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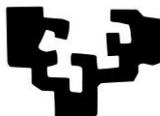
BIOLOGY MAJOR

Is inbreeding avoidance driving female mate choice in Verreaux's sifaka lemurs?

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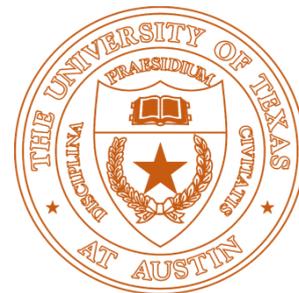
Bachelor's Thesis

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Is inbreeding avoidance driving female mate choice in Verreaux's sifaka lemurs (*Propithecus verreauxi*)?

Abstract

Females of different species might exert female mate choice for different reasons, one of them the aim of avoiding inbreeding. In this study I examine the implication of inbreeding avoidance as a mechanism driving female mate choice in Verreaux's sifaka lemurs (*Propithecus verreauxi*). In fact, in this species females are dominant and appear to be able to choose certain males to mate with, while observations indicate that rank, body size, canine size and proportions of fights won are not factors influencing female mate choice. So I hypothesized that females mate choice is driven by inbreeding avoidance in Verreaux's sifaka lemurs. Tissue and fecal samples were collected in the Kirindy Mitea National Park in western Madagascar as a source of DNA. Parentage was assigned for a sample of the population and relatedness coefficients between dams and sires were estimated and compared to those of between random female and male pairs, dams and other candidate sires within the population and within the groups where the offspring were conceived. I found that there were no significant differences in none of the comparisons which means that Verreaux's sifaka females do not mate more with males that are more distantly related to them. I concluded that inbreeding avoidance does not appear to be the main force driving female mate choice in Verreaux's sifaka lemurs and I addressed explanations for these findings. With this study I contribute to our knowledge of female mate choice in lemurs.

Introduction

Darwin (1859) developed the concept of sexual selection to explain the origin of certain traits in different species that cannot be supported by the theory of natural selection. Based on this theory, members of one sex within a species – usually the males – compete for the access to mates, while members of the other sex – usually the females – are choosy about the individuals they mate with (Darwin 1859). Indeed, females invest more in every reproduction and therefore are more likely to seek optimal matings (Janetos 1980).

Female mate choice has been broadly studied within the field of evolutionary ecology (Sardell et al. 2014). Indeed, there are numerous examples in nature of species that appear to exhibit female mate choice, going from invertebrates as some species of butterflies (Kaitala and Wiklund 1994; Von Schantz et al. 1989) to mammals like hyenas (Höner et al. 2007). We now know that there are different reasons why females choose certain mates (Jennions and Petrie 1997; Sardell et al. 2014). In some cases, females might exert direct selection (Kokko et al. 2003) which means they might choose males to mate with based on direct benefits, such as resources like food or territory (Jennions and Petrie 1997; Tregenza and Wedell 2000; Sardell et al. 2014). Whereas in some other situations, females might exert indirect selection (Kokko et al. 2003) which means that indirect genetic benefits might be the factors driving female mate choice (Jennions and Petrie 1997; Kokko et al. 2003; Sardell et al. 2014). Under indirect selection females might choose males according to their contribution to offspring survival (Kirkpatrick 1987). There are different models that explain female mate choice by indirect genetic benefits

(Sardell et al. 2014; Kokko et al. 2003). Some theories explain that females might seek what researchers refer as to additive 'good genes', genes that will be inherited by their offspring (Kokko et al. 2003) providing them with attractiveness (Fisher 1930) or viability (Andersson 1994). Nonadditive 'compatible genes' models instead point out that females may choose males that are genetically more compatible to them, in spite of males that have better genes – are fitter (Brown 1997; Tregenza and Wedell 2000; Ryder et al. 2010; Huchard 2013; Sardell et al. 2014). For example, females might be looking for males who are less related to them in order to avoid inbreeding (Huchard 2013). In fact, as Keller and Waller (2002) defined, inbreeding is "an increase in offspring homozygosity due to matings among relatives". Inbreeding can result in inbreeding depression which leads to a shift in genotype proportions within the population (as the homozygous individuals become more abundant), the loss of genetic diversity and the fixation of deleterious alleles (Charlesworth and Charlesworth 1987; Keller and Weller 2002). For instance, Chen (1993) and Jimenez et al. (1994), working with land snails (*Arianta arbustorum*) and white-footed mice (*Peromyscus leucopus noeboracensis*) respectively, found out that inbred individuals showed markedly lower survival than outbred ones. Additionally, Keller et al. (1994) found selection against inbred song sparrows (*Melospiza melodia*) and much higher survival for outbred individuals during a population bottleneck caused by severe winter weather.

Female mate choice as a mechanism for inbreeding avoidance has been described in numerous animals, and it is not only limited to mammals or primates. For example, Ode et al. (1995) found that parasitic wasp (*Bracon*

hebetor) females tended to avoid mating with mates that were developed on the same host. Nevertheless, examples are much plentiful among primates. Gagneux et al. (1999) investigating based on nuclear microsatellite markers and behavioral observations found that West African chimpanzee (*Pan troglodytes verus*) females actively seek mating partners outside their social unit, increasing male gene flow between communities and resulting on a lower relatedness among community males. Some species of lemurs also exhibit female mate choice as a way of avoiding inbreeding. For example, Boulet et al. (2009) found out that female ring-tailed lemurs (*Lemur catta*) can detect olfactory markers of genetic relatedness in males' scent marks which prevents them from mating with related males.

There are various features that make Verreaux's sifaka lemurs (*Propithecus verreauxi verreauxi*) particularly interesting to be the subject species for this study. To begin with, females are dominant (Jolly 1966; Kubzdela 1997; Richard 1987; Richard et al. 1993, 2002) and although there is mate guarding (Brockman 1999; Lewis and van Schaik 2007) the males cannot coerce the females because there is no sexual dimorphism (Lewis 2004). In addition, females are aggressive towards males, being these behaviors more pronounced during mating period (Brockman 1999). Indeed, data support that females sometimes mate subordinate males rather than stained dominant males (Lewis 2008). This means that females are very likely to be able to exert female mate choice. It has been observed that females do not mate with males with bigger body size or bigger canine size since these traits are not the target of their aggressive displays (Lawler et al. 2004). The same way, they do not

mate more with males that win more fights (Richard 1992). Furthermore, females have been observed to mate not only with the winners but also with extra-group males who did not participate in aggressive interactions (Lewis 2008). Meanwhile there is evidence of outbreeding, which is probably reduced to the neighboring groups, but that likely helps to maintain the gene-flow between populations (Richard 1974). So there is evidence to believe that females might be choosing males that are less related to them.

In this study I examined the implications of inbreeding in female mate choice in Verreaux's sifaka lemurs, thereby contributing to our knowledge of female mate choice and female dominance in lemurs. I hypothesized that female mate choice is driven by inbreeding avoidance in Verreaux's sifaka lemurs. I predicted that if females were choosing males that were less related to them then, first, parents would be more distantly related than random pairs of females and males within the population. Second, dams would be more distantly related to the sire than to other candidate sires within the population. And third, dams would be more distantly related to the sire than to other sire candidates within the groups where the offspring were conceived.

Methods

Study area

Samples for this study were collected in the Ankoatsifaka Research Station in the Kirindy Mitea National Park (KMNP) in western Madagascar. The forest in this part of the island is dry and deciduous (Richard et al. 2000). The

mean annual temperature is 25°C (range: 9–40°C) (Lewis and Bannar-Martin 2011). There is no available rainfall data for this specific site, although it is probably similar to the nearby Kirindy Forest (CNFEREF) which, placed 100 km to the north, receives approximately 800mm of rain per year (Lewis and Kappeler 2005; Lewis and Bannar-Martin 2011). The park is approximately 140,000 ha where a 1 km² trail system has been cut at 20°47'17" S, 44°10'08" E, approximately 21 km east of Belo-sur-Mer (Lewis and Bannar-Martin 2011). Within this 1 km² a 25 m x 25m grid system has been developed (Lewis and Bannar-Martin 2011).

Subjects

The study subjects are Verreaux's sifaka lemurs. These are Strepsirine lemurs (Lewis 2009), endemic to southwest Madagascar (Mittermeier et al. 2006). They are predominantly arboreal (Ankel-Simons 2000) and mainly folivorous (Norscia et al. 2006). They live in small groups of 2-13 individuals with variable sex-ratios (Richard 1992; Kubzdela, 1997; Brockman, 1999; Lewis and van Schaik 2007). We studied 75 individuals, out of which 48 were adults and 27 were offspring, from groups 1 through 9 within the 1 km² grid system described above. All animals within this area are habituated to the presence of human observers and marked with radiocollars or colored nylon collars and tags as part of an on-going long-term study, so all the subjects in this study are individually identifiable.

Data collection

The first captures and identifications of Verreaux's sifakas in the KMNP were developed in 2006. Senses began in 2007 and have been conducted monthly since then. Data, including individual's id and grid in which it was found, is recorded for the whole population. Throughout the years 9 groups have been identified within the 1 km² of grid system. Nowadays, complete genetic data exists for groups 2, 3, 4 and 5, and almost complete for group 1.

For this study individuals were captured using a blow pipe that delivers darts with a 3/8-inch needle (Lewis and van Schaik 2007; Lewis 2009). Darts were loaded with Telazol™, an injectable anesthetic with a dosage 25 mg per kg (Lewis 2009). Individuals were darted at distances ≤ 20 m by an experienced Malagasy technician (Lewis and van Schaik 2007). Darted individuals were caught in a large cotton cloth when they fell from trees or were retrieved by an assistant when they did not fall from the trees (Lewis and van Schaik 2007; Lewis 2009). Individuals were usually recovered and returned to their social group within 2–4 h (Lewis and van Schaik 2007; Lewis 2009).

Tissue and fecal samples were collected as a source of DNA (Di Fiore et al. 2009). 2 ml x 2 ml tissue biopsy punches were taken from the ears (which is the standard for the species) and stored in 70% alcohol. All the fecal samples were collected immediately upon voiding, and were then placed in aluminum foil, and labeled with time, date, and individual identification (Lewis 2009). After flattened to increase surface area the samples were dried in a Coleman oven within 4 hours of collection (Brockman and Whitten 1996; Brockman 1994).

Dried samples were stored in labeled Whirlpack bags (Nasco, Fort Atkinson, WI), and then combined in a freezer bag with desiccants (Lewis 2009). Samples were sent to The University of Texas at Austin (Department of Anthropology) for analysis.

Laboratory and analytical procedures

We conducted DNA extractions from the tissue and fecal samples. The DNA was extracted from the tissue samples using Qiagen DNEasy Tissue Kits. We followed the manufacturer's protocols and respected the concentrations and measures indicated. We extracted DNA from fecal samples using Qiamp Stool Mini Kits. In this case though, we applied the following modifications to the procedure recommended by the manufacturers: (i) the initial quantity of stool was 250 μ l instead of 180-220 mg, (ii) samples were allowed to lyse initially in ASL buffer for 30–60 min rather than 10 min, (iii) samples were subjected to proteinase K digestion at 70°C for 30 min rather than 10 min and (iv) extracted DNA was eluted in 100 μ l buffer AE heated to 70°C and incubated at room temperature for 30 minutes instead of 1 minute (Di Fiore et al. 2009).

We carried out PCR based genotyping at a panel of 14 variable microsatellite loci isolated in sifaka (Lawler et al. 2001; Rakotoarisoa et al. 2006). We used Qiagen Multiplex PCR Kits and we followed the reaction concentrations and thermal cycling conditions recommended by the manufacturers. We run the PCRs using Eppendorf termocyclers with a total reaction volume of 8 μ l when PCRs were followed by gel-electrophoresis techniques, and 5 μ l when no electrophoresis was carried out after the PCR. In

fact, we confirmed successful amplification via gel-electrophoresis at least once for each sample with each primer.

We mixed the samples with size standard ROX500 and we sent them to a core facility for fragment size analysis. The measurements used were 8.85µl of HiDi, 0.15µl ROX500 and 1µl of PCR product. This core facility provides microsatellite fragment analysis procedures that include the detection of fluorescently labeled fragments by the Applied Biosystems 3730 Genetic Analyzer and the interpretation of those using the GeneMapper or GeneMarker analysis software (DSFCore, 2014). The accuracy reached is less than one base difference between replicates (DSFCore, 2014). In order to confirm our results, we replicated the procedures and sent the samples to analyze at least twice for each sample.

Data analysis

Parentage analysis was estimated using maximum likelihood as implemented in the software CERVUS 2.0 (Marshall et al. 1998). Paternities were assigned with %95 of confidence for 21 out of the 27 offspring. A genotyping error rate of 0.05 was assumed for analyses of males and females. It was assumed that the proportion of males sampled was 0.75 and the proportion of female sampled was 0.90.

We used the software KINGROUP 2.0 to estimate relatedness coefficients between each pair of individuals in the population. This program uses the estimator of Goodnight and Queller (1999) to estimate relatedness values that range from -1 to 1. I compared the relatedness between the

determined parents to the relatedness between random pairs of females and males within the population. I also compared the relatedness between the dams and the sires to the relatedness between the dams and other candidate sires within the population and within the groups where the kids were conceived.

Results

Relatedness coefficients between the parents were not significantly lower than the relatedness coefficients between random pairs of females and males (Figure 1).

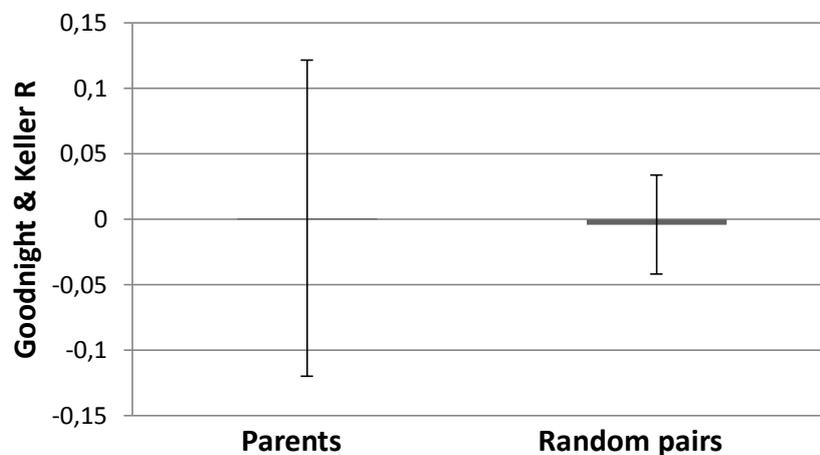


Figure 1. Mean of Goodnight & Queller (1999) relatedness coefficients between parents and between random pairs of females and males.

Relatedness coefficients between dams and sires were not significantly lower than relatedness coefficients between dams and other candidate sires within the population (Figure 2).

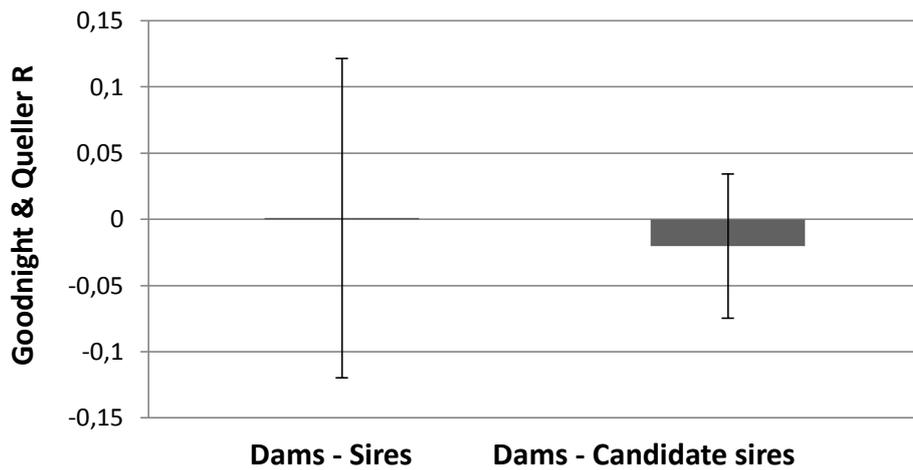


Figure 2. Mean of Goodnight & Queller (1999) relatedness coefficients between dams and sire and between dams and other candidate sires within the population.

Relatedness coefficients between dams and the sires were not significantly lower than relatedness coefficients between dams and other candidate sires within the groups where the offspring were conceived (Figure 3).

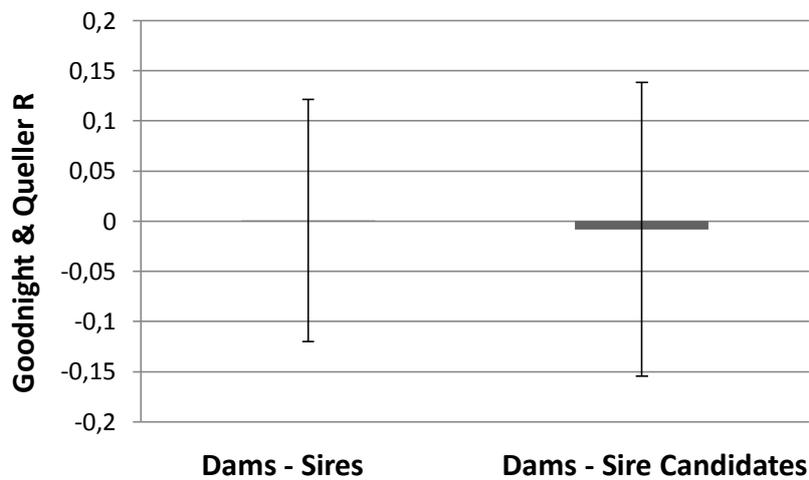


Figure 3. Mean of Goodnight & Queller (1999) relatedness coefficients between dams and sires and between dams and other candidate sires within the groups where the offspring were conceived.

Discussion

This study evaluated whether the avoidance of inbreeding could be the main mechanism driving female mate choice in Verreaux's sifaka lemurs. I predicted that if females were choosing certain males to avoid inbreeding then I would find that dams are more distantly related to the sires than random pairs of females and males between each other. I found no significant difference for relatedness coefficients between parents and between pairs of females and males chosen randomly from the population. I also predicted that if female mate choice was influenced by inbreeding avoidance then I would find that dams are more distantly related to sires than to other candidate sires within the population and within the groups where the offspring were conceived, and I found that in both cases there were no significant differences for relatedness coefficients between parents compared to the relatedness coefficients between dams and candidate sires. Females do not appear to choose males that are more distantly related to them in any of the cases considered so none of my predictions was supported suggesting that inbreeding avoidance is not the main force driving female mate choice in Verreaux's sifaka lemurs.

When looking at the raw data (Appendix A), the relatedness coefficients estimated for the pairs of parents appear to be negative in most of the cases or very close to 0, which means that most of the parents are not related to each other. In fact, there are only 4 cases in which the relatedness coefficients raise and reach values over 0.15. It is interesting that in the 4 cases the males were stained/ dominant. I consider 2 different explanations for these findings. First, it might suggest that male mate guarding is successful in Verreaux's sifaka, at

least for some stained/dominant males. However, previous studies do not seem to support this suggestion. Brockman (1999) observed that although mating was limited by mate guarding, mating frequency was enhanced by clandestine copulations. Lewis and van Schaik (2007) observed that stained males kept both resident and extra-group males away from the estrous females but subordinate males were able to mate with the females. Furthermore, Lewis and van Schaik (2007) also observed aggressive behaviors from females towards stained males that used aggressiveness to keep subordinate males away from them. Second, may be females are choosing stained/dominant males, which probably means they are selecting for inheritable genes that will increase the offspring's fitness as well as provide them with higher reproductive success. In fact, female mate choice appears to be driven by the search for additive good genes (Kirkpatrick 1987; Jennions and Petrie 1997; Kokko et al. 2003; Sardell et al. 2014) that provide the offspring with higher viability (Andersson 1994) or attractiveness (Fisher 1930). This explanation leads to my next consideration.

Females might be selecting for certain males based on several cues: for more compatible/less related males in some cases and males with higher inheritable fitness in some others. Different studies show evidence that supports that females use numerous cues to assess males (Jennions and Petrie 1997; Candolin 2003). Regarding the evolution of the use of several cues for mate choice it is straightforward that the preference for a single trait might result in the selection of various cues (Candolin 2003). The exploitation of several cues can lead to an increase in mate choice costs, but it can lead to a decrease in mate choice errors as well (Candolin 2003). Additionally, the use of different

cues might strengthen sexual selection and provide and maintain variation (Candolin 2003). Females might assess the different cues in an additive way, which means that females might choose males that possess more traits available to be exploited (Künzler and Bakker 2001) or they might select for different cues in different contexts (Candolin 2003). In most of the cases studies refer to cues such as male ornaments and sexual displays, mentioning for example, fish species that have bright colors and prominent courtship displays and bird species that have bright ornaments and perform very elaborated songs (Kodric-Brown 1993; Møller and Pomiankowski 1993; Jennions and Petrie 1997; Candolin 2003). For example, Höglund et al. (1994) found that black grouse (*Tetrao tetrix*) female mate choice does not only depend on tail damage but also on dominance rank and position on the lek. Andersson (1989) found that female mate choice in leks of Jackson's widowbird *Euplectes jacksoni* depends in both display rate and lek attendance. The discern between the importance and strength of different cues driving female mate choice might be difficult, and it only gets more challenging if we contemplate that they follow different cues in different contexts. So further studies might be necessary to find if actually inbreeding avoidance is one of the cues used by Verreaux's sifaka females and in which proportion or/and contexts.

It was also interesting that females did not seem to choose males that were more related to them either. There are various studies in which results show that females do not appear to select for males less related to them, neither do they mate with males more related to them. For example, in a study conducted by Pereira and Weiss (1991) ringtailed lemur (*Lemur catta*) females

showed sexual proceptivity towards unfamiliar and unrelated males, but selection for these males was not exclusive over selection for more closely related males. What this also might suggest is that the 6 paternities that could not be assigned with high confidence might be influencing the results. So further studies might be needed once the sires for this offspring are known.

In conclusion, my hypothesis that female mate choice is driven by inbreeding avoidance in Verreaux's sifaka lemurs is not supported in this study since females do not seem to choose males based on their relatedness. This study might contribute to our knowledge of female mate choice in Verreaux's sifaka lemurs and applicable to other species, so I might also shed light on female mate choice in general.

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Appendix A

Table 1. Goodnight and Queller relatedness coefficients estimated for pairs of parents, and the mean and standard deviation.

Kids	Mothers	Fathers	Goodnight & Queller R
Albert	Abby	Xavier	-0,1162
Ana	Abby	Xavier	-0,1162
Anthony	Abby	Sherlock	-0,1055
April	Abby	Xavier	-0,1162
Asterix	Abby	Xavier	-0,1162
Hira	Hester	Glen	0,193
Hope	Hester	Glen	0,193
Jello	Juliet	Lascaux	-0,0786
Pamella	Petunia	Quincy	0,0004
Peter	Petunia	Quincy	0,0004
Polina	Petunia	Isaac	-0,1736
Prisca	Petunia	Quincy	0,0004
Ratatouille	Rose	Quincy	0,1588
Smithy	Zena	Robert	-0,1322
Stacey	Zena	Omby	0,0198
Velo	Vanilla	Glen	0,156
Victor	Hester	Glen	0,193
Zafiry	Zena	Omby	0,0198
Zara	Savannah	Omby	0,053
Zoma	Zena	William	-0,0673
Zorro	Savannah	Omby	0,053
Mean			0,00088571
StDev			0,12065397