.005	81.64 (8.70)	139.03 (9.14)	<0.001
Pacing	32.7 (4.2)	6.84 (4.2)	<0.001	274.65 (55.65)	176.00 (49.69)	0.187

Additional data
Alongside tiger behaviour, in each data collection period date, time, visitor presence (estimated as low, medium or high), temperature (°C) and feed day (yes or no) were also recorded.

Data analysis
Data were analysed in IBM SPSS Statistics Version 24 (2018). Generalised linear models (GLM) were run to determine if differences were present in the frequency and duration of behaviours after the enclosure move. The Tweedie distribution with an identity link function was used to analyse duration as it exhibited a bimodal distribution. A Poisson regression model was used to determine if there were differences in the frequency of behavioural bouts after enclosure move. The results were then plotted in order to provide the best interpretation.

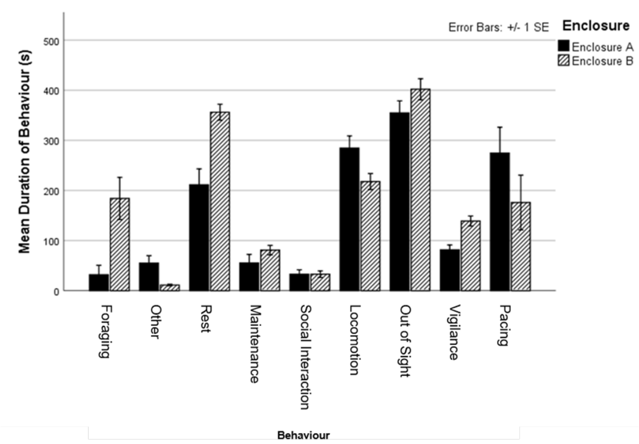

Figure 4. Mean (±SE) duration (sec) of behaviour of tigers in Enclosure A and Enclosure B during behavioural observations at Knowsley Safari.

Consequences

Frequency
In Enclosure A the most frequent behaviours recorded on average per hour of observation (bouts/hr) were, in descending order, locomotion, vigilance, other and out of sight, whereas in Enclosure B they were locomotion, vigilance, social interaction and foraging (Figure 3A). Differences were observed in the frequency of tiger behaviour between enclosure A and B ($X^2(17) = 698.54$, $p<0.001$). Resting, social interaction, locomotion, out of sight, vigilance, pacing and other behaviours significantly decreased (Table 2). The frequency of foraging behaviours did not change between enclosures (Table 2). Although locomotion significantly decreased in frequency (Table 2, Figure 3A), a much wider repertoire of behaviours that could be categorised as locomotion were observed. In total, eight novel locomotion behaviours were recorded in Enclosure B (Figure 3B).

Duration
In Enclosure A, behaviours with the longest duration were, in descending order, out of sight, locomotion, pacing and rest, whereas in Enclosure B they were out of sight, rest, locomotion and foraging (Figure 5). Duration of exhibited behaviours changed between Enclosures A and B ($X^2(17) = 1675.20$, $p<0.001$). The duration of foraging, vigilance and resting significantly increased (Table 2), whereas the duration of other and locomotion significantly decreased (Table 2). The duration of social interaction, out of sight, maintenance and pacing did not differ significantly in any case (Table 2). Overall the observed alterations to the behavioural repetorie of the tigers were largely attributed to features of the new enclosure

Complexity
Enclosure B was designed to be high welfare, practical, easy to manage housing for captive Amur tigers whilst providing a large, complex, stimulating habitat with a variety of topographical features. Locomotion, enclosure size and enclosure complexity are inextricably linked to stereotypical behaviour in big cats (Morgan and Tromborg 2007; Mohapatra et al. 2014; Biolatti et al. 2016). Tigers exhibited in smaller more basic enclosures will exhibit more stereotypic behaviours, such as pacing (De Rouck et al. 2005; Morgan and Tromborg 2007; Breton and Barrot 2014; Mohapatra and Panda 2014).

Less pacing and a greater variety of locomotive behaviours were observed in Enclosure B, with eight novel locomotive behaviours including stalking, climbing, moving backwards, pouncing, swimming, rearing, leaping and trotting recorded. The complexity and size of Enclosure B allowed for the exhibition of these natural behaviours (Lyons et al. 1997; Pitsko 2003; Biolatti et al. 2016). Features such as large trees and felled logs facilitated climbing. Increased cover and more prey availability from naturally occurring fauna drawn to the diverse habitat (e.g., common pheasants *Phasianus colchicus* and grey squirrels *Sciurus carolinensis*) encouraged stalking and pouncing. The water pool—a natural water source that was expanded in the enclosure development—facilitated swimming and provided an area for regular re-exploration with its constantly changing flora and fauna (Biolatti et al. 2016). In contrast, Enclosure A only offered opportunity for basic locomotion, such as running, walking and crawling.

Feeding methods

The feed chute in Enclosure A was a key source of pacing. Constant failure of appetitive behaviour resulted in limited opportunity to perform fulfilling hunting behaviour, driving the performance of stereotypic pacing in front of feeding locations (Lyons et al. 1997; Clubb and Mason 2007; Mohapatra and Panda 2014). As discussed above, in Enclosure B the tigers would exhibit locomotive behaviours associated with hunting as a result of the wildlife species present in the enclosure. This opportunity partially fulfilled the need to perform hunting behaviour (Bashaw et al. 2003). In combination with the absence of a feed chute and a variety of unique feeding locations included in the husbandry routine, this meant that there was no single area for the tigers to expect food, encouraging them to perform a wider range of natural behaviours (Morgan and Tromborg 2007; Szokalski et al. 2012).

Social opportunity

In Enclosure A, the dominant tiger patrolled most of the enclosure, leaving the submissive tiger to only patrol a small area resulting in pacing (Lyons et al. 1997). As Enclosure B offered more space, each tiger was able to patrol a larger territory and avoid negative social interaction, resulting in the observed reduction in pacing behaviour (Lyons et al. 1997; Pitsko 2003) and frequency of direct social interactions.

Social interactions were largely unavoidable in Enclosure A due to the small size and this resulted in aggression between the individuals, which could have had an impact on their stress levels (Miller et al. 2011). In contrast, in Enclosure B the tigers were able to use the large, complex habitat to more effectively avoid conspecifics within the enclosure reducing negative social interactions and therefore stress (Pitsko 2003; Bashaw et al. 2007; Miller et al. 2011; Biolatti et al. 2016). Topographical features such as ponds and boulders have been recorded in other studies to be of use for de-escalating conflict between conspecifics (Mohapatra and Panda 2014; Biolatti et al. 2016). It must also be considered that a reduction in social interactions could be a negative impact of the enclosure move; new routines and housing practices often elevate stress levels within Amur tigers, which could have caused the tigers to separate in search of solitude, reducing social interactions (Miller et al. 2011). Positively, the diversity of Enclosure B enabled indirect social interactions as there were more opportunities for scent and claw marking which are demonstrative of the tigers passively dominating their territory, as wild tigers would (Sunquist 2010; Wang et al. 2018).

Cover

The natural habitat of Amur tigers provides plentiful cover (Carroll and Miquelle 2006). The increased density of vegetative cover in Enclosure B may explain some behavioural differences observed.

Very few behaviours could be categorised as foraging in Enclosure A, as food provided by the keepers in the feed chute was quickly collected and carried from the chute straight into the only extensive cover in Enclosure A (the house), out of sight of the researcher. The increased duration of behaviours grouped as foraging in Enclosure B can be attributed to the tigers choosing to consume their food in the natural cover of the outdoor paddock instead of the house. Resting after food in the cover of the outdoor paddock was also recorded more in Enclosure B (Pitsko 2003), unlike in Enclosure A when resting after food was recorded as out of sight, as it took place in the house (Seidensticker and Doherty 1996; Nilsson 2012). However, further study should be undertaken to understand the true impact of the increased cover on resting behaviour. During data collection in Enclosure B, average temperature was 13°C higher than during data collection in Enclosure A, with a repeated high of 28°C, which may have artificially increased resting behaviour as the tigers attempted to thermoregulate more effectively (Hunter and Adams 1996). This could also account for the decreased frequency of locomotive behaviours. However, the abundant vegetative cover may have counteracted some effects of the heatwave, as availability of shade increases active behaviours of tigers (Stryker et al. 2019).

The density of vegetative cover in Enclosure B can explain why, despite the above link between foraging, cover and out of sight, the duration of out of sight behaviour was maintained through Enclosures A and B. One of the main occupational behaviours for wild tigers is patrolling territory (Law et al. 1997; Clubb and Mason 2007). Whilst patrolling in Enclosure B, the tigers would disappear into the undergrowth for periods of time, which would then be recorded as out of sight. In Enclosure A, the patrols did not pass through dense vegetation and so locomotion behaviour was recorded instead.

Other

It is important to consider the seasonality of the data collection. Maintenance behaviour increased in duration in Enclosure B. Although a sudden increase in grooming can be a sign of increased stress (Morgan and Tromborg 2007), in this case the tigers were moulting their winter coats during Enclosure B data collection, which may account for the increased grooming.

The reduced abundance of species surrounding Enclosure B, most notably the absence of other large predators (lions) may have reduced the tigers' need for frequent vigilance. The increase in duration of vigilance may instead be attributed to the relative newness of the enclosure, despite the month habituation period before data collection commenced in Enclosure B. Increase in anthropogenic noises due to enclosure location, and adjustment to new husbandry routines could also contribute to this increase (Morgan and Tromborg 2007).

Conclusion

The present study provides evidence that moving from a small, sparse enclosure to a large enclosure with features such as vegetative cover and varied, complex topography including large water sources, trees, logs and boulders can benefit captive tigers. The complexity provided by the new enclosure broadened the behavioural repertoire of the tigers allowing them to exhibit locomotive behaviours previously unobserved. It suggests the need to carefully consider the implications of the use of traditional enclosure features such as feeding chutes and instead favouring enclosure designs that allow for mixed feeding methods. Space allowed the tigers to make choices in their social interactions. It is also noted that environmental variables, such as temperature, can also be influencing factors on captive tiger behaviour. Overall, this study highlights that a complex enclosure and environmental enrichment positively changed tiger behaviour to include a more diverse repertoire of behaviours and moved further towards meeting the welfare needs of captive Amur tigers.

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