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SHORT COMMUNICATION

Asynchronous breeding in red brocket deer (*Mazama americana*): seasonal changes in male reproductive characteristics, seminal parameters, androgen levels, and antler cycle

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Abstract

The red brocket deer is the largest species in the genus *Mazama* and one of the most abundant and widely distributed cervid in the Neotropics. Yet it has been classified as data deficient by the IUCN, and the limited knowledge on its reproductive biology indicates that red brocket bucks do not possess an annual antler cycle and are capable of breeding during antler casting and growth. Here, in parallel to antler cycle, we investigated seasonal changes in morphometric (body weight, neck and chest girth, and testicular volume), endocrine [plasma testosterone and fecal androgen metabolites (FAM) levels] and seminal (total sperm count and sperm motility index) parameters from captive adult red brocket bucks collected on a quarterly basis over a 1-year period. Two out of six males kept hard antlers year-round, three cast antlers from winter to spring, and one carried velvet antlers for longer than 6 months. No clear seasonal patterns of variation in gross morphometry, seminal traits, and hormonal levels were found, and mean values of all collected parameters did not show differences among seasons. Body weight was positively correlated with most morphometric measurements and seminal parameters, while chest girth was positively correlated with neck girth, testicular volume, and total sperm count. Neither androgen levels (both plasma testosterone and FAM) nor hard antler phase correlated with seminal characteristics. Our findings support that red brocket bucks not only exhibit aseasonal and asynchronous antler cycles, but also maintain their secondary sexual characteristics and semen quality unchanged over the year. This apparent lack of photoperiodic stimuli for controlling reproduction along with an absence of relationship between seminal parameters and antler status might make red brockets unique in terms of reproductive biology among deer species.

Keywords Cervidae · Deer · Neotropics · Reproductive biology · Aseasonal · Male reproduction

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Typically, cervids inhabiting temperate regions have highly synchronous breeding seasons in which antler cycle correlates with sexual activity through a mechanism that involves photoperiodic control of testosterone secretion (Asher et al. 1989; Bubenik 2006; Haigh et al. 1984; Lincoln 1992; Sempéré et al. 1992). In contrast, tropical deer species exhibit a great variability in their breeding strategies ranging from strong reproductive seasonality to complete asynchronous antler cycle and gonadal function (Asher 2011; Bubenik et al. 1991, 1996; Pereira 2010; Pereira et al. 2005). Some of these aseasonal species apparently resynchronize their reproduction and antler growth when translocated into high-latitude zones, whereas others remain unchanged (Asher 2011; Bubenik et al. 1991; Loudon and Curlewis 1988; Pereira 2010). This response diversity suggests that some tropical deer possess a great plasticity of the photoperiodic template

that allows reproduction to continue as long as environmental conditions (e.g. food availability) are favorable.

Apart from showing little or no synchrony in their breeding and antler cycles, some tropical deer also differ from their temperate congeners regarding the maintenance of spermatogenesis at all antler stages (Chapman and Harris 1991; Loudon and Curlewis 1988; Monfort et al. 1993; Pereira 2010; Reyes et al. 1997). This appears to be the case of most brocket deer species (*Mazama* spp.) as available data indicate that annual antler cycle is absent and stags are capable of breeding during antler casting and growth (Barrozo et al. 2001; Bisbal 1994; Branan and Marchinton 1987; Frädrich 1987; Hurtado-Gonzales and Bodmer 2006; MacNamara and Eldridge 1987; Pinder 1997; Pinder and Leeuwenberger 1997). Moreover, a previous study with captive red brocket bucks (*Mazama americana*) revealed that antler changes and androgen levels do not follow an annual pattern (Versiani et al. 2009), which implies that antler cycle in this Neotropical cervid may not be a reliable indicator of testicular function as it is for temperate species. To date, however, no research has assessed the relationships among antler cycle, gross morphometry, ejaculate characteristics, and sex steroids in red brocket bucks. Such information could help us to better understand which ecological drivers are used by this species for reproductive timing, and the extent to which testicular steroidogenesis and spermatogenesis are linked to secondary sexual characteristics. Thus, we aimed to compare morphometric measurements, ejaculate characteristics, plasma testosterone, and fecal androgen metabolites (FAM) from captive adult red brocket bucks collected on a quarterly basis over a 1-year period.

This study was performed at the Núcleo de Pesquisa e Conservação de Cervídeos (NUPECCE) of the São Paulo State University, Brazil (20° S latitude). Six adult (3–7 years) red brocket bucks (*M. americana*) were housed in individual indoor stalls (4 × 4 m) with auditory and olfactory contact with conspecific males and females, and exposed to natural photoperiod. All animals were subjected to the same environmental, nutritional, health, and reproductive management.

Morphometric measurements (body weight, neck and chest girth, and testicular volume) antler stage, ejaculates, blood, and fecal samples were collected throughout the year in quarterly intervals, and then seasonal differences in these parameters were analyzed.

Under anesthetic effect, red brocket bucks were weighed and their neck and chest girths were measured using a flexible tape, whereas Vernier calipers were used to assess length and width of both testes. Testicular volume was later estimated by using the prolate spheroid formula (volume = length × $[\text{width}]^2 \times 0.52$ − Gosch and Fischer 1989). Antler status (velvet, hard antler or casting) was recorded throughout the year.

Immediately after gross morphometry, semen was collected using a standardized electroejaculation protocol (Duarte and Garcia 1997). A sine–wave electrostimulator and rectal probe (P.T. Electronics, Boring, OR, USA) were used to administer 30 incremental stimuli given in a 3-s on–off pattern in three series consisting of 10 (250 mA), 10 (50 mA), and 10 (750 mA) stimuli. Each series was separated by a 10 min rest interval at which time aliquots of semen were collected and assessed for volume using a micropipette. After collection of the last ejaculate, aliquots from the three series were pooled, diluted in TRIS–egg yolk extender (1:1), and placed in a water bath at 37 °C. Next, sperm motility and forward progressive motility were subjectively determined by placing 10 µL of diluted semen between a prewarmed glass slide and coverslip (37 °C) and observing in light microscope equipped with a heating table (five separate fields − 400 × magnification). Percentage of motile spermatozoa was depicted as percentage (0–100%) while forward progressive motility as scored from 0 to 5 (0 = no movement and 5 = rapid, steady forward progression) (CBRA 1998). Then, both values were used to obtain the Sperm Motility Index (SMI = [motility + (forward progressive motility × 20)] × 0.5) (Howard 1993). To determine sperm concentration, 10 µL of diluted semen was added to 1900 µL of 10% buffered formol saline (1:200) and spermatozoa were counted using an improved Neubauer hemocytometer (400 × magnification). Total sperm count was calculated by multiplying semen volume and sperm concentration.

Blood and fecal samples were collected in the same day of electroejaculation (between 8:00 and 10:00 a.m.) to avoid potential effects of circadian rhythms. Blood samples were withdrawn into EDTA vacutainer tubes soon after anesthesia induction, centrifuged (3000 rpm, 10 min), and plasma was harvested and stored at − 20 °C until assayed. All plasma samples were assayed for testosterone without prior extraction. Parallel to this, steroid metabolites from fecal samples were extracted following methodology described at Versiani et al. (2009). 0.01 mL from each aliquots obtained from extracted fecal sample was diluted in phosphate buffer (1:128) before enzyme immunoassay (EIA).

Plasma and FAM were determined using EIA which used a monoclonal testosterone antiserum (R125/7, C. Munro, University of California, Davis, CA, USA) following methodology described at Versiani et al. (2009). This testosterone EIA was previously validated for red brocket deer (Versiani et al. 2009) by demonstrating: (1) parallelism between serial dilutions plasma pools and fecal extract pools with the standard curve; (2) significant recovery of exogenous testosterone added to plasma pools and fecal extracts, and (3) physiological relevance of plasma testosterone and FAM. Assay sensitivity was 0.046 ng/mL. Inter and intra-assay coefficients of variation for fecal extract and plasma controls were < 15% and < 7%, respectively. The results for plasma testosterone

and FAM were given in ng/mL and ng/g of dried feces, respectively.

All data were evaluated using SAS for Windows (SAS Institute Inc., NC, USA). Due to the small sample size, all variables were analyzed using nonparametric procedures (PROC NPAR1WAY WILCOXON–SAS). Spearman's correlation was used to calculate the relationship between variables studied in each season (PROC CORR SPEARMAN–SAS). The significance level used for all variables was $p < 0.05$.

Annual profiles of the variations in antler cycle, gross morphometry, ejaculate characteristics, and androgen levels are shown in Fig. 1. The number of males showing antlers in velvet was higher in spring than during summer and autumn. Four of the six bucks cast their antlers during our study, but the time of the year when it occurred and the period antlers were in velvet varied among individuals. One male cast antler during autumn–winter while others shed their appendices at different months of the spring. Velvet antlers were carried for periods varying from 1 to 7 months. The remaining bucks kept hard antlers year-round.

Body weight and chest girth changed little throughout the year, and despite neck girths in some bucks had greater fluctuations no clear patterns could be noticed. Half of the males exhibited greater testicular volume during the winter, whereas patterns from the other half were different from one another. None of the seminal and hormonal traits showed any synchrony in their seasonal changes.

Additionally, statistical analysis confirmed that mean values of all collected parameters did not vary among seasons (Wilcoxon tests, $p > 0.05$, Fig. 1). According to Spearman's correlation analysis, body weight was positively correlated with neck and chest girths, total sperm count, and sperm motility index (Table 1). Likewise, chest girth was positively correlated with neck girth, testicular volume, and total sperm count. No correlations between seminal characteristics and androgen levels (both plasma testosterone and FAM) were found, but not surprisingly plasma testosterone positively correlated with FAM.

Our findings provide evidences that red brocket bucks not only exhibit aseasonal and asynchronous antler cycles, but also maintain their secondary sexual characteristics and semen quality stable throughout the year. Previous studies in brocket deer species have likewise documented antler casting at any time of the year and males carrying hard antler for periods longer than a year (Barrozo et al. 2001; Bisbal 1994; MacNamara and Eldridge 1987; Pinder 1997; Pinder and Leeuwenberger 1997; Schneider 1996; Versiani et al. 2009). This peculiarity seems to be shared by other tropical and subtropical species, such as marsh deer (*Blastocerus dichotomus*), chital deer (*Axis axis*), and Indian muntjac (*Muntiacus muntjak*) (Chapman and Chapman 1982; Chapman and Harris 1991; Loudon and Curlewis 1988; Pereira 2010), and contrasts with the classical model of annual antler replacement proposed for temperate-zone species (Bubenik 2006). It also suggests that, considering the close relationship between testicular activity and antler cycle, photoperiodic–pineal link in this species may be absent or only able to entrain the reproductive system weakly.

However, to date indicia that red brockets are aseasonal breeders relied mainly on birth records and little seasonal fluctuations in weight of testes and epididymis (Branan and Marchinton 1987; MacNamara and Eldridge 1987). Herein, we found that red brocket bucks we studied remained reproductively active year-round without seasonal changes in sperm production or quality, and that seminal characteristics were not associated with antler status. These data support earlier reports on the species in which males have bred successfully either during velvet or hard antler (Branan and Marchinton 1987; Pinder and Leeuwenberger 1997). Furthermore, while body weight did not vary considerably throughout the study, testicular volume in red brockets reduced almost 22% in the summer as compared to the yearly maximum (winter). Nonetheless, unlike temperate species, this decline in testicular volume did not lead to azoospermia a circumstance formerly described only in muntjac and chital deer (Chapman and Harris 1991; Lincoln 1985; Loudon and Curlewis 1988). Yet red brocket males differed from both species because semen production and quality were not lowered during the velvet stage.

One possible driving factor for such maintenance in ejaculate parameters is the year-round availability of females in breeding condition (Pereira 2010), which may have evolutionarily favored bucks whose reproductive potential was preserved regardless of season or antler status. Notwithstanding, it seems reasonable to assume that even in this species the reproductive contribution of males in velvet may be smaller than those with hard antlers, due to their inability to use antlers during competition over females or territories (Lincoln 1992). The existence of females ready-to-breed over the year may also explain why some red brocket males carry hard antlers for longer periods (sometimes up to 6 years) to have the advantage of accessing females (Bisbal 1994; Frädrich 1987; MacNamara and Eldridge 1987). In contrast to its larger and temperate congeners, this forest dwelling concentrate–selector is usually solitary and highly territorial, displays small home ranges, and does not establish its dominance by locking its unbranched antlers in an attempt to force the opponent backwards (instead it uses these sharp appendices to injure the adversary) (Pereira 2010; Pinder 1992). Thus, considering that antlers in red brockets rarely break, their need to replace antlers may arise from the habit to constantly sharpen these structures, which periodically induces a reduction in antler size and, in turn, result in disadvantages during male competition for territories.

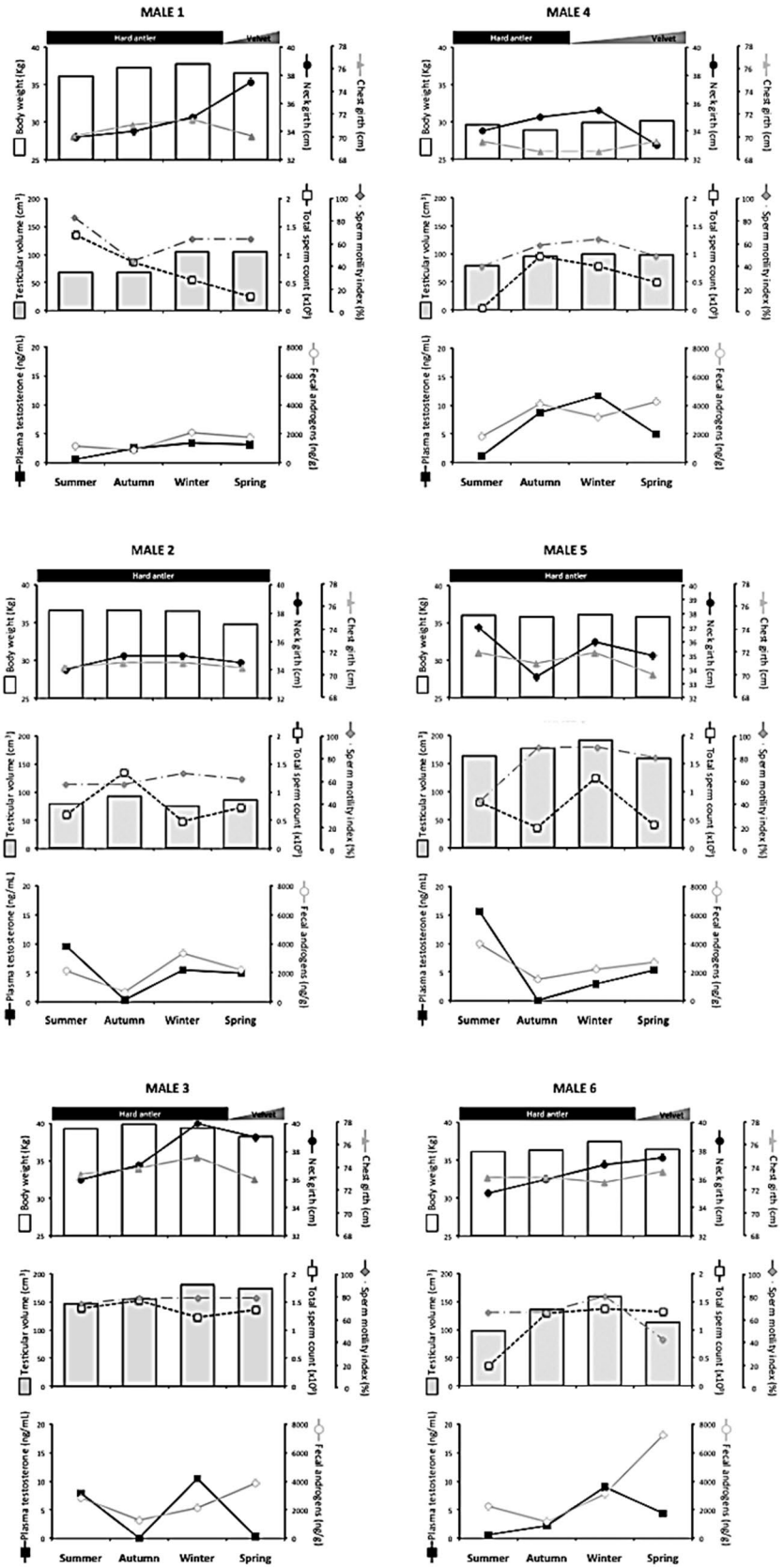

Fig. 1 Individual seasonal profiles of antler phase, morphometric measurements, ejaculate characteristics, plasma testosterone, and fecal androgens from red brocket males. A schematic representation of antler cycle is depicted by horizontal bars on the top of each graph (black and gray bars express hard antlers and antlers in velvet, respectively). None of the analyzed parameters showed significant differences among seasonal means ($p > 0.05$)

Table 1 Summary of the results of Spearman's correlation analysis among hard antler phase, gross morphometry, seminal traits, and hormonal levels in adult red brocket bucks (*Mazama americana*)

Variables	Weight	Hard antlers	Chest	Neck	Testicular volume	TSC	SMI	Plasma testosterone	Fecal androgens
Weight	–	0.06	0.71**	0.43*	0.26	0.42*	0.47*	− 0.14	− 0.27
Hard antlers	–	–	0.10	− 0.20	0.15	0.02	0.17	− 0.14	− 0.31
Chest	–	–	–	0.56**	0.40*	0.44*	0.39	− 0.05	0.00
Neck	–	–	–	–	0.64**	0.56**	0.33	0.17	0.19
Testicular volume	–	–	–	–	–	0.26	0.37	0.03	0.23
TSC	–	–	–	–	–	–	0.42*	− 0.04	− 0.07
SMI	–	–	–	–	–	–	0.01	− 0.22	− 0.07
Plasma testosterone	–	–	–	–	–	–	–	–	0.58*
Fecal androgens	–	–	–	–	–	–	–	–	– and

TSC total sperm count, *SMI* sperm motility index

*$p < 0.05$

**$p < 0.01$

Another species of the genus *Mazama* that share similar ecological and behavioral features, the brown brocket deer (*Mazama gouazoubira*), has also expressed acyclic fluctuations in plasma testosterone, morphological and seminal parameters (Barrozo et al. 2001). In our study, both plasma testosterone and FAM altered slightly among seasons indicating that, as spermatogenesis, steroidogenesis does not show a well-defined annual cycle. These results strengthen the concept that testicular activity in red brockets may be stimulated by continued resources availability rather than photoperiod. According to Bodmer (1989) and Bodmer et al. (1997), many fruits eaten by brockets do not undergo substantial oscillations across seasons, an element strengthens this idea of breeding activity to be more linked to short-term cues. However, we cannot rule out that this lack of seasonal pattern in androgen secretion may derive from small number of animals as well as their heterogenous origin, a hypothesis previously considered by Bubenik et al. (1991) for asynchronized breeding cycles of chital deer and muntjac populations living in Europe.

Intriguingly, our statistical analysis did not find a significant correlations between hard antlers and androgen secretion, an outcome that again contradicts the general pattern described for most deer species (Asher 2011; Asher et al. 1989; Bubenik 2006; Bubenik et al. 1991; Gosch and Fischer 1989; Mirarchi et al. 1977; Pereira et al. 2005; Sempéré et al. 1992). This occurred because all individuals exhibited hard antlers during either high and low levels of plasma testosterone and FAM. Declines in FAM during hard antlers without further shedding have been previously observed in red brocket bucks (Versiani et al. 2009) and, according to our findings they do not seem to influence the male reproductive fitness.

In summary, our data indicate that in addition to having aseasonal and asynchronous antler cycles in which individuals can carry hard antlers for periods longer than a year, the studied red brocket bucks do not show clear seasonal patterns in gross morphometry, ejaculate traits and androgen secretion. Besides, seminal characteristics did not correlate to antler status. Future research addressing the effects of photoperiod on the reproductive axis of red brocket deer and the role of androgens in its antler casting and growth are still needed to confirm whether or not this cervid truly represents an exception to the typical model proposed for temperate and artic species.

This study suggests that red brocket deer bucks can be considered as an aseasonal breeder, explained partly by the lack of seasonal pattern of their reproductive parameters assessed over a 1-year period.

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Compliance with ethical standards

Conflict of interest None of the authors have any conflict of interest to declare.

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