The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK

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The effect of environmental enrichment on play behaviour in white-lipped peccaries (Tayassu pecari)

SSC Nogueira*†, JP Soledade†, S Pompéia‡ and SLG Nogueira-Filho†

† Laboratório de Etologia Aplicada, Universidade Estadual de Santa Cruz – UESC, Rod Ilhéus Itabuna km 16, Ilhéus, BA, Brazil 45662-000
‡ Departamento de Psicobiologia, Universidade Federal de São Paulo – UNIFESP, R Napoleão de Barros 925, São Paulo, SP, Brazil
* Contact for correspondence and requests for reprints: selene.nogueira@pq.cnpq.br

Abstract

*Herds of white-lipped peccary (*Tayassu pecari*) have historically been kept in captivity in order to replace stocks lost to hunting however the lack of knowledge regarding their species-typical behaviour remains an impediment to understanding their captive needs. Environmental enrichment has been suggested as an efficient way of decreasing aggression and apathy as well as increasing the expression of normal behavioural acts — such as play behaviour — which may, in turn, contribute to improved husbandry conditions. Therefore, the aims of this study were to describe play behaviour in this species and analyse the effects of environmental enrichment on such behaviour as well as on agonistic expression and inactivity. The occurrence of solitary and social play acts were recorded, as well as agonistic interactions and inactivity (resting positions) in two conditions (non-enriched and enriched with ball, hose and see-saw). This study included 24 captive peccaries three of which were juveniles, nine sub-adults and 12 adults, with a 1:1 sex ratio. The relationship between social dominance hierarchy and play behaviour was also analysed in each observational condition. Enrichment resulted in increased solitary and social acts of playing both in juvenile/sub-adult and adult peccaries. All the individuals played with the introduced objects and spent less time in resting positions throughout the enrichment phase. However, no decrease in agonistic interactions was observed and dominant individuals played more with the objects. Our study showed that environmental enrichment stimulated play behaviour in white-lipped peccaries as well as decreasing levels of inactivity; this may lead to improvements in the welfare of individuals in captive breeding centres.*

Keywords: *animal welfare, captive breeding, endangered species, play behaviour, social behaviour, social dominance*

Introduction

The white-lipped peccary (*Tayassu pecari*) has suffered due to deforestation leading to its extinction in a number of areas in Neotropical countries (Sowls 1997; Taber *et al* 2009). Herds of peccaries have been kept in captive breeding centres to replace stocks further depleted through hunting (Dubost 2001; Nogueira-Filho & Nogueira 2004). Generally these consist of barren paddocks ranging between 400 and 8,000 m^2 (Nogueira-Filho 1999). The vast home ranges of wild peccary herds (up to 100 km^2; Fragoso 1998) may suggest the need for larger enclosures to maintain adequate welfare in captivity as is the case for the collared peccary (*Pecari tajacu*) (Nogueira *et al* 2010). However, this is not necessarily the case for all species. Perkins (1992) confirmed the suspicions of Wilson (1982) in concluding that more than space, animals require environmental enrichment. This enrichment (for a review, see Shepherdson 1998) may provide a stimulus that serves to enhance cognitive skills (see Shettleworth 2010) and the performance of species-typical behaviour. To-date, little data are available regarding the use of the behaviour of white-lipped peccaries as indicators of welfare. Thus, specific peccary behavioural patterns may be useful for investigating the welfare of this species.

Agonistic behavioural patterns are typically used as an indicator of welfare (Fraser & Duncan 1998). These are extremely conspicuous among peccaries as a result of social dominance (Nogueira Filho *et al* 1999; Dubost 2001). It has been reported that subordinate peccaries in captivity suffer from threatening and aggressive behaviour from conspecifics which can impact on their health conditions (Nogueira-Filho *et al* 1999). However, the white-lipped peccary society is organised into a strictly linear dominance hierarchy (Nogueira Filho *et al* 1999; Dubost 2001) therefore the use of agonistic patterns as unique indicators of welfare may not be completely reliable due to the regular hierarchical displays which may complicate any assessment of animals' welfare. Alternatively, instances of behavioural patterns of play are considered reliable indicators of enhanced welfare (Lawrence 1987; Newberry *et al* 1988; Duncan 1998; Bracke *et al* 2006; Dudink *et al* 2006; Boissy

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et al 2007; Fraser & Yeates & Main 2008; Carrasco *et al* 2009). This can be readily applied to the white-lipped peccary as play among herd members of all ages (with and without other objects) as well as solitary play with objects, have often been observed in both captivity (Nogueira-Filho *et al* 1999; Dubost 2001) and the wild (JMV Fragoso, personal communication 2006). Additionally, a number of authors suggest that play behaviours decrease aggression (Drea *et al* 1996; Soderquist & Serena 2000) thereby having a possible positive effect on welfare, but consensus is yet to be reached on this subject (see Sharpe & Cherry 2003).

One way of increasing play behaviour is via environmental enrichment (see Young 2003) which has been widely implemented in many zoos and laboratories to elicit activity that relieves animals from boredom and encourages the performance of species-specific (Carlstead 1996; Maple & Perkins 1996) as opposed to abnormal behaviour (Mason *et al* 2007). Therefore, the aims of this study were to firstly describe play, agonistic and resting behaviour of captive white-lipped peccaries and then to analyse the effects of environmental enrichment on such behaviours. It was hoped that the introduction of novel objects would decrease animals' aggression and inactivity and increase play. Moreover, there was a desire to explore whether individual dominance status would be related to instances of play behaviour with the supplied objects since they were limited resources raising animals' curiosity.

Materials and methods

Animals and housing

Subjects consisted of 24 captive white-lipped peccaries kept together in a 1,200 m^2 paddock at the Universidade Estadual de Santa Cruz-UESC, Ilhéus, Bahia, Brazil. The herd consisted of 12 adults (six males and six females), nine sub-adults (five males and four females) and three juveniles (one male and two females). The herd mimicked the same sex ratio (1:1) shown by peccaries in the wild (Fragoso 1998). As access to the birth history of all individuals was unavailable, classification of animals' age classes (adult, sub-adult and juvenile) was based upon animals' weight and fur colour (Nogueira-Filho 1999). The enclosure was surrounded by a 1.5-m high wire fence with a dirt floor and coconut trees interspersed with low non-edible arboreal vegetation. Also present were two water troughs (0.6 × 0.3 m; length × width), and three feeders (1.0 × 0.3 m). Animals were identified via individually unique plastic ear tags.

Animals were fed once daily at 0845h with a diet composed of grain corn (83.9%), soybean meal (15.7 %) and cattle mineral salts (Matsuda Inc, São Sebasíao do Paraiso, Brazil). Water was available *ad libitum*. We adhered to the *Guidelines for the use of Animals in Research* as published in *Animal Behaviour* (1991) and following Brazilian federal laws.

Data collection and experimental design

Data were obtained during a 12-week period in two experimental conditions: non-enriched and enriched. During the 20 days prior to data collection, the peccaries were habituated to the presence of the observer, allowing the collection of behavioural data from within 5 m of the paddock fence. Each individual was observed during 10-min continuous-recording focal animal sampling sessions (Altmann 1974; Martin & Bateson 1993), supported by a video recorder (Sony™, Tokyo, Japan), two to three times per week, so that each subject had 20 observation sessions over a six-week period in the non-enriched condition. The same procedures were adopted in the enriched condition in the following six weeks, in such a way that the same number of observation hours were obtained for all three introduced objects. Only one focal individual was sampled in each session, and all herd members were visible continuously. For each individual, observation days and starting times were selected randomly (0900–1100h to avoid feeding and nesting times). During these sessions, play, agonistic, and resting behavioural patterns in which the focal individual was engaged were recorded. Each study condition (non-enriched and enriched) comprised 80 h, totalling 160 h of data collection.

Play behaviour

We followed the definitions of solitary and social play employed by Hall (1968) cited in Fagen (1981) and Bekoff (1972) cited in Fagen (1981), respectively:

Solitary play:

> … Play…is a very broad term which includes almost any activity which, to the observer, seems to have no immediate objective. It therefore includes the manipulation of non-food objects and the whole variety of sensoriomotor performances that are exploratory.

Social play:

> … is that behaviour which is performed during social interactions in which there is a decrease in social distance between the interactants, and no evidence of social investigation or agonistic (offensive or defensive) or passive-submissive behaviours on the part of the members of a dyad (triad, etc), although these actions may occur as derived acts during play.

Furthermore, we classified object play for both situations: without furnished object (leaves, branches or stones found in the paddock) or play with supplied objects (provided by the researchers).

Environmental enrichment procedure

During the enriched condition, the paddock was enriched with three types of object: ball, hose and see-saw, in this order. All individuals were unfamiliar with these objects. A hard, red plastic ball was suspended from a palm tree inside the paddock at a height of 0.3 m. In this way, all animals, including juveniles, were able to reach the ball. Similarly, a rubber hose was suspended from the same tree in such a way that it touched the soil. The see-saw, constructed from a 3.0-m long bamboo branch, was tied at the centre with a 4.0 m length of rope to a high palm branch, allowing it to move freely. The see-saw was also suspended 0.3 m from the soil in order that all individuals could touch it. Enrichment items were situated away from the feeders and water tank.

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For data collection, each object was presented alone and remained in the paddock for 10 days. After this period the item of enrichment was removed and an interval of four days followed before the next object was introduced in the same position. Instances of play events with the novel objects during observation days were also collected along with the pattern of play with the objects throughout the 10-day period of availability.

Social dominance rank analysis

Data on agonistic interactions were recorded to determine the social dominance rank. The dominant-subordinate relationships were analysed using the approach described by Lehner (1996). Each individual was scored either as a winner or a loser after each aggressive interaction. The loser was defined as the animal showing submissive displays or fleeing from the winner, following the procedures described by Nogueira-Filho *et al* (1999). All observed dominance interactions between individuals were organised into a sociometric matrix.

Statistical analysis

The number of events in which each peccary was the actor of social and solitary play acts, and agonistic interactions were compared with a General Linear Model (GLM) which had as factors condition (non-enriched vs enriched), gender (male vs female) and age class category (adult vs combined juvenile and sub-adult due to the small number of individuals in of these ages), followed by *post hoc* Duncan tests when necessary in Statistica version 7.0 (Statsoft, Tulsa, OK, USA). The same statistical model was applied to compare the time the peccaries remained resting, ie sitting or lying down, during the two conditions. Using the same statistical software, the preferences for objects were analysed through two-way repeated measures ANOVA, also followed by *post hoc* Duncan tests. In this model, we included the effects of object (ball, hose and see-saw), gender and age class as factors. We used $\log(x + 1)$ transformations to meet the assumption of normality where necessary.

To test for linearity of hierarchy, we calculated the Landau's corrected linearity index h', adjusted for unknown relationships through the SOCPROG 2.4 (Whitehead 2009) for both experimental periods. This index ranges from 0 (non-linear hierarchy) to 1 (perfectly linear hierarchy). The index h' takes into account the existence of unknown relationships (de Vries 1995) and the statistical significance of h' is provided by a re-sampling procedure using 10,000 randomisations (Whitehead 2009). The SOCPROG also provided a rank order for each individual in both periods through the method I&SI (de Vries 1998). The I&SI method aims to find a rank order most consistent with a linear hierarchy by first minimising the number of inconsistencies *I* and, subsequently, minimising the total strength of the inconsistencies *SI*, subject to the condition that *I* does not increase (de Vries & Appleby 2000).The I&SI method minimises the number of inconsistencies by minimising the sum of the rank differences between individuals whose ranks were inconsistent (de Vries 1998).

In addition, we calculated the Directional Consistency Index (DCI; van Hooff & Wensing 1987). The DCI was calculated across all dyads as: (H – L)/(H + L), where H is the number of times the behaviour was performed in the main direction within each dyad and L the number of times the behaviour occurred in the opposite direction. This value is summed across all dyads and then divided by the total number of times the behaviours were performed by all individuals (van Hooff & Wensing 1987). The resulting values range from zero (complete bi-directional exchange of submissive gestures) to one (complete uni-directionality).

We also analysed the correlations between hierarchy dominance rank and peccaries' live weight, the number of times each peccary was actor or receiver of social play and agonistic acts in both conditions, and the total occurrences of play behaviour with the furnished objects per individual using Spearman rank coefficient (r_S). Means (± SEM) are quoted throughout, and all analyses used a 0.05 significance level.

Results

Occurrence of solitary play acts and social play interactions

The white-lipped peccaries performed 11 different patterns of play behaviour (Table 1) during the non-enriched condition. Here, we recorded a total of 282 occurrences of acts of play behaviour: 73.8% social and 26.2% solitary. In both such categories, the animals played 107 times with a variety of natural/non-furnished objects, such as branches, leaves and coconuts, 23.1% of them in social interactions. We linked three behavioural patterns with play soliciting: running, jumping or beating with head (for descriptions, see Table 1). These acts appeared singly or in combination — beating with head and jumping or jumping and running, for instance.

During the enriched condition, the white-lipped peccaries performed the same 11 play patterns shown during the non-enriched condition, plus the pattern described for play with the furnished objects (Table 1). In this condition, we observed 817 occurrences of play behaviour: 69.6% social and 30.4% solitary. Peccaries played 627 times with objects: 179 (28.6%) with non-furnished objects and 448 (71.4%) with the furnished ones. Most of the time, they played with the objects in social play interactions (283 events or 63.2%) than in solitary acts (165 events or 36.8%).

The effects of enrichment on solitary play acts, social play and agonistic interactions, and the time spent in resting positions

The statistical model showed that, independently of condition and age, the female peccaries were actors of all behaviours analysed (social play interactions, solitary play acts, and agonistic interactions) more frequently than males ($F_{1,20} = 8.45$, $P = 0.009$; Figure 1). There was also a significant interaction between age, behaviour and condition ($F_{2,40} = 7.55$, $P = 0.002$). This interaction revealed that despite adult and juvenile/sub-adult peccaries having been actors of more social and solitary play during the enriched

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Table 1 Description of play behavioural patterns in white-lipped peccaries.

Play behavioural pattern	Occurrence (%)	Pattern category[1]	Age class[2]	Definition
Play run	1.9	SOL or SOC	J, SA, A	One animal alone or engaged with a conspecific runs fast without obvious destination or specific reason
Play digging	0.8	SOL	SA, A	This is a locomotor play in which the animal digs earth/mud and with exaggerated leg movements launches it outwards
Play chase in circle	1.3	SOC	J, SA, A	One animal or the whole group runs following a conspecific in a circular path and frequently they turn and switch direction
Leap	0.7	SOL or SOC	J	A juvenile jumps vertically in front of a conspecific; or after playing with an object; the juvenile releases the object and jumps
Roll onto back	1.3	SOC	J, SA, A	The animal approaches a conspecific and rolls onto its back often with legs raised
Play vicious circle	0.1	SOC	J	Juveniles run in circles amongst conspecifics and throw their head from a horizontal to a vertical position and back again to horizontal in exaggerated fashion
Play beating with head	0.7	SOC	J, SA, A	The animal comes close to a conspecific and solicits play by beating its head at the other individual's head, neck, belly or leg
Play carrying natural object	22.0	SOL or SOC	J, SA, A	The animal grabs branches, leaves or rocks or objects are carried in the mouth while the animal runs away in the direction of conspecifics
Play with furnished object	22.0	SOL or SOC	J, SA, A	Animals interact with offered objects, touching, swinging, pulling, biting and running from them. Also vocalising and carrying the object (hose) and tugging at it with conspecifics
Play squabble	11.4	SOC	J, SA, A	The animals nibble, threaten, bite, squabble, confront face-to-face and turn. This is similar in appearance to the agonistic squabble and is exaggerated and disrupted. Always preceded by another pattern of play
Sexual play	1.6	SOC	J, SA, A	Only during a behavioural sequence of play when one individual mounts another from the front or side

[1] SOL: solitary; SOC: social play; [2] J: juvenile; SA: sub-adult; A: adult.

condition than during the non-enriched condition ($P_s < 0.0004$; Figure 2), during both conditions the two age groups did not differ in the number of social and solitary play acts ($P_s > 0.05$). Conversely, the adult peccaries were actors of more agonistic interactions than the juveniles/sub-adults during the non-enriched and enriched conditions ($P_s < 0.03$; Figure 2). However, the introduction of novel objects during the enriched condition did not change the occurrence of agonistic acts, since both adult ($P = 0.71$) and juvenile/sub-adult peccaries were actors of a similar number of agonistic acts during both conditions ($P = 0.09$) (Figure 2).

The peccaries remained active during most of the observation period. However, the introduction of novel objects affected the time the peccaries remained in resting behavioural patterns, sitting or lying down. The peccaries spent approximately 20% more time resting ($F_{1,20} = 65.94$, $P = 0.000001$) during the non-enriched condition (23.3 [± 0.4] min or 11.6% of the observational time) than during the enriched condition (18.4 [± 0.6] min or 9.2% of the observational time), independently of gender ($F_{1,20} = 1.04$, $P = 0.32$) or age ($F_{1,20} = 1.12$, $P = 0.30$).

Preferences and the effects of objects in time

The statistical model showed differences in the use of furnished objects. Independently of the objects, adult peccaries played more with them than juvenile/sub-adults ($F_{1,20} = 4.8$, $P = 0.04$). There was also a difference in preference for the novel objects ($F_{2,40} = 42.6$,

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Figure 1

Mean (± SEM) number of events in which male (n = 12) and female (n = 12) white-lipped peccaries were actors of social play, solitary play, and agonistic acts in both experimental conditions (non-enriched and enriched).

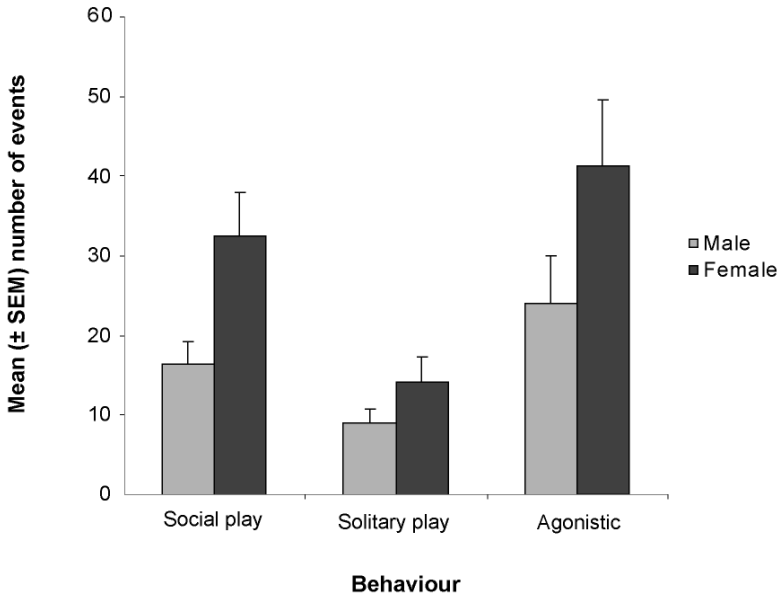
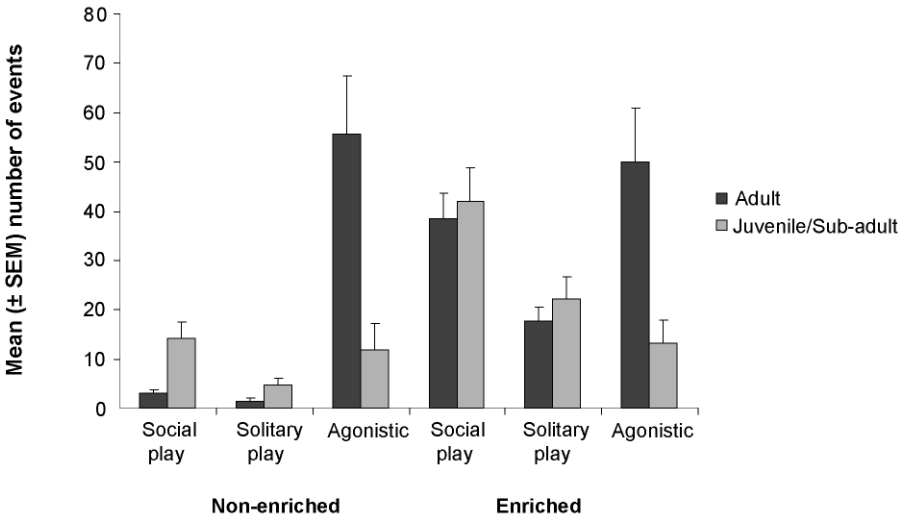


Figure 2

Mean (± SEM) number of events in which adult (n = 12) and juvenile/sub-adult (n = 12) white-lipped peccaries spent on social play, solitary play, and agonistic acts by experimental condition (non-enriched vs enriched).



P = 0.00001): independently of the gender and the age class the peccaries preferred to play with the ball, followed by the see-saw and, last, the hose (P_s < 0.006). The analyses also showed a significant interaction between age class and the type of object ($F_{2,40}$ = 25.6, P = 0.00001): adults played more than juvenile/sub-adults with the ball and the see-saw (P_s < 0.03). The juvenile/sub-adult peccaries played with the hose more than adults (P = 0.01; Figure 3[a]). Additionally, adults played more with the ball, followed by the see-saw and the hose (P_s < 0.0001; Figure 3[a]). Conversely, juvenile/sub-adult peccaries showed no preference among the novel objects (P_s > 0.53; Figure 3[a]). The model also showed an interaction between gender and objects ($F_{2,40}$ = 8.65, P = 0.0008): females played more with the ball (P_s < 0.0001; Figure 3[b]), but equally with the hose and the see-saw (P = 0.70; Figure 3[b]), while the males played less with the hose (P_s = 0.0001; Figure 3[b]) and equally with the ball and the see-saw (P = 1.0; Figure 3[b]). Comparing genders, however, we found that males and females played in the same proportion with all three novel objects (P_s > 0.53; Figure 3[b]).

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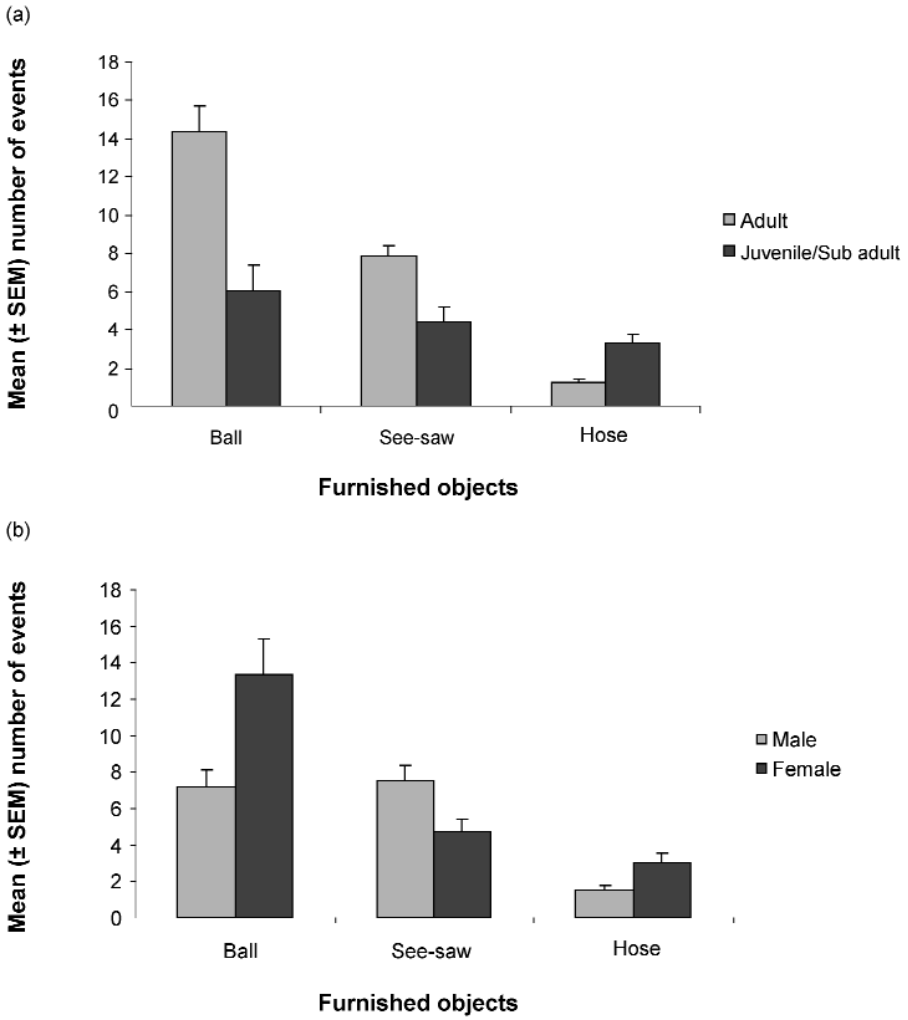
Figure 3



Novel object preferences by the white-lipped peccary according to (a) age classes and (b) gender of subjects during the enriched condition.

Play behaviour and hierarchy dominance status relationships

A linear hierarchy could be constructed based on the frequency of aggressive instances that were followed by submission, and animals could be ranked accordingly in both conditions (Table 2). Linearity of the hierarchies in both conditions was high (h' = 0.67 and h' = 0.69, for non-enriched and enriched periods, respectively), and highly significant ($P_s < 0.0001$). Regarding the direction of social dominance, the directional consistency indexes (DCI) in both periods were high and similar (DCI = 0.970 for the non-enriched and DCI = 0.974 for the enriched period). In both periods, the male AM1 was the dominant individual, while the male AM6 was the most subordinate. The individuals that occupied the highest and the lowest dominance rank positions remained in the same rank throughout both conditions, while the individuals that occupied the intermediate rank, between the 13th and 19th positions, changed their positions (Table 2), indicating dynamic social interactions.

There was a relationship between live weight and hierarchy dominance rank in both conditions: with the heaviest individuals occupying the top of the dominance rank ($r_S = –0.82$, n = 24, $P < 0.0001$ and $r_S = –0.85$, n = 24, $P < 0.0001$, during the non-enriched and enriched periods, respectively). However, only during the enriched period was a correlation found between social status rank and the occurrence of play acts. The dominant individuals played more with furnished objects than subordinates ($r_S = –0.81$, n = 24, $P < 0.0001$) in such a way that the higher an individual's social rank, the more the individual was actor of the social play interactions ($r_S = –0.86$, n = 24, $P < 0.0001$). On the other hand, the subordinate individuals were the main receivers of such interactions ($r_S = 0.43$, n = 24, $P = 0.04$). As expected, a relationship between rank and author of agonistic acts was verified in both conditions: the individuals that occupied the top of the dominance rank were the authors of agonistic interactions ($r_S = –0.54$, n = 24, $P = 0.007$ and $r_S = –0.52$, n = 24, $P = 0.009$, during the non-enriched and enriched periods, respectively). However, only a tendency was found

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Table 2 Hierarchy dominance rank and number of events each peccary was actor or receiver of agonistic and social play acts during the non-enriched and enriched conditions.

Peccary codes*	Weight (kg)	Rank	Act agon	Rec agon	Act soc play	Rec soc play	Play novel objects
Non-enriched condition							
AM1	40	1	118	0	2	13	-
AF1	42	2	82	6	4	5	-
AF2	40	3	153	15	2	2	-
AF3	39	4	87	27	4	3	-
AF4	37	5	103	23	4	4	-
AF5	36	6	57	11	9	6	-
AF6	35	7	35	12	4	3	-
SAF1	19	8	101	30	1	1	-
AM2	34	9	87	45	3	5	-
AM3	33	10	138	89	1	4	-
SAM1	18	11	25	19	15	10	-
JF1	18	12	47	38	34	28	-
SAF2	17	13	47	32	2	5	-
SAF3	8	14	35	28	6	11	-
AM4	16	15	69	51	2	2	-
SAM2	32	16	37	30	9	8	-
SAM3	16	17	64	55	13	9	-
SAM4	15	18	42	39	8	7	-
SAM5	14	19	70	53	2	0	-
JF2	29	20	74	68	1	3	-
JM1	13	21	14	13	30	26	-
SAF4	7	22	18	10	26	18	-
AM5	7	23	105	105	25	33	-
AM6	30	24	10	10	1	2	-
Enriched condition							
AM1	40	1	99	0	99	0	26
AF1	42	2	75	9	66	9	35
AF2	40	3	134	12	122	12	28
AF3	39	4	95	22	73	22	21
AF4	37	5	93	21	72	21	19
AF5	36	6	52	16	36	16	42
AF6	35	7	35	17	18	17	38
SAF1	19	8	87	26	61	26	11
AM2	34	9	77	38	39	38	23
AM3	33	10	123	77	46	77	14
SAM1	18	11	31	22	9	22	27
JF1	18	12	40	31	9	31	25
SAF2	17	13	49	32	17	32	15
SAF3	8	14	41	30	11	30	10
AM4	16	15	69	49	20	49	15
SAM2	32	16	41	29	12	29	19
SAM3	16	17	60	45	15	45	23
SAM4	15	18	45	39	6	39	10
SAM5	14	19	73	54	19	54	12
JF2	29	20	76	63	13	63	11
JM1	13	21	16	16	0	16	4
SAF4	7	22	21	12	9	12	4
AM5	7	23	99	99	0	99	7
AM6	30	24	19	16	3	16	9

* A: adult; SA; sub-adult; J: juvenile; M: male; F: female. Rank: the highest ranking individual is assigned the lowest rank number. Act agon: actor of agonistic acts; Rec agon: receiver of agonistic acts; Act soc play: actor of social play interactions; Rec soc play: receiver of social play interactions; Play novel objects: play with novel objects.

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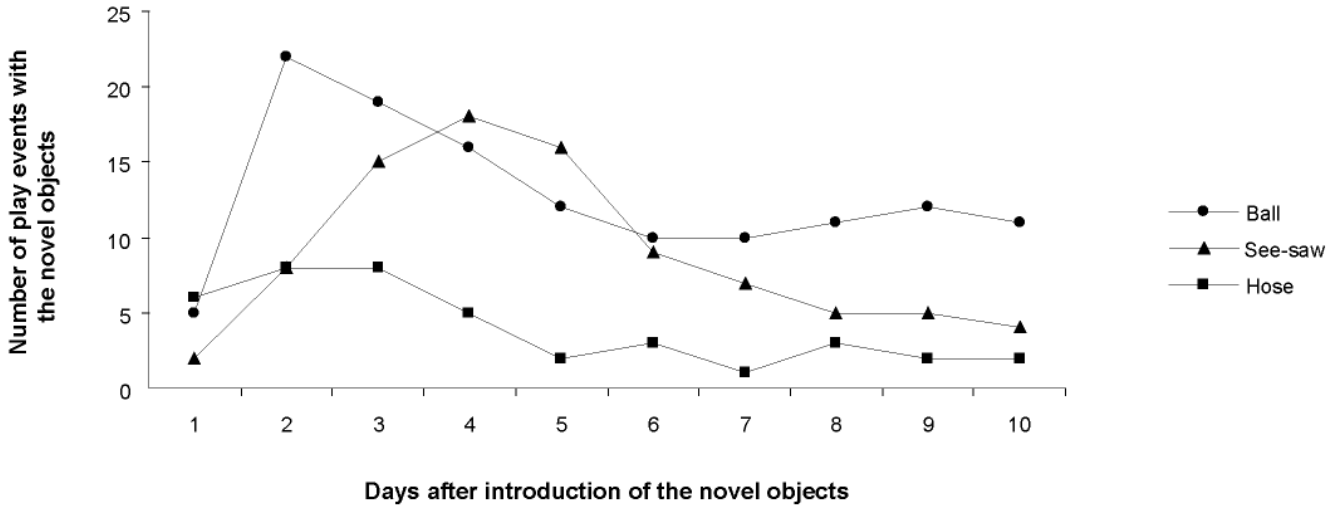
Figure 4



Peccaries' play events with the novel objects during the studied days.

to be in the bottom of dominance rank and the receiver of the agonistic acts (r_S = 0.38, n = 24, P = 0.06) during the non-enriched condition. Otherwise, after the introduction of the novel objects, the individuals that occupied the bottom of dominance rank were the receivers of agonistic interactions (r_S = 0.43, n = 24, P = 0.04).

Generally, animals interacted with all three objects from day one (Figure 4). However, the number of occurrences diverged according the object and the day. The number of play events with the ball increased sharply on the second day followed by a gradual decrease, while the number of play events with the see-saw slowly increased, peaking on the fourth day, followed by a sharp decline after day five. In contrast, the number of play acts with the hose remained virtually constant throughout the first four days. In general, the animals' interest in the objects declined after day five (Figure 4).

Discussion

The findings of our study confirmed the high occurrence of social and solitary play behavioural patterns in captive white-lipped peccaries (Dubost 2001) and allowed the classification of 11 different types of play, which were observed in individuals from all social ranks.

The introduction of novel objects aroused a general excitement irrespective of age category and augmented social and solitary play acts, thus confirming our assertion that environmental enrichment would elicit more play expression in white-lipped peccaries as previously observed for other species of mammal (Maple & Perkins 1996; Wood-Gush & Vestergaard 1991). This is highly desirable in captive animals as play can promote versatility of movement and the ability to cope with emotive situations, such as reversals in dominance (Spinka *et al* 2001). Additionally, we found that the introduction of novel objects reduced the time peccaries spent resting, another potential indicator of enhanced welfare and one advantageous for all captive animals, particularly those in re-introduction programmes (Carlstead 1996).

Furthermore, during play activities, many species are able to communicate clearly their non-competitive intentions and share signals to maintain playful ambience (Palagi 2008). Hence, play in peccary herds may be involved in helping maintain cohesion between individuals as is seen in other species (Bekoff 1977), so any manipulation which enhances play, such as environmental enrichment, could be considered beneficial for herd stability. However, the cohesive power of play behaviour is not yet a consensus for mammals (Sharpe 2005) so this aspect of play behaviour in white-lipped peccaries needs to be better understood before any concrete conclusions can be drawn in this respect.

There were also slight gender-related preferences for objects and despite there being a lack of any evident explanation for this selective pattern, the overall point is that males and females of all ages demonstrate interest in all objects — which are easy to manufacture and could be applied in other captivity centres. Notwithstanding the beneficial effects of this environmental enrichment in boosting play and reducing inactivity, our findings revealed that animals tended to lose interest in the novel objects after a few days as previously described in other species (Bracke *et al* 2006; Mason *et al* 2007). Peccary keepers may therefore have to regularly replace the objects before interest drops. Thus, for a long-term enrichment protocol of husbandry conditions, further studies are required to verify how often new objects must be introduced and/or how the animals react to the repeated presentation of previously known objects.

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During both conditions in this study we found a strictly linear — albeit dynamic — hierarchy in the peccary herd that was related to the individuals' live weight, as previously described for this species (Nogueira-Filho *et al* 1999). Social dominance was also found to play a role whereby dominant individuals played more with the novel objects than juvenile/sub-adults, most of which were subordinate individuals. We also found that females played more with some of the objects than males, perhaps because, notwithstanding the alpha position, the remaining higher ranks were occupied by females.

Although we observed increased play behaviour, our data showed no difference in the occurrence of agonistic interactions between both analysed conditions so we were unable to confirm that animals' aggression would be reduced after the introduction of novel objects (see Byers 1984; Drea *et al* 1996). One possible explanation for this is that peccaries need to define their rank status regularly (Nogueira-Filho *et al* 1999; Dubost 2001). In effect, here the adult peccaries, which need to continuously maintain their hierarchical position with agonistic displays, expressed more agonistic behaviour than sub-adult/juveniles in both enriched and non-enriched conditions. Therefore, lack of change in agonistic behaviour may not necessarily mean that enrichment manipulations do not increase welfare and may depend on the social characteristics of each species under investigation.

Animal welfare implications and conclusion

The present study provides information about the usage of environmental enrichment that will be of interest to zoos and other captive peccary centres to improve their welfare. Our results showed that the introduction of environmental enrichment enhances play behaviour both in juvenile/sub-adult and adult white-lipped peccaries and decreases inactivity. However, the animals tended to lose their motivation to play with the furnished objects five days after their introduction, suggesting that this type of enrichment must be frequently replaced. Finally, we suggest that lack of decrease in agonistic behaviour in the presence of an augmentation of play may serve as a welfare indicator in animals with strict hierarchical characteristics.

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References

Altmann J 1974 Observational study of behaviour: sampling methods. *Behaviour 49*: 223-265

Bekoff M 1972 The development of social interaction, play, and metacomunication in mammals: an ethological perspective. *The Quarterly Review of Biology 47*: 412-434

Bekoff M 1977 Mammalian dispersal and ontogeny of individual behavioural phenotypes. *The American Naturalist 111*: 715-732

Boissy A, Manteuffel G, Jensen MB, Moe RO, Spruijt B, Keeling LJ, Winckler C, Forkman B, Dimitrov I, Langbein J, Bakken M, Veissier I and Aubert A 2007 Assessment of positive emotions in animals to improve their welfare. *Physiology and Behaviour 92*: 375-397

Byers JA 1984 Play in ungulates. In: Smith PK (ed) *Play in Animals and Humans* pp 43-65. Blackwell Scientific: Oxford, UK

Bracke MBM, Zonderland JJ, Lenskens P, Schouten WGP, Vermeer H, Spoolder HAM, Hendriks HJM and Hopster H 2006 Formalised review of environmental enrichment for pigs in relation to political decision making. *Applied Animal Behaviour Science 98*: 165-182

Carrasco L, Colell M, Calvo M, Abelló MT, Velasco M and Posada S 2009 Benefits of training/playing therapy in a group of captive lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare 18*: 9-19

Carlstead K 1996 Effects of captivity on the behaviour of wild mammals. In: Thompson KV (ed) *Wild Mammals in Captivity: Principles and Techniques Managing* pp 317-333. The University of Chicago Press: Chicago, USA

de Vries H 1995 An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour 50*: 1375-1389

de Vries H 1998 Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour 55*: 827-843

de Vries H and Appleby MC 2000 Finding an appropriate order for a hierarchy: a comparison of the I&SI and the BBS methods. *Animal Behaviour 59*: 239-245

Drea CM, Hawk JE and Glickman SE 1996 Aggression decreases as play emerges in infant spotted hyaenas: preparation for joining the clan. *Animal Behaviour 51*: 1323-1336

Dubost G 2001 Comparison of the social behaviour of captive sympatric peccary species (genus *Tayassu*); correlation with their ecological characteristics. *Mammalian Biology 66*: 65-83

Dudink S, Simonse H, Marks I, de Jonge FH and Spruijt BM 2006 Announcing the arrival of enrichment increases play behaviour and reduces weaning-stress-induced behaviours of piglets directly after weaning. *Applied Animal Behaviour Science 101*: 86-101

Fagen R 1981 *Animal Play Behaviour*. Oxford University Press: Oxford, UK

Fragoso JMV 1998 Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the Northern Brazilian Amazon. *Biotropica 30*: 458-469

Fraser D and Duncan IJH 1998 'Pleasures', 'pains' and animal welfare: toward a natural history of affect. *Animal Welfare 7*: 383-396

Hall KRL 1968 Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. *Journal of Zoology 148*: 15-87

Lawrence A 1987 Consumer demand theory and the assessment of animal welfare. *Animal Behaviour 35*: 293-295

Lehner PN 1996 *Handbook of Ethological Methods*. Cambridge University Press: Cambridge, UK

Maple TL and Perkins L 1996 Enclosure furnishings and structural environmental enrichment. In: Kleiman DG, Allen ME, Thompson KV and Poole T (eds) *Wild Mammals in Captivity: Principles and Techniques Managing* pp 317-333. The University of Chicago Press: Chicago, USA

Martin P and Bateson P 1993 *Measuring Behaviour: An Introductory Guide, Second Edition* pp 222. Cambridge University Press: Cambridge, UK

Mason G, Clubb R, Latham N and Vickery S 2007 Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science 102*: 163-188

Newberry RC, Wood-Gush DGM and Hall J 1988 Playful behaviour of piglets. *Behavioural Processes 17*: 205-216

Nogueira-Filho SLG 1999 *A Criação de Cateto e Queixada Viçosa*. MG: Centro de Produções Técnicas. [Title translation: The captive breeding of collared and white-lipped peccaries]

Nogueira-Filho SLG and Nogueira SSC 2004 Captive breeding programmes as an alternative for wildlife conservation in Brazil. In: Silvius KM, Bodmer RE and Fragoso JMV (eds) *People in Nature, Wildlife Conservation in South and Central America* pp 171-190. Columbia University Press: New York, USA

Nogueira-Filho SLG, Nogueira SSC and Sato T 1999 A estrutura social de pecaris (Mammalia, Tayassuidae) em cativeiro. *Revista de Etologia 1*: 89-98. [Title translation: The social structure of the peccary in captivity]

Nogueira SSC, Silva MG, Dias CTS, Pompéia S, Cetra M and Nogueira-Filho SLG 2010 Social behaviour of collared peccary (*Pecari tajacu*) under three space allowances. *Animal Welfare 19*: 243-248

Palagi E 2008 Sharing the motivation to play: the use of signals in adult bonobos. *Animal Behaviour 75*: 887-896

Perkins LA 1992 Variables that influence the activity of captive orangutans. *Zoo Biology 11*: 117-86

Sharpe LL 2005 Play does not enhance social cohesion in a cooperative mammal. *Animal Behaviour 70*: 551-558

Sharpe LL and Cherry MI 2003 Social play does not reduce aggression in wild meerkats. *Animal Behaviour 66*: 989–997

Shepherdson DJ 1998 Introduction: tracing the path of environmental enrichment in zoos. In: Mellen JD and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 1-14. Smithsonian Institution: Washington DC, USA

Shettleworth SJ 2010 *Cognition, Evolution, and Behaviour* pp 136-166. Oxford University Press: New York, USA

Soderquist TR and Serena M 2000 Juvenile behavior and dispersal of chuditch (*Dasyurus geoffroii*) (Marusupialia: Dasyuridae). *Australian Journal of Zoology 48*: 551-560

Sowls LK 1997 *Javelinas and Other Peccaries, Their Biology, Management and Use, Second Edition.* University of Arizona Press: Arizona, USA

Spinka M, Newberry RC and Bekoff M 2001 Mammalian play: training for the unexpected. *The Quarterly Review of Biology 76*: 141-168

Taber A, Chalukian SC, Altrichter M, Minkowski K, Lizárraga L, Sanderson E, Rumiz D, Ventincinque E, Moraes EA Jr, Angelo C, Antúnez M, Ayala G, Beck H, Bodmer R, Salvador BB, Cartes JL, Bustos S, Eaton D, Emmons L, Oliveira L, Fragoso J, Garcia R, Gomez C, Gómez H, Keuroghlian A, Ledesma K, Lizcano D, Lozano C, Montenegro O, Vieira JAP, Paviolo A, Perovic P, Portillo H, Radachowsky J, Reyna-Hurtado, Rodriguez Ortiz RJ, Salas L, Duenas AS, Perea JAS, Schiaffino K, Thoisy B, Tobler M, Utreras V, Varela D, Wallace RB and Ríos GZ 2009 The destiny of the Neotropical forest architects: an evaluation of the distribution and conservation status of the white-lipped peccaries. *Suiform Sound 8*: 17-19

van Hooff JARAM and Wensing JAB 1987 Dominance and its behavioural measures in a captive wolf pack. In: Frank H (ed) *Man and Wolf* pp 219-252. Dr W Junk Publishers: Dordrecht, The Netherlands

Whitehead H 2009 SOCPROG programs: analyzing animal social structures. *Behaviour Ecology and Sociobiology 63*: 765-778

Wilson SF 1982 Environmental influences on the activity of captive apes. *Zoo Biology 1*: 201-209

Wood-Gush DGM and Vestergaard K 1991 The seeking of novelty and its relation to play. *Animal Behaviour 42*: 599-606

Yeates JW and Main DCJ 2008 Assessment of positive welfare: a review. *Veterinarian Journal 175*: 293-300

Young R 2003 *Environmental Enrichment.* Blackwell Science: Oxford, UK

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