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Individual differences in behavior affect total tract fiber digestibility: the example of collared peccary

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*Differences in how individuals cope with stressful conditions (e.g. novel/unfamiliar environment, social isolation and increases in human contact) can explain the variability in data collection from nutrient digestibility trials. We used the collared peccary (*Pecari tajacu*), which is under process of domestication and shows high individual behavioral distinctiveness in reactions toward humans, to test the hypothesis that behavioral differences play a role in nutrient digestibility. We assessed the individual behavioral traits of 24 adult male collared peccaries using both the 'behavioral coding' and the 'subjective ratings' approaches. For the behavioral coding assessment, we recorded the hourly frequency of behaviors potentially indicative of stress during the 30-day habituation period to the experimental housing conditions. The subjective ratings were performed based on the individuals' reactions to three short-term challenge tests (novel environment, novel object and threat from a capture net) over a period of 56 days. During the last 26 days, the collared peccaries were fed diets either high (*n = 12*) or low (*n = 12*) in dietary fiber levels, and we determined the total tract apparent digestibility of nutrients. The individual subjective ratings showed consistency in the correlated measures of 'relaxedness', 'quietness' and 'satisfaction' across the three challenge tests, which were combined to produce *z* score ratings of one derived variable ('calmness'). Individual frequency of BPIS/h and calmness scores were negatively correlated and both predicted the total tract digestibility of acid detergent fiber (**ADF**), which ranged from 0.41 to 0.79. The greater the calmness *z* scores (i.e. calmer individuals), the greater the total tract digestibility of ADF. In contrast, the higher the frequency of BPIS/h, the lower the total tract digestibility of ADF. Therefore, our results provide evidence that by selecting calmer collared peccaries, there will be an increase in their capacity to digest dietary fiber.*

Keywords: coping styles, digestive physiology, feed evaluation, *Pecari tajacu*, stress

Implications

This study is one of the first to show that individual differences in behavior are related to the variability in data collected from *in vivo* digestibility trials. One of the main findings is that, in response to novel/unfamiliar environments, individuals that are better able to cope with stressful situations show improved dietary fiber digestibility. Researchers usually select less excitable animals in response to novel/unfamiliar environments and human proximity to participate in digestibility trials, and this procedure may therefore cause a bias in their results. In turn, our results suggest that the selection of calmer animals has the potential to improve their feed efficiency, productivity and welfare.

Introduction

Many studies show consistent behavioral and physiological differences between individuals within a population of both wild (e.g. squirrels (*Tamiasciurus hudsonicus*: Westrick *et al.*, 2019; bank voles (*Myodes glareolus*): Mazza *et al.*, 2019) and domestic animals (e.g. beef cattle: Neave *et al.*, 2018; pig: Horback and Parsons, 2018). This behavioral variation is an adaptive strategy that can affect the evolutionary fitness of the species (Sih *et al.*, 2004; Koolhas, 2008). Researchers use

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different concepts and terms to study individual behavioral distinctions, such as temperament, behavioral syndromes, coping styles or personality according to the approach used (see MacKay and Haskell (2015) and Finkemeier *et al.* (2018) for critical reviews of terminology, definitions and frameworks).

Overall, personality refers to behavioral and physiological differences that persist throughout time and across different contexts and ecological situations (Sih *et al.*, 2004; Dingemanse and Réale, 2005), which can be evaluated in five major dimensions: shyness/boldness, exploration/avoidance, activity, sociability and aggressiveness (Réale *et al.*, 2007). Assessing the personality of individuals is a very complex task, as researchers need to perform several behavioral tests in different contexts/situations and must repeat those tests at least once throughout the life of the animal (Finkemeier *et al.*, 2018). Thus, under on-farm conditions, researchers usually apply behavioral tests to assess repeatable and consistent individual differences in behavior when facing a range of stressful challenges, such as responses to a novel environment/object or to predation risk, described as 'coping styles' that range along exploration/avoidance, shyness/boldness or activity continuum axes, for instance (Réale *et al.*, 2007; Koolhas *et al.*, 2010). Thus, coping styles represent a sub-aspect of the personality concept (Finkemeier *et al.*, 2018), and this is the approach we adopted here to investigate the differences in how the animals react when confined with close human contact.

Individual differences in behavioral traits stem from individual differences in the response to stress of the hypothalamic–pituitary–adrenocortical axis (e.g. sheep: Fürtbauer *et al.*, 2019; pig: Hervé *et al.*, 2019), and those differences are important from an animal husbandry perspective because they have implications for performance, reproduction, health and welfare (Voisinet *et al.*, 1997; Ruis *et al.*, 2002; Holl *et al.*, 2010). Differing physiological responses to stress can result in differences in food intake, for example. On the one hand, more excitable individuals, i.e. not adapted to handling practices, usually have lower feed intake than the calmer ones, which ultimately results in lower average daily gains (e.g. beef cattle: Cafe *et al.*, 2011; Llonch *et al.*, 2016; pig: Yoder *et al.*, 2011; Rohrer *et al.*, 2013). In turn, these differences in feed intake can either decrease or increase nutrient digestibility coefficients (Robbins, 1993). Therefore, differences in how individuals cope with stressful experimental conditions can be related with the variability in nutrient digestibility trials within the same dietary treatment (e.g. pig: Pérez de Nanclares *et al.*, 2017; Ouweltjes *et al.*, 2018; buffalo: Negesse *et al.*, 2016).

To determine *in vivo* nutrient digestibility coefficients, experimental animals are usually maintained under relative isolation in metabolism cages, allowing separate collection of feces and urine samples. This condition exposes animals to novel/unfamiliar environments, resulting in stress because of increased social isolation and contact with humans. It can compromise the affective state of the experimental animals (Oliveira *et al.*, 2016).

The collared peccary (*Pecari tajacu*) is a key species for food security in Neotropical countries (Nogueira *et al.*, 2010). It is under domestication in Brazil and other Latin American countries (Nogueira and Nogueira-Filho, 2011). Nevertheless, the domestication process of the collared peccary is still in its infancy; thus the species has not yet gone through an extensive process of selective breeding by man for production traits focused on those individuals that are calmer, quieter and less active, which livestock herds of common domestic species have already gone through for millennia (Robert *et al.*, 1987; Rauw *et al.*, 2017). As a consequence, the collared peccary still shows high individual behavioral distinctiveness in reactions toward humans (Nogueira *et al.*, 2015). From a nutrition perspective, the collared peccary is predominantly frugivorous (Kitie, 1981; Olmos, 1993; Keuroghlian and Eaton, 2008). Despite being non-ruminant, it is a foregut fermenter (Langer, 1978 and 1979) that ferments dietary fiber with relatively high efficiency (Comizzoli *et al.*, 1997; Nogueira-Filho, 2005; Nogueira-Filho *et al.*, 2018), thanks to a symbiotic microbiota in its foregut. Additionally, the species benefits from microbial metabolites produced in its complex stomach (Elston *et al.*, 2005; Oliveira *et al.*, 2009; Borges *et al.*, 2017). Therefore, collared peccary has a digestive physiology closer to ruminants than to that of domestic pigs, as originally stated by Langer (1978 and 1979). Collared peccaries fed the same diet showed high variability in the total tract digestibility of neutral detergent fiber (**NDF**) and acid detergent fiber (**ADF**), which ranged from 0.46 to 0.72 and from 0.54 to 0.72, respectively (Nogueira-Filho *et al.*, 2018). Such characteristics make the collared peccary a useful model in which to test the hypothesis that individual behavioral differences are linked to differences in nutrient digestibility.

Therefore, we investigated whether the behavior of collared peccary was related to nutrient digestibility; if so, we predicted that calmer individuals would show higher feed intake, BW gain (**BMG**) and nutrient digestibility than the ones less adapted to experimental conditions.

Material and methods

Animals, housing conditions and procedures

The experiment took place at the Laboratory of Neotropical Animal Nutrition of the Universidade Estadual de Santa Cruz, Bahia, Brazil (14°47′39.8″S, 39°10′27.7″W) in full compliance with the national legislation on animal care (authorization for experiments on captive wild animals, #1/29/2001/00022-7 by the Brazilian government's environmental agency and authorization to experiments on living animals by the Animal Use Ethics Committee of the Universidade Estadual de Santa Cruz through protocol # 0102012). This experiment was conducted in association with a larger study designed, *inter alia*, to evaluate the relationship between individual behavioral differences with total tract nutrient digestibility, gut microbiota diversity and health of the collared peccary.

In the digestibility trials, 24 adult male collared peccaries, with an initial BW of 21.6 ± 0.7 kg and average age of 2.5 years, purchased from a commercial farm, were used in digestive trials. After being weighed and dewormed, the animals were housed in one of the six individual 11.3 m^2 (7.5 m × 1.5 m) pens. Each pen was divided into two sections: a covered area of 3.0 m^2 – named the metabolism pen – had a wooden lattice suspended floor that allowed the feces and urine to be collected separately, and an additional area, comprising a partially sheltered area and a 'solarium', which allowed unobstructed exposure to natural sunlight, with a cement floor, as previously described by Borges *et al.* (2017). The walls between pens consisted of 1.5 m high wire fencing, and these divisions were covered with white canvas to prevent the animals from seeing neighboring pens, thus minimizing visual interference from animals in adjacent pens. The whole experimental procedure described hereafter was repeated four times until all 24 animals had been assessed.

Each experimental trial lasted for 56 days, including 30 days of habituation to the experimental conditions, 20 days of adaptation to the experimental diets differing in fiber content as explained below and 5 days of digestive trials. On the first morning following the end of the digestive trials (56th day), we collected the data of the threat test (described below) and weighed the animals, which were used in a companion study (Cairo, 2018). During the habituation period, peccaries received water *ad libitum* and were fed the same diet as on the farm they were coming from. It was made of grain corn and soybean meal, grass and seasonal fruits, such as banana, papaya and jack fruit mixed with mineral salt, resulting in a diet with 140 g/kg of CP and 14.5 MJ/kg of digestible energy (DE) on a DM basis, following recommendations of Borges *et al.* (2017). Thereafter, animals were adapted to the experimental diets for 20 days, and the last 5 days were used to perform a digestive trial.

Individual behavioral distinctiveness assessment

We assessed individual behavioral differences among collared peccaries under experimental conditions of a digestive trial using both the 'behavioral coding' and the 'subjective ratings' approaches. These methods capture different aspects of behavioral differences between individuals (see Meagher (2009) for a critical review and potential shortcomings of these methods). While the behavioral coding method is more suitable to detect the effects of environment/situation variables, the subjective ratings are more reliable for detecting consistencies in animals' behavior (Vazire *et al.*, 2007). As it is not known which aspect of the individual differences in behavior could be related to the digestibility of nutrients, we used both methods, as recommended by Carter *et al.* (2012). However, unlike Carter *et al.* (2012), we applied the two methods at different times, which allowed us to increase the number and duration of observations to make behavioral coding more reliable, following Meagher's (2009) recommendations.

The behavioral coding method is based on the direct behavioral observation of an individual using a predetermined ethogram, which allows the researcher to measure the variation in some behavioral elements, such as the frequency of *behaviors potentially indicative of stress* (**BPIS**). In the present study, we considered as BPIS for the collared peccary's two agonistic behaviors: 'tooth clacking' and 'whirling'. Both behaviors were originally described by Byers and Bekoff (1981) as follows: tooth clacking – described as 'an explosive series of "pops" or "clacks", made by rapid, orthal movements of the mandible' and whirling – 'one animal rapidly spun to face another (in our case the animal keeper), the mouth was open'.

Behavioral coding data were collected through continuous focal animal sampling (Altmann, 1974), twice a day during the 30 days of the habituation period. Standing 0.5 m in front of the pen door and using a digital camcorder (model GZHD500; JVC, Tokyo, Japan) fixed on a tripod, the animal keeper video recorded each collared peccary's reactions for 10 min before his entrance into the pen to feed the animals and clean the pen.

The individual behavioral characteristics were also assessed by the qualitative behavior assessment (QBA; Wemelsfelder *et al.*, 2001). The QBA has been successfully used to identify individual behavioral differences in domestic species such as Nellore cattle (Sant'Anna and Paranhos da Costa, 2013) and species under domestication, such as the collared peccary used as the model animal here (Nogueira *et al.*, 2015). The QBA approach is based on the use of adjectives as behavioral descriptors, which allows the assessment of the animals' body language as an indicator of individual behavioral differences. In turn, the continuous subjective ratings obtained through the QBA analogue scales detailed below allow the comparison with the results of the behavioral coding approach (Carter *et al.*, 2012).

Each individual went through three challenges: new environment, new object and threat test. In the new environment test, we recorded the first reactions (30 s) of each animal immediately after being released inside the metabolism pen on the first day of the habituation period. Each individual was transported using a wooden cage (1.2 m length × 0.6 m width × 0.6 m height). The transport cage door was opened, releasing the individual into the metabolism pen. In the new object test, we suddenly dropped two coconuts inside the pen and videotaped the animals for 30 s. This test was done 15 days after the new environment test. It started when the collared peccary turned its head toward the coconuts and started to look at them. We chose the coconuts to perform the novel object test because the animals had never seen them before, in the expectation that their introduction would increase the exploratory behavior and activity of the animals, as verified by Oliveira *et al.* (2016). All individuals were randomly tested on the same morning from 0800 to 0815 h. The canvas fixed to the walls of the metabolism pens prevented animals seeing others being tested. After the end of the tests, the coconuts were removed from the pens, as collared peccaries could not open or eat them. Finally, in the threat test, the keeper entered the pen with a capture net, just before the animal was transferred from the pens. Again, the test started only when the collared peccary turned its head toward the capture net and appeared to first notice it, and the test lasted for 30 s. We chose the capture net to stimulate the expression of defensive behavioral patterns, such as tooth clicking, and the animals even attacked the net and/or keepers, while being chased with the net (Nogueira *et al.*, 2015). This test occurred at the end of the digestive trial on the 56th day. The relatively short time window of 30 s for the tests was enough for the observers to rate (see below) the first reactions of the animals to the three challenging situations. Such a procedure was validated for the collared peccary (Nogueira *et al.*, 2015).

The video recording of behavioral reactions during the three tests resulted in 72 video clips of 30 s (3 tests × 24 collared peccaries). The 72 video clips were independently rated by three observers using an analogue scale following the QBA approach procedures (Wemelsfelder *et al.*, 2001) based on 12 adjectives previously validated to assess relatively positive and negative emotional states of the collared peccary (Nogueira *et al.*, 2015). The six adjectives that reflected the positive states were 'active', 'curious', 'quiet', 'docile', 'relaxed' and 'satisfied'; while the six that reflected negative states were 'fearful', 'agitated', 'tense', 'anxious', 'apathetic' and 'stressed' (see Wemelsfelder *et al.*, 2001). All adjectives were given an explicitly written definition to make the subjective ratings more reliable, as recommended by Meagher (2009). In addition, the three observers were experts in collared peccaries' behavior with experience in the subjective ratings method and blind to the experimental treatments. In their assessment, the observers marked a point for each of the 12 adjectives on a 125-mm scale with a minimum value (0) at the left end of the line representing the absence of the behavioral characteristic. At the right end, the maximum value (125) represented the most intense manifestation. The scores were obtained by measuring the distance in millimeters from the left end of the line to the observers' marks.

Digestive trials

In the afternoon of the 30th day of the habituation period, the peccaries were weighed and randomly allocated to one of the two experimental diets in a completely randomized design. These diets provided contrasting levels of dietary fiber (low fiber *v.* high fiber) by varying the proportions of ground corn, soybean bran, tifton hay (*Cynodon dactylon* cv. Tifton 85) and guava fruit (*Psidium guajava*; Table 1). The NDF and ADF proportions in the high-fiber diet were 69.2% and 133.4%, respectively, above the maximum recommendable levels of 281 g NDF/kg of DM and 142 g ADF/kg of DM for collared peccary (Nogueira-Filho, 2005).

Table 1 *Ingredients (g/kg as-is) and chemical composition (g/kg of DM unless otherwise mentioned) of ingredients and experimental diets (as fed basis) fed to collared peccaries*

Ingredients	Low fiber			High fiber
Corn	836			397
Soybean meal	98			97
Tifton hay	1			50
Guava fruit	60			451
Mineralized salt	4			4
Vit. Px.[1]	0.5			0.5
Min. Px.[2]	0.5			0.5
Analyzed nutrient composition (g/kg)		**Low fiber**		**High fiber**
DM		880.2		590.6
OM		857.1		551.9
CP		120.0		122.6
NDF		193.9		546.8
ADF		90.8		268.9
DE (MJ/kg-DM)		15.1		13.3
Ingredients composition	**Grain corn**	**Soybean meal**	**Tifton hay**	**Guava fruit**
DM	930	923	924	190
CP	83	456	24	98
NDF	144	160	923	949
ADF	59	130	399	472
Ash	17	62	105	46
GE (MJ/kg-DM)	16.5	17.6	15.8	15.9

OM = organic matter; NDF = neutral detergent fiber; ADF = acid detergent fiber; DE = digestible energy; GE = gross energy; MJ = mega Joules.
[1]Vit. Px.: vitamin premix with the following composition: Vitamin A, 1 200 000 IU; Vitamin D_3, 1 500 000 IU; Vitamin E, 1 500 000 IU; Vitamin B_1, 2 g; Vitamin B_2, 4 g; Vitamin B_6, 4 g; Vitamin B_{12}, 20 000 g; calcium pantothenate, 15 g; biotin, 0.10 g; Vitamin K_3, 3 g; folic acid, 0.6 g; nicotinic acid, 20 g; Zn bacitracin, 20 g; methionine, 100 g; L-lysine, 300 g; choline chlorine, 100 g; butylated hydroxytoluene (BHT), 10 g; selenium 0.10 g.
[2]Min. Px.: mineral premix with the following composition: iron, 180 g; copper, 20 g; cobalt, 4 g; manganese 80 g; zinc 140 g; iodine, 4 g.

After 20 days of adaptation to the experimental diets (Nogueira-Filho, 2005), each peccary was enclosed in its metabolism pen, and fecal collection was carried out for 5 consecutive days. In each group of six animals, three peccaries received the low-fiber diet, while the other three received the diet with high-fiber levels. Diets were offered twice a day at 0800 and 1700 h, and peccaries had *ad libitum* access to food until the next meal was offered. The feed intake was calculated as the difference between the amount of diet offered and the refused leftovers. Water was offered *ad libitum* at all times.

All feed samples, refusals (if any) and voided feces were collected twice a day, at feeding times. Refusals and feces were pooled per animal and dried to constant weight at 65°C. The dried samples were ground through a 1.0-mm mesh screen in a laboratory mill. Ground samples were analyzed in duplicate following standard laboratory procedures (AOAC, 2012) for contents of total ash in a muffle furnace (Association of Official Analytical Chemists, **AOAC** no. 942.05), nitrogen (N; AOAC no. 977.02; $CP = N \times 6.25$); gross energy (**GE**) was measured using an adiabatic calorimeter (C200; IKA-Werke, Staufen, Germany). The NDF was assayed using a heat-stable amylase (AOAC no. 2002.04) and corrected for residual ash content. The ADF was also expressed without the residual ash (AOAC no. 973.18). Daily DM, DE, digestible protein (**DP**), NDF and ADF intakes were expressed per metabolic BW ($MW^{0.75}$).

Data and statistical analysis

Two observers, who were blind to the experimental treatments during video analysis, scored the total number of BPIS events exhibited by each individual during the 10 min of recorded focal observations using the 'all occurrences' method (Altmann, 1974) by means of the software CowLog 3.0.2 (Hänninen and Pastell, 2009), considering each event as an independent BPIS bout. To increase the method's reliability as recommended by Meagher (2009), previously to the analysis of video-images, the observers were extensively trained to recognize the two coded behaviors (tooth clacking and whirling). They started coding the video-recorded images after reaching high inter-observer agreement (κ coefficient = 0.89).

After the 11th day, 13 of 24 collared peccaries showed no occurrence of BPIS, which they showed before, suggesting that they had become familiar with the experimental conditions, while the other 11 maintained their original reactions. Therefore, we used only the behavioral data collected during the first 10 days of the habituation period for the BPIS analysis, totaling 200 min of data collection per individual. Thereafter, we calculated individual BPIS frequency by dividing the total number of BPIS events by the total time (3.3 h) each animal was observed.

To analyze the subjective ratings, due to the sample size ($n = 24$), we followed the recommendation highlighted by Feaver *et al.* (1986) and used non-parametric analysis to assess individual behavioral characteristics. First, the ratings of the three observers were converted to *z* scores [(individual score - mean)/standard deviation] to reduce the influence of distributional effects. We then determined the inter-observer agreement using Kendall's coefficient of concordance (W), for each adjective and test independently. Further analysis only involved those adjectives that showed inter-observer coefficients of concordance higher than 0.70 ($W > 0.70$). The square of the coefficients of concordance indicates the proportion of the variance which is accounted for by observers' ratings, thus allowing inter-judge agreement on the retained adjective descriptors to account for over half of the variance, as recommended by Feaver *et al.* (1986) and Meagher (2009). For each of these items, we calculated the mean value of the observers' ratings for each collared peccary in each of the three challenging tests (novel environment, novel object and threat tests). Thereafter, we determined Kendall's coefficients of concordance (W) of each adjective among the three tests. We selected for further analysis only the adjectives that showed inter-test coefficients of concordance higher than 0.70 ($W > 0.70$). The selected adjective mean *z* scores across the three tests were then tested for correlations by Spearman rank correlation tests. Subsequently, we determined the mean *z* score of the highly correlated adjective descriptors (Spearman correlation coefficients ($r_{Spearman}$) > 0.70 and $r_{Spearman} < -0.70$), which showed cross-time and cross-situation consistency, to describe a coping style dimension of collared peccaries. We used Spearman rank correlation to test the association between the two approaches to measure individual behavioral differences (hourly frequencies of BPIS – BPIS/h – and *z* scores).

To test our prediction of relationship between feed intake, BWG and nutrient digestibility coefficients of collared peccaries with both the dietary fiber level and the individual behavioral differences, we used a GLM, to compare the DM intake (**DMI**; g/$MW^{0.75}$), the BWG (g/day) and the total tract apparent digestibility of nutrients. The model included the diet (low fiber *v.* high fiber) as fixed factor and the calmness *z* score or the frequency of BPIS/h as co-variable and their potential interactions. The residuals from models were checked for the assumptions of normality of errors and homogeneity of variance. Additionally, Bonferroni corrections for multiple comparisons were determined at $P = 0.05/8 = 0.006$ for GLM analyses. After that, we used the *t* test to compare the mean daily intakes of nutrients. We used the Minitab v. 19.1 software (Minitab Inc., State College, PA, USA) for all analyses, and *P* values less than 0.05 were considered statistically significant for all but the GLM analyses.

Results

Behavioral analyses

During the observations, we recorded 312 events of BPIS, with greater proportion of tooth clacking (86.2%) than whirling (13.8%). A high variability was observed between individuals in frequency of BPIS (BPIS/h), which ranged from 0 to 11.9 events per hour of observation. For the subjective ratings, we verified that 8 of 12 adjectives showed $W > 0.70$ ($P < 0.05$) for inter-judge concordance (Table 2). Of these, we verified that five adjectives (relaxed, quiet, satisfied, docile and anxious) showed concordance ($W > 0.70$ $P < 0.05$) across the three challenge tests (Table 2). Spearman rank correlations among these five adjectives resulted in a single group of the three highly correlated ($r_{Spearman} > 0.70$; Table 3) adjectives – relaxed, quiet and satisfied, which were combined to yield a coping style dimension named calmness as follows:

$$\text{Calmness: mean } z \text{ scores of the adjectives} \\ (\text{relaxed} + \text{quiet} + \text{satisfied})/3$$

Collared peccaries also showed high individual variation in the calmness z score that ranged from −1.0 to 2.6. Additionally, a negative correlation was observed between the frequencies of BPIS/h and the individual mean z scores on the calmness dimension ($r_{Spearman} = -0.45$, $P = 0.03$).

Feed intake, BW gain and total tract apparent digestibility

There was an effect of diet on the DMI ($P < 0.001$; Table 4). There was also an effect of the diet on the BWG ($P < 0.001$; Table 4). Collared peccaries fed the low-fiber diet showed BWG (4.5 ± 4.20 g/day); while animals fed the high-fiber diet lost (−17.8 ± 2.7 g/day) BW (Table 4).

There were effects of the calmness z score ($P = 0.004$; Table 4) and the frequency of BPIS/h ($P = 0.005$; Table 4) on the total tract digestibility of ADF. These effects remained significant after Bonferroni correction for multiple comparisons ($P = 0.006$). The greater the calmness z scores (i.e. calmer individuals), the greater the total tract digestibility of ADF (total tract digestibility of ADF = 0.56 + 0.08 calmness z score, $F_{1,22} = 12.61$, $R^2 = 0.36$, $P = 0.002$, $n = 24$; Figure 1a). In contrast, the higher the frequency of BPIS/h, the lower the total tract digestibility of ADF (total tract digestibility of ADF = 0.61 − 0.01 frequency of BPIS/h, $F_{1,22} = 10.27$, $R^2 = 0.32$, $P = 0.004$, $n = 24$; Figure 1b). There were also effects of the diet on the total tract apparent digestibility of DM ($P < 0.001$), organic matter (**OM**; $P < 0.001$) and GE ($P < 0.001$). The total tract apparent digestibility values for DM, OM, CP and GE were higher for collared peccaries fed the low-fiber diet in comparison to the animals fed the high-fiber diet (Table 4).

The chemical composition of the leftovers did not differ from the diets offered, and the dietary fiber levels resulted in different daily intakes of NDF and ADF (g/MW$^{0.75}$) according to the diets, as expected (Table 5). However, the lower DMI of high-fiber diet (Table 4) resulted in lower intakes of DP and DE, in comparison with collared peccaries fed the low-fiber diet (Table 5), despite the experimental diets being iso-proteic and iso-energetic (Table 1).

Table 2 *Inter-observer and inter-test Kendall concordance coefficients (W) of* z *score ratings of captive collared peccaries*

Adjective	Inter-observers *W*	Inter-observers *P*	Inter-tests *W*	Inter-tests *P*
Relaxed	**0.84**	**<0.05**	**0.84**	**<0.05**
Calm	**0.73**	**<0.05**	**0.88**	**<0.05**
Tense	0.54	<0.05	–	
Apathetic	0.42	<0.05	–	
Satisfied	**0.71**	**<0.05**	**0.88**	**<0.05**
Docile	**0.74**	**<0.05**	**0.82**	**<0.05**
Fearful	**0.80**	<0.05	0.26	>0.05
Agitated	**0.80**	<0.05	0.14	>0.05
Active	0.41	<0.05	–	
Anxious	**0.76**	**<0.05**	**0.86**	**<0.05**
Curious	0.46	<0.05	–	
Stressed	**0.76**	**<0.05**	0.20	>0.05

Items in boldface are those in which the inter-observer and inter-test Kendall concordance coefficients (*W*) were greater than 0.70 and thereby qualified for use in further analysis.

Discussion

Observers rated the reactions of each individual consistently across the three challenging situations on the measures of relaxedness, quietness and satisfaction. This means that the observers picked up on the 'core' of individual behavioral traits that were expressed in a consistent way when they were facing novel situations in the three challenging tests. The resulting calmness z scores were negatively correlated with the frequencies of BPIS/h: the higher the calmness score, the lower the frequency of behaviors that potentially indicate distress. Our results also showed large individual variation in how animals coped with challenges in both approaches (behavioral coding and subjective ratings), which confirms the high individual behavioral distinctiveness in reactions toward humans previously described for the collared peccary

Table 3 *Spearman correlation coefficients ($r_{Spearman}$) of mean* z *score ratings of collared peccaries*

	Relaxed	Quiet	Satisfied	Docile	Anxious
Relaxed	–	**0.80** ($P < 0.05$)	**0.82** ($P < 0.05$)	0.14 ($P > 0.05$)	−0.56 ($P < 0.05$)
Quiet		–	**0.79** ($P < 0.05$)	0.55 ($P < 0.05$)	−0.67 ($P < 0.05$)
Satisfied			–	0.49 ($P < 0.05$)	−0.42 ($P < 0.05$)
Docile				–	−0.56 ($P < 0.05$)
Anxious					–

Boldface values represent $r_{Spearman} > 0.70$ used to combine the 'calmness' behavioral dimension of collared peccaries.

Table 4 *Means*[1] *(standard errors) of the daily DM intake (DMI g/MW$^{0.75}$/day), daily BW gain (BWG g/day) and total tract apparent digestibility (TTAD) of nutrients by collared peccaries according to diets – low fiber (*n = 12*) v. high fiber (*n = 12*) – and their relationships (*$F_{1,20}$ *and (P) values) with personality metrics ('calmness' z score and hourly frequency of behaviors potentially indicative of stress – BPIS/h)*

	Diet		Calmness z score				Frequency of BPIS/h			
	Low fiber	High fiber	Diet	z Score[2]	Diet × z score[3]	R^2	Diet	BPIS/h[4]	Diet × BPIS/h[5]	R^2
DMI	53.17 (2.10)	36.52 (1.00)	51.16 ($P \leq 0.001$)	3.17 ($P = 0.090$)	0.69 ($P = 0.415$)	0.74	43.80 ($P \leq 0.001$)	0.60 ($P = 0.449$)	1.52 ($P = 0.232$)	0.75
BWG	4.50 (4.20)	−17.8 (2.70)	20.34 ($P \leq 0.001$)	1.42 ($P = 0.247$)	0.90 ($P = 0.354$)	0.52	18.37 ($P \leq 0.001$)	1.59 ($P = 0.222$)	0.87 ($P = 0.363$)	
TTAD										
DM	0.91 (0.01)	0.81 (0.01)	63.18 ($P \leq 0.001$)	3.41 ($P = 0.080$)	0.13 ($P = 0.721$)	0.77	38.10 ($P \leq 0.001$)	6.57 ($P = 0.019$)	1.26 ($P = 0.274$)	0.79
OM	0.92 (0.01)	0.73 (0.01)	155.50 ($P \leq 0.001$)	2.82 ($P = 0.108$)	0.73 ($P = 0.402$)	0.89	97.64 ($P \leq 0.001$)	6.56 ($P = 0.019$)	2.95 ($P = 0.101$)	0.90
CP	0.86 (0.01)	0.78 (0.01)	24.81 ($P \leq 0.001$)	0.13 ($P = 0.721$)	0.24 ($P = 0.632$)	0.55	19.10 ($P \leq 0.001$)	0.66 ($P = 0.425$)	0.14 ($P = 0.714$)	0.57
NDF	0.59 (0.04)	0.76 (0.02)	21.20 ($P \leq 0.001$)	4.68 ($P = 0.043$)	1.86 ($P = 0.188$)	0.58	13.57 ($P \leq 0.001$)	3.87 ($P = 0.063$)	0.06 (0.816)	0.57
ADF	0.58 (0.04)	0.54 (0.03)	1.75 ($P = 0.201$)	13.15 ($P = 0.002$)	0.35 ($P = 0.561$)	0.42	0.78 ($P = 0.386$)	9.74 ($P = 0.005$)	0.00 ($P = 0.975$)	0.35
GE	0.91 (0.01)	0.82 (0.01)	63.51 ($P < 0.001$)	2.57 ($P = 0.125$)	0.27 ($P = 0.609$)	0.77	38.17 ($P \leq 0.001$)	5.01 ($P = 0.037$)	0.87 ($P = 0.363$)	0.78

DMI = DM intake; BWG = BW gain; OM = organic matter; NDF = neutral detergent fiber; ADF = acid detergent fiber; GE = gross energy; MW$^{0.75}$ = metabolic BW.
[1]Standard errors of the means are displayed in parentheses.
[2]z Score: calmness z score.
[3]Diet × z score: interaction between diet *v.* calmness z score.
[4]BPIS/h: frequency of BPIS/h.
[5]Diet × BPIS/h: interaction between diet and frequency of BPIS/h.

(Nogueira *et al.*, 2015). The total tract digestibility values of NDF and ADF were similar to the values already observed for collared peccaries fed diets with similar fiber levels (Comizzoli *et al.*, 1997; Nogueira-Filho, 2005; Nogueira-Filho *et al.*, 2018). The digestibility of dietary fiber of collared peccary is also similar to the digestibility determined in both domestic and wild ruminants fed diets with similar fiber levels (Van Soest, 1994). This relatively high efficiency in digesting cell wall contents (NDF and ADF) as verified here can be explained by the collared peccary's forestomach, which has large storage capacity and many folds that slow the passage of food (Langer, 1979).This results in a comparatively high mean retention time of up to 73 h (Nogueira-Filho *et al.*, 2018), allowing more time for active microbial fermentation to occur (Sowls, 1997; Oliveira *et al.*, 2009).

As we hypothesized, there is a strong relationship between the individual coping style and the digestibility of dietary fiber. Indeed, frequencies of BPIS/h and individual calmness scores were both able to predict the digestibility of ADF. We verified an increase of 8.0% in total tract digestibility of ADF for each point in the *z* scores in the calmness dimension. In contrast, there is a decrease of 1.0% in total tract digestibility of ADF for each increment in the frequency of BPIS/h. Therefore, calmer collared peccaries (lower frequency of BPIS/h and higher calmness *z* scores) showed higher efficiency in digesting the ADF.

Contrary to what we expected, no relationship was observed between feed intake and individual behavioral traits. For ruminants, the less excitable individuals and those more adapted to handling practices have higher feed intake (Llonch *et al.*, 2016; Neave *et al.*, 2018). The same was observed in pigs; the calmer and docile ones ate longer meals and spent more time at the feeder, which resulted in faster growing fatter pigs (Rohrer *et al.*, 2013). In this study, the lack of a relationship between feed intake and individual behavioral traits could be explained by the relatively high water content-holding capacity of guava fruit, which composed almost half of the high-fiber diet, as observed by Bindelle *et al.* (2009) in pigs fed sugar beet pulp. The relatively low voluntary intake of the high-fiber diet led to mean daily intakes of 257.6 kJ DE/MW$^{0.75}$ and 3.7 g DP/MW$^{0.75}$. This DE intake was far below the requirement of this species – estimated at 420 kJ DE/MW$^{0.75}$ (Comizzoli *et al.*, 1997) and slightly above this species' requirement of DP – estimated at 3.2 g /MW$^{0.75}$ (Borges *et al.*, 2017) – which resulted in loss of BW, despite the high levels of energy and protein sources (ground corn and soybean meal, respectively) in the high-fiber diet formula. The low voluntary intake of this diet can probably be explained by the relatively high water content-holding capacity of guava fruit, which composed almost half of the high-fiber diet, as observed by Bindelle *et al.* (2009) in pigs fed sugar beet pulp. Therefore, farmers need to dehydrate very juicy feeds given to collared peccaries.

In turn, the comparatively higher DMI of the low dietary fiber diet led to intakes of DE and DP above the requirements of the species, resulting in BWG and higher total tract apparent digestibility of DM, OM, CP and GE, in comparison with

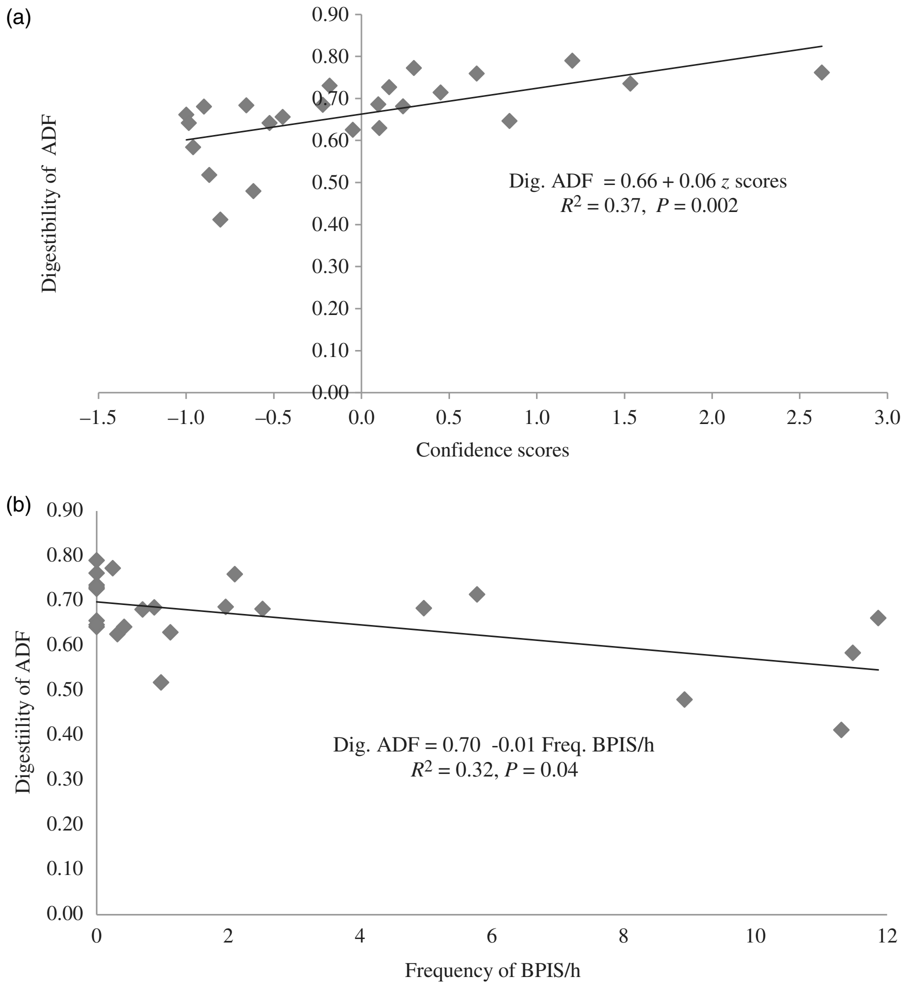

Figure 1 Relationship between the total tract digestibility coefficients of acid detergent fiber (ADF; Dig. ADF) of collared peccaries with the individual 'calmness' *z* scores (a) and hourly frequency of behaviors potentially indicative of stress (BPIS/h) (b).

Table 5 *Mean daily intakes (g/MW$^{0.75}$ unless otherwise mentioned)[1] of nutrients by collared peccaries that received diets either with low dietary fiber level (NDF = 193.9 g/kg DM and ADF = 90.8 g/kg DM,* n *= 12) or with high dietary fiber level (NDF = 546.8 g/kg DM and ADF = 268.9 g/kg DM,* n *= 12)*

Daily intake	Low fiber	High fiber	*t* Value	*P*
NDF (g/MW$^{0.75}$)	7.6 (0.4)	20.0 (0.6)	16.9	<0.001
ADF (g/MW$^{0.75}$)	3.9 (0.2)	8.4 (0.2)	15.8	<0.001
DP (g/MW$^{0.75}$)	6.1 (0.2)	3.7 (0.2)	−8.6	<0.001
DE (kJ/MW$^{0.75}$)	422.0 (16.1)	257.6 (7.2)	−9.3	<0.001

NDF = neutral detergent fiber; ADF = acid detergent fiber; DP = digestible protein; DE = digestible energy; MW$^{0.75}$ = metabolic BW.
[1]Standard errors of the means are displayed in parentheses.

the collared peccaries fed the high-fiber diet. In contrast, we verified lower total tract digestibility of NDF for collared peccaries fed the lower fiber diet. Previously it was reported that the increase in non-fiber carbohydrate in the diet of collared peccary decreases its potential to digest cell wall contents (Nogueira-Filho *et al.*, 2018). Therefore, the higher level of soluble carbohydrates in the low-fiber diet in comparison with the high-fiber diet – which was not determined in the present study – probably explains the lower digestibility of NDF for collared peccaries fed the lower fiber diet, in comparison with the ones fed the high-fiber diet.

As far as we know, this is the first study that highlights the relationships between the individual differences in behavioral traits and the efficiency of dietary fiber digestion, which may have implications for digestibility trial procedures. Researchers usually select less excitable animals in response to novel/unfamiliar environments and human proximity to participate in digestibility trials, which may cause a bias in their results. In turn, as behavioral differences are at least partially inherited (Van Oers *et al*., 2005), the selection for calmer collared peccaries, adapted to handling practices, may improve their nutrient digestibility and, ultimately, their efficiency in converting feed into growth, meat, offspring, etc. However, it is important to highlight that we assessed individual behavioral differences among collared peccaries under the very restricted experimental conditions of a digestive trial. Therefore, further study should seek more practical tests for on-farm conditions, based either on behavioral coding or on subjective ratings, to enable selective breeding programs including behavioral traits not only for collared peccaries but also for other species of domestic animals.

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Declaration of interest

The authors declare no conflicts of interest.

Ethics statement

The protocol for this experiment followed Brazilian laws and was approved by the Animal Use Ethics Committee of the Universidade Estadual de Santa Cruz through protocol # 0102012.

Software and data repository resources

The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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