Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): Implications for harvest sustainability

Hani Rocha El Bizri[a,b,c,d,*], John E. Fa[a,e], João Valsecchi[b,c,d], Richard Bodmer[c,f], Pedro Mayor[c,f,g]

[a] *School of Science and the Environment, Manchester Metropolitan University, Oxford Road, M15 6BH, Manchester, United Kingdom*
[b] *Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Tefé, AM, Brazil*
[c] *ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, 332 Malecon Tarapaca, Iquitos, Peru*
[d] *RedeFauna, Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia, Brazil*
[e] *Center for International Forestry Research (CIFOR), Jalan Cifor Rawajaha, Situ Gede, Bogor Barat, Kota, Bogor, Jawa Barat, 16115, Indonesia*
[f] *FUNDAMAZONIA, Iquitos, Loreto, Peru*
[g] *Universitat Autònoma de Barcelona (UAB), Department of Animal Health and Anatomy, Faculty of Veterinary, Bellaterra, Barcelona, Spain*

ARTICLE INFO

ABSTRACT

Generation length (GL) of a mammal, calculated through the age at sexual maturity, first reproduction and reproductive senescence can be used to assess the capacity of a population of a species to withstand differing amounts of hunting pressure by humans without depletion of animal numbers. Due to the lack of reproductive data for wild mammals, the GL is often difficult to determine for most species. In the present study, the GL parameters were assessed for the wild lowland paca (*Cuniculus paca*) from a sample of 119 female genitalia obtained during a 15-year hunter participatory program in the Amazon. The probability of female pacas being sexually active, with observable ovarian functionality or pregnancy, increased as both body and genitalia masses increased. The average body mass at puberty was 5.46 kg. Puberty was estimated to occur at 4 months of age, from which there was estimation when age at first parturition would occur 9 months after birth. Additionally, there was no indication that there was a decrease in parturition rate at more advanced ages. The estimated age of first reproduction for pacas was much less than previous estimates, most from assessments of captive animals. In addition, because there was no evidence of reproductive senescence, it is suggested that the average age of mature hunted pacas should be used to determine optimal harvesting rates of pacas by humans. The present study highlights the importance of in situ studies on reproduction of animals in their natural habitat because these will yield more accurate reproductive variable estimates than those obtained from captive animals. It is suggested that similar methods be used to accurately assess reproductive parameters of other tropical species that are hunted by humans.

* Corresponding author at: School of Science and the Environment, Manchester Metropolitan University, Oxford Road, M15 6BH, Manchester, United Kingdom.
E-mail address: hanibiz@gmail.com (H.R. El Bizri).

1. Introduction

Generation length (GL) for mammals has been defined as the "average age of parents of the current cohort" (IUCN, 2001; 2012a), and the "age at which half of total reproductive output is achieved by an individual" (IUCN, 2004); the latter calculated as the average age at which reproduction occurs first and last in an animal's life. The GL has been used as a reference time-frame in a multitude of ecological analyses to assess a species extinction risk (Gaillard et al., 2005; Perry et al., 2005; Jiguet et al., 2007; Mace et al., 2008; IUCN, 2012b). An accurate estimation of the GL of any species is also important in determining its capacity to withstand additional death losses imposed by humans.

Although GL is often difficult to determine due to the paucity of detailed reproductive data from species in their natural habitat, overall patterns are based on published metrics as well as taxonomic and allometric species relationships (e.g., Di Marco et al., 2012; Pacifici et al., 2013). Long-lived species are usually characterized by having a large body size, relatively lower reproductive rates, slower sexual maturation, greater parental care and a long GL (Clutton-Brock, 1988; de Andrade et al., 2018). Long-lived species are especially vulnerable to hunting pressures; short-lived species of smaller body size, greater reproductive rates, earlier puberty and a shorter GL are generally more resilient to human hunting pressure (Peres, 2000; Jerozolimski and Peres, 2003; Smucny et al., 2004; Nasi et al., 2008; Ripple et al., 2016; 2017).

Reproductive variables, including the GL of game species, are important elements in most mathematical models used for assessing the capacity of a species' population to withstand hunting by humans at a sustainable level over time (Weinbaum et al., 2013). For example, the intrinsic rate of population increase of a species, $Rmax$, is calculated based on the annual birth rate of female offspring, age at first parturition, and age at last parturition during its lifetime (Cole, 1954), and is useful in predicting how a target species may respond to various harvesting levels (Greene et al., 1998). Gathering empirical data on the reproductive variables of hunted wild species is laborious. This has meant that R_{max} calculations for most game mammals are based on measures derived from captive animals (Robinson and Redford, 1986).

While data from captive animals are important and can be useful, reproductive variables may differ from populations in their natural habitat due to differences in stress levels, lack of natural predation and diseases, and the constancy of resources, mates and territories. Accordingly, if values for reproductive variables from captive animals are used in hunting assessments, they can under or overestimate the numbers of animals that can be sustainably harvested from populations (Milner-Gulland and Akçakaya, 2001). In a study of ten Amazonian mammals, wild populations of five species had birth rates that were less than those derived from captive animals (Mayor et al., 2017). Furthermore, values for reproductive variables currently used to calculate GL such as age at the time of an animal's first and last parturition can differ from estimates for captive animals and, therefore, the data are not reliable for population sustainability assessments.

The lowland paca (*Cuniculus paca*) is a large-sized rodent, currently the most hunted Neotropical species (El Bizri et al., 2015, 2016). Paca reproduction has been extensively studied in captivity for about five decades (see Pérez and Hernández, 1979; Matamoros and Pashov, 1984; Smythe, 1991). The paca is a polyestrous species with spontaneous ovulation and an estrous cycle of 32.5 (± 3.69) days that breeds throughout the year in captivity (Guimarães et al., 2008). Additionally, the paca is a uniparous species with rare cases of twin gestations (Pérez and Hernández, 1979; Merrit, 1989; Oliveira et al., 2003, 2007). In the Amazon, the lowland paca in its natural habitat has 1.37–1.48 annual parturitions that are seasonally distributed depending on the amounts of fruitification and river water, with a long estimated farrowing interval of 247–266 days (Mayor et al., 2013; El Bizri et al., 2018).

In contrast to captive studies, little reproductive data are available for wild pacas. For example, the age at first parturition used for $Rmax$ calculations, 365 days (Robinson and Redford, 1986; Collett, 1981) is known to vary between 225 and 703 days (Merrit, 1989; Smythe, 1991; Nogueira et al., 2006; Belaunde, 2008; Guimarães et al., 2008). Because most estimates were obtained from captive populations, this variation may be explained by using differing diagnostic methods and environmental conditions in studies that can affect the behaviour and physiology of the animals. In contrast, an analysis of paca female reproduction for animals in their natural habitat was conducted using dental cementum and these animals reached a maximum age of around 12.5 years, and were still reproductively active (Collett, 1981). There is no further detailed information on the decrease of reproduction capacity with aging (i.e., age of reproductive senescence) in pacas and other Neotropical game mammals, and few studies have been conducted to investigate reproductive variables by direct examination of reproductive organs.

In the present study, there was examination of a large sample of genitalia of wild lowland paca females, from which there were calculations of age at sexual maturity and first parturition. From these data, there was also an investigation of whether there was reproductive senescence in the species. These refinements allowed for the discussion of potential effects of using new GL values on the results of models assessing sustainable harvest rates of wild lowland paca populations for human purposes.

2. Materials and methods

2.1. Study sites

Materials used in this study were obtained from two study sites, the Yavarí-Mirín River (YMR, 04°19′53″ S; 71°57′33″ W) and the Amanã Sustainable Development Reserve (ASDR, 01°54′00″ S; 64°22′00″ W). The YMR is located in the Western Amazon, and encompasses 107,000 ha of continuous upland forests with one single indigenous community of 307 inhabitants. The ASDR is a 2,313,000 ha reserve of predominantly upland forests in the Central Amazon, between the Negro and Japurá Rivers. Approximately 4000 riverine people inhabit 23 communities and some isolated settlements within ASDR. In both areas, local residents rely mainly on agriculture for income and on hunting and fishing for subsistence. The climate in both study areas is typically equatorial with

annual temperatures ranging from 22 to 36 °C, relative humidity of 80%, and annual rainfall between 1500 and 3000 mm.

2.2. Biological material and data collection

Local hunters from the one community in the YMR and from five communities in the ASDR were trained to remove abdominal and pelvic organs from hunted animals and to store these in buffered 4% formaldehyde solution (v/v). From 2000–2016, local hunters collected and voluntarily donated genitalia from a total of 119 female pacas; 44 in the YMR and 75 in the ASDR. All genitalia were individually labelled with the hunting date and the specimen's body mass.

In addition, between 2002 and 2015, hunters in the ASDR recorded data from all pacas onto datasheets (n = 1027), including sex, body mass and date harvested. Only data related to females (n = 522) were utilized in the present study. All research was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0350 − 2012-DGFFS-DGEFFS), by the Instituto Chico Mendes Institute for Biodiversity Conservation from Brazil (License SISBIO No 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016).

2.3. Laboratory procedures

Genital organs of females were examined for evidence of conceptuses. In addition, the two ovaries of non-pregnant females were sliced and analyzed using a magnifying glass to evaluate the presence of ovarian structures: corpora lutea (CL) and antral follicles larger than 2 mm. Two classes of sexually active females were defined: i) pregnant females with conceptuses (i.e., pregnant females); and ii) non-pregnant females with at least one CL and/or large antral follicles (i.e., non-pregnant estrous cycling females) (Mayor et al., 2013). In contrast, non-pregnant females without a CL or large antral follicles were considered to be anestrous.

The tubular genital organs (uterine horns, cervix and vagina) of non-pregnant females as well as the conceptuses of pregnant females were weighed using a digital weigh scale (0.1 g accuracy; characterized as genitalia mass). Uterine characteristics of pregnant females were not assessed.

2.4. Data analysis

A one-way ANOVA with a *post-hoc* Tukey test was used to assess whether the average body mass differed among anestrus, estrous cycling-non-pregnant and pregnant females, including the body mass of pregnant females with and without the conceptus mass. A *t*-test was used to compare the uterine mass between anestrus and estrous cycling females. Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Stasinopoulos and Rigby, 2007) with the binomial distribution were used to assess the likelihood of females being sexually active (estrous cycles or pregnancy occurring) based on the body mass for all females in the study and to the genitalia mass for non-pregnant females.

Using the probability curve that was developed, there were calculations of the body mass of individuals with a 75% probability of initiation of estrous cycles as a result of pubertal onset and considered this as the average at which most pacas would become pubertal (i.e., pubertal females). There was also calculation of the body mass at which there was a 50% and 100% probability of puberty occurring, using these as the minimum and maximum range of body mass for puberty to occur in females, respectively. There was a subsequent classification as pubertal females of all female pacas that were harvested in the ASDR that were within this body mass range. There was a cross-correlation of the monthly percentages of births in pacas as reported by El Bizri et al. (2018) with the percentages of harvested females that were pubertal to estimate the best fitted time-lag (in months) corresponding to the onset of puberty. The GAMLSS were then used to assess the relationship between the percentage of harvested pubertal females corrected by the selected time-lag and the percentage of births. The same analysis was used to assess the relationship between conceptus mass and pregnant female mass.

To assess whether there is reproductive senescence or a decrease in reproductive rate with advancing age, the GAMLSS analysis was used to evaluate the relationship between the individual body mass of non-pregnant females and the genitalia mass, both in absolute values and relative percentage in relation to the body mass. The existence of an asymptote or decrease in genitalia mass in females with greater body mass may indicate the cessation of capacity to become pregnant at a certain body mass value.

In all GAMLSS models, linear or non-linear relationships and different families of distribution were tested. Families of distribution and final models were selected based on ΔAIC values (Burnham and Anderson, 2004), in which ΔAIC < 2 indicated best fit models. In addition to the AIC ranking, distribution of the residuals (Q-Q Plot) was also checked for selecting the best-fitted family of distribution. The R 3.3.3 software (http://www.Rproject.org/) was used for all statistical analyses, and GAMLSS models were tested using the *gamlss* R-package.

3. Results

3.1. Ovarian structure determinations, genitalia mass and pregnancy diagnosis

Among the females (n = 111) for which there were ovarian structures detected that indicated there had been onset of estrous cycles and in which there was pregnancy diagnoses, there were nine that were anestrous (8.1%) and 102 (91.9%) that had initiated estrous cycles. Among females that were post-pubertal, 18 (17.6%) were non-pregnant and 84 (82.4%) were pregnant (Fig. 1). Post-
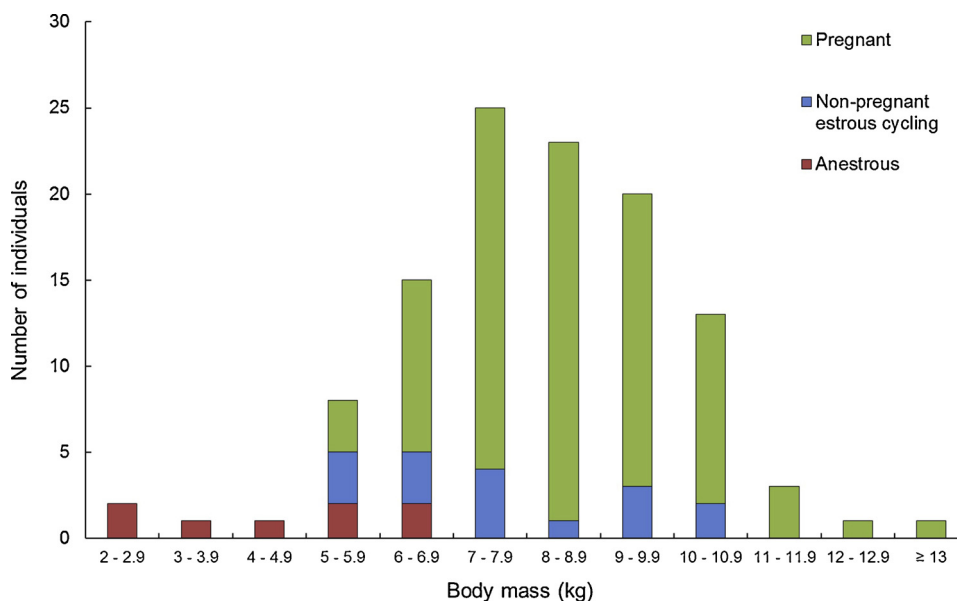
Fig. 1. Distribution of number of lowland paca female genitalia samples characterized by reproductive tract characteristics diagnosed by the presence of ovarian structures and pregnancy ($n = 111$) as related to the increase in female body mass in Amazonia.

pubertal females had a larger body mass (7.4 ± 1.8) compared to anestrous females (4.2 ± 1.6 kg; $F = 18.36$, df = 3, $P < 0.0001$), however, there was no difference between post-pubertal non-pregnant and pregnant females when assessments were made with or without conceptus mass.

Estrous cycling females had a larger genitalia mass compared to anestrous females ($t = 3.22$, df = 25, $P = 0.0035$; Table 1). Ovarian structures, indicating there had been onset of estrous cycles, were observed in pacas with greater than 5 kg of body mass, and all females with more than 65 g of genitalia mass had ovaries that contained a corpus luteum or large follicles. In addition, the probability of female pacas being estrous cycling increased with an increase in both body and genitalia masses (Fig. 2, Table 2).

3.2. Age at sexual maturity, first parturition and onset of reproductive senescence

Based on the curve between body mass and the probability of females being sexually active (estrous cycling or pregnant) (Sexual activity $= e^{(-11.36 + 2.28*\text{Body mass})}/1 + e^{(-11.36 + 2.28*\text{Body mass})}$), there were calculations of the average body mass at the time of puberty to be 5.46 kg (75% of probability), ranging from 4.98 kg (50% of probability) to 6.73 kg (~100% of probability).

Using the probability curve, there was a determination of the number and percentage of pubertal females among all pacas harvested in the ASDR. Monthly percentage of pubertal females peaked in March (24.0%), August (20.9%) and September (25.8%) (Fig. 3). There was a positive relationship between percentage births and percentage pubertal females with a -4 months time lag ($r^2 = 0.31$; Fig. 4; Table 2). There was also a positive relationship ($r^2 = 0.28$) between conceptus mass and pregnant female body mass (Fig. 5, Table 2). Similarly, in non-pregnant estrous cycling females there was an obvious non-linear positive relationship between body mass and the absolute and relative genitalia mass (Fig. 6, Table 2).

4. Discussion

Reproductive variables such as age at sexual maturity, age at first parturition and decreased reproductive rate as a result of aging

Table 1
Categorization of females based on the presence of pregnancy and ovarian structures that are indicative of the onset of estrous cycles along with number of samples and comparison of mean body mass and mass of tubular genital organs; Distinct letters between values within the same column indicate differences at $P < 0.05$.

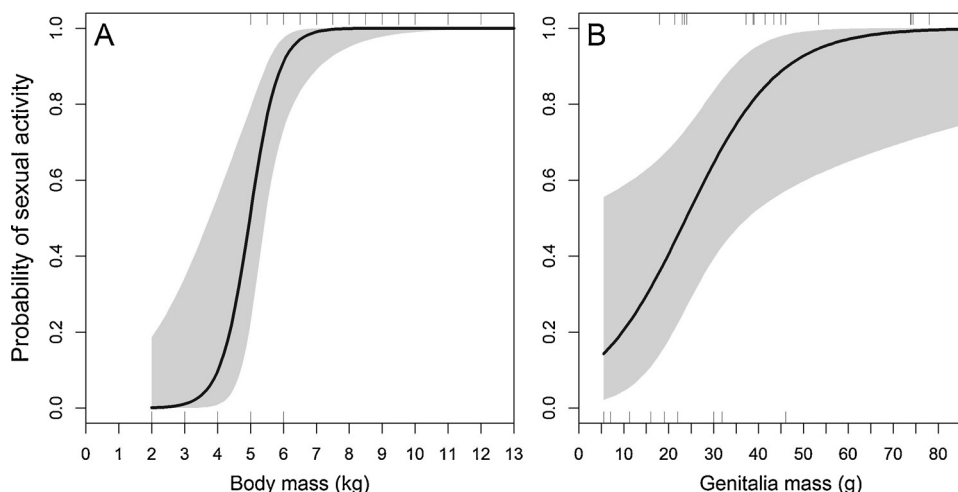| Category	Ovarian functionality	n (Number of samples)	Mean body mass (kg) ± SD	Mean genitalia mass (g) ± SD
Non-pregnant	Inactive	9	4.2 ± 1.6^{a}	20.96 ± 13.16^{a}
	Active	18	7.4 ± 1.8^{b}	46.69 ± 21.92^{b}
Pregnant without conceptus mass	Active	84	8.0 ± 1.5^{b}	–
Pregnant with conceptus mass	Active	–	8.2 ± 1.5^{b}	–
Non-pregnant	Unidentified	8	–	–
Overall	–	119	7.6 ± 1.9	40.61 ± 25.68

Fig. 2. Probability of reproductive tracts being sexual active (estrous cycling or pregnant) in the lowland paca (*Cuniculus paca*), diagnosed A - by the presence of ovarian structures or pregnancy according to body mass; and B - by the presence of ovarian structures according to genitalia mass.

Table 2
Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, delta AIC in relation to the null model (ΔAIC null) and generalized R^2 Non-linear effects were fit using penalized beta splines (*pb*) and cubic smoothing splines (*cs*) functions provided by gamlss R-package; Families of distributions are represented by Binomial (BI), Gumbel (GU), Weibull (WEI3), Generalized Gamma (GG) and Box-Cox t original (BCTo); Generalized R^2 were calculated using the function *Rsq* of the gamlss package.

| Best fitted model		Estimate	P (P-value)	Family of distribution	ΔAIC null	Generalized R^2
Response variables	Predictor variables					
Sexual activity						
Presence of ovaries' structures/pregnancy	Body mass (kg)	2.281	0.0035	BI	37.71	30.07
Presence of ovaries' structures	Genitalia mass (g)	0.097	0.0286	BI	8.82	33.01
% Hunted pubertal females – 4 months	% Births	0.766	0.0376	GU	2.53	31.42
Pregnancy						
Female body mass (kg)	Conceptus mass (g)	0.00033	< 0.0001	WEI3	19.30	27.58
Reproductive senescence						
Non-pregnant genitalia mass (absolute values)	*pb*(Body mass)	0.283	< 0.0001	GG	46.94	57.07
Non-pregnant genitalia mass (relative values)	*cs*(Body mass)	0.114	< 0.0001	BCTo	18.51	53.11
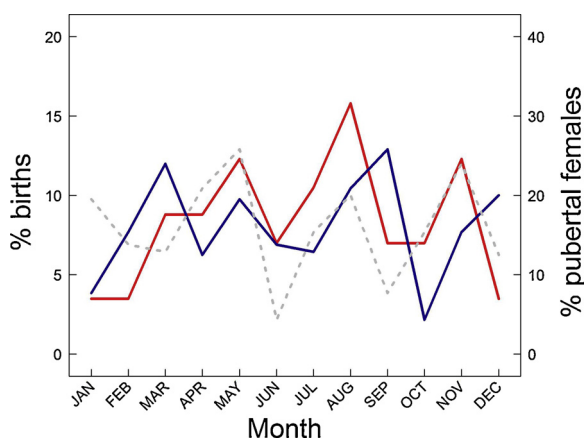
Fig. 3. Temporal trend in the monthly percentage of paca births (solid red line) based on El Bizri et al. (2018) and monthly percentage of hunted pubertal females without time lag (solid blue line) and with a -4 month time lag (dashed gray line) in the Amanã Sustainable Development Reserve, Amazonia (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
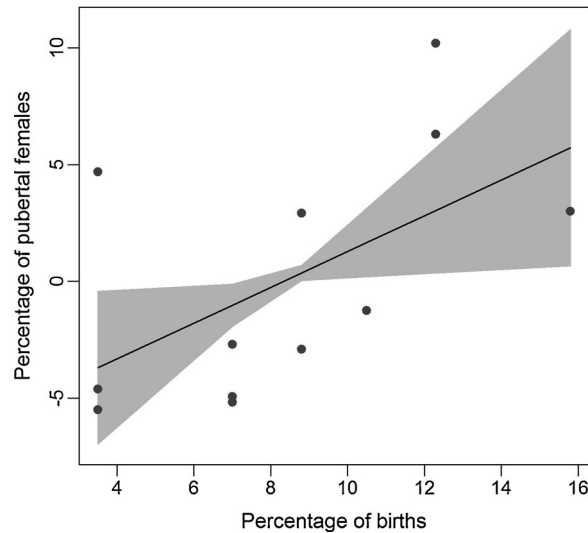
Fig. 4. Association between the percentage of pubertal females and the percentage of births with a -4 month time lag in the Amanã Sustainable Development Reserve; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model.
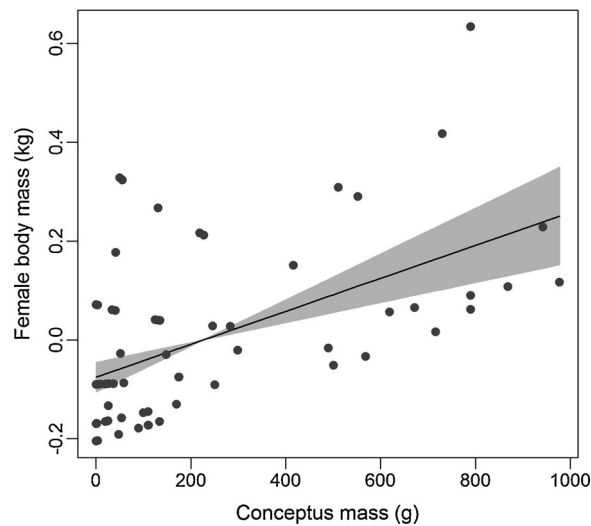

Fig. 5. Relationship between conceptus and body mass of pregnant females; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model.

are important for determining the sustainability of populations of hunted species. In the present study, it was possible to obtain more realistic measures of these variables by using genitalia of animals that were harvested in their natural habitat. Ovarian functionality was initiated in pacas that had about 5.5 kg of body mass. There was determined that these pubertal pacas would have about 4 months of age. In addition, all females larger than 6.5 kg were pregnant or had ovaries that did contained a corpus luteum and/or large follicles indicating there had been onset of estrous cycles, thus all pacas with these ovarian structures or pregnancy were considered to be sexually mature. If a pregnancy length of 149 days is considered (Guimarães et al., 2008), first parturition in the pacas in their natural habitat would occur from 9 months of age onwards. This is much earlier in life than most of these previous estimates for this species where parturition on the average was estimated to occur at about 1 year of age (Collett, 1981; Merrit, 1989; Smythe, 1991; Nogueira et al., 2006; Belaunde, 2008; Guimarães et al., 2008).

Although this estimate indicates that sexual maturity happens earlier in life than was previously thought to occur, this value is validated by body mass growth curves for pacas. Available body mass growth curves indicate that the female paca would weigh 4.54 (Collett, 1981), 4.65 (Rodríguez and Arroyo, 2008), 5.15 (Belaunde, 2008), or 8.35 (Santos et al., 2006) kg at 4 months of age. Realizing that there is a broad range in body weights in these various studies, the average of these values (5.67 kg) is consistent with the estimated average body mass for pubertal females in the present study (5.46 kg, 75% of maturity probability). Furthermore, pacas are considered precocial, having a longer gestation period and a relatively greater intrauterine fetal development than several other
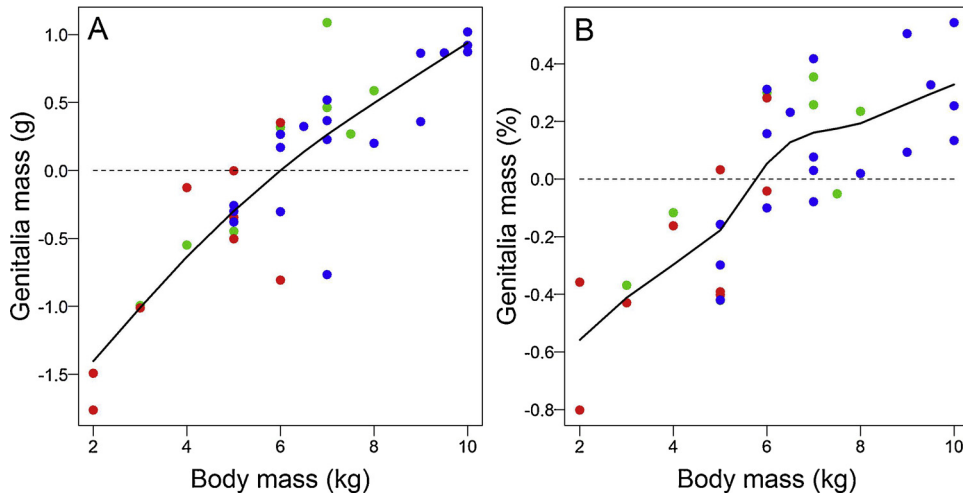
Fig. 6. Relationship between body mass and A - absolute mass of tubular genital organs and B – relative genitalia mass of non-pregnant pacas in Amazonia (*n* = 35); Red dots: anestrous females (*n* = 9); blue dots: estrous cycling females (*n* = 18); green dots: ovarian characteristics unidentified due to lack of ovaries (*n* = 8); dashed line represents the average absolute genitalia mass (40.61 g) and average relative genitalia mass (0.006%), while the y-axis is in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

rodent species. This results in pacas giving birth to well-developed neonates that are relatively independent in their extra-uterine life and with a lesser need for parental care (El Bizri et al., 2017). In precocial species, there is a relatively greater metabolic energy utilization during pregnancy with compensation occurring as a result of less time devoted to lactation and offspring care, leading to earlier maturity of the offspring (Derrickson, 1992; Martin et al., 2005). It is, therefore, unlikely that female offspring would require a long maturation period before the time of pubertal onset and ultimately pregnancy occurring.

Previous studies on reproduction of lowland pacas have been conducted using captive animals, so divergences between age at sexual maturity and first parturition in the present and past studies may be related to this difference. For example, although pacas are solitary in the wild, animals have been maintained in large colony groups of males and females in some studies. In these situations, first parturitions have been recorded between 14.9 and 23.4 months of age (Merrit, 1989; Perez-Torres, 1996; Belaunde, 2008). The grouping of animals has been imposed in confinement to enhance the reproductive performance in several hystricomorphs. In co-lonial hystricomorph rodents, such as the wild cavies, *Cavia aperea*, and domestic guinea-pig, *Cavia aperea* f. *porcellus*, puberty occurs in captive females in the presence of males more than 15 days before those housed without males (Trillmich et al., 2006). Fur-thermore, maintaining individuals in large groups may also result in suppression of reproductive functions (Wasser and Barash, 1983; Kaplan et al., 1986; Abbott et al., 1988).

In many rodents, reproductive suppression is a consequence of the relatively lesser concentrations of luteinizing hormone (Faulkes et al., 1990), urinary chemo-signals or pheromones (Brown and MacDonald, 1984), or by hierarchical competition where a dominant individual induces stress in subordinates through agonistic behavior. Wild Cape ground squirrel (*Xerus inauris*) females in large groups have a delayed sexual maturation compared to those in smaller groups (Waterman, 2002). This reproductive suppression occurs in both captive and wild colonies and it appears as though naked mole-rat (*Heterocephalus glaber*) females in large group environments are reproductively suppressed for their entire lifespan as a result of relatively lesser concentrations of luteinizing hormone than breeding females (Faulkes et al., 1990). In addition, other factors such as photoperiod, temperature and feeding habits in captivity can affect reproduction and may differ substantially from what occurs in the animal's natural habitat (Trillmich, 2000). Thus, it is likely that these factors contribute to a delayed sexual maturation in the captive lowland paca.

The present study is the first in which there has been an attempt to assess the onset of reproductive senescence of pacas in their natural habitat using characteristics of reproductive organs as the biological markers to do so. There was no indication, based on findings in the present study, of reproductive senescence because there was no asymptote of genitalia mass or absence of structures indicative of onset of estrous cycles in ovaries in large females. There was a consistent positive relationship between body weight and uterine mass of lowland pacas in the present study, thus, there were no indications of uterine involution occurring in the older pacas, at least in hunted populations. The largest females in the present study were pregnant at the time tissues were collected. These findings indicate pacas can reproduce as their age advances, and possibly at a high rate. This interpretation is plausible considering there is not generally a post-reproductive female lifespan in mammals with this being limited to humans and a few species of toothed whales (Ellis et al., 2018). Consistent with findings in the present study there have been estimates of lowland paca age in a previous study through dental enamel analyses. Findings indicated that when there was not hunting of wild pacas by humans in their natural habitat sites in Colombia, these pacas could be 12.5 years of age and still be reproductively active, while the maximum recorded age was 8 years in sites where harvesting of pacas for human purposes occurred (Collett, 1981). This means that senescent paca females are unlikely to exist in hunted populations because larger, and therefore older, individuals are generally harvested for human purposes. These factors can have a substantial effect when considering the effect of paca hunting on population sustainability

assessments.

In biological terms, to determine whether there is reproductive senescence in pacas, in-depth studies of pacas in their natural habitat should be conducted because the captive environment may result in an improved fitness and longer lifespan. For example, grey mouse lemur (*Microcebus murinus*) females lived 50% longer in captivity than females in their natural habitat (Hämäläinen et al., 2014). In addition, there needs to be further studies conducted where there is assessment of more precise age data (from skulls) and maturity information from ovaries similar to what occurred in the present study to further ascertain whether there is reproductive senescence in the paca. For paca population sustainability assessments when hunting occurs, the results of the present and a previous study (Collett, 1981) indicate there is no cessation of reproduction, thus, it is suggested that the average age at harvest, as a result of hunting of mature female pacas, be considered the age of the last reproduction event.

The implementation of conservation programs for hunted species is often guided by assessments of their vulnerability to extinction or sustainability of hunting (Bowler et al., 2014). Because previous calculations of reproductive processes of pacas are likely biased, refinements in conservation programs should occur as a result of the enhanced knowledge from the present study regarding the age at sexual maturity. These findings imply that there should be substantial changes to calculations of the GL and, in turn, the calculation of intrinsic rate of population growth (*Rmax*) for this species. Using the most current calculation of birthrate of female offspring (0.71; Mayor et al., 2017), the age of first reproduction calculated in conducting the present study (9 months, or 0.75 years) and the classic measure of age at last reproduction (12.5 years; Collett, 1981), the revised *Rmax* for paca would be 0.60. This is greater than the refined value that was recently published (0.54; Mayor et al., 2017), but still 10.4% less than the established estimate (0.67; Robinson and Redford, 1986). Hence, even when there is consideration of the findings in the present study that pacas sexually mature earlier than what was previously reported, pacas still reproduce less efficiently than expected when calculations were based on data from previous studies. In addition, pacas produce one offspring per gestation and in Amazonia there is an unexpected seasonal pattern of reproduction that converges with periods when there is greater hunting intensity and consequently the harvesting of a large number of pregnant females for human consumption (Oliveira et al., 2007; Mayor et al., 2013, 2017; Valsecchi et al., 2014; El Bizri et al., 2018). When results of the present and previous studies are considered, there needs to be a critical review of previous population sustainability assessments for the species, and calculations of sustainable yields for future in situ management actions (ie., establishment of hunting quotas) should be more conservative.

5. Conclusions

The results of the present study indicate that estrous cycling and pregnant females of lowland paca in their natural habitat have a larger body mass than anestrous females. Ovarian functionality or pregnancy were observed in animals with greater than a 5 kg body mass, and all females with more than 65 g genitalia mass had ovaries containing structures indicative that there had been an onset of estrous cycles before the time of harvest. It is estimated that puberty occurs at about 4 months of age, implying that first parturition occurs at 9 months of age. In addition, there is no evidence that reproductive senescence occurs in the lowland paca. The enhanced information, as a result of the present study, about reproduction of the paca should be considered when conducting population sustainability assessments for the species in areas where hunting occurs.

In addition, results of the present study highlight the importance of in situ studies in understanding the reproduction of species in their natural habitat. These investigations yield more precise information about factors affecting population size of a hunted species in their natural habitat. As ascertained from results of the present study, age at sexual maturity as well as parturition patterns of species in their natural habitat can be obtained and made available to help refine hunting sustainability models. The manner in which the present study was conducted also emphasizes the opportunities to involve local hunter communities in a participatory manner to allow for the collection of large amounts of biological material (see also Mayor et al., 2017). We recommend this method because users of the resource are themselves able to gain directly from the knowledge generated from such studies.

References

Abbott, D.H., Hodges, J.K., George, L.M., 1988. Social status controls LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). J. Endocrinol. 117, 329–339.

Belaunde, S.A., 2008. Determinación de parámetros productivos y reproductivos en la zoocria del "jochi pintado" Cuniculuspaca. Tesis de licenciatura en biología, Universidad Autónoma Gabriel René Moreno. Santa Cruz 95 p.

Bowler, M., Anderson, M., Montes, D., Perez, P., Mayor, P., 2014. Refining reproductive parameters for modelling sustainability and extinction in hunted primate populations in the Amazon. PLoS One 9 (4), e93625.

Brown, R.E., MacDonald, D.W., 1984. Mammalian Social Odours. Oxford University Press, Oxford.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Method Res. 33, 261–304.

Clutton-Brock, T.H., 1988. Reproductive Success. University of Chicago Press, Chicago and London.

Cole, L., 1954. The population consequences of life-history phenomena. Q. Rev. Biol. 29, 103–137.

Collett, S.F., 1981. Population characteristics of *Agouti paca* (Rodentia) in Colombia. Publications of the museum, Michigan state university, East Lansing, Michigan. Biol. Ser. 5, 485–602.

de Andrade, R.D.S., Monteiro, F.O.B., El Bizri, H.R., Vicente, W.R.R., de Araujo Guimarães, D.A., Mayor, P., 2018. Fetal development of the Poeppig's woolly monkey (*Lagothrix poeppigii*). Theriogenology 110, 34–43.

Derrickson, E.M., 1992. Comparative reproductive strategies of altricial and precocial eutherian mammals. Funct. Ecol. 6 (1), 57–65.

Di Marco, M., Possingham, H.P., Wilson, K.A., Blomberg, S.P., Boitani, L., Rondinini, C., 2012. A novel approach for global mammal extinction risk reduction. Conserv. Lett. 5 (2), 134–141.

El Bizri, H.R., Morcatty, T.Q., Lima, J.J.S., Valsecchi, J., 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. Ecol. Soc. 20, 30.

El Bizri, H.R., da Silva Araújo, L.W., da Silva Araújo, W., Maranhão, L., Valsecchi, J., 2016. Turning the game around for conservation: using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. Wildlife Biol. 22, 1–6.

El Bizri, H.R., Monteiro, F.O.B., de Andrade, R.D.S., Valsecchi, J., de Araújo Guimarães, D.A., Mayor, P., 2017. Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): a precocial hystricomorph rodent. Theriogenology 104, 7–17.

El Bizri, H.R., Fa, J.E., Bowler, M., Valsecchi, J., Bodmer, R., Mayor, P., 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. J. Mammal. 99, 1101–1111.

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Bradley, D.L., Giles, D., Balcomb, K.C., Croft, D.P., 2018. Postreproductive lifespans are rare in mammals. Ecol. Evol. 8, 2482–2494.

Faulkes, C.G., Abbott, D.H., Jarvis, J.U.M., 1990. Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. J. Reprod. Fertil. 88, 559–568.

Gaillard, J.M., Yoccoz, N.G., Lebreton, J.D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D., Allaine, D., 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. Am. Nat. 166, 119–123.

Greene, C., Umbanhowar, J., Mangel, M., Caro, T., 1998. Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. In: Caro, T. (Ed.), Behavioral Ecology and Conservation Biology. Oxford University Press, Oxford, pp. 271–305.

Guimarães, D.A., Bastos, L.V., Ferreira, A.C.S., Luz-Ramos, R.S., Ohashi, O.M., Ribeiro, H.L., 2008. Características reprodutivas da paca fêmea (*Agouti paca*) criada em cativeiro. Acta Amazon. 38, 531–538.

Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P.M., Perret, M., Schliehe-Diecks, S., Kraus, C., 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. Proc. R. Soc. B. 281, 20140830.

IUCN, 2001. IUCNRed List Categories and Criteria: Version 3.1. IUCNSpecies Survival Commission. IUCN, Gland, Switzerland and Cambridge, U.K.

IUCN, 2004. Guidelines for Using the IUCNRed List Categories and Criteria. Standards and Petitions Subcommittee. [accessed 2018-9-11]. http://www.globaltrees.org/downloads/RedListGuidelines.pdf.

IUCN, 2012a. The IUCNRed List of Threatened Species. Version 2012.2. [accessed 2018-9-11]. http://www.iucnredlist.org.

IUCN, 2012b. IUCNRed List Categories and Criteria: Version 3.1, second edition. IUCN, Gland, Switzerland and Cambridge, UK [accessed 2018-9-11]. http://www.iucnredlist.org/technical-documents/categories-and-criteria.

Jerozolimski, A., Peres, C.A., 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter–kill profiles in Neotropical forests. Biol. Conserv. 111, 415–425.

Jiguet, F., Gadot, A.S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Glob. Change Biol. Bioenergy 13, 1672–1684.

Kaplan, J.R., Adams, M.R., Koritnik, D.R., Rose, J.C., Manuk, S.B., 1986. Adrenal responsiveness and social status in intact and ovariectomized *Macaca fascicularis*. Am. J. Primatol. 11, 181–193.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Millner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442.

Martin, R.D., Genoud, M., Hemelrijk, C.K., 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. J. Exp. Biol. 208, 1731–1747.

Matamoros, Y., Pashov, B., 1984. Ciclo estral del tepezcuinte (*Cuniculus paca*, Brisson), en cautiverio. Brenesia 22, 249–260.

Mayor, P., Guimaraes, D.A., Lopez, C., 2013. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. Anim. Reprod. Sci. 140, 206–215.

Mayor, P., El Bizri, H., Bodmer, R., Bowler, M., 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. Conserv. Biol. 31, 912–923.

Merrit, D., 1989. The husbandry and management of the Paca (*Cuniculus paca*) at Lincoln Park Zoo, Chicago. Int. Zoo Yearb. 28, 264–267.

Milner-Gulland, E.J., Akçakaya, H.R., 2001. Sustainability indices for exploited populations. Trends Ecol. Evol. (Amst.) 16, 686–692.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G., Christophersen, T., 2008. Conservation and use of wildlife-based resources: the bushmeat crisis. Secretariat of the Convention on Biological Diversity, Montreal, and Center for International Forestry Research (CIFOR), Bogor. Technical Series no. 33. 50 pages.. .

Nogueira, T., Giannoni, M., Toniollo, G., 2006. Observações preliminares sobre a reprodução de uma colônia de pacas *Agouti paca* Linnaeus, 1766 em cativeiro. Cadernos do CEAM-Núcleo de Estudios Agrários 6, 83–95.

Oliveira, F.S., Machado, M.R.F., Canola, J.C., 2003. Real time B-mode ultrasound in pacas pregnancy (Agouti paca, L.1766). Braz. J. Vet. Res. Anim. Sci. 40, 73–78.

Oliveira, F.S., Machado, M.R.F., Canola, J.C., Camargo, M.H.B., 2007. Uniparidade em pacas criadas em cativeiro (Agouti paca, Linnaeus, 1766). Arq. Bras. Med. Vet. Zoo. 59, 387–389.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., Rondinini, C., 2013. Database on Generation Length of Mammals. 5427 Data Records. Online at http://doi.org/10.5061/dryad.gd0m3, version 1.0 (last updated on 2013-08-27), Resource ID: 10.5061/dryad.gd0m3, Data Paper ID:. https://doi.org/10.3897/natureconservation.5.5734.

Peres, C.A., 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conserv. Biol. 14, 240–253.

Pérez, H.C., Hernández, F.Z., 1979. Comportamiento reproductivo y datos de la alimentación de Agouti paca. Acta Zool. Lilloana 35, 283–385.

Perez-Torres, J., 1996. Guía para el manejo y cría de la "Paca" Agouti paca. Convenio Andrés Bello, Bogotá, Colombia.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C., Young, H., 2016. Bushmeat hunting and extinction risk to the world's mammals. Roy. Soc. Open Sci. 3, 160498.

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017. Extinction risk is most acute for the world's largest and smallest vertebrates.

    PNAS 114, 10678–10683.

Robinson, J.G., Redford, K.H., 1986. Body size, diet, and population density of Neotropical forest mammals. Am. Nat. 128, 665–680.

Rodríguez, M.A.B., Arroyo, M.D.B., 2008. Efecto de la dieta sobre la ganancia de peso en individuos de *Agouti paca* (Rodentia: Agoutidae) en cautiverio. Rev. Mex. Mastozool. 12, 6–16.

Santos, R., Lima, A.L., Barbosa, W.A., Vargas Junior, J.G., 2006. Determinação da curva de crescimento em pacas (*Agouti paca* L.) criadas em cativeiro do nascimento ao desmame. IX Encontro Latino Americano de Iniciação Científica e V Encontro Latino Americano de Pós-graduação. Universidade do Vale do Paraíba, Vale do Paraíba: Univap.

Smucny, D.A., Abbott, D.H., Mansfield, K.G., Schultz-Darken, N.J., Yamamoto, M.E., Alencar, A.I., Tardif, S.D., 2004. Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). Am. J. Primatol. 64, 107–121.

Smythe, N., 1991. Steps toward domesticating the paca (*Agouti = Cuniculus paca*) and prospects for the future. In: Robinson, J.G., Redford, K.H. (Eds.), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, Illinois, pp. 202–216.

Stasinopoulos, D.M., Rigby, R.A., 2007. Generalized additive models for location, scale and shape (GAMLSS). R. J. Stat. Softw. 23, 1–46.

Trillmich, F., 2000. Effects of low temperature and photoperiod on reproduction in the female wild guinea pig (*Cavia aperea*). J. Mammal. 81, 586–594.

Trillmich, F., Laurien-Kehnen, C., Adrian, A., Linke, S., 2006. Age at maturity in cavies and guinea-pigs (*Cavia aperea* and *Cavia aperea f. porcellus*): influence of social factors. J. Zool. 268, 285–294.

Valsecchi, J., El Bizri, H.R., Figueira, J.E.C., 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Braz. J. Biol. 74, 560–568.

Wasser, S.K., Barash, D.P., 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. Q. Rev. Biol. 58, 513–538.

Waterman, J.M., 2002. Delayed maturity, group fission and the limits of group size in female Cape ground squirrels (Sciuridae: *Xerus inauris*). J. Zool. 256, 113–120.

Weinbaum, K.Z., Brashares, J.S., Golden, C.D., Getz, W.M., 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? Ecol. Lett. 16, 99–111.