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Female choice in *Trinomys yonenagae*, a spiny rat from the Brazilian Caatinga

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Abstract. ***Trinomys yonenagae*** is a spiny rat endemic to fixed dunes in the Caatinga. It lives in colonies, digs and shares burrows and presents high levels of intra- and inter-group tolerance. Here we tested if females exhibit preference for a long-term partner in a choice test, where each female was free to move and males (partner and unfamiliar) were restricted to their own compartment. Aggression occurred only once against an unfamiliar male and all females spent more time in the compartment with a male than in the empty one, confirming the high degree of affiliation of ***T. yonenagae***. We consider that a choice was made since seventy percent of females exhibited a preference for sitting side-by-side with the partner than with the unfamiliar male. However, the frequencies of visits to both males were not statistically different. Considering the absence of dimorphism, the presence of parental care, delayed sexual maturity, and heterosexual affiliation, shown by the present study, all traits of social monogamy, we suggest that ***T. yonenagae*** is socially monogamous and that the relationship between females and males in this species seems to be a complex balance of partner preferences and kin avoidance strategies.

Key words: Echimyidae, ***Trinomys yonenagae***, female choice, heterosexual affiliation, social monogamy.

Resumo. Escolha de parceiros em fêmeas de *Trinomys yonenagae* **, um rato-de-espinho da Caatinga brasileira.** ***Trinomys yonenagae*** é um rato-de-espinho endêmico de dunas fixas na Caatinga. Estes animais vivem em colônias, cavam e compartilham túneis, apresentando altos níveis de tolerância intra e intergrupal. No presente trabalho testamos se fêmeas exibem preferência por um parceiro de longa convivência em um teste de escolha, onde cada fêmea estava livre para se locomover e os machos (o parceiro e um desconhecido) estavam restritos aos seus próprios compartimentos. Agressões ocorreram uma única vez, contra um macho desconhecido. Todas as fêmeas gastaram mais tempo em um compartimento com um macho do que no compartimento vazio, confirmando o alto grau de afiliação de ***T. yonenagae***. Consideramos que houve escolha, uma vez que 70% das fêmeas preferiram repousar lado-a-lado mais tempo com o parceiro, do que com o macho desconhecido. Contudo, as frequências de visita a ambos os machos não foram estatisticamente diferentes. Considerando que a ausência de dimorfismo, a presença de cuidado parental, a maturação sexual tardia e a afiliação heterossexual, esta apontada no presente estudo, são todas características de monogamia social, sugerimos que ***T. yonenagae*** é socialmente monogâmico e que o relacionamento entre fêmeas e machos nesta espécie aparenta ser um balanço complexo entre estratégias de preferências por parceiros e de evitar parentescos.

Palavras-chave: Echimyidae, ***Trinomys yonenagae***, escolha da fêmea, afiliação heterosexual, monogamia social.

INTRODUCTION

Monogamy has been defined as obligate and facultative (KLEIMAN, 1977). The former is related to a need for male care and the later to social systems where a species exists at low density and both sexes are highly dispersed (for review see WOLF AND SHERMAN, 2007). Social, sexual and genetic types of monogamy have also been described (REICHARD, 2003). Social monogamy refers to a demographic and sociospatial relationship of a female-male pair, where proximity is a prerequisite. In those cases a social pair is formed and last at a time. The temporal component is important because a single partnership for lifetime is a rare phenomenon among reproductive animals. The term "sexual monogamy" is used when it is possible to observe exclusive sexual interactions between a male and female; when DNA analyses can confirm that a male and a female pair reproduce exclusively with each other the relationship is named “genetic monogamy” (REICHARD, 2003).

The occurrence of monogamy is rather rare in mammals (KLEIMAN, 1977), and social monogamy is found in less than 7% of mammalian species. Rodentia is an order where social monogamy is present and has evolved independently in different species. ***Microtus ochrogaster***, the prairie vole, is perhaps the best-studied example of a monogamous rodent (OPHIR ***et al***, 2008). Since rodents frequently are small, cryptic and nocturnal, monogamy has been inferred from: a) studies in laboratories or enclosures; b) field studies using traps or telemetry and c) genetic analyses (see WOLFF & SHERMAN, 2007). Most cases of monogamy in muroid rodents have been inferred from the spatial distribution of male and females, when there is overlapping of their home ranges (in WOLFF & SHERMAN, 2007).

Traits that have been used to infer monogamy in captivity are: the presence of pair-bonding, biparental care with the father carrying, feeding, defending, and socializing offspring, delayed sexual maturation, and the absence of sexual dimorphism (DARWIN, 1871; ALEXANDER ***et al.***, 1979; TRIVERS, 1972; KLEIMAN, 1977; DEWSBURY, 1981; REICHARD, 2003; WOLFF AND SHERMAN, 2007; SILVA ***et al.***, 2008). The relationship is also considered as social monogamy when a male-female pair shares the use of a territory and display behaviors that are indicative of a social pair (REICHARD, 2003).

Trinomys yonenagae (ROCHA 1995), known as rabo-de-facho, is a small rodent endemic to sand dunes fields at the “Área de Preservação das Dunas e Veredas do Médio São Francisco”, in the arid Brazilian Caatinga (ROCHA, 1995). It is fossorial (sensu HILDEBRAND ***et al.***, 1985), colonial and shows high intraspecific affiliation and low aggressiveness (ROCHA, 1995; MANAF & SPINELLI OLIVEIRA, 2000; FREITAS ***et al.***, 2003; MANAF ***et al.***, 2003; FREITAS ***et al.***, 2008). This is in contrast to closely related species that inhabit forested areas, which are considered territorial and less socially tolerant (EMMONS, 1997; FREITAS ***et al.***, 2008).

In captivity, the spiny rats exhibit a complex social repertoire, which includes odorous and vocal communication, a variety of affiliative contacts, and parental care (MANAF & SPINELI OLIVEIRA, 2000; FREITAS ***et al.***, 2003; MANAF ***et al.***, 2003; FREITAS ***et al.***, 2008). Life-history traits are typical of a slow-living mammal: at least in captivity gestation is long, and sexual maturity is delayed (SPINELLI OLIVEIRA ***et al.***, to be submitted).

Field studies indicate that males and females ***T. yonenagae*** spend part of their lives together. They dig communally and inhabit complex burrow systems (ROCHA, 1995), and the frequency of male-female pairs sharing the same burrow is high (SANTOS, 2004). There is not body size dimorphism (ROCHA, 1995).

Taken together, these data suggest that social monogamy is present in ***T. yonenagae***. A test that has been used to study the effect of familiarity in rodents is one where females are given simultaneous access to a former partner and a novel male (SHAPIRO ***et al***, 1986; AVITSUR & YIRMIYA, 1999; CLARK ***et al***, 2004). So we want to use a similar procedure to test the hypothesis whether female ***T. yonenagae*** exhibit social attraction and choose preferentially (***i***) a long-term familiar and breeder partner, or (***ii***) an unfamiliar male, or (***iii***) an empty space. Based on their high sociality and affiliation exhibited both in the field and captivity, we hypothesize that females prefer a place with another animal instead of the empty one (heterosexual affiliation), and further prefer the familiar instead of the unfamiliar male, fulfilling one more condition to be considered socially monogamous.

MATERIAL AND METHODS

Subjects and maintenance conditions

The spiny rats were treated ethically according to Brazilian laws. Subjects were 20 adult ***Trinomys yonenagae*** (10 females: 145 ± 11 g; 10 males: 137 ± 8 g) from an original stock collected in sand dune fields in the Caatinga biome (Ibiraba: 10°48’S, 42°50’W), BA, Brazil, under IBAMA licenses n°097/97 and 129/98-DIFAS. Rabos-de-facho were kept in captivity for 50±24 months (range: 24-84 months) before the tests were conducted.

Routine maintenance and handling procedures were performed according to established standards described elsewhere (Manaf & Spinelli Oliveira, 2000). Briefly, the animals were housed and tested in the Department of Biology – FFCLRP/USP, under controlled conditions (23 ± 1°C; lights off 6:00 a.m. - 6:00 p.m.). All experimental sessions were done during the dark phase, between 3 and 5:00 p.m, when the spiny rats are active (Marcomini & Spinelli oliveira, 2003). The access to water and food was free and the diet (lab chow for mice and rats: Nuvilab CR-1, Nuvital Nutrientes Ltda, Brazil) was supplemented weekly with seeds, fruits, vegetables, and oral vitamins (Rarical, Jansen-Cilag, Brazil).

The spiny rats were grouped as one heterosexual pair per cage (standard plexiglass cages of 40 x 33 x 16 cm) for at least five months prior to the experimental sessions. During these months all females bred and reared at least one litter. Therefore, we have considered "partner" the male with whom the female had litter. To avoid a bias in favor of body size, the mass differences between males tested in the same experimental session were kept smaller than 10 g.

Equipment

The apparatus was modified from Webster ***et al.*** (1982). Briefly, it consisted of three identical wooden compartments (60 x 60 x 60 cm): one central box connected by small doors to two lateral boxes, each one on an opposite side of the central box, to allow females to move freely between the compartments. The floor of all compartments was covered with wood shavings. Each male was confined to a lateral compartment by small leather harnesses made for hamsters (Cinoteck Safe-Belt, Brazil). The harnesses comprised neck and body loops attached to a swivel lashed to a rod positioned at the top of the test box, which restricted locomotion of the male spiny rats.

Procedure

The procedure was modified from Williams ***et al.*** (1992). Each animal had one individual habituation session in the apparatus for one hour, two days before testing. In these sessions males were tethered to the rod in one end-compartment and females were free to move. The reactions of males to the tethering situation, which included scratching and attempts to nibble the leader, were restricted to the first ten minutes of the session.

On the day of testing, the partner and an unfamiliar male were tethered in their respective end-compartments. After 15 min, the female familiar to the partner was introduced in the central compartment free to move in the apparatus for three hours. The experiment was balanced for the male tethered in each end-compartment (partner or unfamiliar). After each test the apparatus was thoroughly cleaned with alcohol solution, and wood shavings were substituted. Females were tested once, and males twice (as a partner and an unfamiliar, designed at random counterbalanced combinations). Sessions were videotaped and the following variables for females were measured: the frequency of entries (all four paws in one compartment), time spent in each compartment, and time spent in resting in body contact (resting side-by-side in physical contact). These variables are considered to indicate a high degree of affiliation to a conspecific (Manaf & Spinelli Oliveira, 2000; Manaf ***et al.***, 2003; Snowdon, 2009)." Nasal-nasal, nasal-lumbar and nasal-anal contacts, nosing, sniffing, freezing and stretched attention postures, as defined by Manaf & Spinelli Oliveira (2000) although not quantified, were registered.

Statistical analysis

Data from the variables (number of entries in the compartments, time spent in the compartments, and time spent resting side-by-side) between familiar and unfamiliar males were analyzed by the paired Student's t-test, two-tailed, with familiar and unfamiliar male as levels, and $p<0.05$ (Zar, 1996). The comparison of time spent with the partner, the unfamiliar male and in the empty compartment was done using ANOVA test, $p<0.05$. Preference for a partner was defined as an individual spending twice as much time in contact with the partner than with an unfamiliar animal (Insel ***et al.***, 1995). Since locomotion may be related to body size in rodents, these two variables were analyzed by the Spearman Rank Correlation Test (Zar, 1996), assuming entries into the central compartment as a measure of locomotor activity.

Table 1. Time spent by each female spiny rat (***Trinomys yonenagae***) resting side-by-side with a familiar, an unfamiliar male, and percent of time spent side-by-side with either male during a session lasting 180min.

	Time spent (min)			**Session (%)**
female	partner	unfamiliar male	with male (total)	with a male
1	124	0	124	69
2	124	4	128	71
3	112	18	130	72
4	101	31	132	73
5	14	128	142	79
6	20	115	135	75
7	40	25	65	36
8	32	4	36	20
9	9	0	9	5
10	11	20	31	17

RESULTS

All females entered the three compartments of the apparatus, crossing the center and reaching the endings where the males were confined. Behaviors displayed during the sessions were grouped in two arbitrary phases. Initially, females showed slow locomotion throughout the apparatus, sniffing walls and floor. The first approach toward the males was generally slow and included freezing and stretched attention postures. This phase lasted up to ten minutes. Thereafter, females moved continuously from one male compartment to the other. In those occasions the pair interacted through affiliative contacts such as nasal-nasal, nasal-lumbar and nasal-anal. Nosing occurred preferentially when females were resting still side-by-side with the male. Eventually, some females briefly nibbled the harnesses without causing visible damages to them. There was only one occurrence of aggressive behavior that lasted the first five minutes of the session: female 9 (tab.1) chased and attacked the unfamiliar male without inflicting wounds. Thereafter this female continued to enter into the unfamiliar male compartment until the session ended, approaching the male without aggressiveness. Nonetheless the pair never rested side-by-side and the male fled from the female every time she approached him until the session ended. Not a single male displayed sexual behavior, like foot-tapping and attempts to mounting, which are commonly seen when males are close to females in estrus (Manaf & Spinelli Oliveira, 2000).

Analysis of individual scores revealed that six out of ten females spent at least 70% of the session time resting side-by-side with a male (tab.1). However 40% of females spent most to the session time in other activities. Seven out of ten females spent approximately twice as much time with the partner (numbers 1-4 and 7-9) than with the unfamiliar male (numbers 5 and 6). However, there was no significant difference in female time resting side-by-side (***t***= 0.9371; p= 0.373; df=9) with a familiar and an unfamiliar males (fig.1).

Time spent in the male compartments was significantly longer (with the partner: 5,520 ± 3,085 min ; with a familiar male: 4,393 ± 3,024 min) than time spent in the central compartment (887 ± 705 min; F=9.12, p<0.001). There was no significant difference (***t***= 0.5875; p= 0.571; df=9) in time females spent between familiar and unfamiliar male compartments (fig.1).

Figure 1 also presents the proportion of entries relative to total in the different compartments. The paired Student's ***t-test*** revealed no significant difference in number of entries between the

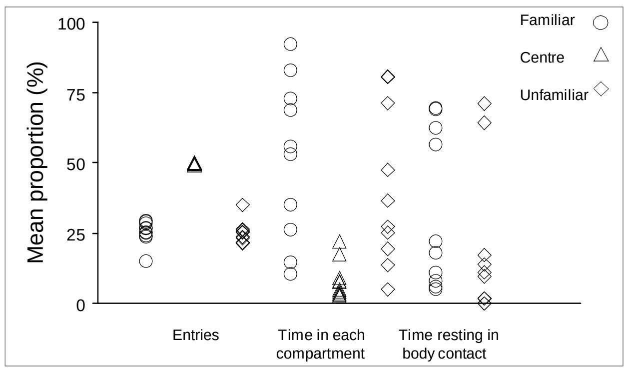

Figure 1. Individual scores as mean proportion of three variables (entries, time spent in compartment, and resting side-by-side) of free females (n=10) during 180min in an apparatus comprising one central (empty) and two end-compartments (with a familiar and an unfamiliar tethered male). Time spent with males (partner and unfamiliar) was longer than in the empty compartment (ANOVA, p<0.001); there were no significant differences when the other variables were compared (paired Student's *t*-test, p<0.05).

compartments of the familiar and unfamiliar males (***t***= 1.0401; p= 0.325; df=9), and there was no correlation between body mass and number of entries in the central compartment (r_s= -0.006, p = 0.987).

DISCUSSION

Time spent together and frequency/ duration of direct physical contact are behavioral measures used to estimate affiliative relationship. It is also considered that heterosexual affiliation is relatively rare among mammals, and it is generally restricted to species with social monogamy and biparental care (SNOWDOWN, 2009). In the present study heterosexual affiliation was estimated by a test were female ***Trinomys yonenagae*** could choose a mate partner, an unfamiliar male and an empty compartment. Results confirm that the species is highly affiliative since females choose to stay close to a male than in an empty place. In most cases time spent in the neutral compartment was below 10% of the session duration. In this aspect, the response of female ***T. yonenagae*** was similar to that of monogamous female prairie voles (***Microtus ochrogaster***), which spent around 20% of their time alone in the neutral chamber in a similar study (CARTER ***et al.***, 1995).

An analysis of the individual scores, based on the criterion of time spent resting side-by-side (INSEL ***et al.***, 1995) showed that the majority of female rested twice as much time with one specific male, either familiar or unfamiliar. This fact suggests that a process of choice and preference took place during the sessions.

It is considered that social preferences in rodents involve a multitude of factors, for example, a history of cohabitation or mating (CARTER ***et al.***, 1988; WILLIAMS ***et al.***, 1992), individual phenotypic traits such as size (SOLOMON, 1993), and sexual or hormonal condition (AVITSUR & YIRMIYA, 1999; LEONARD & FERKIN, 1999). For instance, hormonal status modulates partner preference in a variety of rodent species, as in wistar female rats (CLARK ***et al.***, 2004), and in ***Heterocephalus glaber***, the naked mole rat, a rodent that is fossorial, eusocial, and exhibits high levels of inbreeding (CLARKE & FAULKES, 1996). When females of ***H. glaber*** are reproductively active they prefer unfamiliar males, what is considered a tactic of inbreeding avoidance, whereas reproductively inactive females do not discriminate (CLARKE & FAULKES, 1996).

In the case of ***T. yonenagae*** a history of cohabitation or mating probably played a role since seven out of ten females rested more with the familiar than with the unfamiliar male. Size seemed not important since entries were not correlated with body mass, indicating that basic physical attributes did not influence the locomotor performance of females in the test. Also the hormonal condition seemed not to play a significant role in the performance of ***T. yonenagae*** females. Although in our study the reproductive state was not controlled, we consider that females were in diestrus due to the fact that the cycle in rabo-de-facho is relatively long (SPINELLI OLIVEIRA ***et al.,*** 2007) and the proestrus and estrus are quite short. This assumption is validated by the fact that no single male exhibited sexual behavior, like foot-tapping and mounting, which are commonly displayed by males to females in estrus (MANAF & SPINELLI OLIVEIRA, 2000).

Species differences in selectivity with respect to mate choice have been related to mating strategies in wild rodents, especially among voles (SALO & DEWSBURY, 1995). Monogamous prairie voles (***Microtus ochrogaster***) present a mating system characterized by long-term pair bonds between mates. When female prairie voles were tested on mate choice, they spent more time with the familiar male and also mated preferentially with them (SHAPIRO ***et al.***, 1986). Partner preference developed more rapidly when mating happened, although mating was not essential for the occurrence of choice (WILLIAMS ***et al.***, 1992).

Regarding polygamous species the results depend on the species: montane voles (***M. montanus***) showed no preference (SHAPIRO ***et al.***, 1986), but meadow voles (***M. pennsylvanicus***) preferred mating with familiar versus unfamiliar males, and displayed no preference for unmated versus mated males (SALO & DEWSBURY, 1995). In choice tests with voles the hormonal condition of females usually is not checked since most species are not spontaneous ovulators.

One concludes that choice tests are important to reveal heterosexual affiliation and mating strategies, but are not indicative of mating systems, a distinction that will be addressed below.

Taking in consideration traits typical of social monogamy, such as paternal care, delayed sexual maturation, overlapping of home ranges, absence of sexual dimorphism, and heterosexual affiliation, we suggest that potential social monogamy could be a flexible strategy of ***T. yonenagae*** in an unpredictable physical and social environment. Although density and biomass data for the species is high, its habitat is subjected to oscillations in the intensity of annual rainfall (Reis, 1976) and therefore, oscillations of the annual production of fruits and of population density (Rocha, 1991, Santos, 2004).

A distinction should be made between mating systems, which are characteristic of a population or a species, and mating strategies that refer to all tactics used by an individual to maximize reproductive success. Therefore, mating systems may refer to a variety of specific mating tactics (Waterman, 2007). For instance, ***Mus spicilegus***, the monogamous mound-building mice, presents facultative polygyny in the beginning of the reproductive season. Studies in captivity with this mice, nonetheless also show a deficit in reproduction in polygynously mated females (Gouat, & Féron, 2005).

Another example of the flexibility of mating is provided by prairie voles, a popular model of mammalian monogamy. In a captivity study prairie voles engaged in more extra pair fertilizations than predicted by genetic monogamy but fewer than predicted under random mating, demonstrating that social but not genetic monogamy may exist (Ophir ***et al***, 2008). Social monogamy is multifaceted, far from being a unique phenomenon with a single evolutionary explanation; it seems to have evolved along diverse pathways among different species (Reichard, 2003). So our study can only indicate social monogamy in ***T. yonenagae*** but can not provide insights into its mating system.

An important question brought up by our data is why there are females that, irrespective of a successful breeding and a long period of cohabitation, showed a clear preference for the unfamiliar male, with whom some of them spent more than 50% of session duration, around one hour and half? Field data regarding males of polygynous species point out the fact that they in general move around over larger areas than conspecific females or males of monogamous species, perhaps because wandering around enhances their chances of finding additional mates. Also males of polygynous species of rodents, including rats, mice, meadow voles (***Microtus pennsylvanicus***) and humans, are superior in spatial ability than females of the same species (see Nelson, 2005). Field studies of ***T. yonenagae*** show that some females more often than males (14 in 18 events) were trapped in gallery systems far from their home, a phenomenon not related to dispersion since the spiny rats return to their original burrows (Santos, J.W.A. personal communication). Taking in consideration that male of monogamous species wander around less and the fact that a number of females prefer the company of unfamiliar male we propose that a strategy of kin avoidance could be followed by females of the group, although other explanations are also possible.

The test performed in the present study appears to be an appropriate tool to evaluate social motivation and heterosexual choice in ***T. yonenagae***, which could be applied in studies of other spiny-rats. As reported for voles (Webster ***et al***. 1982), artificiality and tethering did not interfere on the occurrence of social interactions in ***T. yonenagae***.

We also consider that the time spent in captivity did not significantly alter the responses of rabos-de-facho to the test, as have been observed for other variables already studied in laboratory conditions (Spinelli Oliveira, unpublished results; Freitas ***et al***, 2003), since housing and procedures of maintenance were carefully monitored (Manaf & Oliveira, 2000).

We propose that social monogamy is a potential mating tactic of ***Trinomys yonenagae*** since most females showed preference for the partner, characterizing the formation of a social pair. We do not rule out the possibility that females leave temporarily the group following a kin avoidance strategy.

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