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

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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–Grevy's zebra hybrids (*Equus quagga* × *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 animals, 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–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 introgression 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 behaviour 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

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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 subadult 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).