

Reproductive status influences group size and persistence of bonds in male plains zebra (*Equus burchelli*)

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Abstract Animal groups arise from individuals' choices about the number, characteristics, and identity of associates. Individuals make these choices to gain benefits from their associations. As the needs of an individual change with its phenotype, so too we expect the nature of its associations to vary. In this paper, we investigate how the social priorities of male plains zebra (*Equus burchelli*) depend on reproductive state. An adult male is either a bachelor, and lacking mating access, or a stallion defending a harem. Multiple harems and bachelor males aggregate in larger herds. Herds frequently split and merge, affording males opportunities to change associates. Over a 4-year period, we sampled the herd associations in a population of 500–700 zebras. To isolate the effects of reproductive state on male social behavior, we account for potential confounding factors: changes in population size,

grouping tendencies, and sampling intensity. We develop a generally applicable permutation procedure, which allows us to test the null hypothesis that social behavior is independent of male status. Averaging over all individuals in the population, we find that a typical bachelor is found in herds containing significantly more adults, bachelors, and stallions than the herds of a typical stallion. Further, bachelors' bonds with each other are more persistent over time than those among stallions. These results suggest that bachelors form cohesive cliques, in which we may expect cooperative behaviors to develop. Stallion–stallion associations are more diffuse, and less conducive to long-term cooperation.

Keywords Social associations · Permutation test · Equids · Phenotypic state · Group size

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Introduction

In many species, individuals choose to be in groups, to gain benefits such as reducing predation danger (Zuberbuhler et al. 1997) or acquiring resources and information (Horn 1968; Vickery et al. 1991; Beauchamp 1999). The benefits of being in a group weigh against costs such as competition for resources or mates, and enhanced disease transmission (Chapman et al. 1995; Danchin and Wagner 1997). From the perspective of an individual, the costs and benefits of grouping may depend on how many group members it has, the phenotypic characteristics of those associates, and their identity. For example, reduction of predation danger due to dilution alone increases with group size, independent of which individuals are present (Hamilton 1971). On the other hand, potential associates of a certain phenotype may be more effective in warding off predators, for example males in *Cebus* monkeys (Van Schaik and Van Noordwijk 1989). If predation defense depends on coordinated response, then the relationships among individuals become important as well (Burt and Peterson 1993; Boinski 1994). Analogously, an individual's foraging rewards may depend on group size (Janson and Goldsmith 1995), or the information held by those associates about local and distant resources (Caraco and Giraldeau 1991; Couzin et al. 2005). Associates may be known and vary in their helpfulness (Clutton-Brock et al. 2001) or may be strangers unlikely to actively cooperate (Hoare et al. 2000). Thus, in the contexts of finding food, avoiding predation, and various other arenas, an individual's choices about the number, status, and identity of associates may influence fitness (Krause et al. 2009).

The first step to understanding costs and benefits of association choices is to characterize how these choices vary with individuals' priorities. Plains zebra (*Equus burchelli*) are an example of a species with both short-lived and longstanding associations (Rubenstein 1994). An adult male either defends a harem of females as a stallion, or is a bachelor. Over its lifetime, a male may switch one or more times between these two states. Stallions appear to control all the mating opportunities. Harems are relatively stable, maintaining the same adult members for months to years. Plains zebra herds may include one or more harems, as well as bachelor males (Rubenstein and Hack 2004). Herds are fluid aggregations; harems and bachelor males change their herds over a time scale of hours to days.

Past research has identified ecological and social bases for herd formation in plains zebra. High grass availability facilitates larger aggregations. Zebras also form larger herds where predation danger is high (Rubenstein 1994). A social hypothesis for why stallions associate in herds is to reduce the per capita effort necessary to drive away challenging bachelor males (Rubenstein 1986). For bachelors, associating with stallions and females is hypothesized to afford

opportunities for honing social skills (Rubenstein and Hack 2004).

In this paper, we compare the association patterns of stallions and bachelor males. We use two measures: group size and the similarity of group associations over time. By quantifying the association patterns of bachelors and stallions, we gain insight into the mechanisms driving variation in group size, phenotypic composition of zebra herds, and the persistence of social bonds. If stallions cooperate repeatedly with particular other stallions in preventing bachelors from harassing their females, then we are more likely to observe persistent bonds among stallions. If stallions and their harems associate with other harems primarily to dilute predation danger, or find resources, they may break their associations with other stallions quickly, as ecological conditions and resource needs fluctuate.

Students of plains zebra natural history have long noted that bachelors form groups, recognizable within larger herds (Klingel 1975). We may expect bachelors to seek out the company of other bachelors as a form of defense against predators. Bachelors do not enjoy the consistent reduction in predation danger that stallions derive from their several female associates. For a bachelor, harems may not always be attractive associates because of aggression from stallions, or if females have different resource preferences from males. It is not yet known to what extent bachelor associations are fluid or cliquish. Bachelors may seek to dominate other bachelors, so as to position themselves for taking over harems. This may suggest that a bachelor would form strong bonds with some other bachelors, among whom dominance relationships may be worked out over repeated interactions (Goessmann et al. 2000; Chase et al. 2002; Beacham 2003; Rubenstein and Hack 2004).

Comparing the grouping patterns of individuals in two states requires that we account for potentially confounding sources of variation that are common to many field studies. Over the 4 years of our study, the population size changes, and average group sizes fluctuate. Our sampling intensity also varies. We design a permutation procedure in which we randomly reassign males' status histories. This has the effect of breaking the association between group metrics and individual status, allowing us to better isolate the effects of status on group size. We believe this sort of randomization test will be generally useful in investigating how phenotype relates to behavior.

Materials and methods

Study species and field site

Plains zebras are large-bodied (~200–330 kg) grazing ungulates inhabiting grasslands of East and Southern

Africa. The core social group is the harem, composed of one stallion male and one to several females, as well as dependent offspring. Males and females disperse at sexual maturity. Multiple harems form unstable herds, which may also contain bachelor males (Rubenstein 1994).

Since July 2003, we have studied plains zebras on Ol Pejeta Conservancy, a semi-arid bushed grassland in the Laikipia ecosystem of central Kenya. The data presented here are from a 100-sq-km section of the property, formerly known as Sweetwaters Game Reserve and now as the Eastern Sector. Until March 2007, this Sweetwaters population was surrounded by an electrified fence, preventing migration in or out. The data analyzed here extend until June 2007. Over the course of our study, the population declined in size from approximately 700 to 500. High predation pressure is the hypothesized cause of this decline. Estimated lion numbers in Sweetwaters over this period ranged from 15 to over 30.

Field methods

We collected association data by repeatedly sampling the population. We periodically drove set survey routes, searching for herds. We also observed herds visiting waterholes. The interval between successive sampling occasions varied from 1 day to 1 month. There was a 4-month hiatus from data collection, September 2006 to January 2007.

We identify individual zebras based on unique stripe patterns. For each herd sighted, we identified all males present and recorded their status, as bachelor or stallion. We also record the number of adult females present in each harem, and thus in the entire herd. Our study has focused on associations among males. Therefore, we have tended to identify a lower proportion of the females in a group than the males.

In the field, we determine male status based on behavior. A stallion exhibits typical social interactions with females in his harem, such as mutual grooming, “herding” them to induce movement, or closely following females. Within a herd, bachelors tend to be in tight proximity to other males, with frequent male–male interactions such as sniffing, chasing, or fighting.

We consider all individuals in the same herd to have associated with each other at that time. All the individuals of one herd are typically close together, relative to the distance separating them from other herds. If more than 100 m separates two groups of zebras, then we do not consider them to be in the same herd.

Analysis

Permutation test to compare bachelor and stallion herd sizes

We ask how the number of bachelors, stallions and females in a male’s herd is influenced by that male’s reproductive

status. For each observation of a male in the field, we have determined his status based on his behavior and interactions with other animals in the herd. We only include those males observed as adults on at least three occasions. We have observed some males as bachelor and as stallion at different times. Neither juveniles nor foals enter our analysis.

Across all observations of each individual, we find the number of adults, bachelors, stallions, and females in the same herd as that individual. A herd is counted once from the perspective of each adult male within it. Thus, our metric captures the typical group composition and size experienced by an individual in the population.

We exclude the focal individual from group size totals. For example, for a herd observation of a bachelor, we subtract one from the count of bachelors in that herd. When a stallion is the focal individual, we exclude only the focal stallion. In relation to females, we are asking whether the typical stallion has more total associates, including those in his own harem, than does the typical bachelor. Thus, we make no distinction between females within a stallions’ harem and those in other harems of a herd. An alternative approach would be to exclude all of the females in a stallion’s harem; thereby examining only cross-harem interactions at the herd level. The choice we make here is conservative with respect to our result that bachelors have more associates on average than stallions do.

We compute the average number of each type of herd associate—identified adults, bachelors, stallions, and females—across all observations of bachelors and of stallions. We calculate the differences in average numbers of associates between males in the two states, by subtracting the bachelor mean from the stallion mean. We compute four such differences, for all adult associates, bachelor associates, stallions, and females in a male’s herd. We use these differences in numbers of associates to compare the behavior of bachelors versus stallions.

In comparing the grouping patterns of bachelors and stallions, we consider that an individual’s associations may depend on population-level fluctuations in observed herd sizes. Fig. 1 shows the temporal variation in herd size for our population. These fluctuations are shaped by natural factors such as rainfall seasonality, predator movements, and population dynamics. We also note variation in the relative proportions of bachelors, stallions, and females observed. Sample size may depend on natural factors, such as habitat choice and population size. In our study, sampling frequency also varied (Fig. 2).

We design a permutation approach that allows us to compare bachelors and stallions, while accounting for temporal variation in grouping patterns and sampling. We do so by randomizing male status histories to generate a null distribution of expected numbers of herd associates, if these totals were independent of status. We construct a status

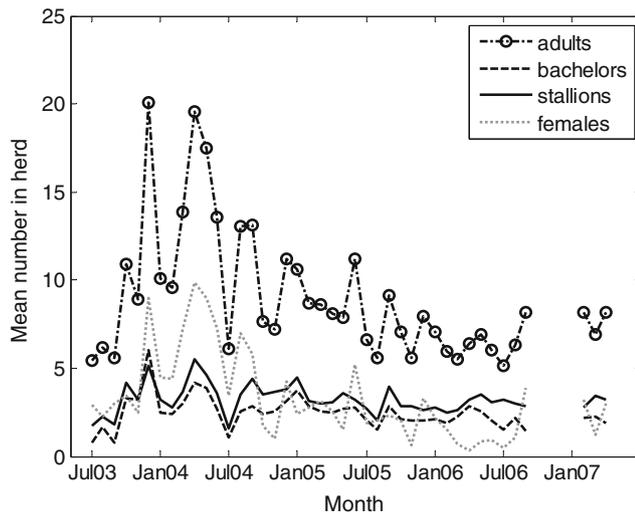


Fig. 1 Temporal variation in herd sizes. For each 30-day period, the mean number of adults is computed across all herds observed. Means are also found for the constituent classes of adults whom we individually identified in the herds: bachelors, stallions, and females. No data were collected from September 2006 until January 2007. Over the entire study period, a total of 5,813 herds were observed

timeline for every male, based on our field observations. If a male has switched status, then we define the transition date from bachelor to stallion, or vice-versa, as the midpoint in time between successive observations of the individual in opposite states. If a male is in the same state in two successive sightings, we assume he has maintained this state through the intervening period when we did not observe him. The complete timeline of states for a male is his status history.

In each randomization run, we reassign the status history of each male to that of a randomly chosen male. The

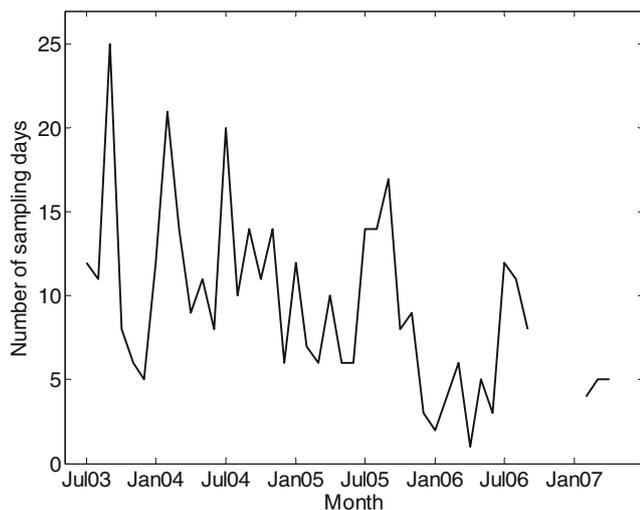


Fig. 2 Temporal variation in sampling effort. The plot indicates the number of days on which we sampled herds, during each 30-day period of the study. The study had a 4-month hiatus, from September 2006 to January 2007

permutation of males' status histories is done without replacement. After permuting the male status timelines, we recompute average number of herd associates for bachelors and stallions, and the mean differences between the two classes in numbers of associates. From the perspective of each individual, we use the original totals of herd associates for each demographic class—all adults, bachelors, stallions, and females. Thus, we retain the exact observed numbers of individuals in association with each male. But each focal individual now has the status history of a randomly chosen individual. Its data on numbers of herd associates are classed accordingly.

The beginning and end of males' status histories vary depending on when we first and last observed them. Some males have entered the adult age class during our study. Others have died before the end of the study, or we have failed to observe them for some period before the end of our dataset. Figure 3a depicts the observed status timelines of three hypothetical males. Male A was initially a stallion, then became a bachelor for a period, before regaining stallion status. Male B was always observed as a stallion. He has a shorter timeline than the other two. Male C was a bachelor throughout.

Variation in the total duration of timelines means that in some cases we have no history from a randomly chosen individual to apply to some, or all, of an original male's sightings. In this situation, we retain the original status history of the focal male, for the dates when no status history is available for the randomly chosen individual. Thus, the period for which no history is available does not contribute to any difference between our statistic and the permutation distribution.

For the hypothetical males of Fig. 3, assume that in one run of our randomization we assign the status timeline of Male B to the herd association data of Male C. For the period over which we have a status timeline on Male B, the herd associate totals of Male C are reclassified from the (original) bachelor column into the stallion column (Fig. 3b). However, Male C maintains his observed bachelor status for the sightings outside the timeline boundaries of Male B. Assume further that the timeline of Male A is assigned to the sightings of Male B. Male A's timeline is only relevant for the shorter period of data for Male B. The timeline of Male C is randomly reassigned to the data of Male A, resulting in all A's observations being classed as those of a bachelor. Our randomization proceeds in this fashion, over all the males in the population.

Based on 1000 randomization runs, we generate a null distribution of differences in numbers of herd associates as seen by bachelors versus stallions. We determine four such distributions, one for each category of herd associate—all adults, bachelors, stallions, and females. We consider bachelors and stallions to have significantly different

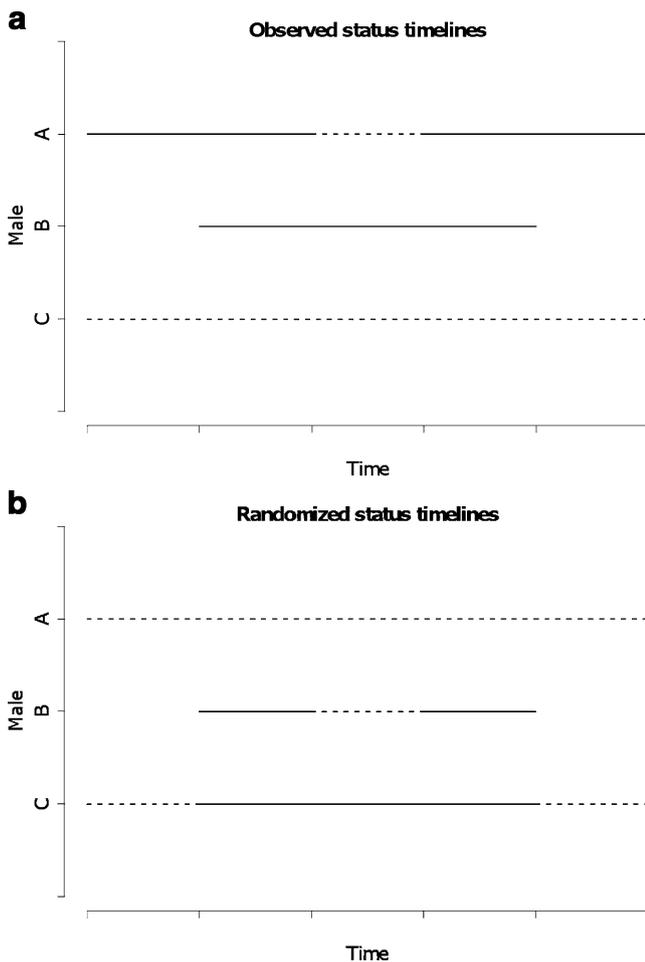


Fig. 3 Status timeline randomization procedure, based on three hypothetical males. **a** Observed status timelines. *Solid lines* indicate time when a male was observed as a stallion, while bachelor periods have dashed lines. **b** Status timelines following randomization. Each individual has the status history of a randomly chosen individual. In this example, Male A's history is reassigned to Male B, B's history is reassigned to C, and A receives the history of C. The history for Male B does not cover the entire period of Male C. For the periods when Male B cannot provide a pseudo-history to Male C, we retain the original status history of Male C. Each male's observed data on numbers of herd associates are classed according to the randomly chosen histories, in computing the averages for group sizes of bachelors versus stallions

grouping behavior if their observed difference lies in one of the extreme tails of the null distribution of differences.

Similarity of group associations over time

We examine whether bachelors and stallions differ in the persistence of their bonds to other males in the same state. We quantify persistence of associations based on the similarity of individual composition between two herd observations, as a function of the time between those observations. For a given time interval, we determine all the pairs of groups observed on sampling occasions with that

interval. For any two of these groups, A and B, we define three quantities: N_A , the number of individuals in group A; N_B , the number in group B; and N_C , the number common to both groups.

Based on these variables, we define the average similarity of groups over the interval as the following quantity:

$$\frac{2 \sum (N_C(N_C - 1))}{\sum (N_C(N_A + N_B - 2))}$$

The summation occurs over all pairs of groups within the time interval of interest. This similarity index gives more weight to groups in which individuals have maintained a greater number of bonds. Maintenance of a high number of bonds reflects a large, cohesive clique.

We compute this quantity separately for bachelor–bachelor group associations and for stallion–stallion associations. To examine how association strength varies with time, we compute the quantity for a series of six 1-day intervals. The first interval contains all groups observed less than 1 day apart, the second interval all groups recorded between one and two days apart, and so on.

Not all pairwise group comparisons are independent. For example, if a set of individuals are common to two groups within an interval, they are unlikely to be present in other groups for this interval. To account for this nonindependence, we use bootstrapping to determine a distribution of similarity estimates. For each sampling interval, we randomly select 50% of the observed group pairs for comparison. We then compute the similarity index based on this set of pairwise comparisons. By repeating such random draws 1,000 times, we generate a distribution of similarity index values. The distribution allows us to draw rough 95% confidence intervals around our observed means. We do not do a formal statistical test in this case.

All analyses were performed using Matlab. Code is available from the authors.

Results

Group sizes of bachelors and stallions

From July 2003 to June 2007, we observed 288 adult males, 241 seen as bachelors, and 232 as stallions. Over 397 days of sampling, we observed these males in a total of 5,546 herds. A herd is counted once from the perspective of each male member. Thus, we have 12,332 instances of bachelors “seeing” a herd, and 16,709 herd observations from the perspective of stallions. As seen by bachelors, the mean size of a herd is 29.3 adults (SE 0.3), compared to a size of 24.0

(SE 0.2) for the mean herd as seen by a stallion (Fig. 4, Table 1). These herd sizes include all adults, male and female, identified with a given male. Thus, the mean difference in herd size between stallions and bachelors is 24.0 minus 29.3, or -5.3 adults (Table 1).

We compare this difference to the distribution of differences generated by our permutation of status histories. Over 1,000 randomizations, the average difference between stallion and bachelor herd sizes is -2.8 individuals (Table 1). The observed difference is more negative than all the thousand randomization outcomes, resulting in a two-tailed p -value of less than 0.002. We conclude that bachelors choose significantly larger groups than do stallions.

We go on to examine the constituent classes of males' herd associates—bachelors, stallions, and females. From the perspective of a stallion, herds contain 3.8 fewer bachelors than are seen in the typical bachelor's herd. Again, the observed difference is significantly negative ($p < 0.002$). Bachelors' herds contain 9.5 stallions (SE 0.1), significantly greater ($p < 0.002$) than the 8.5 stallions (SE 0.1) seen by stallions in their herds. We do not detect a significant difference in the number of females observed with bachelors (8.9 females, SE 0.1) versus stallions (8.4 females, SE 0.1).

Similarity of group associations over time

We compared groups observed at different times, to determine the similarity of individual associates making

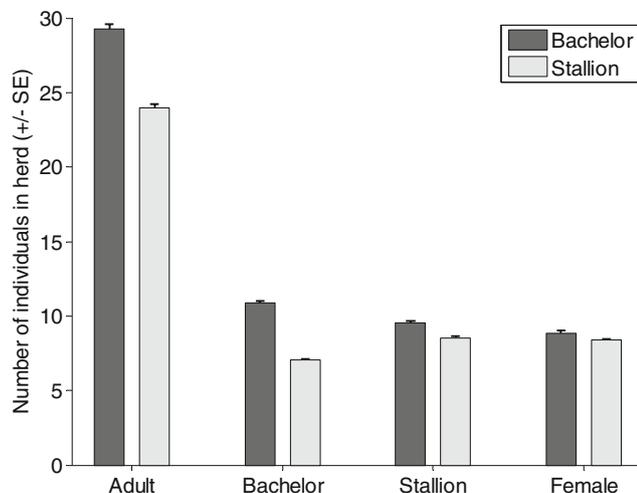


Fig. 4 Herd associates (mean and standard error) for males in the bachelor versus stallion class. A total of 288 males were observed in 5,546 herds, for a total of 29,041 individual observations. From the perspectives of bachelors and stallions, we compute the average number of adults, bachelors, stallions, and females found in these males' herds. A randomization test indicates bachelors are in groups with significantly more total adults, bachelors, and stallions (Table 1)

up these groups. For increasing time intervals between herd observations, from zero to six days, we found all the possible groups to compare. We made comparisons of similarity separately for the bachelor and stallion contingents of groups. In Fig. 5, we plot group similarity over time for bachelor–bachelor versus stallion–stallion associations. The upper and lower bounds are 95% confidence intervals based on bootstrap sampling from all the possible pairwise comparisons of groups over a time interval. The number of possible group pairs within an interval ranges from 57,860 (5 to 6 day interval between herd sightings) to 89,424 (1 to 2 days).

For each time interval, the lower bound on the 95% confidence interval for bachelor similarity is higher than the upper bound of the confidence interval for stallions. Thus, the similarity of bachelor members in groups remains consistently higher, over time, than that of stallion associations. We conclude that bachelors form stronger, more persistent bonds than stallions.

Discussion

In animal societies, individuals employ strategies geared toward retaining, or improving, their station in life. As we seek to identify animals' strategies, and how well they function, the first step is to compare the social patterns of individuals whose state dictates different proximate goals. We examined the grouping patterns of plains zebra males. A male is either a stallion, striving to keep control of a female harem, or a bachelor, aspiring to become a stallion. Stallions and bachelors associate in herds, which split and merge often. The fluidity of zebra herds means males make frequent choices about how many neighbors to have, and the characteristics and identity of those associates.

Past research suggests that stallions seek the company of fellow stallions to dilute the per capita effort of warding off bachelors. In another, smaller plains zebra population, solitary stallions were less likely to ward off a bachelor's approach than were a pair of stallions (Rubenstein 1986). For their part, bachelors are thought to join with other bachelors and harems to improve social skills (Rubenstein 1994; Rubenstein and Hack 2004). Past studies suggest more consistent bonds among bachelor sets than among stallions (Rubenstein 1986; Klingel 1998). We compared bachelors and stallions in their herd sizes and the persistence of their social links.

To examine the effects of reproductive state on grouping patterns, we developed a novel randomization procedure. This permutation test accounts for potentially confounding temporal variation in observed grouping behavior, phenotypic makeup of the population, and sampling effort. For our data, the randomization outcomes bear out the value of

Table 1 Comparison of observed group sizes for bachelors and stallions, tested against outputs of the randomization procedure

Associate type	Observed group size (Mean±SE)		Mean group size difference: stallion–bachelor		Count: Differences _{Rand} >Difference _{Real} (of 1,000 runs)	<i>p</i> -value
	Bachelor	Stallion	Observed	Randomization		
All adults	29.3 (0.3)	24.0 (0.2)	−5.3	−2.8	0	<0.002
Bachelors	10.9 (0.1)	7.0 (0.1)	−3.8	−1.1	0	<0.002
Stallions	9.5 (0.1)	8.5 (0.1)	−1.0	−0.4	0	<0.002
Females	8.9 (0.1)	8.4 (0.1)	−0.5	−0.5	509	0.98

For each category of herd associate, we compare the observed difference between bachelor and stallion means to the differences generated by randomly reassigning individuals' status histories. By comparing observed differences to the randomization distribution, we find that bachelors have groups containing significantly more adults, bachelors, and stallions than are found in stallions' herds. *p*-values are based on a two-tailed test. Where possible, we indicate the exact *p*-value. We determine a *p*-value of less than 0.002 if an observed mean group size falls outside the null distribution resulting from all 1,000 randomization runs.

using such a permutation test. In the randomization distributions, there is a consistent tendency for stallions to be with fewer herd associates compared to bachelors, across the possible classes of associates—all adults, bachelors, stallions, and females (Table 1). The structure of our data thus contains a bias toward observing bachelors in larger groups. In comparing observed differences between bachelors and stallions to those generated by the randomization, we can be confident that our null expectation incorporates this bias. Some of the observed differences between bachelors and stallions are statistically significant. The test for significance is whether males' observed behavior

departs from that expected if association choices were independent of status.

We find that bachelors tend to be in groups with more adults, bachelors, and stallions, compared to stallions' groups. We find no evidence of non-random differences in the number of female associates between bachelors and stallions; this could possibly be due to the countervailing effects of stallions' association with their own harem females, and bachelors' tendency to be with more stallions. Underlying the difference in group size is an apparent difference in how males behave during herd splits. Over time, bachelors are more likely to stick together with their bachelor herd members, compared to stallions with their stallion associates.

We hypothesize that the following behavioral mechanism could explain our observed patterns. Small and relatively stable groups of bachelors wander from one stallion herd to another. Thus, bachelors are in larger groups, overall, due to the presence of the additional bachelors. On average, bachelors have 3.8 more bachelor associates than are found with stallions. This suggests that the size of a bachelor clique tends to be about four to five individuals. The number of females seen by a bachelor is about the same as that seen by a stallion, because bachelors do not bring females with them as they move from herd to herd. An apparent bias towards identifying males is likely responsible for the slightly lower average number of females than stallions observed in herds.

We can posit several potential benefits of persistent bonds among bachelors. By interacting frequently, a bachelor clique may develop cooperative relationships in the context of conflicts with stallions or other bachelors. Strong bonds are predicted to result in stable dominance hierarchies, within tight bachelor cliques (Beacham 2003). Persistent bonds also make it highly unlikely that a bachelor will be in a herd of one, without any male or female associates. Of the 2,555 bachelor groups we

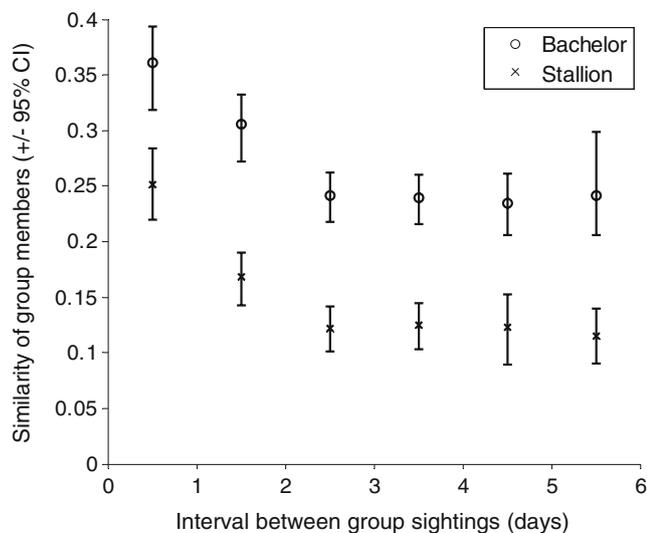


Fig. 5 Similarity over time of associations for bachelors versus stallions. The similarity of group members is compared for all herds observed within a time interval (see “Materials and methods” section for details). Similarity is computed separately for the bachelor and stallion contingents of groups. Bootstrapping defines 95% confidence intervals around the means. Over each time interval, up to six days of separation, bachelors maintain a more similar set of associates, compared to stallions' associations with other stallions

observed, only 165 (6.4%) were solitary males without any adult associates. With many lions around, being alone is dangerous. Plains zebra modify their movements in response to this danger (Fischhoff et al. 2007b); we expect it shapes social choices as well. We predict that bachelors with relatively persistent bonds, toward a large number of bachelors, enjoy benefits of cooperation: lower agonism rates, support in fights against stallions and bachelors who are not in one's clique, and higher survival rates.

Bachelors have more persistent bonds than stallions, but they nonetheless lose associates over time. Bachelors may choose to separate from each other to reduce resource competition. Bulking up is hypothesized to be important for bachelors to win contests with other males (Rubenstein and Hack 2004). Individuals may also want opportunities to test their mettle against less-familiar bachelors, and search for vulnerable stallions or females coming into their first estrus. A group of bachelors may form a clique, but each individual in that set strives for a state in which he has no close male companions: becoming the stallion of a harem. Prior to successful takeover of a harem, we predict that a bachelor enters a period when he associates with fewer bachelors overall, and dissolves strong bonds to any particular clique.

The low similarity of stallion associations over time suggests stallions do not form long-term cooperative bonds. With increasing number of stallion associates, a stallion's herd may become more attractive to bachelors, intent on checking out females and the potential vulnerability of stallions. Stallions may be more likely to lead their females out of herds containing too many other stallions, to escape bachelor attention. This may be the explanation why the average herd, as observed by a stallion, contains fewer stallions than that observed by a bachelor. It may nonetheless be true that stallions enjoy dilution of bachelor harassment from associating with other stallions (Rubenstein 1994). Once a stallion has several other stallions nearby, however, the costs of gaining additional stallion neighbors may outweigh the benefits. Analogously, from the perspective of predation dilution, the marginal gains of adding group members rapidly diminish, as group size grows (Hamilton 1971); as groups grow larger still, they may attract predators (Neems et al. 1992).

The rapid fission of stallion–stallion associations is partly driven by females' choices about when to initiate movement, and whether to follow the movements of other harems. Given the importance of resources to female fitness, we expect that female initiation of movement is shaped most by resource needs, rather than social relationships with animals outside the harem. We may find stronger patterns of harem-level preferential associations based on common resource needs of the females, for example among harems with young foals (Fischhoff et al. 2007a).

In long-term studies such as ours, population characteristics typically change, and so too does the allocation of effort toward various observation methods (Clutton-Brock et al. 1991, 1996; Gibbs et al. 1998; Hasselquist 1998; James et al. 2009). Temporal variation in these factors can confound the comparisons we want to make. In our study, shuffling the status timelines of males effectively accounts for fluctuations over our 4-year study period in herd size, the numbers of individuals in each state, and the frequency of data collection. The procedure allows us to make use of all our data, rather than throwing out information from years when the population or sampling regime differed from the norm (Clutton-Brock et al. 1991; Hasselquist 1998). Our permutation test is generally applicable in addressing questions about how a flexible phenotypic trait, such as reproductive status, dominance rank, or disease status, relates to behavioral outcomes such as grouping, activity, or habitat use.

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