

## **INFANTICIDE IN ANIMALS AND MAN : COMPARATIVE ASSESSMENT IN EVOLUTIONARY CONTEXT, WITH A NEW THEORY.**

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### **INTRODUCTION**

Although infanticide in man and other animals has been known to exist for ages, it did not elicit much scientific interest until its discovery as a regular feature in a nonhuman primate, the Hanuman langur (*Presbytis entellus* : Cercopithecidae) in India in the sixties and seventies (Sugiyama 1964, 1965a, b, Mohnot 1971, Parthasarathy and Rahaman 1974, S.B. Hrdy 1974, 1977, Boggess 1979, Curtin and Dolhinow 1979, and Chapman and Hausfater 1979). Subsequently, the phenomenon has been reported in many other primates. Recently, a wealth of new data and analyses have been brought together (Hausfater and Hrdy 1984).

In the present account I have assessed infanticide comparatively in all animal groups and man in the evolutionary context. The various theories put forward to explain infanticide on the basis of the proximate as well the possible ultimate evolutionary causes have been discussed. As they were found to be inadequate, a new theory is provided.

In mammals the reproductive pattern puts certain constraints on the evolution of infanticide. The reproductive cycle can be broken up into an irreversible sequence of states (events) and stages, e.g., puberty, copulation, fertilisation (conception), implantation, parturition, lactation and weaning. These events and stages also provide the context for infanticidal behaviour which can occur at any stage of the reproductive cycle (Hayssen 1984).

### **WHAT IS INFANTICIDE ?**

#### **1. *General Considerations***

Infanticide is any behaviour that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the performer's own species (Mock 1984). Two principal types of infanticides can be distinguished; viz., *nonkin infanticide* and *kin infanticide*. The latter type results in sacrificing shared genes for some presumed compensating benefits to the perpetrator's inclusive fitness. Kin infanticide can be further divided into two

categories, viz., *parental infanticide* (done by the parent) and *siblicide* (done by a sibling, and sometimes called *patricide* or *cainism*).

S.B. Hrdy (1979) has classified infanticide in animals into five categories, viz., exploitation (i.e., cannibalism), resource competition, parental manipulation, sexual selection and social pathology.

Direct contribution to infanticide indicates that either plain aggression or abusive neglect, or both, are involved. But the death need not be caused by any particular blows. Thus, aggressive intimidation of a nest-mate as an infanticidal act (i.e., siblicide) is included if, as a consequence, the victim starves to death, but the starvation would not be regarded as infanticide if it resulted from aggressive sibling competition. (For a more detailed discussion, vide Hrdy and Hausfater 1984, and Mock 1984.)

## 2. *Infanticide and Cannibalism*

Infanticide may or may not lead to cannibalism. Several cases are known in the animal world where cannibalism is the end and apparently the only purpose of infanticide, and it is not clearly distinguishable from predation ; here we also include 'ovicide', the killing (and eating) of eggs by conspecifics. Many fishes and insects eat their eggs and young ones. A recent example is that given by Roonwal and Rathore (1975) who observed dealated brooding termites, *Microtermes mycophagus* of the Indian Desert, eating young larvae in the colony : "alates often attack and eat up young larvae, a process which is finished in about 5 minutes. Sometimes the larvae are merely bitten and then left over in dead or dying condition" (p. 45) ; it was not possible to say whether the cannibals included the parents of the larvae. Similarly, I have seen the Old World Desert Locust (*Schistocerca gregaria*) attack and eat the older (fourth and fifth stage) hoppers while they were undergoing moulting ; it is possible that the hoppers were eaten not merely for the flesh but also for water. Steiner (1972) reported ground squirrels eating conspecific infants. I have seen a mother rat, *Rattus rattus*, eating young infants from her own litter, and a bitch eating a member of her own litter a few hours after giving birth, in both cases apparently due to hunger.

Cannibalism, however, is rare among the primates, and only a few cases are known, all among the higher apes. The early cases were reported by Suzuki (1971) and Bygott (1972) in the chimpanzee, *Pan troglodytes*, in Africa. In both cases, a group of adult males somehow acquired an infant and jointly tore it apart, limb by limb, and ate it alive. Since the infant could hardly have satisfied the appetite of a group of adults, it seems doubtful if the infant-eating was an immediate food-need. The act is even more surprising when we consider that chimpanzees in their natural habitat are largely vegetarians, and only much less commonly do they throw in animals as a part of their diet — mostly ants and termites, and occasionally the meat of monkeys and other medium-sized and mammals which they kill and eat. Also in the chimpanzee, Goodall (1977) reported two cases of individual females killing an infant of another disabled (polio-affected) and lower ranking female of her own group, and eating it. Fossey (1976) reported a suspected case of infant cannibalism by a dominant female in the mountain gorilla (*Gorilla gorilla beringei*).

Three categories of cannibalism can be recognised, viz., *filial cannibalism* (where the killer is the victim's parent), *heterocannibalism* (where the cannibal is not related to the victim), and *sibling cannibalism* (fratricide which ends up in cannibalism) (Dominey and Blumer 1984).

## INFANTICIDE IN ANIMALS OTHER THAN PRIMATES

### 1. *Infanticide in the Invertebrates*

The invertebrates constitute a vast and varied assemblage of animal forms and include over 95 per cent of all the known animals. Intraspecific killings and cannibalism are widespread and have been recorded in nearly 1,000 species spread over 11 phyla from the Protozoa upward (Pollis 1984), and the phenomenon presents certain general characters which may be summarised as follows :—

- (i) Immature animals form the bulk of intraspecific prey.
- (ii) Predators may be adults, juveniles or even newborn animals, adults being the more common predators.
- (iii) Females are more cannibalistic than males.
- (iv) The rate of intraspecific predation increases with hunger and with a decrease in the availability of alternate foods.
- (v) Predation is often a direct function of density, the rate increasing with overcrowding.

The intraspecific predation of eggs and young ones significantly influences the population structure and dynamics. A large proportion of the entire population or the specific age-class (generally the young ones) may be killed and eaten, so that the population may be heavily skewed in favour of adults.

Cannibalism confers many advantages upon the predator, and the few existing studies suggest that there are genetic strains with different cannibalistic tendencies. In some cases, as in the corn earworm (*Heliothis* sp., Insecta, Lepidoptera) extremely voracious strains are over 20 times more cannibalistic than those that are least voracious.

Infanticide confers one advantage to some invertebrates that has no counterpart among the vertebrates. By killing conspecifics, some arthropods are able to decrease future intraspecific killing and predation on themselves. This is because some arthropods pass through a quiescent stage during larval moulting and pupation during which they are highly vulnerable to predation by the smaller conspecifics, e.g., in the treehole dwelling mosquito larvae (some members of the genus *Toxorhynchites*) whose older stages in the days immediately before pupation embark upon a "killing frenzy"

In some cases sexual selection may operate. Individuals may increase their own fitness by intraspecific predation specially by reducing the fitness of other individuals of the same sex. This may occur by direct cannibalism or killing of sexual competitors or by eating their offspring, as in termites and some social Hymenoptera where eggs and young larvae are eaten along with the defeated adults during territorial wars between rival colonies (Wilson 1971).

Some invertebrates practice sibling cannibalism by eating eggs, embryos and newborn young from within their own clutch.

## 2. *Infanticide in Fishes*

In fishes intraspecific predation of young stages (eggs, embryos, larvae and juveniles) is of common occurrence. Here, infanticide always results in cannibalism which is far more common than in the terrestrial vertebrates. Several factors have contributed to this situation. Among them, the more important ones are the following : (i) High fecundity, and the resulting smaller offspring ; (ii) the predominance of external fertilization, resulting in the deposition of helpless embryos in a potentially hostile environment ; and (iii) filial cannibalism, which is favoured by the frequent occurrence of parental care of offspring by males in contrast to the general prevalence of care by the mother in most other animal groups (Dominey and Blumer 1984).

## 3. *Infanticide in the Amphibia*

As in other animals, in the Amphibia too the highest mortality occurs in the younger stages (eggs and larvae), and the problem has been reviewed by Simon (1984). This is due to various causes, e.g., predation by the vertebrates and the invertebrates, fungal and other infections, competition, disease, starvation, hostile environment (extremes of temperature), etc. In some salamanders and frogs the father guarding the eggs is said to eat them occasionally (filial cannibalism).

Cannibalism by larvae of conspecific larvae is common in the Amphibia. Associated with this in some cases (e.g., in spadefoot toads of the genus *Scaphiopus*) a population may show polymorphism. Within a single population there may exist a noncannibalistic omnivorous morph, a cannibalistic carnivorous morph, and an intermediate morph.

Egg cannibalism by larval siblings has been reported in some tropical frogs that lay eggs in water-filled leaf axils or tree holes.

In most cases, conspecific egg-killing results in cannibalism, but noncannibalistic egg-killing may also occur, as in the frog *Hyla rosenbergi* of Central America and a few others.

In some Amphibia infanticide occurs by the mother deserting her laid eggs that she is guarding, thus exposing them to predation by enemies. This occurs in the salamander *Hemidactylum scutatum* where the desertion occurs when several clutches are clumped together but not when they are widely dispersed.

## 4. *Infanticide in Birds*

According to Mock (1984), infanticide in birds is most common in four broad contexts, viz., brood reduction, desertion, coloniality and communal nesting. He also points out that, contrary to S.B. Hrdy's assertion (1979) that infanticide is never common, field data on birds show that it is regularly the most important source of nestling mortality in some species and thus provides a major selection pressure to evolve various specific adaptations.

**Brood reduction** : In some species females consistently lay more eggs than are successfully hatched on an average. The regular loss of one or more members of the brood (brood reduction) is a density-dependent system for maximising parental reproductive success.

**Desertion (parental infanticide)** : This takes the form of outright killing of eggs (with or without cannibalism) or simple desertion ; outright killing is not common.

**Coloniality** : Infanticide commonly occurs in colonies when dense breeding colonies and unrelated adults are juxtaposed. The density of conspecifics intensifies competition of limited resources, e.g., nest sites, building materials and food. The rate of cannibalism (on eggs and young chick) is often quite high (ca. 23 per cent in herring gulls, one-half of which was performed by only four gulls in a colony of 900).

**Communal nesting** : Several cases of infanticide have been reported in the case of communal nesting. In the groovebilled anis, *Crotophaga sulcirostris*, the socially dominant female lays last after rolling out of the communal nest some of the eggs of the subordinate female. In the Mexican jays, a few group members pilfer eggs and eat them.

## 5. *Infanticide in Mammals other than Primates*

### (a) *Carnivores*

Direct observations on infanticide in wild carnivores are far less numerous than in other groups of animals because of some inherent difficulties. Carnivores are dangerous and not easily approachable ; they are also mostly nocturnal and solitary and are wary of human approach. Consequently, much of the information available is either inferred or otherwise less direct. The results have been reviewed by Packer and Pusey (1983, 1984), and can be grouped into four categories as follows :—

**Infanticide by males** : The most extensive data are from the African lion, *Panthera leo*, in Tanzania. Outside males enter a pride of lions and kill one or more infants. In one case the killer male ate the viscera of one of the cubs. The killer male sometimes takes over the victimised pride, the females coming into oestrus within days or weeks of losing the infant (normally, they remain anoestrus until their cubs are one-and-a-half year old) and mate with the new male (cf. infra, a similar situation in the Hanuman langur, *Presbytis entellus*). The situation could be interpreted as a reproductive strategy by males in S.B. Hrdy's (1974) sense.

**Extragroup infanticide** : Several cases have been reported in which individuals of one breeding group kill the young of another (e.g., in the coyotes *Canis latrans* ; and the African lion).

**Intragroup infanticide by females** : Infanticide by the mother has been observed in the African lion, the mother abandoning healthy single surviving cubs less than three months old. A similar abandonment of a young cub has been reported in the grizzly bear, *Ursus horribilis arctos*. In an untamed pariah dog, near a human colony in India, I have witnessed a mother killing a six-day old infant (out of litter of five) and devour it entirely, the action being probably prompted by acute

hunger. Infanticide by females other than the mother have been recorded in captive wolves (*Canis lupus*), red foxes (*Vulpes vulpes*) and brown hyenas (*Hyaena brunnea*) ; in these cases there is at a time only one breeding female but more than one adult female is present in the group. This seems to be a female reproductive strategy by which a dominant female ensures that she alone can breed at that particular time and also that her offspring receive care from the subordinate female.

Intralitter infanticide : Examples are difficult to come by because of observational difficulties since most cubs are kept in dens. But a few cases have been recorded, e.g., in the Arctic fox, *Alopex lagopus*, in which six of the nine cubs had been killed by a bite at the base of the skull ; and in the spotted hyena (*Crocuta crocuta*) in which two three-fourths grown cubs of a den were each found strangling a 2-month old cub.

#### (b) *Rodents*

For a variety of reasons, such as small size, brief life-history, etc., rodents provide favourable material for the study of infanticide in the laboratory. Consequently, the phenomenon has been well documented and analysed in detail in the laboratory, but field studies on infanticide are scarce. Comprehensive reviews of our present knowledge of both the general and specific aspects have been provided recently by Labov (1984), Brooks (1984), Huck (1984), Elwood and Ostermeyer (1984), Svare et al. (1984) and vom Saal (1984).

As Brooks (1984, p. 334) points out, virtually all direct observations of infanticide in wild rodents are from ground squirrels (Sherman 1981) and marmots (family Sciuridae). In the Californian ground squirrel, *Spermophilus beldingi*, at least 8 per cent of the infants born are killed by conspecifics, mostly adult females, distantly related to the victims ; mothers thus bereft of their infants, abandoned these "unsafe" burrows, making them available to the killer female. Surprisingly, in the Muridae (voles, lemmings, mice, rats, gerbils, etc.), although several field studies on population dynamics have been made, few mention infanticide in the truly wild state. In view of the paucity, I give below my own observations (Roonwal 1949, p. 98) on freshly captured cases of the Manipur White-bellied Rat, *Rattus rattus bullocki*, in 1945 in Manipur (NE India). The litter size is 3-9 ; the young ones are born naked, with the eyes closed ; the eyes open on the 17th or 18th day ; young ones huddle close to the mother who suckles them for at least 25 days after birth ; she fiercely resents any intrusion. In one case when two 14-day old infants from another brood (after the mother's death) were placed in her nest, she instantly killed one of them and ate its head ; the other infant was quickly removed by me.

Huck (1984) has discussed the relationship between infanticide and the evolution of pregnancy block in rodents. Bruce (1959, 1960) had observed the occurrence of the pregnancy block (the Bruce Effect) in rodents. She noted that in the house mice exposure to a strange male (or to his odour) prevented implantation in recently inseminated females (a form of infanticide) and caused a return to oestrus 4 to 5 days later. This phenomenon has been confirmed in several rodent species. To what extent this form of male infanticide is adaptive, if at all, is not clear.

## INFANTICIDE IN THE NONHUMAN PRIMATES

Infanticide in the nonhuman primates in the natural state was first reported in India on the Hanuman langur, *Presbytis entellus*, by Sugiyama (1964, 1965a, b), Mohnot (1971), and S.B. Hrdy (1974, 1977) ; later on by other workers in several species of both the Old World and New World monkeys and apes (vide supra, Introduction). Mitchell and Brandt (1977) reported it in several prosimians in captivity. Examples of infanticide are known in the following species, arranged in a classified way. This is followed by an account of the individual species.

### Suborder 1. PROSIMII

(Tree shrews, lemurs, indris, lorises, tarsiers, etc.)

No field examples of infanticide are available.

### Suborder II. SIMIAE (Anthropoidea of authors)

(Marmosets, monkeys, apes, man)

#### Infraorder (A) Platyrrhina

(New World Monkeys)

#### Family 1. CALLITHRICIDAE

No examples are available.

#### Family 2. CEBIDAE

#### 1. *Alouatta seniculus* (Red howler monkey)

#### Infraorder (B) Catarrhina

(Old World Monkeys)

#### Family 3. CERCOPITHECIDAE

Subfamily : (1) Cercopithecinae (macaques, baboons, etc.)

- (2) *Macaca mulatta* (Rhesus macaque)
3. *Macaca sylvana* (Barbary macaque)
4. *Papio ursinus* (Chacma baboon)
5. *Papio cynocephalus* (Yellow baboon)
6. *Papio anubis* (Olive baboon)
7. *Papio hamadryas* (Hamadryas baboon)
8. *Cercopithecus ascanius schmidtii* (Red-tail monkey)
9. *Cercopithecus mitis stuhlmanni* (Blue monkey)
10. *Cercopithecus campbelli lowei* (Campbell's monkey)

#### Subfamily (ii) Colobinae

(Langurs, colobus, etc.)

11. *Presbytis cristatus* (Silvered leaf-monkey)
12. *Presbytis entellus* (Hanuman langur)
13. *Presbytis senex* (Purple-faced langur)
14. *Colobus badius tahproscalis* (Red colobus monkey)

## Family 4. HYLOBATIDAE

No examples are known

## Family 5. PONGIDAE

15. *Pongo pygmaeus* (Orangutan)
16. *Pan troglodytes schweinfurthi* (Common chimpanzee).
17. *Gorilla gorilla beringei* (Mountain gorilla)

1. *Red howler monkey, Alouatta seniculus*

Infanticide in the red howler monkey has been observed in Venezuela (South America) by Rudran (1979 a, b), Sekulic (1983) and Crockett and Sekulic (1984). One male (the "breeding" or dominant male) does most or all of the mating during a female's period of peak receptivity. Periodically, status changes occur among males, and it seems that infanticide occurs during the period of instability.

Rudran (1979 a, b) recorded (over a period of two years) one observed and three inferred cases of infanticide in three groups, following an invasion by outside males who were the killers. Sekulic (1983) reported one case of infanticide after an inferred status change of male, and 19 infant disappearances as possible cases of infanticide.

By analysing all the available data, Crockett and Sekulic (1984) concluded that most infant disappearances associated with male changes are infanticides, that the killers are new or newly dominant males, that young infants are more frequently killed than older ones, and that mothers and other members of the group attempt to defend the group against potentially infanticidal males.

2. *Rhesus macaque, Macaca mulatta*

In the rhesus macaque group size may vary from small to large (8 to 180 individuals) and the composition is mostly multimale-bisexual, with several adult males and females and a number of immatures (Roonwal and Mohnot 1977). Infanticide has been inferred in one group of 11 (1 adult male, 3 adult females, 4 juveniles and 3 infants) in the Asaroi forest in the Siwalik Hills, northern Uttar Pradesh, by Pirta and Singh (1981). When 10 of the group members were removed, leaving the male alone, he became aggressive. He started visiting 6 mother-infant pairs which were placed in the study area and forcibly snatched 5 infants from their mothers and probably killed them. But he resumed his normal behaviour after some new females were introduced in the area.

Earlier, Carpenter (1942) had recorded suspected cases of infanticide during the group formation process in *M. mulatta*.

3. *Barbary macaque, Macaca sylvana*

Infanticide by adult males in free-ranging population has been recorded by Burton (1972) in Gibraltar (Spain).



#### 4. *Chacma baboon, Papio ursinus*

Infanticide in baboons has been reviewed in considerable detail by Collins, Busse and Goodall (1984). The phenomenon has been reported in four species which are discussed below.

In the chacma baboon groups are multimale. Infanticide in South Africa has been reported by several workers, e.g., Vincent and the South African Parks Board or SAPB, both quoted by Saayman (1971), Busse and Hamilton (1981) and Collins et al. (1984). Vincent observed an adult male killing two young males on the periphery of a group. The SAPB mentioned an adult male seizing an infant from its mother, running off with it and beginning to eat it. W.H. Buskirk (quoted by Collins et al. 1984) observed an adult male attack a 5-month old infant and drag it along the ground as a second male gave chase ; the infant died two days later.

Collins et al. (1984) have recorded three cases of direct observations of infanticide. In two cases the killer was a male ; in the third case, curiously, an adult female who somehow took a 2-day old infant from its mother (the lowest-ranking female of the group), resulting in the infants death two days later. The same authors have recorded circumstantial observations of two infanticides ; one of the dead infants, when abandoned, was partially eaten by a high-ranking female.

#### 5. *Yellow baboon, Papio cynocephalus*

Groups are multimale. A few cases of infanticide in the yellow baboon have been provided by Altman (1980), Rhine et al. (1980), Shopland (1982) and Pereira (1983). Pereira noted, in addition to a case of infanticide, three cases of abortion following the immigration of an outside male into a group.

#### 6. *Olive baboon, Papio anubis*

The olive baboon lives in multimale groups. In Tanzania Packer (1980) and Collins et al. (1984) have recorded several cases of infant killing by conspecifics in four groups (which had been kept under continuous observation for a period of over 10 years) in which infants died as a result of fatal injury or mishandling, including kidnapping. Non-fatal kidnapping by conspecifics is not uncommon ; but in these cases the kidnapper prevented the mother from retrieving the infant (usually by threat or avoidance) who died ; the kidnapper in one case was an adult female, in the other two cases adult or adolescent males. In four cases, an adult male attacked the mother and infant, inflicting fatal injuries, resulting in the death of the infants, and in one case of the mother as well. Packer (1980) and Smuts (1982) have also provided some evidence of infanticide in the olive baboon.

#### 7. *Hamadryas baboon, Papio hamadryas*

Unlike the three baboon species discussed above, the hamadryas baboon generally lives in one-male groups. Infanticide has been reported both in captivity (Zuckerman 1932, Angst and Thommen 1977, Rijkson and Smit 1979, Rijkson

1981) and in the field (Kummer et al. 1974). The last mentioned authors recorded in the field that in two groups, when a breeding male was removed, the arrival of the replacement male was soon followed by the death of an infant in each group—one of the infants showed signs of deep wounds presumably inflicted by the canines of the replacement male.

In a 27-member group (comprising 2 adult and 2 subadult males, 20 adult females and 3 immatures), Rijkson and Smit (1979) removed 7 females (In contrast to the usual practice in zoos faced with infant killings where only the killer males are removed). Before this experimental change, of the over 21 infants born, all but 3 died within a few days of delivery. Post-experimentally, 9 of the 12 infants born survived. The killer male is the established leader of the group and the biological father of his victims. Observations established that mother carrying newborn infants attracted disproportionate attention from all group members, particularly from females in oestrus. The authors surmised that : (i) the male leader's status is seriously impaired by this deviation of attention ; and (ii) by removing the infants he gets rid of the cause of the deviation and restores his social position in group dynamics. The killing of his own offspring is only a side effect (cf. man where similar infant killings occur).

#### 8. *Red-tail monkey, Cercopithecus ascanius schmidti*

Struhsaker (1977, 1978 b) and Leland et al. (1984) have recorded infanticide in the red-tail monkey in the Kibale Forest, Uganda. This species lives in one-male harem groups of about 12-50 individuals. Groups at Ngogo contained one adult male and about 10 adult females with their offspring. During the study period after about four months, the original harem male was replaced by a new adult male who subsequently killed two newborn infants in the group within one to two-and-a-half months of his take over. After about a year this male was replaced by another one (Struhsaker 1977).

#### 9. *Blue monkey, Cercopithecus mitis stuhlmanni*

Infanticide in the blue monkey has been recorded by Butynski (1982) and Leland et al. (1984) in the Kibale Forest, Uganda. Group size is 10-33, with one adult male, several adult females and their offspring. After several months of study, the original harem male was replaced by another male who killed one infant and a suspected two others. After a brief tenure, he was replaced by a new male, and in a 11-month period five new males took over one after the other. The new males were often observed chasing and probably wounding infant-carrying females of the group, but no actual killing was observed.

#### 10. *Campbell's monkey, Cercopithecus campbelli lowei*

In Campbell's monkey in the Ivory Coast (Africa), Galat-Luong and Galat (1979) recorded wounding of infants and their disappearances, believed to be infanticide. this monkey lives in predominantly one-male groups.

11. *Silvered leaf-monkey, Presbytis cristatus*

In a city park in Malaya (SE Asia), Wolf (1980) recorded suspected case of infanticide in the silvered leaf-monkey. It lives in predominantly one-male groups, but groups may sometimes contain up to 3 males and several adult females (Roonwal and Mohnot 1977).

12. *Hanuman langur, Presbytis entellus*

The Hanuman langur lives in two types of medium-sized groups, the bisexual (average size 15-35 individuals, sometimes reaching 80-90, or even 125) and all-male (average 4-15 individuals) (Roonwal and Mohnot 1977, Mohnot 1984 a, b). Bisexual groups again are of two types, viz., unimale (with only one adult male and several adult females), and multimale (with several adult males and females). In Jodhpur, groups are almost exclusively unimale; in central and southern India both types may occur together in a place (Sugiyama 1964, 1965 a, b, Kankane 1980, Newton 1984, 1986, Kurup 1984), but the majority are still unimale.

Infanticide has been observed or inferred in several places in India and Sri Lanka. The first eye-witness account of actual infant killing is that of Mohnot (1971, three cases) in Jodhpur (northern India). The earlier mention of infanticide by Sugiyama (1964, 1965 a, b) was inferred, not eye-witnessed. Subsequently, several accounts of infanticide have been published, along with reviews and hypotheses to account for it, from Jodhpur, Mt. Abu, Dharwar (southern India), Kanha (central India), e.g., by S.B. Hrdy (1974, 1977 a, b, 1979, 1984), Sugiyama (1967, 1984), Makwana (1979), Makwana and Advani (1981), Schubert (1982), Boggess (1984), Hausfater (1984), Vogel and Loch (1984), Sommer and Mohnot (1985), Newton (1986), and Mohnot et al. (1987). Although about 70 cases of infanticide have been reported, the majority of them are inferred by indirect evidence (disappearance of infants; presumed killed). In only 12 cases has the event been eye-witnessed (9 at Jodhpur in Rajasthan, by Mohnot 1971 and Sommer and Mohnot 1985; and 3 in Kanha Park, Madhya Pradesh by Newton 1986). In many cases, the sequence of events is nearly similar. The attacker is usually a male (in only one case out of 12, the attack was by a female) belonging to one of the following 4 categories : a "new resident" who had been with the group for about a year ; an "established resident" who had lived in the group for over a year ; an "interim resident" who had been with a group for a few days to about 3 months ; and male (s) from an all-male band (Mohnot et al, 1987).

Infanticide is often connected with a change in the leadership of a group, but the change is not always accompanied by infanticide. An outside male from another group or an all-male band tries to wrest leadership or sexually possess a female (he is sometimes successfully repulsed by the resident male leader) and is often in a frenzy to do so and repeats his attacks. In this process he attacks and kills, usually by biting, the infant carried by the female. If he is successful, the killed infant's mother comes into oestrus prematurely, within few days or weeks, and mates with the killer male, who is now the new leader. Infanticide is not accompanied by cannibalism.

13. *Purple-faced langur, Presbytis senex senex*

This langur lives in predominantly one-male groups. Rudran (1973 a, b) observed that in Sri Lanka infants, and sometimes juveniles, disappeared in numbers from groups ; they were presumed to have been killed by conspecifics.

14. *Red Colobus monkey, Colobus badius taphrosceles and C.b. rufomitratu*

Infanticide in the red colobus monkey (of the Kabale Forest, Uganda, *C. b. taphrosceles*) has been recorded by Leland et al. (1984). This monkey lives in large, multimale, patrilineal groups of about 8-80 individuals. Males remain in their natal group for life or emigrate only as old juveniles, and rarely join other groups. Females join other groups as old juveniles or subadults, more rarely as adults. (For details, vide Struhsaker 1975, 1978a, 1980.) These groups had been under study for over 12 years. The "CW" group contained 33 individuals (3 adult males, 1 subadult male and 14 adult females and their offspring). No male had ever succeeded in immigrating into this group. In the 12th year of study, a subadult male (named "Whitey") was observed to kill an infant and presumably wounded another in an observed encounter, and probably killed two more which had disappeared. The period of infanticide coincided with the rapid physical and sexual maturation of this male.

In another subspecies, *C. b. rufomitratu* of the Tana river, Marsh (1979) recorded suspected cases of infanticide ; it lives in predominantly one-male groups.

15. *Orangutan, Pongo pygmaeus*

No clear case of infanticide has been recorded in the orangutans. But Galdikas (1980) reported that two young rehabilitant females might have been killed by a young rehabilitant male.

16. *Common chimpanzee, Pan troglodytes schweinfurthii*

This chimpanzee lives in multimale, multifemale "communities", and adolescent females frequently migrate from one community to another. Infanticide has been recorded by several authors in Africa, e.g., Suzuki (1971), Bygott (1972), Goodall (1977), Goodall et al. (1979), Nishida et al. (1979), Kawanaka (1981), and Fossey (1984). Both Suzuki and Bygott observed that in both instances a group of adult males somehow acquired an infant and ate it alive. Goodall et al. (1979) and Nishida et al. (1979) recorded observed cases of infanticide as well as inferred ones. Kawanaka (1981) reported that in the Mahali Mountains study between the years 1965 to 1979, infanticide accounted for 22 per cent of all infant deaths in a sample of 33 live-born infants. From the data of 12 cases summarised by Fossey (1984), it appears that the aggressor was an adult male in 8 cases and an adult female in four. The event happened within the community in 6 cases and outside it in 5 (one case was not clear). In all cases except two, the killed infant was cannibalised—in 6 cases by one or more adult males, and in 3 cases by an adult female and her offspring (in the remaining 3 there was no clear indication).

### 17. *Mountain gorilla, Gorilla gorilla beringei*

The mountain gorilla lives in relatively stable family groups of 2-20 individuals. Each group contains at least one dominant (silverback) male, 1 or 2 subordinate (blackback) males, 3-6 adult females and 4-6 immatures.

Infanticide has been reported by Fossey (1979, 1981, 1984) in groups in Rwanda (South Africa) which had been under observation for over 15 years. During this period, 9 cases of infanticide were recorded. Most of these cases occurred during violent intergroup interactions when one dominant (Silverback) male challenged another for the possession of females. The infanticidal silverbacks were often relatively young and were in the process of forming their own reproductive units. Infanticide often precipitated the emigration of the victims' mother to another group (in three such cases, the new group was in fact of the infanticidal male).

Of the cases of infanticide recorded by Fossey (1984), 3 were observed, and the remainder inferred ; the age of the infant killed varied from 1 day to about 5-11 months, in one case over 36 months.

## INFANTICIDE IN MAN

### 1. *General*

Human infanticide can take many forms ranging from outright physical killing of the infant to its neglect, abuse, etc. It includes destroying the foetus by abortion, or by killing it outright by piercing the abdomen with a sharp instrument, etc. The infant may be drowned in water, placed in a basket and floated down the river; left alone in a jungle or the middle of a desert to die of starvation or be killed by predators. The subject has been reviewed by several authorities, notably Chandrasekhar (1959, India), Dickeman (1975, 1984), S.B. Hrdy (1979), Harris (1977), Williamson (1978), Scrimshaw (1984), Johansson (1984), Daly and Wilson (1984) and Bugos Jr. and McCarthy (1984).\*

Infanticide is found in all societies, from the most primitive to the most civilised, throughout the world and over the centuries. Earliest man, in the hunter-gatherer, horticulturist and early agrarian societies, practised it for supposed purposes as diverse as population control and maintenance of the social structure (Dickeman 1975). In London in the 19th century, infants were commonly left abandoned in parks and ditches to die, and similar practices to kill infants were found in many parts of Europe (Scrimshaw 1984). Although infanticide seems to have disappeared from most parts of the world, it is said to be still practised in China.

\* I have personally knew a man who had committed infanticide. He was a Non-Commissioned Officer from Garhwal (Uttar Pradesh) on the South-East Asia Front during the Second World War. In a moment of rare candour, under the influence of mild drink, he admitted having strangled to death, with the mother's consent, his newborn daughter, because he already had four daughters. He was quite unrepentant and did not regard this act as a heinous crime.

As stated in a large number of cases, human infanticide can be caused in a variety of ways, viz., deliberate killing (sometimes in rituals to propitiate a god or goddess, or to obtain kingship), placing the child in a dangerous situation, abandonment, "accidental" death, excessive physical punishment, and lowered biological support.

Whatever the immediate method or methods used for infanticide, the practice has certain limited biological consequences. Among the most obvious of these is population control, particularly where the infant killed is a female. On the whole, however, it may be pointed out that infanticide in man was on so small a scale compared to the total population in an area, that it probably did not have any large-scale biological consequences, and the various theories advanced to account for infanticide (particularly, comparisons with the nonhuman primates and other animals) are mostly idle speculations. Infanticide in man is simply a case of social pathology.

## 2. Some Theoretical Considerations

Man is remarkable among, and different from, all other primates (including its closest hominoid allies, the higher apes) in having lost the oestrous period in its menstrual cycle and its capacity for successful continuous annual reproduction, almost immediately after parturition and without the loss of the previous infant. This increase in reproductive capacity is to be balanced against a long span of life and slow maturation, the child being more or less dependent upon the parents for the first 17 or 18 years of its life, more so in modern societies with the need for higher education, the incidence of unemployment, etc.

As already stated, infanticide has been a common practice in many human societies, probably from the earliest times, and persists, though in a weak form, to modern times. The practice evidently arose because (in spite of man being ecologically a highly adaptable and successful 'generalist'), the need for some form of population control was present, and infanticide was an easily available means (Dickeman 1975, Ripley 1980). (Other available means of course are adult killings in warfare, abortions, the spread of pestilential diseases, etc., see Divale and Harris 1976, Hirschfield et al. 1978.) Ripley (1980), in fact has gone so far as to assert that "... the possibility of adaptive infanticide is an inevitable accompaniment of the status of an ecologically generalist species and is simply a price our species had to pay in the process of becoming, and remaining, human" (p. 383).

Infanticide in man is different from that in the nonhuman primates. In man it is most often practiced by females (with or without male parental concurrence) on their own progeny. Whether the motivation is 'biological benefit' is doubtful, the more likely motive being socio-economic (e.g., reduction in the number of daughters who are a social liability, as in India). The practice must be considered largely, if not wholly, an example of social pathology. It results in the *post hoc* correction of the following reproductive "errors" undesirable sex ratios or birth orders; reduction of family size for optimal parental care; the elimination of defectives; etc. In the higher apes, both sexes commit infanticide though males seem to do it more often. In the langurs infanticide is almost always done by an outside male for the possession of a female who, after the infant's death, quickly comes into oestrus and mates with the killer male.

## THEORIES OF INFANTICIDE (TOGETHER WITH A NEW THEORY)

1. *The Various Theories*

In recent years various theories have been advanced to account for the unusual and even bizarre phenomenon of infanticide by conspecifics, for, apart from man, the killing of conspecifics irrespective of age, is an uncommon feature. In man, on the contrary, killings of fellow humans on a large, even a vast scale, has been a regular feature of human society from the earliest to modern times.

To discuss these theories, it is necessary to separate the proximate from the supposedly ultimate or theoretical (evolutionary) causes. Most of these theories have been advanced largely on the basis of examples and incidents taken from primates, but we must take a broader view based on all classes of animals.

The theories so far advanced are as follows :—

- (a) Establishing social bonds (Sugiyama 1964, 1965 a,b, 1966, 1967).
- (b) Sexual excitement of males (Mohnot 1971).
- (c) Xenophobia (Carpenter 1942, and others).
- (d) Dominance assertion (Parthasarathy and Rahaman 1974).
- (e) Sexual selection (S.B. Hrdy 1974, 1977).
- (f) Social pathology (maladaptiveness and enforced proximity) (Curtin 1977, Dolhinow 1977, Curtin and Dolhinow 1978, 1979, Boggess 1979).
- (g) Resource competition (Rudran 1979 a,b).
- (h) Population control (density dependent infanticide) and prevention of inbreeding (Sugiyama 1967, Eisenberg et al. 1972, Ripley 1980).
- (i) Following response induction (Pirta 1981).
- (j) Parental manipulation (Alexander 1974, Dickeman 1975).
- (k) Genetic proneness to infanticide (a new theory) (Roonwal, present account).

These theories are discussed below briefly, with examples.

a) *Establishing social bonds*

This theory was advanced by Sugiyama (1964, 1965a, b, 1966, 1967) on the basis of his observations on the langurs (*Presbytis entellus*) in Dharwar, southern India. He noted that the loss of the infant stimulated the onset of oestrus in the infants' mother. This situation helped in establishing social bonds between the group females and the new male. (Also see infra : "Following Response Induction", Pirta 1981.)

(b) *Sexual excitement of males*

Mohnot (1971), who was the first author to eye-witness infant killing by males in the Hanuman langur, *Presbytis entellus*, in Jodhpur (India), stated that infanticide was induced by sexual excitement. He wrote (p. 196) :

"The aggressive attitude of the attackers, their sexual excitement (with the erection of the penis), their probable influence on the oestrus of the females, presentation by the oestrus females towards the invader, subsequent copulations

by them and their overstay with the sexually excited females indicates that the probable motive behind the attacks has some relationship with the sexual urge of the males."

All the infant deprived females came into oestrus quickly (within 6 days of the death of the infant), and mostly copulated with the killer males.

### (c) *Xenophobia*

The killing of conspecific strangers is widespread among animals and has been reported to occur in several groups of animals, e.g., insects, fowl, geese, wolves, hyenas, primates and man. For example, in the Indian termite, *Anacanthotermes macrocephalus*, when two workers from different colonies are brought together, they often attack each other viciously, and within minutes one of them is seen lying fatally wounded or even cleanly decapitated (Roonwal, personal observations).

When infants are the victims, the phenomenon is called xenophobic infanticide. I have observed it in termites. Among primates it has been recorded by Carpenter (1942) in an introduced but free-ranging colony of the rhesus macaque, *Macaca mulatta*, in the Cayo Santiago Island in the West Indies ; in Sri Lanka in the Hanuman langur, *Presbytis entellus thersites*, by S.B. Hrdy (1979) ; and by others in mammals, including the northern subspecies of *P. entellus*, and the chimpanzee (vide supra, Introduction). It is sometimes accompanied by cannibalism, but food-need is only a partial explanation. Its causes remain problematic.

### (d) *Dominance assertion*

From inferred cases in the Hanuman langur, *Presbytis entellus*, Parthasarathy and Rahaman (1974), postulated that infanticide was committed by the male to assert his dominant status. In the red howler monkey, *Aloutta seniculus*, Crockett and Sekulic (1984), who analysed several inferred cases of infanticide, concluded that the infant killers were new or newly dominant males (vide supra).

### (e) *Sexual selection*

The sexual selection theory was proposed by S.B. Hrdy (1974, 1977) to account for infanticide in the Hanuman langur, *Presbytis entellus*, and postulated that it evolved as a result of male-male competition for gaining reproductive advantage. Following infanticide, the mother often comes into oestrus quickly and copulate with the killer male, a situation which provides support to the theory. On the other hand, the expectation that the attacking male attacks and kills only those infants who were not sired by him, is seldom proved for the simple reason that he cannot possibly recognise his own offspring (even man cannot do so).

The theory has been widely discussed, with arguments both for and against it, e.g., by Dolhinow (1977), Curtin (1977), Curtin and Dolhinow (1978, 1979), S.B. Hrdy (1977 a,b, 1979, 1984), Rudran (1979 a,b), Boggess (1979, 1984), Vogel (1979), Makwana (1979), Makwana and Advani (1981), Ripley (1980), Vogel and Loch (1984), Winkler et al. (1984), Hausfater (1984 a,b), Sugiyama (1984), Hrdy and Hausfater (1984), Sommer and Mohnot (1985), Newton (1986) and Mohnot et al. (1987).



Boggess (1979, 1984) in particular has stressed that there is no evidence to suggest that infanticide is the result of organised, goal-oriented behaviour in the long-term evolutionary sense. The contention of Mohnot et al. 1987, p. 23, that a male's repeated attack on the same infant until he succeeds in killing it, is "goal-oriented", is only in the immediate context, not in the long-term sense.

(f) *Social pathology (maladaptiveness) and enforce proximity:*

Infanticide by langur males (*Presbytis entellus*) is a maladaptive behaviour, even a case of social pathology, and occurs in areas where their population density is fairly high (Curtin 1977, Dolhinow 1977, Curtin and Dolhinow 1978, 1979, Boggess 1979, 1980, 1984, ripley 1980.)

It is pertinent to point out, for example, that while infanticide occurs regularly in areas which have a high density of langurs and are disturbed by human proximity and provisioning by man (Jodhpur, Mt. Abu, Dharwar), it is absent in Nepal (Boggess, 1976-1984) and in the Rajaji Wildlife Sanctuary in north-western Uttar Pradesh (Laws and Laws 1983) where langur population is not too high and the area is undisturbed. As Boggess (1984, pp. 307-308), points out, in this "enforced proximity hypothesis", inspite of the above points which may support it, it is difficult to prove that "enforced proximity results in infant killing"

(g) *Resource competition*

On the basis of observations in the New World howler monkey, *Allouatta seniculus*, Rudran (1979 a,b) concluded that increasing male fitness through the reproductive strategy of infanticide (Hrdy's Sexual Selection Theory, supra) is not the primary reason of infanticide but merely a secondary consequence. Infanticide is primarily an extension of the process of eliminating unrelated food competitors who do not benefit the invading male in any way. Regulation of population growth is another consequence of infanticide. According to Rudran, the differences in the ratios of benefits to cost of the process may explain the observed differences in this pattern of social change between the red howler monkey (*Alouatta seniculus*) and other primates (e.g., the langur, *Presbytis entellus*).

(h) *Population control (density-dependant infanticide) and prevention of inbreeding.*

On the basis of data from the Hanuman langur, *Presbytis entellus*, in Dharwar, Sugiyama (1967) suggested that infanticide is the product of high population densities and is a possible mechanism for population control ; Eisenberg et al. (1972) came to the same conclusion. In man, infanticide probably serves as a means of population control and prevents inbreeding (Dickman 1975, Ripley 1979, 1980). The device serves as a means of ensuring genetic polymorphism in the langurs also where the social structure and breeding pattern favour inbreeding (Seger 1977). Boggess (1984) has brought forward several factors which go against this theory. Density dependent infanticide has also been observed in birds (vide supra).

(i) *'Following response' induction.*

Pirta (1981) emphasised that a wide range of behaviour patterns are employed by males to induce a "following response" in females. A male's glance and movement are sometimes enough for this purpose during consort relations. At other times, a male may clasp, pull and bite a female, as in the hamadryas baboon, *Papio hamadryas* (Kummert and Kurt 1965). In the Olive baboon, *Papio anubis*, the male stole an infant from a female several times to induce a following response. In extreme cases, a male wounds (usually by biting) or even kills an infant, as in the Hanuman langur (*Presbytis entellus*) or in the Rhesus macaque (*Macaca mulatta*). (Also vide supra, "Establishing Social Bonds", Sugiyama 1964-1967.)

(j) *Parental manipulation*

Infanticide in traditional human societies, in contrast to other primates, appears to be primarily a sort of parental manipulation of their progeny to achieve various ends (Alexander 1974, Dickman 1975, Roonwal 1977). The death of an infant and the termination of parental investment will sometimes improve the chances of survival of either the mother or her older offspring, or will increase the reproductive fitness of both the parents (Hrdy and Hausfater 1984). (Also vide supra, "Infanticide in Man".)

(k) *Genetic proneness to infanticide (a new theory)*

The new theory presented below is based on happenings in the Hanuman langur.

The clearest details of infanticide by males in the Hanuman langur, *Presbytis entellus* (vide supra), are those provided by Mohnot (1971) and Sommer and Mohnot (1985). They show that only some males are infanticidal and repeatedly attack infants and kill them. In the example from Jodhpur (Mohnot 1971, pp. 187-194), all 3 infants of a group (p. 26) were killed by the *same* male leader (YA —1) after he had assumed leadership. Before each killing he was in an agitated mood and was sexually excited (with the penis erect). But sexual desire alone was not the motive. Earlier, several females had presented themselves to him and he had either copulated with them or ignored them. It was clear that he temporarily became 'abnormal' and prone to killing infants repeatedly, in much the same way as a criminally-minded man repeatedly commits murder.

In the other example from Jodhpur, provided by Sommer and Mohnot (1971), 5 adult males were replaced in three bisexual groups as a result of invasion by males from different neighbouring bands. Of the 5 new males only 3 proved to be infanticidal; the remaining 2 were harmless.

The simplest explanation of these events is that the killer males were genetically prone to killing. All other consequences which followed, or assumed to follow, the killings were secondary and incidental and no long-term evolutionary goal need be assigned to them.

The theory finds support from groups other than the primates. Thus, in the Corn earworm (*Heliothis* sp., Insecta : Lepidoptera), some infanticidal strains are

over 20 times more cannibalistic than others (vide supra, "Infanticide in the Invertebrates"). In the Amphibia (the spadefoot toads of the genus *Scaphiopus*), in a single population, there may be a noncannibalistic morph and a highly cannibalistic one (vide supra).

## 2. Discussion

It will be seen that the majority of the theories of infanticide, as discussed above, refer to the nonhuman primates, and indeed to a single species, the Hanuman langur (*Presbytis entellus*). The reason for this narrow approach evidently is that this species has provided the clearest examples of actually observed infanticide and has attracted the attention of a large number of primatologists both for field observations and for theorisation. The theories so far proposed have inevitably suffered from this restricted approach. I have attempted to correct the imbalance and have proposed a new theory which receives support not merely from mammals but also from various other groups of animals (Amphibia, insects).

Man, however, does not fall fully in line with the other animals, and infanticide here would seem to result from proximate causes (e.g., parental manipulation) rather than from long term evolutionary ones.

On the whole, it can be said that infanticide (though a bizarre phenomenon, of killing one's own conspecifics) is widespread throughout the animal kingdom and has a limited evolutionary purpose to serve. The reasons inducing it are a mixture of proximate and ultimate causes, and a clear-cut evolutionary picture fails to emerge.

## SUMMARY

1. Although infanticide in man and other animals has been known to exist for ages, it is only in the last 25 years or so that it has been examined more scientifically, mainly because of the discovery of its regular occurrence in the nonhuman primates. A large body of information has thus become available, and numerous theories postulated to account for the phenomenon.

2. The object of the present account is to assess this comparative information critically in the evolutionary context. Other aspects such as infanticide and cannibalism, etc. are also discussed.

3. In the invertebrates, which cover a vast field and constitute nearly 95 per cent of all the known animals, infanticide is widespread and occurs in almost all groups from the Protozoa upward.

4. Infanticide in the vertebrate groups (fishes, amphibians, birds and mammals) is analysed. The most numerous and the best documented examples are from the nonhuman primates, and they have stimulated a considerable amount of theorisation about the possible evolutionary motives for committing infanticide.

5. Infanticide in man has occurred from the earliest times and continues to do so even today all over the world in the most primitive and the most sophisticated societies. In the evolutionary context, it does not fit in easily with the animals, and seems to have its own motivations.

6. Infanticide has been the subject of much theorisation. The numerous theories postulated to account for it in the evolutionary context are discussed in considerable detail. They were found to be inadequate as they cover a narrow field, sometimes only isolated cases in a single species. A new theory (of Genetic Proneness to Infanticide) is postulated to cover a wide field and cases of both vertebrates and invertebrates.

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