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Embryonic and fetal development of the collared peccary (*Pecari tajacu*)

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ABSTRACT

The relative timing of the main fetal development events in species determine the extent of fetal development at birth, which range along a gradient of having altricial and precocial traits. The results from this study allow for description of important fetal developments in collared peccary (*Pecari tajacu*) using data from 118 embryo/fetuses from 68 pregnant peccaries obtained over a period of 15 years through collaborative methods with local hunters in the Amazon. The chronological order of emergence of external characteristics in relation to the total dorsal length (TDL) was: differentiated genitalia, limbs and eyelid buds (TDL ≥ 4.5 cm), fusioned eyelids and outer ear (TDL ≥ 5.6 cm), dorsal gland (TDL ≥ 7.3 cm), skin (TDL ≥ 9.2 cm), tactile pelage (TDL ≥ 12.9 cm), coverage pelage (TDL ≥ 17.0 cm), opened eyelids (TDL ≥ 21.5 cm) and tooth eruption (TDL ≥ 24.5 cm). The formula of fetal age was $\sqrt[3]{W} = 0.079\ (t - 27.6)$, with a linear relationship between TDL and gestational age. The relative weight of tubular gastrointestinal organs, lungs, spleen and thymus increased during fetal development. In contrast, the relative weight of kidneys and liver consistently decreased during the fetal development period. Results of this study indicate the collared peccary is a precocial species and that changes during fetal development are very similar to those in other Suiform species.

1. Introduction

In mammals, the intra-uterine development of a species is characterized by the individual's maturational pattern from conception to parturition, during which neonates need to adapt to the extra-uterine environment to maximize their survival (Gluckman et al., 1999). Depending on the extent of fetal development at parturition, mammals are normally categorized into precocial and altricial species. Nevertheless, the proper classification of mammals according to the extent of fetal development is still a challenge. Case (1978) and Eisenberg (1981) tended to focus on the attainment of parental independence through nutritional, sensory, locomotory

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and thermoregulatory development, claiming that precocial species have well-developed neonates, with greater development of the central nervous system, and an improved motor and visual capacity, resulting in the capacity to move and forage independently (Sacher and Staffeldt, 1974). With altricial species, there is completion of fetal development in the early post-natal period, and fetuses are very dependent on maternal care (Flowerdew, 1987). There is likely, however, for mammalian species a continuum of neonatal development (Zeveloff and Boyce, 1980), and survival may be dependent on a myriad of embryonic and fetal development changes that have occurred as a result of natural selection which have occurred during the evolution of the species, which may vary even among species with close phylogenetic relationships.

The collared peccary, a medium-sized artiodactyl weighting from 14 to 30 kg (Desbiez and Keuroghlian, 2009), is one of the most frequently hunted species in the Amazon region (Fang et al., 2008). Due to the trade in meat and pelts, this species is highly important for Latin America economy (Fang et al., 2008) and is also included in captive breeding programs. The collared peccary is aseasonally polyoestrus in their natural habitat in the Amazon (Mayor et al., 2009) with a mean gestation period of 138 days (Mayor et al., 2005), and a litter size of 1.7–1.9 fetuses (Mayor et al., 2005 and 2009; Desbiez and Keuroghlian, 2009), and a yearly reproductive production of 1.98 piglets per pregnant female (Mayor et al., 2010).

The study on the timing of the primary anatomical components of the embryonic and fetal development may clarify the physiological and behavioral changes that have occurred because of natural selection in each species that result in maximal neonatal survival (Derrickson, 1992). The present study was conducted to describe the embryonic and fetal development of the collared peccary and comparing this development to that to other Suiforms.

2. Material and methods

2.1. Study sites

This study was conducted in the Yavarí-Mirín River area (S 04°19.53; W 71°57.33), a continuous area of 107,000 ha of predominantly upland forests located in northeastern Peruvian Amazon. There is a single indigenous community of 307 inhabitants in the region. The inhabitants in the local community rely mainly on agriculture for income and on hunting and fishing for subsistence. The climate is typically equatorial with annual temperatures ranging from 22° to 36 °C, a relative humidity of 80%, and an annual rainfall between 1500 and 3000 mm in the dry and wet/flooded seasons of the year, respectively.

2.2. Biological sample collection and processing

Embryos and fetuses were collected through the collaboration of local dwellers whose income from protein sources depends on the subsistence hunting. Hunters were trained to remove all abdominal and pelvic organs complete with the perineal region and to store these in buffered 4% formaldehyde solution (v/v). This sampling strategy allows for the use of materials that would otherwise be discarded. Because hunters do not consume these materials, any invasive procedure or any additional mortality for the purpose of the study was avoided (Mayor et al., 2017). From 2002 to 2015, local hunters collected and voluntarily donated reproductive tracts from 68 pregnant collared peccaries, including 22 (32.3%) single, 42 (61.8%) twin, and four (5.9%) triplet pregnancies. Among the pregnant females, six (8.9%) were in the embryonic and 62 (91.1%) were in the fetal pregnancy developmental stage at the time of tissue harvesting. Reproductive tracts were dissected and 11 embryos and 107 fetuses were collected. The research protocol was approved by the Research Ethics Committee for Experimentation in Wildlife at the Direccion General de Flora y Fauna Silvestre from Peru (License 0350-2013- DGFFS-DGEFFS) and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (CEUA/UFRA protocol 008/2016). Samples were transferred to UFRA, Belém, Pará, Brazil, after obtaining an export license (CITES/IBAMA) to do so (No 14BR015991/DF).

There was external examination of all embryos and fetuses to describe the presence of the following external morphological features: 1) differentiated genitalia, 2) differentiated limbs, 3) eyelids, 4) skin, 5) covering and tactile pelage, 6) erupted teeth, 7) dorsal gland, and 8) outer ear. The embryo/fetal stage was determined using the criteria of the International Committee on Veterinary Embryological Nomenclature (2017), and the embryos were characterized based on the presence of eyelids, genitalia and limb buds.

Biometry measurements were performed on seven embryos and 96 fetuses from 59 gestations to describe the external biometry. There were damaged or autolyzed embryos/fetuses from nine gestations for which data were not collected. The external measurements included the body mass, total dorsal length (TDL), crown-rump length (CRL), biparietal diameter (BPD), occipital-frontal diameter (OFD), cranial circumference (CC), femur and humerus length (FL and HL), length of thoracic and pelvic limbs (TL and PL), thoracic diameter and circumference (TD and TC), as well as abdominal diameter and circumference (AD and AC). Thoracic and abdominal measurements were obtained from the last rib and the insertion of the umbilical cord, respectively. The biometry measurements conducted with the embryos included the biometry in the same homologous anatomical regions, but there was not consideration of FL and HL. In cases of twin and triplet pregnancies, there was calculation of the average of each biometric variable of all fetuses from peccaries with a single fetus during the gestational period.

There was evisceration of the thoracic and abdominal organs (heart, lungs, thymus, liver, spleen, kidneys and tubular gastrointestinal organs) from one fetus per pregnancy. After excluding embryos and fetuses that were crushed during processing or in poor conservation condition, there was analysis of 43 fetuses from different pregnancies. The summative weight of all organs was considered as the total visceral weight. The difference between the total fetal weight and the total visceral weight was considered as a proxy of the weight of the musculoskeletal system. The relative weight of each fetal organ was calculated as a percentage respective to the total visceral weight and total fetal weight. In parallel, organ samples from three hunted adult collared peccaries were collected and stored using the same procedures as those described for the reproductive organs. The weight of the same organs in the adult individuals was determined to compare the relative weight of fetal organs in advanced pregnancy stages and adults.

There was also measurement of the longitudinal and the maximum width diameter of the placenta of each pregnant female. The mass of the body and fetal organs was quantified in grams using a digital scale (0.1 g accuracy), while a tape measure (0.1 mm accuracy) and a metal caliper (full measurement capability 300 mm) being used to determine values for body measurements.

2.3. Statistical analysis

The gestational age of each embryo/fetus was estimated using the formula developed by Huggett and Widdas (1951), $\sqrt[3]{W} = a$ (t-t0), where *W* is the fetal weight, *a* is the specific fetal growth velocity, *t* is the fetal age in days, and *t0* is the calculated interception on the age axis. Based on the results from the previous study, *t0* was considered to be equal to 20% of gestation length in species gestational period durations of 100 and 400 days. To use that equation, the mean gestational period length was considered to be 138 days (Mayor et al., 2005), and a mean weight 668 g at birth (Sowls, 1984 and 1997; Mayor et al., 2005 and 2010). For the estimation of fetal age *t* (in days), the body mass of each fetus was determined and the value of *a* and *t0* that was previously calculated was used to make this determination.

Logistic regressions were applied to estimate the probability of occurrence of each external morphological characteristic in relation to TDL using the software Statistica 8.0 (StatSoft Inc., Tulsa, USA). Multiple linear and non-linear regression modeling relationships between the TDL and biometric measures, absolute and relative organ weights and placental diameters were conducted using the software CurveExpert 2.4 (© Copyright 2017, Daniel G. Hyams), which defined those functions that best fitted the plots. Regressions were also used to assess allometric relationships between BPD and OFD, TC and AC, HL and FL, TL and PL, and to assess the trends in the relative weight of each organ based on the log of the total visceral weight, considering both fetuses and adults. For absolute measurements, there was forced determination of linear regressions to the origin on the graphic determination and there was only consideration with these calculations of those functions with a starting point on or near zero, because it was expected that both internal and external measurements would be zero on day 0 of fetal development.

There was evaluation of the biometric variation of twins from 34 pregnant females across gestation using linear regressions between the average TDL and the standard deviation (SD) of TDL, body mass, CC and FL.

There was comparison of the relative weight of visceral organs of larger fetuses considering the weight stabilization in fetuses in more advanced stages of gestation (≥25.0 cm TDL) with those of adults by means of T-student tests using the R 3.3.3 software (R Core Team, 2017).

All descriptive values of fetal measurements are expressed as mean ± SD. Differences with a probability value of 0.05 or less ($P \leq 0.05$) were considered significant.

3. Results

In the embryos/fetuses, the average TDL was 14.6 ± 8.1 SD cm (range 0.4–32.8 cm). The body mass was 144.3 ± 170.4 SD g (range 0.1–745 g). The growth formula used to determine fetal age was $\sqrt[3]{W} = 0.079$ (t − 27.6). Both associations between gestational age and TDL ($r^2 = 0.965$, $P < 0.0001$) and CRL ($r^2 = 0.973$, $P < 0.0001$) indicated there were positive associations between values for these variables (Fig. 1). The correlation coefficients between values for TDL and body mass ($r^2 = 0.951$, $P < 0.001$; Fig. 2) and CRL ($r^2 = 0.958$, $P < 0.001$; Fig. 3) indicated there were positive associations between the values for these variables. There were significant associations between TDL and the standard deviation of TDL and body mass indicating the fetal variability for these variables within the same pregnancy increases as the pregnancy advances ($r^2 = 0.391$ and $r^2 = 0.475$, respectively, $P < 0.05$; Fig. 4).

The probability curves and the regression models for the occurrence of external morphological features based on TDL are presented in Fig. 5 and Table 1, respectively. Embryos and fetuses with a TDL of ≤3.1 cm had genitalia, limb and eyelid buds. Differentiated limbs and genitalia (44 females and 45 males) were observed in fetuses with a TDL of ≥4.5 cm and a CRL of ≥2.9 cm. Outer ear and fused eyelids were observed in fetuses that had a TDL of 5.6 cm or greater (≥3.1 cm CRL). The dorsal gland was first observed in fetuses with a TDL of 7.3 cm (≥4.7 cm CRL), and first signs of skin development was detected in fetuses when there was a TDL of 9.2 cm (≥6.7 cm CRL). Fetuses had tactile pelage when the TDL was 12.9 cm or greater (≥10.1 cm CRL) and had a covering pelage when the TDL was 17.0 cm or greater (≥11.9 cm CRL). Opened eyelids and tooth eruption were the last characteristics to be observable in advanced stages of fetal development when the TDL was 21.5 cm or greater (≥14.5 cm CRL) and TDL was 24.5 cm (≥16.7 cm CRL), respectively (Fig. 6).

For all associations between TDL and external biometric measures, there were significant correlation coefficients of determination ($r^2 > 0.916$, $P < 0.01$; Fig. 2). The CC ($r^2 = 0.976$, $P < 0.001$) and TC ($r^2 = 0.975$, $P < 0.001$) had the greatest correlation coefficients with the TDL. For the allometric relationships, there were some significant interactions among values for the variables that were evaluated ($r^2 \geq 0.93$, $P < 0.01$). For the relationship between HL and FL, however, there was a 1:1 proportional growth ($r^2 = 0.953$, $P < 0.001$) for the PL while there was more rapid growth than for TL during the fetal phase ($r^2 = 0.979$, $P < 0.001$, Fig. 3).

For all associations between TDL and the absolute weight of internal organs, there were significant coefficients of determination ($r^2 \geq 0.809$, $P < 0.05$; Fig. 7). The greatest associations were between the thymus ($r^2 = 0.956$, $P < 0.001$), and the total visceral weight ($r^2 = 0.941$, $P < 0.001$).

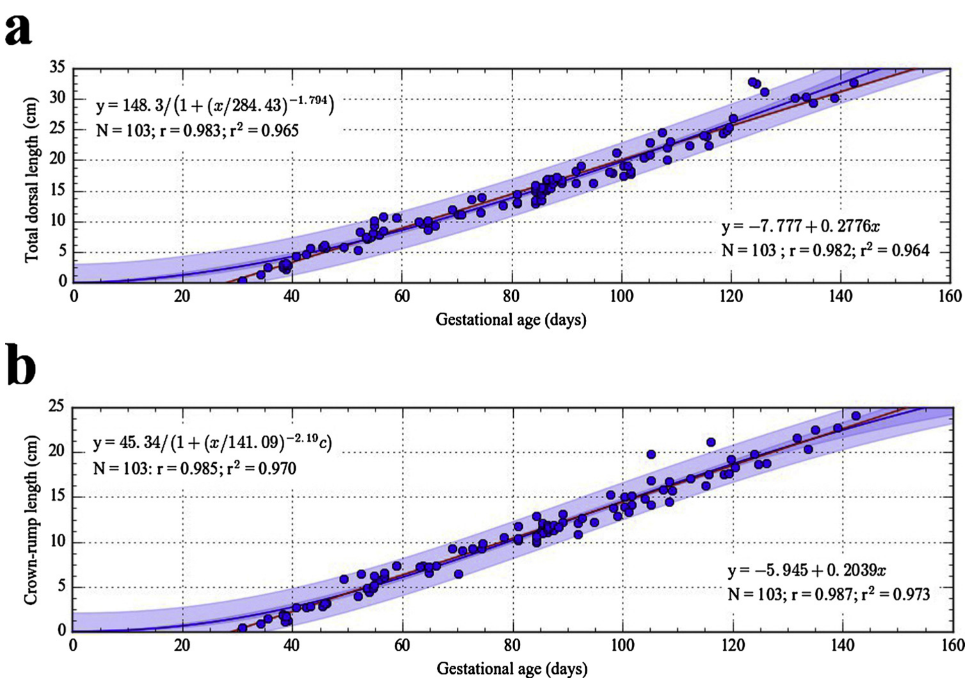

Fig. 1. Relationship between gestational age and total dorsal length (a) and crown-rump length (b) in 103 fetuses from 62 pregnant collared peccaries (*Pecari tajacu*).

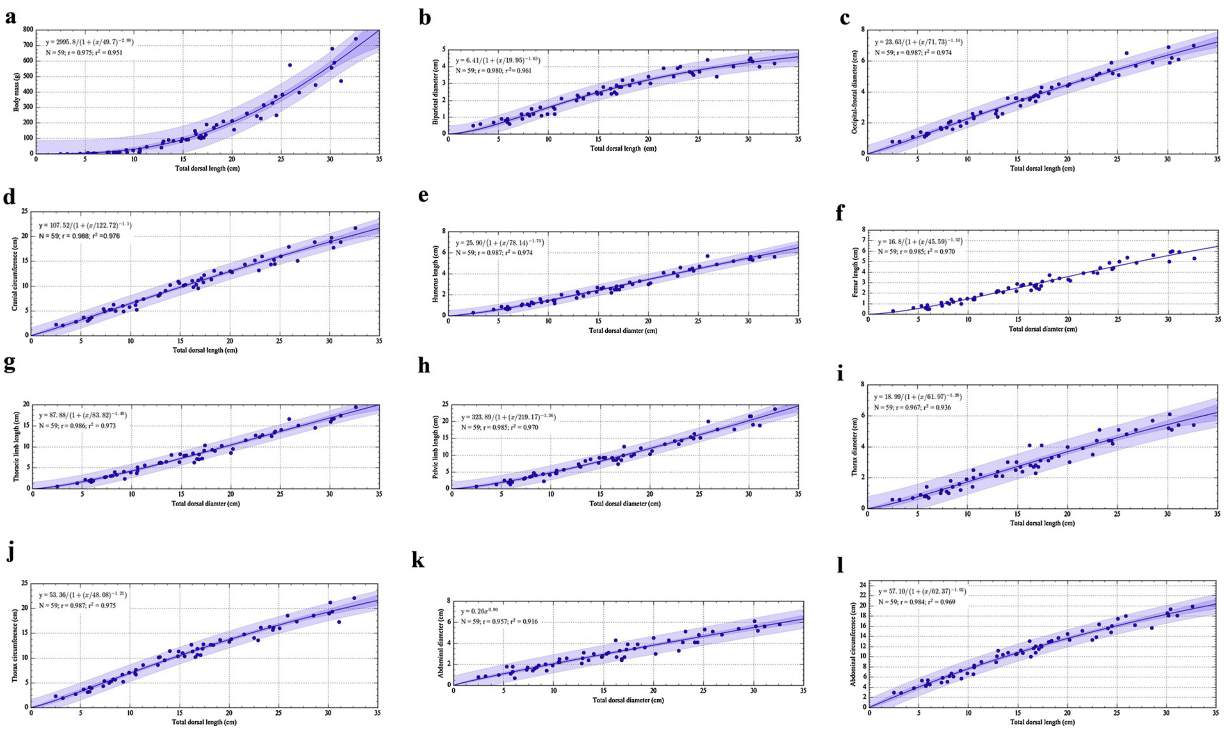

Fig. 2. Relationship between the total dorsal length (TDL) and the body mass (a), biparieral diameter (b), occipital-frontal diameter (c), cranial circumference (d), humerus (e) and femur length (f), length of thoracic (g) and pelvic limbs (h), thorax diameter (i), thorax circumference (j), abdominal diameter (k) and abdominal circumference (l) in embryo/fetuses from 59 pregnant collared peccaries (*Pecari tajacu*).

For the associations between the log value of total visceral weight and the relative weight of internal organs, including fetuses and adults, for which there were significant coefficients of determination (r^2 = 0.596 – 0.863, $P <$ 0.001; Fig. 8), except for the heart (r^2 = 0.008, P = 0.343). There were the greatest associations between the relative weight of tubular gastrointestinal organs

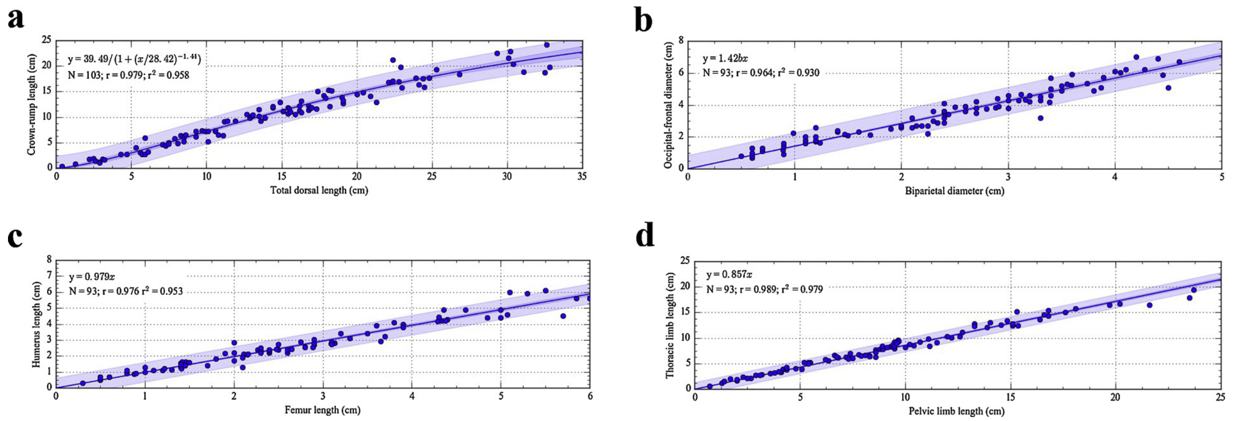

Fig. 3. Allometric relationship of the total dorsal length compared with crown-rump length (a), biparietal diameter compared with occipital-frontal diameter (b), humerus length compared with femur length (c), and length of thoracic limbs compared with length of pelvic limbs (d) in 103 embryo/fetuses from 59 pregnant collared peccaries (*Pecari tajacu*).

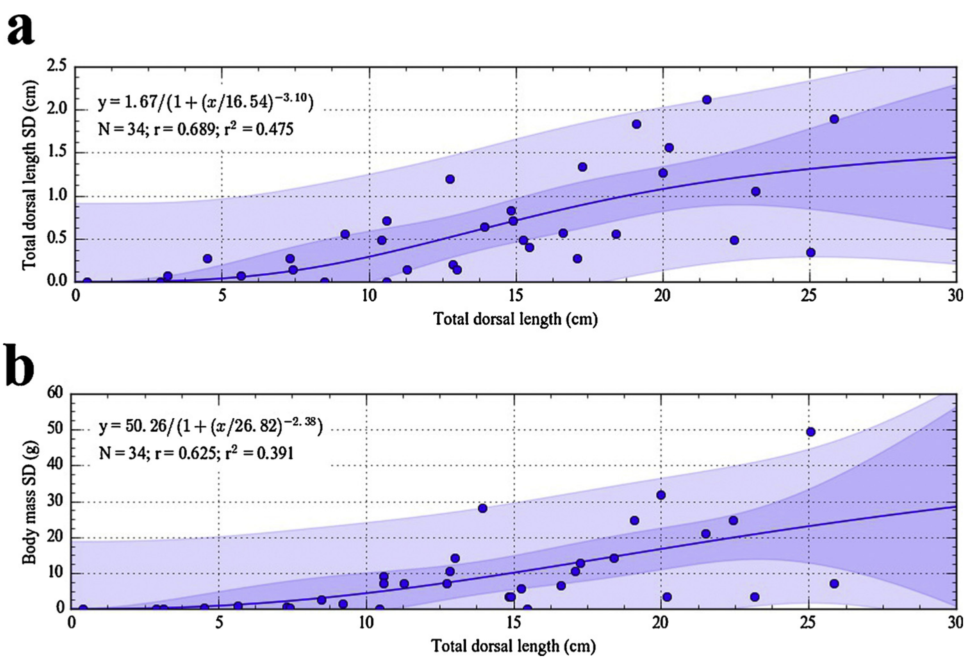

Fig. 4. Relationship between the average total dorsal length (TDL), and standard deviation (SD) of the total dorsal length (a) and body mass (b) in twin fetuses from 34 pregnant collared peccaries (*Pecari tajacu*).

($r^2 = 0.863$, $r = 0.929$ and $P < 0.01$), kidneys ($r^2 = 0.777$, $r = -0.882$ and $P < 0.01$), and the liver ($r^2 = 0.728$, $r = -0.853$ and $P < 0.01$). For the relative weight of the musculoskeletal system, there was a slight increase during post-natal development ($r^2 = 0.772$, $r = 0.596$ and $P < 0.001$). The relative weight of tubular gastrointestinal organs increased during both fetal and post-natal development with the relative weight of the lungs and thymus increasing in rate of growth during fetal development but decreasing during the post-natal development. For the relative weight of the spleen, there was an increase during fetal development and this was proportionally sustained during post-natal developmental period. For the relative weight of kidneys and liver, there was a sustained decrease during fetal development that proportionally continued during post-natal development (Fig. 8). Comparisons between fetuses in the more advanced developmental stages ($\geq$25.0 cm TDL, $n = 7$) and adults ($n = 3$) indicated that for all organs, except the liver, spleen and heart, there were significant differences in relative weights (Table 2).

The diffuse, folded, epitheliochorial and non-deciduate placenta had no trophoblast invasion into the uterine epithelium; however, the fusiform chorionic sac maintained close contact between fetal and maternal microvilli (Fig. 9). Inter-areolar and areolar regions of the feto-maternal interface were identified. The longitudinal diameter of the placenta indicated there was a positive relationship with TDL ($r^2 > 0.303$, $P < 0.0001$), but the maximum width was relatively constant ($r^2 > 0.002$, $P = 0.23$).

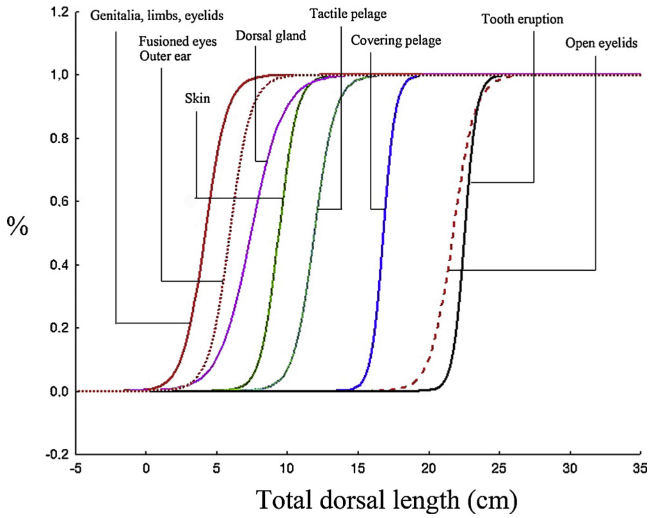

Fig. 5. Probability curves for external morphological features along the increase in total dorsal length (TDL) in 118 embryos/fetuses from 68 pregnant collared peccaries (*Pecari tajacu*).

Table 1
Logistic equations for the external morphological features parameters in 118 embryos/fetuses from 68 collared peccary (*Pecari tajacu*) pregnant females.

Morphological features	Equation	Chi-square (Df)	P value
Eyelid buds	$y=\frac{2.72^{(-5.3832+(1.2949)*x)}}{1+2.72^{(-5.3832+(1.2949)*x)}}$	40.32 (1)	< 0.01
Differentiated genitália	$y=\frac{2.72^{(-5.3832+(1.2949)*x)}}{1+2.72^{(-5.3832+(1.2949)*x)}}$	38.73 (1)	< 0.01
Limbs	$y=\frac{2.72^{(-5.3832+(1.2949)*x)}}{1+2.72^{(-5.3832+(1.2949)*x)}}$	40.38 (1)	< 0.01
Outer ear	$y=\frac{2.72^{(-7.8192+(1.32279)*x)}}{1+2.72^{(-7.8192+(1.32279)*x)}}$	46.90 (1)	< 0.01
Fusioned eyelids	$y=\frac{2.72^{(-8.1934+(1.38259)*x)}}{1+2.72^{(-8.1934+(1.38259)*x)}}$	49.52 (1)	< 0.01
Skin	$y=\frac{2.72^{(-15.057+(1.60324)*x)}}{1+2.72^{(-15.057+(1.60324)*x)}}$	71.54 (1)	< 0.01
Dorsal gland	$y=\frac{2.72^{(-6.4966+(0.873098)*x)}}{1+2.72^{(-6.4966+(0.873098)*x)}}$	50.85 (1)	< 0.01
Tactile pelage	$y=\frac{2.72^{(-16.005+(1.34467)*x)}}{1+2.72^{(-16.005+(1.34467)*x)}}$	76.38 (1)	< 0.01
Covering pelage	$y=\frac{2.72^{(-38.855+(2.31606)*x)}}{1+2.72^{(-38.855+(2.31606)*x)}}$	74.97 (1)	< 0.01
Teeth eruption	$y=\frac{2.72^{(-53.266+(2.3636)*x)}}{1+2.72^{(-53.266+(2.3636)*x)}}$	62.52 (1)	< 0.01
Opened eyelids	$y=\frac{2.72^{(-27.988+(1.28836)*x)}}{1+2.72^{(-27.988+(1.28836)*x)}}$	62.11 (1)	< 0.01

4. Discussion

The results of this study provide useful reproduction information for development of more appropriate reproductive management practices, particularly for use of the modern reproductive biotechnologies, and for improved use of assisted reproductive techniques (Castelo et al., 2010; Peixoto et al., 2012; Maia et al., 2014). These outcomes from the present study also improve the understanding of the natural selection that occurred in different mammalian species to maximize maternal and neonatal survival. The fetal development in mammalian species is of a continuum pattern that results in the neonate having varying altricial or precocial traits (Zeveloff and Boyce, 1980).

The methodology used in the present study has also been used in similar studies conducted with the paca (*Cuniculus paca*, El Bizri et al., 2017), woolly monkey (*Lagothrix poeppigii*, Andrade et al., 2017), white-lipped peccary (*Tayassu pecari*, Andrade et al., 2018) and red brocked deer (*Mazama americana*, Mayor et al., 2019). In these studies, results were consistent with those obtained using B-mode ultrasonography and with measures in neonates born in captivity the values for measurements in the present study can be used as accurate standard values for these variables. In addition, the CRL data curve developed in the present study is similar to those developed in previous studies of fetal development in collared peccaries conducted using ultrasonography (Mayor et al., 2005)

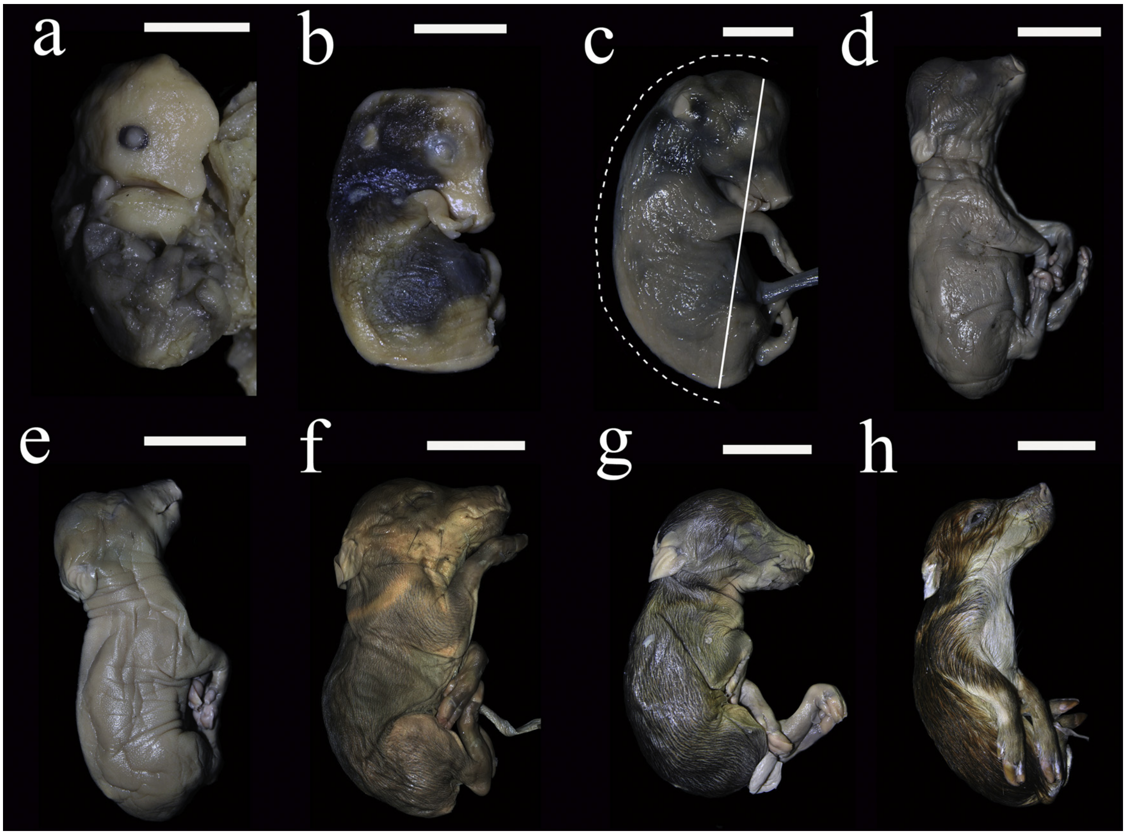

Fig. 6. Embryos and fetuses of collared peccary (*Pecari tajacu*) at different stages of development based on total dorsal length (TDL): (a) Embryo of 2.5 cm TDL and at 38 days of the gestational period with genital and limb buds, but no eyelid buds and any other external fetal characteristic (bar: 1 cm); (b) Embryo of 4.3 cm TDL and at 41 days of the gestational period with differentiated limbs and outer ear, and eyelid buds (bar: 1 cm); (c) Fetus of 5.7 cm TDL and 45 days of the gestational period, with fused eyelids, outer ear, and differentiated limbs and genitalia (bar: 1 cm); (d) Fetus with a 10 cm TDL and at 67 days of the gestational period, with fused eyelids and the initial development of the skin (bar: 2 cm); (e) Fetus with a 13 cm TDL and at 82 days, of the gestational period with fused eyelids, and development of the skin and tactile pelage (bar: 2 cm); (f) Fetus with a 16 cm TDL and at 89 days of the gestational period, with the developed skin, and tactile and coverture pelage, and the white collared mark on the skin (bar: 2.5 cm); (g) Fetus with a 20 cm TDL and at 103 days of the gestational period, with greater development of the tactile and coverture pelage (bar: 3 cm); (h) Fetus with a 30 cm TDL and at 130 days of the gestational period, with all fetal external characteristics, including opened eyelids (bar: 5 cm); Fetus (c) includes the performed biometry measurements of TDL (curve white dashed line) and CRL (straight white line).

indicating results obtained using the methodologies conducted in the present study are accurate.

As with other ungulates, the neonates of the collared peccary have several precocial characteristics, with development of body structures for autonomous postnatal survival and relatively lesser dependence than many animals for parental care. For example, all external morphological characteristics evaluated in the present study are already present and well developed in fetuses at the end of gestation. In regards to the timing of the emergence of main external body tissues, there are no visible eyelids in embryos at 39 days (28% gestation length) but these are already fused at and subsequent to 48 days of the gestational period (35% of gestational period length), whereas eyelid opening occurs around 106 days of pregnancy (77% of gestational period length). This result is very similar to that reported for the white-lipped peccary (Andrade et al., 2018) and domestic pig (Evan and Sack, 1973), in which eyelids fuse on day 49 and 50 of pregnancy (31% and 43% gestation length), and eyelids open on day 125 and 90 of the gestational period (77% and 78% of the gestational period length), respectively (Evan and Sack, 1973; Andrade et al., 2018). In the wild pig (*Sus scrofa*), eyelids fuse on day 50 of the gestational period (42% of the gestational period length; Henry, 1968). The opening of eyelids during the latter phase of gestation has direct effects on the capacity of neonates to detect stimuli from the environment (Patten, 1952; Derrickson, 1992). Furthermore, this timing of eyelid opening determines how well species (especially prey species such as Suiform members) are able to detect imminent dangers, food sources and communicate with individuals from the same social group (Sarko et al., 2011; Anthwal and Thompson, 2016). The capacity to perceive environmental stimuli is also affected by the early formation of the outer ear on day 48 (35% of the gestational period length) and tactile pelage on day 75 of the gestational period (54% gestation length) in the collared peccary. The similar and early development of the sensory system in both peccaries, and in the wild and domestic pig indicates that all the neonates of all these species have development of anatomical components that when stimulated allow for an early individual autonomy in sensing environmental stimuli.

The detection of early development of the dorsal gland around day 54 of the gestational period (39% of the gestational period

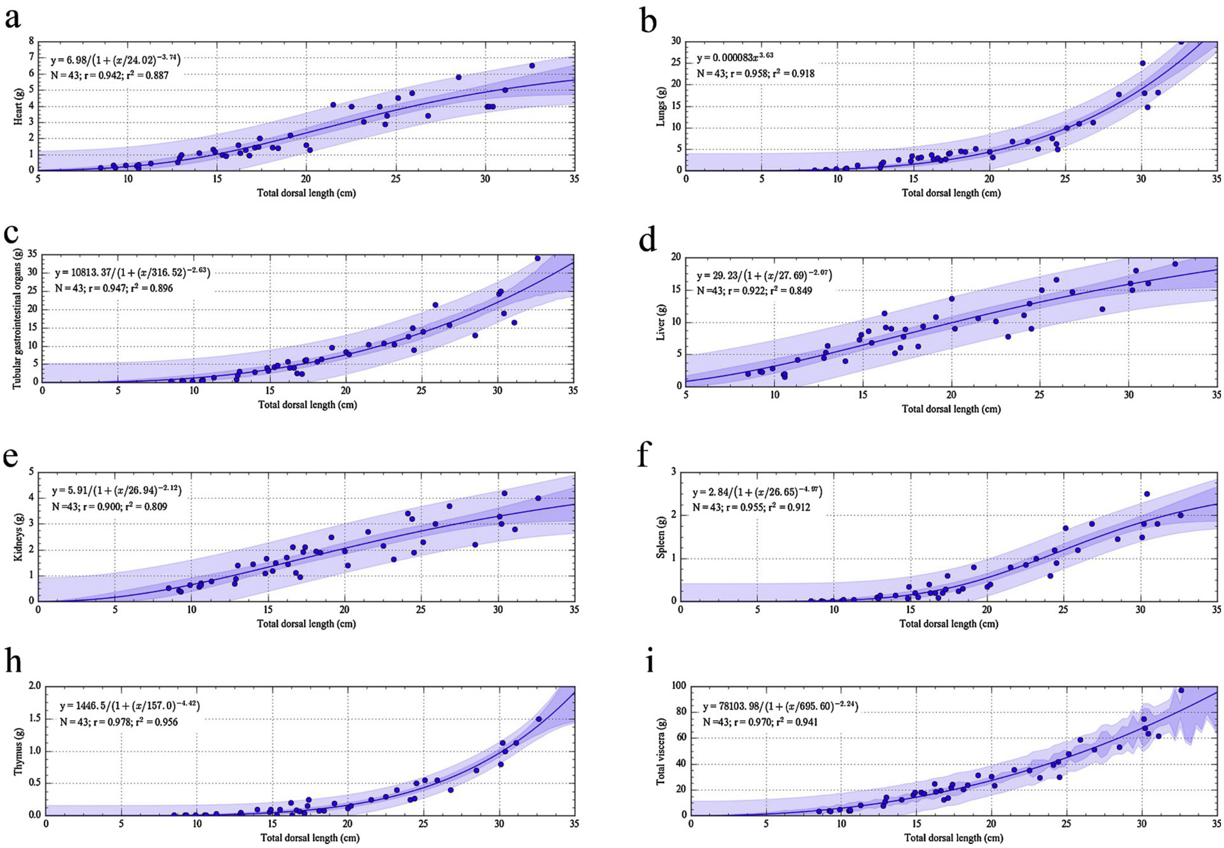

Fig. 7. Relationship between the absolute weight of the (a) heart, (b) lungs, (c) digestive tract, (d) liver, (e) kidneys, (f) spleen, (g) thymus, and (h) total visceral tissues with the total dorsal length (TDL) in 43 fetuses from different pregnant collared peccaries (*Pecari tajacu*).

length) in the present study is similar to other observations in peccaries (Smith and Sowls, 1975; Andrade et al., 2018). There is an importance for development of this gland for the individual recognition within the group, and for territory demarcation and threat signaling (Werner et al., 1952; Hannon et al., 1991).

In the collared peccary, the presence of covering pelage was detected around day 87 of the gestational period (63% of the gestational period length), and this pelage is fully formed at the end of gestation. Similarly, in other studies conducted in the wild pig (Henry, 1968) with the collared (Smith and Sowls, 1975) and white-lipped peccary (Andrade et al., 2018), there was covering pelage observed on the day 90, 100 and 120 of the gestational period (75%, 72.5% and 75.5% of the gestational period length, respectively). The pelage is fully formed at the end of gestational period (Margarido and Mangini, 2001) allowing for independent temperature control (Derrickson, 1992).

As observed previously in the collared peccary (Smith and Sowls, 1975), dogs have the first teeth eruption at about day 116 of the gestational period (84% of the gestation length). In the domestic pig (Bivin and McClure, 1976) and the white-lipped peccary (Andrade et al., 2018), teeth eruption starts at about day 80 and 116 of the gestational period (70% and 73% of gestational period length), respectively. In both peccary species, dentition in newborns allows for early and independent foraging (Bivin and McClure, 1976), and the start of solid food intake between 4 and 6 weeks after birth (Sowls, 1997).

The reproductive performance of any species is related to the amount of predation for the species (Case, 1978; Greene et al., 1998). Large felids inhabiting tropical moist forests have often been classified as opportunistic predators (Rabinowitz and Nottingham, 1986) of mainly medium-to-large-sized mammalian prey, such as the collared peccary (Weckel et al., 2006; Cascelli de Azevedo and Murray, 2007), and preferentially kill young individuals or individuals with diminished locomotor capacity (Mitchell et al., 1965; Palmqvist et al., 1996). The optimal foraging theory assumes that there is an energy maximization in foraging, and the amount of resources obtained is a result of a trade-off between the energetic costs and the benefits to the forager (MacArthur and Pianka, 1966; Shoener, 1971). Because neonates are vulnerable prey for natural predators, the collared peccary produces precocial neonates with an early autonomous functionality for detection and response against predation. Thus, the reproductive pattern of the collared peccary is apparently an adaptation response that has developed during evolution of the species to natural predation to maximize neonatal survival (Case, 1978).

The results of the present also allowed for development of a description of the development of the primary visceral organs in the fetus. In the collared peccary, the relative weight of the liver decreases from 13.2% to 2.9% between days 60 and 70 as well as between 125 and 140 days of the gestational period (44%–50% and 90%–100% of the gestational period length, respectively), and is

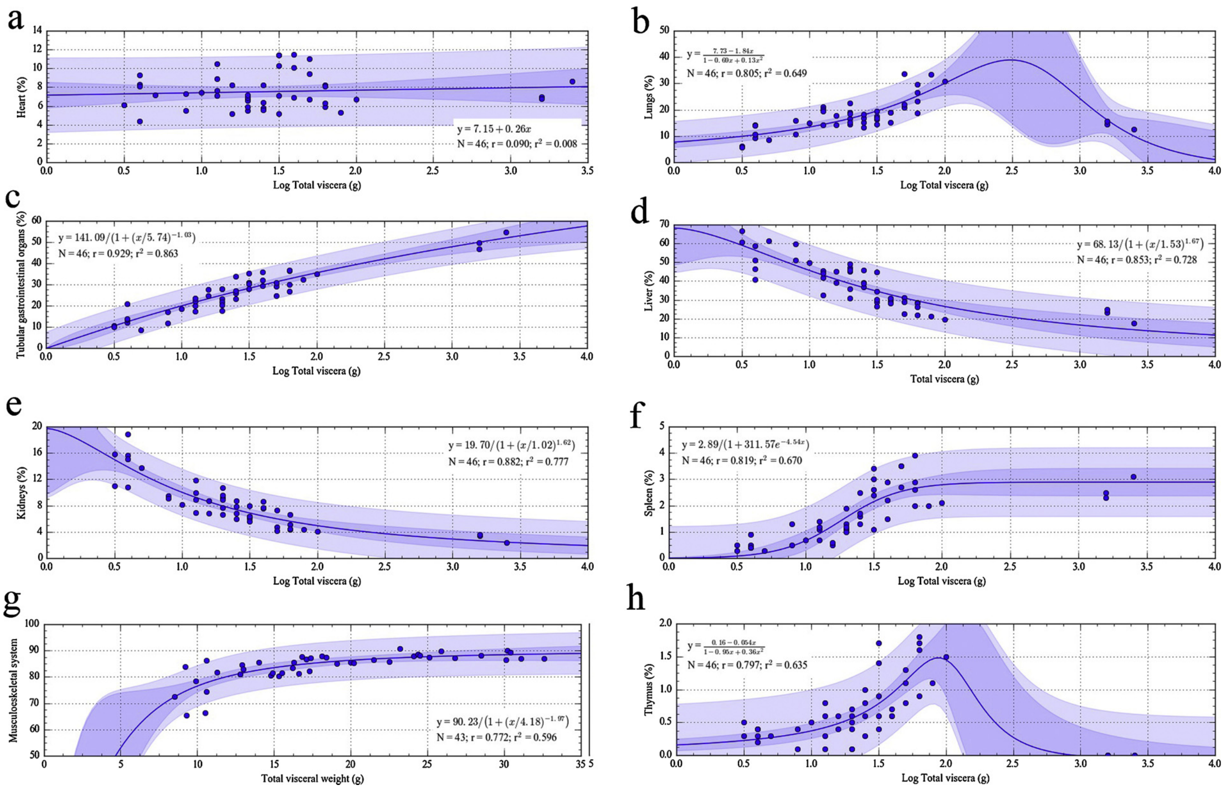

Fig. 8. Relationship between the relative volume of the (a) heart, (b) lungs, (c) digestive tract, (d) liver, (e) kidneys, (f) spleen, (g) thymus, with the log values of the total visceral volume, and relationship between the relative volume of the (h) total visceral tissues and (i) proxy weight of the musculoskeletal system with the total dorsal length (TDL) in 43 fetuses from different pregnant and three adult collared peccaries (*Pecari tajacu*).

Table 2
Absolute and relative volume of the visceral organs of the collared peccary (*Pecari tajacu*) in advanced pregnancy stage (TDL > 25.0 cm; *n* = 07) and adulthood (*n* = 03).

Organ	Absolute volume ± SD (ml)		Relative volume ± SD (%)		T value	df	P-value
	Fetus	Adult	Fetus	Adult			
Heart	4.3 ± 1.1	154.9 ± 66.7	7.2 ± 1.7	7.4 ± 1.0	0.189	6.971	0.856
Thymus	0.8 ± 0.3	0	1.3 ± 0.5	0	−6.713	6	0.001
Lungs	15.3 ± 8.3	283.7 ± 49.8	23.5 ± 5.7	14.3 ± 1.5	−3.648	7.568	0.007
Liver	15.7 ± 2.1	427.4 ± 38.7	26.7 ± 5.3	21.8 ± 3.8	−2.216	4.362	0.085
Tubular gastrointestinal organs	21.0 ± 8.9	1036.6 ± 386.4	33.2 ± 3.2	50.3 ± 4.0	7.182	2.677	0.008
Kidneys	3.1 ± 1.0	61.1 ± 3.8	5.1 ± 1.5	3.1 ± 0.6	−3.107	7.942	0.015
Spleen	1.8 ± 0.3	66.0 ± 43.2	3.1 ± 0.8	3.0 ± 1.1	−0.386	2.745	0.727
Total visceral volume	61.9 ± 20.3	2029.6 ± 587.8	–	–	–	–	–

maintained at this relative weight during post-natal development. The timing during the gestational period in development of the liver is very similar to that observed in the white-lipped peccary. There is a decrease in the white white-lipped peccary from 12.3% to 1.7% in the relative liver weight during same gestational period (Andrade et al., 2018) as observed in the present study for the collared peccary. Similarly, in domestic pigs there is a decrease from 9.8% on day 45 (40% of the gestation length) to 2.1% on the day 110 of the gestational period (97% of the gestational period length; McPherson et al., 2004). The liver is the first organ responsible for the erythropoietic function during fetal development (Gale, 1987), but as hepatoblasts are matured to hepatocytes (Shin and Monga, 2013; Golub and Cumano, 2013), its hepatic prenatal erythropoiesis is progressively substituted for by medullary erythropoiesis (Reece, 1997).

The relative weight of the tubular gastrointestinal tract increases from 13.4% to 31.0% between days 60 and 70 as well as 125 and 140 days of the gestational period (44%–50% and 90%–100% of gestational period length, respectively), with there being a 50.3% relative weight in adult collared peccaries. The development of the tubular gastrointestinal tract in the collared peccary is very similar to that observed in the white-lipped peccary where there are increases from 15.2% to 38.5% during the same period (Andrade et al., 2018) that this development occurs in the collared peccary. In the domestic pig, a similar growth pattern occurs from 3.0% to

Fig. 9. (a) Dorsal view of the genital organs of a pregnant collared peccary; Lumen of the uterine horns was accessed to observe the relation between maternal and fetal membranes (bar: 3 cm); (b) View of the diffuse, folded, epitheliochorial and non-deciduate placenta membranes (bar: 3 cm); and (c) View of the amnion, chorioallantoic membranes and fetus membranes (bar: 3 cm). Ovary (Ov), uterine horn (UH), cervix (UC), vagina (VG), urinary bladder (UB), chorioallantoic membranes (AC), and fetus contained within the amnion (F) (bar: 1.5 cm).

6.2% of the total body weight during the last third of the gestational period (Lowrey, 1911; Sangild et al., 2002; McPherson et al., 2004), mostly due to the increase of the small intestine weights (Sangild et al., 2002). In adult peccaries, due to the increasing fermentative process of plant material that occurs with development, the multi-cavity stomach resembles the stomach of true ruminants with glandular and non-glandular portions and two blind sacks (Lochmiller et al., 1987; Schwarm et al., 2010). The stomach accounts for most of the weight and volume of the digestive tract, weighing about 1.5% of body weight in the white-lipped peccary, in contrast to the 0.7% in the domestic pig (Schwarm et al., 2010). The incremental increase in weight of the tubular digestive tract in final stages of the gestational period is important because of the nutritional requirement of the neonate (Barszcz and Skomia, 2011), and during the postnatal period its relative size increases most markedly when the animals begin to ingest solid matters (Zabielski et al., 2008).

The relative heart weight in the collared peccary did not change during fetal development of the collared peccary, decreasing from only 0.7% (from 1.6% to 0.9%) between days 60 and 70 as well as 125 and 140 days of the gestational period (44%–50% and 90%–100% of the gestational period length, respectively). There were similar results in the white-lipped peccary with a relative heart weight reduction from 1.0% to 0.8% during the same gestational period (Andrade et al., 2018) when these data were collected in the present study. In the domestic pig there was a slight decrease from 0.8% to 0.6% between days 60 (53% of gestational period length) and 115 (100% of gestational period length) of the gestational period (Lowrey, 1911; Ullrey et al., 1965; Sangild et al., 2002; McPherson et al., 2004). Due to the commercial farming selection process to maximize meat production, the heart of domestic pigs is < 45 kg with there having been a reduction to 0.4% of body mass for heart weight while the heart is 0.2% of the body weight in pigs weighing > 200 kg. This selection has resulted in cardiovascular anomalies that can cause death of stressed animals (van Essen et al., 2011). The similar relative weight of the heart in neonates from both types of peccaries indicates that animals of both species may be also predisposed to cardiovascular overload.

The relative weight of the spleen was relatively consistent in growth during the fetal developmental phase, from 0.10% to 0.34% with respect to the fetal body between days 60 and 70 as well as 125 and 140 days of the gestational period (44%–50% and 90%–100% of gestational length, respectively). There was maintenance of this relative spleen weight in the adult developmental phases of the collared peccary. There were similar results in the white-lipped peccary, with a relative spleen weight increasing from 0.06% to 0.35% during the same gestational periods (Andrade et al., 2018) in the collared peccaries in the present study. The increase of the splenic volume in the fetal developmental phase in mammals is related to the erythropoietic function, shared by the liver and bone marrow; but in the postnatal phase the spleen function is related to the control of erythrocyte cell functions and the induction of immune reactions against systemic antigens (Rothkötter, 2009). In contrast, the relative spleen weight in the domestic pig decreases from the 70% value during the gestational period and subsequent to birth (Ullrey et al., 1965; Sangild et al., 2002), and during the first 5 months of the post-natal development (Tess et al., 1986).

The relative volume of kidneys decreased during the fetal developmental phase from 3.3% to 0.6% between days 60 and 70 as well as 125 and 140 days of the gestational period (44%–50% and 90%–100% of the gestational period length, respectively), and there was maintenance of this proportional weight during postnatal development. There were similar results in the white-lipped peccary, with the relative weight of kidneys decreasing from 1.8% to 0.5% during the same gestational period (Andrade et al., 2018) as that of the collared peccary in the present study. In the domestic pig, the relative weight of the kidneys decreased from 1.2% to 0.6% between days 80 (70% of the gestational length) and 100 (90% of the gestational length; (Lowrey, 1911; Sangild et al., 2002; McPherson et al., 2004). During the fetal developmental phase, the kidneys function in the excretion of hypotonic urine inside the amniotic cavity (Caruthers, 1999). In the domestic pig, there is a continuous formation postnatally of nephrons until the day 21, after which the kidneys undergo differentiation of the existing nephrons (Friis, 1980).

Similar to other mammals (Andrade et al., 2018), the thymus had a relatively consistent growth pattern during the fetal developmental period, but there was no longer development of the thymus postnatally. In the domestic pig, the thymus size decreases during the pubertal phase (10–18 months) and there is disappearance of this organ in adults (Igbokwe and Ezenwaka, 2017). During the embryonic developmental phase, the growth of the thymus is related to the maturation of the immune system and subsequently hematopoiesis (Vasil'ev and Polevshchikov, 2015), and then there is a decrease in size when the bone marrow becomes the primary cells responsible for the animals' immunity (Reece, 1997).

Classification of the intrauterine development in mammals should be more focused on a gradient of development of altricial or precocial traits (Case, 1978; Eisenberg, 1981). The study of the relative timing of developmental functions (rather than presence or absence of morphological characteristics) are important for understanding the relationship between neonatal development and other physiological and behavior traits (Derrickson, 1992).

5. Conclusions

The present study was conducted to describe the most important changes occurring during the external and internal fetal development in the collared peccary, which are very similar to those in the white-lipped peccary, a phylogenetically close species, and also in the wild and domestic pig, a species that has undergone genetic selection for increasing the efficiency of pork production. The results of the present study provide useful information for the development of more appropriate *in situ* and *ex situ* reproductive management practices in the collared peccary and other wild Suiform species, such as for used of the modern reproductive biotechnologies and assisted reproductive techniques.

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