

Male harassment influences female movements and associations in Grevy's zebra (*Equus grevyi*)

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In traditional models for social organization, female movements and association patterns track resource distribution, whereas males track females. More recently, this model has been expanded to include feedback effects of male behavior, especially sexual harassment, on female decisions. In Grevy's zebra (*Equus grevyi*), males defend territories containing resources attractive to females, who form unstable groups. Past research has explained female behavior based on resource distribution and needs alone. Lactating females have been found to have restricted movements and fewer male associates than nonlactating females, a pattern we find in our study. This pattern has previously been attributed solely to the higher water needs of lactation. However, in our population, both lactating and nonlactating females are typically close to water. We test the hypothesis that male harassment also influences female ranging and associations with males. This effect is predicted to be greater for lactating females because harassment has higher costs to them. We find that lactating females experience higher harassment rates than those of nonlactating females. Lactating females tend to move faster during harassment periods, whereas nonlactating individuals do not. Lactating females experience lower harassment rates if they spend more time with a particular male, whereas nonlactating females' harassment rates do not depend on their allocation of time to a primary male. We suggest that females concentrate their time with one male in order to reduce male harassment. Even in species such as Grevy's zebra without strong male–female bonds, social interactions may be a significant driver of female distribution. *Key words*: animal movement, associations, Equids, Grevy's zebra, sexual harassment, social organization. [*Behav Ecol*]

In the most widely used model for the ecological basis of social organization, female reproductive success is thought to be limited by access to resources, whereas male reproductive success depends on access to females (Emlen and Oring 1977). Female behavior, including space use and social associations, are therefore predicted to be most strongly influenced by resource distribution. Male behavior, by contrast, is most strongly adapted to the behavior of females (Bradbury and Vehrencamp 1977). This model has been widely and successfully applied to explain social systems in diverse taxa, including antelopes (Jarman 1974; Gosling 1986), weaver birds (Crook 1964), primates (Crook and Gartlan 1966; Wrangham 1979; Terborgh and Janson 1986), bats (Bradbury and Vehrencamp 1977), and equids (Rubenstein 1986).

In many species, males may not only follow females but also attempt to force them to mate. Such sexual coercion or harassment has been found to have high costs to females (Smuts BB and Smuts RW 1993; Cluttonbrock and Parker 1995; Arnqvist and Rowe 2005). Costs to females of harassment include increased energy expenditure in water striders (Watson et al. 1998), higher exposure to predation and lower reproductive output in crustaceans (Jormalainen 1998; Jormalainen et al. 2001), decreased foraging returns in the solitary bee (*Amphiphora plumipes*) (Stone 1995), and injury or death in elephant seals (*Mirounga angustirostris*) (Leboeuf and Mesnick 1991). In response to these costs, females have adapted diverse behavioral strategies to reduce their exposure to male aggression (Smuts BB and Smuts RW 1993; Cluttonbrock and Parker 1995; Arnqvist and Rowe 2005). Females may choose to accept male advances in situations where resistance would

result in injury or death (Mesnick and Leboeuf 1991). Females may form alliances among themselves against male attacks (Packer and Pusey 1979; Smuts BB and Smuts RW 1993), change their movements to avoid areas frequented by males (Trillmich and Trillmich 1984; Krupa et al. 1990; Cluttonbrock et al. 1992; Stone 1995), or associate more with a single male who offers protection from other males (Rubenstein 1986; Leboeuf and Mesnick 1991; Smuts BB and Smuts RW 1993). Thus, the effect of male harassment on female behavior has become a widely recognized feedback in the structure of animal societies.

For equids, this model has been used to explain differences in social organization and space use among species (Rubenstein 1986, 1994). We find 2 themes in equid societies: harem defense polygyny and resource defense polygyny. In plains zebra (*Equus burchelli*), horses, and mesic feral asses, females form stable groups, which males directly defend (Rubenstein 1994; Moehlman 1998). In the more arid-adapted equids such as Grevy's zebra (*Equus grevyi*) and Asiatic wild ass (*Equus hemionus*), males defend territories containing resources valuable to females, who live in unstable groups. Past research on Grevy's zebra shows that females segregate by reproductive state, with lactating females moving less and associating with fewer males (Rubenstein 1986; Ginsberg 1988). This difference has been attributed solely to the greater water needs of lactating females.

In equids, researchers have examined the effects of male harassment on female behavior in the harem-dwelling species but not those with resource defense polygyny. In wild horses, mares form strong bonds with stallions, who provide them greater protection from harassment (Rubenstein 1986; Rutberg 1990; Rubenstein 1994; Kaseda et al. 1995; Linklater et al. 1999). Plains zebra stallions bring their harems together into herds to counter bachelor harassment (Rubenstein and Hack 2004). For the territorial or resource defense species, the feedbacks of harassment on female behavior have not yet been examined. This may be because females have been thought to only care about resources that males defend.

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Received 9 November 2006; revised 21 April 2007; accepted 3 May 2007.

Here we investigate how male harassment affects female associations and space use in Grevy's zebra. In this species, sexual coercion begins with a male chasing a female. Such chases may extend over as far as 500 m, last for 10 s to 5 min, and separate females from other group members, including their dependent offspring (Sundaresan SR, personal observation). We expect harassment to be more frequent when females are lactating because they come into a predictable postpartum estrus. Lactating females come into estrus twice every month following birth (Ginsberg 1988). By contrast, nonlactating females cycle approximately once every 29 days. Harassment during lactation stage is more costly for the female because disruption to her activities may reduce the resources she can acquire or allocate to her foal. We expect that females experience less harassment when they have spent more time with a male. Greater time spent together may allow a pair to establish a more cooperative relationship and for the male to be familiar with the female's estrus state. If a male learns that a female has become a regular associate, he may be less motivated to chase her and force copulations (Ginsberg and Rubenstein 1990). We predicted that harassment rate is lower when a female is with her primary male associate, compared with secondary males with whom she spends less time. Females may experience overall lower harassment rates if they spend more of their time with a single male. We suggest that females modify their behavior to reduce exposure to male harassment by associating with fewer males and restricting their movements. We expect that lactating females respond more strongly to male harassment because of its greater cost to them.

METHODS

Study species and sites

Grevy's zebras are large-bodied (~400 kg) grazing ungulates primarily inhabiting the semiarid and arid rangelands of central and northern Kenya. This species is endangered with less than 3000 individuals living in the wild (Williams 2002).

We study a population of approximately 500 Grevy's zebra in the Lewa Wildlife Conservancy, central Kenya. Lewa is approximately 200 km². Data were collected from September to October 2003. Lewa is a semiarid bushed grassland. The woody vegetation is dominated by *Acacia* species. Grasses are primarily of the genera *Themeda*, *Cynodon*, and *Pennisetum*. Annual rainfall averages approximately 600 mm. Lions are a key predator of Grevy's zebra in this site.

Field methods

Each day, we searched the area for a set of focal zebra that included 9 lactating females and 8 nonlactating females. All were adults, at least 3 years of age. It is not possible to differentiate age, in the field, among individuals over 3 years old. We focused our observations on 2 areas, each of approximately 20 km², surrounding water holes popular with Grevy's zebra. For this paper, we consider females with foals less than 6 months old as lactating females. We can recognize individuals by their unique stripe patterns. In addition, 3 lactating and 3 nonlactating were wearing very high frequency radio collars that facilitated locating them. When found, a focal individual was followed for between 1 and 5 h. We used a global positioning system to record the individual's location at the start and end of every observation period. We recorded the identity of the female's nearest territorial male associate, if one is within 200 m. Females are always found in groups with other females. We watched the focal zebra and its group members and recorded all occurrences of sexual harassment by

males. For each harassment event, we noted the location, time, and identities of the harassing male and target female.

Analysis

We first compare lactating and nonlactating females in their male associations and ranging patterns. Second, we examine the harassment rates experienced by the 2 female classes and the immediate effects of harassment on their movements. We use permutation tests for all comparisons because our data are generally not normally distributed (Good 2000). In a permutation test, we compare a test statistic from our observed data with the distribution of test statistic values generated by a series of 1000 randomizations. For our comparisons between lactating and nonlactating females, the test statistic we use is the group mean. A significant *P* value is indicated by an observed test statistic that is an extreme value, compared with the distribution from the randomizations. To perform one randomization, we randomly reassign the group (treatment) labels for all observations and compute the randomized test statistic. We repeat these steps 1000 times to obtain the test statistic's randomized distribution. For each test, we present the 2-tailed permutation *P* value, the estimated difference between the group means, and the 95% confidence interval (CI) around this difference. We estimate the 95% CI around the difference in group means using the method prescribed by Good (2000). The CIs provide an indication of the statistical power of each test and the magnitude of differences between group means.

Female-male associations

For each female, we tally the total number of males with whom she has been observed. We determine if lactating females differ from nonlactating females in their number of male associates. Across all observation hours for a female, we sum the total time spent with each of her male associates. We then compute the fraction of time a female has been with each of her male associates. We compare the fraction of time spent with the primary male for lactating versus nonlactating individuals. We define the primary male as the one with whom the female was observed for the greatest fraction of time.

Ranging patterns

As a measure of an individual's space use, we use the maximal distance between any 2 of its locations. We compare this maximal distance between lactating and nonlactating females. We only include those individual for whom we have at least 8 locations.

Previous studies have found that lactating females constrain their movements around water holes (Ginsberg 1988). We compared distances with closest water hole for lactating versus nonlactating females. For each individual, we compute the average distance to the nearest water, over all her sightings.

Harassment rates

For each female, we compute her harassment rate as the total number of harassment events divided by the total observed time. We test whether lactating females differ from nonlactating females in their harassment rates. Next, we compared harassment rates experienced by females with their primary versus secondary males. Harassment rate is computed separately for a female's time with her primary male versus all secondary males. Within each female reproductive class, we test whether a female experiences different levels of coercion from their primary versus secondary males. We pair primary and secondary male harassment rates for each female. Finally, we use a linear regression to test for a relationship between the proportion of time a female allocates to her primary male

and her overall harassment rate. We perform this regression separately for data from lactating and nonlactating females.

We examine whether female reproductive state mediates the relationship between harassment rate incurred by a female and how much time she spends with her primary male. We test this by determining whether the slope of the regression line is different for lactating females from that of nonlactating females. To test for this difference, we use a permutation analysis of covariance (ANCOVA) adapted from the methods suggested by Good (2000) and Manly (1997). First, we use linear regression to fit 2 parallel lines to the 2 groups—lactating and nonlactating females. This represents the null hypothesis that the relationship between time spent with primary male and harassment rate is the same for both lactating and nonlactating females. We do a permutation ANCOVA test by using a randomization of the residuals of the 2 regression lines, as fitted with identical slope. If the null hypothesis is correct, then the observed slopes of the regression of the residuals, against time spent with primary male, should be the same for lactating and nonlactating females. On the other hand, if the regression slopes of the residuals differ for the 2 female reproductive states, then we can conclude that lactating females experience a different relationship between male association and harassment. Thus, we randomized the group labels of the residuals and compared the regression slope of the randomized residuals data with the observed case. We perform the permutation test in the following way.

For lactating females, we compute the slope of the regression of their observed residuals against the associated values for the x -variable, the proportion of time with primary male. We compared this observed slope for the residuals to the distribution generated from a series of 1000 randomizations. In each randomization, we permute the group labels (lactating or nonlactating) for the residuals. We then recompute the regression slope of the residuals for the relabeled lactating data against their associated x -variable value, which remains unchanged. A significant P value is indicated if the observed slope is an extreme value relative to the distribution from the randomized cases. This would indicate that we should reject the null hypothesis that lactating and nonlactating females exhibit the same relationship between harassment rate and proportion of time with a primary male.

Effects of harassment on female movement

We examine whether females move more rapidly during observation periods when they have been harassed. For a female, we compute her mean speed over all observation periods when she was not harassed and pair that to her mean speed in all periods when harassment occurred. Within each reproductive class, we perform a paired test.

RESULTS

We have a total of 130 observation hours over 70 periods for the 9 lactating females. We observed the 7 nonlactating females over 165 h in 67 periods.

Female–male associations

Lactating females associate with significantly fewer males than their nonlactating counterparts ($P = 0.002$, difference in means = 2.05 males, 95% CI [1.00, 3.00]). Lactating females average 1.67 male associates (standard error [SE] = 0.29, $N = 9$). Nonlactating females associate with an average of 3.75 males (SE = 0.31, $N = 8$).

Lactating females spend a significantly greater fraction of their time with a primary male than do nonlactating females ($P = 0.001$, difference in means = 0.46, 95% CI [0.31, 0.60]).

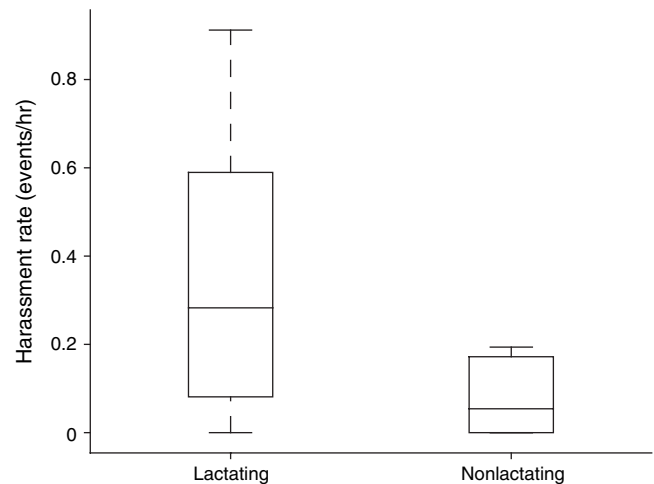


Figure 1

Box plot of harassment rate experienced by lactating females ($N = 9$) versus nonlactating females ($N = 8$). The horizontal lines of each box represent the lower quartile, median, and upper quartile of each distribution. Whiskers represent the bounds of the observed data up to a maximum of 1.5 times the quartile range. Lactating females experience significantly greater harassment rates than do nonlactating females.

The average fraction of time that a lactating female is with her primary male is 0.87 (SE = 0.05, $N = 9$), whereas nonlactating female only spends on average 0.41 (SE = 0.03, $N = 8$) of her time with her primary male. We conclude that lactating females tend to constrain their associations to fewer males and to concentrate their time with one particular male.

Ranging patterns

The maximal distance spanned by the locations of a lactating female is significantly less than that of a nonlactating female ($P = 0.004$, difference in means = 2.43 km, 95% CI [0.60, 4.21]). Mean maximal distance for lactating females is 2.09 km (SE = 0.23, $N = 7$), and for nonlactating females it is 4.53 km (SE = 0.78, $N = 8$). Thus, we find that lactating females have more limited movements than nonlactating females.

We find that lactating females tend to be significantly closer to water than nonlactating females ($P = 0.001$, difference in means = 0.21 km, 95% CI [0.12, 0.32]). The mean distance from water for lactating females is 0.54 km (SE = 0.03, $N = 9$). For nonlactating females, this distance is 0.75 km (SE = 0.03, $N = 8$).

Harassment rates

Lactating females suffer significantly higher harassment rates than do nonlactating females ($P = 0.018$, difference in means = 0.27 events per hour, 95% CI [0.03, 0.53]) (Figure 1). Lactating females average 0.35 harassment events per hour (SE = 0.10, $N = 9$), compared with 0.08 events per hour for nonlactating females (SE = 0.03, $N = 8$).

Of the 9 lactating females, only 4 associated with multiple males. For these 4 females, all experienced higher harassment rates with secondary males. Harassment with secondary males averaged 1.2 events per hour higher than the rate with primary males. The small sample size results in low power to detect a difference ($P = 0.12$). Sample size is insufficient to compute a 95% CI. All 8 nonlactating females had multiple male associates. We find no evidence for harassment rates being different between primary versus secondary males

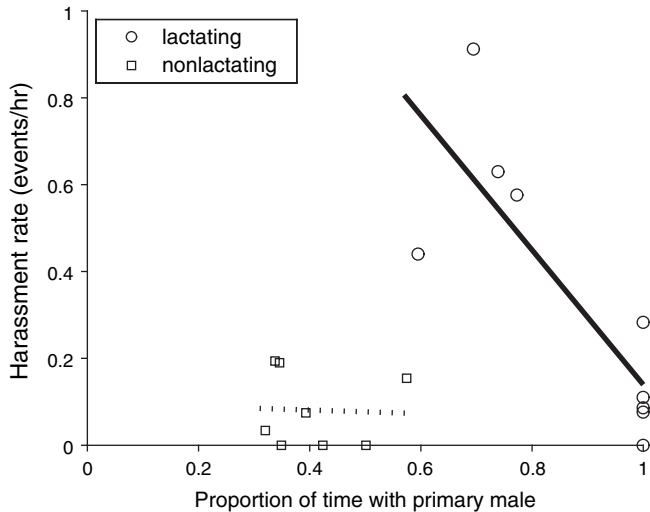


Figure 2
Regression of individuals' overall harassment rate versus time spent with primary male. The primary male is the male with whom a female has spent the greatest proportion of time. Harassment rate incurred by lactating females (circles) significantly decreases as time spent with primary male increases. By contrast, nonlactating females (squares) exhibit no such relationship.

($P = 0.62$, difference in means = -0.04 events per hour, 95% CI [$-0.18, 0.06$]).

For lactating females, overall harassment rate declines with increasing proportion of time spent with a particular male (Figure 2) (linear regression; $R^2 = 0.67$, $F = 14.14$, $P = 0.007$, $N = 9$). For nonlactating females, we find no relationship between their overall harassment rates and time with the primary male (Figure 2) (linear regression; $R^2 = 0.01$, $F = 0.01$, $P = 0.91$, $N = 8$). We conclude that lactating females are able to reduce their harassment by lengthening their association with a single male. Our permutation ANCOVA further supports the hypothesis that lactating females exhibit a relationship between overall harassment rate and time with primary male that is different in slope from that of nonlactating females ($P = 0.004$).

Effects of harassment on female movement

We find evidence for short-term effects of harassment on movements in lactating females but not in nonlactating females. Seven lactating females have been observed both in periods with and without harassment. During observation periods in which a lactating female has been harassed, her speed over this period is significantly higher than in periods without harassment ($P = 0.031$, difference in means = 0.30 km/h, 95% CI [$0.02, 0.65$], $N = 7$) (Figure 3). We detect no significant difference in speeds of nonlactating females between periods of harassment compared with harassment-free periods, for the 5 nonlactating females observed in both conditions ($P = 0.12$, difference in means = -0.17 km/h, $N = 5$) (Figure 3). For nonlactating females sample size is too small to construct CIs. There appears to be a trend toward nonlactating females moving slower during periods of harassment.

DISCUSSION

The original behavioral ecology model is that females typically pattern their distribution to maximize resource access, whereas males track female distribution (Jarman 1974; Emlen

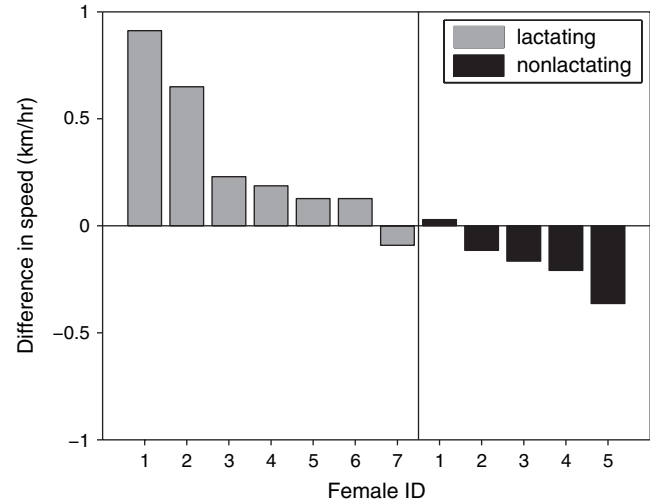


Figure 3
Difference in speed of females during periods when harassed versus periods without harassment. Each bar represents an individual. Speed is calculated from the distance moved from start to end of an observation period. Positive values indicate more rapid movement during periods of harassment. Gray bars are lactating females and black bars are nonlactating females.

and Oring 1977; Gosling 1986). This model has been elaborated to include a role for male behavior toward females as a factor shaping female movements and associations (Rubenstein 1986; Smuts BB and Smuts RW 1993; Cluttonbrock and Parker 1995; Sterck et al. 1997; Arnqvist and Rowe 2005). In invertebrates, many studies have shown that females reduce harassment by moving in ways that reduce their encounters with males (Parker 1970; Krupa et al. 1990; Stone 1995). Among many mammal species, females reduce harassment by associating more with particular males who provide protection from aggression by others (Rubenstein 1986; Cluttonbrock et al. 1992; Smuts BB and Smuts RW 1993). In a group with multiple males, females may accomplish this by spending more time in close association with one male (Smuts 1985). In species where males defend territories, females restrict movements to one territory whose owner guards her against others (Trillmich and Trillmich 1984; Rubenstein 1986; Cluttonbrock et al. 1992; Cluttonbrock and Parker 1995).

In equids, attention to such feedbacks has been limited to harem defense species, in which males and females form strong bonds (Rubenstein 1986, 1994). In the resource defense Grevy's zebra and wild ass, females typically form unstable bonds with both males and other females. Female movements and association choices have been thought to depend principally on water and forage distribution. Differences in resource needs between lactating and nonlactating females prevent females forming stable bonds among each other. Unable to directly and continuously guard a set of females, males defend territories containing resources attractive to females (Emlen and Oring 1977; Rubenstein 1986; Ginsberg 1988; Ginsberg and Rubenstein 1990). Researchers have not examined how male behavior influences female decisions. In this paper, we tested the hypothesis that male harassment influences female movements and associations with males.

As found previously (Rubenstein 1986; Ginsberg 1988), lactating females in our population have fewer male associates and more constrained movements than nonlactating females. Past explanations for this difference have focused on lactating females' greater water needs in habitats where water points are scarce. Lactating females were significantly closer to water than

nonlactating females by an estimated difference of 0.21 km. This distance appears minor, given that a female could traverse it in several minutes. Overall, the furthest we observed any female from water was 2.22 km, a distance that an individual can easily move within a day. In our study site, it seems unlikely that remaining close to water is the only, or even primary, reason why lactating females are constraining their movements and the number of male associates in our population. Within the areas close to water that they share with lactating females, nonlactating females associate with more males.

We find that lactating females are harassed at a rate more than 4 times that of nonlactating females. Harassment appears to have greater costs, in the short term, to lactating females than for nonlactating females. If we assume that each harassment event disrupts a female's activities for 1 min, then each hour a lactating female loses 4 min more to harassment than a nonlactating female. Over 24 h, this difference may accumulate to as much as 96 min of time that could be spent foraging or in other activities. As hindgut fermenters, Grevy's zebra must feed throughout the day.

Lactating females move faster during periods of harassment, whereas we find no evidence for nonlactating females exhibiting this response. For females with young foals, moving faster may deplete their energy reserves, leave them less time to forage or nurse and increase the risk of separation from their foals. On 2 occasions, mothers were separated from their foals for 45 min following a harassment encounter (Sundaresan SR, personal observations). Such harassment-induced separation may sharply increase foal susceptibility to predation in a setting such as Lewa where predator density is high. We have observed foal mortality following harassment in a different population. In another case, a foal died when a harassing male trampled it (Rubenstein DI, personal observations). Thus, harassment may present large energetic and fitness costs to lactating females.

One strategy that lactating females may employ to minimize their harassment is to focus their time on a particular male. We find that lactating females' harassment rates decline with increasing proportion of time spent with a primary male. By contrast, nonlactating females' harassment rate does not depend on the time they spend with their primary male. There is a trend toward lactating females being harassed more often when with a secondary male than with their primary male.

Our results indicate that social interactions may shape female movement and association patterns that were formerly assumed to emerge from resource distribution alone. The feedback effects of male behavior on females have been studied more widely in species with strong male–female bonds. Here we demonstrate its importance even in a population with only transient male–female associations. Similar processes have been found in female decision making about space use and mate choice in other species where males defend territories rather than defending females (Cluttonbrock et al. 1992; Cluttonbrock and Parker 1995). Based on our study, we can hypothesize 2 factors expected to increase the strength of these feedbacks. First, if male sexual coercion can impose high costs, then females should develop strategies for avoiding these costs. Second, for females to benefit from constraining their movements and associations, males must be able to protect their females from encounters with other males. In Grevy's zebra, females can limit their interactions to one male by remaining in that male's territory.

Given the high costs of harassment and potential to reduce it by remaining with a single male, we may ask why some lactating females associate with multiple males. One possible explanation is that females whose male associate has a relatively poor territory may seek better resources elsewhere. This predicts that females associated with males on superior terri-

ories will exhibit greater fidelity. Females who range more may be trading off increased costs of harassment for other potential benefits, including searching for better forage sites or higher quality males with whom to mate.

Our results suggest that male harassment may be a unifying factor in the emergence of equid societies. Among the harem defense species of horses and plains zebra, females bonded to a male derive protection from harassment by other males (Rubenstein 1986; Linklater et al. 1999). In plains zebra, stallions bring their harems together into herds in order to dilute costs of protecting females against bachelor males (Rubenstein and Hack 2004). In this paper, we have shown that male harassment is important to social organization in equid species without stable male–female bonds because it can force lactating females to temporarily bond to particular males for protection.

FUNDING

National Science Foundation (IOB-9874523 to D.I.R. and I.R.F., IBN-0309233 to D.I.R. and S.R.S.); Pew Charitable Trusts award 2000-0002558 “Program in Biocomplexity” to Princeton University Department of Ecology and Evolutionary Biology (I.R.F., S.R.S., and D.I.R.); the Wildlife Conservation Society Research Fellowship Program to S.R.S.; the Teresa Heinz Environmental Scholars program to I.R.F.; Princeton University Department of Ecology and Evolutionary Biology.

The authors thank the Kenya Ministry of Education for permission to carry out the research. Lewa Wildlife Conservancy staff generously supported the fieldwork, in particular Ian Craig, Belinda Low, David Njonjo, and Edwin Kisioo. We thank Patrick Akilong and Lesiri for field assistance. Jonathan Dushoff assisted in designing our statistical tests including permutation ANCOVA. He also provided code for performing the permutation tests. We thank Goran Arnqvist and 2 anonymous reviewers for comments on an earlier version of the article.

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