Lemur Social Behavior and Primate Intelligence

The step from prosimian to monkey intelligence probably took place in a social context.

Alison Jolly

Primates are extraordinary among mammals for their complex social relations and their ingenuity in handling (or destroying) objects. The evolutionary trends which led to the excellence of *Homo sapiens* in these lines began long before the transition from ape to man.

All monkey species are social. Although individuals may be solitary for a time, a monkey is usually part of a group throughout his life. And when he is taken from his wild group and loosed in laboratory or house he unlatches doors, solves hardware puzzles (*1*), and carefully stuffs aquariums with brass lamps and shredded medical texts (*2*). He can even be trained to drive tractors (*3*), or show the rudiments of symbolic thought (*4*).

Some primates are not social, however, or even particularly clever. Three great modern branches diverged from each other during the Paleocene: the Old World monkeys, or Cercopithecoidea (which gave rise to apes and men); the New World monkeys, or Ceboidea; and the Prosimii (Fig. 1) (*5–7*). Many prosimians still live solitary lives (*8*), and none seem to manipulate laboratory tests like even the lowliest simian (*9*). In Madagascar, though, the prosimian Lemuroidea, unhampered by competition with true monkeys, have radiated to fill the ecological niches of monkeys and apes. I recently spent 11 months in Madagascar, mainly studying two social lemurs: *Lemur catta* (L. 1708), the ringtail (400 hours of observation), and *Propithecus verreauxi* (A. Grandidier, 1867), the great white sifaka (250 hours of observation) (*10*).

The work largely centered on a few troops in one place, a stretch of gallery forest by the Mandrary River. Troops even of the same species, at other seasons or in different forests, may behave differently (*11*). However, at the moment this one intensive study and the extensive pioneering survey of J. J. Petter and A. Petter-Rousseaux (*9, 12*) are all we know of lemur behavior in the wild. These studies at least reveal some of the possibilities of prosimian social organization.

I went to Madagascar with two main questions. How much do these lemur societies resemble the troops of other primates? And what bearing has primate social behavior on the evolution of intelligence? Since, in fact, the lemur troops seemed much like those of monkeys, the lemurs show that primate society could develop without the peculiar cleverness of our own ancestors.

Troop Structure

An infant monkey, unlike an infant tiger or beaver or gnu, is likely to remain for life in the troop of its birth. The result is a social group of all ages, with several adults of either sex. When too large the group divides into smaller troops of roughly similar composition. This sort of social structure is rare in nonprimate mammals (*13*), but about half the primate genera studied conform to the rule (*14*).

Both the genera of lemurs I studied in Madagascar shared the normal primate troop structure. They differ from each other, though, much as many genera of monkeys do.

Propithecus (Fig. 2) lived in small troops with a range of two to ten members and an average of four to five. The members of a troop followed each other in single file, silently soaring against the blue sky in great ballet leaps, propelled by their jumping hindlegs. Any member of the troop might lead, and they stopped in loose formation to feed with no fuss or bickering. There was no apparent dominance order outside the breeding season. The 13 troops I studied usually contained more than one male—in fact, adult males outnumbered females, averaging 2.4 per troop as compared to 1.7 adult females. [The only other primate among which such a sex ratio has been observed in several troops is the black lemur, *Lemur macaco macaco* (*8*).]

Each *Propithecus* troop defended a minute territory—0.26 square kilometer of the forest I studied. Geography was very important in their lives. They frequently scent-marked branches, and their most highly ritualized behavior was the territorial "battle," a kind of arboreal chess-game in which opposing knights hopped to strategic branches, occasionally landing back-to-back as each faced outward from his own territorial base. Of 40 animals I knew well, after a year 37 remained in the same troops, in the same territories. The three who died or disappeared were a very old male and two juveniles.

Propithecus babies were born in July and matured to semi-independent juveniles by the breeding season, which probably falls in February. They remained smaller than adults at least through the birth of the next year's young. Five such juveniles, which I left in September 1963, were still with their same troops on my return in March 1964, though by now they seemed fully adult. I suspect, however, that they may not usually breed until 2½ years of age, because only half the females I knew gave birth in 1963 and because the smaller *Lemur catta* breeds at 2½ years.

It seems clear that at least these *Propithecus verreauxi* troops were as stable as those of other primates, with the typical sort of primate structure. Troops of *Lemur catta* had quite a different allure: 12 to 24 animals tumbled through the trees, grunting and clicking, or sauntered along the ground with their ringed tails in the air (Figs. 3 and 4). The three troops I studied in 1963 averaged six adult males and six adult females each. In Troop 1, the only one in which I knew individuals, most of the adults were the same in 1963 and 1964, though

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the dominant male died or disappeared. At least seven of the nine adult females bore infants in 1963, with birth probably occurring only in September. During the mating season in April 1964, the seven young chased and played as independent 7-month juveniles. Two nonbreeding animals, one male and one female, could be distinguished by their small genitalia and were presumably 19-month-old subadults. They would then breed the following year, at the age of 31 months. [If this is true, it contrasts with a captive female *Lemur macaco*, which mated at 1½ years and gave birth at 2 years of age (*15*)].

We do not know how widespread this type of society is among lemurs. Several genera of Lemuroidea are solitary, others form pairs. However, *Lemur* and *Propithecus* belong to two different families, the Lemuridae and Indriidae, so it is significant that these two have each arrived at the usual primate kind of troop structure.

Cohesive Forces

Two strong cohesive forces in many primate troops are attraction to infants and the "friendly behavior" of contact, grooming, and play (*16, 17*). Friendly behavior may even be related to mother-infant attachment, because it includes the gestures of maternal care and because we see in it the mother-infant emotions of trust, dependence, and solicitude. What role had such behavior among the lemurs?

Lemurs' grooming differs in form from that of monkeys. Monkeys, even primitive Ceboidea, part the fur with both hands, then pick out particles with hand or mouth (*18*). The Lemuroidea (and Lorisoidea) tooth-scrape instead. Their lower incisors and canines are narrow and procumbent, much like the teeth of a comb. They lick and scrape their own and each other's fur, using repeated upward sweeps of the head. Occasionally *Propithecus* chiselled *Albizzia* seeds from the pod with their tooth-scraper, but otherwise they used it only for grooming. It seems a peculiarly specialized structure, but a "well-grooming" lemur probably had great selective advantage, once tooth-scraping took on social significance (*19*).

Although the form differs, lemur grooming has similar frequency and functions to grooming among higher primates.

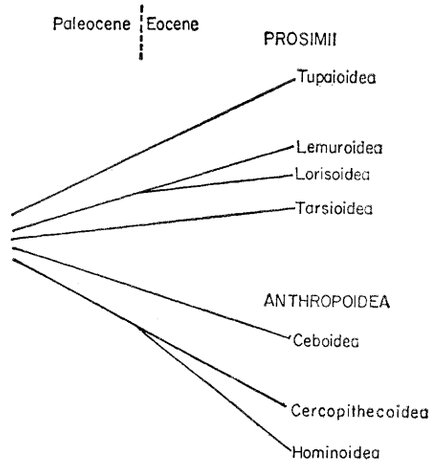

Fig. 1. Primate phylogeny (*6*).

Propithecus initiated friendly behavior (contact, grooming, or play) only 0.6 time per hour of observation, in troops of about five animals. A bout once started, however, often lasted 20 minutes. One animal would leap beside another and seize the second's nose in its long, curved hand. The second one, if it wished to be groomed, extended its neck, so the first could tooth-scrape under the jaw, or bent down to be groomed on the occiput. Then both would groom, alternating at intervals of 10 seconds or 1 minute, or both heads moved at once like reciprocating pistons. Often the bout ended with wrestling, as each struggled to groom the other's genitalia. They would sit facing each other in a slow-motion flailing of arms and legs, then seize each other's ankles with their great toes and bicycle round and round.

Unlike baboons and macaques, the uncompetitive *Propithecus* never really tried to gain advantage. When one grew tired of the play, he would spring away, and the other returned to feeding.

In *Lemur catta* troops, I observed about two friendly interactions per hour, with perhaps ten animals visible at a time. Their bouts of grooming were shorter, though again mutual and reciprocal. Their play was much rougher, in keeping with their irascible temperament. The favorite game was jump-on-and-wrestle, in which one animal would leap, hard, on top of another, preferably on a springy branch or sapling. The advantage lay with the jumper, because he used all four hands and feet to pull fur, while the one beneath needed at least one hand to hold them both on the branch.

Although friendly behavior has appeared by parallel evolution in nearly all groups of social mammals, it is far more important in the primates (*13*). Primates, including these social lemurs, groom in greeting, in pacification, in sexual overtures, in mother-infant relations, in juvenile relations, when waking up, and when settling to sleep. Even adults play—adult male *Propithecus* groom and play with each other as much as with females. Just as in monkeys, one is tempted to interpret these friendly relations as the "social cement" of the group.

Newborn infants of both kinds of lemur attracted much attention. *Propithecus*' friendly behavior was four times as frequent after the babies were born, for every member of the troop crowded near, attempting to groom the young. The mother, during the first day or two, sat apart from the others, but later simply boxed her great jumping thighs round her infant. The troop then fell to grooming her instead, or one would distract her by grooming while others tried to reach the baby. Again, the males were as doting as the females. The first time I saw a mother relinquish her baby for 5 minutes, she hopped off to feed while her 2-week-old infant clung to the belly of a battle-scarred male.

Lemur catta males, on the other hand, ignored infants. Females and juveniles crowded round, but the mother cuffed them or shoved the others away with her nose. Only other mothers were privileged to groom a new infant, while allowing their own to be groomed. In spite of this, since most *L. catta* females in a troop gave birth together, there were always many available "aunts" (*20*).

These differences between the two lemurs seem little greater than differences between various monkeys. The lemurs again fall in the usual spectrum of primate behavior.

Sexual Behavior

Monkeys were originally thought to breed all year round, but many actually have a breeding peak or season (*21*). Prosimians, including the lemurs (though perhaps not tree shrews), breed seasonally (*7, 12, 22*).

Propithecus verreauxi and *Lemur catta* each had an extremely short mating season—probably only 2 weeks long for *L. catta* in the area I studied (*23*). Their births were similarly

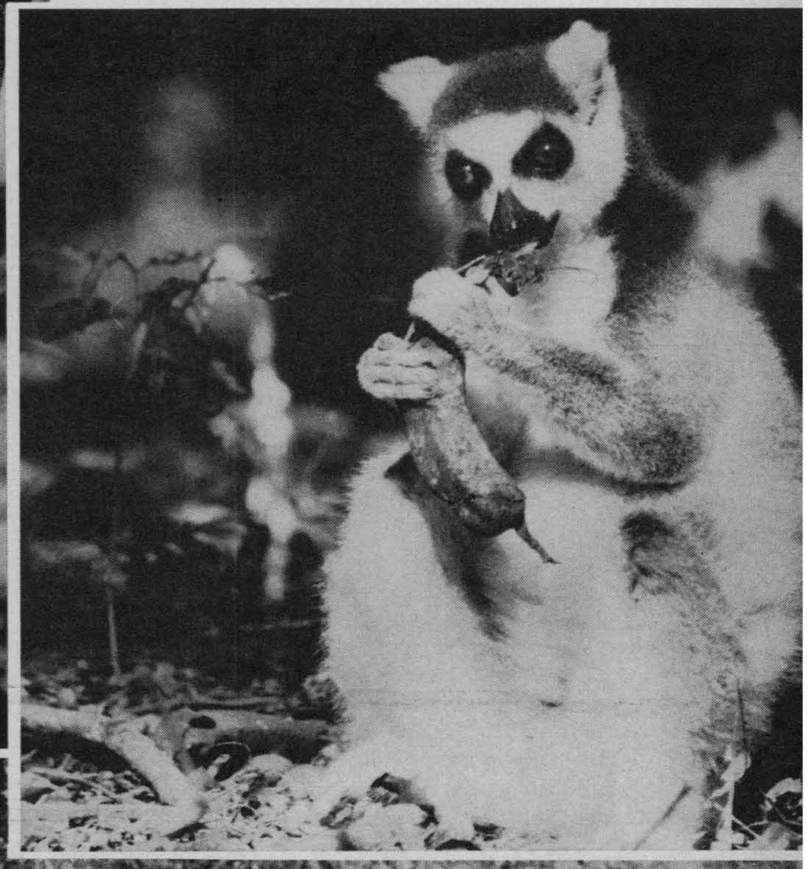

Fig. 2 (left). *Propithecus verreauxi verreauxi.* Fig. 3 (below). *Lemur catta* eating a fermented tamarind pod. Fig. 4 (bottom of page). Lemurs from Troop 1. [Photographs by C. H. F. Rowell]

concentrated, in July for *P. verreauxi* and in September for *L. catta*. Before mating, *L. catta* males of Troop 1 fought, raking each other's limbs and flanks with gashes as much as 10 centimeters long, though none suffered permanent injury. *P. verreauxi* are said to fight as well, with blood streaming down their white fur (*24*).

Here, these social lemurs appear at the extreme end of the primate spectrum: their annual mating season is probably one of the shortest in mammals and is almost certainly the shortest in primates (*25*). Mating causes maximum disruption of the social order. Nevertheless, as in other primates, troop compositions remained unchanged.

To sum up, the lemurs, like many monkeys, form troops composed of all ages and both sexes, which is unusual among nonprimate mammals. They have the cohesive bonds of contact, grooming, social play, and troop attraction to infants, although the actual grooming gesture of lemurs is different from that of monkeys. The lemurs' compressed sexual season is different from anything known in monkeys, but monkey genera also differ widely from each other in length of season. Therefore, in social behavior, as in anatomy, it seems reasonable to say that lemurs are generally primate in structure, though with their own peculiarities.

Thus, the lemurs seem to have "monkey-type" societies without having evolved monkey-level intelligence.

Uses of Intelligence

What does one mean by monkey-level intelligence? One usually means an ability to solve problems with objects, under controlled laboratory conditions. This is a limitation of history and technique. In fact, whenever a psychologist tests learning, it is of inanimate objects: symbols on the alleys of a maze, plaques covering food-wells, hardware toys or sticks and boxes. Whether the aim is "learning" or "insight," whether the reward is food, sight of another monkey, or just the chance to play, intelligence is measured in relation to gadgetry.

This use of intelligence is our own forte, but not the monkey's. Zimmerman and Torrey ruefully remark, "For example, a monkey that may require lengthy pre-training and adaptation to an apparatus as well as 20 to 100 trials to solve one two-choice object-discrimination problem will, in a matter of seconds, or, at most, minutes, become thoroughly adapted to a particular dominance status when introduced for the first time to a social situation with three or four cagemates (*26*). Or, as Washburn *et al.* conclude, "learning is not a generalized ability; animals are able to learn some things with great ease and others only with the greatest difficulty. Learning is . . . the process of acquiring skills and attitudes that are of evolutionary significance to a species when living in the environment to which it is adapted" (*11*).

There are three main uses of learning or insight in the wild: toward objects, including food; toward other active species, including predators; and toward fellow members of one's own species. It is clear that the speed and subtlety of primate learning differs in these three contexts.

Social Uses of Learning

Monkeys, more than any other mammals except their descendants, the apes and men, learn to be social. A rhesus raised in isolation from its kind may not mate normally or rear its own young (*27*). Primates have a long youth, compared to mammals of their size, and during this period, through association, exploration and play, the juveniles learn the ways of the troop (*16*). It is even possible that primates exploit the full capacity of their brain only during youth. Man, after all, accomplishes the gigantic feat of learning to speak, and may never again face such a daunting intellectual task (*28*).

Social lemurs also learn much about their fellows. A lemur must learn the rank and idiosyncrasies of all troop members. They share the primate character of long youth: a 3- to 5-month gestation (even in the mouse-sized *Microcebus*), one young, or at most twins, each year, 1½ years to full growth, and, in the groups I studied, possibly 2½ years to first breeding. Hand-raised *Lemur macaco* may be strongly imprinted on humans, to the extent of never acquiring the full grooming patterns.

We have unfortunately few measures of the complexity of learned social relations in adult monkeys. Altmann has attempted stochastic analysis of chains of rhesus interactions (*29*). However, such quantitative methods become really useful only when the completeness and accuracy of observation and the complexity of the computer program outdo the monkeys' own powers of observation and memory. Most field primatologists have not yet achieved this.

At present one is limited to making qualitative comparisons. In general, the organization of *Lemur catta* troops seems as complex as that of the troops of many monkeys. In Troop 1 there was a linear dominance order among the five males, and long chains of interactions: approaches, spats, stink-fights, redirected aggression. The males did not, however, have a "central hierarchy" (*17*) of friends who would support each other. Also, most single interactions could be considered as involving only two animals at a time. I did not see "protected threat," in which an inferior, say male No. 3, challenges a superior, No. 2, while standing directly in front of No. 1, so that No. 2 cannot attack No. 3 without seeming to challenge No. 1 (*30*).

After further study, it may be possible to say categorically that such subtle behavior does exist or that it never exists among lemurs. When more primate species have been studied, it may also be clear whether such interactions are common to most monkeys, or only to the active, argumentative rhesus and baboons. Therefore, though we know that lemurs, like other primates, learn much of their social behavior, we have no scale by which to compare their relative sophistication.

In summary, the social use of intelligence is of crucial importance to all social primates. As the young develop, they depend on the troop for protection and for instruction in their role in life. Since their dependence on the troop both demands social learning and makes it possible, social integration and intelligence probably evolved together, reinforcing each other in an ever-increasing spiral. And, although it is very likely that the learned social relations of monkeys are in fact more complex than those of lemurs, our present techniques of description emphasize the similarity between lemur and monkey social interactions.

Andrew (*31*) pointed out that the mammals of both America and Afro-Asia, have, as a whole, increased in brain size since the Eocene. He suggested that the increase was due to interaction between species: as prey species grew cleverer, their predators

and competitors survived only by also becoming cleverer, and vice versa. The mechanism works best with a large number of species and close competition: mammalian intelligence evolved faster and farther on the large, interconnecting continents than on Australia or Madagascar.

Most primate species ignore each other when they meet, even while feeding in the same tree. Occasionally, one group chases another (*32*). *Lemur catta* actively teased the peaceful *Propithecus*, and investigated such varied primates as *Lepilemur* and *Dr. C. H. F. Rowell*. One can only speculate whether such behavior might help disperse related genera (*33*).

Few primates eat meat, except for insects. Both baboons (*11*) and chimpanzees (*34*) sometimes hunt to kill, but it seems unlikely that carnivorous habits played much part in primate evolution, outside the hominid line.

Predation, however, is a major factor, evoking social defensive behavior in primates ranging from howlers to gorillas (*32, 35*).

A primate learns from his troop what to fear—not from innate recognition patterns, nor by himself narrowly escaping from every foe. Whether his enemy is a wriggling snake or the menace inside a Land Rover (*16*), he takes his cue from others of his own species, as much as or more than from the predator's behavior.

Lemurs gather round to mob carnivores, *Propithecus* hiccuping "sifak, sifak," and *Lemur catta* yapping like terriers. However, when a hawk flies past, lemurs compulsively roar or scream. If the lemurs' response to hawks should be innate, one may see here a truly primitive mechanism. Again, though, there is no scale by which to compare the lemurs' responses with those of other primates, though Andrew's hypothesis remains the most reasonable evolutionary explanation of the difference in "general" intelligence.

Learning and Objects

Finally, there is intelligence with respect to objects. Much rigorous and skillful testing has shown that monkeys do not necessarily surpass other mammals in the ability to learn simple discriminations. Instead, rhesus monkeys excel in their ability to transfer learning from one problem to the next: they rapidly form learning sets, accept reversal tests, and so forth (*36*). At least one genius rhesus succeeded in elevating this capacity to learning a "symbol"—circle means blue (*4*)—and *Cebus* monkeys, like chimpanzees, can use tools (*37*).

There have been two great gaps in this sort of study, though—the capacities observed are rarely considered either in relation to object manipulation in the wild or to social behavior.

In the wild, it is unusual to see the sort of intelligence toward objects one can demonstrate in captivity (*38*). Not even Goodall's (*34*) tool-making wild chimpanzees approach the ingenuity of Kohler's (*39*) or Shiller's captives (*40*), Hayes's cake-baking ape (*41*), or the creative mania of Morris' chimpanzee artists with their poster-paints (*42*). At a far lower level, *Lemur* in captivity actively played with new objects (*9*), whereas in the wild they apparently never manipulated inedible objects.

There are two related aspects to learning about objects: willingness to pay attention to the object in the first place, and learning capacity proper. Obviously, the capacity is there in the wild primates, or they could not show it when brought into the laboratory. On the other hand, it is the circumstances of the experiment which direct their attention to objects. There seems to be almost an excess capacity for learning about objects, possibly developed as a by-product of the all-important ability for social learning.

When primates do learn about objects, it is rarely a "discovery," but more commonly social "imitation" (*38, 43*). (How far would most human discoverers go without first having learned from their predecessors?). In the laboratory, when a normal primate has the choice of responding to a social cue or to objects, he turns first to the social cue. During early insight tests, primates from lemur (*37*) to chimpanzee (*44*) would beg from the experimenter before attempting to solve a new problem (in fact, a quite accurate assessment of the real relationships of the situation).

In the wild, preference for social cues is even clearer. The Japanese workers have repeatedly shown that wild macaques learn object relations from each other. Generally, playful juveniles "discover" a new food or action, then the rest of the troop gradually learns by imitating those animals with whom they have close social ties. One might have predicted this for very complicated actions such as washing sweet potatoes or placer mining for wheat. However, tasting and eating a new food must be the most straightforward case. In this situation one would expect any animal to form its own learning set, yet even this is mediated through social channels (*38, 43, 45*).

This emphasizes the whole question of the relation of "intellectual" skills to social learning in the individual. Harlow kept rhesus without any social contact for the first 6 or 12 months of life. Though these animals later failed to make any effective social contacts, they were able to solve an extensive battery of "learning problems" nearly as well as the control monkeys (*46*). If the uses of learning are really so compartmentalized, this is a fascinating discovery. One hopes that either the Yerkes or the Wisconsin primate laboratories might re-examine their huge bodies of data and sum up longitudinal profiles of social and object learning in individual animals rather than just the cross-sectional results of separate experiments.

To return to the lemurs, *Propithecus* and *Lemur*, like other prosimians, fail miserably on tests of monkey "intelligence." Here, at least, there are standard scales of comparison, though one must take account of lemurs' preference for manipulating with their mouths, not their hands. On the whole range of tests that have been tried, from object discrimination and delayed response to "insight" problems of opening boxes and pulling strings, the lemurs fall below other primates, even the primitive New World marmosets (*9, 31*).

This is, in part at least, a failure to direct their attention to the relevant cues (*31*), which, in turn, is related to their willingness to manipulate objects at all. In the laboratory, lemurs may actively play. As with other primates, though, the attention is greatly modified by the social situation. A tamed *Lemur* often accepts a toy it would otherwise ignore, when the toy is offered by a human friend. On the other hand, when five caged groups of *Lemur* were given a hasp-and-pin puzzle (*1*), four groups of two to three animals repeatedly opened the puzzle, whereas the fifth did not touch it. This fifth group consisted of two males and two females in a large cage, who had formed a sort of "troop" with well-differentiated social roles and who indulged in much social and locomotor

play. This laboratory "troop" may have approached the situation of wild troops observed by Petter (*8*) and by myself, where there was much social play, and locomotor play in springy branches, yet the lemurs were never seen to manipulate or investigate an object other than food.

The lemurs, then, clearly lack much capacity to learn about objects, and it takes the extraordinary situation of captivity to turn their attention to objects. Yet they have evolved the basic characteristics of primate society, including relatively long youth and probably a fairly large dependence on social learning.

Primate society, thus, could develop without the object-learning capacity or manipulative ingenuity of monkeys. This manipulative, object cleverness, however, evolved only in the context of primate social life. Therefore, I would argue that some social life preceded, and determined the nature of, primate intelligence.

Summary and Conclusion

Our human intellect has resulted from an enormous leap in capacity above the level of monkeys and apes. Earlier, though, Old and New World monkeys' intelligence outdistanced that of other mammals, including the prosimian primates. This first great advance in intelligence probably was selected through interspecific competition on the large continents. However, even at this early stage, primate social life provided the evolutionary context of primate intelligence.

Two arguments support this conclusion. One is ontogenetic: modern monkeys learn so much of their social behavior, and learn their behavior toward food and toward other species through social example. The second is phylogenetic: some prosimians, the social lemurs, have evolved the usual primate type of society and social learning without the capacity to manipulate objects as monkeys do. It thus seems likely that the rudiments of primate society preceded the growth of primate intelligence, made it possible, and determined its nature.

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