

**Title**

Leadership in plains zebra movements: Individual and phenotypic effects

**Short title**

Leadership in plains zebra

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## Abstract

Animals typically move as they seek resources and avoid dangers. In social groups, movement often emerges as a consensus decision, group members collectively determining the timing and direction of each move. The decision-making process may be relatively evenly distributed, with each member equally likely to lead a move, or certain individuals may dominate as more frequent leaders. Heterogeneity among individuals in their propensity to lead may arise due to differences in needs, knowledge, or social relationships. We investigate group movements within the stable social groups of plains zebra harems. We design permutation tests to examine how evenly leadership is distributed, and the effects of sex and age on leadership. These permutation tests can be readily extended to examine how leadership is influenced by other traits, or in other sorts of group behaviors. Our results show that leadership is significantly uneven; individuals vary in their propensity to lead. Controlling for individual differences in leadership, we further find that adults are more likely to lead than young, and males exhibit a (non-significant) tendency to lead more often. Controlling for differences between these groups, our investigation indicates that leadership remains uneven. This suggests that individual differences in leadership run deeper than differences due solely to age or sex.

**Keywords:** *Equus burchelli*, permutation test, collective movement, consensus decision-making

## Introduction

Movement is among the most basic aspects of animal biology. Animals move seeking resources, mates, and safety (Smith 1974; Turchin 1998; Bartumeus et al. 2005; Moorcroft et al. 2006). In many species, individuals move in cohesive groups. Aggregations range in size from several individuals to swarms of billions, and exhibit a diversity of configurations and activities. Moving collectives have major impacts on their environment, as they use resources, and attract or repel other species.

The behavior of an aggregation arises through the interactions of its members. Group behavior may appear to be coordinated from the top, but a variety of models suggest it can instead emerge based on purely local interactions among close neighbors (Hamilton 1971; Gueron et al. 1996; Grunbaum 1998; Couzin & Krause 2003; Simpson et al. 2006). Simulations show that in a group following simple, local rules, a small minority of target-oriented individuals can lead the rest to a distant target (Couzin et al. 2005).

In nature, as well as models, we may discern leaders. As a group changes speed and direction, certain members may transition first, while others follow. If group members are to remain together, then each choice must be a collective, consensus decision (Conradt & Roper 2005). Over the course of many moves, we may ask whether decision-making is relatively evenly distributed, with group members being equally likely to initiate group moves, or if it is more unevenly distributed, with certain individuals being consistently more likely to lead (Vehrencamp 1983; Hemelrijk 1999). Individual variation in the tendency to lead may arise because certain members of a group want to move more often, due to resources needs. Thus there may be phenotypic traits that predispose an individual to initiate movement. For example, lactating females, who have higher water and nutrient needs, tend to lead group movements in

plains zebra (Fischhoff et al. 2007). Females tend to lead males in white-handed gibbons (*Hylobates lar*) (Barelli et al. 2008). In both zebras and gibbons, the leaders have priority of access upon reaching a resource location. Older individuals are more likely to lead in rhesus macaques (*Macaca mulatta*) (Sueur & Petit 2008). If members of a group interact repeatedly, they may develop social relationships that further influence how strongly individuals want to follow particular neighbors. In plains zebra, we found significant individual-level differences in leadership within harems, core social groups that have stable membership for months to years (Fischhoff et al. 2007). In gorillas (*Gorilla gorilla beringei*) (Schaller 1963), chacma baboons (*Papio ursinus*) (King et al. 2008), and African elephants (*Loxodonta africana*) (McComb et al. 2001), the dominant group member tends to be the most frequent leader.

In this paper, we investigate individual-level and phenotype class (age and sex) differences in leadership, within the harems of plains zebra. We ask first whether leadership in initiating movement of group members is distributed more or less evenly among individuals than we would expect by chance. Leadership may be distributed unevenly due to both phenotypic effects and individual variation within phenotypic classes. We next examine whether two phenotypic factors -- age and sex -- influence leadership. Finally, we test if individual differences remain even when accounting for differences between sex or age classes. Based on our past analysis of zebras' order in single-file walking lines, we expect to find significant individual variation between and within phenotypic classes (Fischhoff et al. 2007). In particular, we expect that adults are more likely to lead than the young. Adult group members may exhibit stronger preferences about the best places to go, and may be more rewarding for others to follow than less experienced neighbors. Alternatively, the same pattern of adults tending to lead may result from youngsters choosing not to lead the group. Males and females differ in the factors limiting their

fitness and, thus, the major drivers of their behavior (Rubenstein 1986; Rubenstein & Wrangham 1986). We expect to find differences in their propensity to lead the mixed-sex harem groups, but we do not have an *a priori* hypothesis for the direction of this difference. Age and sex are only two of many possible factors influencing individuals' tendency to lead. Other potential causes of individual differences include past experience with the landscape, and relationships with group members. We expect variation in such additional factors results in inequality among individuals even when we control for possible differences due to age or sex.

To investigate how phenotype affects leadership, we have designed a set of permutation tests. These tests allow us to investigate whether leadership occurs randomly among individuals in a harem, and with respect to phenotypic traits. In addition to producing novel findings about the factors shaping leadership in zebras, this paper illustrates how permutation tests may be more widely usable for examining how individual and phenotypic factors affect leadership in other sorts of group behaviors and species.

## **Methods**

### *Study population and field site*

Since 2003, we have studied plains zebras in Ol Pejeta Conservancy (0°00 N, 36°56 E), a semiarid bushed grassland in the Laikipia ecosystem of central Kenya. The data presented here are from Ol Pejeta's former Sweetwaters Game Reserve, a 100 sq km area fenced off from the rest of the property until 2007. The Sweetwaters population was approximately 500 in 2005 and 2006, the years in which we collected the data analyzed here.

A zebra harem comprises a stallion male, the females defended by him, and their dependent offspring (Klingel 1975). Harem membership remains stable for months to years. Both sexes disperse at maturity, approximately 2 years of age. We determine the membership of

each harem within the herd, based on spatial proximity of harem members and social interactions among them (Fischhoff et al. 2009). We track harem membership through population surveys, taken approximately once every two weeks. In these surveys, we record the identity of individuals in each herd we observe. Each individual is uniquely identifiable by its stripes, using our photo database of the population.

### *Field methods and dataset*

We gather data on leadership by observing harems, for periods of at least one hour. For each observed harem, we note the identity of individuals and ages of all individuals. For the purpose of the present analysis, we define two age classes: adult (three years and older), and young (less than three years old).

While following a harem, we record each time a member of the harem walks for an estimated distance of at least five meters (equivalent to two zebra body lengths). We record the identity of the walking individual and its compass bearing. If any other group member walks in the same direction ( $< 30$  degrees difference in bearing), within one minute, then we consider it to be following the initiator. We define the leader of a group movement as the individual who initiates a move and is followed by at least one group member. A leadership event is an instance of an individual being initiating movement and being followed.

We gathered data from July to August 2005 and again in July and August 2006. In 2005, we only recorded leads and follows made by adults. In 2006, we included walking events by both age classes. The data from 2005 include 15 harems, containing 55 adults. From 2006, we have leadership data on nine harems, including a total of 9 young and 36 adults. Two harems were observed in both years. We observed harems on one to seven sampling periods, for a total of 63 sampling occasions. Each individual has been observed in only one harem, over the course of our

data collection. All individuals in our dataset were observed in only one age class over the two years.

### *Analysis*

We designed a series of randomization tests to generate null models for the distribution of leadership. Appropriately constructed randomization tests are valid even though we don't expect our variables to be normally distributed, and our sample size varies widely (Good 2000). We provide scripts for performing the tests (Electronic Supplementary Material). All scripts are written for use with the freely available software R (R\_Development\_Core\_Team 2005). The supplementary material also includes the raw observational data used in our analyses and all the steps for recreating our results.

#### Randomization test for individual differences in leadership

We want to know whether leadership events are distributed randomly among the members of a harem. To characterize the observed distribution of leadership, we compute the variance in the number of times each individual in the population has led. We compare this variance to the distribution that would be expected under the null model that each individual within a harem is equally likely to lead a move, at random. Thus, for each harem, we randomly sample from the harem's members to fill the observed order in which individuals began walking in each event. Having randomized leadership across all harems, we recompute the variance of the counts of leads by each individual in the randomized dataset.

By repeating this whole procedure (selecting an order for each event) 1000 times, we generate a null distribution of expected variance in leadership. We then ask whether the observed variance is statistically significant with respect to this null distribution. It is worth noting that in principle, the observed variance could be significantly high (representing a tendency for some



individuals to lead more than others) or low (representing a pattern that is more egalitarian than would be expected by chance).

#### Randomization test for phenotypic differences

The distribution of leadership may depend partly on differences due to phenotype. Here, we investigate the effects of age and sex on the propensity to lead. The test statistic is the number of times one phenotypic class has led, minus the number of leads by members of the other class. For example, to examine the effects of sex, we subtract the number of leads by males from the number of leads by females; to compare adult and young zebras, we subtract the number of leads by young zebras from the number of leads by adults. In designing a null model for the effect of a phenotypic factor, we consider that individuals may significantly differ in their leadership tendencies, independent of phenotypic class. For example, personality traits may predispose certain individuals to lead independent of age (Kurvers et al. 2009). Thus we wish to control for possible individual differences, in our null model of leadership with respect to phenotype. We do this by permuting individuals, rather than events, thus maintaining the observed distribution of the number of leads by each individual. Within each harem, we randomly permute the observed phenotypic class labels (age or sex) among the members. We then recompute the difference in the number of leads between the two phenotypic classes of interest over all of our observed events. By repeating the procedure 1000 times, we determine a null distribution of the expected difference in lead frequency between phenotype classes, if all variation were due to individual effects rather than phenotype. We compare this distribution of differences to the observed difference in leads by phenotype, to arrive at a p-value (Good 2000).

In testing for effects of age class, we limit our analysis to data from 2006, when our observation of leads was unbiased with respect to age. We compute the p-value for the one-tailed

test, with the *a priori* hypothesis that adult zebras lead more frequently than we would expect by chance.

We test for effects of sex among adults for data from 2005 and 2006. In this case, we randomly permute the sex labels among the stallion and adult females of each harem. We do not have an *a priori* hypothesis for differences between adult males and females, so we perform a two-tailed test.

#### Randomization test for individual differences, controlling for phenotype

Finally, we ask whether individual differences remain, after our phenotype classes are accounted for. As in our first test for individual differences, the null model involves resampling among the members of a harem to fill the leader spots. The test statistic remains the variance in the individual counts of leads. In this case, however, we want to limit our choices of potential “random leaders” to harem members of the same phenotypic class as the observed leader. For each observed lead, we randomly resample among those individuals of the same phenotypic class as the observed leader, when choosing the random leader. For example, for each occasion in which a female was observed to lead, we randomly sample among the harem’s female members to fill the initiator spot. Indeed, given that the harems observed typically have only one young member and always only one stallion, this is effectively an examination of leadership distribution among adult females.

## **Results**

### *Individual differences*

We observed 1,485 harem leads, initiated by 91 individuals in 22 harems. The variance in the number of times each individual has led is 244.0. We compare this observed variance to the distribution of variance values generated by our randomization. The observed variance is greater

than that generated by all 1000 runs of the randomization. We conclude that leadership is distributed significantly unevenly among individuals, with a two-tailed p-value of less than 0.002.

#### *Phenotypic effects: Age*

We observed 36 adults and 9 young in 2006. Among the 780 leads observed, 72 were initiated by young zebras, and 708 by adults. Thus there is an observed difference between adults and young 636 (708 minus 72) leads. We compare this observed difference to the distribution of differences generated by the randomization, which permutes age labels among individuals in each harem. The null distribution indicates that if leadership had been random with respect to age, we would have observed a narrower gap in the count of leads by young and adults. All 1000 randomizations produce a difference in the count of leads that is smaller than that in the observed data. Thus young zebras led significantly less frequently than the adults, at a two-tailed p-value of less than 0.002. We conclude that adults are more likely to lead than young.

#### *Phenotypic effects: Sex*

We have leadership data on 78 adults, including 57 females and 21 stallion males. We observed group leads by females 972 times and by males 416 times, for a difference of 556 leads (972 female leads minus 416 male leads). Males were 0.27 of all adults, and led 0.30 of all group moves led by adults. Comparing the observed difference to the differences generated by the null distribution, we do not detect a significant effect of sex on the propensity to lead group moves. In Figure 1, we show the observed fraction of leads by males, compared to the distribution of values obtained from the randomization.

#### *Individual differences, controlling for age and sex*

For the 780 leads made by 45 individuals in 2006, we find an observed variance of 127.8. The observed variance is greater than that obtained from any of the 1000 randomizations in which we control for the age of the leader when resampling. Thus we conclude that individuals significantly vary in their tendency to lead, controlling for differences in age, at a two-tailed p-value of less than 0.002. In a separate test, controlling for both age and sex, we again find that the observed variance is significantly high ( $p < 0.002$ ). We conclude that leadership is unevenly distributed among harem members, when we account for the possible effects of age and sex. Figure 2 illustrates the differences between observed and null variation in individual behavior. For this plot, we pair the original distribution in individual propensity to lead with that obtained from one single run of the randomization. We choose the run of the randomization having the median variance value, out of all 1000 runs. The figure demonstrates the flatter distribution we would observe if individuals were equally likely to lead, respecting differences due to age and sex. Compared to the results of the randomization run, the observed data include more individuals responsible for either a very low or a very high proportion of leads.

## **Discussion**

Our analysis shows that leadership in plains zebra harems is significantly uneven. Controlling for individual variation in leadership, we can partly explain variation in leadership due to adults being more likely to lead than young individuals. We also find a (non-significant) trend towards adult males being more likely to lead than females. However, individual differences persist, even when we control for both age and sex.

The difference between old and young individuals is consistent with our expectations about age-based variation in knowledge and motivation to move. Young zebras are less familiar with the landscape, and depend on adults for resources and protection. Hence we expect they

have weak preferences about where to go and therefore may not attempt to lead the group. Older group members may also find following young zebras a relatively unattractive option, when the young do make a move, due to the poorer knowledge of young zebras.

We did not detect a significant difference between males and females in their tendency to lead. We may expect that males' and females' tendency to lead depends on the ecological and social context. For both sexes, the impetus to move is to acquire resources and avoid dangers. The factors limiting fitness tend to differ for males and females, in polygynous species such as plains zebra (Emlen & Oring 1977). Male fitness is limited by access to females, while female fitness is limited by the resources needed to raise offspring. We may hypothesize that males lead more frequently in times and places of interactions with other males; following such encounters, a stallion may seek to lead his females away from other males. By contrast, we may expect that females more frequently lead movements toward new grazing areas or water, as these are resource choices that we expect to be important to female reproductive success. This is the case in horses. In a population of free-ranging feral horses, females within harems initiate about 70% of the moves towards new grazing locations or water, whereas males initiate approximately 80% of the moves either towards or away from other harems or bachelor groups, both of which contain reproductive competitors (Rubenstein 1994). If the contexts in which zebra movements are initiated are approximately equally divided among sexual and nutritional contexts, then overall differences in leadership by males and females would be small, as we observed.

We hypothesize that differences between the sexes in resource priorities, which are seen in horses, may also lead to differences in initiation behavior in plains zebra. In leading females away from other males, a stallion would likely be forcing his females to abandon a preferred area, or preventing their attempts to contact foreign males. Thus males may need to initiate leads

more forcefully, by aggressively herding females. On the other hand, when a female wants to move to a new resource location, other females' needs are more likely to coincide with the aspiring leader. The male, in this case, need only follow to continue guarding his females. We would expect females to more often lead simply by walking away from the group. In a future paper, we can test for potential differences between the sexes in whether individuals initiate movement by aggressively herding each other or walking away.

We designed our permutation framework with the goal of a logical, flexible progression of hypothesis testing. In our case, we first found an uneven distribution of leadership, indicating individual-level differences. This prompted us to examine likely phenotypic drivers, while controlling for individual differences. Finding phenotypic effects, the next logical step was to ask whether individual differences remain, once we controlled for phenotype.

We can continue, in this iterative fashion, to disentangle the bases for variation in individual roles. Our past work has shown that lactating females, which have higher nutrient and water needs, are more likely to lead than non-lactating females (Fischhoff et al. 2007). Lactating females are further more likely to drink when their group reaches small waterholes, showing a possible resource payoff of leadership. We could also examine, as possible predictors of leadership, an individual's seniority within a harem, dominance rank (Sueur & Petit 2008), health, genetic markers, or personality (Samuel & Oliver 1999). In addition to phenotypic traits, we can extend the current analysis to ask how the social or ecological context influences the process of consensus decision-making. We may hypothesize, for example, that leadership is relatively evenly distributed across a group in situations for which all are likely to have the same preferred response, such as the approach of a predator. It is possible to test these hypotheses

within the framework of the permutation tests described here. These tests allow the user to investigate individual or environmental variables in models of increasing complexity.

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## Figure legends

Fig. 1. Leadership by males versus females. The observed value (hollow diamond) is the fraction of observed leads by adult males, out of all leads made by adults. The boxplot is the distribution of values obtained from a randomization procedure that holds constant the number of leads by each individual, but randomly permutes the sex labels within each harem. Comparing the observed value to the randomization, we do not detect a significant difference between the sexes in the tendency to lead.

Fig. 2. Individual variation in leadership. We compare histograms of observed variation in leads (dark bars), with the variation generated by a randomization (light bars). For each individual, we compute the proportion of leads it made within its harem. In the randomization, observed leader slots are filled randomly, choosing among individuals of the same age and sex as the original leader. We display the results from the randomization run having the median variance, out of all 1000 runs.



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