INFANTICIDE

Comparative and Evolutionary Perspectives

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Comparative and Evolutionary Perspectives on Infanticide: Introduction and Overview

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INTRODUCTION

Infanticide has only recently come to be regarded as a biologically significant phenomenon. The fact that infanticide is considered an abhorrent practice in our own society is only a part of the reason why researchers for so long failed to realize how widespread infanticide is in the natural world. A second reason had to do with evidence. Early field reports of infanticide among langur monkeys and lions were sketchy; data were even sparser for other wild mammals. In the case of birds, researchers knew that egg destruction by conspecifics and siblicide occurred but the true frequencies of these acts was unknown and they were generally considered to be isolated phenomena. Eventually, detailed information emerged from laboratory studies of rodents, but infanticide and cannibalism in these species was typically attributed to overcrowding or to other features of captivity itself.

Yet a third reason why the importance of infanticide was so long unrecognized was that reigning intellectual traditions in the biological and social sciences evaluated behaviors according to their contributions to survival of the species and the group. From this perspective there could be only two explanations for infanticide: either the behavior was pathological or else it functioned adaptively to regulate population size through prevention of overcrowding (Calhoun, 1966; Christian *et* *al.,* 1963). Any behavior which resulted in death or injury to offspring was by definition "abnormal" (see for example King, 1963: 85–6).

According to classical ethology, animals (with the notable exception of humans) rarely kill members of their own species under natural conditions (Lorenz, 1966). Nevertheless, it was widely accepted that if sufficiently stressed, as through crowding, animals might become infanticidal or cannibalistic (Calhoun, 1962); such behavior was considered maladaptive. By the late 1970's however, intraspecific killing, including infanticide, had become more widely documented. In many cases there was no indication of either crowding or "abnormal" conditions. The focus of research shifted from *whether* infanticide occurred under natural conditions to *why* it occurred, and *how* frequently. Some researchers even began to ask if there were circumstances under which infanticide might be reproductively advantageous for one or more of the individuals involved.

This shift in thinking about infanticide can be traced in large part to Williams' influential critique of current evolutionary thinking (1966) and to seminal writings on kin selection and sexual selection by W. D. Hamilton (1964a) and Robert Trivers (1972). Once infanticide began to be explained in evolutionary terms (Hrdy 1974), published reports of infanticide in mammals increased dramatically. Ethologists began to recognize how widespread intraspecific killing, infanticide, and cannibalism—behaviors long considered "unnatural"—actually were. As several papers in this volume amply demonstrate, infanticide and cannibalism are for many animals everyday occurrences during those seasons when infants are present (Dominey and Blumer, Chapter 3, this volume; Polis, Chapter 5, this volume). Likewise, in certain species of birds, the first-hatched chick inevitably kills its younger sibling (Mock, Chapter 1, this volume). For many other species, infanticide is far less common than in the cases just cited, but it nevertheless plays an important role in shaping reproductive biology and social behavior.

DEFINITIONS

According to a conventional definition, such as the one used by Mock (Chapter 1, this volume), *infanticide* is any behavior that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the perpetrator's own species. This definition has the merit of being easily comprehended across a spectrum of disciplines. However, as Mildred Dickemann points out in the introduction to Section IV of this volume, the decision to focus only on elimination of an embryo or newborn is somewhat arbitrary. In agreement with Dickemann, we feel that from the standpoint of development of theory, it may be useful to formulate a single broad definition that includes any form of lethal curtailment of parental investment in offspring brought about by conspecifics. Included in this definition would be curtailment of parental investment through destruction of gametes (see Charnov, Chapter 7, this volume) or reabsorption of a foetus. Because this definition applies throughout the period of offspring dependence (Hayssen, Chapter 6, this volume) no distinction between infanticide or pedicide (killing of children) is implied unless specified. In some species (such as humans) parental investment continues well after weaning and the decision by a parent to terminate investment may occasionally take place late in the overall reproductive process. At this level of generality, contraception, abortion, direct killing of an infant, or nutritional neglect of a child are seen as related phenomena, differing only in the stage of the reproductive continuum at which curtailment of parental investment occurs. Furthermore, as Dickemann stresses, only by viewing foeticide-infanticide-pedicide in the context of the whole range of possible manipulations of the reproductive continuum can we make meaningful statements about the selective value of infanticidal behavior in cost-benefit terms.

Our chief concern in recommending the use, at least over the next few years, of such a broad definition is to avoid at this early stage in research narrowing our focus to the point that we arbitrarily exclude from consideration any of the remarkably diverse array of intraspecific social behaviors which lead to decreased survival of immatures. This point may be particularly pertinent in the case of humans where so-called *deferred infanticide* takes many forms and where reduced investment by parents in unwanted children may continue long after weaning (Scrimshaw, Chapter 22, this volume).

FUNCTIONAL CLASSES OF INFANTICIDE AND ULTIMATE CAUSATION

The above definition reflects our view that infanticide is a protean phenomenon. Between and within taxa, patterns of infanticidal behavior exhibit wide variation. Adults of either sex, and even other immatures, have been implicated in infanticide and the perpetrator may be either a close or distant relative of the victim, or not related at all. About the only consistent feature in all cases of infanticide, as broadly defined, is the relative vulnerability of the victim and the fact that offspring, with a few exceptions, represent a costly accumulation of resources contributed either by one or both parents. Where parents themselves are implicated in the elimination of offspring, it is often because continued demands by the offspring on scarce resources are anticipated.

Among the many surprising forms of infanticide described in the following chapters are the cases of siblicide in birds, a phenomenon that parents themselves facilitate by laying eggs at intervals so that the first-hatched chick is typically larger and stronger than the second. Furthermore the parents generally do not intervene when the older chick attacks the younger (Mock, Chapter 1, this volume). Sand sharks provide another striking example: siblings begin to devour one another while still squirming inside the mother's oviduct, a hitherto undreamed of hazard of viviparity (Dominey and Blumer, Chapter 3, this volume). Here, as in the avian cases, the individual gain to the surviving sibling apparently overrides losses in inclusive fitness incurred by itself and its parents from the death of close kin. In other fish species, and in many vertebrates, cannibalism by relatives may be an occasional byproduct of the way that these organisms obtain food, e.g., through filter feeding (Fox, 1975a; Dominey and Blumer, Chapter 3, this volume; Polis, Chapter 5, this volume).

For most mammals, however, with the exception of humans and other species where mothers in certain circumstances may opt to abandon offspring, infants tend to be killed by unrelated individuals who either exploit the infant as a resource (i.e., cannibalism) or who thereby gain access to physical resources (such as food or a nest site) or to the breeding capacity of one of the infant's parents. The death of an unrelated infant also reduces the net reproductive success of a competitor of the infanticidal individual.

In organizing our thinking about the range of behaviors which fall under our broad definition of infanticide, we have found it helpful to use Hrdy's (1979) five functional categories of infanticide: (1) *exploitation* of the infant as a resource, usually cannibalism; (2) *competition for resources* where death of the infant increases resources available to the killer or its lineage; (3) *sexual selection*, where individuals improve their own opportunities to breed by eliminating dependent offspring of a prospective mate; and (4) *parental manipulation* of progeny, where parents on average increase their own lifetime reproductive success by eliminating particular offspring. Obviously, though, not all cases of infanticide are adaptive for the killer. Thus we have reserved the term (5) *social pathology* for cases where infanticide on average decreases the fitness of the infanticidal individual. It is also possible that researchers may eventually document cases in which infanticide is selectively neutral, but for a variety of reasons, this is highly problematic.

Several earlier theories emphasized the role of infanticide in population regulation. Not surprisingly, this emphasis was most strong in studies of infanticide in rodents, since many species are characterized by marked fluctuations in population density and associated density-dependent changes in behavior, but population regulation has also been invoked to explain infanticide among primates (Ripley, 1980). There is little question that under circumstances of high population density infanticide-foeticide not only occurs with increased frequency, but also has the effect of reducing recruitment to the population through births. However, as Brooks (Chapter 17, this volume) points out, in many cases the population has already begun to decline well before the increase in infanticide is observed. Although it is theoretically possible that infanticide might serve as an adaptive mechanism to regulate population size, this would be limited to cases of isolated populations characterized by low migration and high rates of extinction. Hence, the conditions permitting such group selection would be rare among most vertebrates. More often, population regulation will be a secondary consequence of infanticide. By and large then, one should look for benefits to individuals rather than groups for the primary selection pressure in infanticide (Williams, 1966; Bates and Lees, 1979).

Available evidence on infanticide from wild populations is not nearly as complete or as precise as one might wish. For no single animal population have the costs and benefits of infanticidal behavior been determined for all parties involved. Nevertheless, even at this early stage, there is sufficient evidence to allow us to evaluate roughly the relative frequency of different types of infanticide in various taxa.

Not surprisingly, exploitation of immatures as a resource, usually through cannibalism, turns out to be most common among predatory species, particularly insects, spiders, amphibians, and fishes where there are substantial size differences between adults and immature forms, and where there is often little parental protection (see Simon, Chapter 4, Dominey and Blumer, Chapter 3, and Polis, Chapter 5, this volume). Sometimes infants are eaten by close relatives, and occasionally even by their own parents. However, most species where this might otherwise be a problem appear to have evolved specific mechanisms to reduce its chance occurrence, e.g., parents and offspring occupy separate feeding niches.

Of all classes of infanticide, the most difficult to document convincingly is resource competition since one must first demonstrate that some resource is actually limiting, and, second, that infanticidal individuals thereby gain increased access to the resource (cf. Leland *et al.*, Chapter 8, this volume). Conversely, it could be argued—admittedly at a fairly high level of abstraction—that virtually all classes of infanticide ultimately relate to competition for resources. At present, the best documented cases of infanticide due to resource competition seem to be among birds (Mock, Chapter 1, this volume) and ground squirrels (Sherman, 1981). Infanticide is a major source of infant mortality among ground squirrels and adult females turn out to be the primary killers. Mothers whose infants are killed often vacate their "unsafe" burrows, leaving an available nest site for subsequent use by the infanticidal female.

In sexually selected infanticide, breeding opportunities rather than ecological resources are at issue. This form of infanticide appears to be most prevalent among polygynous mating systems where breeding occurs throughout the year, and where male tenure of access to females is on average short (Hrdy, 1977; Chapman and Hausfater, 1979). Typically infanticide follows male takeovers when a male from outside the troop usurps the resident male. However, cases are known in which a male currently residing in a troop kills infants after rising from nonbreeding to breeding status in the troop hierarchy (Wolf, 1980 for wild *Presbytis cristata;* Busse and Gordon, 1983 for captive *Cercocebus atys;* and Leland *et al.,* Chapter 8, this volume for wild *Colobus badius*). In either event males are "entering" a breeding system from which they were previously excluded and hence are unlikely to be the fathers of infants killed. Relatives of the infants, including the mother and probable father defend the infant [see Chapters by Leland *et al.* (8); Crockett and Sekulic (9); Collins *et al.* (10), and Fossey (11), in Section II of this volume].

Infanticide by immigrant males was first observed by scientists among Hanuman langur monkeys at Dharwar in South India (Sugiyama, 1965b, and this volume, Chapter 15). Unweaned infants were attacked by males from all-male bands which had invaded the one-male harem groups (the basic breeding unit in this population) and evicted the resident male. Similar take-overs followed by attacks on unweaned infants have now been reported among langurs at Jodhpur (Mohnot, 1971a; Vogel and Loch, Chapter 12, this volume) and Mount Abu (Hrdy, 1977b), but not at certain other study sites in both Nepal and India (Curtin and Dolhinow, 1978; Boggess, Chapter 14, this volume). This within-species variation has led to considerable controversy concerning the causes and adaptive significance of langur infanticide (Dolhinow, 1977; Curtin, 1977; Curtin and Dolhinow, 1978, 1979; Boggess, 1979, 1980, and this volume Chapter 14; Vogel, 1979; Schubert, 1982; Harraway, 1983) and viewpoints voiced in this controversy have become part of the intellectual background for subsequent studies of infanticide in other animal species.

In contrast to other primates, infanticide as practiced in traditional human societies appears to be primarily a form of parental manipulation of their progeny (Alexander, 1974; Dickeman, 1975, and this volume). The death of an infant and termination of parental investment will sometimes improve the chances for survival of either the mother or her older offspring or will otherwise lead to greater net reproductive fitness for the mother of the infant, the father, or both. The circumstances surrounding infanticide in humans include the existence of older offspring whose chances for survival might be diminished if resources were diverted to a new infant, illegitimacy, deformity, poor ecological conditions, or economic patterns that give one sex lower breeding or resource accrual potential than the other, or else make one sex more expensive than the other. A woman confronted with stressful conditions (including the prospect of little or no paternal support) may spontaneously lose her infant prior to birth (Baird, 1945; Berle and Javert, 1954) Roberts and Lowe, 1975; Bernds and Barash, 1979). Interestingly, sonograms of women in the first trimester of pregnancy reveal that twins are conceived two to four times more often than they are born; in the majority of cases, the smaller of the two foetuses disappears by the third trimester and is apparently reabsorbed by the mother (Robinson and Caines, 1977; Varma, 1979). Even where parental investment is not terminated outright through abortion or infanticide, nurturance may be reduced and offspring neglected or abused (Daly and Wilson, 1978).

In sum, from the standpoint of understanding the evolution of infanticide, it is critical to recognize that many different kinds of social, ecological, and parental interactions can reduce an infant's chances of survival or reflect a parental decision to terminate further investment in an offspring. There is no unitary mechanism across species, and the infanticidal individual may gain a reproductive advantage in any of a number of different ways. Nevertheless, it is possible to restate each of the above functional classes of infanticide as an explanatory hypothesis which in turn leads to its own set of testable predictions. In the case of sexually selected infanticide among primates, for example, it is predicted that (1) infanticidal behavior is heritable; (2) that an infanticidal male will typically not be the father of any infant he kills; (3) that on average the killer will gain sexual access to the mother sooner than if the infant had lived; and (4) that the reproductive gain to the killer will be a function of the average tenure length and age of the infant at death. These predictions as well as those generated for other functional classes of infanticide are summarized in Table I.

Although for various reasons the most sustained thought has been given to deriving predictions suitable for testing the first four functional categories of infanticide listed above, Glass (1983) has recently suggested several novel ways of testing both the social pathology hypothesis and the idea that infanticide is brought about by high levels of social stress. Clearly, considerable overlap exists in the specific predictions drawn from these various hypotheses. Thus, nearly all hypotheses—except the sexual selection hypothesis—predict that both sexes should engage in killing of unrelated infants where possible. Nevertheless Table I suggests that the possibility of distinguishing between these

Table I. Predictions generated by five explanatory hypotheses for infanticide[a]

Class of infanticide	Degree of relationship	Age of infant	Age and sex of killer	Nature of gain
1. Exploitation as resource	Distant	Size and vulnerability more important than age	Either sex at any age large enough to subdue victim	Nutritional gain by killer
2. Competition for Resources	Distant	Vulnerability more important than age	Either sex usually (but not always) adults	Increased availability of resources for killer and killer's kin
3. Sexual selection	Distant	Unweaned (but specifically younger than age at which ovulation resumes or amenorrhea terminated	Adult of sex investing least in offspring, typically male	Additional breeding opportunity
4. Parental manipulation	Close (~.5)	Just after birth (but any age possible depending on time-course of parental investment)	Either sex, but most likely an individual of the sex investing most in offspring, typically female	Increased inclusive fitness for one or both parents
5. Social pathology	Relationship not critical for this hypothesis	Size, proximity, and vulnerability more important than age	Adult of sex most likely to respond to social disturbance with increased aggressiveness	None for the killer directly, although decrease in population density may eventually result

[a] Specific predictions concern the degree of relationship between the infanticidal individual and the infant, age of the infant killed, sex of the killer, and the nature of the gain accruing to the infanticidal individual.

five explanatory hypotheses, as applied to any given case of infanticide, does exist.

INFANTICIDE AS A SELECTIVE PRESSURE

Zoologists have long taken it for granted that predation was a significant pressure selecting for a variety of morphological and behavioral attributes, such as, the large body size of terrestrial primates (relative to arboreal ones), their retreat at night to sleeping trees, or their social traits like gregariousness or alarm calling. However few field workers (mainly terrestrial and diurnal) have actually witnessed predators (mainly aerial or nocturnal) kill and eat a monkey. Nevertheless, comparisons with other taxa, the occasional disappearance of healthy animals, the obvious alarm exhibited by monkeys confronted by a leopard or other potential predator, as well as the complex of adaptations mentioned above, have been sufficient to convince virtually all primatologists that predation has been an important factor in primate evolution.

As with predation, eyewitness observations of infanticide are uncommon except among laboratory rodents and certain species of birds, fish, and invertebrates. Except for a few groups, infanticide tends to be only sketchily documented among wild mammals. Nevertheless, the majority of scientists present at the Wenner-Gren symposium at Cornell University—admittedly not a random sample—now take for granted that the destruction of infants by conspecifics is a chronic hazard in the lives of many animals and, in some cases, even the major source of infant mortality. This assumption has radically altered the way that we interpret certain well-known behaviors.

In his review of infanticide among amphibians, Simon (this volume, Chapter 4) notes the high correlation between the occurrence of egg cannibalism and the existence of parental care, and asks the question: Is this correlation due to the need of brooding parents to supplement their energy intake during the long period of egg attendance, or might parental care itself have evolved in these species as a defense against cannibalism? It is an easy enough idea to test. The first hypothesis predicts that a male will eat eggs that he himself has fertilized, while the second predicts that he will not do so.

The more important point, however, is that if one accepts infanticide as a frequent occurrence in the social life of a species, an occurrence more costly to one sex than the other, it then becomes reasonable to look for evolved counterstrategies to infanticide. Thus, adult male baboons who carry infants on their ventrum during fights, were believed to be using the infants as "agonistic buffers" to shield themselves from attack by more dominant males. However, according to a more recent interpretation, some adult males in such situations are carrying infants in order to protect them from infanticidal attacks by unrelated, immigrant males (Busse and Hamilton, 1981; Collins *et al.*, Chapter 10, this volume).

Preventive measures may have been taken even further in the case of tree hole-dwelling mosquitoes of the genus *Toxorhynchites* (reviewed by Polis, Chapter 5, this volume). Just before pupation, a highly vulnerable quiescent phase in the life cycle of these insects, the larvae embark on a "killing frenzy," cannibalizing all accessible conspecifics. The apparent selection pressure behind this massacre is the *prospect* of infanticide: if even one younger larva survives, it would consume the negligent killer once pupation rendered it vulnerable. A primary selective pressure for the killing frenzy can thus be thought of as an infanticidal act which has not yet occurred and which will rarely ever be seen!

Another example of how the recent awareness of infanticide has led to reinterpretation of well known phenomena is the case of the "Bruce effect" (Bruce, 1960). Among a wide array of wild and laboratory-housed mice and voles (*Mus, Peromyscus, Microtus, Clethrionomys*) a recently inseminated female who is exposed to a strange male, other than her mate, spontaneously terminates her pregnancy. Recently, Wilson (1975) and others have pointed out that reproductive advantages would accrue to the strange male who caused a female to divert investment from the offspring of competitors. But as Wilson aptly queried, how could such an ostensibly wasteful and disadvantageous trait evolve among females? However once the possibility was considered that strange males present a threat to the survival of the female's impending litter, a number of researchers simultaneously arrived at the same answer. Faced with a potentially infanticidal male it might well be advantageous for a female to terminate further investment in an ill-fated reproductive venture until she could conceive a litter under more stable social conditions conducive to the infants' survival (Schwagmeyer, 1979; Hrdy, 1979; Labov 1980; 1981b; Huck, Chapter 18, this volume).

Such an interpretation is very new, and its acceptance will depend in large part upon the demonstration that both the Bruce effect and infanticide by strange males do indeed occur in the wild; at present both phenomena have only been observed among captive animals. Alternative interpretations, namely that reabsorption of litters is brought about through crowding and serves to reduce population growth (Chipman *et al.*, 1966), that the Bruce effect is an artifact of laboratory conditions and handling (Bronson, 1979; and others), or that the Bruce effect is an artifact of endocrine process which evolved for reason unrelated to either strange males or infanticide (Keverne and de la Riva, 1982), can not currently be ruled out.

The hypothesis that the Bruce effect evolved as a female counterstrategy to infanticide by males has in turn led to additional speculation about the adaptive significance of spontaneous abortions in animals other than rodents. Hence researchers who have recorded pregnancy termination at the time of male invasions among wild horses, baboons, and lions (Berger, 1983; Pereira, 1983; Packer and Pusey, Chapter 2, this volume) have wondered if a tendency to abort at such times might not sometimes be adaptive. No doubt, some will see these speculations as the construction of sand turrets upon sand castles but it is our opinion that there do exist substantial grounds for taking such ideas seriously, and that they merit considerable further investigation.

Along these lines, Huck (Chapter 18, this volume) designed a series of investigations to test the idea that infanticide has been a selective pressure in the evolution of an analogue of the Bruce effect among hamsters. Taking advantage of the fact that among hamsters females are dominant to males and also infanticidal, he predicted that a strange female should be more likely than a strange male to induce abortion. As predicted, pregnancy was blocked in nearly one-half of the recently mated subordinate female hamsters who were exposed to near-term dominant females.

The realization that infanticide may be a chronic hazard for many species has far-reaching implications for the likelihood that female counterstrategies to infanticide have also evolved. Because female mammals typically invest more care and resources in offspring than do males, maternal counterstrategies to infanticide should be selected for at the level of morphology, reproductive physiology, and temperament. Paternal counterstrategies ought to evolve also and may be manifested in the protection by males of particular infants likely to be their own progeny, as well as in general defense by males of females or territories (Hrdy, 1979). However, the issue of counterstrategies is a complex one and raises questions such as why females have not been *more* successful in eliminating behavior patterns so detrimental to their fitness (Hrdy, 1981; Hausfater, Chapter 13, this volume).

The capacity of females to conceive again soon after losing an infant is, of course, a crucial precondition for sexual selection to favor infanticide in males. Mathematical models presented by Hausfater (Chapter 13, this volume) illustrate that a lag of even relatively short duration between death of a female's offspring and her next conception can make infanticide untenable as a male reproductive strategy. Hence, we predict that sexually selected infanticide will rarely be found among seasonal breeders or in any other setting where environmental or social cues preclude an immediate return to breeding condition by females following the death of their most recent offspring. Nevertheless, even in the case of strictly seasonal breeders infanticide might still confer on males a limited reproductive advantage were it the case that a female who loses her litter in one season is more likely to breed successfully or to produce a larger litter in the subsequent breeding season (H. Hoeck, personal communication; Andelman, 1984).

PROXIMATE CAUSATION

Whereas field researchers have tended to focus on questions about the ultimate causation of infanticide, laboratory scientists, primarily working with rodents, have focused most closely on questions about proximate mechanisms. *How* are infanticidal behaviors elicited or inhibited? What makes some individuals, but not others, kill young? Why are some offspring but not others killed and by what means do infanticidal individuals avoid killing their own offspring?

As in sexual behavior and aggression, male and female rodents exhibit quite different patterns of infanticidal behavior. For this reason, many of the early hormonal studies of infanticide focused on the role of testosterone (reviewed in Svare *et al.,* Chapter 20, this volume). In certain strains of mice for example, pup-killing behavior begins in males at about 1 month of age, approximately the same time that levels of circulating testosterone show a sharp increase. Furthermore, castration reduces infanticide in mice and hormone replacement therapy with testosterone restores infanticide in males and elicits it in females.

Clearly, the evidence is compelling that testosterone is implicated in infanticide by males and females, but it is only part of the story. The effects of gonadal hormones may vary from strain to strain and in some wild strains females are far more infanticidal than males (Jakubowski and Terkel, 1982; Labov, this volume, see Introduction to Part III). Furthermore, adult sensitivity to steroid hormones may be influenced by hormonal levels during prenatal and neonatal life. For example, vom Saal (Chapter 21, this volume) has shown that positioning *in utero* and the sex of adjacent foetuses affect embryonic levels of circulating testosterone which, in turn, appear to influence infanticidal tendencies in adulthood. Since uterine placement of embryos is presumably dictated by chance, vom Saal's findings underscore the existence of stochastic components in the production of infanticidal and noninfanticidal phenotypes.

Other factors influencing infanticide include timing and the nature of social encounters. Hence, when a male mouse is introduced into a cage containing a female and her newborn pups, one of three things happens: the male ignores the pups, attacks them, or engages in caretaking behaviors such as retrieving the pups and keeping them warm. Whether a male kills the pups or cares for them depends both on his recent mating experience, particularly whether or not he mated at about the time the pups might have been conceived (vom Saal and Howard, 1982; vom Saal, this volume), and on his familiarity or past consort relationships with the mother (Labov, 1980; Huck et al., 1982). In the case of monogamously mated gerbils, the situation may be more nearly deterministic. Pup-killing is permanently inhibited in males that have been previously pair-bonded with a breeding female (Elwood and Ostermeyer, Chapter 19, this volume).

Dominance status is another mediating variable in rodent infanticide. Among mice, the achievement of dominant status by a male apparently facilitates infanticide, although this effect may be overridden by prior sexual experience (vom Saal, Chapter 21, this volume). Social rank is also important in infanticide by females though its precise role is not yet well understood (Wasser, 1983a; Fossey, Chapter 11, this volume).

In marked contrast to many invertebrates and nonmammalian vertebrates (Dominey and Blumer, Chapter 3, this volume; Polis, Chapter 5, this volume), there apparently exist among most mammals mechanisms which ensure that parents avoid killing their own offspring. For mothers, endocrinological changes during pregnancy, and the inviolability of young within particular locales (e.g., near the nest, within the group) make it unlikely that mothers would kill or eat their own progeny.

Fathers are more problematic, especially when they have not been paired with the mother in a monogamous arrangement. Although technically it might sometimes be feasible for fathers to identify phenotypes of probable offspring (Holmes and Sherman, 1983), such powers have not yet been documented for progenitors in any species (Labov, 1980). More commonly, one finds that males show a generalized inhibition that forestalls them from killing any infant which they might possibly have fathered, even though this may sometimes result in their being tolerant of infants sired by other males (see McLean, 1983). Given that males who killed their own offspring would usually be drastically selected against, it makes sense for males to be conservative when confronted with uncertain paternity. As vom Saal (Chapter 21, this volume) shows, males in some strains of mice are inhibited from killing *all* infants, regardless of paternity, for a period of weeks after they have mated. Such males do not resume killing infants until after all offspring potentially resulting from this prior episode of mating would be past the age of weaning.

In situations where the targeting of victims is more specific, it appears that males use the mother rather than the infant itself as the cue either to attack or tolerate it. This suggestion, originally proposed for wild langur monkeys (Hrdy, 1977b), has only been systematically tested in the case of rodents (Labov, 1980; Huck *et al.,* 1982). Prior mating experience with an individual scented with the urine of a pregnant female reduced the likelihood that a male would subsequently kill offspring of a female with the same scent. Conversely, males can be "tricked" into killing their own offspring by placing them in the nest of a strange female (Huck, Chapter 18, this volume).

Nevertheless, the detailed workings of most infanticidal mating systems are far from understood. For example, are males generally tolerant of infants and only incited to infanticidal behavior by a particular sequence of stimuli, such as those that might occur in the nest of an unfamiliar female or in an unfamiliar group? Or, as in the case of the monogamous gerbils studied by Elwood and Ostermeyer (Chapter 19, this volume), do generally infanticidal individuals *become* tolerant in the course of a prolonged consortship with a pregnant female? The confounding effects of female counterstrategies and female behaviors which confuse paternity must also be taken into account (Hausfater, Chapter 13, this volume). In the case of higher primates it also seems likely that individuals are making sophisticated evaluations about the risk of retaliation by other group members (Collins *et al.,* Chapter 10; Leland *et al.,* Chapter 8, both this volume), evaluations that may border on conscious decisions (Fossey, Chapter 11, this volume). Whatever the answers to such questions, they will be rooted in the ecology and evolutionary history of the particular species, and pursuit of these answers is likely to be a focus of research in behavioral biology for some years to come.

HUMAN INFANTICIDE VIEWED IN EVOLUTIONARY PERSPECTIVE

Infanticide in Traditional Societies

Virtually every category of infanticide which has been described for other animals can be documented anecdotally for the human species. Given the apparent prevalence of infanticide by alien males in other higher primates, it is plausible that this nonparental form of infanticide may have been important in the course of hominid evolution (Alexander, 1974), but this will be almost impossible to prove. For contemporary western societies there does exist some evidence indicating that infants with alien males living in the same household run an elevated risk from child abuse and even death (Daly and Wilson, 1978 and this volume, Chapter 24), but we doubt that it will ever be possible to conclusively demonstrate *sexually selected* infanticide among humans. Not least among the problems would be the need to discover a genetic component underlying infanticidal behavior (Lenington, 1981). Furthermore, the contemporary data fail to show that males benefit reproductively from child abuse, child homicide or infanticide, and indeed, the opposite could be argued more forcefully.

Whether or not infanticide is sanctioned by a particular society, such practices are rarely recorded. Infanticide must therefore be derived primarily from interviews with individuals who recount—with varying degrees of reliability—personal experiences or village hearsay (Shostak, 1981). Bugos and McCarthy (Chapter 25, this volume) describe from firsthand experience informant evasiveness and other difficulties encountered by researchers attempting to collect information about infanticide. Ironically, only when infanticide is outlawed in societies with centralized governments do we begin to have fairly extensive documentation of infanticide in the form of sex ratio data derived from censuses (Miller, 1981 for India) and court records (Sauer, 1978 for Great Britain). Even with such data, analysis must often be inferential or indirect so that, for example, female preferential infanticide is inferred from censuses showing a preponderance of males at different ages. It should be noted that these problems are as serious for conventional historical demography (Johansson, Chapter 23, this volume) as they are for more controversial sociobiological analyses (Daly and Wilson, this volume), and that the methods used to cope with them are not substantially different.

In reviewing ethnographic and historical sources Dickeman (1975) Scrimshaw (Chapter 22, this volume), and others, have all reached the same conclusion: the most reliably documented cases of infanticide in humans involve parents and are best described as parental manipulation of their progeny (Alexander, 1979). In contrast to all other primates, but similar to some birds (Mock, Chapter 1, this volume) and fish (Dominey and Blumer, Chapter 3, this volume) close relatives tend to be the perpetrators. Among humans one or both parents appear to make a conscious or unconscious calculation concerning the cost of the infant, probable current and future demands on parental resources, alternative uses to which those resources might be used as well as the future breeding options that the parents might have. The infant's own future survival and breeding or marriage prospects may also be taken into account.

Although it is rare to have firsthand information from parents who have decided to commit infanticide, when parents do talk about it they can be quite explicit about the practical imperatives. Diamond Jenness (1922:166) an ethnographer who worked among the Copper eskimo of the Canadian Arctic describes the rationale for a young couple who decide, for the second time in a row, not to keep an infant daughter: the timing was bad, they were confident they would have other children and hoped that they would have a son who could hunt and care for them in their old age. However, whether such decisions represent parental efforts to maintain their social and economic status and quality of life or whether they represent an effort to maximize the inclusive fitness of the family or lineage remains unresolved (Scrimshaw, Chapter 22, this volume). Such questions will be answerable only when we have precise information on the life historical context within which decisions are made and data on long-term reproductive success of lineages which permits us to test subtle differences between these two closely related hypotheses. Not the least of the problems is the likelihood that the long-term success of lineages has typically been linked in human history with socioeconomic status.

A recent study of infanticide among the Ayoreo indians of Bolivia and Paraguay by Bugos and McCarthy (Chapter 25, this volume) is a first effort toward analysis of the maternal decision-making process. They provide a unique and important body of marital and reproductive histories which illustrate the close link between infanticide and environmental and social conditions, particularly scarce resources and lack of paternal support. From their data, Bugos and McCarthy are able to document a decreased probability of infanticide with maternal age, a finding that is clearly in line with the hypothesis that these mothers are taking into account their own "reproductive value" (i.e., likely future reproduction) as well as prevailing environmental conditions when they decide to terminate investment in a particular infant. At present, however, it is not possible to differentiate between the two most likely explanatory models, namely the hypothesis that mothers are attempting to maintain their own quality of life, or alternatively that they are striving to enhance their inclusive fitness over the course of a lifetime, even at the expense of a particular infant (Alexander, 1979).

As Scrimshaw (Chapter 22, this volume) describes in some detail, parental elimination of unwanted infants tends to be carried out with a minimum of violence; rarely are wounds inflicted. In this respect, humans appear to be unusual among primates but scarcely unique among vertebrate animals generally since abandonment of young is known to occur in many birds and mammals (e.g. lionesses during food shortage may abandon a litter; a mother kangaroo pursued by a predator may jettison her joey). Insofar as humans articulate conscious rationales for infanticide, however, they are unique.

Several recent studies aimed at evaluating causes and frequency of infanticide in human societies have drawn on ethnographies encoded in the Human Relations Area Files. In addition to the analyses carried out by Scrimshaw and by Daly and Wilson (Chapters 22 and 24, respectively), Whiting *et al.* (1977) examined infanticide for 84 societies in which reliable data on the presence of the behavior were available. For fully one-third of the societies in the Whiting study infanticide was reported as a means of eliminating defective offspring. Birth spacing was another frequently cited reason for infanticide. In 72 societies for which it was possible to make a judgement, 36% reported the practice of killing an infant born too soon after its older sibling. Interestingly, the likelihood was greatest in hunting-gathering-fishing societies, which tend to be nomadic, and relatively lower in pastoral and agricultural ones (but see also the discussion in Howell, 1976b, suggesting that due to lactational amenorrhea and consequent long birth intervals the rate of infanticide among hunter gatherers like the !Kung would have been very low, on the order of 2% of births). Such cross-cultural findings have led to a fairly general consensus among anthropologists that as originally suggested by Birdsell (1968), infanticide by parents has deep roots in human history, and has probably been part of our adaptive repertoire since Pleistocene times.

Infanticide may entail intentional destruction of the infant soon after birth, or take a less direct form (see Scrimshaw, Chapter 22, and Johansson, Chapter 23, this volume). There are a wide range of human behaviors which may decrease the likelihood of infant survival. Such practices are extraordinarily elaborate and include neglect and nutritional discrimination (Cassidy, 1980; McKee, 1982); sending the infant away to be suckled by hired, often inadequate wet nurses (Sussman, 1975; 1977; Badinter, 1980); sending infants away to foster homes for a period of harsh apprenticeship associated with lower than average rates of survival (Bledsoe, 1983); or abandonment. The latter may take the form of either exposing the infant to the elements or of deserting it in a location where there is some possibility that others will adopt and care for it (Scrimshaw, this volume, Chapter 22; Balikci, 1967; Trexler, 1973a).

It should be clear from this discussion that infanticide as most often documented for humans differs markedly from its occurrence among other primates. While human infanticide appears to be most often perpetrated by the biological parents, among nonhuman primates infants tend to be killed by unrelated males or by females belonging to a matriline different from the infant's mother. We know of no case among wild monkeys where a mother has been observed to kill her own offspring. Although occasionally inexperienced, primiparous mothers will handle infants roughly, such treatment typically improves within days after birth (Hrdy, 1976). Murderous abuse by mothers is only reported among captive primates, most often among animals which have been socially isolated (e.g. Harlow *et al.*, 1966) but not always (e.g. Troisi *et al.*, 1982). Such abuse has never been reported among wild monkeys and apes. Because distinctions between naturalistic and captive behaviors are often ignored, considerable confusion has emerged in both the popular (Herbert, 1982) and technical literature (Caine and Reite, 1983) concerning "the evolution" of child abuse. It may well be true that simian and human mothers respond to stress in the same way and thus that social isolation results in offspring abuse by both human mothers and monkey mothers (Suomi and Ripp, 1983), but it is extremely unlikely that adaptation could be at issue since no monkey or human ever evolved in social isolation.

Sociobiological Analyses and Contemporary Child Abuse

From a sociobiological perspective, humans are viewed as "strategists" whose ultimate goal is to increase inclusive fitness (that is, the sum of individual fitness plus the fitness of his or her relatives weighted according to their degree of genetic relatedness). Because long-term rather than immediate reproductive success is at issue, an infant may be eliminated if the parent or step-parent thereby enhances overall reproductive prospects. It is assumed that individuals have at their disposal limited resources which can be translated into reproductive effort (Alexander, 1979; Daly and Wilson, Chapter 24, this volume). Just how individuals allocate such resources among offspring in their charge should depend on their assessment of (1) degree of relatedness to the offspring; (2) worth of the offspring in terms of its ability to translate parental investment into subsequent reproduction; and (3) alternative uses to which the parent could devote the resources, such as diverting the same resources to an older or stronger child, or delaying reproduction until conditions are more favorable. To what extent can such an evolutionary approach elucidate the problem of contemporary child abuse?

Infanticide occurs when conspecifics bring about an infant's death, but "abuse" is much more difficult to ascertain since species and cultures differ greatly in respect to caretaking. For example, many societies might find it cruel that Western mothers force infants to sleep in separate cribs, whereas we find repugnant the "circumcision" of young girls to make them marriageable. Hence, some anthropologists would define abuse and neglect as "harsh treatment of children unrelated to purposeful socialization and unsupported by cultural norms" (Poffenberger, 1981). However, while very useful in considering contemporary child abuse in the West, this definition excludes institutionalized forms of mistreatment obviously detrimental to fitness of the victims (e.g., harsh treatment of adopted daughters in traditional Chinese culture, described in Wu, 1981). Furthermore, many behaviors which cultures rationalize as "good" for children (e.g., the practice of denying infants colostrum) are almost certainly detrimental. Hence, we concur with Korbin (1981:205) that it would be virtually impossible to set up cross-culturally valid standards for either optimal child rearing or for behavior which is abusive. Hence in a rural Indian community where female infanticide is probably still practiced with at least passive support from the community a father can nevertheless frown upon corporal punishment of surviving children: "When we work so hard to provide food for children to become strong, should we beat them and make them weak?" (cited in Poffenberger, 1981). Balikci (1970:150) makes a similar point. Infanticide among the eskimoes he studied can not be considered as "callousness" toward children. Children allowed to live were dearly loved.

Yet, by any standards, the bizarre pattern found in some contemporary cases (and perhaps earlier cases, deMause 1974) where chronic mistreatment and even torture of young by a biological parent alternates with ambivalent expressions of solicitude by that same parent must be considered maladaptive. Nevertheless, some portion of the cases of contemporary child abuse may be attributed to emotions which might well have been adaptive at one time. Indeed, as Scrimshaw suggests, some victims of child abuse might—in some other era—have been eliminated at birth. This is the dimension of child abuse currently being explored by sociobiologists (Daly and Wilson 1980; 1981a; 1981b; Chapter 24, this volume; Lenington, 1981; Lightcap *et al.*, 1982).

In line with predictions generated by a sociobiological model of child abuse the children in contemporary western societies who appear to be most at risk from neglect or abuse tend to be those born to families with scarce resources, children with birth defects, children later in the birth order, and children with unrelated males in the home. However, as Lenington (1981) points out, the same findings would be predicted by alternative, nonevolutionary hypotheses. For example, if child abuse were a pathological response brought about through stress, we would still expect a higher incidence among families with few resources or many children. The majority of cases of child abuse and child homicide involve the biological parents and many of these can be explained by economic and developmental factors in the lives of the adults involved. In particular, parents who were themselves abused as children are most likely to abuse their own children (Kempe and Kempe, 1978). As Lenington cautions, then, evolutionary models will at best explain only a portion of cases of violent mistreatment of human immatures.

In a society where stringent legal sanctions against child abuse exist and where children abandoned to institutions have fair prospects for survival, it would virtually never be advantageous for a parent to inflict injuries on his or her own child. Accordingly, if one invokes evolutionary models (as opposed to social pathology) to explain contemporary child abuse, one must either assume that violence toward immatures is vestigial, evolved in some different era and no longer adaptive or else argue, as do Daly and Wilson (Chapter 24, this volume) that abuse patterns can be traced back to differential parental solicitude and reflect an evolved intolerance or reduced solicitude toward particular kinds of infants (e.g., unrelated; poor quality), or toward infants under certain conditions (e.g., insufficient resources) rather than selection for abusive behavior per se. Were societal norms different, psychological motivations causing parents to discriminate against certain children might—however cruel—nevertheless enhance the inclusive fitness of parents.

Sex-Biased Infanticide

Evolutionary biology has produced a body of sophisticated theories to explain parental preferences for one sex or the other in nonhuman species (Charnov, 1982; Chapter 7, this volume) but currently, only a few such models are applicable to humans (Williams, 1979) and efforts by anthropologists to apply them are still very preliminary. One of the few models that theoretically ought to apply to humans is the *Trivers-Willard hypothesis.* According to Trivers and Willard (1973), a parent in good condition should bias investment toward sons among polygynous species whenever males in good condition enjoy better than average reproductive success (e.g., Clutton-Brock *et al.,* 1982; Dittus, 1979; McClure, 1981); a parent in poor condition, however, should preferentially produce daughters.

Under different social and ecological conditions, however, other models would be needed. Where daughters inherit their status from their mothers, and where high female status is correlated with better than average reproductive success for daughters (but not sons), one would expect high-status mothers to prefer daughters and low-status mothers to prefer sons. In fact, high-ranking mothers in some monkey species produce up to twice as many daughters as sons (Simpson and Simpson, 1982; Silk, 1983; Altmann, 1980). This model has only been tested among animals, but it ought also to apply in human societies with the appropriate marriage and mating systems—although it must be noted that humans, unlike the monkey and deer examples cited above, appear to lack the capacity to bias their sex ratios *in utero* and must rely on the more physiologically wasteful practice of infanticide after birth.

In our view, the work of Dickemann (1979a; 1981) provides the only compelling application to date of the Trivers-Willard or, in fact any such model, to human societies. Dickemann's analysis focuses on the widespread occurrence of preferential female infanticide among high-status families living in stratified social systems where the marriage system is hypergynous and the access to an unpredictable resource base is determined by status. Drawing on ethnographic studies from North India and Imperial China—both societies characterized by intense competition for scarce resources and extreme variance in male reproductive success—Dickemann (1979a:323) pointed out that "men of high rank [acquire] access to a disproportion of females through polygyny, and in addition [enjoy] greater health and earlier entry into reproduction, while those at the bottom are disproportionately excluded from reproduction through delayed marriage, heavy mortalities and the imposition of celibate roles, [and] their reproductive success is further reduced through heavy mortalities among their progeny."

These societies were also hypergynous, that is, a significant proportion of women are able to marry "up" the social scale into families of higher standing than their own. Such a marriage benefits not only the bride but her entire family. Her parents can look forward to grandchildren born into a world of improved opportunities. But marriage prospects for these daughters from high-status families entailed high costs in the form of dowries which their families must provide. To avoid these costs, daughters would be eliminated at birth, yielding the extraordinarily high sex ratios characteristic of many groups in North India in the nineteenth century (Miller, 1981). Parental investment, and the wealth that otherwise would have been diverted to daughters, was directed exclusively toward sons.

However, direct infanticide as traditionally practiced in North India is only one of several ways of biasing sex ratios. Recently, attention has been directed toward the allocation of food among family members. Sons are nursed for up to twice as long as daughters in societies as distant in space and time as peasants from ninth century France (Coleman, 1974), contemporary Equador (McKee, 1982), and modern India (Miller, 1981). Indirect evidence on this same point is provided by the finding that birth intervals in many cultures tend to be longer after the birth of a son than a daughter (Haldar and Bhattacharyya, 1969; Khan, 1973). Current explanations for preferring offspring of one sex over the other (e.g. greater valuation of male labor, marriage patterns that make sons more valuable) are discussed in some detail in the chapters by Johansson (Chapter 23) and Scrimshaw (Chapter 22). With only a few exceptions (Hartung, 1976; 1982; Dickemann, 1979a; 1979b), little attention has been paid to the evolutionary dimensions of parental sex preferences.

Whatever the ultimate cause of sex preferences, infanticide as a means of biasing parental investment toward either sons or daughters probably has a long history. It is widely accepted that a hunting-gathering-fishing way of life has characterized human existence for more than 90% of the history of our species. The majority of such societies are known to practice infanticide as a means of birth spacing. Hence, as Jane Lancaster noted during symposium discussions, once conditions arose which made one or the other sex offspring more desirable, parents might have viewed the preexisting mechanism of control over the reproductive process, that is, infanticide, as a natural and quite acceptable means for biasing family sex ratios.

A NOTE ON THIS VOLUME

The chapters that follow explore in some depth topics outlined in this Introduction. In Part I, taxonomic reviews of infanticide among birds (Mock), carnivores (Packer and Pusey), fishes (Dominey and Blumer), amphibians (Simon), and invertebrates (Polis) are followed by two theoretical review papers, a description of phylogenetic constraints on the evolution of infanticide (Hayssen), and a précis of both new and previously published work which bears on the question of why parents would invest preferentially in offspring of a particular sex (Charnov). In Section II new data on infanticide among Old World cercopithecine monkeys (LeLand *et al.;* Collins *et al.*) and New World howler monkeys (Crockett and Sekulic) are presented along with a review of infanticide among the great apes (Fossey). New observations of infanticide among the langurs at Jodhpur (Vogel and Loch) serve as an introduction to the use of such langur data to test theoretical models with computer simulations (Hausfater). Finally some longstanding controversies concerning interpretation of langur field studies are reviewed (Boggess, Chapter 15, and Hausfater, in his introduction to the primate section).

In the introduction to Section III, Labov briefly contrasts the merits and disadvantages of performing experiments with laboratory rodents with those of studying wild primates. Labov stresses the need for more information concerning the natural history of wild mice. The rodent section begins with a review article by Brooks on the cause and consequences of infanticide among natural populations of rodents which provides the essential (if still sketchy) framework for interpreting experimental results. Such studies have involved a variety of rodent species (hamsters, mice and gerbils) and are described in detail in papers by Huck, vom Saal, Elwood and Ostermeyer, and Svare *et al.*

The introduction to the human section provides a critique of some current thinking about infanticide in our own species (Dickemann). This discussion is followed by a review of the ethnographic and historical literature on infanticide in humans (Scrimshaw). The remainder of the volume is devoted to the analysis of data. Johansson provides an historical and demographic case study of deferred infanticide in pre-modern Europe; Daly and Wilson provide a sociobiological analysis of cross-cultural data from traditional human societies as well as child homicide data from Canada; and Bugos and McCarthy provide a case study of infanticide among a lowland South American population which is in transition between its traditional culture and incorporation into the modern world.

Most of these chapters grew out of papers presented at the Wenner-Gren Symposium on "Infanticide in Animals and Man" which was held at Cornell University between August 16 and 22, 1982. Several papers presented at this conference were deleted, while several others were added later (in fact, the last chapter by Bugos and McCarthy was added after the book was in press).

During the conference, participants were assigned particular papers to comment on both in writing and during panel discussions. Several of these commentaries are published following the original contribution (Sugiyama, Hrdy) but, by and large, the most useful portions of the commentaries were either incorporated into the relevant chapter or else were summarized in the three section introductions. Hence, we believe we speak for most authors when we state that contributors to this volume were mutually indebted to one another for the final versions of their papers; this is certainly true of this introduction.

As with any symposium volume there are a few holes in our coverage of comparative and evolutionary perspectives on infanticide. In retrospect, it would have been useful to include a chapter on kin recognition and certainly it would have been valuable to have more historically oriented reviews of infanticide in human populations. Nevertheless, we believe that the volume fairly represents the "state-of-the-art" with regard to research on infanticide and should provide readers a broad, and occasionally deep, perspective from which to view an astonishingly widespread complex of behaviors which characterizes so many animals, including humans.

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