Caught between two worlds: genes and environment influence behaviour of plains × Grevy's zebra hybrids in central Kenya

Jennifer M. Schieltz [a, 1], Daniel I. Rubenstein [a, b, *]

[a] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, U.S.A.
[b] Mpala Research Centre, Laikipia, Kenya

Hybridization between related species has been documented in many animal groups, but little work has been done on the behaviour of hybrids relative to the parental species. Hybrid individuals generally possess physical characteristics of both parents, but behaviour may vary depending on complexity of gene interaction and the extent to which behaviours are learned from one species or the other. Studying hybrid behaviour can be an opportunity to separate environmental or learned traits from genetic ones. Here we report on the behaviour and sociality of natural plains e Grevy's zebra hybrids (*Equus quag- ga* × *Equus grevyi*) from central Kenya. All hybrids were born to plains zebra mothers and raised exclusively in the plains zebra society. When leaving natal groups, hybrids showed no interest in and did not interact with Grevy's zebras. Therefore, any behavioural differences between hybrids and plains zebra may result from genetic influences of their Grevy's zebra fathers. We found several significant behavioural differences between hybrids and plains zebra. Hybrid females were more vigilant than plains zebra females and showed equivalent levels of vigilance to Grevy's zebra females. Male hybrids were seen alone more often (a Grevy's zebra trait) and in a greater diversity of behavioural states (bachelor, satellite, challenger, stallion, alone), and changed state more often than plains zebra males, indicating conflicting environmental and genetic cues. Adult hybrid males appear to show a divergence in behavioural paths, with some behaving like plains zebra males challenging for harems and others setting up territories as Grevy's males do. Both male and female hybrids stayed with their natal harems longer than either plains or Grevy's juveniles.

Hybridization between closely related species has been observed in nearly all major plant and animal taxa (Dowling & Secor, 1997), and is now recognized as an important evolutionary force (Arnold & Hodges, 1995). While hybridization in animals is generally thought of as rare compared to plants, it does occur in a number of mammals, both in captivity and in the wild (Gray, 1971). Natural hybridization has been observed in a range of mammalian species (e.g. macaques: Bernstein, 1966; baboons: Alberts & Altmann, 2001; Bergman & Beehner, 2004; porpoises: Willis, Crespi, Dill, Baird, & Hanson, 2004; coyotes and wolves: Lehman et al., 1991), especially under conditions of disturbance. In ani- mals, hybridization may be more likely in poor habitats or small populations, where low mate availability and skewed sex ratios may lead to exclusion of some individuals from mating (Jansson, Thulin, & Pehrson, 2007; Mace & Waller, 1998). Here we report on the behaviour and social organization of natural plains e Grevy's zebra hybrids (*Equus quagga* × *Equus grevyi*) from an area of range overlap in central Kenya where hybridization has not been known to occur until the past decade (Cordingley et al., 2009).

In any species pairing, the effect of hybridization on phenotype can be quite variable depending on the levels of genetic intro- gression and differences in gene expression. Particular traits may be determined by one parent only, or be intermediate between the two. Hybrid individuals generally possess physical characteristics of both parents, while behaviour may vary depending on the complexity of gene interaction and the extent to which behaviours are learned from one species or the other. Studying hybrid behav- iour can, therefore, be an opportunity to separate environmental or learned traits from genetic ones. For example, Alberts and Altmann (2001) reported on the hybridization of yellow, *Papio cynocephalus*, and anubis baboons, *Papio anubis*, around Amboseli, Kenya over a span of 30 years. The authors found evidence that, despite being members of a yellow baboon social group, hybrid males dispersed

* Correspondence: D. I. Rubenstein, Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall, Princeton, NJ 08544, U.S.A.
E-mail address: dir@princeton.edu (D. I. Rubenstein).
[1] *E-mail address*: schieltz@princeton.edu (J. M. Schieltz).

at an earlier age than yellow males. The earlier age of dispersal suggests that hybrids may have inherited this trait from their anubis fathers, despite the environmental influence of the yellow baboon social group in which they were raised.

In a different hybrid zone between hamadryas baboons, *Papio hamadryas*, and anubis baboons in Ethiopia's Awash National Park, extensive hybridization has led to the formation of hybrid-only groups. One hybrid group studied displayed elements of both hamadryas and anubis social organization (Bergman & Beehner, 2004). Overall, the group resembled a multimale, multifemale group that lacked cohesion, typical of anubis baboons. However, there were several hamadryas-like one-male units nested within this group. Interestingly, the subgroups displaying more hamadryas-like behaviour also contained the physically more hamadryas-like individuals, suggesting that individual ancestry may determine many of the behaviours that affect social systems (Bergman & Beehner, 2004).

EQUINE HYBRIDS

The mammalian family Equidae is unusual in that interbreeding and production of viable, though usually infertile, offspring is possible between nearly every pair of its member species. A considerable range of hybrid foals have been born in captivity, despite significant chromosomal differences between the parent species (Allen & Short, 1997; Benirschke & Ryder, 1985). The number of chromosomes in the genus *Equus* ranges from a high of 66 in Przewalski's horse, *Equus ferus przewalskii*, to 32 in the mountain zebra, *Equus zebra*. The most common and well-known equine hybrid, the mule, is a cross between a female domestic horse, *Equus ferus caballus* ($2n = 64$) and male donkey, *Equus asinus* ($2n = 62$). The reciprocal cross (female donkey × male horse) produces the less common hinny. Both the mule and hinny have an intermediate number of chromosomes to the two parents ($2n = 63$) and both are generally sterile, although rare cases of fertility in females have been reported. The sterility of equine hybrids is generally attributed to an incompatibility between the paternal and maternal sets of chromosomes, leading to a block in meiosis (Allen & Short, 1997). Not all equine hybrids are sterile, however. Both male and female Przewalski's horse × domestic horse hybrids are fully fertile (Short, Chandley, Jones, & Allen, 1974).

Like many hybrids, the mule possesses morphological characteristics of both of its parents. In their dominance and social organization, mules appear to be intermediate between the parental species, holding the middle ranks of the dominance hierarchy in a mixed group, with ponies at the top and donkeys at the bottom (Proops, 2006). However, the mule has been bred for centuries by humans for commercial use because of its hybrid vigour, showing that some traits of hybrids may diverge from either parent. Mules tend to be stronger and more sure-footed than a horse, better able to withstand thirst and hunger, show a quicker recovery after strenuous effort (Savory, 1970), and are capable of growing taller than either parent (Travis, 1990). In a study on cognition, mules showed significantly better performance on a visual discrimination learning test than either of the parent species (Proops, Burden, & Osthaus, 2009).

PLAINS–GREVY'S ZEBRA HYBRIDS

Hybrid offspring have been produced in captivity between a male Grevy's zebra, *Equus grevyi* ($2n = 46$) and a female plains zebra, *Equus quagga* ($2n = 44$), and these offspring possessed the expected intermediate chromosome number of 45 (Benirschke, 1977). Further studies have shown a close chromosomal correspondence between the two species (Musilova et al., 2007). Recently, the first evidence of natural hybridization between these two species was reported from an area of range overlap in central Kenya (Cordingley et al., 2009). Both male and female F1 hybrids have been observed and molecular genetic testing showed that all F1 hybrids have a Grevy's zebra father and a plains zebra mother. Interestingly, one backcross (female hybrid × male plains zebra) has produced a viable B1 offspring surviving to adulthood, indicating that at least some F1 hybrids are fertile.

Natural hybridization between these two species is unexpected as the two have existed together in an overlap zone for centuries, often associating in mixed herds, without any apparent interbreeding (Keast, 1965). This recent hybridization appears to be the result of both increased range overlap and the small size and skewed sex ratio of the endangered Grevy's zebra population at our study site. Historically, the Grevy's zebra range extended from Kenya into present-day Ethiopia and western Somalia. However, today they number fewer than 2500 individuals globally (following a decline from 15 000 in 1977) and occur only in northern Kenya and Ethiopia, making them one of Africa's most endangered mammals (Moehlman, Rubenstein, & Kebede, 2008). The range of the more common plains zebra stretches from Ethiopia in the north to South Africa. In recent years, the Grevy's zebra range has extended south onto the Laikipia Plateau. Grevy's zebra have become increasingly concentrated in the south of their range due to habitat loss in the north and increased competition with livestock, leading to increased contact with plains zebra (Williams, 2002). In addition, the small population at our study site began with a male-biased sex ratio over 30 years ago (9 males and 4 females) and remains small and male skewed.

Plains and Grevy's zebra have distinct morphology and social systems. Grevy's zebra are larger, with large rounded ears. Plains zebra are smaller with pointed ears. Grevy's zebra have a pattern of thin black and white stripes, a prominent dark dorsal stripe and a white belly (Kingdon, 1997; Rubenstein, 2001). Plains zebra have broader stripes that extend to the ventral line (see Fig. 1). Grevy's and plains zebra are adapted for different habitats, which has also led to significant differences in their behaviour and social structure. The core social group in the plains zebra is the harem, comprising a stallion, several females and dependent offspring (Klingel, 1975; Rubenstein, 1986). Males compete for harems that they then protect and mate with exclusively, until usurped by another male. Grevy's males, by contrast, establish and defend territories around valuable resources such as waterholes and forage patches in an attempt to control access to unstable groups of females that enter their territory (Klingel, 1975; Rubenstein, 1986).

In both species, all juveniles leave their natal groups. Juvenile males typically join bachelor groups. Bachelors fight among themselves to establish positions in the dominance hierarchy until they can take over a harem or establish their own territory. Young plains zebra males also have several other possible pathways to adulthood. In addition to the typical harem route, experienced young males can leave a bachelor group and bond with an emigrating female (monogamous route). Two low-ranking sub-adult males can join together and bond with an emigrating female (polyandrous route). Alternatively, some males forgo joining a bachelor group and take up residence as a secondary male in an existing harem (satellite route) (Rubenstein & Nuñez, 2009). Young plains females either join an existing harem or bond to a high-ranking bachelor male.

Plains–Grevy's zebra hybrids (verified genetically in Cordingley et al., 2009) show physical characteristics intermediate to both parents. Hybrids' stripes are narrower than the plains zebra, but not as narrow as the Grevy's zebra, and their stripes do not meet under the belly. Hybrids also have a distinctive ‘waffle-iron’ stripe pattern on top of the rump that is not found in either of the parents (Fig. 1).

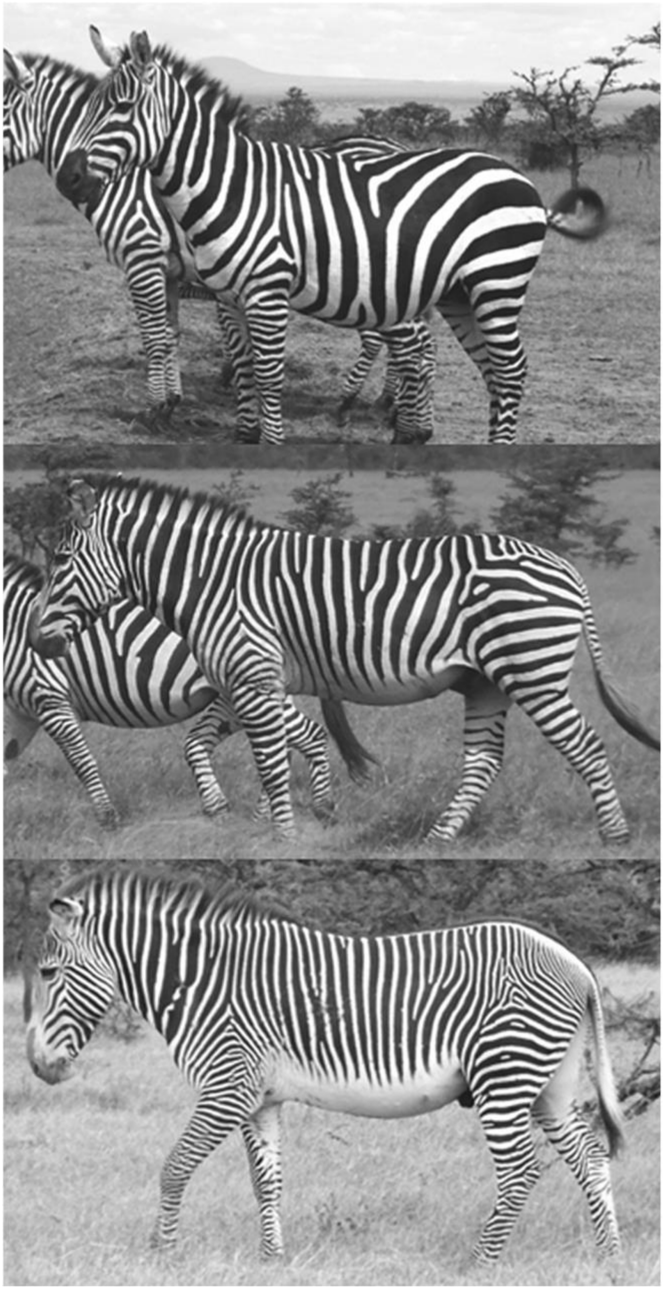

Figure 1. Comparative photos of a plains zebra, *Equus quagga* (top), a hybrid (centre), and a Grevy's zebra, *Equus grevyi* (bottom).

Hybrids are noticeably larger than plains zebra of the same age, but not as large as Grevy's zebra. The one backcross female is, as expected, slightly more plains zebra-like, with pointed ears and stripes that do meet under the belly (Cordingley et al., 2009).

Little is known about the behaviour of these hybrids relative to both parental species. Because they are born to plains zebra mothers, hybrids have been raised exclusively in the plains zebra society. If social behaviour is the outcome of only learning and not influenced by genetics, we would expect hybrids to behave just like plains zebra, because hybrids have virtually no interaction with Grevy's zebras. This is true as long as hybrids are not treated differently by plains zebra with whom they interact, a consider- ation we try to keep in mind and take note of in our observations. However, work on hybrids of other species suggests that genetics can play a role in determining social behaviour. Therefore, if genetics is the primary determinant of the behaviour of hybrids, we predicted that hybrids would display behavioural phenotypes intermediate to the two parents and show some behavioural characteristics of Grevy's zebras. Each individual hybrid may show behaviour more strongly resembling one parent or the other, depending on their unique genetic make-up and the relative contribution of genetic material from each parent. In either case, if these behaviours are determined by genetics alone and not modi- fied by learning, then they should be fixed from birth and not change over an individual's lifetime. This study is the first to identify how genes and socialization throughout ontogeny affect a variety of social behaviours exhibited by male and female Gre- vy's–plains zebra hybrids.

METHODS

Field Site and Population

This study was conducted at Ol Pejeta Conservancy, which lies on the equator ($0^\circ 00'$N, $36^\circ 56'$E) in Laikipia District, Kenya, at the southwestern limit of the Grevy's zebra range. By 1990, Grevy's zebra had already moved to within 20 km of Ol Pejeta and in the early 1990s 13 individuals were translocated to Ol Pejeta to accelerate the movement of their expanding range. Plains zebra have always been common on Ol Pejeta. The vegetation is a mosaic of savannah grassland, *Acacia* woodland, *Euclea* scrub woodland and riverine woodland. The area of the conservancy open to wildlife is 305 km^2. A perimeter fence surrounds the conservancy, but several corridor gaps along the northern boundary allow animals, including zebra, to move in and out, connecting the Ol Pejeta population with populations to the north. Ol Pejeta currently sup- ports about 4000 plains zebra and 13 Grevy's zebra. Apparent hy- brids between plains and Grevy's zebra were first observed in 2004. Molecular analysis of the 10 individuals identified at that time (6 female, 4 male) demonstrated that they were true genetic hybrids (Cordingley et al., 2009). One of these six females was a backcross individual born to an F1 female hybrid. As of December 2014, the total number of hybrids on Ol Pejeta was 25 individuals: 10 female and 15 male. The 15 additional hybrids identified since 2004 have not been genetically tested. However, they all have strong inter- mediate stripe patterns, especially with respect to the unique 'waffle iron' pattern on the top of the rump that is conspicuously absent in both parental species, and are very similar to the 10 hy- brids previously tested. Consequently, we are confident in identi- fying them as true hybrids as well. All hybrids included in the present study had a different plains zebra mother. Cordingley et al. (2009) were able to identify the paternal species in each case, but were not able to assign paternity to individual Grevy's zebra males. Using our long-term data set, we attempted to compare home ranges of plains zebra females who later gave birth to hybrids to the known territories of several Grevy's zebra males around the time of presumed conception, but we were unable to determine whether one or several Grevy's males sired these hybrids.

Because of the small Grevy's population at Ol Pejeta and the unusual behaviour of at least some of the males (as evidenced by the birth of hybrids), most of the data on normal Grevy's behaviour was collected in June–August 2006 at nearby Mpala Ranch ($0^\circ 17'$N, $36^\circ 53'$E). Mpala is a 200 km^2, unfenced property, 35 km north of Ol Pejeta, but with a larger Grevy's population that can be as large as 300 individuals depending on season. Mpala also supports around 800 plains zebra. One hybrid was recently spotted on Mpala, but was not included in the present study. Mpala contains the same habitats as Ol Pejeta, but with lower average rainfall (10- year average: Mpala ¼ 471 mm/year, Ol Pejeta ¼ 613 mm/year).

Vegetation differences between Ol Pejeta and Mpala do exist because of topography and rainfall, but overall the habitats are similar and both contain predators. Only Grevy's zebra data were collected at Mpala. All hybrid and plains zebra data and some additional Grevy's zebra data were collected at Ol Pejeta.

Field Methods

Targeted behavioural data were collected from June to August 2006 and June to August 2010. The zebra population on Ol Pejeta is also part of a long-term study being conducted by D. I. Rubenstein. Plains, Grevy's and hybrid individuals have been identified and monitored since 2003. This long-term data set was used to determine life history and behavioural characteristics of plains and hybrid individuals. Life-history trajectories of known individuals identified by unique stripe patterns have been recorded over life- times, and periodic samples of their social and ranging behaviour have been recorded.

Targeted behavioural data gathering consisted of both focal and scan sampling (Altmann, 1974). Since hybrids are relatively rare, we drove loops each day searching for hybrid individuals. When a hybrid was located, we recorded the GPS position of the animal, the size and composition of the herd it was with, its relative position in the herd, and a qualitative assessment of the vegetation (sensu Rubenstein, 2010; Rubenstein & Hack, 2004). We then observed this individual for up to several hours, following it when possible, until it disappeared completely from view. Individuals were sighted between 1 and 12 times within the 2-month sampling period each year (average of 5.5 sightings/individual in 2010), but time budgets were only obtained up to three times per individual per sampling period (during sightings when we were able to view the hybrid for more than 1 h). For time budgets, we used instantaneous scan sampling every 5 min during 1 h blocks within the observation period to record the time and occurrence of grazing, drinking, walking, standing, lying, vigilance and socializing by the hybrid and any plains zebra within approximately 15 m of the hybrid. Indi- vidual zebra were identified by their unique stripe patterns. To collect sufficient data on plains and Grevy's zebra time budgets for comparison to the hybrids, we also performed 15 and 30 min focal samples of individual zebra of all three species. This was necessary because hybrids were never within 15 m of a Grevy's zebra during observation periods, so data on Grevy's time budgets needed to be collected separately. Some data on plains zebra was obtained dur- ing the scan sampling of individuals in groups with hybrids, but focal samples of individual zebra allowed for additional data to be collected on an appropriate range of ages of each sex.

Data Analysis

Time budgets

For each observation period, we calculated the proportion of time spent grazing, drinking, walking, standing, lying, vigilant and socializing for each individual. For scan samples, the number of occurrences of each activity was divided by the total number of interval scans for that sample to obtain the fraction of time spent engaged in each activity. For focal samples, the number of seconds engaged in each activity was divided by the total number of seconds of observation. Males and females were analysed separately. All hybrid females were nonlactating at the time of observations. Because time budgets can differ between lactating and nonlactating females, we excluded any lactating plains or Grevy's females and used only nonlactating females for time budget comparisons. Males were separated by both species and breeding status (bachelor or stallion at time of sample) for analysis. Data were not normally distributed, so nonparametric tests were used. We used Kruskal–Wallis tests to compare the proportion of time that the three equids (plains, Grevy's, hybrid) spent engaged in each activity. When behaviours differed significantly among the three equid types, we used nonparametric Dunn's post hoc tests to compare pairs of equid types separately.

Life histories

We used the long-term data set to examine group membership and reproductive status of all hybrids and a subset of plains zebra males and females for which we had sufficient data, for all sightings from 2003 through 2012. Males were classified into one of six status categories for each sighting: with natal harem, bachelor, satellite male, challenger, stallion, or alone. A male was classified as a bachelor when he was sighted only with other males or when seen in multiple consecutive sightings with the same group of males (a bachelor group). He was classified as a satellite male when seen on two or more consecutive sightings at least 2 weeks apart as the only other adult male in a harem with a plains stallion (not his natal harem). A male was classified as a challenger when seen as the only adult male within 15 m of a plains stallion and harem, but on that occasion only, and not subsequently seen with that harem again (distinguishing a challenger from a satellite male). Some challenger sightings were also confirmed by parallel walking or fighting between the challenger and harem stallion. A male was classified as a stallion when he was the only adult male with a group of plains females. This classification was usually supported by multiple consecutive sightings of the male with the same group of females. A male was considered alone if he was >250 m away from any other zebra. In some cases, male status could not be determined because the male was spotted in a large group with multiple males and females and no consistent bachelor group or harem members were identified. In these cases, the status was listed as unknown. Females were never seen alone. We simply noted whether the harem they were in was their natal harem, not their natal harem, or unknown.

Plains zebras are a highly social species, yet males are occasionally seen alone. Casual observation suggested that hybrid males appeared alone more frequently than plains zebra males. To test this, we took all sightings of males over 2 years old from the long-term data set and counted the number of sightings of males alone and not alone. We also determined the number of individual males over 2 years old that had been seen alone at least once versus the number that had never been seen alone. We then used a two-tailed chi-square test to compare hybrids to plains zebra for the number of sightings and a Fisher's exact test for the number of individuals seen alone.

Males change roles over their lifetime. Again, casual observations suggested that hybrid males appear to show a greater diversity of behavioural states and to change status more often than plains zebra males. To examine this, we compared the 13 hybrid males over age 2 to 13 plains zebra males over age 2 chosen randomly from the subset of plains zebra for which we had regular sightings. To control for age, we separated sightings into two age classes: subadult and adult. Subadult sightings began when the male left his natal harem and continued until he became a poten- tially breeding male. Therefore, subadult sightings could be clas- sified as bachelor, satellite, or challenger. Adult sightings then began when the male was first seen as a harem stallion (not a satellite) or alone, and continued until the last sighting. Adult sightings thus had two additional possible states and could be classified as bachelor, satellite, challenger, stallion, or alone. We then calculated the proportion of sightings in each status category for each male by dividing the number of sightings in each category by the total number of sightings for that male.

To examine diversity of states, we calculated a Shannon diversity index score for each male as $-\sum p_i \log p_i$, where p_i is the proportion of sightings in each class. We then used ANOVAs to compare the diversity index values of hybrids versus plains zebra in each age class. We also compared the diversity values for individuals of the same type between age classes. To compare proportions in each category between hybrids and plains males, we ran nonparametric Wilcoxon tests for each status category for subadults and for adults. For each male, we then used a sliding window of 1 month between sightings to look for the number of status changes over time after leaving the natal harem. For each pair of consecutive sightings, we determined whether they were within 1 month or less of each other and, if so, noted whether the male's status category changed or stayed the same between these two sightings. Pairs of sightings greater than 1 month apart or while the individual was still with his natal harem were not included. We counted the number of ‘status change’ and the number of ‘no change’ events for each male, then summed these for hybrid males and for plains males. A Fisher's exact test was used to compare hybrids to plains zebras.

We also wanted to know the age at which individuals left their natal harem. About half of the hybrids were first sighted as adults, or the mother was not identified (7/15 males and 6/10 females) and we, therefore, could not determine the age of emigration for these individuals. Two females were not sighted for 6 months to 1 year during the time when each left her natal harem, and one male was still a juvenile. However, for seven males and two females, we were able to determine the age at which they left their mothers and joined bachelor groups or new harems. We also examined the life histories of the subset of plains zebra for which we had regular sightings and determined the age of leaving the natal harem for 45 male and 16 female plains zebra. We then counted the number of individuals that left their natal harems before age 3 (i.e. as yearlings or 2-year-olds) versus the number that stayed with their mothers until age 3 or older. Fisher's exact tests were used for males and females to compare the number of hybrids versus plains zebra leaving before age 3 or staying until age 3 or older.

By 2013, we noticed that most of the adult hybrid males appeared to have adopted one of two distinct behavioural states: defending a territory as a Grevy's male would, or challenging harems to take over as stallion as plains males do. Therefore, we noted the ‘outcome’ for each adult hybrid male in 2014 as one of three classes: territorial Grevy's zebra-like; plains zebra-like (if the male had ever been a harem stallion or satellite male); or inter- mediate (never a stallion, satellite, or territorial). To test whether males with different outcomes differed in their life-history trajec- tories, we compared the males in these three outcome classes using a chi-square test on the number of sightings in each status category prior to April 2014 for each outcome class.

RESULTS

Time Budgets

Females

Females of the three equid types did not differ significantly in the proportion of time engaged in any activity, except vigilance (mean ± SE vigilance: Grevy's ¼ 0.067 ± 0.016; hybrid ¼ 0.098 ± 0.024; plains ¼ 0.026 ± 0.009; Kruskal–Wallis test: H_2 8.476, P ¼ 0.0144). The post hoc test for all pairs showed that hybrid females were significantly more vigilant than plains females (Dunn's test: Z ¼ −2.619, P ¼ 0.026) while hybrid and Grevy's females showed equivalent levels of vigilance (Z ¼ 0.109, P ¼ 1.000). Grevy's and plains females did not significantly differ in this analysis (Z ¼ −2.109, P ¼ 0.105), likely due to our small number of Grevy's observations (N ¼ 8), but Grevy's females did have a higher mean vigilance rate than plains females. We did not have enough data to analyse the single backcross female separately, so she was included with the other female hybrids. When we removed this backcross female and repeated the analysis with only F1 hybrids, the results remained the same.

Males

We had a small sample size of hybrid males as single harem stallions (eight sightings of four hybrid males in this role since 2004). In addition, all of the observations during the targeted behavioural sampling of hybrid males with harems were of hybrid males as satellites in multimale harems with plains zebra stallions. Comparing these hybrids to plains zebra stallions may not be appropriate. Moreover, since there were no sightings of plains zebras as satellites, a direct comparison of both types as satellites was not possible. Therefore, we were only able to compare time budget data for hybrid, plains and Grevy's zebra males as bachelors and hybrid and plains zebra males as members of the same harem. When comparing bachelors to bachelors, there was no significant difference between the three equid types in time spent engaged in any activity. Time budgets on two different satellite hybrids with harem plains zebra males were recorded and no consistent behavioural pattern emerged.

Group Membership

Hybrid zebras were always located with groups of plains zebra, except for several hybrid males that were seen alone on a number of occasions. Grevy's zebra were sometimes visible in the vicinity, but never within 50 m of a hybrid. All female hybrids were in recognizable harems with plains zebra stallions. Hybrid males were seen in multiple different status categories, with some individuals seen in all six categories over their lifetimes. When seen as bachelors, hybrid males appeared to be typical members of bachelor groups, sometimes remaining with the same plains males for up to a year. As challengers, hybrids were seen following harems and aggressively interacting with the stallion in an attempt to gain access to females. These hybrid challengers then often wandered from group to group after unsuccessful challenges. Several hybrid males were observed as satellite males in multimale harems with plains zebra stallions. Five separate hybrid males were observed as satellites to at least one harem and sometimes two different harems from 2003 to 2011. Plains males, in contrast, were almost always bachelors or stallions, and occasionally challengers, but were never seen alone or as satellite males in the subset of 13 plains males that were used for comparison to the 13 hybrid males. In a population of over 4400 plains zebra, with approximately 450 harem groups existing at any point in time, only one or two harems with multiple plains zebra males were considered to be stallions with plains zebra satellite males. As noted above, we had few observations of hybrid males as the sole stallion of plains zebra females. When a hybrid male was with a harem, females did not appear to actively shun him. However, in every case, the next time the male was sighted he was no longer with the harem and appeared to be a bachelor or challenger again.

Life Histories

Hybrid males were seen alone significantly more often than plains males (chi-square test: χ^2_1 ¼ 315.334, $P < 0.0001$). Hybrids were seen alone in 13 out of 107 total sightings (12.15%), while plains zebra were seen alone only in 37 out of 11383 total sightings (0.33%). The number of individuals seen alone also differed significantly between hybrids and plains (Fisher's exact test: $P < 0.0001$).

Seven out of 14 hybrid males over age 2 (a full 50%) were seen alone at least once, while only 25 out of 1535 plains zebra males over age 2 (1.63%) were seen alone.

Shannon diversity index values for the proportion of time seen in each status category were higher for hybrid males than for plains zebra males in both the subadult (ANOVA: $F_{1,15}$ ¼ 4.902, $P < 0.05$) and adult ($F_{1,15}$ ¼ 44.024, $P < 0.0001$) age classes. In addition, the diversity values for hybrids were higher in the adult age class than in the subadult age class ($F_{1,13}$ ¼ 15.296, $P < 0.002$), while there was no difference between the diversity values for subadult versus adult plains zebra males ($F_{1,17}$ 0.117, P ¼ 0.7366; Fig. 2).

Comparisons between hybrid and plains zebra males for the proportion of sightings in each status category showed that for subadults, hybrids were seen as bachelors less often (Wilcoxon: H ¼ 5.962, P ¼ 0.015) and seen as satellite males more often (H ¼ 5.416, P ¼ 0.020) than plains zebra males, and that there was no difference between the two in proportion seen as challengers (H ¼ 0.203, P 0.652; Fig. 3). For adults, hybrids were seen as bachelors (Wilcoxon: H ¼ 8.324, P ¼ 0.004), challengers (H ¼ 9.164, P ¼ 0.003) and alone (H ¼ 11.735, P ¼ 0.0006) more often than plains zebra males. Plains zebra were seen as stallions more often than hybrids were (Wilcoxon: H ¼ 12.340, P ¼ 0.0004), but there was no difference between the two in the proportion seen as sat- ellites (H 1.429, P 0.23; Fig. 4). ¼ ¼

Hybrid males also switched status more frequently than plains zebra males (Fisher's exact: $P < 0.0001$). For pairs of consecutive sightings within 1 month of each other, hybrid males changed status 41 times and did not change status 60 times. Plains zebra males, in contrast, changed status only 4 times and did not change status 572 times. In addition, although the number of 'change' to 'no change' events varied among individuals, 8 of the 10 hybrids (for which we had consecutive sightings after leaving the natal harem) changed status at least once, while only 3 of the 13 plains zebra males did so (Fisher's exact: P ¼ 0.0123).

In 2013, we noticed that several male hybrids appeared to have established territories that they patrolled, often alone, similar to Grevy's male behaviour. Camera traps set up for a separate project by J.S. confirmed that these males were frequently alone and each stayed within a defined spatial area. Each of these males was also seen on at least one occasion aggressively chasing plains zebra bachelor males that were on their territory (as in the camera trap photo in Fig. 5). Five hybrid males established territories. One of these males maintained the same territory for over 2 years. Two of these males established a territory shortly (within 1 year) after leaving their natal harems. After determining the outcome for each adult hybrid male, five were classified as territorial Grevy's zebra-like, eight as plains zebra-like and one as intermediate. The males

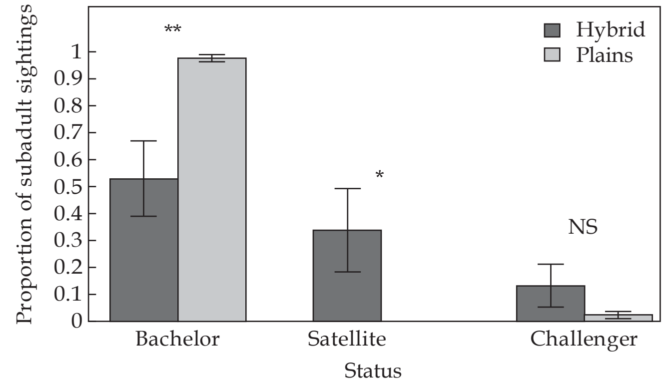

Figure 3. Proportion of sightings in each status category for hybrid and plains zebra subadult males. *$P < 0.05$; **$P < 0.02$.

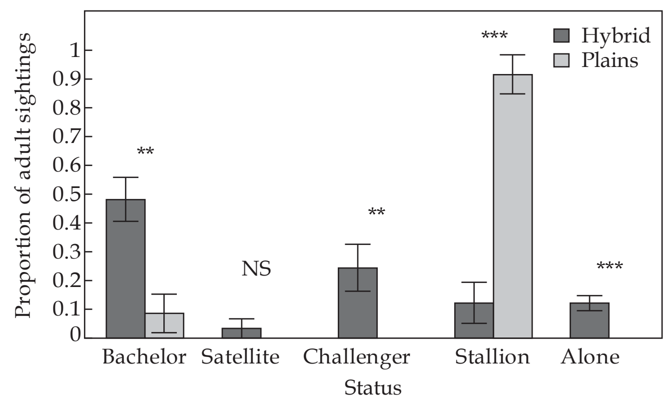

Figure 4. Proportion of sightings in each status category for hybrid and plains zebra adult males. **$P < 0.005$; ***$P < 0.001$.

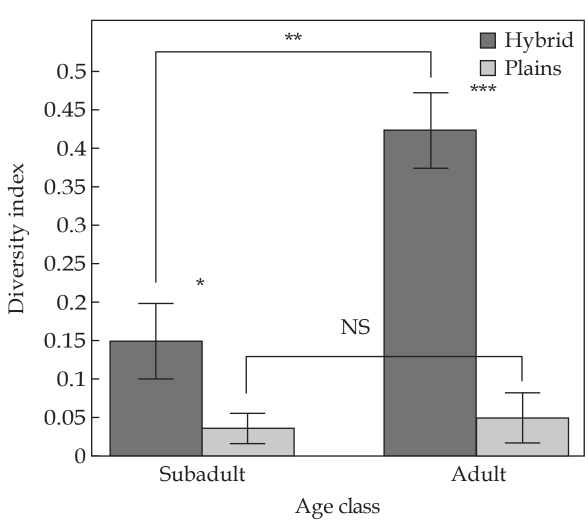

Figure 2. Diversity index values for the proportion of time seen in each status class for hybrid and plains zebra subadult and adult males. *$P < 0.05$; **$P < 0.005$; ***$P < 0.001$.

Figure 5. Camera trap photo of a hybrid male defending his territory by chasing away a plains zebra bachelor male.

in these three outcome classes differed significantly in the number of sightings in each of the five status categories ($\chi^2_8 = 38.05$, $P < 0.001$; Table 1). Differences between the observed and expected numbers of observations in the satellite and stallion categories accounted for most of the chi-square value. Territorial males were never seen as satellites or stallions.

Hybrid males and females also stayed with their natal harems longer than plains zebra. Six of seven hybrid males stayed with their mothers to age 3 or older (85.71%), while only two of 45 plains zebra males (4.44%) did so (Fisher's exact: $P = 0.0001$). One hybrid male even stayed with his natal harem to age 5. We had a smaller sample size for females. We were only able to determine age of emigration for two hybrid females (one F1 and the single B1 backcross female), but both of these females stayed with their natal harems to age 3 . Only 3 of 16 plains zebra females (18.33%) stayed with their mothers past age 2. Despite such a small sample, this suggests a tendency for juvenile hybrid females to also remain in their natal groups longer than their plains zebra counterparts (Fisher's exact: $P = 0.0654$).

On 15 October 2014, we observed the formation of a novel and unique group of zebras. Two adult hybrid males formed a harem with the B1 hybrid female and one plains zebra female. In examining the life histories of these individuals, we noted that both of these hybrid males were classified as plains zebra-like and not territorial. We also noticed that these two hybrid males had interacted in the past. In 2010, the older hybrid male was a satellite to a plains zebra stallion in charge of the harem in which the younger hybrid male was a juvenile. After leaving this harem as a satellite, the older hybrid male was subsequently seen as a lone stallion twice, taking over a harem, but each time only keeping it for a day or two. The younger hybrid male left his natal harem in 2012 and was seen as a bachelor and challenger before forming this new group. In this new group, the younger, 6-year-old hybrid appeared to be the dominant male, herding the females and aggressively displacing the other male if he got too close to the females. The older, 10-year-old hybrid male appeared to be a satellite to the younger hybrid. The B1 female hybrid and the plains female in this group have been together since 2008. This is the first known instance of adult hybrid males taking over a group with an adult hybrid female in it. However, on 3 December 2014, these females were sighted with a new plains zebra stallion and without the two hybrid males. Therefore, this group appears to have persisted for fewer than 7 weeks in total.

DISCUSSION

At first glance, hybrids seem superficially integrated into plains zebra society. However, we discovered a number of important behavioural differences between hybrids and plains zebra. The expression of Grevy's zebra-like behaviour by hybrids suggests that behaviour is not the result of only environment or socialization in these hybrids. We believe this supports our general hypothesis that genetics do play a role in affecting hybrid zebra behaviour, independent of social learning. By examining the differences between hybrids and plains zebra more closely, we can begin to get an idea of the relative strengths of environmental versus genetic cues and explore the interaction of these cues through time across development and maturation.

The data on females appear less complex than those for males and we believe they support the prediction that hybrid females show behaviour intermediate to the two parents. Our main finding for females was that while hybrid females were all members of harems with plains stallions, hybrid females were significantly more vigilant than plains zebra females. Hybrids in fact showed vigilance rates equivalent to Grevy's females. Plains zebra females join harems in order to gain material benefits associated with enhanced feeding (Rubenstein, 1986, 1994). Females can enhance feeding by decreasing the amount of time they must spend vigilant, not only for predators, but for bachelor males and neighbouring stallions that harass and attempt to mate with them. To prevent harassment, plains females bond to a male who assumes the responsibility of guarding the females by chasing off intruding males. This gives females extra time for grazing, which enhances their reproductive success (Rubenstein, 1986, 1994). Grevy's zebra females, on the other hand, do not form long-term bonds with males. Differences in resource needs between lactating and nonlactating females prevent stable groups of Grevy's females from forming (Rubenstein, 1986). Instead, Grevy's males establish territories around valuable resources and attempt to mate with all females that pass through their territory (Rubenstein, 1989, 1994). Therefore, Grevy's zebra females do not have the benefit of a harem male to assume vigilance duties, and thus, they show higher vigilance rates than plains females. Even though we observed hybrid females in harems with plains zebra stallions, genetic influences from Grevy's genes may be influencing their vigilance levels more than the environment. Socialization seems not to have modified the vigilance behaviour of hybrids to bring them into line with their plains zebra peers. Hybrids were often spotted in the centre of groups, not marginalized to the edges where there may be higher predation risk. Therefore, the higher vigilance level in hybrid females does not appear to be the result simply of their physical position in the group. From our current data set, we do not have enough information to determine whether behaviours change through time in females. This would be an interesting follow-up study.

While differences between hybrid and plains females are subtle, male hybrids display significant differences from male plains zebra in the trajectories they take to adulthood. These differences again support our general hypothesis that environment alone is not the sole determinant of behaviour, and that genetics can have a significant effect. For example, hybrid males were seen alone more often than plains zebra males. This is a behaviour characteristic of Grevy's zebra males who are often alone patrolling their territories or wandering in search of females. One potentially confounding factor is whether the phenotypic appearance of male hybrids may affect their 'social acceptance'. In other words, are hybrid males alone more often due to their own behaviour or due to diminished acceptance by plains zebra bachelors? We believe that the former explanation is more likely for several reasons. First, there were no significant time budget differences between hybrid and plains males when in bachelor groups. Both behaved similarly when together as bachelors. In addition, hybrid bachelor males fought with plains bachelor males on numerous occasions, as plains males do with each other to establish dominance hierarchies, and both males always remained in the bachelor group at the end of fights. This is typical behaviour of plains bachelor males where both in- dividuals return to the group at the end of a fight regardless of who is the winner and who is the loser. We did not ever witness plains

Table 1
Number of sightings in each status category for plains–Grevy's hybrid male zebras in three outcome classes

Outcome	N	Stallion	Satellite	Challenger	Bachelor	Alone
PZ-like	8	9	44	44	65	12
Territorial GZ-like	5	0	0	23	35	5
Intermediate	1	0	0	14	20	3

PZ: plains zebra; GZ: Grevy's zebra. N = number of individuals in each outcome class. The three outcome categories differed significantly from each other ($\chi^2_8 = 38.05$, $P < 0.001$).

males attempt to 'kick out' a hybrid from the bachelor group. Also, from the life-history data we know that several hybrid males were in consistent bachelor groups with the same individual plains zebra males for several months to a year. This indicates that plains males do tolerate hybrids. Therefore, it seems more likely that hybrid males choose to leave bachelor groups and wander alone rather than plains males refusing to accept hybrids into groups.

While hybrid males resemble hybrid females in displaying Grevy's behaviour, for males there is also evidence of behaviour changing over time. First, hybrids had significantly higher Shannon diversity values in both age classes (subadult and adult) than plains males. This indicates that hybrid males are seen in a wider variety of states than plains zebra males of a similar age. Moreover, the diversity values of hybrid males were significantly higher in adults than in subadults, but there was no such difference between plains adults and plains subadults. This suggests that plains zebra males transition from one state to another as they mature from subadult to adult. Grevy's males also generally transition as they mature, from a bachelor to a territorial male. This is the only known route to adulthood in Grevy's males (Ginsberg, 1987). Once a Grevy's male becomes a territorial adult, he usually remains in this state. Of 54 known territorial Grevy's males whose fate had been followed for 4 consecutive years between 2010 and 2013 on Mpala, only one (<2%) switched from territorial back to bachelor (and then became territorial again). All others remained territorial once they transitioned to being territorial. Hybrids, on the other hand, expanded their repertoire of states and continued to be seen in many different states as they aged. No canalization with age appears to occur in hybrids.

Hybrid males also changed status more frequently than plains zebra males. Examination of group compositions across consecutive sightings showed that hybrid males did not often appear with stable groups in the long term, but wandered from group to group. One interpretation of these results is that this represents the consort-inspect-mate-leave type of behaviour typical of Grevy's males searching for females, or what we will refer to as the 'Grevy's mating cycle'. However, another possibility is that hybrid males may be contending with conflicting social–environmental and genetic cues causing them to oscillate between plains zebra-like and Grevy's zebra-like states. We believe the latter may be a more likely explanation because of the timescales involved and the types of associations that hybrids do form, if only temporarily. Transitions through stages in the 'Grevy's mating cycle' usually happen over short timescales on the order of minutes to days. While hybrid males do change state more frequently than plains zebra males, these state changes are interspersed with periods of weeks to months where they remain with a group of plains zebras and appear to be an integrated member of the group. This is especially true of hybrid males who join harems as satellite males, a behaviour not seen at all in Grevy's males.

Hybrid males were also seen as satellites much more often than plains zebra males. Five of the 15 hybrid males (33%) were observed as satellites to one or more harems with plains zebra stallions, while this behaviour was rare among plains zebra (<1%). This type of coalition illustrates how dominants sometimes offer concessions to retain the services of subordinates. However, work with feral, free-ranging horses (where the proportion of subadult males who become satellites is ~10%) has shown that harems headed by single males are always dominant to those led by two males, and males that are the sole harem leaders sire more total offspring and have higher yearly siring rates than males in dual-male harems (Rubenstein & Nuñez, 2009). Therefore, allowing a secondary male to join the harem represents a cost–benefit trade-off to the dominant. For a subordinate it provides an alternative route to early reproduction even if it means initiating more of the fighting than the dominant stallion.

If this behaviour is rare among plains zebra, and nonexistent in Grevy's, why does it occur at a fairly high rate in hybrid males? The size difference between hybrids and plains may be one factor. Hybrid males are physically larger than plains zebra males, and we observed several instances of hybrid bachelors winning fights with plains bachelors. Therefore, one reason a plains zebra stallion may let a hybrid male join his harem is that the hybrid acts as a deterrent to bachelors who may try to take over the harem. The plains stal- lion, because of his smaller size, may also simply be unable to prevent the hybrid from joining. However, the benefit to a hybrid male of joining an existing harem as a satellite male is less clear. On the one hand, their large size relative to that of subadult plains zebra males may make it easier to share copulations with the stallion. On the other hand, the physical superiority of the hybrid male should make taking over a harem by himself easier than for most plains males. One possible explanation for a hybrid joining a harem, but not displacing the harem stallion, is that the influence of his Grevy's zebra genetic background may be providing a conflict- ing signal. Social cues learned while associating with plains zebra males should cause the male to attempt to take over a harem of females and, if successful, to stay with them and guard them. However, Grevy's males do not form long-term bonds with females. Instead, they inspect and attempt to mate with all oestrous females they encounter. When females are not in oestrus, Grevy's males simply inspect them and let them leave, and then the males return to searching for females with whom they can mate. Because of these conflicting tendencies, hybrids may be less likely to form long-term bonds with females, which would allow them to main- tain their own harems.

This hypothesis of conflicting cues may also help explain why hybrid adults were seen as stallions much less often than plains adult males. Hybrid males do sometimes succeed in taking over harems of plains zebra females, but they do not keep them for more than a few days. On numerous occasions, we have observed hybrid males challenging plains stallions (e.g. parallel walking, kicking, biting and chasing) and trying to interact with harem females. At least four hybrid males over eight sightings appeared to be the sole stallion of a harem, but in every case, the next time the male was sighted he was no longer with the harem and appeared to be a bachelor or challenger again. This indicates that these males either voluntarily left the harem, were forced out, or were ignored or not encouraged by the females to remain. Although the role of female choice cannot be ruled out, we currently have no evidence from our observations that plains females actively shun hybrid males that take over their harem or that they treat them differently from plains zebra stallions.

In October 2014, we observed the formation of a harem composed of two adult hybrid males, one hybrid female (the B1 female) and one plains female. This group is interesting for several reasons. First, the two hybrid males did not appear to be equal leaders of this group, but one male seemed to be dominant while the other was acting as a satellite. This group remained together for almost 2 months, which is the first time a harem headed by a hybrid male persisted longer than a few days. We do not know why this new group was able to persist. Perhaps the pairing of two male hybrids together allowed them to maintain control of the two fe- males in their harem, while single hybrid stallions are unable to do so. Alternatively, the dominant hybrid male in this group, because of his unique genetic make-up or his particular socialization as a juvenile, may possess more of the plains zebra skills or behavioural tendencies necessary for maintaining a harem. However, by 3 December 2014 this harem had dissolved. While many plains stallions retain control of the same females for years, this hybrid harem lasted fewer than 7 weeks, indicating that this pairing of hybrid males was still unable or unmotivated to maintain a harem in the long term. We do not know whether the hybrid males chose to leave the females or were outcompeted by a plains challenger, or whether the females voluntarily left and chose a new stallion.

This unique harem is also the first and only time to date that adult male and female hybrids have formed a harem together. Until 2014, adult hybrids were only seen to actively interact with other adult hybrids of the same sex. Hybrid males and females were sometimes in proximity to each other when in large herds of multiple harems, but adult hybrid males did not appear to show any interest in hybrid females, or vice versa. The reasons for this are unclear. It is possible that socialization in the plains zebra society led hybrids to develop a search image for plains zebra mates, pre- cluding opposite-sex hybrids as potential mates. Although this new hybrid group seems to challenge that thinking, the one female hybrid in this group was the backcross B1 hybrid, which was somewhat more plains zebra-like in appearance and, therefore, may still fit a ‘plains zebra’ search image.

In contrast to the harem-type behaviour discussed above, five hybrid males behaved like adult Grevy's males by establishing and defending territories. This shows that genetic influences can actually trump socialization in some instances. However, not all hybrid males are territorial. This suggests a bifurcation of routes, with males generally following one of two paths: plains zebra-like or territorial Grevy's zebra-like. The strategy a male adopts could be the result of genetics alone, or may be the product of a gene×environment interaction. Genetic make-up may ‘predispose’ individuals toward one path or the other, or cause them to oscillate between the two early in life, but positive or negative reinforcement during social interactions may also be important in affecting the eventual outcome. Some individuals seemed to adopt one behavioural route over the other fairly early in life. For example, we know that two of the males who established territories did so within a year of leaving their natal harems. However, feedbacks from social learning during maturation may also be an important component of determining future behaviour. As seen in Table 1, none of the hybrids observed as satellite males went on to establish territories. These males may simply have had a genetic make-up more predisposed towards plains zebra-like behaviour. But joining an existing harem as a satellite may have also provided reinforcement to behave as the harem stallion does, and not go on to establish a territory. Alternatively, any negative reinforcement that hybrids receive when displaying plains zebra-like behaviour may push them more towards a Grevy's zebra-like state.

We also note that both male and female hybrids tended to stay with their mothers and natal harems to age 3 or older, a behaviour that differs from both of the parental species. We found that plains zebra in our study population usually emigrated as yearlings or 2-year-olds. Previous work on plains and Grevy's zebra found that the average age of dispersal for plains juveniles was 19.6 ± 3.9 months of age and even younger for Grevy's zebra at 12.4 ± 0.8 months of age (Becker & Ginsberg, 1990; Ginsberg, 1987). Therefore, our observation that hybrids stayed with their natal harems longer than did either parent represents a novel behaviour, different from what would be expected by environmental or genetic cues (Rubenstein & Hack, 2004), and different from what has been found in studies of other hybrid populations.

In baboons, age of maturity and dispersal in annubis×cynocephalus male hybrids are intermediate between the two parental species and are advanced relative to yellow baboons in proportion to the degree of annubis ancestry. For females, the philopatric sex, hybridity has a much smaller effect on maturation than do maternal factors and environmental conditions (Charpentier, Tung, Altmann, & Alberts, 2008). The fitness benefits of earlier sexual maturity can be great. Although the baboon hybrids mature earlier than yellow baboons, heterosis, or hybrid vigour, is unlikely to be the mechanism underlying selection for the attainment of early maturity since hybrids do not mature earlier than both parental species. It is much more likely that the hybrids represent an intermediate fitness phenotype that has an advantage over the cynocephalus, but not the annubis, parental species. For equids in general, both sexes disperse from their natal groups, so an early onset of sexual maturity would potentially provide fitness benefits for both males and females. In our plains×Grevy's hybrids, both males and females showed delayed time to dispersal, suggesting either some form of negative heterosis (hybrid disvigour), a difference in hormonal maturation, or some process making it difficult for hybrids to reach certain socialization milestones.

The reason for staying with the natal harem longer is not clear, especially for males. Hybrids grow taller than plains zebra, and male hybrids reach a size that should allow them to compete well in fights at a younger age than plains zebra males. Three-year-old hybrid males exhibit variable behaviour when they are still in their natal harems. One 3-year-old male left his natal harem for up to several hours at a time to fight with plains zebra bachelor males, but then returned to his natal harem. Another 3-year-old male stayed with his mother in his natal harem and was never seen to fight with bachelor males. Perhaps hybrid males stay in their natal harems longer because conflicting genetic and environmental influences make them unsure of the best route to take to adulthood. In a proximate sense, conflicting feedbacks may prevent males from reaching threshold reinforcement levels for adopting either behavioural option. Joining a harem as a satellite male can also be thought of as delaying independence, which may be another reason why we see a fairly high occurrence of this behaviour among hybrid males.

The benefit of remaining longer with the natal harem for female hybrids is also unclear. Because of our low sample size of females, we cannot be completely sure whether this is a consistent pattern of behaviour in females as it is in males. Data on age of dispersal for additional hybrid females may help clarify this question. Interestingly, of the two females that were known to stay with their mother to age 3, one was the single backcross individual. While a sample size of one does not reveal a pattern, the age of dispersal for this backcross female seems to match the F1 hybrids. Additional backcross individuals would be needed to determine whether backcross individuals do disperse at an age similar to F1 hybrids or perhaps at an age intermediate to hybrids and plains zebra.

In conclusion, we believe our data support the hypothesis that the behaviour of hybrids is not determined by environment alone. Plains×Grevy's zebra hybrids showed behavioural phenotypes that contrast with what we would predict if the social environment were the only factor shaping behaviour. In some cases, hybrid behaviour was intermediate to the two parents, in other cases it more closely resembled one parental equid type or the other, and in the case of age of dispersal, it differed from both parental species. However, at least for males, behaviour also does not appear to be the result of only genetics. Behaviours are not set from birth but can change over time, and we suspect they may be modulated by positive and negative reinforcement, suggesting a strong gene×environment interaction. Therefore, we believe that it is this interaction of genes and environment over time that ultimately shapes behaviour of many hybrids.

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