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Original Article

Understanding mammary activity in red-rumped agouti and implications for management and conservation of this Neotropical game species

M. D. Singh[a]*, *S. Singh*[b] *and G. W. Garcia*[a]

[a]Department of Food Production, Faculty of Food and Agriculture, The University of the West Indies, St. Augustine, Trinidad and Tobago

[b]Biochemistry Unit, Department of Preclinical Sciences, Faculty of Medical Science, The University of the West Indies, St. Augustine, Trinidad and Tobago

*michele.singh@gmail.com

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(With 4 figures)

Abstract

The red-rumped agouti (*Dasyprocta leporina*) produces precocial young and is the most hunted and farmed game species in several Neotropical countries. An understanding of the reproductive biology, including the relationship between litter size and teat functionality is crucial for conservation management of this animal. In precocial mammals, as the red-rumped agouti, maintaining maternal contact to learn foraging patterns may be more important than the energy demands and nutritional constraints during lactation and suckling may not play important roles when compared to altricial mammals. Therefore, in this study we evaluated the relationship between mammary functionality with litter size, litter birth weight, and parturition number in captive red-rumped agouti. Functionality was assessed by manual palpation of teats from un-sedated females (N=43). We compared the average birth weight of all newborns, male newborns and female newborns among agoutis with different litter sizes and different parturitions by one way ANOVA's, while Pearson's Chi-squared tests were used to detect relationships between teat functionality, litter size, and parturition number. Parturition number had no effect on the mean birth weight of all young ($F_{0.822}$, $P > 0.05$), male young ($F_{0.80}$, $P > 0.05$) or female young ($F_{0.66}$, $P > 0.05$) in the litters. We found (i) no significant correlations ($P > 0.05$) between teat functionality and litter size and (ii) no significant correlations ($P > 0.05$) between teat functionality and parturition number. This suggests that whilst all teat pairs were functional, functionality was a poor indicator of litter size; suggesting that female agouti young may not have a high dependency on maternal nutrition; an possible evolutionary strategy resulting in large wild populations; hence its popularity as a game species.

Keywords: animal reproduction, agouti, *Dasyprocta leporina,* teat functionality, weaning age.

Compreendendo a atividade mamária na cutia e as implicações para o manejo e a conservação desta espécie cinegética Neotropical

Resumo

A cutia (*Dasyprocta leporina*) produz filhotes precoces, e é a espécie cinegética mais caçada e criada em muitos países neotropicais. O entendimento da biologia reprodutiva, incluindo a relação entre o tamanho da ninhada e a funcionalidade das glândulas mamárias é crucial para o manejo conservacionista deste animal. Nos mamíferos precoces, como a cutia, manter o contato materno para a aprendizagem de padrões de forrageamento pode ser mais importante do que a demanda energética e de restrição nutricional durante a lactação, e a amamentação pode não desempenhar um papel importante quando comparado aos mamíferos altriciais. Portanto, neste estudo nós avaliamos a relação entre a funcionalidade mamária com o tamanho da ninhada, peso ao nascer da ninhada, e o número de partos em cutias cativas. A funcionalidade foi avaliada por meio de palpação manual das glândulas mamárias em fêmeas não sedadas (N=43). Nós comparamos a média do peso ao nascer de todos os recém-nascidos, macho e fêmeas recém-nascidos entre cutias com diferentes tamanhos de ninhadas e diferentes parturições, por meio da análise one–way ANOVA unifatorial; enquanto o teste do chi-quadrado de Pearson foi utilizado para detectar as relações entre a funcionalidade da glândula mamária, o tamanho da ninhada e o número de partos. O número de partos teve efeito na média de peso ao nascer dos filhotes ($F_{0,822}$, $P > 0,05$), filhotes machos ($F_{0,80}$, $P > 0,05$) ou filhotes fêmeas ($F_{0,66}$, $P > 0,05$) nas ninhadas. A análise bivariada de Pearson (i) não mostrou correlação ($P > 0,05$) entre a funcionalidade da glândula mamária e o tamanho da ninhada e (ii) nenhuma correlação significativa ($P > 0,05$) entre a funcionalidade da glândula mamária e o número de parições. Os resultados sugerem que, embora todos os pares de tetas fossem funcionais, as cutias recém-nascidas podem não depender da nutrição materna para sobreviver; .embora todos os pares de tetas sejam funcionais, as cutias recém nascidas aparentemente não dependem da nutrição materna para sua sobrevivência; esta é, provavelmente, uma estratégia evolutiva que resulta em grandes populações da cutia em vida livre; e que pode explicar sua popularidade como espécie cinegética

Palavras-chave: reprodução animal, cutia, *Dasyprocta leporina*, funcionalidade mamária, idade ao desmame.

1. Introduction

The length of lactation in mammals is influenced by the quality and quantity of milk produced, body size, and age of the mother (Oftedal, 2000). The mammal's ability to produce milk is determined by the level of activity and number of secreting cells (Hughes, 1950; Kim et al., 1999). Teat functionality can be measured by the increased activity of the mammary glands through the ability of the teat to yield milk (Farmer, 2013; Hughes, 1950). The quality and quantity of milk, however, may change according species, maternal nutrition, habitat, and water availability (Kim et al., 1999). Each one of these glands is comprised of tubular-alveolar epithelium, mainly composed of epithelial cells where milk is synthesized (Hughes, 1950; Robinson et al., 1999) and is then secreted into the alveolar lumen through a network of ducts to the glandular cistern.

Mammary cell activity and milk yield is stimulated by increased milking frequency (Knight and Wilde, 1987; Knight and Wilde, 1993) and suckling from one parturition to the next (Farmer, 2013). The mammary glands are located in varying positions in the thoracic to inguinal region of the body (Gilbert, 1986; Pagels, 2013). The number of activated mammae/functional teats may have acted as a selective constraint in litter size of wild mammals (Korhonen, 1992). Thus, teat functionality is an aspect that may be considered in domestication of new species (Deem, 2012). Within these species, the agouti (*Dasyprocta leporina*) (Linnaeus, 1758) is highly prized for its meat and one of the most consumed game species in Neotropical countries (Cummins et al., 2015; Robinson and Redford, 1991). Despite the species classification as 'Least Concern', overhunting may compromise its survival (Emmons and Reid, 2016). To avoid this, some authors suggested the agouti and other Neotropical species for captive production systems (Nogueira and Nogueira-Filho, 2011; Perez and Ojasti, 1996). In Brazil, there were just 21 legal agouti farms (Le Pendu et al., 2011), while in Trinidad and Tobago over 400 wildlife farmers rear the agouti in captivity (Rackal et al., 2013). Hence the question arises on whether this species maintains teat functionality for extended periods of time, and whether teat functionality is related to litter size, parturition number or litter birth weight. This will inform on the need for a weaning period in captive colonies of agouti, influencing gestation interval and reproductive efficiency and ultimately conservation activities.

The agouti is a rodent of an average weight of 4.5 kg. The female agouti has eight mammae, two pairs in the thoracic region and two pairs in the abdominal region (Baas et al., 1976; Deem, 2012). It is a non-seasonal breeder (Baas et al., 1976; Campos et al., 2015; Guimarães et al., 2011; Singh et al., 2014) and under captive conditions, when receiving an abundance of food with a high plane of nutrition may produce larger litters (Singh and Garcia, 2015). Agoutis reach puberty at eight months and go through gestation for 104 to 120 days

(Guimarães et al., 2011; Lopes et al., 2004; Weir, 1971) producing litters between one and six young (Brown-Uddenberg et al., 2004; Dollinger et al., 1999; Lopes et al., 2004; Singh and Garcia, 2015). Gestational intervals of 115 to 190 days (Korz, 1991; Meritt, 1983; Roth-Kolar, 1957) and 219 days (Dubost et al., 2004) have been reported for the agouti. This long interval can potentially be manipulated in captivity, especially as agoutis do not exhibit lactational anestrous (Guimarães et al., 2009; Weir, 1971).

In captive breeding programs for conservation and production, the rate of reproduction and offspring survivability are crucial factors which affect conservation efforts and farmers' production and profitability; thus, the parameters which affect these are important. Hence, to improve agouti production in captivity the relationship between mammary functionality and litter size needs to be understood. In mammals that bear precocial young like agouti (Smythe, 1978), maintaining maternal contact to learn foraging patterns may be more important than the energy demands and nutritional constraints during lactation (Pond, 1977), suggesting that lactation and suckling may not play important roles when compared to altricial animals. As female agoutis do not experience lactational anestrous (Guimarães et al., 2009), we considered that lactation may not be as important for nutrition and survival of newborn agouti. Thus, we predict that we will find no relationships between mammary functionality with litter size, litter birth weight, and parturition number.

2. Materials and Methods

2.1. Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

2.2. Animals and housing

Forty-three pregnant female agoutis, aging between 2-4 years, were individually housed with their young in wire mesh cages (0.6m wide x 0.6m deep x 0.9m high) over a period of 10 months in 2014 at the Agouti Unit, Department of Food Production, Faculty of Food and Agriculture, The University of the West Indies, St. Augustine, Trinidad and Tobago. Females had a mean (± SD) body weight of 4.3 (± 1.2) kg before mating and comprised of primiparous (N=10) and multiparous females (N=33). The animals were watered and fed *ad libitum* with diets consisting of *Mangifera indica, Musa spp., Curcubita pepo, Anacardium occidentale, Cocos nucifera, Manihot esculenta, Ipomea batatas, Leucaena leucocephala,* and *Trichanthera gigantea*.

2.3. Milk and data collection

Milk collection began one day after birth and continued three times weekly until weaning at four weeks. Each female agouti was manually restrained and milk collected from each teat using a modification of the method described by De Peters and Hovey (2009). Briefly, each teat was gently massaged and plucked for milk yield. Based on its location, each pair of agouti teat was identified as the cranial pair (CrP), abdominal pair 1 (AP1), close to the head, abdominal pair 2 (AB2), close to the rear and the caudal pair (CaP) (Figure 1).

The presence or absence of milk droplets from the functional teats over a four-week period was recorded. A mammary teat pair was considered functional if both teats produced milk at the same time or non-functional if it did not produce milk simultaneously. Subsequently, the longitudinal data for each pair of teat (CrP, AP1, AP2, and CaP) was dichotomized and recoded to reflect functionality for an entire 28 day period *vs*. non-functionality for any part thereof. Frequency tables were generated to describe the data set according to litter size and parturition number and also to report the functionality of each teat pair. Newborns were weighed on the day of birth and examined by manual palpation to determine sex.

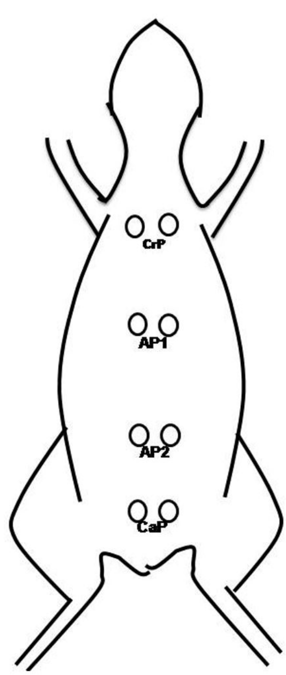

Figure 1. Diagram of agouti in lateral recumbence showing location of the Cranial teat Pair (CrP), Abdominal teat Pair 1 (AP1), Abdominal teat Pair 2 (AP2) and Caudal teat Pair (CaP).

2.4. Statistical analyses

The dependent variable was teat functionality, while litter size, litter birth weight, litter sex and parturition number were independent variables. The data set was recorded into agoutis with litter sizes ranging from one to two and those with litter sizes greater than two. Pearson's Chi-squared test was used to detect possible associations between teat functionality (at the various pairs), litter size, litter birth weight and parturition number. Pearson's bivariate correlation analysis was used to detect significant relationships between teat functionality and litter size/parturition number. One-way Analysis of Variance (ANOVA) was used to compare the birth weight of all young, male young and female young among agoutis from different litter sizes and different parturition numbers. The Bonferroni and Least Squares Difference post-hoc tests were used to determine where significantly different means existed. All statistical analyses were performed using the Statistical Package for Social Sciences (SPSS) 20 software for Windows (IBM, NY, USA).

3. Results

The CrP was functional in 42 (98%) female agoutis (Figure 2a), while AP1, AP2, and CaP was functional in 22 (51%) (Figure 2b), 9 (20%) (Figure 2c) and 19 (44%) (Figure 2d) female agoutis, respectively. Thirty four (79%) of female agoutis had a litters of one or two young and nine (21%) had litters with more than two young (Figure 3). Ten (23%) of the agoutis had one parturition, while 13 (30%) had three, 11 (26%) had 2, eight (19%) had four, and just one (2%) had five parturitions (Figure 4).

There were no significant associations between the functionality of teat pairs CrP (χ^2_1 = 0.27, P > 0.05), AP1 (χ^2_1 = 1.45, P > 0.05), AP2 (χ^2_1 = 0.01, P > 0.05) or CaP (χ^2_1 = 0.0003, P > 0.05) and litter size. There were also no significant associations between the functionality of teat pairs CrP (χ^2_4 = 2.98, P > 0.05), AP1 (χ^2_4 = 2.05, P > 0.05), AP2 (χ^2_4 = 0.44, P > 0.05) or CaP (χ^2_4 = 3.77, P > 0.05) and parturition number. Pearson's bivariate analyses revealed (i) no correlations between teat functionality and litter size for CrP (R = -0.20, P > 0.05), AP1 (R = 0.29, P > 0.05), AP2 (R = 0.24, P > 0.05), and CaP (R = 0.28, P > 0.05), and (ii) no correlations between teat functionality and parturition number: CrP (R = -0.07, P > 0.05), AP1(R = -0.20, P >0.05), AP2 (R = -0.02 P > 0.05) and CaP (R = 0.20, P > 0.05).

Mean (± SE) birth weight of young in litters with single births (N=10) was significantly higher ($F_{4,20}$, P < 0.05) than young from litters of two young (N=24) and three young (N=6) births (Table 1). Mean (± SE) birth weight of male young in litters with single births (N=5) was significantly higher ($F_{2,29}$, P < 0.05) than male young from a litter of two young (N=24) births (Table 1). Parturition number had

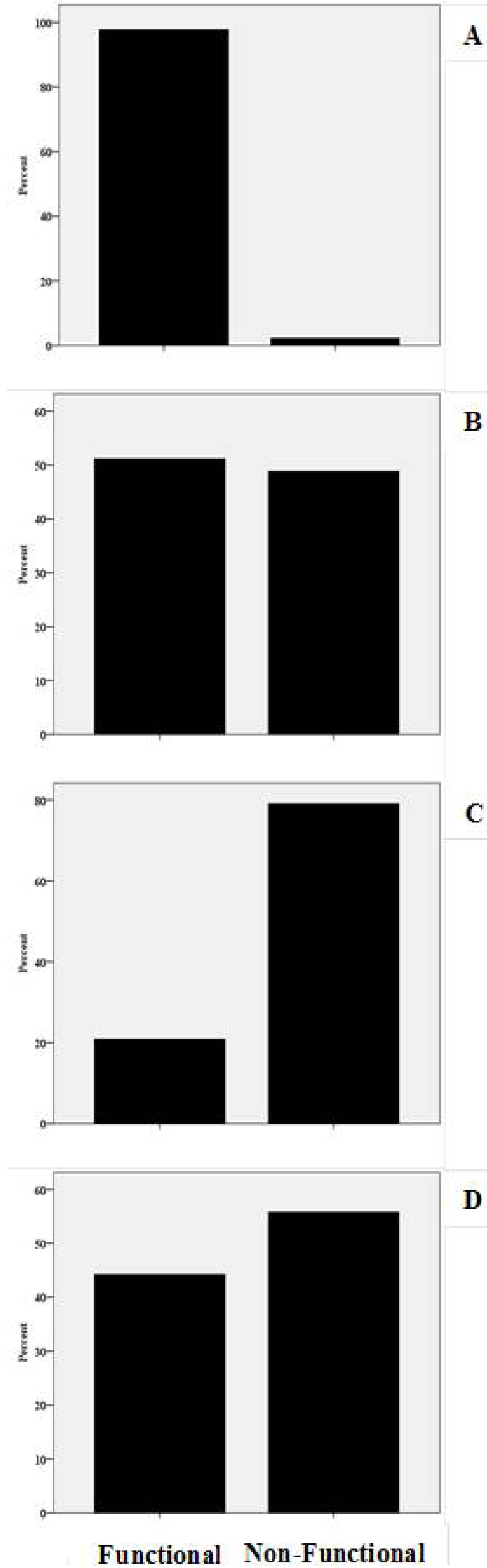

Figure 2. Percentages of functional teat pairs in female agoutis (N=43). (a) Cranial teat Pair (CrP); (b) Abdominal teat Pair 1 (AP1); (c) Abdominal teat Pair 2 (AP2), and (d) Caudal teat Pair (CaP).

no significant effect on the mean birth weight of all young ($F_{0.822}$, $P > 0.05$), male young ($F_{0.80}$, $P > 0.05$) or female young ($F_{0.66,}$ $P > 0.05$) in the litters (Table 2).

4. Discussion

In the agouti, the cranial pair was functional in a great majority of the females, making it the most functional pair. Teat functionality varies, and mammals that are primarily monotocous like cattle have four functional teats, whereas humans, primates, elephants, sheep and goats have two (Anderson et al., 1982). In polytocous species, like the agouti, teat functionality has never been investigated, however, the number of active nipples can vary with litter size, and may be considered inversely proportional as litter size can exceed available nipples as seen in guinea pigs (2 nipples), rats, dogs, cats and pigs (7-12 nipples) as well as in marsupials (5-12 nipples) (Hayssen, 1993; Senger, 2013).

As we expected, due to the precocial characteristic of agouti young (Sikes and Ylonen, 1998; Smythe, 1978), the teat functionality was not related to litter size, litter birth weight, and parturition number in female agouti. In mammals that bear precocial young, as agoutis (Smythe, 1978), young can rapidly obtain relatively large amounts of milk with each compression of the teat, as these species represent prey to large predators, hence the ability to feed rapidly and flee quickly is highly adaptive survival traits (Pagels, 2013). It has been suggested that with increasing litter size, there is an associated increase on energetic requirements and this may limit litter size due to energy requirements of the mother for lactation and maintenance (Sikes and Ylonen, 1998). Precocial young, as agouti,

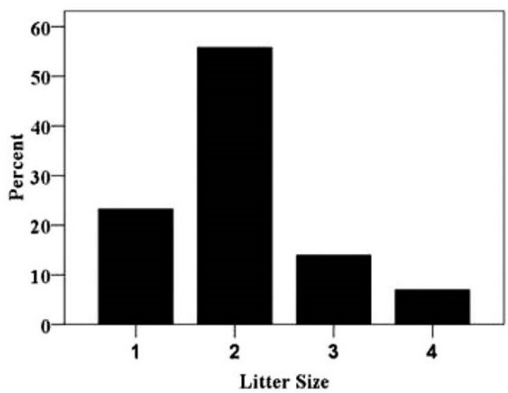

Figure 3. Litter sizes among female agoutis (N=43).

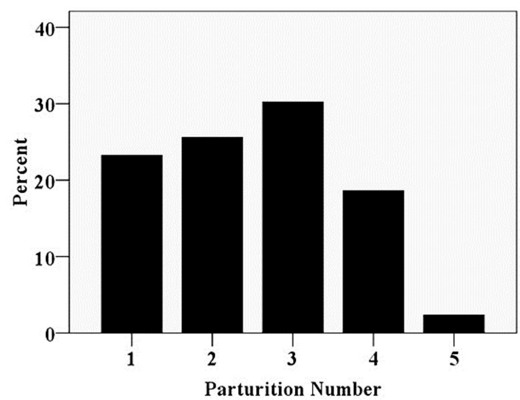

Figure 4. Parturition number among female agoutis (N=43).

Table 1. Mean (± SE) birth weight (g) of all young, male young and female young in different litter sizes.

Variable	Litter Size			
	1	2	3	4
All	$310^{a} \pm 17$ n=10	$255^{b} \pm 8$ n=24	$249^{b} \pm 17$ n=6	$275.78^{ab} \pm 24$ n=3
Male	$321^{a} \pm 33$ n=5	$259^{a} \pm 12$ n=24	$234^{b} \pm 20$ n=6	$245^{b} \pm 12$ n=3
Female	300 ± 9 n=5	251 ± 11 n=24	264 ± 24 n=6	304 ± 34 n=3

[ab]Means in the same row followed by different superscript letters differed by the t test ($P < 0.05$).

Table 2. Mean (± SE) birth weight (g) of all young, male young and female young in agoutis with different parturition numbers.

Variable	Parturition Number			
	1	2	3	4
All	288 ± 17 n=10	270 ± 18 n=11	260 ± 12 n=13	256 ± 10 n=9
Male	281 ± 20 n=10	249 ± 31 n=8	253 ± 16 n=11	264 ± 14 n=9
Female	289 ± 23 n=9	263 ± 14 n=10	255 ± 18 n=12	248 ± 15 n=7

however, are born with eyes open, well furred and little dependence on maternal nutrition (Sikes and Ylonen, 1998; Smythe, 1978). In such precocial mammal species, maintaining maternal contact to learn foraging patterns may be more important than the energy demands and nutritional constraints during lactation (Pond, 1977), suggesting that lactation and suckling may not play important roles when compared to altricial animals. In contrast, species that bear altricial young, like the opossum (*Didelphis marsupialis*) with litters ranging from 4 to 25 young born in the embryologic state, there is a strong positive correlation between litter size and teat functionality and number, since neonates which do not attach to a nipple perish (Feldhammer et al., 2003).

Parturition number (one to four) had no effect on neither individual nor total litter birth weight in captive agoutis. This is in contrast with reports on captive capybaras (*Hydrochoerus hydrochaeris*) as litter size was apparently affected by maternal age, with a sharp decrease occurring by the fourth birth (Nogueira-Filho and Nogueira, 2013). These differences may be due to the duration of this study as data only up to the fourth parturition was collected, while in the capybara study, the authors analyzed up to the eighth parturition. Usually, life history variables like parturition number has often shown a negative relationship between litter size and offspring weight, with multiparous females producing increasingly larger litters (Sikes and Ylonen, 1998). This can be explained by body mass. As the animal ages, body mass increases, thereby improving the physiological adaptations for larger litters (Westlin and Gustafsson, 1983). Thus, further study with older agoutis may confirm our results.

In this experiment, birth weights were higher for male and female newborn agoutis (251g, 310g), than reports by Lopes et al. (2004), who recorded 149g for both sexes in black-rumped agouti, 172g from *D. prymnolopha* and *D. aguti* and 148g and 146g. These were similar to weights reported by Meritt (1983) who stated a value of 258g (range 210-308g) from male newborn agoutis and female newborns of 272g (range 210-355g) in captivity. This can probably be attributed to the diet and space under captive conditions in this study. Moreover, whilst the average birth weight of male newborn agoutis decreased as parturition number increased from one to four, this was not significant and there was no difference between birth weight of female young and parturition number. In the consulted literature, we found no explanation for the obtained results. We can suggest a higher intrauterine competition between males than females, which can be test in future research.

The obtained results in this study suggests a low of dependence of newborn precocial agouti on maternal nutrition and may explain the large populations of wild agouti, since newborn agouti may not necessarily need to suckle and possess the ability to feed themselves from birth (Sikes and Ylonen, 1998), the generation interval may be decreased, resulting in growing populations of wild agouti in the Neotropics. Agouti population density ranges from 8-84 individual agouti per km^2 (Dubost et al., 2004; Jorge and Peres, 2005; Nasi et al., 2011; Robinson and Redford, 1991) in hunted areas, making the agouti one of the most common forest mammal. This species reproduces quickly (Dubost et al., 2004; Ojasti, 2000; Roth-Kolar, 1957; Weir, 1971) and hence has a better chance of surviving hunting pressure. The tolerance to harvesting may be related to the biology of the agouti; the reproduction potential and survivablility of the animal which influences the recruitment of agoutis into the population (Robinson and Redford, 1994). The higher the number of animals recruited into the population, the greater numbers are available to be harvested. This evolutionary survival strategy would explain the popularity of the agouti as a game species and also make it an ideal species for captive production systems.

The teat functionality, as we expected, due to the precocial characteristics of the species, was not correlated to litter size or birth weight in captive agouti. This suggests that newborn agouti may not be dependent on suckling for nutrition, as is seen in other precocial mammals, and can be used to guide management of captive agouti production systems for conservation and production as it may be possible to wean neonatal agoutis almost immediately, returning the mother to breeding thereby reducing the parturition interval, increasing productivity in captivity. Our data also may help to explain the large populations of wild agouti, which persist even in heavily hunted Neotropical areas, as young, apparently, have little dependence on maternal milk.

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