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Senior Thesis

The effect of kinship on male chimpanzee behavior

Cooperation in animals creates fascinating research questions (Dugatkin 2002). In animal behavior, cooperation is defined as behavior that increases the fitness of other individuals and is selected because of its positive effects on others (West et al. 2007). Such behavior poses an evolutionary paradox because natural selection typically operates to favor the survival and reproduction of individuals (Mitani 2009a). Why then do animals help others at a potential cost to themselves?

W.D. Hamilton (1964) provided one solution to the puzzle of animal cooperation. He reasoned that while individuals are the units upon which the process of natural selection operates, individuals are not the units of inheritance. Instead, genes are passed down from generation to generation, and these genes are shared differentially between individuals. Specifically, closely related individuals share more genes with each other than do unrelated individuals. From this, Hamilton hypothesized that natural selection will favor the evolution of traits that helped others survive and reproduce insofar as those others share genes with the actors. This process was dubbed kin selection to differentiate it from natural selection (Maynard Smith 1964). To formalize the concept, Hamilton specified the conditions under which kin selection is expected to operate. If b is defined as the fitness benefit derived by the recipient of a cooperative act, c is the fitness cost suffered by the actor, and r is coefficient of relatedness between recipient and actor, then cooperative behaviors will evolve when $rb > c$. This simple equation, which has come to be known as Hamilton's rule, makes the prediction that cooperation will occur more often between closely related individuals than it does between non-relatives.

Coalitionary behavior is a prime example of cooperation among animals, particularly primates. Coalitions involve two or more animals cooperating by directing aggression toward third parties. In a typical interaction, one animal intervenes into an ongoing dispute between two others, helping one of the latter individuals in the process. The behavior of individuals who intervene is puzzling because by providing help they run the risk of getting injured and negatively affecting their relationships with other members in the group (van Schaik et al. 2004). Why then do animals form coalitions? Several studies suggest primates form coalitions with their relatives to gain indirect fitness benefits via kin selection (Langergraber et al. 2007)

Several studies indicate that females form coalitions selectively with their maternal kin. In New World monkeys, female white-faced capuchins (*Cebus capucinus*) form coalitions more often with their maternal relatives than they do with non-kin (Perry et al. 2008). Similar findings have been made in several species of Old World monkeys including baboons, macaques, and vervets (Chapais 2001). While these studies reveal that maternal kinship affects coalition formation, whether paternal kinship exerts a similar influence continues to be debated. Observations of baboons and macaques suggest that females in these species affiliate more often with their paternal half siblings than they do with non-relatives (Widdig et al. 2002; Smith et al. 2003). In contrast, female capuchin monkeys do not bias their behavior towards their paternal kin (Perry et al. 2008).

Male chimpanzees are particularly appropriate subjects to investigate the effect of kinship on coalition formation. First, they are quite social, interacting and forming coalitions frequently with each other (Mitani et al. 2002). Specific pairs of males sometimes support each other in consistent fashion in long-term alliances (Nishida and Hosaka 1996). Additionally, unlike most primate species in which males typically leave their natal groups after reaching or nearing sexual maturity, female chimpanzees disperse (Mitani 2009a). Therefore, chimpanzee communities often contain males who are closely related to each other, providing opportunities for kin to support each other (Mitani et al. 2000).

In this paper, I investigate the effect of kinship on coalition formation in a community of wild chimpanzees. I examine the effects of maternal and paternal kinship on coalition formation separately. given the current controversy regarding whether primates form coalitions with their paternal kin.

METHODS

Study Site and Subjects

Chimpanzees were observed by John Mitani at Ngogo, Kibale National Park, Uganda, during five years between 2004 – 2008. The Ngogo study site is covered primarily by old growth rainforest interspersed with patches of *Pennisetum purpureum* grassland. Straddling the equator ($0^0$29'53" N, $30^0$5'0"E), Ngogo is relatively high lying at an altitude at about 1400 meters above sea level. As a consequence, temperatures there are comparatively mild, fluctuating between average daily lows of 16.8 C^0 (SD = 0.3) and highs of 23.8 C^0 (SD = 0.3) during the five-year study period. Ngogo experiences two wet seasons during March – May and August – December, with annual rainfall averaging 1429 mm (SD = 32, N = 5 years, 2004 – 2008).

The Ngogo chimpanzee community is unusually large. During the five-year study period, the community contained approximately 150 individuals, including 25 – 29 adult males.

Behavioral Observations

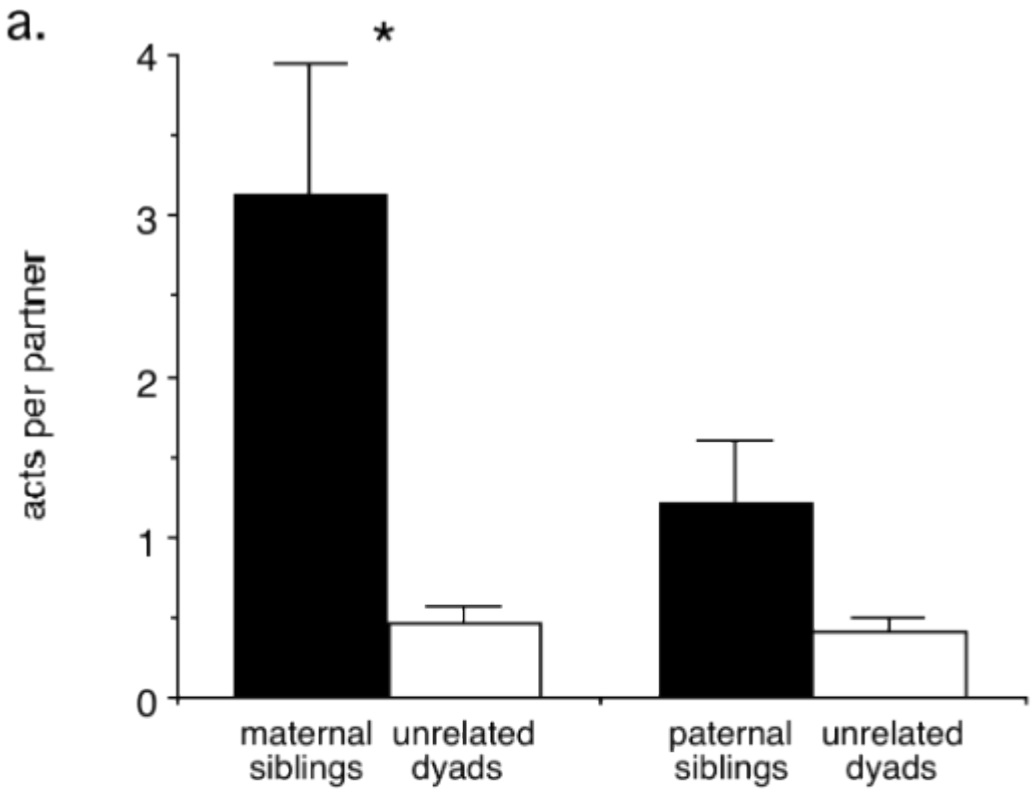
The behavioral observations analyzed here were collected by John Mitani. He followed chimpanzees for 16 months during the 5 year study period, making observations for 6 months in 2005 and for 2 – 3 months in the remaining years. Adult male chimpanzees were observed during 2,832 one hour focal animal sampling sessions. The observations of coalitions reported in this paper were collected *ad libitum* during these times. Mitani recorded who participated in each coalition, including the males who provided support, the recipients of support, and the identities of targeted individuals. I used these observations to determine whether male chimpanzees formed coalitions selectively with their kin. For purposes of these analyses, I considered relatives to be maternal and paternal half-siblings. All other pairs, excluding father-son dyads, were classified together into a category of non-relatives. I performed two analyses to examine whether kin supported each other more than they did non-kin. In one analysis, I controlled for variation in the number of potential partners by computing the number of related and unrelated individuals each male had in the community during each year of observation. I used these to calculate the average number of kin and non-kin each male had over the five year study period. I then divided the number of times males supported each type of recipient, kin and non-kin, by the average number of beneficiaries present during the study. I compared these ratios, using males as their own controls, in a Wilcoxon signed rank test. In a second analysis, I accounted for variation in the number of opportunities males had to support kin and non-kin. I assayed

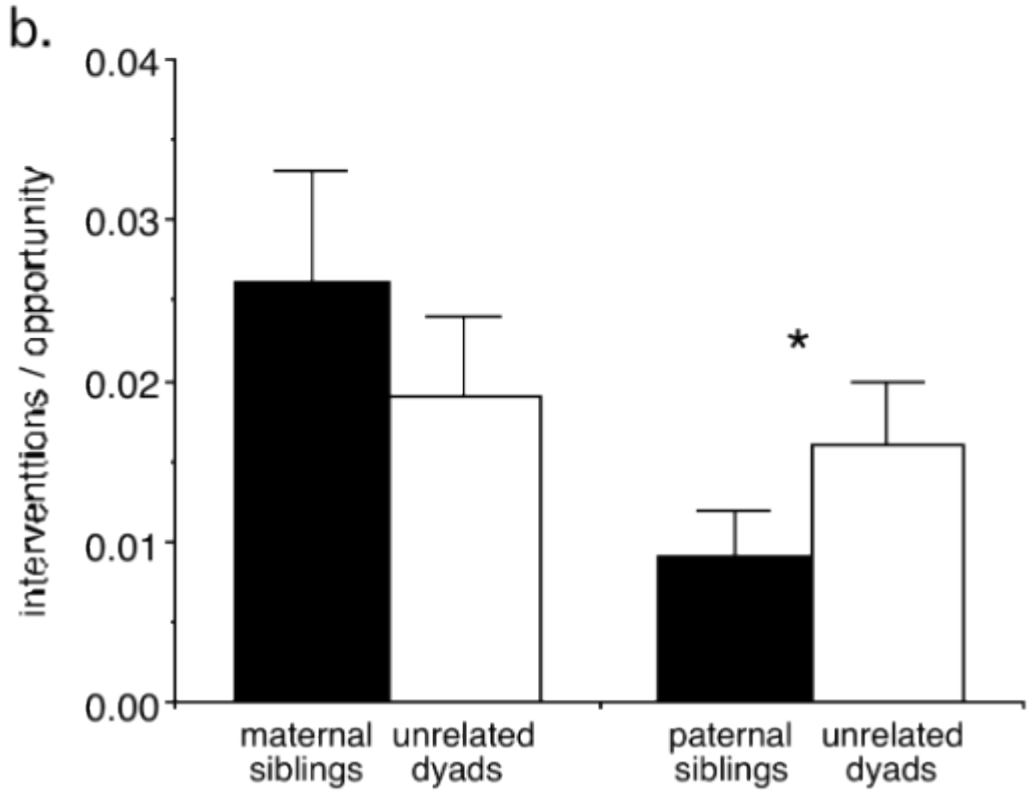
opportunities to support others by tabulating the number of times each male's relatives and non-relatives were involved in aggressive acts. In these tallies, I excluded aggressive episodes that involved focal subjects. I counted the number of times males supported kin and non-kin and divided these by the number of opportunities, comparing these ratios in a Wilcoxon test.

RESULTS

There were 84 coalitions between maternal siblings, 45 between paternal siblings, 5 between father-son pairs, and 626 between unrelated males. Males supported their maternal siblings significantly more often than they did unrelated males when support was assayed in terms of acts per partner (Wilcoxon $Z = 2.98$, $P < 0.01$, $N = 21$; Figure 1a). Males also formed coalitions with their maternal brothers more often than they did with nonkin when support was evaluated with respect to the number of opportunities to intervene, but this difference was not statistically significant (Wilcoxon $Z = 0.38$, $P = 0.70$, $N = 21$; Figure 1b).

Paternal kinship did not influence the formation of coalitions between males. Males supported paternal siblings and unrelated males at similar rates when support was computed in terms of acts per partner (Wilcoxon $Z = 1.45$, $P > 0.10$, $N = 21$; Figure 1a). In contrast, males supported their nonkin significantly more often than their paternal half-siblings when support was calculated in terms of the number of opportunities to intervene (Wilcoxon $Z = 1.45$, $P > 0.10$, $N = 21$; Figure 1b).





DIscussion

The preceding analyses indicate that male chimpanzees supported their maternal siblings more often than they did unrelated individuals. This effect held when coalitions were

assayed in terms of acts per partner, but not when they were assessed in terms of number of opportunities. In contrast, male chimpanzees formed coalitions with their paternal kin no more often than they did with unrelated animals.

My results are consistent with a large body of research, which reveals that maternal kinship affects several aspects of primate behavior. Previous research at Ngogo indicates that maternal kinship influenced the social bonds between individuals. Maternal half brothers formed long-lasting bonds and groomed each other more equitably than did pairs who were unrelated (Mitani 2009b). Studies of other primates have yielded similar results. For example, female baboons form strong and enduring social bonds with their maternal kin (Silk et al. 2006). Maternal kin also support each other in coalitions more often than do nonrelatives (Silk et al. 2004). Female rhesus macaques form close social bonds with their maternal sisters (Widdig et al. 2001), while female white-faced capuchins provide more coalitionary support to their maternal sisters than they do to nonkin (Perry et al. 2008).

The findings reported above are also consistent with prior research that reveals primates do not bias their behavior toward their paternal kin. Observations of white-faced capuchins and chimpanzees indicate that individuals cooperate with their paternal relatives no more frequently than they do with unrelated animals (Langergraber et al. 2007; Perry et al. 2008). These data, however, contrast with those derived from additional studies. Widdig and colleagues were the first to report that female rhesus macaques selectively associate with their paternal half-sisters (Widdig et al. 2001). Similar findings were subsequently published on female baboons (Smith et al. 2003; Silk et al. 2006).

It is not immediately clear why different studies have produced different results. At first blush, maternal kin recognition facilitates the ability of primates to bias their behavior toward maternal kin. Because primate infants experience prolonged periods of dependence on their mothers, who provide extensive care to them, individuals are likely to be able to recognize their maternal relatives. In contrast, primates may not bias their behavior toward their paternal kin because they are unable to identify them (Chalmeau & Gallo 1996; Widdig 2007). In many primate species, single females mate multiple males. Combined with internal fertilization, this would make it difficult for mothers, fathers, and offspring to determine paternal relationships (Mitani 2009b). While these considerations suggest why there are consistent biases in behavior toward maternal kin, they fail to explain cases in which paternal kin have been reported to cooperate selectively with each other. Smith and colleagues proposed that the differences in the size and composition of kin networks may play a role in this (Smith et al. 2003). In cases where matrilineages are larger than patrilineages, maternal kin might be expected to show clear preferences for each other than do paternal kin. Where patrilineages are larger than matrilineages, the opposite is expected to occur. While this is an interesting possibility, additional data from chimpanzees does not bear out this prediction (Langergraber et al. 2007). In sum, additional work will be required to determine why paternal kin biases have been reported in some primate species, but not others. Such studies will depend critically on identifying a viable mechanism that primate individuals can use to reliably recognize their paternal kin. Until such a mechanism has been documented, the issue is likely to remain unresolved.

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