Primate Behaviour, Ecology and Conservation

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INTRODUCTION

Aim: This one-day course will introduce the student to primates and to some basic principles that govern primate evolution, ecology, and social organization. Major topics covered in the lecture will be illustrated with observations on and experiments with free-living monkeys in the Udawattakele Sanctuary in Kandy.

Why Study Primates? Man is a primate. We know this from every detail of our physical form, from our fingernails to our blunt big toes, and in the colours we see with our eyes. The evidence for our close kinship to non-human primates (the monkeys and apes) is overwhelming, and lies not only in our anatomy, but also in our physiology, biochemistry, genetics, and even some behaviors. Zoologists, therefore, have classed man in the 'Primate Order' along with monkeys and apes.

The interest in our primate relatives rests largely on our affinity to them. Rightly or wrongly, the development of many of our modern drugs and medical treatments was possible only because nonhuman primates served as experimental models of the human condition. On a more critical level, primates are of heuristic interest because by studying them, we can reconstruct our human ancestry and better understand ourselves. Such study goes beyond primate fossils to include living forms. Primates living in their natural habitats today represent life forms that have successfully survived millions of years of environmental changes and challenges.

The more urgent question in primate evolution is not what it reveals about the past. The real question is: What happens in the future? Studies of primates provide knowledge concerning our human limitations and potentials for surviving in a modern world where man's activity is destroying natural environments and other life forms at a rate of such great magnitude that it is unprecedented in the earth's known history. We are creating an impoverished and vulnerable world, quite alien to that of even 100

years ago. The message is: we must come to terms with ourselves as a biological entity, and our place in this world, lest we too follow the way of the dinosaurs.

PRIMATES AND THEIR HISTORY

Primates belong to the class of vertebra te animals known as mammals, which are distinguished from other vertebrate classes; the birds, reptiles, fish, and amphibians. Mammals typically have fur covering their skin, are warm -blooded, bear their young in the womb, and feed their young with milk f rom breasts or 'mammae' (hence the word 'mammal').

Palaeontologists have shown that the first mammal -like creatures (Pantotheres) evolved from therapsid reptiles during the Jurassic Period, about 150 million years ago, a time when reptiles, including large dinosaurs, dominated the earth's landscapes (Figure 1).

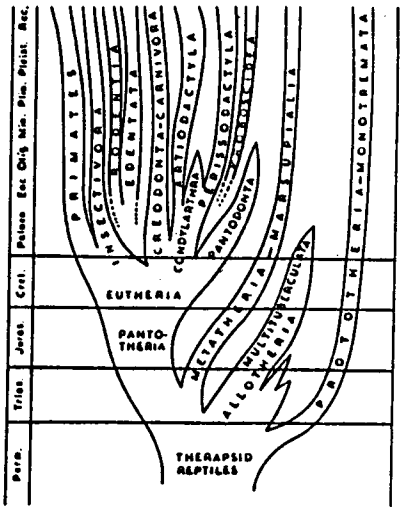

Fig 1. Schema showing the progressive differentiation of the Orders of Mammals during the Mesozoic and Tertiary epochs. The geological subdivisions of these epochs are shown on the left.

The 'Age of Reptiles' came to an end with the extinction of dinosaurs between 60 and 120 million years ago. At this time the ancestral stock (Eutheria) to modern mammals were represented by small, primitive and mostly nocturnal creatures. The extinction of the reptiles afforded these early mammals the opportunity to vastly expand their geographical ranges and lifestyles into habitats formerly dominated by reptiles. Thus, by about 40 to 60 million years ago (Oligocene to Paleocene) these mammals had evolved into several different types that were ancestral to the modern mammalian orders such as the Insectivores (shrews), Artiodactyles (deer, buffalo), Perissodactyles (horses, tapirs), Probiscidea (elephants), Rodents (rats, mice, squirrels), Carnivores

(leopards, jackals), and Primates. Some early mammalian orders also became extinct (Pantodonta).

The first ancestral primates appeared in the fossil record about 50 million years ago as small, primitive nocturnal mammals with arboreal habits and having a well-developed sense of smell, creatures closely resembling modern tree-shrews (Figure 2).

These early creatures gave rise to the main stocks of modern primates as well as to man (Figure 1). The ancestors to Old World monkeys (family Cercopithecidae) appeared first in northern Africa about 18 million years ago. They were well-differentiated into either macaque-like or langur-like by about 15 million years ago(middle Miocene). In this same period, the ancestor common to both apes and man (Dryopithecus) was also roaming northern Africa. African ape and human-like ape (hominid) stocks were distinct by about 6-15 million years ago. But modern humans had not evolved until about 1-2 million years ago.

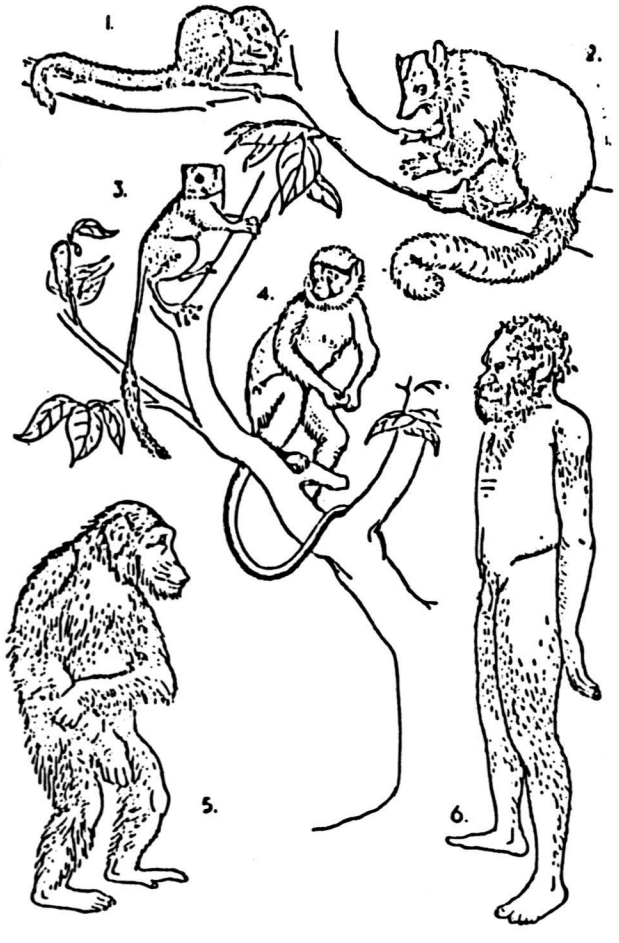

Fig 2. Some of the living members of the Order Primates, representing a graded series which, broadly speaking, links man anatomically with some of the most conservative of placental mammals .(1) Tree-shrew, (2) Lemur; (3) Tarsier; (4) Vervet monkey; (5) Chimpanzee; (6) Australian Aboriginal.

PRIMATE PHYLOGENY

As an order of the mammals there is no single anatomical character that typifies all primates. Instead, primates are distinguished as a group by a set of common evolutionary trends (Table 1). If there is an essence of being a primate, it is the progressive evolution of intelligence as a way of life.

Table 1. Primate evolutionary trends

1. Preservation of a generalized structure of the limbs with a primitive pentadactyl (5 digits on hands and feet) and the retention of certain features such as the clavicle (collar bone) which tend to be reduced or disappear in other mammalian orders.
2. Freely movable digits (fingers) and an opposable thumb (and big toe) for grasping and climbing trees.
3. Development of flat nails on the fingers and toes and sensitive tactile pads on the digits.
4. Abbreviation of the snout or muzzle.
5. Elaboration of visual acuity, color vision, and binocular vision for depth perception.
6. Reduction of the sense of smell.
7. Loss of certain primitive mammalian teeth (e.g., wisdom teeth) and preservation of simple cusp pattern of molar teeth.
8. Elaboration of the cerebral cortex of the brain.

Zoologists classify animals into categories based on similarities. Degrees of genetic affinity between existing (and also fossil) forms are determined by noting degrees of resemblance in anatomical details. The most elementary unit in this classification is the 'species'. The anatomical details between animals of the same species will be identical. Also, under natural conditions, animals will breed only with those of their own species. The next category of classification is referred to as the 'genus' and it takes into account that different species may be very similar (but not identical) in form. For example, all macaque monkeys belong to the genus *Macaca.* The genus is subdivided into 16 different species, of which the Sri Lankan macaque (or toque macaque) is labeled as *Macaca sinica.* The South Indian Bonnet macaque, which is related to the Sri Lankan one, is known as *Macaca radiata.* All macaques belong to the family Cercopithecidae, which includes the African baboons (genus *Papio*), vervet monkeys (genus *Cercopithecus*), and mangabeys (genus *Cercocebus*). A classification of the primates is given in Figure 3.

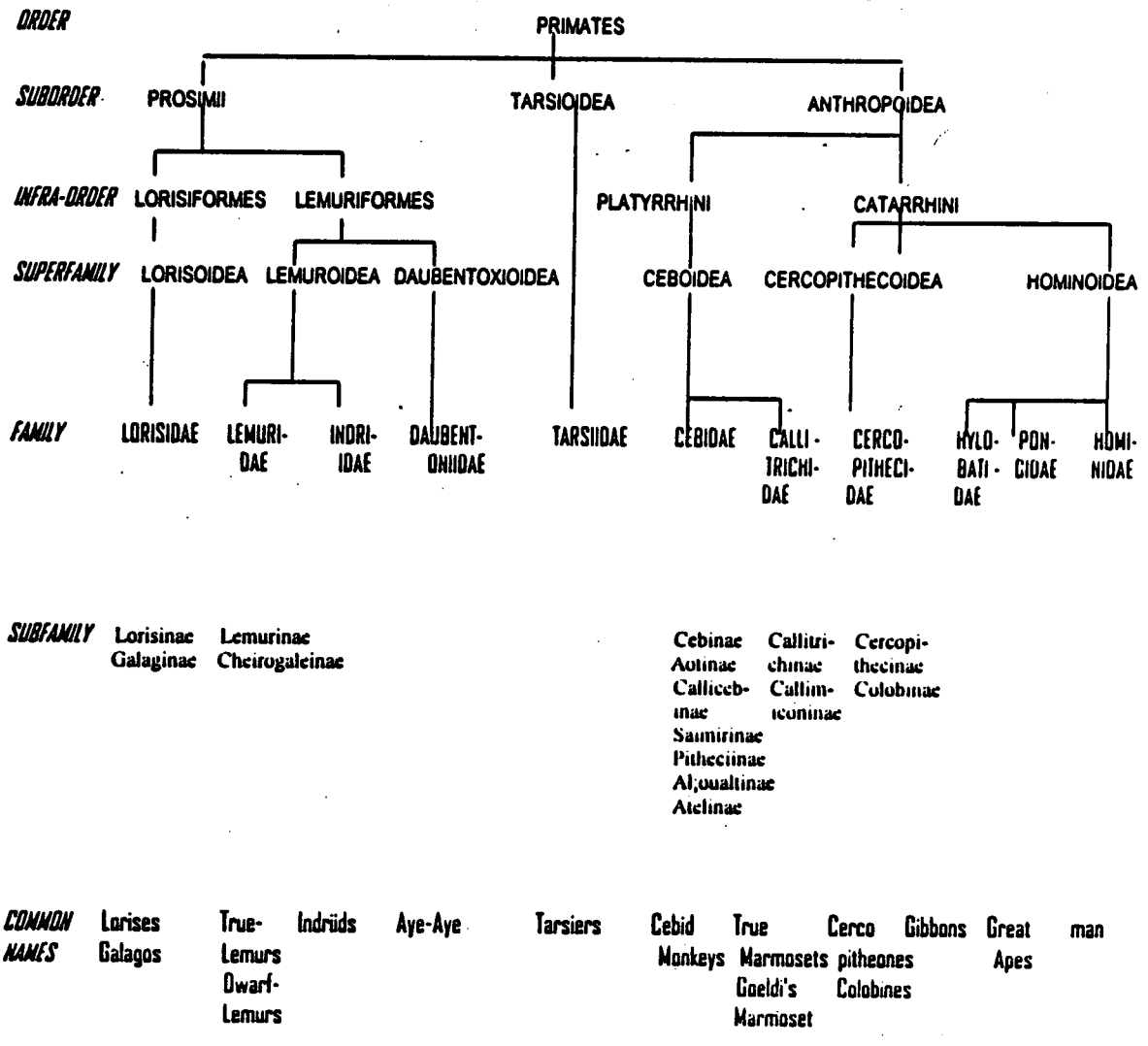

Figure 3. Classification of living primates.

PRIMATES OF SRI LANKA

For its size, Sri Lanka has a remarkably diverse fauna of primates. As with other plants and animals of Sri Lanka, the primates too are most closely related to those of southern India. Unlike in India, however, there are no apes in Sri Lanka. Table 2 gives a classification of Sri Lankan primates. Of the four species of primates, two – *Semnopithecus vetelus* and *Macaca sinica* -- are endemic species to Sri Lanka (found

only in Sri Lanka). The gray langur has the most restricted geographical distribution in Sri Lanka and is represented by only one subspecies. All the other species have at least three subspecies each and these subspecies correspond to the three major climatic zones; the lowland wet zone, the lowland dry zone, and the montane zone. In the lowland wet zone, the purple-faced langur has two different subspecies that are separated by a major river, the Kalu Ganga.

Table 2. Classification of living primates of Sri Lanka

ORDER PRIMATES
- SUBORDER I. PROSIMII
  - A. FAMILY LORISIDAE
    - *Loris tardigradus* (Slender loris)
      - a) *L. t. tardigradus* (lowland dry zone)
      - b) *L.t. grandis* (lowland and midland wet zone)
      - c) *L.t. nordicus* (northern dry zone)
      - d) *L.t. nycticeboides* (highland wet zone)
- SUBORDER II. ANTHROPOIDEA
  - A. FAMILY CERCOPITHECIDAE
    - SUBFAMILY 1. COLOBINAE
      1. *Semnopithecus entellus* (Gray langur)
         - a) *S.e. thersites* (dry and intermediate zones)
      2. *Semnopithecus vetelus* (Purple-faced langur)
         - a) *S. v. senex* (northern dry zone)
         - b) *S. v. vetulus* (lowland and midland wet zone south of Kalu Ganga)
         - c) S. v. *nestor* (lowland wet zone, north of Kalu Ganga)
         - d) *S. v. monticola* (montane wet zone)
    - SUBFAMILY 2. CERCOPITHECINAE
      1. *Macaca sinica* (Toque macaque)
         - a) *M.s. sinica* (dry and intermediate zones)
         - b) *M.s. aurifrons* (lowland and midland wet zones)
         - c) *M.s. opisthomelas* (montane wet zone)
  - B. FAMILY HOMINIDAE
    1. *Homo sapiens* (Man) (recent immigrant)

Members of the same subspecies share similar morphological traits that are adaptations to a local habitat type (such as rainforest) and they differ from the traits of subspecies living in contrasting habitats (such as dry forest). Members of different subspecies are capable of interbreeding because they belong to the same species. However, they rarely do so because of the geographical barriers separating subspecies. The formation of subspecies is usually the beginning stage in the evolution of a new and separate species.

PRIMATE ECOLOGY

Ecologists study the way in which animals interact with their physical and biotic (plant and animal) environment. Such studies indicate the kinds of food that a species eats, the predators it is vulnerable to, and its climatic tolerances and means of coping with climatic extremes. All of these aspects are influenced by the morphological attributes and behaviours of a species.

Ecological Niches

Surviving is a daily challenge for most animals. It involved finding food, eating and digesting it, locating mates and caring for the young, avoiding predators, and coping with the extremes of weather and climate. Each animal species is an expert for 'earning a living' in its own specialized way in a particular environment. These specializations involve both its anatomical structures that serve as 'tools' and its behaviours that guide the animal in the proper use of the tools. For example, the teeth and guts for eating a diet of leaves differ from those used for eating primarily insects or fruit. Likewise, leaf-eating monkey species behave differently from those whose main diet consists of fruit.

These specializations in anatomy and behaviour are accompanied by constraints in the kinds of environmental resources that a species is best capable of using. For example, a leaf-eating monkey, with its leaf-cutting teeth and large gut for processing leaves, would make a poor predator. A cat's specialized limbs, teeth, gut, and stalking behaviours are much better suited for hunting and a carnivorous (meat-eating) way of life (and of course it cannot survive by eating leaves).

The particular array of environmental resources that a species exploits in its specialized way of life is referred to as its ecological niche. Ecologists have found that each species has its own particular niche. That is to say, two or more species cannot occupy the same niche in the same habitat. This situation results from the fact that only one species is likely to be the most 'expert' in a particular niche. Less expert ones, having been unable to compete in an environment with limited resources, have either died out or have changed their life-style and so their niche. Ecologists refer to this fact as the Principle of Competitive Exclusion. In other words this means that species which are complete competitors cannot co-exist.

Specialists and Generalists

Species differ in the degree of specialization to their particular niche. One of the most specialized mammals in the world is the koala bear of Australia. It can survive only on a diet of a few species of eucalyptus trees. Because of this very narrow niche it is also very vulnerable to extinction, for if anything should happen to its main food source, the eucalyptus trees, it would have no alternative way of surviving. Among the Sri Lankan primates, the purple-faced langur has the most restricted niche. It is highly specialized for a diet of mature leaves from a few tree species. At Polonnaruwa, for example, about 60 percent of its diet involves a single tree species, *Adina cordifolia.*

Generalists are species with a very catholic diet and flexible lifestyle. The Sri Lankan toque macaques are a good example of a species with a broad niche. At Polonnaruwa, for example, they make use of about 65 different tree species for their foods. Although these macaques prefer mature fruit, they will also eat almost any soft vegetal matter (except most mature leaves) including young leaves, flowers, herbs, grass, tubers, mushrooms, insects, and small prey items such as eggs, lizards, birds, and even young mice and squirrels.

Preferred Habitats, Home Ranges, and Territories

Primates and other animals are not distributed randomly across the landscape. Rather, their dietary and other niche adaptations will determine the kinds of habitats in which

they can live. Each species tends to have its own preferred habitat. Habitat qualities that are important to primates are as follows:

- Climate.
- Forest type (rainforest, dry forest, scrubland, savannah).
- Availability of critical plant species for diet.
- Water sources (river, lake, waterhole).
- Availability of water (seasonal or constant).
- Predators and parasites.
- Human disturbance (electrical wires, traffic, hunting, cultivation, garbage, toxic products, harassment).

Within their preferred habitats, individual monkeys use only a small portion of the habitat available. The home range is that area of habitat to which an individual (or a group of monkeys) confines all of its life's activity. The size of a home range of a group of monkeys is usually anywhere between 5 and 60 ha, and depends on its quality and one the number of animals in the group. Thus, in poor habitats, where food trees are scarce, home ranges will be larger than in rich habitats. Similarly, in the same quality of habitat, bigger groups with many animals will require a larger home range area than smaller groups.

Food and water resources are generally scarce so that neighbouring monkeys will compete for whatever resources there are. When the residents of a home range defend the boundaries of their living space against neighbouring intruders, we refer to their ranges as territories.

Ecology of Sri Lankan Primates

The ecological principles and constructs outlined above apply well to the Sri Lankan primates. A summary of the major differences in habitat preferences and ecological niches of Sri Lankan primates is given in Table 3.

Because of their niches specializations, several different primate species can co-exist peacefully in the same habitat. In the Nature Sanctuary of Polonnaruwa, for example, all four primate species share the same land area, a phenomenon ecologists call sympatric. The four species share the same land, but eat different foods from it. Or, when their diets do overlap, they eat at different times. For example, both the macaque and the loris eat insects. But, the loris is most active at night, when the macaques sleep. Also, of course, macaques eat fruit and other vegetal material in the absence of insectivorous prey.

Table 3. The ecological niches of Sri Lankan primates.

	Loris tardigradus	*Semnopithecus entellus*	*Semnopithecus vetelus*	*Macaca sinica*
Free water dependent	Partly	Independent dependent	Partly	Wholly dependent
Diet Insectivore-frugivore	Insectivore	General folivore	Specialized folivore	
Gut	General	Special	Special	General
Locomotion & walker	Slow climber	Leaper bounder	Leaper	Climber
Active	Nocturnal	Diurnal	Diurnal	Diurnal
Preferred habitat forest	Closed forest	Open dry woodland	Closed wet forest	Closed
Preferred & forest layer	Arboreal: mid & low canopy	Arboreal: low canopy & terrestrial	Arboreal: upper canopy	Arboreal terrestrial
Land tenure home range	Small territory	Large home range	Small territory	Large
Social order size	Solitary groups	Large groups	Small group	Variable

Both langur species, especially the gray langur, will also eat fruit. However, they do not eat fruit in the presence of macaques. The macaques will simply chase the langurs out of any fruited tree where they wish to eat. The langurs are not much affected by

their inferior status, because, when unable to eat fruit, they eat leaves. This, the macaque cannot do because they lack the gut morphology and biochemistry to digest leaves and to neutralize the poisons that occur in mature leaves.

Competition between the two langur species is minimized in a similar way. The purple-faced langur feeds heavily on the leaves of the tallest trees, whereas the gray langur survives on a more varied diet gleaned mostly from the lower forest strata.

Ecology and Population Density

A basic tenet in ecological studies concerns the carrying capacity if a habitat for a particular species. It refers to the total number of animals, or their total weight (biomass), that a given area of land can support. The size of any animal population is determined by basically two factors: 1) the amount of food which promotes survival and reproduction and 2) mortality factors such as predation which keep numbers in check.

For most primate populations predation is not a major factor limiting their numbers. But food and water resources are important. The amount of food in a habitat is determined by a set of interrelated factors:

- Climate (rainfall, temperature, and number of months of drought). Climatic factors have a major effect on plant growth.
- Forest diversity (number of different plant species). Tree species produce new leaves, flowers, and fruit at different seasons. The availability of edible plant parts is better assured the greater the number of different tree species.
- Forest density (number of trees per unit area).
- Forest productivity (amount of fruit, leaves, and flowers produced).
- Plant defense mechanisms against vegetarians. Most plants produce chemical defenses (poisons and tannins) in their leaves that make them inedible to folivores. Thorns and siliceous fibers constitute physical defenses to being eaten.
- Primate digestive ability and diet preferences.

Of the above factors, primate diets are of special interest because they directly affect the amount of food available. For example, besides wood, most vegetation in a forest consists of mature leaves. Young leaves, fruit and flowers constitute only a small fraction of total vegetal matter, and their availability is very seasonal. Thus any animal that can digest mature leaves and can detoxify the plant's chemical defenses has an abundant food supply available to it. This is exactly what leaf-eating monkeys are able to do. For this reason, leaf-eating monkeys are always more numerous in any forest than the fruit-eating macaques (Table 4) or insectivorous lorises.

Table 4. Differences in biomass among species of primates in three forest habitats and climatic zones of Sri Lanka.

	Wilpattu	Polonnaruwa	Horton Plains
Plains			
Climate			
Average annual rainfall	1200 mm	1671 mm	2000mm
No. months drought per year	4-5	2-4	none
Forest type	Arid scrub	Dry evergreen	Montane rain evergreen
Forest productivity tons/ha/yr	2	4.5	5
Tree species diversity	Low	Moderate to high	Moderate
Primate biomass (kg/km2)			
Macaca sinica	1	300	<40
Semnopithecus entellus	19	730	0
Semnopithecus vetelus	0	1430	630

The above relationships are well-illustrated by the biomass of Sri Lankan primate species in different habitats (Table 4). The data indicate that poor habitats, such as

Wilpattu National Park, support a much lesser biomass of primates than do richer habitats where climatic factors are more favorable and plant productivity is high (Polonnaruwa and Horton Plains). Although plant productivity at Horton Plains is about the same as at Polonnaruwa, it supports fewer primates. This is because the plants on the Horton Plains are adapted to a cold and cloudy environment, where the leaves of most plants are thick, heavy in toxins and therefore difficult to digest by leaf-eating monkeys. Macaques, too, find little food on the Horton Plains and gray langurs avoid the cold rainy mountains altogether.

At Polonnaruwa, the purple-faced langur is the most arboreal, being confined to the top layer of the tree canopy, where it eats a greater proportion of leaves than the more terrestrial gray langur. Probably for this reason the biomass of purple-faced langurs is greater than that of gray langurs (Table 4).

Primate Ecology and Conservation in Sri Lanka

The Yala and Gal Oya National parks are similar to Wilpattu in providing very little favorable habitat for primates (Table 4).

Virtually all primates in these parks are confined to riverine forest or to that bordering permanent water holes. For this reason, it is of utmost importance to safeguard additional habitats that are suitable for primates and those that are located outside the National Parks. The drive to convert every acre of arable land to agriculture is detrimental to the preservation of biological diversity not only of primates but also of plant life and of the faunae that they support.

Population Regulation

In the absence of environmental perturbations, the number of primates inhabiting a given area of land tends to be constant over time. That is, many primate populations, in their natural state, experience more or less zero population growth rate. This occurs because rates of birth an immigration more or less cancel rates of death and emigration. But, major declines in population size do occur during periods of drought or cyclones, when the forest food supply is less than normal. Such food shortages

cause malnutrition and increased mortality. Which animals in the population are most likely to die at times of environmental shortage and hardship is determined by the social structure and organization of the species.

PRIMATE SOCIAL ORGANIZATION

The social structure of a species refers to the manner in which animals of different age and sex distribute themselves in space and time in relation to other members of their species. This distribution is never random. Instead, each species has its own typical social organization, which is influenced by basically three factors: 1) phylogenetic history, or innate social tendencies; 2) ecology, or the species' niche; and 3) the environment. The social organization of the four primate species inhabiting the dry evergreen forest at Polonnaruwa serve to illustrate these principles.

Solitary Life, (e.g., *Loris tardigraus*)

The loris is a member of the suborder Prosimii, or 'pre – monkeys.' Living prosimians are today's least-changed representatives of the most ancient primates, which appeared first in the fossil record in Africa during the Miocene Period (about 20 million years ago). This early stock (the Adapids) were ancestral to two main primate lineages, the anthropoids (monkeys, apes, and man) and modern day prosimians (lorises and lemurs). Through evolutionary time, most prosimians did not compete well with the more developed anthropoids. Therefore, in areas of Africa and Asia where today's lorises are sympatric with monkeys and apes, the lorises are confined to nocturnal habits. However, prosimians were most successful, evolving into many species of lemurs, on the island of Madagascar, where competing anthropoids have always been absent.

The fossil records indicate that the anatomical structure of loris-like animals has changed very little in the past 11 to 20 million years, attesting to the evolutionary success of the design and lifestyle of these animals. Therefore, by studying living lorises, we gain knowledge of the habits of an ancient ancestral lineage.

At Polonnaruwa, the basic social structure of the loris includes an adult female and her most recent infant. We refer to this social order as 'solitary' because these animals mostly live alone, especially the males. Typically, each loris occupies its own small territory of land, which it defends against its neighbours. The territories of the males are larger than those of the females and overlap with them. Thus a territory of male will encompass several territories of females. Males and females come together only briefly to mate. A mother will share her territory with her infant and possibly one older offspring to form a 'temporary mother-family.' Eventually, her young leave her territory to establish their own elsewhere.

Lorises in neighbouring territories communicate with one another every night by calling back and forth with high pitched squeals. They use special scent glands to place smelly marks on branches and also urinate on the areas that they use. Other lorises find these olfactory signals in their travels and so monitor the movements and reproductive status of their neighbours. Communication by olfactory cues is an ancient mammalian trait.

The solitary social life of the loris is well-suited to its ecological niche of nocturnal insectivory. Such hunting for small prey items would be inefficient in groups. Groups, therefore, have not been promoted by natural selection.

Evolutionary Trends in Social Organization

The social organization of the loris represents an ancient pattern not only for primates but also for other mammals. Within the primate order, more complex societies have evolved from the solitary way. this evolution has involved the following trends.

- Extended mother-family. Retention of daughters with the breeding mother, so that the social group consists of a matriarch and her adult breeding daughters and their progeny. Males are temporary visitors to these matriarchal groups.
- One-male group. Incorporation of a single adult male as a semipermanent resident in the extended mother-family (e.g., *Semnopithecus vetelus*). All-male bachelor groups are common as independent temporary groups.

- Multimale group. Incorporation of more than one male as residents in the extended mother-family, (e.g., *Semnopithecus entellus*, *Macaca sinica*). Temporary bachelor groups roam near these social groups, but are not common.

One-Male Groups (e.g., *Semnopithecus vetelus)*

The purple-faced langur lives in small groups (4 to 12 members) consisting of 2 to 5 adult females, a single adult male, and their progeny. These primates live in the upper canopy of the forest and feed heavily on the mature leaves of certain favored trees. As these food sources are common and concentrated he forest, the langurs need not move great distances in search of food. Instead they live in small territories, the boundaries of which hey defend vigorously against their competing neighbours. Purple-faced langurs announce their claim to a territory and their location by loud vocal hoots early in the morning. They are diurnal and monitor their territorial boundaries visually, driving off any neighbouring intruders by leaping at them while uttering loud 'whoop' shouts.

Multimale Groups (e.g., *Semnopithecus entellus*)

Gray langur groups are usually much larger (10 to 40 members) than those of the purple-faced langur and may include more than one male. Their groups have more adult females than males.

Although gray langurs too can digest mature leaves, their dietary preference is much more varied than that of the purple-faced langur and their diet includes fruit and terrestrial herbs. Generally, gray langurs move over long distances during any one day in order to fulfill their dietary requirements. Their home range boundaries, therefore, are too great to monitor effectively against intruders. Instead, their home ranges overlap between neighbours, and when neighbours meet in the same area, one group will chase off the other by leaping and making vocal 'whoop' shouts similar to those made by the purple-faced langur. Olfactory marks, like those used by the loris,

are not used by either the gray or purple-faced langur. Instead, vision plays a much more important role in these diurnal primates.

Multimale Groups (e.g., *Macaca sinica*)

Groups of toque macaques vary in size from 4 to 80 animals, averaging around 20. Large groups tend to have more than one adult male, and in all groups there are more adult females than males. Females never leave the group in which they were bore, whereas all males emigrate to other groups at puberty. Consequently, groups consist of one or more matrilineal families. The adult makes, being immigrants from a neighbouring group, are not closely related to the females.

Toque macaques are unable to digest most mature leaves and their diet is more varied than that of the langurs. Their home range use patterns are similar to those of the gray langur, except that they lack the loud vocal territorial displays typical of the langurs. Macaques have larger home ranges than the gray or the purple-faced langur. Given the diverse diet and sometimes difficult to harvest foods that the macaques rely on, their manual manipulative ability and intelligence are highly developed.

SOCIAL DYNAMICS AND DEMOGRAPHY

The relationships among primate ecology, social behaviour, and demography are best known from studies of the toque macaques at Polonnaruwa. No other study of any primate (or mammal) has devoted so much effort and time to clarifying these important relationships. I will, therefore, use the discoveries from that study to exemplify some established trends and principles.

Dominance Hierarchy

Members of a social group recognize each other individually and establish a peck-order amongst themselves. When two monkeys squabble, the winner of the fight is

labeled as 'dominant' and the loser as "subordinate". Once a monkey wins against another it usually maintains its dominant status over the loser in all future encounters. Therefore, when these same two monkeys meet again, a fight is not necessary to settle any dispute because the subordinate one respects the winner's dominant status and merely gives way. These dominant-subordinate relationships are established for all possible pairs of individuals residing in the group. As a consequence, there exists a hierarchy of dominance relations. The highest ranking, or the most dominant, monkey can supplant and exploit all other monkeys in the group. The second ranking is dominant to all monkeys except the first ranking. The third ranking is dominant to all monkeys except the first and the second ranking, and so forth down to the lowest ranking animal which is subordinate to all others in the group.

Dominance by Age, Sex, and Kinship

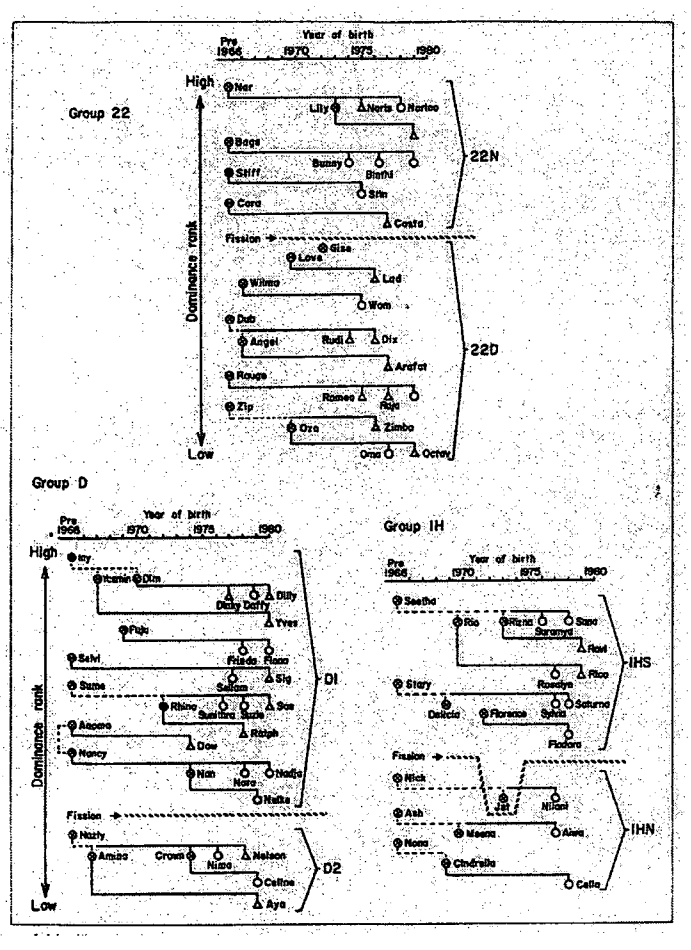

Figure 4. Matrilineal kinships among the natal members of the three different groups that fissioned, and the dominance rank relationships among matrilines within these groups. Solid lines indicate kinships known through birth, broken lines indicate estimated ones. The names of all individuals more than 6 months old at the time of fission are indicated. Circle: female; triangle :male; black: dead individual at the time of group fission; crossed circles: adult; open: juvenile or infant. Brackets indicate the daughter groups created by fission. In group 22, the female 'Gise' is an assumed daughter of 'Dub.' (after Dittus 1988).

Among adult males, kinship is less important than physical size and fighting ability in determining social rank. Since most adult male monkeys are very much larger in body size and physically stronger than adult females, they are generally dominant to the females and all of the young.

A monkey's rank in the dominance hierarchy is determined by its age, sex, and kinship. To a certain degree males and females have separate hierarchies. In the female hierarchy, a young monkey's rank in determined by that of its mother. For example, sons and daughters will be dominant to the offspring of any female that is subordinate to their own mother. Hence, families within a group can be ranked by their status. Within families, mothers dominate their offspring dominate the younger. In general, kinship and 'social connections' are important in determining a monkey's social status.

Competition and Survival

The ultimate biological purpose of any monkey (or any organism) is to survive and to reproduce. Apart from avoiding predators and other life-threatening circumstances, survival is a matter of eating well, and reproduction involves successful mating and taking care of one's young.

More monkeys are born each year than can ever survive. The food supply in the natural forest environment is limited and can support only a certain number of monkeys. One consequence of social life is that the monkeys themselves influence who in their society survives. Such 'decisions' are not made consciously, of course, but result from the monkeys' competitive behaviours.

Monkeys compete for a variety of resources that are essential for their survival, and the most important of these is food. About 81 percent of all aggressive interactions in toque macaque society involve strife over food or water, at least during the non-mating season. A careful study of 'who threatens who' in toque macaques indicated that these competitive acts closely follow the hierarchy of dominance ranks.

A monkey's social rank in its group has a profound effect on its foraging efficiency, or 'ability to make a living', and hence on its survival and success in raising its young. Compared to high-ranking animals, low-ranking ones:

- are supplanted from contested feeding sites more often,
- feed at slower rates because their feeding sites are poor,
- spend more time and energy (work harder) in fulfilling their daily nutritional needs , and
- eat a larger proportion of poor-quality foods.

These socially imposed ecological hardships have a direct bearing on the health and mortality of the monkey. Thus, compared to high-ranking monkeys, low-ranking ones:

- grow at slower rates,
- reproduce at slower rates (female birth rates are lower),
- reach sexual maturity at a later age, and
- die at greater rates.

During the mating season the overall frequency of aggression increases, but is confines mostly to male-male fights over access to estrous females. Such fights often result in serious injury and death. For this reason, the rate of death (mortality) in adult males is greater than that in adult females (who do not fight for males)

The most life-threatening phase in a male's life occurs during adolescence. At this time, males are evicted from the natal group and attempt to transfer into a new group, where, as unwelcome competitors for limited resources, they are mostly harassed by resident xenophobic group members. Also, adolescent males try to compete with older, larger-sized males for rights to male with estrous females, and often lose and are injured in the attempt.

Figure 5 illustrates rates of death a different ages of males and females. Several trends are evident from these considerations, and research has shown that much of this mortality is caused y social factors.

- As in all mammals (including man) mortality is greatest early in life and in old age. The reasons for this are greater vulnerability to diseases as well as low social status.

- During infancy and the juvenile period, females die at a greater rate than do the males, largely as a consequence of the low dominance status of the females in relation to food competition.
- Male mortality reaches a peak during adolescence, when all males are evicted from their natal group and are subject to the stresses associated with emigration to group of strange monkeys.
- During adulthood, males continue to suffer greater mortality than females largely as a consequence of injuries from male-male for mates.

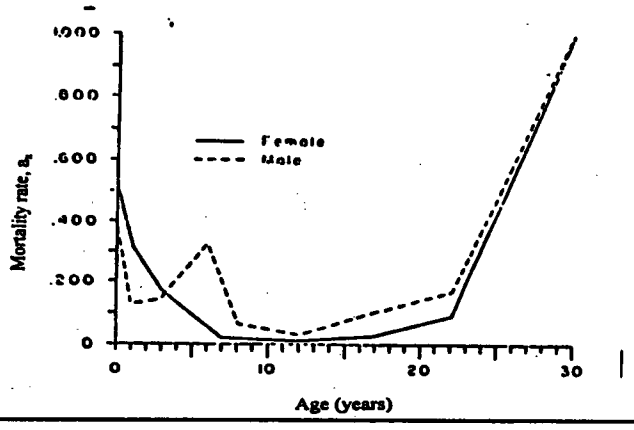

Figure 4. Age-specific mortality rate curves for male and female toque monkeys (After Dittus, 1975)

Female Mortality and Interfamily Competition

Females in macaque society never leave the group in which they are born , whereas the males emigrate at puberty. Home ranges, therefore, are inherited by successive generations of females. Since resources are limited, mother-families within a group compete for available resources on any give day ad for the eventual inheritance of the entire home range. To prevent the daughters of low-ranking families from competing with their own daughters, high-ranking mothers are spared such harassment because, by leaving the group and home range at puberty, they pose no threat to the inheritance of the home range. For this reason, mortality is so much greater in infant and young females than in like-aged males (Figure 4).

MAN'S RELEASE FROM ANCIENT CONSTRAINTS

It was noted earlier that populations in stable environments tend to approach zero growth rates and remain more or less in equilibrium with the available food resources. Individual competitive behaviours, over both food and mates, play a major role in influencing the vital statistics (rates of birth and death) that ultimately determine population size. Being subject to such constraints, primate societies and the environments which they had inherited from their ancestors have been safeguarded.

Man differs from this ancient tradition in one major way, and in so doing jeopardizes not only his own survival but also that of most life on earth. Man makes little effective attempt either to limit his own population size or to preserve the environment which had sustained him and his predecessors. In evolutionary history, population explosions and environmental destruction of the kind and magnitude that man is undergoing today have ended in disaster. The challenge to man is to use his superior intellect to override his biological drives and those cultural traditions which are inappropriate in the modern world, and so to alter the current course to nowhere.

Are you willing to rear two children or less in order to assure a reasonable standard of living for them and your grandchildren?