Why fight? Selective forces favoring between-group aggression in a variably pair-living primate, the white-faced saki (*Pithecia pithecia*)

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Abstract

Between-group aggression is a common feature of many group-living animals. Yet aggressive behaviors are often costly, involving risk of injury, increased energy expenditure and the potential to reduce feeding time. For aggression to be evolutionarily advantageous these costs must be outweighed by the benefits gained from exclusive access to resources and/or mates, or through committing infanticide. However, the dynamics favoring aggression in species living in small groups may differ from those in larger groups since mating exclusivity is higher and the potential to numerically dominate opponents is lower. We examined the selective factors influencing between-group aggression in a primate that lives in both pairs and small groups, the white-faced saki monkey (*Pithecia pithecia*). Data were collected on three free-ranging groups at Brownsberg Naturepark (Suriname) over 17 months. Intergroup encounter frequency and intensity of aggression during encounters were compared to temporal changes in diet, variation in ovarian hormones, frequency of copulations and the presence of dependent infants. Participation in between-group aggression was heavily male-biased and the presence of cycling females was a significant predictor of aggression frequency. Percentage of mesocarp in the diet also had a significant effect on the frequency and the intensity of aggression, with high mesocarp consumption corresponding to increased aggression. Presence of dependent infants did not affect between-group aggression. Our results support both the male mate defense and male resource defense hypotheses, suggesting that male reproductive interests are the principle selective pressures acting on between-group aggression in white-faced sakis. White-faced sakis’ rigid conformity to traditional expectations of male intrasexual intolerance appears to be unique among primates living in small groups with variable mating systems.
Keywords
intergroup encounters, mate defense, resource defense, infanticide, pair-living, dear enemy, small groups.

1. Introduction
For social animals, between-group interactions are a competitive element which can influence individual access to feeding resources and mates, thereby influencing reproductive success. Intergroup relationships play an integral role in socio-ecological models and the predicted competitive regimes individuals will face (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). In group-living primates encounters are often aggressive, but can also be neutral or affiliative (Cheney, 1987). While groups occupying the same environment can be expected to occasionally converge in time and space [either by chance, such as in an ideal gas model (Hutchinson & Waser, 2007) or by mutual attraction to a resource (Harris, 2007)], such meetings do not explain the decision to engage in aggression. Intergroup aggression (IGA) can result in injury (Crockett & Pope, 1988; Palombit, 1993; Mech, 1994; Miller, 1998; Cords, 2002; Gros-Louis, 2003; Watts et al., 2006), entail energetic costs of participation (Marler et al., 1995) and potentially decrease the amount of time available for feeding. The willingness of individuals to engage in such costly IGA is generally attributed to four non-mutually exclusive explanations:

H1. Female resource defense (Wrangham, 1980; Ostfield, 1990). Between-group aggression allows groups to gain exclusive access to food resources within their home range. Since feeding resources in mammals are more limiting to female than male reproductive success, female(s) are expected to be the main aggressors.

H2. Male resource defense (Emlen & Oring, 1977; Fashing, 2001; Williams et al., 2004). Male(s) defend food resources within an area, possibly in exchange for access to mating opportunities and/or to maintain female membership in the group. Effective resource defense may also promote female transfer, as females should prefer males who provide better access to resources.

H3. Male mate defense (Trivers, 1972; Kitchen & Beehner, 2007). Aggression toward other groups grants males exclusive mating access to female(s) within their group, increasing the probability that they will sire...