Male cooperation despite high reproductive skew may be explained by reproductive queuing in white-faced capuchin monkeys

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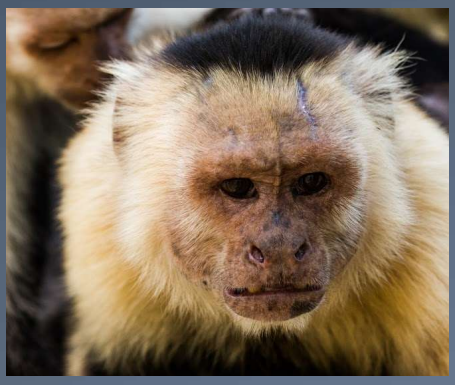
Introduction

Cooperation in animal societies with high reproductive skew presents a paradox in which subordinates promote the reproductive success of a dominant animal, seemingly at the expense of their own reproduction. The *concession model* suggests that the alpha male benefits from the presence of subordinate males and therefore offers reproductive opportunities as staying incentives (1-3). The *queuing model* is an extension of the concession model that also takes future reproductive opportunities into account (4, 5). Subordinate males that outlive the alpha male may gain the alpha position after the current alpha male disappears from the group. The effect of queuing can be so powerful that the subordinate male does not require any current reproductive opportunities as staying incentives (4, 5).

Research objective and questions

To further our understanding of how male coalitions are maintained in populations with high reproductive skew, we investigate whether the following underlying assumptions of the concession and queuing models are true in our study population:

1. Do alpha males benefit from the presence of subordinate males via increased offspring production?
2. Do immediate reproductive opportunities act as staying incentives for subordinate males?
3. Are there alternative long-term strategies to obtain high reproductive success?



White-faced capuchins (*Cebus capucinus*)

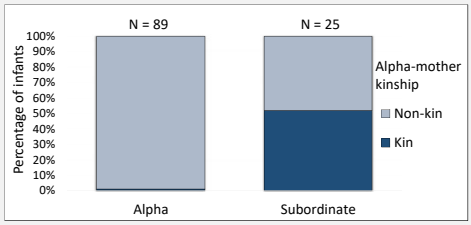
- Males immigrate alone or in parallel with other males
- Coalitions of males are more successful in taking over groups
- Males become alphas by aggressively taking over the position or by queuing until the position becomes vacant by the death or dispersal of the former alpha male
- Males in multi-male groups cooperatively defend the group from predators, extra-group males, and other bisexual groups
- Female reproductive output increases with number of males
- Despite the importance of male coalitions, male reproductive skew remains high

Methods

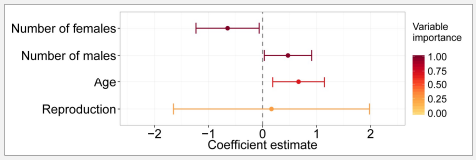
- Four white-faced capuchin groups
- Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica
- Demographic, behavioral, and genetic data collection between 1993 and 2012
- Non-invasively collected fecal samples from infants, mothers, and males (>6 years)
- Genotyping at 20 short-tandem repeat loci
- Parentage assignments in the software CERVUS (72, 73) and COLONY (74) at the 95% confidence level

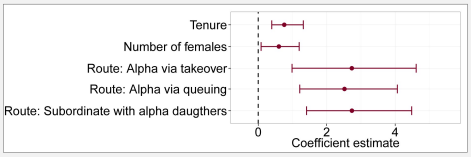
Data set

- 114 genotyped infants
- Alpha males sired 50% - 100% of the infants
- Subordinate males sired 0% - 88% of the infants
- Half of the infants sired by subordinate males were born by the mature daughters of the alpha male



Group	% infants sired	Tenure (years)	# females	Interbirth interval	Expected reproductive success (# offspring)
Uni-male	100	4	3.2	3.4	3.7
Multi-male	85	4.7	6	2.7	8.9





1. Expected alpha male reproductive success

- Higher in multi-male than uni-male groups
- Based on the mean percentage of infants sired, mean tenure, mean number of females, and mean interbirth intervals
- *Alpha males benefit from the presence of subordinate males*

2. Likelihood of subordinate male dispersal

- Decreases with number of females
- Increases with number of males and male age
- Not affected by reproductive opportunities
- *Reproductive opportunities do not act as staying incentives*

3. Total male reproductive success

- Increases with number of females and tenure
- Higher for alphas via takeover, alphas via queuing, and subordinates residing with alpha daughters than for other subordinate males
- *There are three alternative routes to high reproductive success*

Acknowledgements

We gained permission from the Costa Rican Park Service, the administration of the Área de Conservación Guanacaste, the University of Calgary's Life and Environmental Sciences Animal Care Committee, and Tulane University's Institutional Animal Care and Use Committee. The study was funded by Japan Society for Promotion of Science, NSERC, Canada Research Chairs Program, LSB Leakey Foundation, Tulane University's Department of Anthropology, Stone Center for Latin American Studies, Newcomb Institute, and Research Enhancement Fund.

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