A comparative study of the influence of social housing conditions on the behaviour of captive tigers (Panthera tigris)

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Abstract

Nowadays, zoos are increasingly concerned with animal welfare as public expectations and knowledge of the needs of captive animals increases. Although many zoos try to provide all sorts of enrichment for their big cats, the importance of social enrichment is not yet fully understood. This study investigates the effect of different social housing conditions on the behaviour exhibited by captive tigers (Panthera tigris). It was found that paired tigers performed a wider variety of behaviours than single tigers (mostly direct social interactions). Single animals spent significantly more time rolling, auto-playing and performing flehmen. Moreover, paired tigers without neighbouring tigers exhibited significantly less pacing than those with neighbouring tigers. These results suggest that housing tigers in pairs is preferable for the animals as they are able to perform a wider range of natural behaviours, and that the presence of neighbouring tigers causes stress and frustration, and hence more pacing.

Keywords: animal welfare, behaviour, captivity, social conditions, tiger

Introduction

During the last few decades, zoo exhibits have been made increasingly complex to try to reduce abnormal behaviours and to increase the potential for an array of natural behaviours to be performed by the animals. One factor that may be important for the welfare of captive animals is the presence of conspecifics sharing the same enclosure (Carlstead 1996; Koontz & Roush 1996; Shapiro et al 1996, 1998). For some species, the social life of the animals in the wild is obvious; for other species, it is less obvious and hence little is known about it (Berger & Stevens 1996).

Studies of the social organisation of wild felids are difficult as felids tend to live at low population densities in vegetation or terrain that makes them difficult to observe (Robinson 1992). Most wild cats live in forest and/or forest-edge habitats that produce far less biomass of terrestrial prey than the more open savannah and grassland plains; therefore, these species are unable to live in social groups (Eaton 1974). Consequently, they are solitary hunters that have dispersed social systems with limited specific, direct social interactions (Jackson 1990; Barnes 1994; Kitchener 2000). The sightings of most tigers (Panthera tigris) are of solitary males, solitary females, or females with their cubs (Schaller 1967; Leyhausen 1979; Richardson 1992; Robinson 1992; Turner 1997). However, an increasing number of observations of social groupings of tigers have been reported, suggesting that tigers may

not be as solitary as was previously thought. Males associate with females for breeding, and with females and their cubs when feeding, resting and bathing (Sunquist 1981; Thapar 1989; Tyabji 1991; Sunquist & Sunquist 1992; Seidensticker et al 1999). In addition, Bragin (1986) and Wright (1989) cite reports of tigers socialising and travelling in groups. Furthermore, cooperative hunting in pairs and groups of tigers has also been observed (Pocock 1939; Corbett 1953; Thapar 1986).

Although some observations about tiger sociality exist, researchers have not yet conclusively determined what the influence of social interactions might be on the well-being of captive tigers. In fact, there have been very few studies investigating how the scarce knowledge about the social life of wild tigers could be applied to the management of captive tigers. For example, it is not yet known whether it is more stressful for a tiger to be housed alone, thereby lacking all forms of social interaction with conspecifics, or adjacent to other tigers, where limited social interaction is possible, or in a social unit, where conflicts and the lack of an individual home range may also cause stress to some animals (Koontz & Roush 1996; Mellen et al 1998).

The aim of this study is to examine whether differences in social conditions cause significant differences in the behaviours performed by captive tigers and whether these differences might give an indication of what housing conditions are most beneficial for the animals.

Table 1   Details of the studied animals.

Animal	Zoo	Sub-species	Age (yrs)	Single /Pair	Tiger neighbours	Rearing	Enrich-ment	Feeding	Enclosure size (m²)	Locked in at night	Comments
1	1	Siberian	11	Pair	No	Parent	Yes	1530 (daily) Friday: no feed	1080	No	Housed with unrelated male
2	2	Indian	14	Single	Yes	Parent	Yes	Twice weekly	400	No	
3	2	Indian	14	Single	Yes	Parent	Yes	Twice weekly	480	No	
4	3	Siberian	3	Pair	No	Parent	No	1500 (public feed), remainder in the evening	1200	Yes	Housed with unrelated male
5	4	Sumatran	6	Pair	No	Parent	Yes	Variable feeding schedule	600	No	Housed with unrelated male
6	5	Hybrid	4	Pair	Yes	Hand	Yes	In the evening, when locked in	200	Yes	Housed with brother
7	5	Hybrid	5	Pair	Yes	Hand	Yes	In the evening, when locked in	280	Yes	Housed with half-sister
8	5	Hybrid	10	Single	Yes	Parent	Yes	In the evening, when locked in	270	Yes	On rotational basis in same enclosure
9	5	Hybrid	10	Single	Yes	Parent	Yes	In the evening, when locked in	270	Yes	On rotational basis in same enclosure
10	5	Hybrid	4	Single	Yes	Parent	Yes	In the evening, when locked in	130	Yes	On rotational basis in same enclosure as unrelated male
11	6	Indian	4	Single	Yes	Parent	No	In the evening, when locked in	140	Yes	On rotational basis in same enclosure as unrelated male
12	6	Sumatran	4	Pair	Yes	Parent	No	In the evening, when locked in	170	Yes	Housed with sister, proba-bly in oestrus
13	7	Sumatran	15	Pair	No	Hand	No	1500 (daily) Friday: no feed	160	No	Housed with unrelated male
14	8	Siberian	13	Pair	No	Parent	No	1200 (daily)	370	Yes	Housed with unrelated male
15	9	Siberian	14	Pair	No	Hand	No	In the evening, when locked in	730	Yes	Housed with unrelated male

Materials and methods

Questionnaire

All institutions that are current participants of the European Endangered Species Programme (EEP) for the tiger in the UK, Belgium, and The Netherlands, together with a selection from France and Germany, were contacted. In total, 93 institutions were sent a question-naire to determine those that were most suitable for this study. The purpose of the questionnaire was to identify suitable tigers according to subspecies, age, sex, housing conditions, management, enrichment used and social conditions so that the pair- and single-housed groups could be balanced for these main variables. Ideally, all of the studied animals would be maintained under the same management practices. However, as only about one third of the contacted institutions responded and only a limited number of these institutions housed tigers in the social conditions suitable for this project, it was not possible to eliminate many of the influencing variables. Finally, nine institutions were selected for observation: from the UK (5), Germany (2), France (1) and The Netherlands (1).

Animals

Veasey (1993) found a difference in activity between female and male tigers. Furthermore, females are thought to be influenced more by the presence of a male than males are by the presence of a female (G Law and A Kitchener, personal observation). Therefore, all animals in this study were females. Most study animals belonged to one of the following subspecies: Amur/Siberian — *Panthera tigris altaica* (4), Sumatran — *Panthera tigris sumatrae* (3) and Indian — *Panthera tigris tigris* (3); the remaining animals were subspecific hybrids (5). The animals were 3–15 years old. Details of the animals studied are summarised in Table 1.

In this study, 15 female tigers were observed. Of these, 6 were housed singly with neighbouring conspecifics, and 9 were housed in pairs, 3 of which had neighbouring conspecifics and 6 of which did not. The 3 pairs of tigers with neighbouring conspecifics were housed with a related animal (Table 1).

Enclosures

The animals were housed in enclosures ranging from 130 to 1200 m^2 (Table 1). Some animals were housed in very naturalistic enclosures, with several trees and bushes, whereas others had rather barren enclosures.

Observations

All animals were observed live by M De Rouck, therefore avoiding inter-observer bias. The observations were carried out in May, June and July 2002. During the study, each animal was observed for 5 days, following an observation schedule (Table 2) designed in such a way that the observation periods were 'balanced' over the 5 observation days (Crockett 1996). Each 30 min period between 0900h and 1800h constituted one time block. The observation periods were scheduled so that consecutive days' observations were never conducted during the same time blocks. This reduced bias imposed by time-of-day effects (Crockett 1996). At the end of the study, 18 h of observations had been carried out for each tiger over the 5 day observation period.

Thirty-two behaviours were defined from six behavioural categories: locomotory, scent-marking, olfactory-response, ingestive, social, and other behaviours (Table 3). All of the individuals' behaviours were recorded using instantaneous focal sampling every minute of each observation period (Martin & Bateson 1993; Crockett 1996). A sample interval of 1 min ensured that relatively infrequent and short-duration behavioural occurrences (eg rolling, rubbing, elimination, drinking and aggression) were not missed, and that the overall behaviour of the tigers was accurately recorded. As the sample interval was shorter than the duration of the average behavioural pattern, the recorded data enabled relatively precise calculations to be made of the percentages of time for which the animals were performing the observed behaviours.

Activity was also recorded for each tiger. The activities were divided into five categories: lying, sitting, standing, moving, and out of view (Table 3). Activity was recorded simultaneously with the behavioural observations.

Data analysis

Calculations on data before analysis

For all behaviours, the percentage of time spent performing each behaviour was calculated over the whole observation period. However, the weather conditions varied greatly between observation days, as well as between observed animals. For some animals, the observations were carried out in mainly sunny conditions; for other animals it was cloudy or drizzly most of the time. De Rouck *et al* (in preparation) found great fluctuations in activity with different weather conditions, so the percentages of active time were analysed, rather than the percentages of the whole observation period.

Table 2   Observation schedule.

Time	Day 1	Day 2	Day 3	Day 4	Day 5
9.00-9.29	■			■	
9.30-9.59		■		■	
10.00-10.29		■			■
10.30-10.59			■	■	
11.00-11.29	■		■		
11.30-11.59				■	
12.00-12.29		■		■	
12.30-12.59					■
13.00-13.29			■		
13.30-13.59	■				
14.00-14.29				■	
14.30-14.59		■			
15.00-15.29		■			
15.30-15.59			■	■	
16.00-16.29	■		■		
16.30-16.59				■	
17.00-17.29		■		■	
17.30-18.00		■			■

■ Observation period

☐ No observations

To calculate the percentages of the active time, the inactive behaviours (resting and sleeping) were subtracted from the total observation time. In addition, the behaviours that could only be performed by some of the observed animals were also subtracted; therefore, all occurrences of behaviours that were directly related to given food and enrichment were excluded from the analysis. The percentage of 'out of view' was also subtracted in order to calculate the percentage of the total active time because during almost all 'out of view' observations the animals were not visible for a prolonged period; therefore, it was very likely that the tigers were sleeping and resting during these periods (Veasey 1993).

Consequently, all observations for resting, sleeping, bathing, and eating meat, as well as those observations when tigers bit specific enrichment devices (such as sheep fleeces and cardboard tubes), were excluded from the statistical analysis. Additionally, mounting, vomiting and aggression (no occurrences of these behaviours were scored during the study), and 'other behaviours' were excluded from the analysis. Table 4 shows the percentage of the total observation time spent as active time for each animal.

Statistical analyses

Before analysis, the data were transformed using an arc-sine transformation. Subsequently, these values were analysed using stepwise discriminant analysis (Hatcher & Stepanski 1994). In this analysis, the frequencies of each of the different behaviours were used as dependent variables and were compared multivariately between the different study groups. Because the number of individuals was lower than

Table 3   Ethogram of tigers' behaviours.

Observed behaviours	
Locomotory behaviours	
Walking	Forward motion at slowest gait
Running	High speed forward locomotion
Jumping	Leaping with all four legs off the substrate from one point to another
Pacing	Walking in a fixed pattern, the animal completing at least three repetitions of circuit/line
Marking behaviours	
Spraying	Horizontal ejection of jet of urine against vertical surface
Rubbing object	Sliding of facial area/head over any non-animal surface
Biting object	Biting behaviour directed towards an object (not part of playing behaviour)
Rolling	Rubbing of dorsal and lateral sides on the ground (or other horizontal substrate)
Scratching	Claws being drawn down a tree trunk to leave a visual mark behind
Elimination	Deposition of urine and/or faeces onto the ground from a squatting position
Olfactory response behaviours	
Sniffing	Taking air through the nose in repeated small sniffs, the nose being held close to the object or raised into the air
Flehmen	Grimacing facial expression with the tongue out of the mouth while drawing scent over the facial glands
Social behaviours	
Vocalising Prusten	Friendly greeting call, sounds like 'iff iff iff'
Vocalising growl	Loud call to signal discontentment with other tiger's attempts to engage in an interaction
Head-to-head rubbing	Rubbing the facial area/head over a conspecific's body
Mounting	Sexual behaviour involving placement of the male directly behind or over the female, may involve biting, slapping and growling
Aggression	Usually short bouts of 'boxing' behaviour, may involve a threatening gesture, the ears turned back, striking motions, hissing, growling
Allo-playing	Directing 'non-serious' behaviours at conspecific
Allo-grooming	Licking and/or biting the fur or paws of a conspecific's body
By-allo-grooming	Licking and/or biting the fur or paws of observed animal by a conspecific
Ingestive behaviours	
Eating (meat)	Consumption of meat
Eating (plants)	Consumption of plant particles
Drinking	Consumption of water
Vomiting	Expelling the stomach contents via the mouth
Other behaviours	
Auto-playing	Directing 'non-serious' behaviours at an object/self
Auto-grooming	Licking and/or biting the fur or paws of own body
Observing	Interruption of the current behaviour to stare at a specific stimulus
Resting	Lateral/ventral lying with the eyes mainly open
Sleeping	Lateral/ventral lying with the eyes closed
Stretching/Yawning	Extended forelegs, depressed body from standing position/Fully extending then closing the jaw (with the eyes closed)
Bathing	Entering a water feature with any part of the body other than the mouth
Other	Behaviours not described so far
Activity categories	
Lying	Animal is in a horizontal position with the belly or a flank on the substrate
Sitting	Animal is supporting most of body weight on haunches and the upright body is supported by the extended front legs
Standing	Animal is upright, supported on all four extended legs, but not in motion
Moving	Animal is upright supported by all four legs, and in motion
Out of view	Animal is in an area which is visually inaccessible to observer

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Table 4   Active time as a percentage of the total observation time for each individual animal.

Animal	Active time/Total observation time (%)
1	55.73%
2	37.43%
3	38.17%
4	60.42%
5	65.73%
6	64.00%
7	56.75%
8	46.30%
9	60.61%
10	75.81%
11	64.58%
12	64.54%
13	37.75%
14	48.26%
15	50.72%

the total number of behaviours scored, a stepwise analysis was performed. In this analysis the frequencies of the different behaviours were added to/removed from the model in a stepwise fashion so that only behaviours that differed significantly between groups remained in the model and all non-significant ones were excluded.

As the single animals were very restricted in the social interactions in which they were able to engage (no direct social interactions were possible for single animals), the behaviours that could be performed by all observed animals and the behaviours that could only be performed by the paired animals were analysed separately. The differences between the behaviours of the three test groups (singles with neighbours, pairs with neighbours, and pairs without neighbours), for which a significant difference was found, were examined using the average percentages for all behaviours per group.

Results

The stepwise discriminant analysis revealed a significant difference between the test groups for pacing, rolling, flehmen and auto-playing (Table 5). Furthermore, the squared distances between the groups' average values indicate that overall, the greatest differences can be found between the pairs without neighbours and all tigers with neighbours (both pairs and singles $F = 26.26837$, $P < 0.0001$ and $F = 65.76275$, $P < 0.0001$ respectively). Additionally, it can be seen that between the paired and single tigers with neighbours the difference is only just significant ($F = 3.62531$, $P = 0.05$) (Table 6). The multivariate statistic, using the Wilks' Lambda test, shows that the results generated by the stepwise discriminant analysis are highly significant ($F = 13.49$, $df = 8$, $P < 0.0001$).

A significant difference was found for pacing ($F = 107.35$, $P < 0.0001$), with the paired tigers without neighbours pacing much less (approximately 5% of active

Table 5   Results of the stepwise discriminant analysis for the behaviours that could be performed by all animals.

Behaviour	F value	P value
Walking	0.06	ns
Running	0.16	ns
Jumping	1.64	ns
Pacing	107.35	< 0.0001
Spraying	2.81	ns
Rubbing object	0.51	ns
Rolling	25.58	< 0.0005
Scratching	0.14	ns
Elimination	0.41	ns
Biting object	0.05	ns
Sniffing	0.45	ns
Flehmen	5.09	< 0.05
Auto-play	8.14	< 0.01
Auto-groom	1.04	ns
Prusten	0.44	ns
Growl	0.65	ns
Eating (plant substances eg grass, weeds)	2.39	ns
Drinking	1.17	ns
Stretching/Yawning	0.66	ns
Observing	1.15	ns

ns = no significant difference

Table 6   Pairwise squared distances between the groups (1 = pair-housed animals without neighbours, 2 = pair-housed animals with neighbours, 3 = singles with neighbours). NDF = degrees of freedom for numerator; DDF = degrees of freedom for denominator.

Between groups	Squared distance	F value (NDF = 4, DDF = 9)	P value
1 & 2	70.04898	26.26837	< 0.0001
1 & 3	116.91155	65.76275	< 0.0001
2 & 3	9.66750	3.62531	0.05

time) than the single and paired tigers with neighbours (both > 20% of active time) (Table 7). Single animals performed significantly more rolling (up to twice as much) than the pairs ($F = 25.58$, $P < 0.0005$), and performed flehmen up to five times more than pairs ($F = 5.09$, $P < 0.05$). Auto-play was also found to differ significantly between groups ($F = 8.14$, $P < 0.01$). The paired tigers with neighbours were rarely observed auto-playing (0.06%), the pairs without neighbours a little more frequently (0.36%), and the single animals with neighbours most often (0.62%).

A significant difference was found for head-to-head rubbing ($F < 0.05$, $P = 6.45$) (Table 8). Paired tigers with neighbours were never seen performing head-to-head rubbing, whereas the pairs without neighbours rubbed heads approximately 0.5% of the active time (Table 7). Finally, there was a significant difference between the two groups of paired animals for allo-grooming ($F = 16.06$,

Table 7   Average percentages for all behaviours per group (1 = pair-housed animals without neighbours, 2 = pair-housed animals with neighbours, 3 = singles with neighbours).

Group	Walking	Running	Jumping	Pacing	Spraying	Rubbing object	Rolling	Scratching	Elimin-ation	Biting object	Sniffing	Flehmen
1	22.06%	0.38%	0.35%	4.67%	0.69%	0.45%	0.15%	0.46%	1.07%	0.28%	3.81%	0.19%
2	11.85%	0.58%	0.26%	21.30%	1.05%	0.99%	0.16%	0.19%	0.30%	0.06%	3.45%	0.16%
3	11.06%	0.53%	0.24%	23.91%	1.76%	0.74%	0.31%	0.22%	0.83%	0.31%	4.21%	0.56%

Group	Auto-playing	Auto-grooming	Vocal-ising Prusten	Vocal-ising Growl	Eating (plant substances)	Drinking	Stretching / Yawning	Observing	Head-to-head rubbing	Allo-playing	Allo-grooming	By-allo-grooming
1	0.36%	8.55%	0.39%	0.71%	0.88%	0.57%	2.47%	50.08%	0.57%	0.46%	0.15%	0.08%
2	0.06%	6.97%	0.56%	0.18%	0.05%	1.18%	1.07%	47.75%	0.00%	0.42%	0.89%	0.37%
3	0.62%	5.89%	0.16%	0.12%	1.67%	0.92%	1.70%	44.22%				

Table 8   Results of the stepwise discriminant analysis for the behaviours that could only be performed by the pair-housed animals.

Behaviour	F value	P value
Head-to-head rubbing	6.45	< 0.05
Allo-play	0.04	ns
Allo-groom	16.06	< 0.01
By-allo-groom	0.35	ns

ns = non significant

$P < 0.01$); pairs without neighbours groomed significantly less (0.15%) than pairs with neighbours (0.89%).

Discussion

Ideally, all of the studied animals would have been maintained under the same conditions. However, data gathered from studies on zoo animals are prone to all kinds of differences attributable to differing management practices. Because of the fairly limited number of zoos that responded to our questionnaire, it was not possible to eliminate a number of variables that could have influenced the animals' behaviour (eg subspecies, age, hand-rearing versus parent-rearing, naturalistic versus barren enclosure, enclosure size, feeding regime, locked in at night or not, use of enrichment, presence of specific features such as ponds, platforms). In addition, this study involved a relatively small number of tigers. To get a better idea of the variation within the population we would have liked to study a larger number of animals. Moreover, a better representation of the animals' time budgets would have resulted from doing more than 5 days' observation. This needs to be taken into account when interpreting the data.

The analyses revealed that the occurrence of pacing was much higher in animals with neighbouring conspecifics. As pacing is generally considered to be associated with increased stress levels and hence poor welfare (Broom 1983; Wiepkema 1983; Broom & Johnson 1993; Wemelsfelder 1993; Carlstead & Shepherdson 2000), we can conclude that the welfare of tigers with neighbouring conspecifics is probably lower than that of tigers without neighbouring conspecifics. A possible causal factor for this higher level of pacing might be 'social experience', ie the influence of stereotyping in neighbouring animals (eg Palya & Zacny 1980; Kiley-Worthington 1983). All of the observed tigers that paced regularly were housed next to tigers that also paced regularly, and it is very likely that the presence of a pacing tiger could trigger pacing in neighbouring tigers. However, it is very difficult to determine the extent to which this might have caused, or increased, the pacing in the observed animals. Furthermore, there must have been an earlier trigger to initiate pacing in the first animal. On the other hand, the fact that these animals pace might result from being housed in the same environment and reacting to the same stimuli.

Another factor directly linked to the presence of neighbouring conspecifics could be sexually related motivation (Carlstead & Seidensticker 1991). One of the animals observed, animal 12 (a female in a single-sex pair), was thought to be in oestrus at the time of the observations. This animal paced for one third of the active time, which was very high compared to the other pairs. This observation suggests that the mere presence of a conspecific could cause an animal to start pacing when in oestrus (Lyons *et al* 1997); therefore, pacing could be interpreted as a frustrated attempt to get closer to this neighbouring conspecific (Hediger 1950; Clubb & Mason 2001).

Furthermore, as practically all tigers showed pacing to some degree, it is very likely that aside from the presence of conspecifics, the presence of other cats (regardless of the species), other 'competitors', and prey species in neighbouring enclosures (Shorey & Eaton 1974; Roynon 2000) may influence pacing. Pacing may have originated from normal patrolling of the territory (Clubb & Mason 2001) and gradually evolved into a fixed pattern because of the location of the neighbouring animals' enclosures and/or activities. The presence of neighbouring animals may even have reinforced the pacing of the observed animals. Both positive and negative reactions by the neighbouring animals

possibly contribute to satisfying the pacing animal's hunger for socialisation and interaction (Priest 1993). On the other hand, Mellen and Shepherdson (1997) found that by providing animals with barriers so that cats could hide from each other, pacing was reduced or even absent, suggesting that the animals do not necessarily try to socialise with their neighbours. Therefore, pacing may be an attempt to 'get away' from the social source of the stress. However, this result was confined to smaller cats, where incipient gregariousness is virtually unknown in the wild (Mellen *et al* 1998). Roynon (2000) found that visual barriers do not necessarily reduce or stop pacing, and might cause the pacing to be transferred to a location further along the barrier where the animals can still see out of the enclosure. However, in this study, animal 3 had a visual barrier along one side of the enclosure, and, although other tigers were housed on the other side of the fence, animal 3 did not pace along this side of her enclosure. Therefore, visual barriers probably can eliminate or reduce pacing, as opposed to simply moving it to another location. However, the creation of visual barriers along the whole circumference of the enclosures would make interaction between the neighbouring animals (almost) completely impossible and may cause as much stress as the original situation without barriers, although vocal and some degree of olfactory communication would still be possible.

Analyses of the behavioural data per group (Table 7) revealed that lower occurrences of pacing appear to correspond with higher occurrences of walking. Furthermore, lower occurrences of walking did not appear to be compensated for by a significant increase in running or jumping. The total amount of time spent performing locomotory behaviours was quite similar for all tigers (about 30%), indicating that the animals' lack of normal walking was compensated for by performing stereotypic pacing. Therefore, part of the reason for pacing might be found in the animals' need to perform locomotory behaviours (Nicol 1987; Hughes & Duncan 1988; Hughes *et al* 1989; Rushen *et al* 1993), or after the animal no longer feels the need to pace, there is only limited time for daily walking.

Nevertheless, the social conditions and the 'behavioural need' are not the only factors that might influence the occurrence of stereotypic pacing. It is generally accepted that all kinds of environmental restrictions also influence the animals' behaviour and cause the development of stereotypies (Hediger 1955; Morris 1964), including feeding regime (Rushen 1984, 1985; Terlouw *et al* 1991a,b; Weller & Bennett 2001), space allowance/enclosure size (Draper & Bernstein 1963; Terlouw *et al* 1991a), and enrichment methods (Ödberg 1987; Bryant *et al* 1988; Lam *et al* 1991; Law 1991; Mellen & Shepherdson 1997). Furthermore, the expression of stereotypic behaviours is also thought to be dependent on the animals' age (Bernstein & Mason 1962; Berkson 1967, 1968; Ridley & Baker 1982) and may even be genetically predisposed (Mittelman & Valenstein 1984). Boredom might also be causing stereotypic behaviour, highlighting the need for effective social and/or environmental enrichment (Dantzer 1986; Wemelsfelder 1993; Carlstead 1996).

There was also a significant difference in the frequency of flehmen performed by tigers depending on their housing conditions. Single animals performed significantly more flehmen than paired animals. As no significant difference was found in the percentages of time spent performing scent marking, which in itself indicates the importance of scent marking to all captive tigers, we can conclude that the higher percentage of flehmen is likely to be due to the fact that flehmen is one of the few ways in which the single tigers can obtain information about their neighbouring conspecifics. Any form of close investigation is almost completely obscured by the separating fences. Some sniffing of scent-marks and rub-marks of the neighbouring tigers was observed, as well as some vocal communication. However, flehmen is predominantly used by tigers to find out more about the sexual state of their conspecifics (Estes 1972; Robinson 1992), whereas more general information about the other tigers in the neighbourhood may be gathered visually, vocally and using other forms of scent marks.

De Rouck *et al* (in preparation) suggest that rolling is a form of play. This appears to be supported by the results of our statistical analysis, as rolling and auto-playing show the same trend: both behaviours were performed much more by the single-housed animals than by the pairs. Playfulness could be the expression of the animals' relaxed state; therefore, one would expect the animals to play more in conditions they favour. If we look at the average percentages of allo-playing, it can be seen that the lower frequency of auto-playing in the paired animals is completely compensated for by allo-playing. Consequently, one could argue that the animals are equally 'happy' in both conditions as they play for approximately the same proportion of time. Therefore, the difference in auto-playing might simply reflect the fact that single animals cannot engage in allo-play. Alternatively, it has been suggested that animals may become bored when they are in an unstimulating environment (Wemelsfelder 1993) and auto-playing may be one way for single animals to amuse themselves. If so, auto-play may be the result of an inadequate environment rather than an expression of the animal's contentment with its situation.

Head-to-head rubbing was never seen in the paired tigers with neighbours, whereas pairs without neighbours rubbed heads relatively often. Feldman (1994) stated that head-to-head rubbing is a social contact behaviour, enabling the animals to get to know one another's odour (Gorman & Trowbridge 1989). As all pair-housed animals with neighbours were related to their enclosure mate, the lack of head-to-head rubbing in the latter might indicate that the scents of the related animals might be very similar or at least very familiar, thereby rendering head-to-head rubbing unnecessary. Alternatively, perhaps head-to-head rubbing occurs only in relaxed situations, which the paired tigers with neighbours did not experience sufficiently. Additional observations on unrelated pairs with neighbours should allow us to confirm or reject these hypotheses.

In cats and other carnivores, auto-grooming, in some cases, has been found to be an acute stress response in conflict situations (Campbell 1975; Kiley-Worthington 1990; van den Bos 1998), and it is possible that allo-grooming may also be such a stress response. The paired tigers with neighbours allo-groomed much more than the pairs without neighbours and this may be a consequence of the higher stress levels caused by the presence of neighbouring tigers. However, as all paired tigers with neighbours were housed with a related animal (brother, sister or half-sister), the difference might indicate that affiliative behaviours are more frequent between littermates (Bradshaw & Hall 1999).

Interestingly, the paired animals were seen lying next to one another while performing all kinds of behaviours for a huge proportion of the day. In a truly asocial species, individuals would be expected to avoid each other (Barry & Crowell-Davis 1999); this clearly was not the case. Tigers appear to be well adapted to living in pairs (Berger & Stevens 1996) and may even live in social groups in the wild when the ecological and environmental circumstances are favourable (Kitchener 2000). One must always ensure that animals housed together in captivity are fully compatible. Over all, there are very few problems when introducing an unrelated male and female, as long as the introduction is well prepared (Weston 1991), and the fear that tigers might engage in severe fights and hence injure each other does not appear to be a sufficiently strong argument to condemn tigers to solitary confinement.

The differences in behaviour discussed above indicate that keeping tigers in pairs allows the animals to perform a wider variety of behaviours than single animals. Mellen (1991) found that exotic cats maintained in groups of three or more were less likely to reproduce than those maintained in pairs, and Mellen *et al* (1998) found that small cats maintained in groups of three or more spent significantly more time pacing than did animals in pairs. These findings, and those of this study, suggest that pair housing appears to be preferable if we want tigers to behave as normally as possible and apparently to suffer minimal levels of social stress. However, separation of animals to prevent breeding is still a common practice. This is more reliable and has fewer potential deleterious side effects than alternatives such as hormonal contraception. Hence, if we want to keep tigers in pairs, reliable population management methods would be needed to avoid over-population. The easiest way to pair-house, and ensure no breeding, would be to house the tigers in same-sex pairs. However, further research is needed to determine the practicability of male and female same-sex pairs.

The presence of neighbouring conspecifics caused stereotypic behaviours in the studied tigers, regardless of whether they were kept singly or in pairs. Therefore, in order to eliminate, or at least reduce, some sources of stress that elicit stereotypies, one should consider avoiding housing these animals next to one another, or at least try to ensure that sufficient distance or barriers exist between their enclosures. As we were unable to observe single-housed animals without neighbours, we were unable to determine whether single-housing without neighbours was preferable to single-housing with neighbours, as the former excludes all possibilities of social interactions with a conspecific. Further observations on single tigers without neighbours are needed to clarify this issue.

Conclusion

In this study several differences in behaviour were found between tigers housed in different social conditions. These findings suggest that housing tigers in pairs is probably preferable for the animals than housing singly. In addition, neighbouring conspecifics appear to be a cause of stress resulting in higher levels of pacing.

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