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Original investigation

Comparison of the social behaviour of captive sympatric peccary species (genus *Tayassu*); correlations with their ecological characteristics

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Abstract

Comparison was made of the social behaviour of two congeneric peccary species, the white-lipped (*Tayassu pecari*) and the collared peccary (*T. tajacu*), coexisting in South American rain forests and observed in captivity. In the former species, herd cohesion is strong, and strangers generally are violently attacked. White-lipped peccaries have 2–3 times more contacts with partners of their herd than collared peccaries. In many social behavioural situations, the dominant female is the most active individual in the white-lipped peccary herd, whereas the dominant male is the focal member of the social unit in the collared peccary. Subordinate and subadult males participate in all social behaviour, including sexual, and are very well integrated into the white-lipped peccary herd. In contrast, subordinate collared peccary males are more or less neutral and peripheral individuals. Unlike the latter species, aggressiveness is noticeable in most behaviour of the white-lipped peccary; the dominant male is the main effector of these agonistic contacts, which are frequent and intense. In this species, both sexes belong to only one hierarchic order, with males always superior to females. Conversely, in the collared peccary, there are two distinct monosexual hierarchic orders, and the females dominate the males. These interspecific differences, as well as the total lack of ground marking in the white-lipped peccary, fit well the ecological characteristics of both species: the white-lipped peccary lives in wandering, large multiple-male herds, and the collared peccary in small stable and locally resident troops.

Key words: *Tayassu*, social behaviour, peccaries

Introduction

Unlike species in open habitats, terrestrial mammals of tropical forests are generally encountered alone or in small social units. While there are very few exceptions to this ecological rule, the Bovids (Estes 1974) and the Suiforms (Frädrich 1974; Barrette 1986; Caldecott et al. 1993) each have one or more gregarious forest species on every continent. There has been no specific study to date to examine the behavioural mechanisms underlying the formation of permanent social groups in closed terrestrial habitats.

Two peccary species (Tayassuidae), the white-lipped peccary (*Tayassu pecari* or

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Table 1. Percentage of agonistic encounters during which the two individuals are equal to each other. (CP – collared peccary; WLP – white-lipped peccary).

	CP	WLP
Male-male interactions		
adult male-adult male	0.0%	0.0%
adult male-juvenile male	20.0%	0.0%
juvenile male-juvenile male	44.4%	0/0
Total	(9/58) 15.5%	(0/101) 0.0%
Female-female interactions		
adult female-adult female	10.3%	0.0%
adult female-juvenile female	20.0%	0.0%
juvenile female-juvenile female	45.5%	1/1
Total	(11/60) 18.3%	(1/129) 0.8%
Male-female interactions		
adult male-adult female	45.6%	3.2%
adult male-juvenile female	0/4	0/0
juvenile male-juvenile female	60.0%	?
adult female-juvenile male	41.7%	0.0%
Total	(42/95) 44.2%	(5/207) 2.4%

interactions are marked and frequent, even between individuals of very different ranks (Fig. 1). Agonistic interactions between two individuals generally reveal a clear dominance of one of them. Cases of equalities are non-existent or very rare within each sex (0/101 among males, 1/129 among females), as well as between adults of different sexes ($5/154 = 3.2\%$; Tab. 1). There are therefore no or very few events where the relative status of each individual is not respected. Thus, contrasts in frequencies of equalities between the two species are always evident in each age or sex category.

In contrast to the CP, the most frequent agonistic interactions in WLP occur between males (1.39 times the frequency expected) and the least frequent between females (0.86 times the frequency expected). Adult males dominate females in 72.7% of the 154 cases observed ($X^2 = 15.84$; df = 1; $P < 0.001$). As expected, status differences are less evident between juvenile or subadult males and adult females, appearing in only 60.4% of the 53 encounters ($X^2 = 0.76$; df = 1; not significant).

In both peccary species, all 4 subordinate adult females were elevated to the top of the hierarchy immediately after giving birth. They subsequently became equal to the dominant CP female, and to the dominant WLP male.

Comparative role of different individuals within the group

Rates at which naso-body contacts, chin-layings, and mountings are seen in each social category (in average number per animal, per hour of observation and per potential partner) are similar in the two peccary species (respectively, $r_s = 1.0$, 0.95 and 0.90; $P < 0.01$ and < 0.05; $n = 6$). These behaviours are most frequent in adults: generally, rates are highest in the dominant male, next highest in females, third highest in subordinate males (Fig. 2).

For mounts occurring outside oestrus, the hierarchical order is respected among CP males. The dominant male is implicated in such behaviour 3 times more often than subordinate males: a rate of 0.027 vs 0.009 ($U = 0$; $P = 0.005$; $n_1 = 4$; $n_2 = 6$), and juveniles never. In the WLP, on the contrary, subordinates are involved as often or even more often than the dominant male: respectively 0.077 vs 0.067 ($U = 1$; $P < 0.05$; $n_1 = 3$; $n_2 = 5$) and the juveniles also participate in this behaviour (0.018). Thus, mounting has a lower hierarchical value in WLP than in CP.

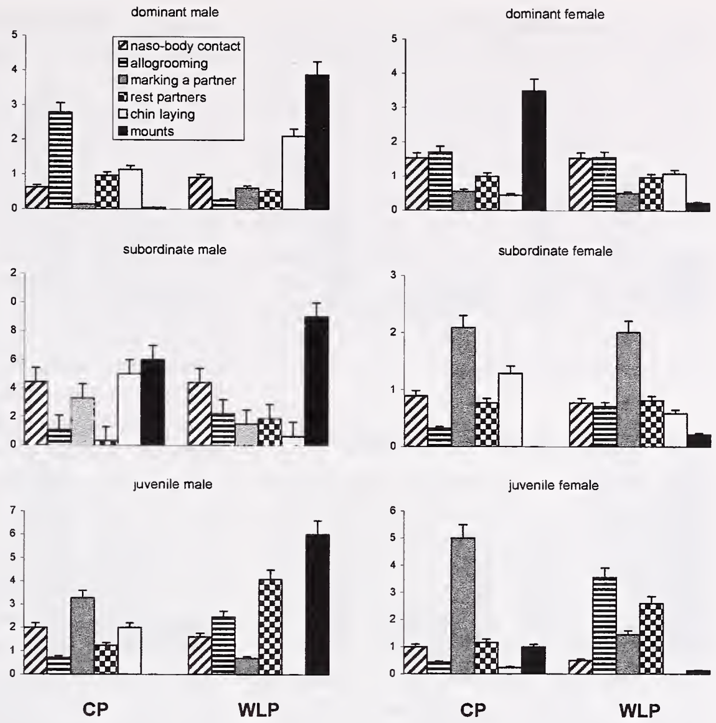


Fig. 2. Number of social behaviours or rest partners recorded in the collared peccary (CP) and white-lipped peccary (WLP) for each member of the troop per animal, per hour of observation and per potential partner (mean ± - standard error).

The relative frequencies of other behaviour vary among the different social categories from one species to the other, but without any correlation (rs varying from 0.1 to 0.8; $n = 6$; not significant). Nevertheless, some specific features appear, as shown in figure 2.

Allogrooming and marking a partner are particularly indicative of the role played by an individual in group cohesion. The major role is held by the dominant male in the CP (respectively, 0.399 vs 0.041–0.238 and 0.558 vs 0.049–0.326 in the other animals: $U = 8$; $P < 0.01$; $n_1 = 4$; $n_2 = 20$) and by the adult males and females in the WLP (respectively, 0.481–0.760 vs 0.152–0.217 and 0.468–0.802 vs 0.091–0.142 in the other animals: $U = 6$; $P < 0.01$; $n_1 = 5$; $n_2 = 14$).

CP females show an increased frequency of social play and number of rest partners compared to males: respectively, 0.030–0.033 vs 0.008–0.029, and 0.220–0.251 vs 0.080–0.193 ($U = 0$; $P < 0.001$; $n_1 = 11$; $n_2 = 13$). In the WLP, subordinate males and juvenile females are more involved in these behaviours than are other individuals: respectively, 0.076–0.102 vs 0.047–0.084 ($U = 22$; $P < 0.025$; $n_1 = 9$; $n_2 = 12$), and 0.392–0.414 vs 0.211–0.341 ($U = 0$; $P < 0.001$; $n_1 = 9$; $n_2 = 12$).

Agonistic behaviour is mainly performed by adults. Adult males and females are nearly equivalent in the CP: 0.073–0.081 vs 0.076 ($U = 32$; not significant; $n_1 = 8$; $n_2 = 12$). In the WLP, however, the dominant male is far more involved in such behaviour than the other adults: 0.288 vs 0.122–0.153 ($U = 0$; $P < 0.01$; $n_1 = 3$; $n_2 = 11$). In this species, the level of aggressiveness of each individual corresponds to its hierarchical rank.

As shown in figure 2, subordinate CP males have a limited social role, often restricted to play or agonistic contact. They do not seem to have many partners for allogrooming, marking, resting or mounting. They live more or less as satellites to the troop. In contrast, subordinate WLP males are more involved in the various social behaviours than are the juvenile males ($U = 13$; $P = 0.025$; $n_1 = n_2 = 8$). Among the WLP males, they show the most intense contacts with the different partners of their social group, especially for allogrooming, play, resting and mounting, and they are very well integrated socially.

Performer and receiver of social behaviour

In both species, naso-body contacts are made mainly by the dominant male, the dominant female and the subordinate male; the dominant male is also the main receiver (46.1–54.5% of all behaviour performed). Thus, both species appear quite similar to each other ($rs = 0.77$; $P \sim 0.05$; $n = 6$).

Social category and marking of partners also show similar associations in the two species ($rs = 0.77$; $P \sim 0.05$; $n = 6$). This behaviour is frequently performed by the second ranking female, the dominant of both sexes being the principal receiver (66.5–77.4% of all behaviour performed).

The initiation of allogrooming shows an opposite association with social categories in the two species ($rs = -0.83$; $P < 0.05$; $n = 6$). In the WLP, such initiations are common in the dominant female and the subordinate male, and the main receivers are the dominant male (26.0%) and the adult females (an average of 18.3% each). In the CP, on the contrary, initiations are chiefly performed by the dominant animals of both sexes, especially the dominant male, without any particular receiver.

There are no noticeable differences between CP individuals in rest partners, the dominant individual of each sex being both the principal donor and receiver. On the contrary in the WLP, subordinate adult males and juvenile females often join the other animals, particularly the dominant male (25.5%). Thus, the same individuals do not play the same social role in the two species, as shown by the lack of correlation between them ($rs = 0.60$; $n = 6$; not significant).

The dominant male and the second ranking female are the chief performers of chin-laying in the CP, the behaviour being mainly directed to the dominant female. In the WLP, this role is played by the dominant male and female, both also being the main receivers of such behaviour. Nevertheless, there is globally no similarity in the roles played by different individuals in the two species ($rs = -0.01$; $n = 6$; not significant).

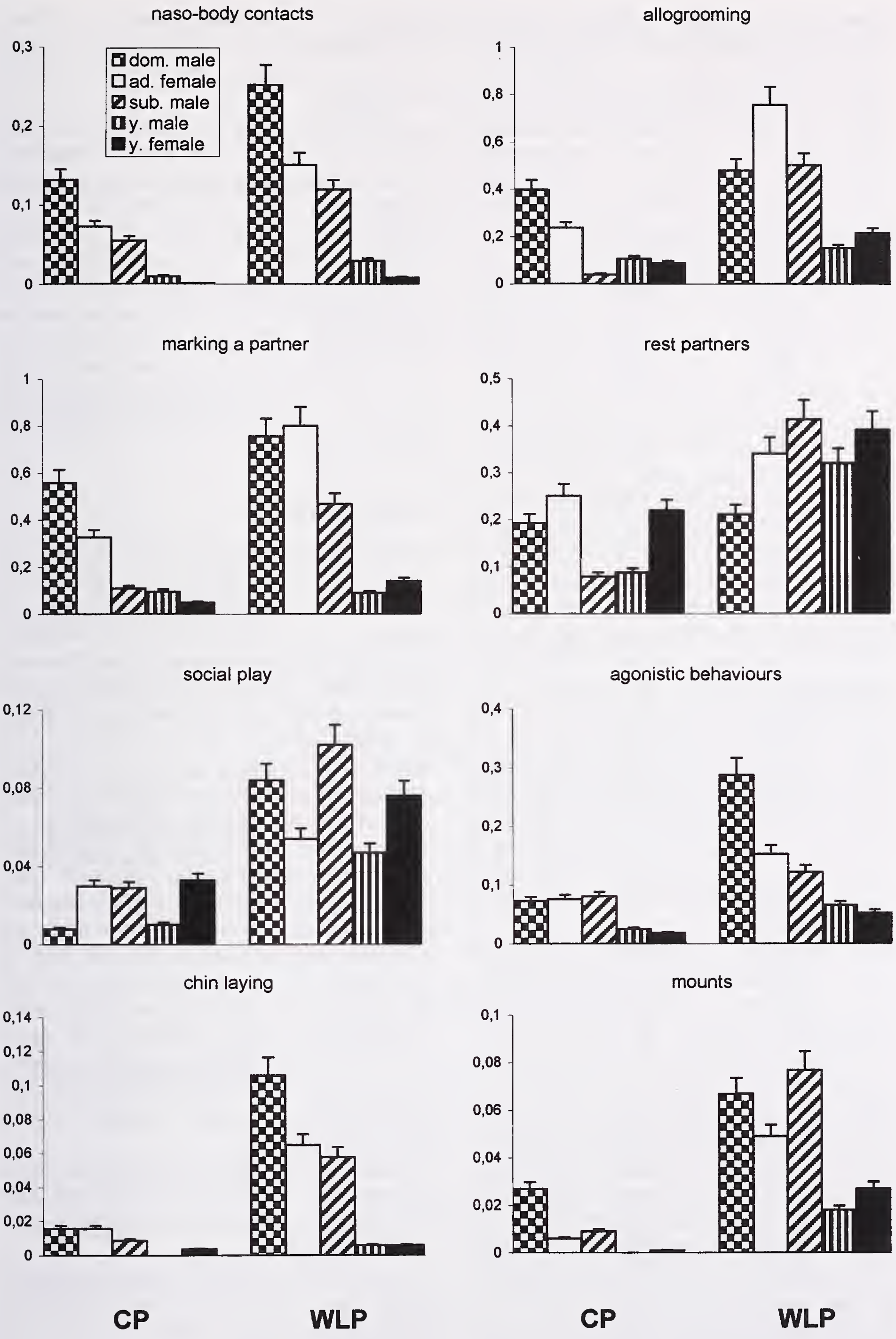
Mounts outside oestrus are usually performed by the subordinate male and by the dominant female in the CP, the dominant male being, curiously, a great receiver of such behaviour. In contrast, mounting is the prerogative of any male in the WLP, all the females being receiver animals. Thus, again, individuals behave differently in the two species and without any link between them ($rs = 0.04$; $n = 6$; not significant).

Taking into account all these behaviours, there are many differences between the two species concerning the role played by different individuals within their social group. This is evident for the juvenile males, whose involvements in the different behaviours are almost opposite in the two species ($rs = -0.81$; $P \sim 0.05$; $n = 6$). The major exception is the similarity in the social functions of subordinate females ($rs = 0.83$; $P < 0.05$; $n = 6$). Nevertheless, some other features seem shared between both species.

By calculating the ratio of the number of behaviours performed by an individual and the number received, it is possible to determine if an individual is significantly a donor or receiver of a given behaviour (Fig. 3). On the whole, the dominant CP male is a re-

▶

Fig. 3. Ratio of the number of behaviours performed to the number received by different individuals of the troop (mean ± standard error) in the collared peccary (CP) and the white-lipped peccary (WLP). Ratio >1: the animal is chiefly a performer of the behaviour; ratio <1: the individual is a receiver.


naso-body contacts
0,3
0,2
0,1
0
▩ dom. male
☐ ad. female
▨ sub. male
▥ y. male
■ y. female
allogrooming
1
0,8
0,6
0,4
0,2
0
marking a partner
1
0,8
0,6
0,4
0,2
0
rest partners
0,5
0,4
0,3
0,2
0,1
0
social play
0,12
0,08
0,04
0
agonistic behaviours
0,4
0,3
0,2
0,1
0
chin laying
0,14
0,12
0,1
0,08
0,06
0,04
0,02
0
mounts
0,1
0,08
0,06
0,04
0,02
0
CP
WLP
CP
WLP

ceiver of partner marking (24/174: $X^2 = 64.58$; df = 1; $P < 0.001$) and of mounting (1/20: $X^2 = 8.64$; df = 1; $P < 0.01$), but a donor of allogrooming (267/96: $X^2 = 41.64$; df = 1; $P < 0.001$). Conversely, the dominant WLP male is a receiver of allogrooming (72/267: $X^2 = 59.90$; df = 1; $P < 0.001$) and a donor of mounting (31/8: $X^2 = 6.18$; df = 1; $P < 0.02$). The dominant CP female is neither receiver nor donor of any behaviour, whereas its WLP equivalent is a receiver of mounting (5/21: $X^2 = 4.16$; df = 1; $P < 0.05$) and of partner marking (118/233: $X^2 = 19.30$; df = 1; $P < 0.001$). Thus, the social role of the dominant animal of both sexes differs greatly between the species.

The subordinate males of both species are more often donors than receivers. In the CP, they are donors of naso-body contacts (31/7: $X^2 = 7.08$; df = 1; $P < 0.01$) and of partner marking (33/10: $X^2 = 5.52$; df = 1; $P < 0.02$), but receivers of resting partners (8/26: $X^2 = 4.04$; df = 1; $P < 0.05$). In the WLP, they are donors of naso-body contacts (66/15: $X^2 = 16.46$; df = 1; $P < 0.001$), allogroomings (252/114: $X^2 = 24.18$; df = 1; $P < 0.001$), and mounts (45/5: $X^2 = 17.20$; df =1; $P < 0.001$), but never receivers. The same is true for the juvenile males which are, in the CP, only donors of partner marking (36/11: $X^2 = 6.06$; df = 1; $P < 0.02$), but, in the WLP, only donors of allogrooming (69/28: $X^2 = 8.22$; df = 1; $P < 0.01$) and of resting partners (53/13: $X^2 = 12.04$; df = 1; $P < 0.001$).

The subordinate females are as often receivers as donors of behaviours in both species. In the CP, they are receivers of allogrooming (45/140: $X^2 = 25.02$; df = 1; $P < 0.001$) and donors of partner marking (71/34: $X^2 = 6.02$; df = 1; $P < 0.02$); in the WLP, they are receivers of mounting (9/41: $X^2 = 10.02$; df = 1; $P < 0.01$) and donors of partner marking (239/119: $X^2 = 20.00$; df = 1; $P < 0.001$). The juvenile females are also both receivers and donors. In the CP, they receive allogrooming (31/72: $X^2 = 7.68$; df = 1; $P < 0.01$) but carry out partner marking (35/7: $X^2 = 9.06$; df = 1; $P < 0.01$); in the WLP, they receive mounts (3/22: $X^2 = 10.66$; df = 1; $P < 0.01$), but are effectors of allogrooming (192/54: $X^2 = 40.80$; df = 1; $P < 0.001$) and resting partners (135/52: $X^2 = 18.46$; df = 1; $P < 0.001$).

Except for mounts in both sexes of the WLP, there are no cases where both the dominant and the subordinates or juveniles of the same sex are both performers or receivers of the same behaviour, and many similarities exist between subordinate and juvenile individuals in both species. In contrast, the subordinate adult males tend to seek contact with more troop members in the WLP than do their equivalents in CP ($U = 2$; $P = 0.057$; $n_1 = n_2 = 4$). The same difference exists in partner choice for social play.

Partner choice

Twelve different pairings were identified in each species according to sex, age and social status of the individuals. For each behaviour, the mean number of observations made on each pair was calculated. The most active pairs (number of observations ≥50% that of the best pair) are particularly distinguished in table 2.

Looking at all pairs, there are detectable differences between the species in choice of partners for playing, allogrooming or resting. The differences are principally due to the fact that the dominant male and the adult females have more frequent contacts with juveniles of both sexes for allogrooming and rest in the CP than in the WLP ($U = 1$; $P = 0.029$; $n_1 = n_2 = 4$). In contrast, the subordinate WLP adult males tend to seek contact with more troop members than do their CP equivalents ($U = 2$; $P = 0.057$; $n_1 = n_2 = 4$). The same difference exists in partner choice for social play.

As a rule, young of both sexes are preferred play partners in both species. Nevertheless, the dominant CP male never plays with a juvenile female.

Allogrooming is more frequent between adults than with or between juveniles in the WLP ($U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$), in contrast to the CP.

Table 2. Mean number of behaviours performed by each pair of partners, according to different social categories. *: number of observations equal to or greater than 50% that of the best pair. CP: collared peccary; WLP: white-lipped peccary.

Pairs of partners	Behaviour	CP	WLP
MALE-MALE INTERACTIONS			
dominant male-subordinate male			
	naso-body contacts	4.17*	8.00*
	allogrooming	0.33	27.02*
	marking a partner	4.50	26.80*
	rest partners	0.33	12.60*
	social play	0.00	4.20
	agonistic behaviours	4.00*	12.80*
	chin-laying	0.00	4.00*
	mounts	1.00*	0.80
dominant male-juvenile male			
	naso-body contacts	1.00	2.00
	allogrooming	14.67*	4.00
	marking a partner	8.00	7.33
	rest partners	9.67*	2.33
	social play	0.67*	1.33
	agonistic behaviours	2.67*	1.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
subordinate male-juvenile male			
	naso-body contacts	1.33	1.33
	allogrooming	0.67	3.33
	marking a partner	1.67	0.67
	rest partners	3.33	9.00*
	social play	0.00	7.00*
	agonistic behaviours	2.00*	0.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
FEMALE-FEMALE INTERACTIONS			
adult female-adult female			
	naso-body contacts	0.89	2.06
	allogrooming	3.22	26.86*
	marking a partner	7.28	28.42*
	rest partners	4.63	12.40*
	social play	0.11	0.86
	agonistic behaviours	2.17*	2.07
	chin-laying	1.06*	1.17
	mounts	0.00	0.38
adult female-juvenile female			
	naso-body contacts	0.08	0.17
	allogrooming	1.89	7.67
	marking a partner	0.34	5.27
	rest partners	6.94*	9.11*
	social play	0.48	0.45
	agonistic behaviours	0.50	1.06
	chin-laying	0.00	0.00
	mounts	0.00	0.00
juvenile female-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.00	5.33

Table 2. (Continued).

Pairs of partners	Behaviour	CP	WLP
	marking a partner	0.33	0.66
	rest partners	11.00*	11.67*
	social play	1.00*	13.67*
	agonistic behaviours	0.00	0.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
MALE-FEMALE INTERACTIONS			
dominant male-adult female			
	naso-body contacts	3.31*	2.20
	allogrooming	15.53*	9.50
	marking a partner	20.34*	19.95*
	rest partners	6.39*	4.13
	social play	0.17	2.00
	agonistic behaviours	1.20	6.77*
	chin-laying	0.89*	2.12*
	mounts	0.47	1.19
subordinate male-adult female			
	naso-body contacts	0.61	2.50
	allogrooming	1.09	14.93*
	marking a partner	1.39	11.40
	rest partners	1.17	11.27
	social play	0.22	2.70
	agonistic behaviours	2.31*	1.73
	chin-laying	0.22	0.83
	mounts	0.06	2.83*
juvenile male-adult female			
	naso-body contacts	0.00	0.33
	allogrooming	3.83	6.33
	marking a partner	4.50	2.78
	rest partners	8.50*	7.45*
	social play	0.00	0.45
	agonistic behaviours	1.50	0.33
	chin-laying	0.00	0.33
	mounts	0.00	0.33
dominant male-juvenile female			
	naso-body contacts	0.00	0.50
	allogrooming	4.17	5.17
	marking a partner	5.50	5.83
	rest partners	3.13	8.50*
	social play	0.00	2.17
	agonistic behaviours	0.00	0.50
	chin-laying	0.33	0.78
	mounts	0.25	2.83*
subordinate male-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.67	5.17
	marking a partner	0.66	1.17
	rest partners	1.25	10.33*
	social play	0.44	7.33*
	agonistic behaviours	0.08	0.00
	chin-laying	0.00	0.17
	mounts	0.00	0.67

Table 2. (Continued).

Pairs of partners	Behaviour	CP	WLP
juvenile male-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.89	3.00
	marking a partner	3.94	0.34
	rest partners	7.17*	9.33*
	social play	0.08	6.67
	agonistic behaviours	0.78	0.00
	chin-laying	0.22	0.00
	mounts	0.00	0.67

In the CP, but not in the WLP, resting groups including juveniles tend to be more frequent than those comprising only adults ($U = 6$; $P = 0.055$; $n_1 = 4$; $n_2 = 8$). Thus, an adult CP female generally lies with her juveniles of different litters. The dominant male may take part in such groups, in contrast to the WLP, where the dominant male rarely lies near a juvenile male or an adult female.

In other behaviours both species show comparable partner choices. Thus, significant similarities exist between CP and WLP for marking, chin-laying and agonistic behaviour ($rs = 0.6$; $P < 0.05$; $n = 12$) as well as for naso-body contact and mounting ($rs = 0.8$; $P < 0.01$; $n = 12$).

In both species, naso-body contacts are more frequent between adults than with or between juveniles ($U = 4$; $P = 0.024$; $n_1 = 4$; $n_2 = 8$ in the CP; $U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$ in the WLP) and are chiefly performed by the subordinate males on the dominant, or by the dominant and subordinate males on adult females. Contacts between adults are also or tend to be more frequent in both species for agonistic behaviour ($U = 5$; $P = 0.036$; $n_1 = 4$; $n_2 = 8$ in CP; $U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$ in WLP), and for mounting ($U = 5$; $P = 0.036$; $n = 4$; $n_2 = 8$ in CP; $U = 6$; $P = 0.055$; $n_1 = 4$; $n_2 = 8$ in WLP).

Marking a partner and chin-laying are also more frequent among adults in the WLP ($U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$), but not in the PC. Partner marking occurs chiefly between adults of the same sex in the WLP (dominant male with subordinates, adult females with adult females), and between adults of different sexes (dominant male with females) in the CP. Apart from the dominant male-adult female pair in both species, chin-laying often occurs between adult females in the CP, and conversely between adult males (dominant-subordinate) in the WLP.

The most frequent agonistic contacts in the CP take place between males, or between a given adult female and another adult except the dominant male. In the WLP, most behaviour results from the dominant male performing agonistic acts towards subordinate males or adult females.

An important difference between both species therefore resides in the fact that in the WLP the subordinate male is a favoured partner of the dominant male for many behaviours, whereas in the CP the same role is held by the adult females.

However, these specific preferences are inverted for mounts occurring outside oestrus, 56.5% of them involving two males in the CP (the subordinate males mounting very often the dominant one), whereas, in contrast, 87.8% of the mounts in the WLP occur between partners of different sexes (48.1% between a subordinate male and an adult female). Thus, in both species mounts play a social role that differs from the other behaviours.

Frequency of interindividual contacts within the group

Frequency of social behaviours

Taking into account the average number of pooled social behaviour involving one given individual (per hour and per potential partner), it appears that each WLP has generally 2 to 3 times more social contacts with its partners than an equivalent CP (Tab. 3). On the other hand, both species are very similar in the relative frequencies of individual social behaviour (rs = 0.94; P = 0.01; n = 6), although sexual behaviour is more frequent in the WLP. In both species, marking a partner and allogrooming are the two most frequent social behaviours.

Compared to the CP, this greater degree of social contact within a WLP group is also noticeable during rest periods. Each individual rests on the average with 0.35 partners/hour (number of rest partners observed/number of potential partners), compared with 0.20 in the CP. Thus, group sizes during resting periods are significantly 1.75 times larger in the WLP than in the CP (t = 6.02; df = 85; P < 0.001). This is the case despite the smaller number of individuals in the WLP groups (4–11 animals in WLP vs 7–16 in CP).

Group cohesion

The degree of grouping of individuals during activities is indicative of the cohesion level of each group. In this respect, several differences between the two species are apparent.

In the CP, one or more individuals frequently remain apart from the group in a portion of the enclosure distant from the group's location. These individuals are neither socially expelled nor actively chased out. At feeding time, they approach the food long after the others. In contrast, all the WLP individuals come together in a very homogeneous unit.

During diurnal activities, the grouping of individuals is lower in CP than in WLP: in the former, only 3% of the individuals being separated from the group, compared to 4.5% in the latter ($X^2 = 4.7$; df = 1; $P < 0.05$). In the CP, this trend is more apparent during the afternoon than in the morning (1.6% isolated individuals against 4.4%: $X^2 = 14.94$; df = 1; $P < 0.001$), in contrast to the WLP whose percentages are quite similar for both periods (respectively 4.0% and 5.0%: $X^2 = 0.47$; df = 1; not significant). This could mean that there are qualitative changes in the CP behaviour throughout the day: more movements and foraging in the morning, and frequent social interactions in the afternoon.

On the whole, CP shows also a weaker allomimetic behaviour than WLP: individuals perform a behaviour different from that of the rest of the group in 19.6% of the cases in the former, against 16.0% for the latter species ($X^2 = 64.5$; df = 1; $P < 0.001$). Unlike WLP, CP copy each other less during the morning than in the afternoon: respectively, 23.2% and 15.8% of the animals perform activities different from the rest of the troop ($X^2 = 19.39$; df = 1; $P < 0.001$).

During resting periods, the dominant male and female of both species are encountered more often alone than the juveniles: respectively 28.4–48.6% cases against 3.2–11.1% ($X^2 = 28.6$ to 52.5; df = 1; $P < 0.001$). Subordinate adult males usually rest more often alone in the CP than in the WLP (70.8% vs 30.9%: $X^2 = 31.7$; df = 1; $P < 0.001$). The same is true for subadult males (20–22 months old): CPs rest alone 4 times more often than the WLPs (30.8% vs 7.6%:

Table 3. Average number of social behaviours recorded for each individual, per hour and per potential partner. CP: collared peccary; WLP: white-lipped peccary.

	CP	WLP	WLP/CP
Marking a partner	0.23	0.57	2.48
Allogrooming	0.17	0.52	3.06
Agonistic behaviours	0.06	0.16	2.67
Naso-body contact	0.05	0.13	2.60
Social play	0.03	0.06	2.00
Sexual behaviours	0.02	0.10	5.00
Total	0.56	1.54	2.75

$X^2 = 11.8$; df = 1; $P < 0.001$). On the other hand, subordinate WLP adult females rest alone more often than the CPs (43.9% vs 26.0%: $X^2 = 6.95$; df = 1; $P < 0.01$).

Integration of new members into the group

During tests of sexual receptivity with penned animals, it was always possible to present a female to a new male without any risk in the CP. The opposite often occurs in the WLP: on several occasions under enclosure conditions, a male attacked a "new" female so violently that we had to urgently remove the female and abandon the test.

Discussion

The behavioural repertoires of these two forest peccary species are broadly similar to each other with few exceptions (Dubost 1997). Contrary to many other suiforms which live either in permanent pairs or in unisex social units outside the reproductive period (Bigourdan 1948; Gundlach 1968; Frädrich 1974; Beuerle 1975; Kiltie and Terborgh 1983), mixed groups are the basis of the peccary social system. This fact is favoured by the persistence of sexual activity throughout the year. There is never any sexual segregation, even before or after birth. The two species mainly diverge in the frequency or mode of appearance of behaviours rather than in any real inequality in behavioural repertoire. However, some qualitative or quantitative differences, especially concerning social interactions, are sometimes significant enough to reveal a true divergence in their biology. These follow directly from specific etho-ecological characteristics of each species.

Behavioural differences between both species

In both species, young or subordinate animals of both sexes frequently mark partners. This observation, also made by Schmidt (1976) for the CP, contradicts the assertion of Sowls (1974) that dominant animals are the main effector of such behaviour. Likewise, allogrooming in the WLP is commonly initiated by juveniles of both sexes and subordinate males, and to a lesser degree by dominant females. In the CP, on the contrary, this behaviour is chiefly performed by the dominant animals of both sexes, especially the dominant male. This fact, also noted by Schmidt (1976), distinguishes the CP from most other mammals where dominants are generally groomed by subordinates, e. g. *Papio hamadryas* (Kummer 1968), *Bos taurus* (Walther 1979).

Contrary to evidence on several ruminants (Walther 1979), mounts in peccaries do not have any aggressive significance; they do not play the same role in both species. In male CPs they occur in accordance with hierarchical order, but not so in the WLP. This means that mounting has a different social role and a lower hierarchical value in WLPs than in CPs.

As previously noted by Sowls (1974) and Schmidt (1976), female CPs are slightly dominant to males, but in the WLP, males dominate females, as in several suids (Frädrich 1965) as well as in ruminants living in mixed herds – e. g. *Taurotragus*, *Bison*, *Syncerus* (Estes 1974; Walther 1979). However, in both peccary species, subordinate females are elevated immediately after giving birth to the top of the hierarchy, a fact also observed by Schweinsburg and Sowls (1972) in the CP.

In the CP, but not in the WLP, resting groups often include an adult female with her juveniles of different litters, which led Schmidt (1976) to use the term "clan". Furthermore, according to Lochmiller and Grant (1982), groups of CP are highly bonded units, whose members are intolerant of strangers of the same sex. As reported by Schmidt (1976) and Byers and Bekoff (1981), individuals which were temporarily separated from the group lost their former social status and were never completely reintegrated. However, this exclusion does not seem to exist between sexes, because it was always possible to present a CP female to a new male without any risk, contrary to the WLP. We do not know if the intolerance observed in the latter species is triggered by the odour of the stranger and corresponds to a type of group defence, but it fits well with the high level of natural agressiveness observed in this species (Dubost 1997).

Social behaviour in relation to group size

WLP live in large herds, comprising generally from 30 to 200 animals, and including many adult males, females, and juveniles of all ages (Kiltie and Terborgh 1976, 1983; Sowls 1984; Mayer and Wetzel 1987; Benirschke et al. 1989; Hernandez et al. 1995; Peres 1996; Fragoso 2000; Judas pers. comm.; pers. data). Such social structure appears relatively unique among the artiodactyls, permanent aggregations of so many mature individuals of both sexes being only known seasonally in several migratory, open country ruminants, such as *Antilope cervicapra* (Mungall 1978), *Connochaetes taurinus* (Estes 1969) and others (Walther 1979), but exceptionally also among some forest suids, like *Sus barbatus* (Pfeffer 1959; Frädrich 1974; Caldecott et al. 1993).

Conversely, the social unit of the CP is generally composed of a limited number of individuals: 1–2 adult males and 1–3 adult females, with several young of different ages. Such small groups are found in French Guiana (Judas pers. comm.) as in other forest regions (Kiltie and Terborgh 1976, 1983; Robinson and Eisenberg 1985; Bodmer et al. 1988; Peres 1996).

When individual WLPs search for food, they are frequently at a distance from each other, the whole herd being spread out over several tens or hundreds of meters. Because the physical forest environment is largely obstructed at ground level, individuals need mechanisms for intercommunicating efficiently at short and medium distances to ensure herd cohesion. In contrast to CP, visual, acoustic or olfactory signals are particularly well developed in WLP, both in expression and in intensity: spectacularly bristled hairs; prolonged yawning as intimidation, loud blowing, grunts, teeth snaps or cries of the young (Kiltie and Terborgh 1976, 1983; Sowls 1984; Mayer and Wetzel 1987; Hernandez et al. 1995; Dubost 1997); strong odor (Benirschke et al. 1989; Dubost 1997).

The WLP is heavier than the CP: a mean of 37.1 kg for the adult males and 35.7 kg for the adult females in French Guiana, versus, respectively, 22.1 kg and 19.5 kg (Dubost 1997). Unlike the CP, the large body size of individual WLPs belonging to a well-populated and powerful herd provides protection against potential predators and dispenses with the need for cryptic behaviour. This species has the reputation of attacking jaguars en masse (Kiltie and Terborgh 1983).

Herd cohesion of the WLP must also be facilitated by the behaviours themselves. The results of this study indicate that social behaviours are from 2.5 to 6.4 times more frequent in this species than in CP. Likewise, during resting periods, the grouping of individuals at the same spot is almost twice as high in the former than in the latter. Furthermore, in comparison with the CP, the WLP shows a generalization of some behaviours, which are performed by most members of the herd, rather than just by one or several individuals. Such behaviours include collective fear, body rubbing on the ground in all individuals, play often being contagious, penis trembling and mount by all males. Several other behaviours occur in a very demonstrative manner, including strong reactions to anxiety situations, urinary marking on the standing female, play with objects, marked body displays in threat or submission situations, frequent and strong attacks (Dubost 1997).

In the WLP, the involvement of most individuals of the same herd in different social behaviours is also noticeable in sexual behaviour. In this species, all the numerous adult or subadult males are reproductive and may copulate with the females, regardless of their relative hierarchical position (pers. obs.), as described in some other mammals (SMUTS 1987).

On the contrary, only the dominant male is reproductive in the CP. It is the only one to court and copulate with the few reproductive females of the group (BISSONETTE 1976; SCHMIDT 1976; pers. obs.). All the other males show much lower sexual hormone levels (HELLGREN, in HANNON et al. 1991; pers. data); they avoid the proximity of the receptive females. Unlike most other artiodactyls and many mammals, they were never observed to be pushed away by the dominant male, as also noted by SOWLS (1974), SCHMIDT (1976), and BYERS and BEKOFF (1981). Furthermore, they do not leave the social unit to live alone or grouped together in a bachelor herd, like *Sus scrofa* and *Phacochoerus* (BIGOURDAN 1948; FRÄDRICH 1974; BEUERLE 1975; BARRETTE 1986), the tylopods and many ruminants (KOFORD 1961; DAVID 1973; ESTES 1974; FRANKLIN 1974; GOSLING 1974; JOUBERT 1974; SPINAGE 1974; MUNGALL 1978), and several *Equus* species (KLINGEL 1974). The fact that these surplus adult males can stay inside the social unit is perhaps due to their sexual inactivity, provided they behave submissively, as in *Hippopotamus* (KLINGEL, in ELTRINGHAM 1993) or *Hylochoerus* (D'HUART 1993).

The life within a rather considerable herd does not allow individual WLPs to establish such an elaborate and fine contact with each other as in the CP, whose groups function as very well coordinated and stable units. In the WLP, there are, indeed, frequent encounters between animals with little knowledge of each other, each individual having to define its own place in relation to its partner. One can understand why, contrary to the CP, most interindividual contacts, even sexual ones, are of a very aggressive nature in the WLP, as noted also by FRÄDRICH (1986) and BENIRSCHKE et al. (1989). In contrast, there are pronounced displays for appeasement and submission purposes (DUBOST 1997). Likewise, this species shows a rather strict social organization, where all individuals of both sexes are included in the same linear hierarchy. Finally, since social units need to remain distinctive within a complex herd, its members are forced to stay close to each other. This would function to strengthen the bonds uniting them and to guarantee their relative isolation within the herd, when necessary, as displayed by the female WLP with her young (DUBOST 1997).

Thus, the WLP herd can be considered as a multi-male society, whereas the social unit of CP corresponds more to a harem or pseudo-harem. Moreover, some intermediate situations between these specific social organizations have been observed. Indeed, the formation of a harem in the CP seems directly dependent on the group size. SOWLS (1974), BYERS and BEKOFF (1981), PACKARD et al. (1991) observed, both in captivity and in nature, instances of sexual promiscuity within large groups.

Differences of social life between wandering and locally fixed groups

Another main difference between both species lies in the fact that herds of WLP travel more or less constantly throughout a huge area. In the absence of precise biological data, this species was considered nomadic and capable of travelling great distances (KILTIE and TERBORGH 1983; SOWLS 1984; HERNANDEZ et al. 1995; PERES 1996). But recently, FRAGOSO (2000) produced data indicating that herds of WLP can live for a long time on vast home ranges of 22–110 km^2, where they move over long distances but do not migrate. Quite the contrary, each group of CP is permanently attached to a well-defined terrain, covering an average area of only 190 ha in French Guiana (JUDAS pers. comm.). One finds here the classical link uniting the social behaviour of a species with the characteristics of its environment, as noted in many other artiodactyls.

Life in a moving herd does not require to deposite marks on the ground. Thus, the WLP does not show the behaviours that allow the CP, especially the dominant male, to assert its presence in the area where the group resides. Indeed, the WLP shows no sign or behaviour indicating any direct bond with the ground occupied, like defecation site or glandular marking. The home range of a WLP herd studied by Fragoso (2000) was almost completely encompassed by that of another, and the two herds were found together several times at the same site. The WLP sociality is thus nearly exclusively dependent on the exchanges existing between the individuals themselves; inter-individual contacts are particularly frequent in this species. It is also significant that WLP males never urinate on a female lying on the ground, as do CP males, but only on standing or moving females (Dubost 1997).

Finally, the more or less continuous travelling of a WLP herd demands that individuals be well synchronized during their activities. This is achieved by mass effects and allomimetic behaviour. In counterpart, the great social cohesion, as observed also by Fragoso (2000) in the wild, engenders a marked intolerance towards strangers.

On the other hand in the CP, each home range is generally distinct and belongs to only one social group, even if neighbouring home ranges overlap greatly. Each home range has several rest places (Hernandez et al. 1995; Judas pers. comm.) and defecation sites (Hernandez et al. 1995; pers. obs.). According to Bissonette (1976), the home range is regularly marked by the locally resident adult male which asserts both his status and presence by many behaviours, including surveillance, defence of the group in case of danger, display with bristled hairs and ceremonial gait, continuous olfactory control of all partners, emission of urine when walking, scraping and glandular marking of the ground and dropping of faeces on distinctive places (Dubost 1997). The behaviour of the CP appears therefore comparable to that found in many ruminants, and perhaps also in hippopotamuses and several suids (Frädrich 1974).

The harem or pseudo-harem of the CP differs from those of many ruminants by including several subordinate adult males (David 1973; Estes 1974; Gosling 1974; Joubert 1974; Spinage 1974; Mungall 1978). The fact that it stays constantly with the same dominant male within one locally fixed home range differs also from the ruminant harem, but resembles what is known in *Vicugna* (Koford 1961; Franklin 1974). Nevertheless, this similarity is only apparent, because the harem of *Vicugna* lives on two small territories separated from each other by neutral ground.

Most behavioural differences between both peccary species thus appear to be the direct result of the way of life adopted by each. In this context, it is reasonable to suppose that the Chacoan peccary, *Catagonus wagneri*, shows a social organization similar to that of the collared peccary, owing to the great resemblances of these species in both behaviour and group composition (Mayer and Brandt 1982; Mayer and Wetzel 1986).

Similar variations in social behaviour could exist in Old-World primates. Indeed, between primate species living in multi-male troops and those forming harems, obvious differences exist in the size of the social units, level of sociality, marking, function of the dominant male as the nucleus of the group, nature of the male-female relations, and hierarchical system (Rowell 1988).

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Zusammenfassung

Vergleiche des Sozialverhaltens zweier sympatrischer Pekariarten (Genus *Tayassu*) in Menschenobhut; Beziehungen mit ihren ökologischen Merkmalen

Die Vergleiche des Sozialverhaltens wurden zwischen dem Weißbart-Pekari (*Tayassu pecari*) und dem Halsband-Pekari (*Tayassu tajacu*) in Menschenobhut durchgeführt, die beide im südamerikanischen Regenwald leben. Beim Weißbart-Pekari gibt es einen engen Rudelzusammenhalt und Gruppenfremde werden im allgemeinen heftig angegriffen. Die Individuen haben zwei- bis dreimal mehr Sozialkontakt mit Gruppenmitgliedern als die Halsband-Pekaris. In vielen sozialen Verhaltensweisen ist beim Weißbart-Pekari das dominante Weibchen das aktivste Individuum, während beim Halsband-Pekari das ranghöchste Männchen das meistbeachtete Mitglied der Sozialeinheit ist. Randniedere und subadulte Männchen beteiligen sich bei allen sozialen Interaktionen und sind bestens in das Rudel integriert. Beim Halsband-Pekari dagegen leben rangniedere Männchen mehr oder weniger als neutrale und periphäre Individuen. Völlig verschieden verhält sich das Weißbart-Pekari mit beträchtlicher Aggressivität in der Mehrzahl der Auseinandersetzungen, wobei das ranghohe Männchen der Hauptinitiator der häufigen und intensiven agonistischen Interaktionen ist. Bei dieser Art unterliegen beide Geschlechter einer einzigen, alle Rudelmitglieder einschließenden Rangordnung, in der die Männchen den Weibchen stets überlegen sind. Beim Halsband-Pekari dagegen gibt es zwei getrennte, geschlechtsspezifische Rangordnungen und beim zwischengeschlechtlichen Kontakt dominieren die Weibchen über die Männchen. Diese zwischenartlichen Unterschiede und das völlige Fehlen einer Bodenmarkierung beim Weißbart-Pekari verdeutlichen die ökologischen Merkmale beider Arten. Während das Weißbart-Pekari in großen Mehrmännchen-Rudeln umherzieht, lebt das Halsband-Pekari in kleinen stabilen und lokal seßhaften Rotten.

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