CAREL P. VAN SCHAIK AND CHARLES H. JANSON

Infanticide by males: prospectus

Infanticide refers to the killing of dependent offspring, or more formally, to "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" (Hrdy & Hausfater 1984). Although this seemingly bizarre behavior is often rare in the species in which it occurs, it is nonetheless remarkably widespread in the animal kingdom. Gathered under the unitary label "infanticide" is a diverse set of behaviors that differ in social context, the sex of the perpetrators, and the relationship between the perpetrators and the infant. This variability suggests similar variability in the nature of the selective factors that favored the evolution of infanticide. Hrdy (1979), therefore, distinguished five functionally distinct "classes" of infanticide. Infanticide could be an adaptation that (1) increases resource acquisition (cannibalism), (2) excludes competitors for the agent or its kin, (3) increases the inclusive fitness of one or both parents, or (4) increases the reproductive success of adult males unrelated to the infant. Alternatively (5), it could be a reflection of social pathology, thus not serving any adaptive function.

Among primates (and in this book "primates" refers to non-human primates unless otherwise specified), infanticide is relatively more homogeneous. Most infanticide is committed by males, and in most of these cases, adult males kill unweaned infants not related to them, usually without consuming them. After the first and often fragmentary observations of infanticide by adult males in primates in the 1960s (Sugiyama 1965, 1966), a protracted and heated debate ensued about the proper interpretation or interpretations of infanticide in primates, which focused on its possible selective advantage (Angst & Thommen 1977; Boggess 1979; Hrdy 1979). For most biologists, this debate was satisfactorily resolved in

the mid 1980s, with the appearance of the first edited volume devoted largely to the problem (Hausfater & Hrdy 1984), in favor of the male reproductive strategy hypothesis. Better known as the sexual selection hypothesis, this idea proposes that a male increases his reproductive success by killing unrelated dependent infants if the infant's death makes the female return to receptivity sooner than would otherwise have been the case and if he has a higher probability of siring her next offspring (Hrdy 1979).

This idea is thoroughly embedded in contemporary evolutionary biology. Infanticide by males is only one expression of a more general conflict between the sexes that has its origins in fundamental reproductive asymmetries between the two sexes. Where females have internal fertilization and gestation, and in mammals also lactation, females are associated with the young much more intensely and much longer than males. As first noted by Darwin (1871), this sex difference is the basis for sexual selection, because the differential parental investment and thus differential latencies following fertile matings (Clutton-Brock & Parker 1992) produce operational sex ratios that are heavily skewed toward the sex with the shorter association with the offspring. For each female that is ready to engage in fertile mating, there will be many males. As a result, male reproductive success tends to be limited by access to mates, and selection will favor traits that favor success in competing with other males in acquiring mating access to females, resulting in the evolution of enlarged body size, weaponry, etc.

Female reproductive success is usually limited by access to resources that would enhance the number of offspring they can produce. With respect to mating, females usually do not suffer from a lack of access to mates. However, they can enhance their reproductive success by mating preferentially with mates of superior intrinsic viability, provided there is heritable variation in this trait and it can be assessed by females. Consistent female choice has therefore selected for male traits that indicate the intrinsic viability of the males (e.g., Petrie 1994).

Most of the time, female preferences and male mating interests diverge. The profound impact of this conflict of interest was not realized until relatively recently (Parker 1979; Smuts & Smuts 1993; Gowaty 1997a). Natural selection will favor traits that make males more likely to mate with females who do not prefer them, whereas selection will favor traits in females that will allow them to express their preferences. This conflict has set up an "arms race", where male traits are favored that allow them to

force females into mating with them (e.g., grasping appendages or penetrating sperm delivery organs) and female traits are favored that allow them to overcome such male tactics. Where males can gain the upper hand, sexual coercion may ensue. Sexual coercion, as defined by Smuts & Smuts (1993) is "use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female". The most obvious expressions of sexual coercion in mammals such as primates are harassment and forced matings of sexually attractive females, and infanticide. Thus infanticide by males can now be regarded as one component of nearly ubiquitous intersexual conflict.

Nonetheless, many still regard infanticide by males in primates as a non-adaptive phenomenon, if it exists at all. In the Foreword to this volume, Sarah Hrdy mentioned the long and acrimonious debate over infanticide, in particular among anthropologists. In Chapter 1, Sommer examines the various positions, from those who disagree with the interpretation of the data to those who disagree with the data or even with the fact that infanticide is a valid object for study in the first place.

The first, albeit subsidiary, aim of this book is to review the recent primate literature to reassess the evidence for sexually selected infanticide by males, to summarize and respond to the criticisms raised against it, and to identify remaining weaknesses. In Chapter 2, van Schaik expands the careful review of Struhsaker & Leland (1987), to evaluate the sexual selection hypothesis in detail, and to contrast it with other possibilities. The emphasis on primates in this book is not due to the taxonomic myopia of which primatologists so often stand accused. In Chapter 3, van Schaik proposes that this primate bias has a biological basis, by linking vulnerability to infanticide by males to features of life history and reproductive biology.

Subsequent chapters present detailed studies of red howlers (Crockett & Janson, Chapter 4), hanuman langurs (Borries & Koenig, Chapter 5), chacma baboons (Palombit *et al.*, Chapter 6) and Thomas's langurs (Steenbeek, Chapter 7). Each of them supports the sexual selection hypothesis, but also examines in some depth some puzzling aspects of the phenomenon of the sexual selection hypothesis, such as infanticide in highly seasonal breeders and the roles of diet, of group size and of group composition, or the effect of infanticide on the social organization.

Although the phenomenon is both best documented and most studied

in primates, sexually selected infanticide is not limited to this taxon. Excellent work on lions has demonstrated that infanticide is an adaptive male reproductive strategy in that species, and has documented some of the effects on social organization (Pusey & Packer 1994). Outstanding work on the regulation of infanticidal behavior has been done in rodents (Perrigo & vom Saal 1994). In this volume, Blumstein (Chapter 8) takes an evolutionary approach, and reconstructs the phylogenetic history of infanticide by males in rodents in relation to the evolution of infanticide by females and of Bruce effects. Veiga (Chapter 9) reviews the evidence for sexually selected infanticide by male birds, and finds that it may be more common than is generally accepted. We hope that the obvious gaps in taxonomic coverage spark new attempts to document sexually selected infanticide in other taxa.

The continuing controversy has made many students of primate behavior conservative in their interpretation. While it is a scientifically proper attitude to avoid rushing prematurely to judgment over competing hypotheses, it has also prevented us from fully appreciating the pervasive importance of the threat of infanticide for the social lives of the animals vulnerable to it. Because critics insisted on the importance of directly observed cases, few realistic estimates of the rate of infanticide have been published. Now that realistic estimates show that infanticide can be a major source of infant mortality (see Chapters 2, 4–7), there is no reason to postpone any longer a thorough exploration of the consequences of infanticide: the various counterstrategies and infanticide's impact on other aspects of physiology and behavior, especially on primate social systems. Ironically, 20 years ago Hrdy (1979) had defined this as a pressing research agenda, but relatively little progress has been made since then in studies of infanticide by males. Similarly, Sherman (1981) proposed the importance of infanticide by females for territoriality in rodents, but serious studies of this suggestion have appeared only in the past few years (Wolff 1993; Hoogland 1995; Wolff & Peterson 1998). The second, and major, aim of this book, then, is to take up this challenge.

While the detailed case studies of Chapters 4 through 7 already hint at the possible consequences of infanticide by primate males on social organization, most of the following chapters have this possible impact as their major theme. We should stress that none of these explorations requires that infanticide by males be adaptive, only that its context be predictable enough to provide cues to favor counterstrategies. Both critics and proponents of the adaptive nature of infanticide by males

agree that infanticide is far more frequent shortly after replacement of a top breeding male (Bartlett *et al.* 1993; van Schaik, Chapter 2). However, a more serious obstacle for such explorations is that, paradoxically, where counterstrategies are quite effective, the *rate* of infanticide will be so low that infanticide by males may never be observed in the average field study. In various chapters, authors escape from this by defining the *risk* of infanticide independently from direct observations of actual infanticide.

Infanticide by males may have affected the evolution of infant features and aspects of infant care (Treves, Chapter 10), of male–female relationships (Palombit, Chapter 11), of male–infant and male–male relationships (Paul *et al.*, Chapter 12), of female dispersal (Sterck & Korstjens, Chapter 13), of sexual behavior (van Noordwijk & van Schaik, Chapter 14) and features of female reproductive physiology (van Schaik *et al.*, Chapter 15), and finally of aspects of social organization as a whole (Nunn & van Schaik, Chapter 16). All these chapters take an explicitly comparative approach, although, with the exception of Chapters 11 and 14, their taxonomic scope is limited to primates.

The book's focus on infanticide by males allows us to maintain a reasonable functional homogeneity. However, infanticide by females is quite common in some mammalian taxa, and functionally more diverse. Digby (Chapter 17) examines the multiple contexts in which it is observed in mammals, and establishes a framework for functional interpretation. Voland & Stephan (Chapter 18) connect infanticide by females to this volume's main theme, infanticide as a sexually selected reproductive strategy, by arguing that in humans infanticide by mothers can reasonably be interpreted as a mating strategy. This new approach complements the more traditional approach of considering infanticide by mothers as an adaptive response to resource scarcity and the associated reduced probability of survival of the current offspring (Daly & Wilson 1984).

Most of these chapters are exploratory, in the sense that far more questions are raised than are answered, and we encouraged authors to speculate. The possible impacts of infanticide on other aspects of social behavior and individual physiology and life history need to be tested both on a broader comparative scale and against competing hypotheses within smaller clades. In the final chapter, we try to take stock and develop priorities for further research. The success of this book will be measured by the speed with which new studies will replace or refine the insights we have gained so far, and by the extent to which it inspires students of non-primate mammals and of birds to explore infanticide and its implications

more than in the past. We hope that in the future, researchers exploring the evolutionary consequences of infanticide can publish their work without the controversy that has dogged the issue of the adaptive value of infanticide to males.

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Part I

Introduction

VOLKER SOMMER

1

The holy wars about infanticide. Which side are you on? And why?

Introduction

The topic of infanticide has been a staple theorem of sociobiology ever since this discipline – the study of social behavior from an evolutionary perspective – was born two and a half decades ago (Wilson 1975). The killing of conspecific young is still hotly debated. Does it occur at all, does it reflect an adaptation, a pathology or even a political agenda? Infanticide – observed among such varied taxa as birds, rodents, carnivores, pinnipeds and primates (Hausfater & Hrdy 1984; Parmigiani & vom Saal 1994) – therefore remains a litmus test upon which the validity of a sociobiological interpretation of behavior depends. I attempt to trace some intellectual roots of the controversy: those of defenders of adaptationist explanations, those of critics from within the paradigm of evolutionary biology, and those of critics who operate from other paradigms such as the social sciences. My ultimate aim is to defend the adaptationist interpretation as a valid and fruitful approach, while acknowledging that its narrative is anchored in a time-dependent framework of interpretation.

Cute and brute

People are fascinated by animals, not least because people are, in their own right, animals who can empathize with similar organisms. The average viewer of a natural history documentary will feel good if a monkey mother cuddles her newborn: "It's so cute." But different emotions flare up if, over television dinner, wild chimpanzees eat an infant of their own kind: "It's so brute."

These complementary sets of emotions are readily served by our brains

and will often grow into thinly veiled judgments. The cute stuff animals do is "natural" because we like it, whereas the brute stuff is "animalistic"because we do not like it. Nevertheless, egg cannibalism in wasps will upset us less than seeing a little chimpanzee being torn apart. The repugnance is stronger if we are phylogenetically close to the victim.

Natural scientists are, of course, supposed to shrug their shoulders no matter what behavior is at stake and take refuge to the advice offered by David Hume in his 1740 *A Treatise of Human Nature* not to stroll from "Is to Ought", or else be in danger of committing the *naturalistic fallacy*. Still, scientists are governed by the same mechanisms of empathy that lay nature lovers possess. I will not forget 9 July 1981, the first time I witnessed a male monkey sinking his canines into an infant I had grown fond of during a study of hanuman langurs in India. Later in the fieldwork I shouted and threw stones at the aggressor. It did not prevent infant-killing. The first attack took me by surprise. My academic mentor, Christian Vogel of Germany's Göttingen University, had instilled in me disapproval (Vogel 1979) for the "out-of-America" hypothesis that infanticide occurs regularly amongst langurs and is caused by male competition over females (Hrdy 1974). Vogel's views still reverberated with the idea that animal behavior serves the good of the species. Accordingly, monkeys were expected to perform "group serving" and "group bonding" acts (Vogel 1976). As an evolutionary biologist, Vogel represented a *within-paradigm critic*. Data subsequently gathered by his students and Indian colleagues changed Vogel's *Weltanschauung* radically: he transformed into a vigorous defender of the theorem that infanticide amongst animals including humans reflects evolutionary adaptation (Vogel 1989), such as exploitation of the infant for cannibalistic purposes, or parental manipulation of progeny (cf. Hausfater & Hrdy 1984; Parmigiani & vom Saal 1994). With respect to langurs, the theory (Hrdy 1974) maintains that infanticidal males increase their relative genetic representation in future generations by eliminating unweaned offspring of other males, particularly those of their predecessors as harem residents in populations with one-male/multifemale group structures. Infanticide will shorten the waiting time of a new male until he can impregnate a female, because the loss of an infant terminates the period of temporary infertility associated with lactation. In addition, infanticide may be adaptive if it reduces resource competition for a male's kin.

I for my part learned to rationalize the gruesome events (Sommer 1987, 1994, 1996; Böer & Sommer 1992). I now publicly lecture and write about

infant-killing in more or less the same way as about grooming, presenting both as functional behaviors. However, occasionally somebody from the audience or readership will call me a fascist (cf. Schües & Ostbomk-Fischer 1993: 17). I tend to reply that few people hold meteorologists responsible for the destruction and grief caused by tornadoes; by the same token, I should not be held morally accountable for the aggressive behavior of the monkeys that I study.

This excuse is an easy escape when dealing with benign minds who accept that they are committing the naturalistic fallacy. However, the route from "Is to Ought" is a two-way street and various apostles actually travel in the opposite direction: from "Ought to Is". They preach that our values construct the reality around us, and that it is imperative to possess the right values. Cute mother–infant interactions are OK, acceptable testimony to how the world should be, but brute male–infant interactions are not OK because reports about aggression are borne out of aggressive minds and breed more violence. This can be labeled as the *moralistic fallacy*: what should not be, cannot be.

Donna Haraway, American scholar of History of Consciousness, figures prominently as an *outside-paradigm critic* sympathetic to such conviction: "To center the debate on the biological meanings of infanticide among primates too easily plays into the culturally overdetermined lust for sexualized violence" (Haraway 1989: 311). There is some truth to this if we look at how the popular media disseminate findings about infanticide: as a story about sex and crime in which the theory is often not only trivialized but distorted. Headlines of, for example, German magazines were only at times acceptable ("Der neue Chef des Harems tötet seine Stiefkinder" [The harem's new boss kills his stepchildren]), but more often barely bearable ("Affen morden ihre Kinder" [Monkeys murder their young], "Mord im Harem" [Murder in the harem]) and at times blatantly sensational ("Anklage Mord" [Accused of murder], "Das Killer-Gen" [The killer-gene]; "Blutrünstige Rivalen" [Bloodthirsty rivals]) (references in Sommer 1996). But then, purging language and employing euphemisms will not in itself foster desired political change. It may, on the contrary, just cover up fields of conflict. Moreover, any paradigm can be used to incite a war – prime examples being such diverse ideologies as the Christian doctrine to love one's neighbor, Buddhist belief in the vanity of life, or Marxist utopias of equality. I cannot see what harm talk about infanticide has done, but the fear that it *could* certainly generates much of the heat of the debate.