

## Commentaries

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### Infanticide Is No Fallacy

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The *American Anthropologist* recently published a critique by Anne Innis Dagg (1998) claiming to refute a series of scientific publications on infanticide in male African lions. Joan Silk and Craig Stanford (1999) rebutted Dagg's paper, providing a concise summary of prior work on this topic. In brief, Bertram (1975), Packer and Pusey (1984; Pusey and Packer 1994) showed that cub mortality increases dramatically when new males first join a pride. Although incoming males have only occasionally been seen to kill cubs, direct observations are difficult to obtain and most of the mortality has been inferred from demographic records. Mothers quickly return to estrus after losing their dependent offspring and then mate with the incoming males. Infanticidal behavior thus accelerates the males' opportunity to father their own offspring. This pattern is consistent with the hypothesis first articulated by Sarah Hrdy (1974) concerning the adaptive significance of infanticide by incoming males.

Dagg (2000) has written a rejoinder to Silk and Stanford that repeats many of her original assertions. First, she claims that infanticide is not as common as generally believed, basing her reply on an apparent discrepancy between the observations of George Schaller (1972) and all subsequent observers in the Serengeti. Schaller provided the first comprehensive description of lion biology and natural history, and his book was certainly a landmark in its time. However, Schaller's study only lasted 3.25 years, and it preceded the great infusion of evolutionary theory into the behavioral sciences in the mid-1970s. So it is not surprising that many of his ideas and interpretations have been superseded. For example, Schaller tabulated the foraging success of different-sized hunting groups, and numerous "armchair" lion ecologists later used his data to predict the optimal group size of hunting lions. These data proved inadequate to test such detailed predictions, and further field studies came to very different conclusions (Packer et al. 1990). This is not to say that Schaller was wrong or unreliable; he just hadn't collected an appropriate dataset to test the hypotheses that his initial observations had inspired.

Many of Schaller's ideas about lion social behavior have stood the test of time. Lion prides are certainly fission-fusion social groups; male coalitions enter the pride from elsewhere; daughters may be recruited into their mothers' pride. However, some of his conclusions were misleading. For example, he categorized lions as either "residents" or "nomads," implying that while most animals were sedentary, a proportion of the population wandered permanently over the Serengeti. We now know that most "nomads" only wander temporarily: they are either

dispersing subadults or males who have lost residence in a pride. Schaller's comments about nomads were not wrong, they were incomplete; he only watched lions for a few years. Without long-term records, he couldn't have seen the larger pattern.

Similarly, there was no way that he could have appreciated the larger pattern of infanticide. Although Schaller monitored over a dozen prides, most of his observations were based on only two prides, the Masai Pride and the Seronera Pride. As it happened, his observations of the Masai Pride coincided with a long period of social stability—the original breeding coalition maintained residence until August of 1969 (when Schaller was busy preparing to leave the Serengeti), and Brian Bertram witnessed the first recorded takeover of this pride. A new set of males briefly entered the Seronera Pride in September 1967, and a second coalition established long-term residence in December 1967. The Seronera Pride suffered considerable cub mortality over these months, including three cubs killed by the second coalition (p. 49 of Schaller's book). However, since Schaller saw no reason to pay special attention to male takeovers, he was in no position to comment on the frequency of infanticide in this context.

In contrast, Bertram monitored four takeovers of the Masai Pride as well as an additional takeover in the Seronera Pride. He was struck by the recurrent loss of cubs and the rapid return to sexual receptivity by the mothers (Bertram 1975). His analysis measured the effects of seven takeovers, and he found a significant statistical relationship between the timing of male takeovers and high cub mortality.

Several of Bertram's papers were inspired by evolutionary logic, and he introduced important theoretical concepts to the study of lion behavior. However, many of his hypotheses have been discarded in the light of more comprehensive studies. Indeed, we wrote two papers as correctives to his more fanciful ideas (Packer and Pusey 1982, 1983). Nevertheless, our larger database clearly confirmed his conclusions on infanticide (Packer and Pusey 1984), and we have continued to see a remarkable consistency in the effects of male takeovers on cub survival.

We have recently analyzed the effects of 270 takeovers over a 30-year period in the Serengeti and Ngorongoro Crater (Packer et al., in preparation). In the absence of a takeover, 56% of 2,091 cubs survived until the age of 9 months, and over 90% of 18-month-old cubs survived to the age of 27 months ( $n = 439$ ). In contrast, cubs that were exposed to male takeovers showed only a 14% survival rate until the age of 9 months ( $n = 398$ ), and less than 70% survived from 18 to 27 months ( $n = 436$ ). The effect of a takeover was statistically significant at all ages.

As her second major point, Dagg incorrectly claims that we have overlooked mortality due to disease, neglect, or starvation. In fact, our first infanticide paper showed that females were more likely to abandon singleton cubs (Packer and Pusey 1984)—a point that we reiterated in our later analysis on the

“optimal litter size” (Packer and Pusey 1995). We also showed that cub mortality was statistically higher in periods of poor food availability (Packer et al. 1988; Packer and Pusey 1995), but since only one cub has ever been seen to drop dead from starvation (A. E. Pusey, personal communication), it is difficult to say what proportion of “poor-season” mortality is due to malnutrition, disease, or abandonment. Finally, we have recently completed an extensive epidemiological analysis of the effects of viral infection (based on serological data collected over an 11-year period). However, none of the six tested pathogens consistently inflicted significant cub mortality (Packer et al. 1999). We have therefore been more willing to publish estimates of the overall impact of infanticide simply because (1) male takeovers are easier to monitor and (2) their effect on cub survival is so large.

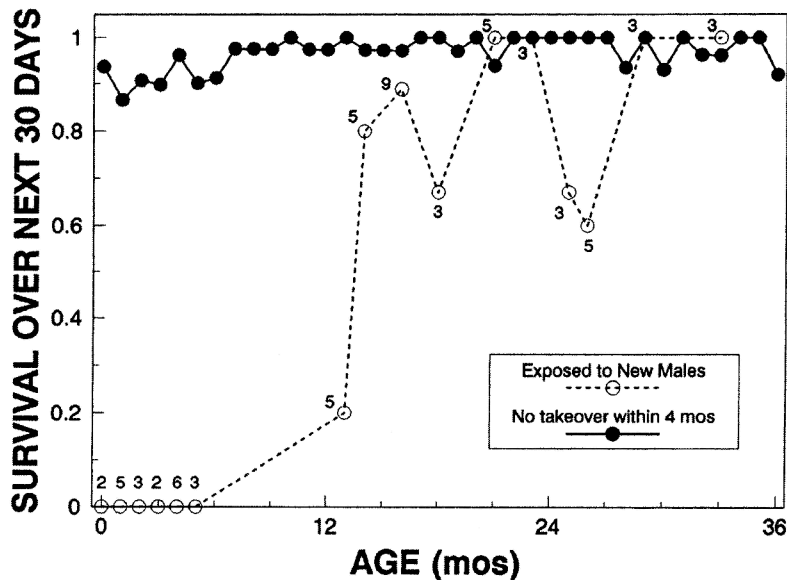
Third, Dagg states that mortality of older offspring at male takeovers runs counter to the sexual selection hypothesis. However, her perspective is too narrow. While a female’s reproduction is only accelerated by the death of a dependent offspring that is less than 14 months of age, the presence of older cubs will reduce the survival of her next litter. This effect is strongest when the subadults are 15–21 months older than the next set of cubs (Packer et al., in preparation). Thus by removing older cubs and subadults from their new pride, incoming males enhance the survival of their own offspring.

Fourth, Dagg proposes that when infanticide does occur, it is merely a random by-product of social disruption. Readers can judge this hypothesis for themselves by watching footage of an infanticidal male on our Web page ([www.lionresearch.org](http://www.lionresearch.org)).

This sequence shows a male systematically killing three cubs. None of our observations have ever suggested that these deaths are “accidental.” Males are not in a hyperkinetic frenzy, and the cubs are not accidentally caught in the middle. The males are focused; the cubs are the targets. In lions, infanticide is one of the fundamental facts of social life.

The value of scientific theory lies in its ability to make novel predictions. The risk of infanticide by incoming males represents a major loss of fitness to females, and we have shown that mothers are relatively indifferent to the vocalizations of resident males and highly nervous of nonresidents (McComb et al. 1993). In addition, females show numerous counter-strategies to minimize their risk from incoming males, including periods of infertility and cohesive nursery groups (Pusey and Packer 1994). While the total number of direct observations of infanticide may still be small, the phenomenon is sufficiently predictable that we have routinely helped documentary film teams to photograph the behavior. Indeed, they have been successful in all three occasions that we deemed cubs to be “at risk” during filming.

Dagg’s original paper stated that there was no direct evidence of an infanticidal male fathering offspring with the mother of his victims. We use the term “incoming males” to define the initial residency of a new coalition. Most mating occurs in the first weeks or months after the takeover; coalitions compete against each other on a continual basis. Successful males make the transition from “incoming males” to fathers. Our DNA study (Packer et al. 1991) was based on a representative sample of incoming males, and the analysis confirmed that these same males



**Figure 1.** Age-specific survival of cubs according to their exposure to a male takeover. Analysis is restricted to cubs born prior to the entrance of the seven coalitions studied in Packer et al. (1991). Survival is measured over a 30-day interval; numbers indicate the number of “exposed” cubs at each age. Data on “unexposed cubs” are based on 80 cubs born over the same period in the same prides, but who were not subject to a takeover either (a) before they reached the age of 37 months or (b) within four months of their deaths. The effect of male takeovers is highly significant ( $p < .001$ ).

subsequently sired every cub born during their tenure. Figure 1 presents the extent of cub mortality at the takeovers of the seven male coalitions in this study. Cubs less than 15 months old suffered massive mortality, whereas the control group enjoyed excellent rates of survival. Given everything we know about the behavior of new males during a takeover, the increased mortality in Figure 1 was almost certainly due to infanticidal behavior by these males.

Although our view of lion infanticide is largely statistical, the magnitude of the effect is huge, and the lions are highly sensitive to the associated risks. It would be irresponsible to ignore a pattern that stands out so prominently from a 35-year study. Throughout Africa, wildlife biologists routinely consider the risks of infanticide whenever they manage endangered populations of lions. No one would encourage the introduction of new males into the last population of Asian lions, for example, nor would anyone introduce an unfamiliar male to a captive female and her cubs. Dagg writes with a surprising air of authority, but she has never studied lions, nor has she ever made any attempt to contact us. Her penchant for inflammatory rhetoric may be entertaining to read, but she would be better served by a more constructive approach to scholarship. We have built a productive research program on the basis of our understanding of male infanticide. Schaller's book may be absorbing, but there is no reason to view it as scripture. Bertram got it right, and his work has provided an important foundation for us all.

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