

Introduction

The study of primate behavior and social systems is very important, as they are a link to the evolutionary past of humans. Here, the behavior of the *Indri indri* will be examined. The aspects of their mating system, grouping patterns, kinship, dispersal, and social relationships as well as others will be discussed.

Taxonomy

Indri indri, commonly known as the indri, are in the order Primates, suborder Stepsirhini, infraorder Lemuriformes, and included in the family Indridae. (Quinn & Wilson 2002) This species is very unique, being the only genus to include *Indri indri*. Indris are located on the island of Madagascar, restricted only to the northeastern rainforests. They are in dispersed subpopulations from the Mangoro River to Sambava, not including the Masoala peninsula. (Glessner 2004) (Thalmann 1991) In Madagascar, *Indri indri* are the largest existing lemuriform primates. (Thalmann 1991)

Conservation

The IUCN Red List of Threatened Species lists the indris as an endangered species, facing a very high risk of extinction in the wild in the near future. (Ganzhorn 2000) With the presence of humans, indris are vulnerable to extinction. Humans pose many threats to the indris. These threats include habitat loss and degradation, and harvesting through hunting and gathering. (Ganzhorn 2000)

The dwindling population of indris can be based on the destruction of habitat. Humans take over the land with slash and burn agriculture and commercial logging. As a result, the amount of inhabitable rain forest is reduced. (Glessner 2004) This takes out many trees, a source of food in the indris' folivorous diet and downgrades the quality of the habitat.

Another main issue is the hunting of these species. Most tribes in the indri's areas are aware of the conservation of these species; even some consider hunting indris "taboo." (Thalmann 1991) It is those who are not native to the regions who hunt down these species. This is a result of the creation of paths through the indri's habitat. Paths and trails were created for easier access through the terrain; a consequence of this was that people believed that access to this area was permitted. (Thalmann 1991) Due to easier access, more people settled in the area. As time went passed, these trails were upgraded into a passable road, which puts stress on the habitat of the indris. (Thalmann 1991)

There are many solutions that can be accomplished to help conserve the indris. The simple act of educating the population would decrease many threats. Informing the public about the irreplaceable state of the rainforest can help further the conservation of this species. Another possible solution is protecting the land from commercial use. This can be executed by having patrols guarding the boundaries of the rain forests. These ways of conservation seem the most plausible.

An extreme form of conservation would be the translocation of close to extinct populations to suitable habitats. This would keep the indris in a protected environment. The only difficulty in this solution would be to find a location suitable for food and habitat sources. Another extreme form would be to raising indris in captivity. Those raised in captivity have resulted in poor outcomes, as seen in a Forest Station at Ivoloina, where only one individual has been able to be kept alive for more than a year. (Thalmann 1991)

Humans have posed a huge threat on the indris. Only with public information about the unique condition of the indris and its habitat will help with the major issues of conservation.

Spacing and Feeding

Many studies have focused on the size of home range in Indri indri. The size of home ranges has varied within different studies. According to a study by Glessner and Britt (2005), the estimated home range size is 27 ha. In study by Pollock (1979), home ranges averaged a size of 18 ha. Another researcher, Powzyk (2003), observed that the size was about 35-40 ha.

There are many reasons to why there is such a difference in home range size. Obvious reasons include forest destruction and other factors dealing with the disruption of habitats. Another reason could be due simply to the location. Differences in the altitude affect the growth and composition of the forest. (Glessner 2005) Different plants grow at different elevations. Due to different growths of plants, indris place themselves where food is most abundant. (Quinn 2002) Feeding is a major part of the indri's life, sometimes even defining home range territories. Feeding moves groups about 300-400 m a day traveling to find food sources. (Quinn 2002)

The diet of Indri indri is extremely folivorous. Majority of the food comprises of leaves, fruits, buds, and flowers from all levels of the canopy. (Quinn 2002) The diet is very high in young leaves; this seemed to be the predominant of all the food types throughout the year. (Britt 2002) Other foods were consumed depending on the season, more over the availability of young leaves.

During the transition of the seasons, rainfall is very low. The climate shifts from cool winter to hot summer, and vice versa. Thus, young leaves are not easily available and consumption of mature leaves increases. During the winter period, bark and fruit consumption is increased due to the reduction of young leaves. (Britt 2002) The transitions from winter to summer also show an increase in feeding of fruits, flowers, bark, and seeds. (Britt 2002) Dirt consumption was also observed in the indris. This coincides with the peak in mature leaf consumption; studies have found that eating dirt neutralizes chemicals in the digestive system. (Britt 2002) Indris are very selective, only choosing 3-4 species of certain leaves and fruits while other possible food sources are available. (Quinn 2002) With so much specificity in leaves, the indris devote much time to feeding.

Indris spend majority of their day feeding. Feeding totals between 8 and 16 hours a day. This takes up 41.1% of all activity. This is behind resting which takes up 44.9% (Britt 2002). Within this time spent for feeding, indris an average of 72.3% of its feeding time on young leaves, 16.4% on fruits, and 6.7% on flowers. (Powzyk 2003)

Indri indri has special adaptations for its folivorous diet. The alimentary tract is specialized for this animal. The stomach is large, caecum is elongated, and the intestine is uniform and lengthy, and the colon is capacious and compactly folded. (Quinn 2002)

Feeding is a main part of Indri indri lives. Majority of their day is spent feeding; with time devoted for finding specific foods. Feeding is so crucial that even the home range territories are determined by the food location.

Mating System

Most primates are polygynous; living with multiple mates. Yet, *Indri indri* is monogamous, living with a single partner. This is rare because monogamy is seldom observed among mammals. It is only found in about five percent of all species. (Dunbar 1988) There are many hypotheses on what determines the mating systems of a species.

Dunbar (1988) provided an explanation of the existence of mating systems, mostly about polygyny. His explanation describes whether or not a male could defend a large enough territory that surrounds the ranges of several females. These female ranges would have to be fairly small. This is difficult because dispersal of females could be due to many reasons, like predation and feeding competition. If the male could defend the territory, the males could support a polygynous system. (Dunbar 1988) Due to the costs to male indris, this is not the case.

Indri males would have to make the choice of having multiple female mates, or a large territory. The cost of having both would be energetically expensive. Males cannot defend a large territory and have multiple female mates. It would be difficult to monitor the females, most especially when scattered about. For instance, this would be very demanding to defend outside males from mating with females within the territory. In order for indris to have a large territory, it would benefit the male to be monogamous with a single female. (Dunbar 1988) (Kappeler 1997) There is much time and energy put in by the male, but the female also has her own share in costs.

Female indris bear the offspring, have to collect food, and have to care and nurture the offspring. Much energy is purely devoted for the offspring. Due to this expensive investment of breeding, it would be to the benefit of the female to have help in rearing the offspring. (Pollock 1979) The best mating system for this would be monogamy. The female then could have a male partner that would provide paternal care to the offspring, splitting the costs with the female, so that the offspring could be successful. (Dunbar 1988) There is also an advantage to this monogamous relationship to the male. The male would be able to help foster the development of the offspring and invest in the health of the adult female both for present and future offspring. (Pollock 1979)

Indri indri are monogamous primates. They live in exclusive families and are very territorial. One main reason why indris are monogamous is due to the dispersal of females at the cost of territory. It would be difficult for a male to defend many mates in a large area compared to one mate in a large area. The other main reason is that the costs of parenting are expensive. Having a monogamous relationship helps the female by having a mate that will not abandon her and that will help in rearing the offspring.

Grouping Patterns and Kinship

Group living is very important in *Indri indri*. Indris live in groups which consist of small families. Group sizes are primarily small, ranging from two to six individuals. These groups contain a reproducing adult male and female, and their offspring. (Pollock 1975) There are various benefits to this type of grouping pattern.

Group living is very advantageous. Primates and other animals form groups for protection against predators, defense of resources, efficiency of foraging, and improved care-giving opportunities. (Dunbar 1988) Indris mainly form groups for protection of food sources and extra parental help.

Indris are territorial animals. Indris have been seen to outline their boundaries by scent markings. (Pollock 1975) They can actively defend their area from invading groups, guarding such sources like food. Indris also use vocalizations or "songs" to ward away intruders. (Pollock 1975) Thus, by living in groups, there is an advantage for protection of their territories and resources. Group living also helps with the development of the offspring.

Due to small family groupings, there is much care that is devoted to the young, most specially, the infants. As mentioned previously, bearing offspring is extremely costly. The female spends an expensive amount of energy due to gestation and lactation. (Dunbar 1988) Living in groups provides extra care, primarily from the male parent, which helps split the cost with the female so that the offspring could be successful. (Dunbar 1988) Investment in offspring is extremely important to the indris.

Young indris are of high importance in the group. In fact, they are placed behind the adult females who are dominant. This can be observed in feeding. (Pollock 1977) Females and young are placed higher in the canopy. (Pollock 1977) The canopy contains the most leaves and is the most nutrient rich. The males are placed lower in the trees, which usually had less leaves. Females and young also had longer feeding periods compared to males. (Pollock 1977) Also in feeding, it has been observed that stealing food from an adult male or female by infants is allowed, but very rare among older offspring. (Pollock 1977) Young indri importance can also be seen within sleeping patterns.

Within indris, the group displays nocturnal group dispersion while sleeping. (Pollock 1977) Young indri infants sleep with their mother every night for the first year. The next youngest in line occasionally sleeps with the male. (Pollock 1977) During the second year, sleeping with the mother is reduced, eventually disappearing. (Pollock 1977) These behaviors show that the young of indri groups are very important.

Indris live in groups due to many advantageous reasons. These reasons include defense against invading groups, protection of food sources, and extra care due to the high costs of rearing offspring. The young of indris are placed of high importance, ranking behind of the dominant female. This can be seen within the feeding and sleeping patterns of the indris.

Dispersal

As previously mentioned, the species *Indri indri* live in small groups. The adults in these groups have a monogamous relationship. This type of mating system affects the dispersal of both sexes.

In monogamous, mating systems, both male and female offspring leave their natal home range, sometimes following aggression from the same sexed parent. (Kappeler 1997) There have been many hypotheses on why both sexes would disperse. Dispersal has many advantages: it helps species avoid inbreeding and helps to increase mating opportunities.

Since indris live in small family groups, there are not many opportunities to find a mate. Incestuous mating would not be advantageous. Dispersal decreases the chances of inbreeding within small family groups. Dispersal also helps increase mating chances. Since group numbers are small and inbreeding is disadvantageous it would be to the benefit of the indris to disperse to find other mates.

Social Relationships

Adult female indris dominate adult males. (Quinn 2002). There are many behaviors that were observed that show that females are dominant. This can be seen in grooming, feeding, and reproductive behaviors.

All indris participate in allogrooming. (Pollock 1979) Here, the roles of the groomer and the one being groomed can be reversed. Allogrooming helps groom body parts which cannot be clean on their own. These parts include the face, neck, ears, and back. Pollock (1979) observed that the subadult and adult males were the most frequent groomers. Whenever females groomed, it was very momentary, whereas the grooming time of the males were prolonged. Females only participated in reciprocal grooming; they only groomed when they wanted to be groomed in return. Besides grooming, female dominance in indris can be seen in situations of social displacement.

Again observed by Pollock (1979), agnostic behavior was seen between group members in a form of social displacement. Individuals were threatened and thus tried to avoid aggressive confrontations. Adult females would always displace the male adult. The adult male never displaced the adult female. In most reproductive acts, attempts to mate with an adult female by an adult male were rejected by the female acting with violent reactions. (Pollock 1979) Displacement is strongly seen in feeding behaviors.

In most primate groups, where there is food, there is always competition. In another study by Pollock (1977), adult indri females spent more time in the higher canopy compared to the adult males who spent more time in the lower canopy. When in trees the adult male would always be lower than the female. Females would have priority in the food bearing parts of the trees. (Pollock 1977) extraneous

This was a result due displacement of the adult male. (Pollock 1977) Females were observed to spend more time feeding than males. Females were also observed never to be displaced for food. Reasons for this feeding displacement could be due to the costs of offspring. As previously mentioned, offspring care is very expensive, most especially for females who need energy to nurse an infant. Female dominance in feeding would be highly advantageous when food is scarce. The pregnant or lactating female would be less nutritionally deprived than the male partner. (Pollock 1977)

Due to the behaviors of female indris in grooming, feeding, and reproductive situations, it can be seen that they are dominant over the adult males. Female displacement of males has been seen in these activities, where male displacing females is seldom observed.

Female Dominance

In many mammal groups, the male is dominant over the female. This dominance is also observed in most primate groups. Usually, sexual dimorphism is clear predictor of which sex is the dominant. In these types of systems, the sex with the larger body (male) is dominant over the smaller sex (female). Yet, in the species Indri indri, there is no obvious sexual dimorphism. Both adult males and female are typically the same size, sometimes difficult to distinguish. Which sex would be the dominant? In the indris, the female is dominant over the male. (Hemingway 1999) Why does female dominance exist in the indris? Surely there must be some sort of advantage to both sexes in why this dominance pattern exists.

There are three main arguments for the existence of female dominance. Males defer to females in order to conserve energy for male-

male competition that occurs during the breeding season. (Hrdy 1981) Male subordination could possibly be a form of paternal investment, giving resources to the female, which in turn help the male's offspring. (Pollock 1979) Another reason why female dominance exists could be due to a behavioral strategy that allows females to cope with high expenses of reproduction, as they have more at stake, in terms of fitness. (Jolly 1984) Female dominance can be seen as a male strategy.

During the reproductive season, there is much competition. Finding a mate is very difficult, as there are little opportunities. As mentioned before, this is due to the small family groups and dispersal patterns of the indris. Much time and energy is spent by the male, as finding a mate is difficult. In order to conserve energy, males could possibly give up their dominance to females in order to compete against other males during the breeding season. (Hrdy 1981) This male-male competition can drastically change behaviors.

Throughout the breeding season, males are aggressive towards other males. The indris demonstrate this aggression through singing. The male indris would actively sing to defend their mate against intruding males. (Pollock 1975) Males at this time would feed very little in order to remain alert and sing to protect their mate. (Pollock 1975) Male indris also use to scent markings to mark their territories. These marks also assist in deterring outside males. These types of behaviors require a great deal of energy and are associated with plenty of physical risks. Thus, for most of the year, in order for males to conserve energy, males would defer dominance to females. It is observed that allowing dominance to females could help males save costs during the breeding season; it can also benefit the offspring.

Males are not the only individuals that benefits from this dominance pattern. Males could defer dominance to allow females access to resources. These resources, such as food, help with the development of the offspring. This can be seen as a form of paternal investment, where it is to the advantage to the father. The male helps with the development of his young, and in the long run, invests in the health of the female both for present and future offspring. (Pollock 1979) As mentioned previously, parental investment is strong in the indris.

Indris take high importance in their offspring. A male indri would sacrifice his fitness for the sake of his offspring. As mentioned before, this can be observed in feeding situations where females and young are placed higher in the canopy, which contain the most nutritious leaves. Males are placed lower in the canopy which usually had less leaves. Even when males had the chance to eat preferred food items, the males ate less and fewer on average. (Hrdy 1981) An extreme case of paternal investment is observed during the dry season. The dry season yields less sources; food is scarce. The male would give priority to the female and the young. (Jolly 1984) Thus, subordination of males to females helps increase the fitness of the offspring by allowing females access to resources. The care of offspring is energetically costly; female dominance could also be a way for females to adapt to the great expense.

Raising offspring is energetically expensive; this is especially true in the indris. Female dominance is part of a behavioral strategy that allows females to manage the huge expense of reproduction. Females would be dominant over males because females have more at stake than

males, in terms of fitness. (Young 1990) There are many costs due to reproduction.

Indris, part of the Strepsirrhines, are less developed at birth compared to the Haplorhines. Indris, are altricial, in which the young are helpless at birth, requiring parental care for a period of time. (Jolly 1984) This care includes lactation and child carrying. These activities require a huge deal of energy. In fact, most energy is used in lactation, due to the feeding of a large, active baby. (Jolly 1984) Carrying a child by the fur is also energetically exhausting. Because of this, females need extra food during the period of pregnancy and lactation.

The gestation period of an indri female is about five months. (Jolly 1984) The same amount of time is devoted for weaning. During this time, the indris are nourishing their young during the dry season. This causes much stress to the females; they might be under pressure to synchronize reproduction with favorable environmental conditions. (Young 1990) Here, dominance can be seen as a behavioral response to energetic expense. Because the female requires much energy, the female would take dominance over the male. This in turn can be incorporated with the idea that female dominance is linked to the paternal investment of the males, to allow females to gain access to sources.

The idea of males deferring to females in order to conserve energy for male-male competition, during the breeding season is a likely possibility. This idea can be argued that males can compete year round to gain an aggressive edge over the other males. The most plausible idea of why female dominance exists would be for the benefit of the offspring. This can be a combination of both strategies used by the male and female. The male gives priority to sources for the well being of his offspring. The female gains dominance due to the expensive costs that are related to reproduction. These two ideas work hand in hand to benefit the male and female, most especially the young.

Conclusion

The species *Indri indri* is a unique primate in which some of their behaviors are uncommon compared to the rest of the primates. This can be observed within their mating system; being one of the few species to be monogamous. Their uniqueness can also be seen in a pattern of female dominance; they are part of a select few that displays this type of behavior. Because indris are part of the early primates, their behaviors can show insight into the understanding of humans.

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Format: MLA