

zaftig, pale-skinned nudes in the nineteenth century gave way to anorexic models of the 1960s and then the tanned and athletic ones of today. If male choice of female physiques is going on, why the swings in fashion? Underlying this variation is a stable measure: Psychologist Devendra Singh of the University of Texas at Austin showed that the ratio of female models' chest to waist to hips varied very little over that century-long time span.<sup>23</sup> If women are presenting themselves to the world with an eye toward sexual attraction by men, a reasonable assumption to make, then they unconsciously maintained certain visual cues in their figures.

But are these signals aimed at men, or at other women? At least some scholars believe that women are the intended targets of women's appearances. We used to think that the swellings borne by female chimpanzees were there to signal their availability to males. We now know that they more likely exist to excite lots of males, allowing the females to choose among them, or to choose all of them and mask the paternity of the ensuing baby. But swellings and other female primate traits may also be signals by a female that she is genetically healthy enough to bear the costs of such a metabolically burdensome organ.

—five

## The Infanticide Wars

I have steadily endeavored to keep my mind free, so as to give up any hypothesis, however much beloved. . . . as soon as facts are shown to be opposed to it.

*Charles Darwin's Autobiography,*  
edited by Sir Francis Darwin

Of all the behaviors primatologists have observed, none has fascinated and appalled us like infanticide. When Jane Goodall reported a mother-daughter team among her Gombe chimpanzees (the infamous Pom and Passion) preying on the infants of other females, we were shocked by yet another brutal behavior from a species so like ourselves. We now know that both male and female chimpanzees sometimes kill neighbors' offspring. Among mountain gorillas the behavior accounts for a high percentage of the mortality to newborns.

But apes and monkeys don't have a monopoly on infant-killing. Over the past several years, infanticide has also been reported among lions, wild horses, dolphins, and a wide range of other animals. The reports have often led to bitter debates. When an article appeared in a prestigious anthropological journal arguing that infanticide in lions is a myth, twenty-eight scientists cosigned a letter of protest to the journal's editor. Reports of infanticide among langur

monkeys led, as we shall see, to one of the most acrimonious disputes in behavioral biology.

Perhaps most notably the infanticide reports have not been limited to cats and horses. They include human infanticide, sometimes in our own backyards. Two teenage girls killed their newborn babies (one at her high school prom) in the mid-1990s; at least one cognitive scientist argued that Darwinian theory offers a plausible rationale for them to do so. His explanation evoked widespread outrage from groups across the political spectrum.

These incidents can mean only one thing; the infanticide wars are heating up again. The battle is not fought over the infants themselves but over the way we explain this horrifying but evolutionarily fascinating behavior. As the recent salvos show, campaigns fought and won by animal behaviorists and evolutionary biologists in the 1970s have cycled around, and a vocal minority of scholars opposed to Darwinian models of social behavior are crying foul.

The supremacy of biological versus environmental influences on social behavior has been fought about for centuries. Over the past three decades, it has been well demonstrated that many aspects of social behavior in animals are subject to natural selection. Most biologists who study animals in their natural habitat assume that most if not all aspects of behavior have evolved in response to ecological and social pressures, such as the need to find and compete for food and mates. But while evolutionary interpretations of most behaviors have become part of mainstream behavioral biology, a few have remained highly controversial.

The killing of infants happens in many different circumstances and in many different animal species, from birds to monkeys to humans. The history of infanticide research in animal ethology has been a road map of the course of scholarly thinking about the role of evolution in animal behavior. In 1871, Charles Darwin noted its occurrence in both animals and humans, and attributed its motivation in human societies to population control.<sup>1</sup> Darwin, however, was

talking about infanticide committed by mothers who abandoned their offspring or killed them outright when they could not care for them. Mothers sometimes kill their own babies. Fathers may do the same. But most of the debate has centered around infants killed by a male other than the biological father.

There was a time when we believed that the ultimate goal of animals living in a social group was the attainment of group harmony. Events that disrupt the harmony, such as fights or sexual jealousy, were thought to disrupt the behavioral equilibrium of the group. The rise of Darwinian theory to explain social behavior changed all that. Beginning with the work of the evolutionary biologist Robert Trivers, we recognized that every organism has a genetic agenda: the perpetuation of itself in the next generation. This agenda often conflicts with those of other individuals. Even kin, like mothers and daughters or siblings, have conflicting goals. This is not to say that harmonious relationships are not sometimes in the best genetic interests of all parties—much cooperative behavior occurs due to benefits to the participants—but when push comes to shove, both males and females are expected to selfishly look after their own interests.<sup>2</sup> This Darwinian paradigm can also be extended to explain infanticide in human societies, though not without much controversy.

One Harvard graduate student who took Trivers' teachings to heart was Sarah Blaffer Hrdy. In the early 1970s Hrdy, now at the University of California, Davis, was planning a doctoral thesis on Hanuman langur monkeys, a large and graceful monkey ubiquitous across the Indian subcontinent. Hrdy had heard reports from the arid western regions of India that langurs living at high population density committed infanticide. She set off to investigate, settling in Mount Abu, a resort town in the red hills of southernmost Rajasthan. Mount Abu offered lots of langurs, living both in the wooded hills surrounding the town and in the town itself. (I visited Abu for several days in 1987; there were langurs in the forest, lan-

gurs on the polo grounds, and langurs roaming like street gangs through the bazaar.)

Across India, langurs live in two types of social groups: one-male and multi-male. One-male groups predominate at Abu, and in this social setting the lone resident male becomes a target for attack by bands of males that lack a group of females of their own. As it turned out, some of the Abu langurs were killing infants, and they did not seem to be acting pathologically. Instead, Hrdy observed bands of males invading established social groups, ousting the resident male, and in some cases killing infants he had sired. Over a five-year period she saw four infanticides and strongly suspected numerous others.<sup>3</sup>

Hrdy viewed the killings in the light of Darwinian principles, previously untried in the explanation of infanticidal behavior but powerful in their ability to account for the deaths she reported. Far from pathological reactions to overcrowding or stress, Hrdy saw infanticide as an evolutionarily sensible reproductive strategy by otherwise bachelor males. By ousting a resident male and then fending off other competitors, a marauding male langur reaped a sudden windfall of reproductive opportunities with the group's females. The catch was that some or all of the females were likely preoccupied, reproductively speaking, because they were pregnant by the previous resident male or were nursing his infant. In either case, the females would be unavailable for a new male eager to sire his own progeny. It was well-known that in some rodents, the introduction of a novel male can induce a pregnant female to abort, probably because the male would kill her litter anyway.<sup>4</sup> Hrdy reasoned that if the tendency toward infanticide were an inherited trait, males who engaged in the behavior would have enhanced reproductive success relative to other, non-infanticidal ones. This suggested the heinous act was actually sexually selected, an adaptive strategy evolved to promote a male's genes at the expense of other males. Female langurs who preferred non-infanticidal males as mates lost the evolu-

tionary arms race, since their sons, by failing to kill rivals' offspring, would leave fewer descendants.

The results of Hrdy's long-term field research at Abu appeared in her book *The Langurs of Abu* in 1977. The langur infanticide data were not unassailable. Her Darwinian interpretation was a good fit if you were a believer, but it was not a skeptic's dataset. The reaction was swift and vituperative. Many primatologists denied that the infanticides she reported had occurred at all. Others, when it became clear that the infant-killing was not only real but occurs systematically in other populations of Hanuman langurs as well, acknowledged that infanticide occurred but denied its evolutionary importance. The most vehement disagreement came from primatologist Phyllis Dolhinow and her graduate students at the University of California, Berkeley. Dolhinow had been one of the early langur researchers in India, where she described largely peaceful societies in which group upheavals occurred gradually, never accompanied by attacks on infants. Employing a defense lawyer's argument, she and her students noted that most of the reported infanticides were only circumstantial; the prime evidence was often an infant found dead with bite wounds shortly after a group takeover. Others had been reported secondhand by local people rather than observed directly by the researchers. Dolhinow also charged that the explanation for langur infanticide at Abu was social pathology, not reproductive strategy. The high langur population density and level of human disturbance in and around Abu, she argued, made it impossible for males to take over new groups in the normal, unaggressive and gradual fashion.<sup>5</sup> Instead, in the melee of male-male encounters, aggression directed at other males and at females sometimes injured or killed infants accidentally. In other words, Hrdy's langurs were suffering from the same sort of social chaos that researchers have described in lab rats kept at unnaturally high density. Why had no previous researcher reported infanticide by primates? As Einstein said, the eyes rarely see what the mind does not expect. The debate

over langur infanticide raged until other researchers could produce field data supporting or refuting the reproductive adaptation model. Dolhinow's students came back from the far reaches of the Indian subcontinent with field data showing more or less peaceful social relations in their study populations. But trouble was brewing for the anti-adaptationists. German primatologist Volker Sommer studied langurs living in the arid scrubland of Jodhpur, Rajasthan, in collaboration with an Indian team led by S. M. Mohnot of Jodhpur University. Between 1969 and 1985 they documented fourteen cases of infanticide, plus twenty other suspected killings and fourteen nonfatal attacks on infants. They also showed that the pattern of aggression was consistent with the sexual selection hypothesis. Females whose babies were killed by incoming males began to cycle again significantly sooner than those whose infants survived, thus rewarding a marauding male with procreative opportunities months earlier than if he had waited for the infants to mature.<sup>6</sup>

Elsewhere in India, Oxford University zoologist Paul Newton documented infanticide in a pristine forested region in Kanha National Park. Unlike Abu, where langurs live among villagers, bus stops and trash heaps, Kanha langurs live in a natural state, preyed upon by tiger and leopard while foraging among Kanha's richly diverse wildlife. Newton demonstrated that infanticide and heightened male aggression were not correlated with either langur or human population density, thus doubly refuting Dolhinow's idea that infant-killing was caused by living at high density in human-disturbed environments.<sup>7</sup>

Meanwhile, reports of infanticide mounted for a wide range of species throughout the 1980s. David Watts of Yale University showed that among Dian Fossey's mountain gorillas of the Virunga Volcanoes, infanticide by silverback males is a leading cause of infant mortality. In species as different as marmosets and macaques, the killing of infants was witnessed, often in scenarios that were consistent with the Darwinian model. Infanticide is also relatively com-

mon among wild chimpanzees, with a total of at least twenty known cases plus several other unsuccessful attempts. Seven of these infanticides have been committed by the chimpanzees of the Mahale Mountains of Tanzania. In each case in which the killer could be identified, he was an adult male, and all seven victims were infant males.<sup>8</sup> Most intriguing is that most of the infants were the offspring of females who had recently immigrated to the community. The adult males may thus have had an incentive to eliminate male babies who could someday become mating rivals. The explanation for chimpanzee infanticide is, however, less than entirely clear; in most cases the killers eat part of the infants they capture, suggesting that nutrition may be either a primary or secondary motive in a species that craves meat but rarely gets it.

The grisly behavior is not limited to primates. A recent report by Scottish researchers described infanticide by male bottlenose dolphins.<sup>9</sup> Some of the best field data on infant killing come from the Serengeti plains and Ngorongoro crater of Tanzania, where a research team led by Craig Packer and Anne Pusey of the University of Minnesota has documented infanticide in lions. The pattern is similar to that in langurs; coalitions of male lions invade new prides, driving out or killing the resident males. Pregnant lionesses in the new pride nearly always lose their infants within six months of birth, the only exceptions being lionesses who bear a close genetic relation to the new males. In many cases, all cubs in every litter born in the early months of the new males' tenure die. Older cubs are typically driven out of the pride. Lionesses ferociously defend their cubs against infanticidal males, probably because such takeovers greatly reduce their overall reproductive success.<sup>10</sup>

Infanticide has even been experimentally induced in the wild. Ornithologists, who are able to manipulate social groups of bird subjects in ways that researchers studying large mammals cannot, have been able to establish situations in nature in which infant-killing can be predicted. Stephen Emlen and colleagues from Cornell Univer-

sity studied the polyandrous wattled jacana, a wading bird in which normal sex roles are reversed; one female jacana mates with several males, and the males raise the brood of chicks. This leads to competition among females over access to males. Such an exception to the rule of animal mating systems supports the idea that the sex that invests time and energy in offspring will be competed for by the other sex. Emlen and colleagues predicted that if the sexual selection theory is correct, instead of the more usual pattern of male infanticide it ought to be female jacanas that commit infanticide of other females' offspring. That is exactly what the researchers observed. When resident females were removed from their broods of chicks, replacement females killed or ousted the original broods and began to sexually solicit the resident males. Jacanas may thus be the exception that proves the rule; incoming mates eager to produce their own progeny and loathe to waste their time raising those of others should try to eliminate the unrelated offspring.<sup>11</sup>

For the past two decades the anti-Darwinians have fired back salvos of their own. Dolhinow's claims of langur social pathology in the 1970s were dusted off by other scholars in the 1990s. Robert Sussman and colleagues at Washington University pointed out that twenty-five years after Hrdy's work, only a few infanticides have been reported among primates, and most of those have been in just a handful of species.<sup>12</sup> Recently, Anne Dagg of the University of Waterloo, Canada, writing in *American Anthropologist*, charged that Packer and Pusey's reports of lion infanticide failed to meet the accepted criteria for being adaptations; she even cast doubt on whether male lions commit infanticide at all.<sup>13</sup> Dagg's article was immediately attacked by a wide range of scholars of both animal and human behavior (including me) in a letter of protest written to the journal's editor. Meanwhile, the behavioral evidence in support of the sexual selection model continues to mount. A recently published volume edited by Carel van Schaik of Duke University and Charles Janson of the State University of New York at Stony Brook

brought together and synthesized much new evidence of infanticide by male primates and other animals.

Many in the anti-adaptationist school argue that unless a gene or complex of genes can be found that causes infanticidal behavior, we should not speak of infant-killing as an evolved trait. This is an unreasonable standard of proof in the behavioral sciences. Although there are examples of direct gene-behavior relationships (some captive-bred strains of mice will commit infanticide, while other strains do not), higher social animals are simply too complex, genetically and behaviorally, for simple gene-behavior links. Instead, scientists seek to establish correlations between certain behaviors and their likely reproductive payoffs as a way to hypothesize the behavior as adaptive and, therefore, evolved. Male langurs that commit infanticide should kill only those infants they have not sired themselves, and should then father new infants. With the advent of modern DNA analysis, we can test this hypothesis directly. A team of researchers led by Carola Borries of the German Primate Institute in Göttingen, Germany, recently conducted a paternity analysis of a langur population in southern Nepal using DNA from the monkeys' feces. They showed that in all cases, the infanticidal males were not the fathers of the infants they killed.<sup>14</sup> This is the most conclusive evidence that infanticidal males behave in accordance with the predictions of Darwinian theory.

On the other hand, some adaptationists may have gone overboard, invoking infanticide as the driving force behind the social systems of all primates, including humans. A few researchers assert that in every species where male infanticide has been reported, it can only be explained as an evolved behavior. They also argue that in those species in which infanticide has never been seen, nor even suspected to occur, its absence is explainable because the species has evolved effective adaptations to avoid it. In other words they try to have it both ways. If you see the behavior then it must have evolutionary importance. If you don't see it you can therefore as-

sume that it was important sometime in the past, and has molded the present accordingly. This amounts to a theory that cannot be falsified, which leaves many cautious Darwinians more than a little uneasy.

The persistence and acrimony of the infanticide debate leads us to ask whether this is merely another esoteric academic controversy, or something larger. The answer should be obvious: we care about the explanation for animal infanticide because it is mirrored in human societies. In the West we regard infanticide, whether committed by mothers or their male partners, as a heinous behavior, forbidden by moral values and punishable by law. Infanticide is seen by some right-wing political groups as the next choice society will offer its citizens once abortion rights are granted. Sarah Hrdy has pointed out that in bygone eras, infanticide was a common practice, while abortion was rare.<sup>15</sup> The fact is that in spite of cultural prohibitions, infanticide happens in many societies and contexts. In many non-western cultures, newborns die at the hands of their mothers and other family members under circumstances consistent with the Darwinian paradigm.

Can the same theories that account for infant-killing by male langurs and lions also explain infanticide, even child abuse, among humans? Martin Daly and Margo Wilson, psychologists at McMaster University in Canada, conducted a careful study of homicide patterns, including murders of infants. They found that younger mothers, in both Amazonian Indian tribes and modern Canada, are much more likely to kill their infants than older ones. The risk to the infant declines steadily with maternal age. This would accord with the diminution of a mother's reproductive value as she ages; later children are much less replaceable than those born to a teenager. Single mothers in Canada were also much more likely to be infanticidal than those with spouses, and single mothers at any age were more often infant-killers than married women of the same age. The latter finding suggests that women lacking the economic and emotional

support of a partner are more likely to suffer the despair about a baby's future that can lead to either a conscious decision or an uncontrolled moment resulting in the death of the child.<sup>16</sup>

These data, however, concern maternal infanticide, whereas the animal killings that provoke so much controversy are done by males. What do the human data show regarding the likelihood of biological fathers versus other, unrelated males in the family attacking or injuring their spouse's infant? Daly, Wilson and other researchers have found that stepfathers are far more likely than biological fathers to become infant-murderers. A child under two years of age is at far greater risk when living with one natural and one stepparent than children of the same age living with two biological parents. Since, due to custody laws, the stepparent is almost always a stepfather (or at least was in the 1980s when the study was done), the risk of infanticide is greatly elevated for small children who live with a non-biological father.

In 1997, linguist Steven Pinker wrote an opinion piece in the *New York Times*, arguing that the infanticidal behavior of two teenage girls who left their newborns in trash bins might have been influenced by sound evolutionary urges rather than by social pathology.<sup>17</sup> He pointed out that in many cultures, neonates are abandoned at birth if the mother makes the harsh but rational judgment that investing her time and energy in them is not in her own best interest. The young mother's reactions are played out at the level of raw emotion, but underlying this may be a deeper and more calculated motivation as well. Although Pinker's casual rationalization of such an awful act struck many readers as facile, there are good reasons for considering both the biological and cultural influences on a mother's treatment of her.

Nowhere are biological and cultural values more tightly linked in the treatment of children than in India. There, infanticide and abortion are part of a harsh cultural feedback loop. The ratio of men to women in India has been rising throughout the twentieth century, to

a current high of 107 males per 100 females.<sup>18</sup> In other words, about fifty million women are “missing” from the Indian population. During the years of British colonial rule, census-takers conducting village-to-village demographic surveys noted that girl babies were in shorter supply than boy babies. Further study showed that infanticide of newborn daughters is widespread in rural India. Distraught mothers, overwhelmed by the birth of yet another girl in a society in which dowries must be paid by the parents to the groom’s family at marriage, choose to kill their last born daughters. Daughters are perceived as expensive, while sons are considered a blessing. This is the cultural element of female infanticide; as in many societies, boys are preferred due to long-standing cultural traditions that place wealth and power in the patriline rather than the matriline. This bias is even played out at the prenatal level. In 1996 India outlawed all forms of prenatal sex-determination in an attempt to stem a tidal wave of abortions of female fetuses. One much-cited study from a Bombay hospital showed that during the 1980s, virtually 100 percent of elective abortions performed were of female fetuses.<sup>19</sup>

Evolutionary biologists who study human behavior are caught in a dilemma; they must generate comprehensive theories that explain both animal and human actions without oversimplifying the cultural and psychological complexities of human social behavior. Perhaps this explains why attempts to understand biological influences on our own behavior are often met with scorn by those who do not think in biological terms. Animals are not behaving immorally when they commit infanticide. They are behaving amorally. Of all the traits most uniquely human, we would like to place morality at the pinnacle. Dagg’s critique of the lion infanticide research ends with a warning that viewing infanticide from an evolutionary perspective is dangerous because it will “make the possibility of change for society seem more difficult.” In other words, she fears that behaviors with demonstrated biological influences will be accepted as inevitable and therefore unworthy of efforts to effect social change. This is

nonsense. If anything, viewing behaviors that most of us consider morally wrong in a biological light will allow us new reflections on their roots. Whether the crime is infanticide, homicide, or just bad behavior, this reflection can only improve our quest to remedy social ills.