Mating strategies in primates: A game theoretical approach to infanticide

James E. Lyon [a], Sagar A. Pandit [a], Carel P. van Schaik [b], Gauri R. Pradhan [c,*]

[a] Department of Physics, University of South Florida, Tampa, FL, USA
[b] Anthropological Institute and Museum, Zurich University, Zurich, Switzerland
[c] Department of Biology, University of South Florida, 4202 East Fowler Ave, SCA110 Tampa, FL 33620, USA

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ABSTRACT

Infanticide by newly immigrated or newly dominant males is reported among a variety of taxa, such as birds, rodents, carnivores and primates. Here we present a game theoretical model to explain the presence and prevalence of infanticide in primate groups. We have formulated a three-player game involving two males and one female and show that the strategies of infanticide on the males' part and polyandrous mating on the females' part emerge as Nash equilibria that are stable under certain conditions. Moreover, we have identified all the Nash equilibria of the game and arranged them in a novel hierarchical scheme. Only in the subspace spanned by the males are the Nash equilibria found to be strict, and hence evolutionarily stable. We have therefore proposed a selection mechanism informed by adaptive dynamics to permit the females to transition to, and remain in, optimal equilibria after successive generations. Our model concludes that polyandrous mating by females is an optimal strategy for the females that minimizes infanticide and that infanticide confers advantage to the males only in certain regions of parameter space. We have shown that infanticide occurs during turbulent changes accompanying male immigration into the group. For changes in the dominance hierarchy within the group, we have shown that infanticide occurs only in primate groups where the chance for the killer to sire the next infant is high. These conclusions are confirmed by observations in the wild. This model thus has enabled us to pinpoint the fundamental processes behind the reproductive decisions of the players involved, which was not possible using earlier theoretical studies.

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1. Introduction

In a variety of mammals such as primates, carnivores and rodents, newly immigrated or newly dominant males are known to attack and kill dependent infants (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994; van Schaik and Janson, 2000). Hrdy (1974) was the first to suggest that this unusual behavior was the product of sexual selection: by killing infants they had not sired, males advanced the timing of the mother's next estrus, and due to their new social position would have a high probability of siring this female's next infant. Infanticide would therefore be one of the most dramatic expressions of inter-sexual conflict (Smuts and Smuts, 1993; Gowaty, 1997). This is particularly true for primates with slow life history and the propensity to resume cycling when dependent infants are lost. These conditions provide ideal circumstances for reproductive gains, thereby making infanticide an adaptive strategy for the male but extremely costly for the female, who has a substantial investment in the form of lactation and gestation (van Schaik, 2000). Indeed, among primates this phenomenon is remarkably common: It is reported

in more than 40 species and may account for up to 25% of infant deaths (Hausfater and Hrdy, 1984; Smuts and Smuts, 1993; Hiraiwa-Hasegawa, 1988; Van Schaik et al., 1999). Although both the phenomenon and its interpretation have been questioned by some (Bartlett et al., 1993; Sussman et al., 1995; but see Hrdy et al., 1995), this hypothesis provides a far better fit with the observations on primates than any other alternatives (van Schaik, 2000). Moreover, strong empirical data supporting the infanticide hypothesis have been found in recent years (van Schaik and Janson, 2000; Bellemain et al., 2006), including studies that determined paternities (Borries et al., 1999; Soltis et al., 2000). Since infanticide almost always follows usurpation or incapacitation of the former dominant male, who is the likely sire, it is clear that male protection plays an important role in infant survival (van Schaik, 2000). Thus, considering the costs involved, infanticide is expected to have driven selection on counterstrategies by both the mother and the likely sire from the point of view of reduction in infanticide (van Schaik et al., 1999, 2004; Hrdy et al., 1995; Hrdy, 1979; de Ruiter, 1996).

Since infanticide is inherently adaptive for the males and at the same time, extremely costly for the female it is important to study its impact formally on the overall reproductive behavior of primate males and females. Our earlier mathematical models are based on a phenomenological approach. We have demonstrated

* Corresponding author. Tel.: +1 813 974 5188; fax: +1 813 974 3263.
  E-mail address: gauri@usf.edu (G.R. Pradhan).

the existence of a basic conflict of interest between the dominant male and the female and also between the dominant and other competing males (van Schaik et al., 2004; Pradhan and van Schaik, 2008; Boyko and Marshall, 2009). We have derived conditions under which infanticide is adaptive and its resulting impact on social composition of primate groups. Furthermore, one of our models has shown that despite having a conflict with the subordinate male and/or the rivals, occasionally, the dominant male earns a higher payoff by conceding some paternity to other males; this prediction has been supported with empirical data on baboons (Henzi et al., 2010; see also Reeve and Ratnieks, 1993).

It would be of interest to know the fundamental processes behind male–female reproductive decisions in this social situation of conflict and cooperation and we thus propose a framework that will complement our earlier theoretical investigations (van Schaik et al., 2004; Pradhan and van Schaik, 2008). We propose that, starting from first principles and with a minimum number of assumptions, it can be best approached by using the mathematical theory of games because there is involvement of multiple players and the reproductive decisions made by each player has an impact on the fitness of every player involved. In this framework, every player chooses its strategies from a fixed set and then rather than searching for a globally optimal outcome, we look for combinations of strategies, where each player's strategy gives the best outcome to that player based on the others' strategies. Such combinations are known as Nash equilibria. Furthermore, we need to determine the stability of these strategy equilibria against competing strategies.

Our model differs from that of Broom et al. (2004) in that we also consider the options of the female and of both insider and immigrant males. It is similar to other social strategy games on deforestation (e.g. see Rodrigues et al., 2009) or on decision-making in political systems and large organizations (Stokman and Stokman, 1995). In this paper, we will demonstrate that the reproductive decisions made by males and females are in Nash Equilibria, and that only small regions of parameter space lead to stable Nash Equilibria that admit infanticide which, for the first time, will also produce a theoretical explanation for the adaptive but rare nature of infanticide on the whole.

2. Model

We have developed a game theory model that describes the mating strategies of females and attitudes towards infants by males in primate groups. Standard Game Theory assumes a finite number of players and a finite number of strategies for each player. Although many primate groups contain numerous potential players, we limit the game to a two-male, one-female system. This game involves one female because in species with estrous asynchrony, female mating decisions are largely independent of each other (e.g. Pereira, 1991). The two-male approximation is justified because most of the male–male interactions are dyadic (unless coalitions among males are present (Pandit and van Schaik, 2003)). A male's dominance is based on his strength relative to the other (σ). The species modeled here are iteroparous and hence females give birth multiple times in a lifetime, up to a dozen times for some species (Stearns, 1992).

In constructing our model, we assign a set of pure strategies to each player. Both males possess the same set of pure strategies, viz. "attack (A)," "defend (D)," and "show indifference toward (I)" the offspring. The female's pure strategies are to mate solely with male 1 (M1) and mate solely with male 2 (M2). Each player may also utilize a mixed strategy, with different weights attached to their pure strategies. A strategy profile is denoted by an ordered n-tuple of individual strategies. For example, a pure strategy

profile could be $S=(A,D,M1)$. A mixed strategy is denoted as $M=(X_{A,D},X_I,X_{M1})$, where the subscripts are the supporting pure strategies.

In the previous example, male 1 is playing a strategy with non-zero weights attached to his attack and defend strategies, male 2, strictly the ignore strategy, and the female, strictly "mate with male 1" (see Weibull, 1995).

The physical interpretation of a mixed strategy in game theory has been contested in recent decades (Aumann, 1985; Rubinstein, 1991). In the female's case, the interpretation is straightforward. Each weight to her pure strategy represents the proportion of matings with that particular male among all her matings with both males within one turn of the game, i.e. one full birth interval. Thus, if she is playing a mixed strategy with 0.3 weight assigned to her M1 (denoted in our game by the variable p) pure strategy and 0.7 weight assigned to her M2 pure strategy, out of all her total matings with males 1 and 2, 30% of them are with male 1 and 70% with male 2.

For the males, various interpretations of their mixed strategies can be put forward. For this game, we chose the multiple-action interpretation, in which the males have multiple opportunities to act against the infant, and their pure strategy weights represent the percentage of times they take that action at every opportunity. However, in this interpretation, the number of opportunities n a male has is ambiguous: it is assumed to be a finite number, dependent on external factors, but is not necessarily constant, because if the infant is successfully killed early on, n could be smaller. Also, the order in which a male takes his actions is undefined. It is unclear how these two features of the multiple-action interpretation affect the outcome of this model. Regardless, the model treats these multiple actions as if they are equivalent to a single action.

Apart from the strategies, the model relies on five external parameters that depend on environmental factors such as group composition, duration of male tenure, length of gestation and lactation periods, life history, and the physiological conditions of the males. The values of these parameters range between 0 and 1, exclusive. The parameter μ is the probability of a male siring a subsequent offspring with the female after committing infanticide (where $1-\mu$ is the corresponding chance of the other male siring the next offspring), σ is the normalized relative strength of the males (corresponding to the likelihood that male 1 wins a conflict with male 2), c is the normalized cost, weighted by σ, to a male while defending an offspring attacked by another male. In the model, there is no cost to an attacking male because it is assumed that attacks are always opportunistic, that is, at a time favorable to the attacker. Since the attacker has the choice of the timing and conditions of the attack, costs for an attack are negligible compared to the cost of defense. The cost of defense is always assumed to be less than 1, even though defense might incur losses of future potential infants, because the game only considers the presence or absence of one infant for the male at the end of the turn, and does not take into account future game turns. The parameter l is a "lookout" cost borne when a male defends an infant not immediately threatened, and k is the normalized reproductive cost to the female, in either time or energy, from the loss of the initial infant. Table 1 gives concise descriptions of these parameters. The probabilistic interpretation of external parameters is founded on the possible existence of ensembles of primate groups, i.e. given multiple simultaneous instances of the game by any group of players. Thus, the parameters may be interpreted as the expected value of that parameter over those instances.

The payoff for each player is the number of offspring sired at the end of the turn minus the costs imposed upon the player. Since our payoff tables are three-dimensional, Tables 2–4 represent them as a pair of two-dimensional tables, one for each of the female's pure strategies.