Behavioral correlates of extra-pair copulation in Indri indri

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Behavioral correlates of extra-pair copulation in Indri indri

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Abstract

Active pursuit of extra-pair mating has been reported for *Indri indri*, the socially monogamous largest living lemur. This study, conducted in a mountain rainforest in eastern Madagascar, presents the first evidence for extra-pair mating of indri and discusses the alternative mating strategy and alteration of the social, territorial, spatial, and vocal behavior of the adult female of a group of wild indris. Further studies may investigate whether extra-pair copulation is an attempt to breed with a partner of superior quality and thus lead to extra-pair paternity. If so, it could potentially play a role in maintaining genetic variability within a population.

Keywords Extra-pair copulation · *Indri indri* · Monogamy · Spatial behavior · Vocal behavior

Introduction

Monogamy is limited to 5 % of extant living mammalian species (Kleiman 1977). According to Trivers (1972) monogamy is common in birds because parental care may be shared by both sexes. Polygyny, on the other hand, is most likely to occur in mammals, in which parental care is mainly borne by females. Males, less involved in parental care, may incur fewer costs in engaging in additional matings, but it is also known that paternal care is a poor predictor of monogamy in primates (Wright 1990; Tardif 1994; Komers and Brotherton 1997). To increase their reproductive success, males must gain access to as many females as possible, but if complete monopolization is not possible males must maximize their number of copulations (Kappeler and Van Schaik 2004) coercing females (Isbell and Van Vuren 1996; Packer 1979; Samuels et al. 1984; Shively and Smith 1985; Bercovitch 1988) or pursuing extra-pair copulations (EPCs) (Trivers 1972). However, the benefits a male may gain from EPCs must reconcile:

(1)   The costs of pursuing such additional matings; and

(2) The gains from parental efforts (Maynard Smith 1977; Westneat et al. 1990)

such that male reproductive behavior may be seen as a tradeoff between mating and parental effort.

Previous studies of birds (Wagner 1991; Kempenaers et al. 1992; Birkhead and Møller 1992; Kempenaers and Dhondt 1993) have shown that extra-pair paternity is likely to be largely controlled by females, which may resist, accept, and/or actively seek EPCs (Westneat et al. 1990). Females may gain genotypic benefits from initiating extra- pair mating: in particular, ''good genes'', increased heterozygosity of their offspring, or fertilization insurance (Westneat et al. 1990). By actively seeking an EPC a female may copulate with a higher quality reproductive partner, if its mate is not the best available partner (Gray 1997).

The occurrence of EPC has been documented for several socially monogamous mammal species (Isvaran and Clutton-Brock 2007), including primates (gibbons: Palombit1994b; Oka and Takenaka 2001; marmosets: Digby 1999; dwarf lemurs: Fietz et al. 2000; sifakas: Lawler 2007; fork-marked lemurs: Schulke et al. 2004; and red-bellied titis: Mason 1966). It has never been observed for indri (*Indri indri*), a socially monogamous primate (Pollock 1975a, b; Reichard and Boesch 2003) inhabiting the mountain rainforests of eastern Madagascar and living in territorial family groups typically consisting of a breeding pair and their offspring (Petter and Peyriéras 1979; Pollock 1975a, b, 1979; Powzyk and Thalmann 2003). Indri family groups, actively defend their territories both through direct fights at the boundaries and by singing. The indris' song is a long sequence of vocal utterances (Pollock 1986; Giacoma et al. 2010; Gamba et al. 2011; Sorrentino et al. 2013) that serve to regulate spacing between neighboring groups and maintain group cohesion (Pollock 1986; Torti et al. 2010). The mating season usually lasts from late November to February (Pollock 1975a, b), but breeding behavior is more often observed in December and January, when territorial behavior, social interactions, and the timing and frequency of indri singing activity steadily increase (Pollock 1975a, b, 1986); Mittermeier et al. 2006).

In this paper we report an EPC, observed for the first time in this species, during a long-term field study. We provide a detailed description of the social, singing, and spatial behavior of an indri group before, during, and after the EPC.

Methods

Study area and subjects

The Maromizaha forest (18°560 4900 S–48°270 3300 E) is 1880.8 hectares in size, extending around the village of Anevoka, in eastern Madagascar, 29.6 km east of Moramanga, province of Toamasina, in the Alaotra Mangoro region (Hervieu 1960). We observed a habituated group of indris (designated 3MZ) for a total of 143 h and 19 min, during 23 days of sampling activity, between October 10, 2011 and December 16, 2011. The group was composed of an adult breeding couple, a sub-adult male, and a juvenile. The male involved in the EPC was from a wild, non-habituated group (designated XMZ). We found group XMZ twice before the day of the EPC. This enabled us to identify its composition: an adult male, an adult female, and a juvenile (born in 2011). We carried out observations daily from 06:00 to 13:00 h, the most active period for indris (Pollock 1975a, b).

Behavioral observations

Behavioral data were collected by using the focal animal sampling method (Altmann 1974). Each day, each researcher followed a focal animal using a 30-s scan every 5 min and collected data on distance between the study subjects and on displayed behavior (additional data are provided in

Online Resource 1). We termed advertisement song the indris' song used for territorial announcement (Pollock 1986; Torti et al. 2010). We randomly chose focal animals, to enable equal sampling of all the individuals during the study period. We followed a group for a maximum of five consecutive days, according to its detectability. We conducted all-occurrences sampling (Altmann 1974) of selected behavior, for example aggressive interactions, geophagy, and marking.

For this research we had the research permit 2011 (no. 274/11/MEF/SG/DGF/DCB.SAP/SCB), from the Direction des Eaux et Forets, Antananarivo, Madagascar.

Results

Indri family groups occupy exclusive territories whose shape and extent is directly regulated through inter-group encounters at the boundaries of the territories. In 2010, 3MZ's home range size was 12.09 hectares (Torti 2013). In 2011, we observed a shift in group 3MZ's spatial distribution, with a loss of 2.66 hectares of the northwestern portion of the territory along the boundaries with group XMZ (unpublished data).

On December 7, at 8:00 am, group 3MZ was found in the eastern part of its territory (additional data are provided in Online Resource 2). We noticed sexual approaches between the resident adult male and the adult female of group 3MZ. When the male sexually approached, the female rejected and moved away using vertical clinging and leaping jump. During the day, the adult male was vigilant and kept a short distance from the female. Every time the female interacted with the sub-adult male the adult male moved towards them.

On December 12, the group moved toward the western portion of its territory and we saw the female making ano-genital (N = 8) and cheek marks (N = 11).

On December 13, at 9:00 am, we found the female outside the boundaries of 3MZ territory, alone in the territory of the neighboring group XMZ. The juvenile and the sub-adult male from 3MZ were in their own territory, approximately 50 m away from the female. Between 9:00 am and 9:40 am, the female changed her location to eat *Tavolo manitra* fruits and uttered kiss–wheeze vocalizations (Maretti et al. 2010) at 9:19 am and 9:21 am. At 9:40 am the female moved toward a *Menahihy* tree and began an advertisement song, the adult male of 3MZ (approx. 15 m away) participated in singing. The female was at rest until 9:53 am, then moved 15 m away to a *Hetatra* tree, where at 10:00 am the adult male of the group XMZ suddenly and rapidly reached her. This male immediately approached the female, first sitting just behind her on the same branch, and then mating with her. The female did not try to reject him, as she had previously rejected the adult male of her group. At 10:02 am the male XMZ stopped mating and moved. Immediately after, the female followed the XMZ male, but shortly after that we heard an advertisement song coming from XMZ's territory, and the female moved back in the direction of her own territory. The male of group XMZ sang together with the other members of group XMZ. We were not able to identify the other callers of group XMZ because the animals were far away and not visible and we continued to follow the female of group 3MZ. Immediately after hearing the neighbors' song, the adult male and the sub-adult male of group 3MZ started an advertisement song in their own territory, but the female did not participate. Of the 34 songs recorded in study period this was the only song that the female of group 3MZ did not take part in. Indeed, apart from this instance, we always observed the adult couple singing together. At 12:05 pm, the sub-adult of group 3MZ uttered roars and then the adult male and female of 3MZ simultaneously emitted an advertisement song. The sub-adult and the juvenile came closer to the female and the adult male, which had always been far from the group, stayed 20–30 m from

the female for the rest of the day. The female of group 3MZ made fewer ano-genital (N = 1) and cheek marks (N = 2) on December 13 than on the previous day.

On December 16, the amount of marking was comparable with that observed on December 13 (ano-genital N = 2, cheek marks N = 2).

Discussion

Our study reports an EPC in indri, which is a deviation from their usual pattern of social, territorial, spatial, and vocal behavior. The female, unusually, moved away from her offspring, entered the territory of a neighboring group and did not join her male singing when outside their occupied territory. The obligate monogamous breeding system of indris seems more flexible than expected from early studies, similar to that observed for gibbons (Palombit 1994a; Reichard 1995; Brockelman et al. 1998). The behavior of the adult male of group XMZ reflects the hypothesis of a mixed reproductive strategy in this species. Engaging in an EPC may produce benefits for both the female, in terms of selection of a fitter male, and for the male, in that he will sire more offspring (Fisher 1930; Zahavi 1975; Hamilton and Zuk 1982). When females are not fertilizable simultaneously (female estrus asynchrony), more mating partners are available for males during the breeding season (Matsumoto-Oda et al. 2007).

The male of group XMZ may also have engaged in EPC to maximize his reproductive success by copulating with a potentially receptive female. The adult female of group XMZ may have been unreceptive because she gave birth the year before, whereas the 3MZ female was 2 years postparturition and thus potentially receptive (Pollock 1975a, b).

On the other hand, females may copulate with extra-pair males because of their genetic quality, gaining indirect genotypic benefits from EPC, for example better genes and increased genetic variability of the offspring (Smith 1988; Lawler 2007). Females may also gain direct benefits, e.g. gaining tolerance of the neighboring male when defending his territory from intrusion (Barlow 1970) or increasing mate guarding by her own male (Kempenaers and Dhondt 1993).

The existence of EPC in indris may lead to re-assessment of the mating strategy of this species. We submit that EPC between individuals of different groups is potentially underestimated, because it is difficult to detect, and that researchers need to increase knowledge about the behavioral and genetic consequences of EPC.

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Behaviors	Short description
Feeding - Eating	Eating includes all the actions that animals make to take food. The food usually consist of leaves, flowers, fruits or other plant parts (Powzyk 1997). The animal can take the food directly with its mouth or it can use one or both hands to reach and take the food, normally sitting on a branch or hanging on a trunk.
Play	Solitary and social play. Solitary Play includes a number of different actions, such as running, jumping or wriggling. Sometimes the animal can interact with inanimate objects, like lianas. In social play two or more individuals play together in a chaotic and disorderly manner. They fight without a set pattern of sequences. During these actions they can produce vocalizations.
Allogrooming	An animal inspects the fur of a partner using its fingers or a toothcomb. The animal that is grooming sits while the target can assume different postures during the action. More than 2 individuals can participate in a grooming session, but individuals always start grooming actions alternatively: they keep a sequence in which they change the roles of groomer and groomed. Allogrooming can sometimes be associated with social play.
Scent mark - Neckband (cheek mark)	Animals scent-mark by rubbing their neck and the cheeks on horizontal and vertical substrates, with sebaceous glands located in the neckband region.
Scent mark - Anogenital mark	Animals scent-mark by rubbing their ano-genital region on horizontal and vertical substrates.
Vocalizations - Song	Males and females of the group participate in a chorusing song, mainly consisting of harmonic frequency modulated notes, usually introduced by three or four "roars". It plays a role in intergroup communication, proclaiming the occupation of a territory and transmitting cues for inter-group avoidance (Maretti et al. 2010; Powzyk and Thalmann 2003; Pol-

	lock 1975).
Vocalizations - Kiss	In response to disturbance indris react with calls of medium intensity. In stress-related contexts these vocalizations are often produced during a grunt bout or before a song. Kiss is often the first unit of the so-called "cri d'amour", followed by a wheeze (Maretti et al. 2010).
Vocalizations - Wheeze	Typically closely associated with a kiss, the wheeze is a rapid air expulsion blown through open lips. It is often emitted in competitive intragroup situations or in response to potentially dangerous or noxious stimuli and intruders (Maretti et al. 2010).
Vocalizations - Roar	Loud and harsh vocalization used as a standalone vocal signal in the presence of aerial predators (Maretti et al. 2010).
Locomotion - Vertical clinging and leaping	Progression along discontinuous supports, jumping from branch to branch, making contact with the hands and feet and maintaining a vertical position.
Reproductive behavior - Approach	Adult males become agitated and attempt the mount, almost disregarding aggression from the female.
Reproductive behavior - Reproduction	The male is standing on its legs, behind the female, introducing his penis in the vagina. The two animals are in mounting posture and pelvic thrusting is clearly visible.

ESM. 1. Description of the behaviors cited in the text, for the species *Indri indri*.

Fig.1 Home range of the indri group 3MZ. The Minimum Convex Polygon (MCP 100%), calculated on the totality of the waypoints collected in 2011, is shown in solid grey. Kernel density estimation (95%) is shown with a dotted line. The EPC waypoint was not included in home range size estimates because it was outside the territorial boundaries of group 3MZ.

Legend

● 2011 GPS waypoints

★ Extra Pair Copulation waypoint

-- Kernel 95%

MPC 100%

N

0   50   100   200 m