Follow the Leader: Correlates of Juvenile Leadership in Wild Chimpanzees

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B.S. in Anthropology, December 2016, Michigan State University

A Thesis submitted to

The Faculty of
The Columbian College of Arts and Sciences
of The George Washington University
in partial fulfilment of the requirements
for the degree of Master of Science

May 19, 2019

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Acknowledgements

This thesis would never have been possible without the support from numerous individuals. I would like to thank my advisor, Dr. Carson Murray, who has offered countless insights during every step of the process. Thank you for your guidance and humor throughout these past two years and reminding me that even a null result is interesting. Additionally, I would like to thank Dr. Shannon McFarlin as the second reader of my thesis; thank you for your invaluable comments.

Thank you both to Kaitlin Wellens and Sean Lee for your help and insights throughout this process. To the George Washington University’s Primate Behavioral Ecology Lab interns, past and present, thank you for digitizing the data that I used for my research and commenting on the many iterations of my work in lab meetings.

I would like to thank Tanzanian National Parks, the Tanzania Wildlife Research Institute, and the Tanzanian Commission for Science and Technology for granting access to research at Gombe National Park; as well as the research assistants who work tirelessly to collect data. Additionally, I would also like to thank the Jane Goodall Institute for providing access to these data.

To the CASHP graduate students, thank you for all of your support and advice. I am so proud to belong to this wonderful community of researchers. To Courtney Sexton and Louis Gorgone, thank you for the endless laughs, constant support, and frequent reality checks. I couldn’t have asked for a better cohort; I look forward to clump reunions for years to come. An incredibly important thank you to Kristen Tuosto. You have encouraged and supported me in more ways than you know. Thank you for making me
laugh, listening to my ideas, and opening up my world to the culinary miracles of mushrooms.

Finally, to my mom, dad, and Andrew, nothing that I am is without you. Thank you all for your unwavering support and constant encouragement throughout the years. I could not have done this without all of you.
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Most primate species are socially-cohesive. Group-living primates enjoy the benefits of sociality—such as lower predation risk and better foraging efficiency—but must coordinate movements despite differences in kinship, affiliation, sex, age, and reproductive status. The majority of research on primate group movements has focused on species that travel as a socially cohesive unit. However, in fission-fusion living primates, in which members of a community associate in temporary subgroups, leadership is poorly understood. Chimpanzees (Pan troglodytes schinfurthii) represent an ideal species to study the complexities of leadership and followership as the fission-fusion nature of this genus may allow for a broader range of individuals to influence leadership, such as juveniles, compared to group-living primates in which membership is relatively stable and cohesive. Juveniles, represent an interesting class in which to consider leadership as this period is hypothesized to be an important time for young primates to develop the social and foraging skills needed for adulthood.

Using 34 years of data collected on wild chimpanzees in Gombe National Park, I investigated juvenile leadership in chimpanzee family groups. I first explored the relationship between juvenile age and sex on consensus movement (i.e. joint travel initiations by both the mother and juvenile). My results indicate that both sex and age of the juvenile affect the frequency of consensus movements. Second, I investigated multiple variables of juvenile leadership. My results indicate that the sex of the juvenile affects juvenile leadership, as juvenile males lead more than juvenile females.
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Chapter 1: Introduction

Primates are characterized by slow development, delayed maturation, and long life spans compared to similar sized mammals (Harvey & Clutton-Brock, 1985; Charnov & Berrigan, 1993). The juvenile period between weaning and sexual maturation has been hypothesized to be an important time for immature primates to learn both social and ecological skills needed for adulthood (Joffe, 1997). Unlike humans who are weaned young and require both parental and alloparental nutritional provisioning to survive, non-human primates achieve nutritional independence once weaned (Watts & Pusey, 2002). However, despite the ability to support themselves calorically, newly weaned primates remain in their natal community where they are likely to benefit from familiar social and ecological surroundings as well as continued association and support from their mothers (Fairbanks, 2000). Continued association with a juvenile, however, can be costly for mothers. Previous research has noted that continued association with a juvenile decreases maternal traveling speeds and constrains day ranges (chimpanzees: Wrangham, 2000; Pontzer & Wrangham, 2006).

The majority of research on post-weaning association between mothers and juveniles comes from various female philopatric cercopithecine species that live in stable social groups and attain rank through maternal inheritance (Fairbanks, 2000). Cercopithecine mothers play a substantial role in both juvenile and adult female reproductive success through support in agonistic interactions, in which rank may be attained or solidified, and access to preferred food resources (long-tailed macaques: van Noordwijk and van Schaik, 1999; vervet monkeys: Horrocks and Hunt, 1983; chacma baboons: Cheney, 1977; yellow baboons: Altmann and Alberts, 2005). Rank has been
documented to affect both the health of a female (Sapolsky, 2005), as well as her reproductive success (Dunbar & Dunbar, 1977; Altmann & Alberts, 2003). In group living species, juveniles have few opportunities to lead due to small body size, low social dominance, and inexperience (but see Tonkean macaques: Sueur & Petit, 2008), and so chimpanzees provide an interesting system in which to investigate the factors that impact juvenile leadership in family movements.

Chimpanzees (Pan troglodytes) live in a fission-fusion social system in which individuals belong to a permanent community but associate in temporary parties that may last from minutes to days (Pusey and Schroepfer-Walker, 2013). Additionally, males are the philopatric sex and females typically disperse at adolescence (Mitani et al., 2002). Chimpanzees are nutritionally dependent on their mothers until they are weaned between the ages of 3-5 years old (Pusey, 1983). Once weaned, juveniles continue to travel with both their mother and younger sibling for 4-5 more years (Pusey, 1983). Due to to both caloric and time restraints, chimpanzee mothers must face competing pressures between investing in an infant and continuing to associate with the juvenile. As such, continued association with a juvenile may lead mothers to opt for activities and social groups that are not beneficial from the mother-infant perspective (Pontzer and Wrangham, 2006).

Optimal ranging patterns can vary substantially between individuals, though conflicts may be less pronounced between kin given inclusive fitness benefits. Social factors—such as sex, age, rank, and social relationships—ecological knowledge, and physiological requirements have been observed to influence leadership in group-living animals (Van Belle et al., 2013; King et al., 2009; Fichtel et al., 2011). Multiple studies across primate taxa have noted that more experienced individuals—i.e. adults—lead
group movements at higher frequencies than subadults or juveniles (Costa Rican squirrel monkeys: Boinski 1991; white-handed gibbons: Barelli et al., 2008; white-faced capuchin monkeys: Campbell & Boinski, 1995). These experienced individuals may emerge as recurrent leaders due to their knowledge about resource availability and location unknown to younger or less experienced individuals; this knowledge may be important to the overall foraging success of the group (Van Belle et al., 2013). For example, in killer whales, post-reproductive females have been documented to lead collective group movements more often when food abundance is low (Brent et al., 2015). In other taxa, members of the dominant sex, with a skew towards the highest ranking individual, have been observed to lead more, or all, group movements compared to the subordinate sex, regardless of age or experience (Verreaux’s sifakas: Trillmich et al., 2004; gray wolves: Peterson et al., 2002; mountain gorillas: Schaller, 1963).

Male and female chimpanzees experience different reproductive strategies as adults. Therefore, sex differences in the selective pressure on immature behavior are expected to influence leadership patterns in juvenile chimpanzees (Watts and Pusey, 2002). Eastern chimpanzee males are more gregarious than females, forming strong social bonds with other adult males that can endure for years (Mitani, 2009). Males engage in a variety of affiliative and cooperative behaviors including coalitions that function in rank maintenance, hunting, and territory border patrols (Mitani, 2000). Conversely, though inter-site variation exists, eastern female chimpanzees are less gregarious than males, with anestrous females spending up to 70% of the time alone with their offspring (Watts and Pusey, 2002; Pusey and Schroepfer-Walker, 2013;). Putatively, due to selection on behaviors associated with adult strategies, studies have reported sex
differences during development (Lonsdorf et al., 2014). Juvenile males express a greater interest than females in associating with other individuals in the community as males have been documented leading their mothers to groups of chimpanzees at higher frequencies than females (Watts and Pusey, 2002; Pusey, 1983). Juvenile females, on the other hand, have been documented to exhibit higher rates of playing and food sharing with younger siblings than do juvenile males (Pusey, 1983).

The juvenile period may provide an opportunity for newly weaned individuals to learn from their mothers how to find and process seasonal foods (Wrangham, 1977; Joffe, 1997; Pusey, 1983). Indeed, juvenile chimpanzees have been documented to watch their mothers while foraging, often joining their mothers in food trees and responding to feeding grunts (Pusey, 1983). Leadership, however, presents a distinct challenge to juvenile individuals as they must face competing pressures of maintaining both the protection and ecological knowledge offered by their mothers while also benefiting from social exposure by associating with conspecifics.

In this study, we investigated juvenile leadership in long-range movements by examining 1) at what age does conflict between the mother and juvenile emerge in travel bouts and 2) what factors (i.e. biological, behavioral, environmental) influence the appearance of a travel leader. We hypothesized that juvenile age and sex will affect leadership based on previous studies and sex differences in social strategies. Specifically, we predicted that juvenile leadership will increase with age, as juveniles gain more social and ecological knowledge. Furthermore, we predict that males are more likely to lead than females, and behavioral context will influence juvenile leadership. We predicted that juveniles will lead more often towards a social opportunity. Pusey (1983) noted that
juveniles, particularly males, appeared to be attracted to social groups and regularly led their mothers to them. Finally, we hypothesized that seasonality will affect leadership patterns. We predicted that mothers will lead more often during the dry season in which food resources are scarce due to increased ecological knowledge (Wrangham and Smuts, 1980; Williams et al., 2002a).
Chapter 2: Materials and Methods

2.1 Study Site and Subjects

The data analyzed for this thesis was collected from chimpanzees in the Kasekela community in Gombe National Park, Tanzania. This community has been studied continuously since 1960. We used detailed behavioral and party composition data on mother, infant, and juvenile chimpanzee family groups collected from focal follows during a 34-year period from 1979 to 2013. During follows, teams of two Tanzanian field assistants collected behavioral data at 1-minute point samples on the mother, infant, and juvenile. Behavioral information includes activity—e.g. traveling, resting, foraging—and the ID for individuals with whom the focal subjects are interacting. Mother-offspring follows occurred almost daily, with researchers collecting data on each family group once per month, with a goal to collect at least 6 hours on each family per month. Follows began once the chimpanzees of interest were located, often at the night nest of the previous day. Additionally, party membership scans are conducted at regular intervals during each follow (5-minute intervals are recorded until 2011 and 15-min intervals are recorded thereafter). We defined the start of juvenility in this study at the birth of a younger sibling. As immature chimpanzees began to enter the dominance hierarchy around age 12, we only included juvenile chimpanzees < 12 years of age.

2.2 Behavioral Metrics

Most movement was associated with local foraging and had no clear directionality or leader. Thus, in this study, we focused on long-range movements which represent a substantial energetic costs and a substantive change in location. Long-range movements
were defined as sustained travel by both the juvenile and the mother for 6 minutes or longer, which is equivalent to the average travel bout (2.2 minutes) plus 1 standard deviation.

Consensus movement was assigned when both the mother and juvenile started traveling at the same point sample. Leadership was assigned when one individual started traveling prior to the other, representing that they started traveling at least one minute in advance of the other individual. Disjoint initiations of the mother and juvenile can be interpreted as either stronger leadership by one individual and/or resistance by the other. Our analyses address two questions: (1) How does juvenile age and sex relate to consensus movement? Older juveniles, particularly males, may be more likely to have increasing knowledge and social status, face lower predation risks due to large body size, and movement strategies that conflict with their mothers, particularly males; and (2) Under what contexts do juveniles lead their mothers?

2.3 Predictors of Consensus Movement and Leadership

Corresponding with our analytical structure, the response variables were consensus movement (Y/N) and juvenile leadership (Y/N). Predictor variables included the following:

1. **Sex**: prior studies have suggested that juveniles, particularly males, regularly lead their mothers to social opportunities (Pusey, 1983).

2. **Age**: older juveniles expected to have increased ecological knowledge compared to younger juveniles (Joffé, 1997).
3. **Season:** the size of chimpanzee social parties varies with season as food resource abundance changes (Wrangham, 1977). Therefore, season may limit potential social interactions that influence juvenile leadership; alternatively, but non-exclusively, due to high core fidelity, mothers have increased ecological competency which may influence maternal leadership as food abundance changes.

4. **Group Composition:** the total number of individuals within a social party (i.e. potential social partners) may influence juvenile leadership; alternatively, female chimpanzees may lead to smaller groups as this decreases feeding competition. Change in group size was used as a proxy for sociality.

### 2.4 Statistical Analyses

All statistical analyses were conducted in R version 3.5.2 (R Core Team 2018). No interactions for our predictors were significant and so are not included in our models. We first tested the influence of juvenile age and sex on consensus movement. Initiation type was converted into a binary Y/N and fit with separate general linear mixed models (GLMM) with a binomial error distribution and a logit link function (Bates et al., 2015). Fixed predictor variables were juvenile age and sex. Each model included a random effect of juvenile ID to control for repeat measures of the same individual. As the rates of consensus movement may vary with age between males and females, we first tested the interaction between juvenile age and sex. If the interaction did not have a significant effect, it was removed and juvenile age and sex were included as main effects. We excluded any juvenile that had less than 5 follows per yearly bin from this analysis to
minimize variance in number of long range movement observations between age categories. This resulted in 658 follows of 20 juveniles (11 females and 9 males) and 10 mothers.

To test what factors influence juvenile leadership, we only included follows in which either the mother or the juvenile were identified as the leader due to disjointed initiation. This resulted in 164 observations of 30 juveniles (15 males and 15 females) and 16 mothers. Juvenile leadership was converted into a binary Y/N. We fit a single GLMM to examine the influences of juvenile age, change in group composition and season on disjointed initiations. Each model included a random effect of mother ID to control for repeat observations of the same individual since work in other species has demonstrated that some mothers have a more lassez-faire maternal style (Fairbanks & Mcguire, 1987; Bardi & Huffman, 2002). We first tested relevant interactions; if these interactions were not significant, they were removed from the model and ran as independent predictors. Testing the relationship of juvenile sex on juvenile leader resulted in a singular fit warning. Thus, we ran a general linear model (GLM) to investigate the influence of juvenile sex on leadership.
3.1 Consensus Movement

When tested as main effects, both age ($\chi^2=10.67$, df=1, $p=.001$) and sex ($\chi^2=4.26$, df=1, $p=.039$) were significant in predicting consensus movement (Table 1). Visualization of this data suggests that during long range movements, females share more initiations with their mothers than males (Figure 1).

<table>
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<td>5.186</td>
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<tr>
<td>Juvenile Sex</td>
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Table 1. Results of generalized linear mixed model examining the effects of juvenile age and sex on shared leadership. If the interaction between variables were not significant, we tested each variable independently. P values that are significant ($p < .05$) are bolded. The reference category for juvenile sex was male; juvenile age was ran as a continuous variable.
3.2 Leadership

Juvenile sex influenced leadership ($X^2=5.0941$, df=1, $p=.024$), with males leading more often than females. This complements the previous result: when leadership is unshared between a female juvenile and her mother, the mother leads more often than the daughter. Additionally, although not significant, a negative change in party size is reported as a trend ($X^2=3.08$, df=1, $p=.079$). Surprisingly, this suggests that when the juvenile leads, they lead more often away from larger parties and towards smaller parties. Season was not a significant predictor as shown in Table 2.
<table>
<thead>
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<td>Juvenile Age</td>
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<td>Season</td>
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**Table 2.** Results of generalized linear mixed model examining predictors of disjointed initiations in which the juvenile leads. P values that are significant (p < .05) are bolded. The reference category for season is dry.

<table>
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<th>Predictor</th>
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<tbody>
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<td><strong>0.0254</strong></td>
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</tbody>
</table>

**Table 3.** Results of generalized linear model examining predictors of disjointed initiations in which the juvenile leads. P values that are significant (p < .05) are bolded. The reference category for juvenile sex is male.
Chapter 4: Discussion

Understanding the factors that drive movement in group-living species is central to the field of evolutionary biology, since individuals may range suboptimally in order to remain in a group. Fission-fusion social systems characterize few mammalian species (giraffes: Carter et al., 2012; elephants: Wittemyer et al., 2005; dolphins: Conner et al., 2001; hyenas: Holekamp et al., 1997; spider monkeys: Chapman et al., 1995; bonobos: Hohmann and Fruth, 2002; chimpanzees: Boesch & Boesch-Achermann, 2000; and humans: Marlowe, 2005). These dynamics allow for species to mitigate costs of group living, such as feeding competition and fighting, maintain the benefits associated with collective action (Aureli et al., 2008; Smith et al., 2008) and even allow for juvenile leadership (Pusey, 1983), which is rarely observed in other taxa. Little is known about sub-group travel decisions prior to fusion events; particularly, we lack an understanding of the social and ecological variables that potentially drive leadership (Smith et al., 2015). Previous research has suggested that leaders may emerge in fission-fusion societies, as certain individuals possess ecological knowledge that may increase the foraging efficiency of a subgroup (bottlenose dolphins: Lewis et al., 2010; forest elephants: Fishlock and Lee, 2012). However, higher ecological knowledge seems an unlikely factor in juvenile leadership in wild chimpanzees since mothers have had substantially more experience than juveniles.

This study investigated the correlates of juvenile leadership in a species characterized by fission-fusion dynamics. Our findings indicate that, regardless of juvenile sex, consensus movement decreases with age. This suggests that as juvenile chimpanzees grow older, they increase their travel autonomy from their mothers, which
could represent either conflict or reduced reliance on mothers for protection and socio-ecological knowledge. Our result for sex differences in juvenile leadership support findings from previous research; Pusey (1983) measured the percentage of change in time a juvenile spent traveling in front of the mother for any bout lasting longer than 5 minutes. Indeed, using an increased sample size, our results indicate that the sex of a juvenile significantly impacted juvenile leadership, with male juveniles leading more than female juveniles. Two alternative, although not necessarily exclusionary, hypotheses may explain the effect of sex on leadership: 1) males are more likely to lead than females in general, as observed in some other species (reviewed in Smith et al., 2015), and 2) males and females are likely to initiate travel bouts at the same rate, however, mothers are more likely to follow males.

Previous research suggests that juvenile males are more likely to lead to social opportunities (Pusey, 1983). As males are the philopatric sex in chimpanzees and rely on alliances and coalitions to acquire and maintain rank later in life (Bygott, 1979), it is reasonable to predict that males are more likely to lead than females in order to gain more social exposure. Alternatively, sex-based bias in maternal investment may account for variation as well. Trivers-Willard’s hypothesis suggests that if maternal investment influences the lifetime success of her offspring, and investment influences the success of the offspring differently, then mothers are expected to invest more in the sex that gives greater fitness returns in the form of grand-offspring (Trivers and Willard, 1973). As males show higher variation in the potential for reproductive success than females, mothers should invest more in sons than daughters (Smith, 1980). As such it is possible that mothers in our study were more likely to follow males than females when a travel
bout was initiated as a form of sex-biased maternal care. Future studies should investigate if females are more likely to follow sons, i.e. differentially invest in males, given differences in other aspects of maternal behavior (Murray et al., 2014).

In contrast to previous research, we found a trend that juveniles lead to smaller party sizes than do their mothers. As group size was used as a proxy for sociability, this result is not only surprising due to the “need to learn” hypothesis, but deviates from previous studies in which juveniles are observed to regularly lead their mothers to social groups (Pusey 1983). One reason for this discrepancy may result from differences in sampling bias; the Pusey study relied on a smaller sample size. Alternatively, juveniles may prefer to associate with similarly aged individuals in nursery parties and not large social groups, as was tested in this study. The occurrence of nursery parties, which consist of multiple mothers and their offspring, has been reported by previous studies (Wrangham and Smuts, 1980; Goodall, 1986). Pusey (1983) observed that post-weaning, one anestrous female frequently associated with other females who had similarly aged offspring. As such, these parties may represent an opportunity for juveniles to interact with peers without the associated risks of larger parties.

Leadership, and subsequent followership, are prevalent throughout the animal kingdom in gregarious species (King and Cowlishaw, 2009a). All social animals, regardless of species, adopt strategies in order to maximize the benefits, and minimize the costs of group living for the individual (King and Cowlishaw, 2009; King and Sueur, 2011). Juveniles represent an interesting class in which to consider leadership as this period has been hypothesized to be an important time for immature primates to learn both social and ecological skills needed for adulthood (Joffe, 1997). Our results indicate that
1) as juvenile chimpanzees grow older, they increase their travel autonomy from their mothers; 2) juvenile males lead more than juvenile females; and 3) juveniles appear to lead towards smaller parties than their mothers. Future studies should explicitly test the energetic tradeoffs faced by mothers for their continued association with juveniles as well as deference to juvenile leadership.
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