



# Dominance hierarchy and social network in a captive group of white-lipped peccary males: what happens after the alpha male leaves?

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## Abstract

Dominance hierarchies are typically stable, with dominants occupying central positions in social interaction networks. However, system perturbations, such as the removal of individuals, may cause instability, which varies according to the group's resilience. If the hierarchy undergoes a restructuring, this can occur through a dynamic process of self-organization (Social Dynamics hypothesis) or through the influence of individuals' attributes (Previous Attributes hypothesis). We analyzed the resilience of the white-lipped peccary hierarchy after the alpha's death and observed how the rise of a new dominant occurred. Additionally, we evaluated the validity of these two hypotheses in the restructuring of the system. We observed the group of white-lipped peccary males of the Municipal Zoo of Curitiba, PR, Brazil, from May to October 2018. We recorded and analyzed the agonistic and affiliative interactions, and we collected data from the attributes: weight, testicle size, testosterone serum and age, before and after the dominant's death (August). Due to this perturbation, the hierarchy started to show instability, but proved to be resilient. There was an increase in agonism and more than one individual pleading for the new dominant position, which was occupied by a subordinate male. Affiliative interactions were also important in the rise of the new alpha. The hierarchy was well ordered by the social dynamics among individuals, but weight and testicular volume were also correlated with the status of the individuals before, and with the serum testosterone after the alpha's death. Thus, both hypotheses affected the restructuring of this system.

**Keywords** Previous attributes · Self-organization · Social interactions · Social network analysis · *Tayassu pecari* · Tayassuidae

## Introduction

Group life favors individuals through obtaining food resources, mating possibilities, better offspring survival, and reducing the predation risk (Bonabeau et al. 1999; Horová et al. 2015). However, when resources become

scarce, animals start to dispute them, which creates agonistic conflicts (Holekamp and Strauss 2016) and a consequent attempt to monopolize the resource, which can also lead to fitness monopolization (Vervaecke et al. 2007; Sánchez-Tójar et al. 2018). As these confrontations occur, the group may show an organization that becomes stable with the establishment of dominant and subordinate relations among all group members, until the dominance hierarchy formation (Bonabeau et al. 1999; Holekamp and Strauss 2016).

The hierarchy structure is related to the level of social information that individuals have access to, that is, how they can or cannot assess themselves and their opponents, to then decide which struggles they should fight for (Hobson 2020). In the low level of social information, individuals use only their own experience in making decisions (Hobson 2020). So, in the "Social Dynamics" hypothesis, the hierarchy would be formed through a process of self-organization, mediated mainly by a double reinforcement effect, the "winner-loser"

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effect, which is when winners are more likely to win subsequent clashes and losers, to lose (Dugatkin 1997; Bonabeau et al. 1999; Hsu and Wolf 1999; Chase et al. 2002; Franz et al. 2015b). At moderate levels of information, individuals can assess the specific characteristics of their opponents (Hobson 2020). This mechanism is called “Previous Attributes” hypothesis and suggests that animals have, a priori, characteristics that would indicate their ability to dominate the hierarchy (Bonabeau et al. 1999; Chase et al. 2002; Franz et al. 2015b). At higher levels of information, individuals can infer their own status and that of their opponents, even without interacting with them (Hobson 2020).

The individual attributes frequently related to the rise of the dominance hierarchy are physical, physiological or genetic (Chase and Seitz 2011). One of the most studied physical attributes is the size of individuals, in weight or length, with larger individuals showing dominance over smaller ones (Brace and Pavey 1978; Haley et al. 1994; Matthews and Wong 2015; López-Segoviano et al. 2018; Gilpin and Chadwick 2019). Another physical attribute is the testicle size (Setchell and Dixson 2002; Aguirre et al. 2007), since in many species the hierarchy also establishes individuals with priority in accessing sexually receptive females (Spong et al. 2008; Miller et al. 2010). Among the physiological attributes, hormone concentrations stand out, mainly testosterone, which seems to mediate dominance behaviors, which may or may not include aggression (Muller and Wrangham 2004; Beehner et al. 2006; Eisenegger et al. 2011). In addition to these, age, sometimes related to the size of the body and testicles in young and adult individuals, has been investigated as a predictor of dominance, when older animals are dominant over younger ones (Šárová et al. 2013; Lukianchuk and Doucet 2014; Moreno-Opo et al. 2020).

In addition to the establishment of dominance hierarchies, the social context of a species can be investigated through the dynamics of interactions between the group, which constitutes the approach of social networks (Shizuka and McDonald 2012). Constant variations in the network structure, expected in response to changes in the environment, directly influence groups, especially their survival and reproductive success (Pinter-Wollman et al. 2014; Shizuka and Johnson 2020). This influence can be more or less significant, depending on how the system and interactions are modified (Kurvers et al. 2014). However, little is known about the permanence of individuals in their social roles in face of structural changes (Pinter-Wollman et al. 2014) or high turnover of elements, as in demographic processes (Shizuka and Johnson 2020).

So-called “knockout experiments” or disturbance experiments have been applied with the withdrawal of specific individuals or interactions (Pinter-Wollman et al. 2014). These studies are mostly simulated removal (Williams and Lusseau 2006; Manno 2008; Kanngiesser et al. 2011;

Puga-Gonzalez et al. 2018; Wiśniewska et al. 2020), while true experiments in removing (Flack et al. 2006; Naug 2009; Firth et al. 2017; Rueger et al. 2021) or observing natural suppression of individuals (Goldenberg et al. 2016) are scarcer. In general, all of them cause instability and show how networks can be restructured and how resilient they are (Kurvers et al. 2014; Pinter-Wollman et al. 2014), that is, whether they manage to maintain cohesion in the face of the loss of individuals (Puga-Gonzalez et al. 2018). However, with the exception of some studies with insects (Theraulaz et al. 1989), primates (Reynolds 1970; Flack et al. 2005; Franz et al. 2015a), fish (Piefke et al. 2021) and birds (Kubitza et al. 2015), the dynamics of dominant substitution is still poorly studied. Given that these individuals usually also occupy central roles in the networks, it is important to understand how these positions are filled, to restore the cohesion of the system (Pinter-Wollman et al. 2014).

Therefore, we studied a species of artiodactyl in captivity, the white-lipped peccary, before and after the natural suppression of the alpha male. Our objective was to analyze whether the species’ social system is resilient and how the alpha’s position and its central role in networks are replaced by another individual. Given the linear configuration of hierarchy already observed in this species (Nogueira-Filho et al. 1999), we expect that the beta individual will replace the alpha and the relationships below them will be maintained. We also investigated the validity of the hypotheses of “Social Dynamics” (winner-loser effect) and “Previous Attributes” (physical: weight and testicular volume; physiological: serum testosterone; and age) acting alone or together, in replacing the dominant.

## Material and methods

### Study species

The white-lipped peccary, *Tayassu pecari* (Link, 1795), is a social species that lives in stable and mixed groups of 50 to 200 individuals (Kiltie and Terborgh 1983), and is hierarchically organized (Nogueira et al. 2016). At given moments, according to food availability, groups can be divided into subunits, or a main group and other satellite groups, which may consist of individuals of the same sex (Margarido 2001). Under captive conditions, Nogueira-Filho et al. (1999) evaluated the social structure of a mixed group of white-lipped peccaries, which allowed the establishment of a linear hierarchy with a male as the highest-ranking animal (Nogueira-Filho et al. 1999), although females can also occupy the highest status in captivity (Nogueira et al. 2016).

The species has a promiscuous mating system (Leite et al. 2018) and breeding occurs according to environmental

conditions to maximize the offspring's chances of survival (Bronson 2009). In regions with well-defined dry and rainy seasons, they synchronize reproduction in the period of greatest food availability (Altrichter et al. 2001), but in regions without marked climatic seasonality, they reproduce throughout the year (Gottdenker and Bodmer 1998; Mayor et al. 2009). It is expected that in these specific periods, the testicular volume (physical attribute), mediated by androgen concentration (physiological attribute), may vary (Johnston et al. 1994). But in a previous study with the same group (Grossel et al. in preparation), no difference in organ volume or serum testosterone was obtained throughout the year.

## Data collection

The group of white-lipped peccaries (*T. pecari*) was part of the Curitiba Zoo (State of Paraná, Southern Brazil) animals' squad, which was composed of adult males ( $n = 7$ , age 5–9 years old) and was studied from May to October 2018. Animals remained in the same enclosure (321 m<sup>2</sup>), with an additional covered area (12 m<sup>2</sup>) that was used for handling. They were fed once a day and had water available *ad libitum* in three drinking fountains. On August 18, 2018, an individual (#180: alpha male) died during the management procedure ( $n = 6$ ).

The individuals were recognized through earrings with different colors and numbers. From May to July 2018 (before alpha's death) and August to October 2018 (after alpha's death), we observed the group one week per month, between 8:00 and 10:30 a.m., which corresponds to the feeding period and during which most of the confrontations occurred (Nogueira et al. 2016). We sampled all the agonistic and affiliative interactions (sampling all occurrences cf. Altmann 1974), based on the behavioral states and events recorded by Sowlis (1997) (Online Resource 1), with the addition of events and variation in descriptions, as needed. We recorded sequentially the winner, loser, and type of interaction in agonistic confrontations, and sender, receiver, and type of interaction for each affiliative event.

To collect physical and physiological data, the animals were anesthetized using blowguns in two periods (May: before alpha's death, and August: after alpha's death) and transported to the Veterinary Sector. This anesthetic procedure is necessary due to the aggressiveness presented by the species, and guarantees both the safety of the animals and the team. We weighed the animal on a scale graduated in grams (Balmak®, Brazil), and we measured the length and width of the testicles with a 0.05 mm precision caliper (Disma®, 150 mm, Brazil). For the quantification of testosterone, we collected blood samples by venipuncture in tubes without anticoagulants and kept refrigerated. We aliquoted the serum in 1.0 ml volumes in tubes and kept the samples refrigerated (− 20 °C) until hormonal analysis. Lastly, we obtained the ages from the zoo archives.

## Data analysis

To see if there were differences in the number of interactions, before and after the alpha's death, we used a chi-square test. We compared the total number of interactions (agonistic and affiliative) from the months before (May to July) and after (August and October) the death; the number of interactions in the months adjacent to the death (July and August), both weighted by the number of individuals (before  $n = 7$ , after  $n = 6$ ), and the percentage of agonistic and affiliative interactions for each month.

To establish the hierarchy and social networks among males, we organized the observed interactions, monthly, in frequency matrices of interactions for each behavioral state targeted by this study (agonism and affiliative). We gave values of 1.0 for victory, 0.0 for defeat, and 0.5 for apparent tie in each agonistic interaction and values of 1.0 for each behavior emitted, 0.0 for each behavior received, and 0.5 for mutual behavior in each affiliative interaction (Croft et al. 2008).

We performed the metric analysis of the hierarchy and networks plotting using the R software 4.1.0 (R Core Team 2020). With the *compete* (Curley 2006) and *steepness* (Leiva and de Vries 2014) packages, we evaluated three hierarchy metrics. (I) Linearity corresponds to the index that evaluates how linear the system is (if A dominates B and B dominates C, then A dominates C) (De Vries 1995). It is calculated using the Landau's modified  $h'$  index (De Vries 1995) and the values range from 0, when all individuals dominate an equal number of other individuals, to 1, when linearity is perfect (De Vries 1998). Reversal is a complement to linearity and widely used in primates (Isbell and Young 2002). It suggests the level of stability of the hierarchy, indicated by the number of observations below the diagonal matrix, and generally represents less than 5% of total observations. (II) Directional Consistency Index (DCI) of behaviors indicates the direction of interactions, ranging from 0, if all connections are directed and received with the same frequency, to 1, if interactions are initiated by a few individuals towards others (So et al. 2015). (III) Steepness is the dominance gradient index that quantifies the intensity of individuals' success in confrontations and varies from 0, when the difference between individuals is small and reflects little depth, to 1, when the difference is large and the hierarchy is steep (De Vries et al. 2006; Balasubramaniam et al. 2013).

We estimated the dominance rank using two different methods. First, we used David's Score (DS) method, which weighs the total number of wins and losses according to the proportion of interactions of each individual (David 1987) and uses the frequency matrices of agonistic interactions developed during behavioral observations. To calculate the score of individuals, we applied the Individual Score Index ( $P_{ij}$  = proportion of victories by the number of dyadic

interactions), since it is the most suitable for species with high values of directional asymmetry, that is, with a high DCI (Balasubramaniam et al. 2013). Then, we used the Elo-rating (ER) method, which gives each animal a score after a confrontation and varies accordingly to the probability of an individual winning the other, as it is mediated by the “winner-loser” effect (Hsu and Wolf 1999; Albers and De Vries 2001) based on the sequential interactions observed during the sampling period (Sánchez-Tójar et al. 2018). The Elo-rating allows you to monitor temporal fluctuations at the individual hierarchical level, such as when an animal is inserted or removed from the group (Neumann et al. 2011). To calculate the score of each animal, we used a package of the same name (*EloRating*; Neumann and Kulik 2020) and the standard parameters of initial score = 1000 and constant  $k = 100$ . To assess whether both methods showed concordance with respect to recovered ranks, we applied a monthly Kendall’s coefficient of concordance with monthly results of individual positions in the hierarchy.

To visualize the social dynamics in the group, we used the *igraph* package (Csardi and Nepusz 2006), where the total number of agonistic and affiliative interactions was plotted on directed and weighted social networks (Social Network Analysis). We performed the analyses of the metrics of the affiliative networks using the UCINET 6.0 software (Borgatti et al. 2000). The metrics applied to the networks included evaluation of general and individual measures and were chosen according to our need to highlight the directionality of the interactions (Sosa et al. 2020). Thus, to assess network connectivity, we measured the density, that corresponds to the proportion of interactions existing in the system (So et al. 2015). To assess the properties of each individual in the networks, we measured the degrees (in-degree and out-degree), representing the number of interactions or partners for each

individual (Farine and Whitehead 2015), and the betweenness centrality, which indicates the proportion of times that an individual is contained in the shortest path between each dyad (Sosa et al. 2020).

To test the social dynamics hypothesis, we observed the sequential development of individuals’ rank positions using the Elo-rating. This method works because it considers the “winner-loser” effect, which results in the system’s self-organization, if acted on (Franz et al. 2015b).

To test the previous attributes hypothesis, if the attributes of weight, testicular volume, serum testosterone, and age of the animals before (May) and after (August) dominant’s death were related to the individuals’ hierarchical position, we used Spearman’s correlation. For this purpose, we used the testicular biometric data (length and width) to calculate the volume of each testicle, using the formula for ovoid structures:  $\text{Volume} = 4/3 \cdot \pi \cdot (L/2)^2 \cdot (h/2)$ , where  $\pi = 3.1416$ ;  $L$  = width (cm) and  $h$  = length (cm), according to Bailey et al. 1998 (CBRA 2013). Adding the volume of each testicle, we calculated the total testicular volume of all individuals for the months. We performed serum testosterone measurements using the enzyme immunoassay method (ELISA — enzyme linked immunosorbent assay), as described by Brown (2004).

## Results

We recorded a total of 105 observation hours and 1323 interactions during feeding periods, with behaviors previously described by Sowls (1997), two new affiliative behavioral events and four variants of agonistic behaviors (Table 1). Also, due to the frequent emission of aggressive sound emissions (grunts and teeth clicking), with the

**Table 1** Variants of agonistic interactions and new descriptions of affiliative interactions recorded after observation of the white-lipped peccary (*T. pecari*) males from Curitiba Zoo (State of Paraná, Southern Brazil)

Term	Definition
<b>1. Agonistic interactions</b>	
Intimidation	One individual remains static, making it difficult for another to move, who either deviates or stops moving, until the first individual moves away, releasing the passage
Retreat	With the approach of one individual, another individual walks away in the opposite direction, without any apparent conflict
Threat	One individual moves towards another without physical contact. Grunts and teeth clicking may be present. The threat can be retaliated or not. If not, the threatened individual retreats
Attack	One individual moves towards another by making physical contact, usually with an open mouth and exposed teeth. Chases, bites, grunts and teeth clicking may be present. In response, the attacked individual may respond with an equivalent attack or with retreat
<b>2. Affiliative interactions</b>	
Friction (various parts of the body)	An individual leans against the side of its head on some part of another's body, who may be standing or lying down, and then rubs vertically
Poking (various parts of the body)	An individual touches with the snout some part of the body of another that may be standing or lying down, and performs frictional movements

**Table 2** Agonistic and affiliative interactions of white-lipped peccary (*T. pecari*) males from Curitiba Zoo (State of Paraná, Southern Brazil) and monthly dominance hierarchy indices

	May	June	July	August	September	October
	Before death ( <i>n</i> = 7)			After death ( <i>n</i> = 6)		
Total interactions	280	244	291	162	170	176
Agonistic (%)	51	52	50	53	61	59
Affiliative (%)	49	48	50	47	39	41
$\chi^2$ <sup>a</sup>	0.04	0.16	0	0.36	4.84	3.74
$p(\chi^2)$	0.84	0.68	1	0.54	0.02*	0.07
$h'$ <sup>b</sup>	1	0.80	0.98	0.80	0.94	0.88
$p(h')$	0.003*	0.02*	0.002*	0.05*	0.02*	0.07
Reversal <sup>c</sup> (%)	0.73	1.70	1.71	23.83	4.48	2.78
DCI Agonistic <sup>d</sup>	0.98	0.96	0.96	0.54	0.91	0.94
DCI Affiliative <sup>e</sup>	0.24	0.26	0.26	0.22	0.47	0.42
Steepness ( <i>Pij</i> ) <sup>f</sup>	0.90	0.62	0.95	0.63	0.89	0.83

\*statistical significance ( $p < 0.05$ )

<sup>a</sup>Comparison of the number of agonistic and affiliative interactions

<sup>b</sup>Modified  $h'$  index (linearity) of Landau ( $h'$ )

<sup>c</sup>Percentage of interactions below the diagonal matrix

<sup>d</sup>Direction of agonistic interactions

<sup>e</sup>Direction of affiliative behaviors

<sup>f</sup>Dominant gradient index, with the *Pij* method

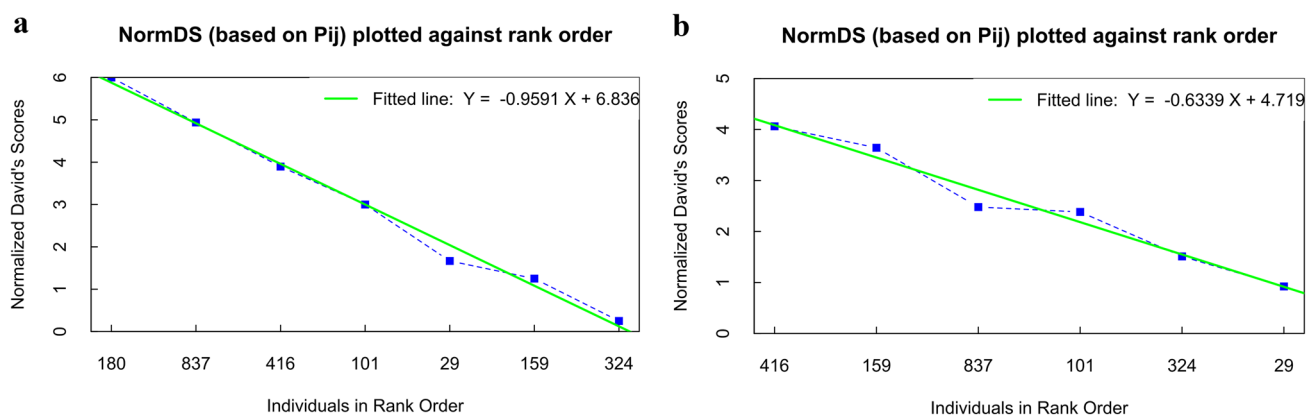
display of agonistic behaviors, we did not consider these different emissions a separate behavior, but a variant of the displayed agonism. All behavioral data generated during this study are included in this published article (Online Resource 3).

## Dominance hierarchy structure

There was a significant reduction in the total number of interactions (agonistic and affiliative) in the months before (May to July:  $116.1 \pm 97$  interactions per individual) and after (August to October:  $84.7 \pm 29.1$  interactions per

individual) the alpha's death ( $\chi^2 = 4.91$ ;  $df = 1$ ;  $p = 0.02$ ), but not between adjacent months (July:  $41.6 \pm 37$  interactions per individual, August:  $27 \pm 15.5$  interactions per individual) ( $\chi^2 = 3.11$ ;  $df = 1$ ;  $p = 0.07$ ) (Table 2). From August onwards, the proportion of monthly interactions showed more agonism in relation to affiliative interactions, with this difference being significant in September ( $\chi^2 = 4.84$ ;  $df = 1$ ;  $p = 0.02$ ).

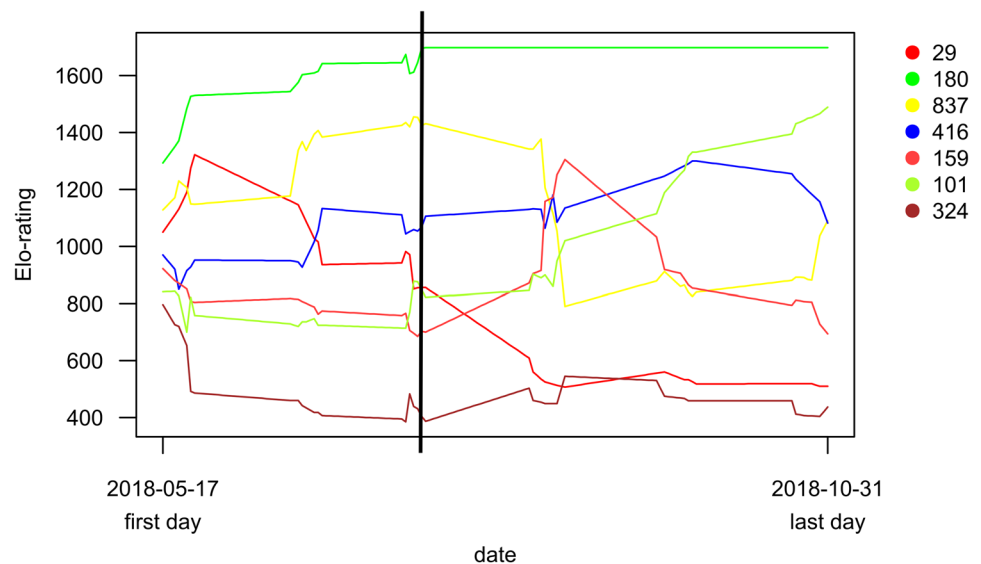
In the months prior to the alpha's death, the dominance hierarchy was strongly linear ( $h' > 0.9$ ), except in June (Table 2). Agonistic behaviors were unidirectional ( $DCI > 0.9$ ), and affiliates showed directional symmetry



**Fig. 1** Steepness (dominance gradient index) in the months of July (a) and August (b) of male white-lipped peccaries (*T. pecari*,  $n = 7$ ) from Curitiba Zoo (State of Paraná, Southern Brazil)



**Fig. 2** Hierarchy dynamics through Elo-rating, showing the position of all individuals according to their respective classifications after the result of each agonistic confrontation. Representation of individuals by colors on the right side. Start (May 17, 2018) and end (October 31, 2018) observations. Vertical black bar represents the moment of death of individual alpha (#180)



(DCI=0.2), while steepness values were high ( $>0.9$ ), except again for June. Immediately after death (August), the hierarchy lost its obvious previous linearity, but recovered in the following month ( $h' > 0.9$ ). The highest percentage of reversal was recorded in August (23.83%), when agonistic behaviors were also more distributed among individuals (DCI=0.5), while in the following months the affiliation interactions were less targeted (DCI  $> 0.4$ ). The steepness was reduced in August (=0.6), but later recovered (Fig. 1).

Assessing the trajectory of individuals by Elo-rating, animals' classification experienced minor changes before the alpha's death, except for the #29 male, which showed a gradual decline over the months (Fig. 2). After death, the rank of individuals underwent major changes. Individual #101 showed a marked rise, along with #416. At the same time, the individual #837, until then the beta male, presents an abrupt drop in the hierarchy, while the animal #159 exhibits a rapid rise also followed by a clear fall. In October, however, the positions of #416 and #837 males are reversed and #837 returns the beta position, this time, preceded by individual #101 as alpha. Male #324 was the most subordinate individual over the analyzed period.

With the Elo-rating, we observed that the initial results of the confrontations (victory and defeat) resulted in the

establishment of hierarchically classified individuals. And even though we have slightly different ranks according to the applied method (David's Score and Elo-rating) (Online Resource 2), both showed a high and significant Kendall's coefficient of concordance in all months ( $p < 0.05$ ) (Table 3).

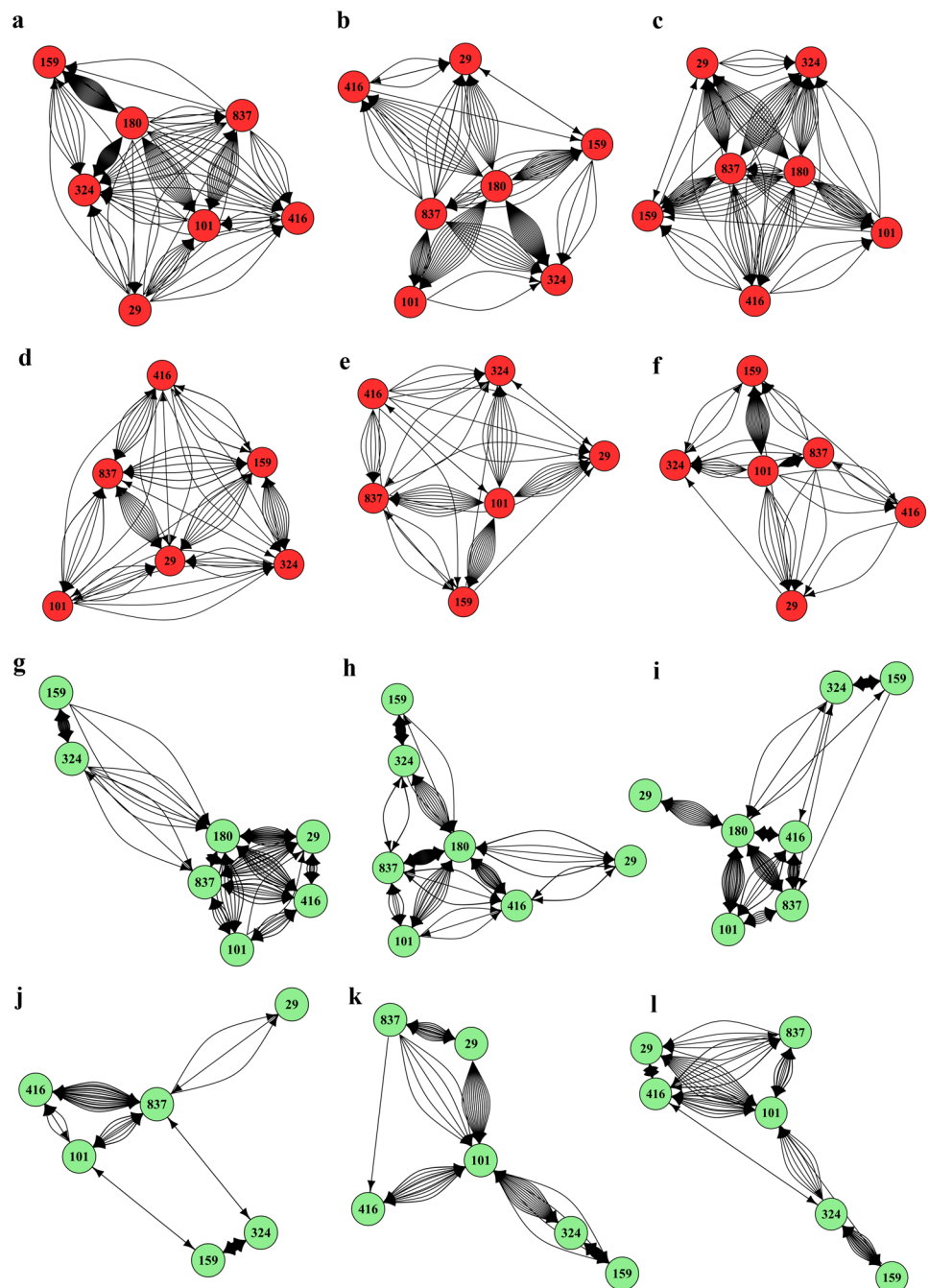
### Social networks

In the networks of agonistic interactions, in the months before death, the individual #180 (alpha) won confrontations with all others (Fig. 3a), while individual #29, who at the beginning lost the confrontations only to the dominant, went on to be defeated in most clashes in the following months (Fig. 3b, c). At the same time, the one who was defeated only by the alpha was the individual #837 (beta). Male #101 won fights only of male #324 and this male, with #159, lost practically all fights (Fig. 3a–c). After the alpha's death, defeats were more homogeneous among the individuals (Fig. 3d), but in the following month (Fig. 3e), the #101 male won almost all the confrontations with the others. Two males, #416 and #837, started to lose fewer fights, mainly to #101, which was evident in the last month (Fig. 3f), and #837 male start to behave again as beta.

**Table 3** Kendall's coefficient of concordance with monthly ranks obtained through both methods and  $p$  of statistical significance ( $<0.05$ ) of white-lipped peccary (*T. pecari*,  $n = 7$ ) males' hierarchy from Curitiba Zoo (State of Paraná, Southern Brazil)

	May	June	July	August	September	October
	Before death ( $n = 7$ )			After death ( $n = 6$ )		
$\tau$	0.90	0.80	0.90	0.73	0.69	1
$p$	0.002*	0.01*	0.002*	0.05*	0.05*	0.002*

**Fig. 3** Directed (between individuals) and weighted (actual number of interactions between individuals) agonistic (a–f) and affiliative (g–l) interaction networks obtained between the months of May and October of white-lipped peccary (*T. pecari*,  $n = 7$ ) males from Curitiba Zoo (State of Paraná, Southern Brazil). Individuals are represented by the nodes, while interactions by arrows, which occurred unidirectional or bidirectional



With the networks of affiliate interactions, in the months before death, we observed that the only individual who interacted with everyone else was #180 (alpha). With #324 male, the alpha enabled a network connection with individual #159 (Fig. 3g, h), and alone, he joined #29 to the system (Fig. 3i). After his death, a marked reduction in interactions was observed and a few interactions occurred with one or two other animals (Fig. 3j). In the following months (Fig. 3k, l), #101 male assumed the central position in the hierarchy, although interactions were not bidirectional with everyone

else and allowed subordinates #324 and #159 to connect, keeping the system cohesive.

In general, the density of affiliative networks was lower in the period after death (Table 4). The metrics of the affiliative networks showed that from May to July, with few exceptions, the alpha male (#180) had the highest degrees (both in- and out-degree) and betweenness (Table 5). Males #817, #416, and #324 also had outstanding betweenness values in this period. From August to October, after the alpha's death, high degree values are more evenly distributed among individuals. The

**Table 4** Affiliative network density over six months of white-lipped peccary (*T. pecari*,  $n=7$ ) males from Curitiba Zoo (State of Paraná, Southern Brazil)

	May	June	July	August	September	October
	Before death ( $n=7$ )			After death ( $n=6$ )		
Density (%)	59	57	57	47	40	63

highest betweenness are displayed by the new alpha (#101), although #324 male also have consistent values (Table 5).

### Previous attributes

There were strong correlations between individuals' hierarchical position and previous attributes, body weight and testicular volume with both methods (DS and ER) before alpha's death, and serum testosterone only with DS after death (Table 6).

### Discussion

The perturbation of the social system of the white-lipped peccaries, caused by the alpha male's death, evidenced a resilient and robust structure, but it went through a period

of instability and changes in positions in the hierarchy and roles in the networks, until a gradual return to stability. The alpha position was filled by an individual of low status, who gained rank using agonism and affiliative interactions, keeping the network cohesive. As for the level of information used by individuals in the reorganization of the system, our data supported the two hypotheses considered, Social Dynamics and Previous Attributes.

Before the alpha's death, the hierarchy had high linearity, as already observed by Nogueira-Filho et al. (1999), as well as a marked and stable difference between individuals' hierarchical positions, mediated by the high rate of directed agonistic behaviors. This period is in agreement with the proposed theories, where in periods of stability one alpha male dominates all the others, one beta dominates all, except the alpha, and so on (Chase et al. 2002), with some individuals showing greater success in agonistic encounters

**Table 5** Metrics for each individual in the friendly networks (in percentage) over the 6 months of white-lipped peccary (*Tayassu pecari*,  $n=7$ ) males from Curitiba Zoo (Parana, Brazil)

	May			June			July		
	Degrees <sup>a</sup>		Betweenness <sup>b</sup>	Degrees		Betweenness	Degrees		Betweenness
	In	Out		In	Out		In	Out	
180	<b>44.5</b>	27	17.8	<b>41.5</b>	<b>39.5</b>	<b>43.3</b>	<b>47.5</b>	<b>41.5</b>	<b>48.9</b>
837	22	<b>28.5</b>	<b>32.8</b>	26.5	17.5	6.7	22	29	3.9
29	22.5	21.5	0	5.5	4.5	0	12.5	4.5	0
416	21.5	20.5	1.11	17	12	6.7	26	20	4.4
101	12	16	0	7	14	0	14.5	23.5	0
159	12.5	8.5	0	11.5	16.5	0	14	9	0
324	6	19	18.3	18	23	3.3	8.5	17.5	2.8
Alpha's death (#180)									
	August			September			October		
	Degrees		Betweenness	Degrees		Betweenness	Degrees		Betweenness
	In	Out		In	Out		In	Out	
837	12	21	<b>55</b>	5	16	2.5	11	10	0
29	1.5	0.5	0	10	20	0	<b>29.5</b>	18.5	0
416	16	9	0	10	4	0	16	<b>33</b>	15
101	6.5	5.5	20	<b>41.5</b>	9.5	<b>42.5</b>	28	16	<b>27.5</b>
159	17	<b>23</b>	5	17.5	22.5	0	9.5	9.5	0
324	<b>23</b>	17	10	19	<b>31</b>	20	10	17	22.5

<sup>a</sup>In-degree (In): the sum of interactions that other nodes have with the individual, and Out-degree (Out): the sum of interactions the individual has with other nodes

<sup>b</sup>Betweenness (Be): the number of times a node appears on the path connecting each pair of nodes. The values in bold correspond to the maximum values recovered for each metric each month



**Table 6** Values of  $\rho$  of the Spearman correlation between the individuals rank obtained using David's Score (DS) and Elo-rating (ER) methods and previous attributes and p of statistical significance ofwhite-lipped peccary (*T. pecari*,  $n=7$ ) males' hierarchy from Curitiba Zoo (State of Paraná, Southern Brazil) before and after alpha's death

	Body weight (kg)		Testicular volume (cm <sup>3</sup> )		Serum testosterone (nmol/L)		Age (months)	
	Before	After	Before	After	Before	After	Before	After
DS	<b>1</b>	−0.14	<b>0.85</b>	0.25	0.37	<b>0.94</b>	−0.10	0.2
P	0.0003*	0.8	0.02*	0.6	0.4	0.01*	0.8	0.7
ER	<b>0.96</b>	−0.37	<b>0.89</b>	−0.14	0.54	0.77	−0.07	0.6
p	0.002*	0.4	0.01*	0.8	0.2	0.1	0.9	0.2

\*statistical significance ( $p < 0.05$ ). In bold, high correlations values ( $< 0.85$ )

than others (De Vries et al. 2006). Affiliative behaviors, on the other hand, were independent of any type of hierarchy and were exhibited with great frequency in both directions, dominant-subordinate and vice versa.

According to the proposal by Nogueira-Filho et al. (1999), due to large groups that can be formed in nature, it would be expected that a well-defined organization would be predominant, although not exactly linearly. The possibility of establishing social subunits in nature would allow different degrees of linearity to be exercised within each subunit (considering our group of 6 individuals as a subunit of a large group) and with greater pressure from the alpha male toward the possible leaders of each subunit. In addition, the maintenance of the beta without major conflicts would tend to increase the fitness of the alpha since beta strengthens the role of alpha over possible subunit leaders. This type of structure would allow the maintenance of hierarchical relationships even in large natural groups.

With the absence of an alpha male and the establishment of disputes between potential successors, the hierarchy lost its marked linearity and became highly unstable, since agonistic behaviors occurred more homogeneously among all individuals, as the difference between individual successes was reduced. Due to the absence of females in the study group, which could also encourage increased confrontations during reproduction, the post left by the alpha male reinforces that this is the main explanation for the observed instability. Similar episodes were observed in groups of pigtailed macaques (*Macaca nemestrina*; Flack et al. 2005, 2006), house sparrows (*Passer domesticus*; Franz et al. 2015a), and cichlids (*Astatotilapia burtoni*; Piefke et al. 2021), where the absence of individuals with high hierarchical positions increased agonism and a reduction in affiliate interactions among individuals in the groups.

The increase in agonistic behaviors was necessary for the relations between dominants and subordinates to be established for a later restructuring, with the emergence of a new alpha. After the death of the dominant individual, this position was not filled naturally by the individual who succeeded him in the hierarchy, but gradually by a male of lower status. Computer simulations predict little restructuring in

the hierarchy in the absence of alpha, if the difference in initial forces between the group members, which contribute to their success in the results of the confrontations, are sufficiently high (Bonabeau et al. 1999). Under these conditions, only the lowest positions would be modified since their respective occupants have smaller differences between them (Bonabeau et al. 1999). This simulation leads us to assume that the differences between the initial forces of the individuals in our group were low, so as to allow for shifts in positions throughout the hierarchy. Experimental work produced results similar to ours. In *A. burtoni* groups, there are several territorial dominants and nonterritorial subordinates. The removal of a dominant caused, in some cases, a status shift among individuals, and subordinates began to ascend and conquer the territories left vacant, but, in other cases, the remaining dominants expanded their territory and occupied those areas (Piefke et al. 2021). Also, in rhesus monkeys (*Macaca mulatta*), the death of the dominant female was not followed by the filling of this position by the beta female, but by the ascension of another lower-ranking female, who did it through agonism toward the other females and bidirectional affiliate interactions with the alpha male. Similar to our study, the rise was gradual, with slightly aggressive behaviors becoming more violent as they were reinforced by the alpha male's position (Reynolds 1970). In short, our data reinforce that the beta position is not a prerequisite for becoming alpha, but subordinate individuals, in the midst of instability caused by the permanent absence of the dominant, can, through increased agonism, occupy this position. However, we found that other types of behavior can help explain this transition in dominance.

The status of the dominant male belongs to an individual who not only exhibits greater or total success in agonistic confrontations, but who also demonstrates a greater ability to relate in an affiliative way with others. The two individuals who occupied the alpha male position when the hierarchy was stable (#180) or, gradually becoming stable (#101), played a central role, exhibiting relationships with all or almost everyone else and allowing all individuals to be connected in some way in a solid and cohesive network of interactions (high betweenness). In the social networks of

agonistic interactions, these individuals were winners in all confrontations in which they were involved. Already in the networks of affiliative interactions, alpha males received and emitted most affiliative behaviors (high degree), although this behavior was more evident with the first alpha. In chimpanzees (*Pan troglodytes verus*), Kanngiesser et al. (2011) also observed that dominant individuals had a greater ability to connect the group. Additionally, the transition of dominance in wasps (*Polistes dominulus*; Theraulaz et al. 1989) and rhesus monkeys (*M. mulata*, Reynolds 1970) occurred through the replacement of the suppressed alpha by another individual with greater capacity to interact socially with others, although he occupied a more subordinate position. These initial betas, as well as the beta in our study, did not have the basic skills to fill the position left open by the alpha, acting as a central element and interconnecting the entire network affiliative. Still, we observed that other individuals with lesser hierarchical status also exhibited an influence on the system, acting as bridges or connections between more isolated individuals and the group and, therefore, assisting in the cohesion of this system alongside the alpha male (high degree and betweenness values). This assistance shows that members can play different roles in networks, even those without a leadership position (Williams and Lusseau 2006), and exemplifies why structures lose stability when key nodes are removed, compared to removing random nodes (Manno 2008; Puga-Gonzalez et al. 2018; Wiśniewska et al. 2020). Central individuals can act in specific situations of tension and stress during social relationships, maintaining the cooperative structure of groups (Flack et al. 2005, 2006; Funkhouser et al. 2018).

We found that the Social Dynamics hypothesis, which predicts that attributes may not be essential in maintaining a hierarchical organization, but rather a process of self-organization, is supported in this captive population. The winner-loser effect works as a predictor of this hypothesis and is evidenced by the Elo-rating sequential interactions methodology (Franz et al. 2015b). This method generated a hierarchy according to the positions recovered using the traditional method (David's score), that considers only the number of wins and losses (David 1987). This agreement of results reinforces that an analysis that considers the probabilities of outcomes in confrontations based on past events has reflected the real positions of individual status, through the dynamics of dyadic interactions.

Additionally, the Previous Attributes hypothesis, where certain characteristics of individuals can influence their status in the hierarchy in periods of social instability and hierarchical establishment, also played an important role in this restructuring. Before the alpha's death, body weight and testicular volume were correlated with the status positions of the animals, regardless of age. In the period that followed

the death of the alpha male, these attributes were not correlated with the hierarchy, possibly because in this period of hierarchical instability generated by the absence of a dominant, individuals of different subunits and physical attributes could plead for new positions. However, the testosterone concentration was related to status only in this season, that is, with the lack of dominance, other males, who also had high testosterone levels, ascended in the hierarchy, even if not definitively (see individual #416; Fig. 2). The production of sexual steroids can influence several types of behaviors, including aggression between individuals. This behavior, in turn, mediates the relationships of dominant and subordinate (Tennenhouse et al. 2017). Therefore, it is expected that in this period of struggle, the hierarchical status reflects the concentration of testosterone produced individually. The "Challenge hypothesis" predicts this: individuals do not maintain high levels of testosterone continuously, due to high costs, but increase testosterone production during the breeding period, when competition for mates intensifies (Wingfield et al. 1990). Even in species with non-seasonal reproduction, this hypothesis fits the explanation of hormonal peaks during social instability. Among primates, events that increase hormone production are related to hierarchical instability and aggressive confrontations in search of high social status (Eberhart et al. 1980; Beehner et al. 2006; Mendonça-Furtado et al. 2014). Therefore, during unstable periods, individuals with higher testosterone production are more aggressive, and as a consequence, more likely to ascend to the dominant position (Beehner et al. 2006). As this pattern was not repeated before the disturbance, it seems that the concentration of androgens exerted influence during the hierarchical organization of the group, but, in agreement with the Challenge hypothesis, it is not an attribute correlated with dominance in periods of social stability. The two hypotheses are not mutually exclusive, and other studies have found that both can explain social systems in some way (Bonabeau et al. 1999; Chase et al. 2002; Franz et al. 2015b).

Thus, an event of instability, represented by the absence of the most dominant individual, showed that the hierarchical system of white-lipped peccaries in captivity is resilient, but that it faces a complex restructuring, with increased agonism between individuals and changes in social positions. In addition, affiliative interactions also contribute to the emergence of a new dominant. Moreover, both hypotheses of hierarchical structuring seem to have affected this group, with the attributes of weight and testicular volume being more active in maintaining the stability of the system (prior to the death of the alpha male; Previous Attributes hypothesis), and the concentration of serum testosterone and social interactions, exerting a greater influence on the reorganization of the status of individuals during the period of instability (after death; Social Dynamics hypothesis).

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**Availability of data and material** Supplementary Information.

**Code availability** Not applicable.

## Declarations

**Ethics approval** This study was conducted according to the Ethical Principles of Animal Experimentation, adopted by the Conselho Nacional de Controle de Experimentação Animal (CONCEA), and was approved by the Comissão de Ética no Uso de Animais (CEUA) under protocol No. 31/2017 (UFPR – Palotina) with license of the Sistema de Autorização e Informação em Biodiversidade (SISBIO–ICMBio) under protocol 59628–1.

**Consent to participate** Not applicable.

**Consent for publication** The authors declare consent for publication in this journal.

**Conflict of interest** The authors declare no competing interests.

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