



Original investigation

Lack of mate selectivity for genetic compatibility within the red brocket deer *Mazama americana* complex

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ABSTRACT

Red brocket deer *Mazama americana* includes at least two lineages that differ at the level of karyotypes and phylogenetic relationships based on mtDNA. Also, hybrids between them have been proved to be nonviable or infertile. Since successful breeding is hampered, we expect selection to have produced a precopulatory barrier between these lineages based on courtship behaviour, to prevent investment in unsuccessful breeding. Here we made experiments with specimens in captivity to investigate mating preferences for partners belonging to the same or different karyotypes or lineages, along with a white-tailed deer buck (*Odocoileus virginianus*) as an outgroup control. Behaviours were video recorded and analysed by using Generalized Linear Mixed Models, with the interacting females and males as random subjects. The results show that although red brocket females never accepted copulations with the control male, trials involving pairs of red brocket deer may or may not end with copulation regardless as to whether the partners belonged to the same or different lineages. Although some male and female behaviours differed when pairs belonged to the same or different lineages, our results do not support the existence of a precopulatory barrier between lineages in the red brocket deer complex. We discuss the implications for sympatric speciation and species conservation.

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Introduction

The processes of sympatric speciation have puzzled evolutionary biologists for decades (Coyne and Orr, 2004; Dobzhansky, 1937; Futuyma, 2005; Mayr, 1963). In the absence of geographical barriers that produce isolation, simple distance in geographically continuous areas has been shown to allow the genetic differentiation of populations up to reproductive isolation (Futuyma, 2005). One example are the ring species, or series of populations wrapping around a geographical barrier where the two terminal populations do not exchange genes directly but are connected by a chain of interbreeding populations (Irwin et al., 2001). But distant populations in fairly homogeneous areas may also suffer differentiation processes in a chain of intermediate forms. These changes may be adaptive but also random, the latter being especially relevant when ecological conditions maintain over large geographic areas. One of

these forms of random processes of change is karyotypic evolution. In some taxa, karyotypes tend to experience changes within short periods of time giving rise to reproductive incompatibility, such as the reported rapid chromosomal evolution in mice (Britton-Davidian et al., 2000). Chromosomal evolution may be a source of rapid, non-adaptive changes producing accelerated rates of radiations, but examples are very scarce for this type of speciation processes (Britton-Davidian et al., 2000). Populations differing in chromosomal composition can produce hybrids that may be sterile or infertile owing to the complex chromosomal configurations that would occur in meiosis (Baker and Bickham, 1986). Once the chromosomes have differentiated after a short period of time (e.g. as short as 500 years in mice: Britton-Davidian et al., 2000), a question arises about the consequences for other reproductive processes. For example, post-zygotic reproductive isolation such as karyotypic divergence is expected to promote adaptive pre-zygotic barriers since resources devoted to offspring production will have no fitness return.

The red brocket deer (*Mazama americana*) is one of the best examples for a large mammal of karyotypic diversification leading to true sympatric speciation (see Amato et al., 2000, and Huang

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et al., 2006, for a similar case in *Muntiacus reevesi*). Members of this species complex (Abril et al., 2010; Aquino et al., 2013; Cursino et al., 2014), currently occur in forest habitats (Bodmer, 1997; Duarte, 1996; Escobedo-Morales et al., 2016; Varela et al., 2010) throughout a wide distribution range from México to the north of Argentina (Eisemberg, 1989; Emmons, 1990). Earlier studies described up to eight different species within the red brocket deer complex (Allen, 1915) that were later included in one with a variable number (9–15) of subspecies (Cabrera, 1960; Czernay, 1987; Rossi, 2000). A cryptic species, the small red brocket deer *M. bororo*, was initially included within the complex but lately identified as a separated species based on chromosomal and morphological differences (Duarte, 1996; Duarte and Merino, 1997; Duarte and Jorge, 2003). More recent work based on cytogenetics and mtDNA sequencing have provided improved tools for the assessment of taxonomic diversity within the complex and its relationships with other neotropical deer, evidencing the explosive diversification during the late Pliocene (2.5–3 MYA), soon after their ancestor arrived in South America through the Panamanian land bridge, giving rise to a number of morphologically cryptic species within the red brocket clade (Duarte et al., 2008; Escobedo-Morales et al., 2016; Heckeberg et al., 2016).

The analysis of the cytogenetic evolution has recently shown the existence of two karyotypic lineages that evolved from a common ancestor by chromosomal rearrangements: Lineage A, which includes the Rondônia and Juína karyotypes; and Lineage B, which includes the Jarí, Carajás, Santarém, and Paraná karyotypes (Abril et al., 2010). Both lineages are also well differentiated at the level of mtDNA (Abril et al., 2010) and maintain reproductive isolation, with hybrids showing sterility or subfertility (Aquino et al., 2013; Cursino et al., 2014; Salviano et al., 2017). All these results clearly point to the existence of at least two separate species within the current *Mazama americana* specific nomination, which need to be formally described, and probably a deeper investigation could reveal further subdivisions under an ongoing process of rapid sympatric speciation based on chromosomal rearrangements (Abril et al., 2010).

Genetic compatibility is a central element in reproductive isolation and speciation (Coyne and Orr, 2004; Piálek and Albrecht, 2005) and there is increasing support for the role of sexual selection in sympatric speciation (van Doorn et al., 2009; Wagner et al., 2012). For mammalian females, the production of hybrids may entail high costs of gestation and lactation that compromise mothers' success. These potentially high costs of matings leading to subfertile hybrids are expected to fuel selection favouring pre-zygotic barriers known as reinforcement in speciation (Servedio and Noor, 2003), which may include mate choice strategies to discriminate among mating partners and reject as mates those that would give rise to less successful offspring (Andersson, 1994; Trivers, 1972).

Sexual selection has an important role in maintaining species isolation by the evolution of signal divergence between species (Ptacek, 2000), and female choice is an important mechanism for both species recognition and intraspecific mate selection (Andersson, 1994; Kokko et al., 2003). Sexual signals during courtship (Andersson 1994; Johnstone 1997), such as visual displays or sex pheromones, play a crucial role as premating barriers between closely related taxa (Ptacek, 2000; Bradbury and Vehrencamp, 2011). Little is known on the courtship behaviour and mating system of the red brocket deer. As forest dwellers, individuals are solitary, with females using mostly exclusive ranges and male ranges overlapping with those of more than one female. Although the geographic ranges of distribution for both lineages have not been delimited, the species occurs throughout a large, continuous geographic area in which interactions between members of both lineages could occur along contact zones. Here we focus on the behavioural barriers that could prevent gene flow between both

Table 1
Description of the individuals used in the study.

Individual	sex	Cytotype	Karyotypes
1	F	Paraná	2n = 52/NF = 56
2	F	Paraná	2n = 52/NF = 56
3	F	Paraná	2n = 52/NF = 56
4	M	Paraná	2n = 53/NF = 56
5	M	Paraná	2n = 53/NF = 56
6	M	Paraná	2n = 53/NF = 56
7	M	Paraná	2n = 53/NF = 56
8	F	Rondônia	2n = 42/NF = 49
9	M	Rondônia	2n = 43/NF = 49
10	M	Carajás	2n = 51/NF = 54
11	M	Juína	2n = 44–45/NF = 48

lineages. In particular, our goal was to study courtship behaviour of captive pairs during mating trials with members of the same and different karyotypic lineages, as a potential pre-mating barrier contributing to reproductive isolation between both putative species.

We were interested in testing whether the two red brocket deer lineages are fully reproductively isolated and will not engage in courtship behaviour and mating with members of the other lineage. The null hypothesis, therefore, is that there are no differences in copulation probability, and in the behaviour of males and females in couples formed by animals belonging to the same or different lineages.

Material and methods

Animals

The study used eleven adult animals from a red brocket deer species (*Mazama americana*), 4 females (aged 3.1–14.3-years-old, 37.5–45.2 kg body weight) and seven males (aged 2.9–15.3-years-old, 37.8–41.7 kg body weight). These animals belonged to four different cytotypes. The experimental subjects belonged to cytotypes Juína (J) and Rondônia (R) of Lineage A, and cytotypes Paraná (P) and Carajás (C) of Lineage B. In particular, three of the four females belonged to the Paraná cytotype and one to Rondônia. In males, four of them belonged to the Paraná cytotype, one to Juína, one to Carajás and another one to Rondônia (see Table 1).

Seven of these animals were born in the research centre and the rest came from confiscations, either directly sent by the authorities to the research centre or after spending some period in a zoo.

Animals were maintained in individual indoor stalls visually isolated from one another, although they probably got olfactory information from each other since all of them were kept in the same building. Three of four females had previous experience with males, either mating or simply having physical proximity when assessing their oestrus status. Regarding males, only two had previous experience with females. All animals were subjected to similar management and olfactory or other casual contacts might have occurred among the individuals, so there was no evident reason for a bias towards knowledge of their own or different cytotypes. However, previous experience was obviously variable among individuals and this represents an uncontrolled variable in our experiments, hence included as random subject in the analyses (see below).

Animals were maintained in captive conditions housed individually in indoor holding areas all day (individual stalls of 12 m²) at the Deer Research and Conservation Centre (NUPECCE) of the Department of Animal Science of the FCAV-UNESP in Jaboticabal, São Paulo, Brazil. Animals from all cytotypes were fed *ad libitum* with a diet consisting of a pelleted feed (12% crude protein, 2% crude fat, 10% crude fibre; Purina Co., Paulínia, Brazil) and approxi-

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