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Social Structure, Vigilance and Behaviour of Plains Zebra (*Equus burchellii*): a Five-Year Case Study of Individuals Living on a Managed Wildlife Reserve

Short Title: Behaviour of Individual Plains Zebra

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ABSTRACT

Most studies of plains zebra (*Equus burchellii*) have focused on population ecology and have not included long-term observations of identified individuals. Over a five year period we studied the crepuscular activities of 13 individual zebras within a focal group held within a managed game reserve. We also examined individual residency within the group by recording births, mortalities and longevity of group membership by adults. Residency of individuals living in other groups on the reserve was similarly monitored to examine variability in social structure within this closed population over an extended period of time. Stable, female groups were the mainstay of group sociality with male mean residency at 31.6 months being variable in length or even absent. Social interactions across all categories of zebra were free from aggression. Despite an absence of non-human predators, the proportion of dusk time-budget allocated to vigilance was high, at 41% for males during periods when they accompanied stable female groups and 12% for females during these same periods. Female vigilance increased significantly to 19% when males were not resident. Females spent 70% of the time grazing and males just 36%. Due to its long-term nature, we concluded this study established a base line for plains zebra activity that could assist in understanding the factors that influence the successful management and conservation of healthy populations.

Keywords: Behaviour; hunting; social structure; vigilance; zebras.

INTRODUCTION

Much has been learnt about the social organisation and population ecology of plains zebra (*Equus burchellii*) in the wild (Fischhoff et al. 2007a; Fischhoff et al. 2007b; Fischhoff et al. 2009; Gasaway et al. 1995; Georgiadis et al. 2003; Grange et al. 2004; Klingel 1969a; Klingel 1969b; Rubenstein 1994; Rubenstein and Hack 2004; Smuts 1976a). The highly flexible and dynamic social organisation of this species may be a response to solving challenging and unpredictable social and ecological problems such as resource availability and risk of predation (Rubenstein and Hack 2004). A two-tiered social organisation has been reported: a long-term core group social structure of one-male-to-many-females (other males form all male groups) and a more unstable and transient herd pattern when groups become loosely affiliated for hours to days (Fischhoff et al. 2007a). Some studies have focused on aspects of reproduction (Klingel 1969b; Smuts 1976b; Ncube et al. 2011) whilst others showed core stable groups may provide females with protection from harassment by other males with increased chances of reproductive success (Rubenstein 1994).

Separately, captive zebra populations have been examined by Andersen (1992); Ford and Stroud (1993) and Schilder and Boer (1987), the latter comparing the social organisation, time budgets and reproduction of zebras in safari-parks with Klingel's (1967) data collected for wild zebras. Some similarities in both social organisation and time budgets of captive and wild zebras were noted but conclusions were limited by paucity of data and stressful methods of food provision for the captive population. Other studies have found social factors can influence the reproductive success of plains zebras in zoos with higher-ranked females having shorter inter-birth intervals than those of low-rank (Pluháček et al. 2006) and males newly-introduced to breeding females more likely to show infanticide than fathers (Pluháček & Bartoš 2000).

Pluháček and colleagues (Pluháček & Bartoš 2000; Pluháček et al. 2006) were able to study known individual animals in the zoo environment but to our knowledge, there are no long-term

observations of the behaviour of individual plains zebras living in the wild. Where studies of wild individual zebras have been undertaken, they have been short-term (three month study; Neuhaus and Ruckstuhl 2002) or have focused on specific aspects of behaviour (movement patterns; Brooks and Harris (2008) or reproductive state and leadership; Fischhoff et al. 2007a) or on groups where not all of the individuals were identified (Neuhaus and Ruckstuhl 2002). By contrast, longitudinal studies of individual African elephants (*Loxodonta africana*) (Moss 2000) and chimpanzees (*Pan troglodytes*) (Williams et al. 2002) have brought nuanced insights into social behaviour, revealing characteristics undetected by population-level studies. For example, incompatible social organisational models were ultimately harmonised by subsequent studies that showed the space use patterns of individual females were influenced by both feeding competition and male territorial behaviour (Williams et al. 2002). Long-term studies of individual zebra could similarly help to develop accurate models of social behaviour.

A need for such data is further emphasised by the trend towards declining plains zebra populations (Hack et al. 2002) with continued habitat destruction and hunting likely to lead to an increasing proportion of the world's zebra being kept on reserves. Studying reserve-kept zebra is therefore directly relevant to conservation efforts, with exploration of the factors that influence costly activities, such as vigilance, having particular relevance. Zebra vigilance strategies have been documented in habitats where predators such as lion are resident (Fischhoff et al. 2007b; Mills and Shenk 1992; Valeix et al. 2009) but not in habitats where large predators are absent. It has been argued that the prime cost of vigilance is a time opportunity cost such that high vigilance activity reduces the time available for alternative behaviours such as foraging or sleeping (Caro 2005). Accordingly, where no salient predators occur, it should be adaptive for vigilance to decrease. In contrast, others have argued that there is little cost involved in predator-detection and therefore it makes no sense to jettison this capability (Coss et al. 1993). Both views are represented in studies that reveal great variation in the extent to which anti-predator strategies have been retained in predator-free environments (Blumstein 2002; Byers 1998). There is currently insufficient information on the costs of vigilance in zebra to predict how they might adapt to a reserve free of large predators.

Male ungulates are usually more vigilant than females (Burger and Gochfeld 1994). One reason may be (as has been proven in many species) that females have greater energy requirements for themselves and their offspring so they tend to prioritise foraging (Clutton-Brock 1991). Males, with lower feeding pressures, might therefore be able to allocate more time to vigilance, potentially enhancing their reproductive success by protecting both their investment in their existing offspring and future mating opportunities. Although higher bite rates during grazing in lactating females can mitigate some of the energetic costs of reproduction (Neuhaus and Ruckstuhl 2002), female Grevy's (*Equus grevyi*) and plains zebra appear to benefit additionally from the presence of vigilant males (Rubenstein and Hack 2004). These studies were undertaken in reserves where large predators were present and where costs of failing to maintain anti-predator vigilance could be disastrous. However, little is known about sex difference in vigilance behaviours under conditions where large predators are absent.

Our aim was to provide information about the social structure, group residency and crepuscular activities of individually-identified wild zebras living on an extensive managed reserve with no resident large predators. Because the reserve was fenced with no migration possible, we could examine a closed population over a five-year period. Vigilance activity of a focal group was studied to determine the amount of time allocated to this anti-predator activity. If vigilance remained a prevalent behaviour in this environment, we predicted that adult males would allocate more time to this activity than adult reproductively-active females with greater energy requirements.

MATERIALS AND METHODS

Ethics Statement

This observational study of Plains zebra was approved by the University of Bristol ethical review group (UB/09/031). The zebra were undisturbed by our observations which were conducted from within a vehicle parked at a distance of at least 700m using *Nikon 8 x 50* binoculars.

Field site

The zebras were resident on a 4200 ha, fenced private wildlife reserve, Moolmanshoek, in the Orange Free State, South Africa (GPS 28 37'58 S and 27 59'56 E) in an area of both historical and current distribution of plains zebra. The reserve was part of the Clarens Formation, a mixture of savannah plains (at altitudes of approximately 2400 m) and mountains (up to altitudes of 3 200 m). The mountains comprised mudstone and sandstone topped with volcanic basalt which produced the highly fertile soil of the grass plains. The reserve contained flora and grasses of the southern African Highveld type (a combination of palatable, nutritious 'sweet grasses' and bitter, less nutritious 'sour grasses') and the rare Fynbos biome, with the latter occurring only at elevations of over 3 000 m. As the reserve was located in a high rainfall area, food resources were abundant and water, from mountain streams, was accessible throughout the year. Other large herbivorous mammals resident included black wildebeest (*Connochaetes gnou*), blesbuck (*Damaliscus pygargus*), springbuck (*Antidorcas marsupialis*), mountain reedbuck (*Redunca fulvorufula*), common eland (*Tragelaphus oryx*), oryx gazelle (*Oryx gazella*) and red hartebeest (*Alcelaphus buselaphus*). Medium-sized predators in the form of black-backed jackal (*Canis mesomelas*), serval (*Felis serval*), caracal (*F. caracal*) were all resident on the reserve and although these were unlikely to be a threat to healthy adult zebra, black-backed jackal in particular were a potential threat to neo-natal foals. Leopard (*Panthera pardus*), African lion (*P. leo*) and spotted hyena (*Crocuta crocuta*) all occurred previously in the area but had been locally extinct for decades.

Study period

Between October 2004 and 2009, the zebra were studied during 16 blocks spread across different months of the year. Blocks were defined as periods variable in length in which both identification of zebras and observations of their activities were made, with the shortest block being 7 days and the longest 72 days (Table 1). Information on group social structure and residency was obtained in all blocks, with behavioural observations taken during 10 blocks.

Study subjects reserve population

An initial group of seven zebras had been introduced to the reserve in 1993 with two further groups added during the next three years. No information was available for these groups. At the commencement of the study, 32 zebras were resident with a female: male ratio of approximately 4:1. The skewed ratio had occurred because between approximately 1995 and 2004, male zebras of two years and older had been targeted for trophy hunting. As a result, only six males had survived. The remaining 26 zebras comprised adult females with offspring of three years of age or less. A moratorium on trophy hunting of zebra commenced six months prior to the start of this study in 2004 although other large male mammals continued to be hunted. The hunting practices on the reserve occurred throughout the year (peaking in the winter months at a frequency of approximately three days out of seven) and throughout the area with some hunting parties having a profound effect on the movement of the zebras, for example, when hundreds of animals were killed in one night.

At the start of the study, the zebra were distributed in three nursery groups and one all-male group. Defining a group can be difficult because individuals can be found at varying distances from each other or can stray from the group or be only loosely attached (Caro 2005). We therefore defined a nursery group as a group of three or more adult mares sighted together more than 70% of the time accompanied by their offspring, attended typically, but not always by a male, and who performed their behavioural activities within a radius of less than 20 m of each other. We chose the term 'nursery group' rather than harem (after Rubenstein and Hack 2004; Fischhoff et al. 2007a) to avoid any anthropomorphic connotations that female behaviour might be coerced and to reduce the implicit risk of bias in interpretation of behaviours of both sexes. Despite the initial biased sex ratio, at the beginning of the study all nursery groups were accompanied by a resident male.

All-male groups were defined as a group of two or more males who were approximately three years of age or older sighted together more than 70% of the time and who performed their behavioural activities within a radius of less than 20 m of each other.

Zebras were individually identified by making photographic records of their left and right sides. Photographs were taken from a vehicle positioned at a distance of at least 700 m from the group so as to give a clear view of the majority of the individuals in a social group but without disturbing the animals. Where individuals were obscured or only partial photographs could be taken, these were retained until improved versions could be obtained in later visits. In this way, over time, the entire population of zebras on the reserve was identified and a clean, unobscured set of photographs of both sides of all individuals was achieved. This complete accuracy of identification in all samples allowed for the activities of specific individuals to be monitored as well as the recording of movements of individuals with respect to group residency. It also allowed for individuals to be recognised on sight so that fast identification of individuals, sometimes observed in unexpected places, could be made. Individual sex was either deduced in heavily pregnant mares and those with foals at foot, or based on observation of urination posture.

Maternal relationships (through suckling interactions with no allosuckling observed) were identified in over 90% of cases (those whose maternal relationship was not identified included young males that were in the process of dispersing at the start of the study). Group composition and longevity of residency within the nursery groups was recorded. A proportion of foals that died were investigated post-mortem for cause of death.

Study subjects focal group

The focal group was chosen originally for relative ease of identification of the original adult male associated with this group. As for the general study, we recorded variations in the social make-up of this group and longevity of residency of individuals but additionally we recorded the crepuscular activities of 13 of the group members (two adult males, four adult females, seven foals of which one was female and six were male).

The focal nursery group initially comprised a stable group of three adult females. Over the period of the study, this was augmented by two daughters (one of these dispersed to a different nursery group) and a newly arrived female who joined from another group, their offspring and the variable presence of one, two or no males. As all individuals were identified, we could be certain when males had left a group because before commencing an observation session, we were able to locate them elsewhere. Paternity was not assessed but maternal relationships were identified in 100% of cases within the focal group.

Lead and second-lead females were identified in the focal group. Following Petit and Bon 2010, we defined leadership in terms of individual ability to cause other group members to follow in a single-

file walking pattern as previously used in studies of plains zebra (Fischhoff et al. 2007a) and horses (Waring 2003). When an individual at one end of the group (the front or the back) consistently took the lead either by initiating uni-directional movement forwards, or by causing the group to turn around and then move off uni-directionally in an opposing direction (in the case of a female positioned at the back), then they were identified as leaders. In this focal group, the lead female initiated movement first more than 90% of the time whilst the second-lead female usually positioned at the opposite end of the group, took the lead in commencing movement approximately 10% of the time. Remaining females in the group were typically centrally positioned and were rarely successful at initiating group movements themselves (approximately 0.001% of total group movements observed).

Focal group activity

Activity data were collected at dusk, a period recognised for peak activity in wild and feral equids (van Dierendonck et al. 1996). It was also apparent from our pilot observations that the zebra were more active at dusk. The behaviour of pre-selected individuals in the focal group was continuously recorded during 30 min. observation sessions (between one and eight per day) conducted at dusk between 16:00 and 19:00 h. The temperature was recorded once at the beginning of each session using a vehicle-mounted thermometer. At this high altitude mountain reserve, daytime temperatures remained stable throughout the year without the seasonal highs experienced in the summer in other parts of South Africa. Male presence or absence was also noted once at the beginning of a session.

Selection of order of observation of individuals was based on whether a clear view was likely for the session. Vigilance activity was defined as occurring when an individual animal was stationary, alert, with its head raised and scanned the surroundings. The duration of 18 other activities was also recorded so that the investment of time in vigilance by an individual could be measured against its other activities. These included: graze, suckle, walk, trot, canter, stand rest, lie alert, lie rest, roll, vocalise, nuzzle, nip, object play, social play, flehmen, pandiculation, aggression and other (for example, yawning, galloping). The behavioural descriptions used by Nicol and Badnell-Waters (2005) were used to define the behavioural categories for this study. Data were collected over a total of 831 sessions (415.5 hours) with the number of observation sessions per individual zebra averaging 63.9 (sd 53.3).

Statistical analysis

There has been much debate about the degree of independence that is likely when observations are taken on animals living in groups, and how non-independence should be treated statistically. One approach is to acknowledge hierarchies in a dataset and to account for these using statistical methodologies (Knowles and Green 2002). Here we used the statistical package *MLwiN 2.2* (Rasbash et al. 2005) and built a base (random effects logistic regression) model that acknowledged the hierarchical structure of the dataset where repeated observations (sessions) occurred within blocks, and were taken of the same zebras. Hierarchical models allow each level of the hierarchy to be treated as a random, rather than a fixed effect. The model for the dependent variable grazing (for example) contained fixed terms based on the mean rate of grazing across all observations for the slope of the correlation between the variables, the intercept with the y axis, and the effect of ambient temperature. The random part of the model, e , an error term, denoted random variation in rates of grazing partitioned into components, between observations, blocks and individuals. In this way, dependence between responses due to repeated observations of the same individual was accounted for. Having accounted for this structure, the influence of the following independent categorical variables was examined. First, we examined the effect of role, where adult male was taken as the arbitrary reference category and the behaviour of adult males compared with that of

adult females or foals. Then we examined the effect of adult male presence, where the presence of an adult male was taken as the arbitrary reference category. The behaviour of all categories of zebra was compared during periods when at least one adult male was present and periods when no adult male was present. Adult male absence occurred either for one or more blocks or just for temporary periods within a block (Table 1).

RESULTS

Changes in population structure

Because the reserve was free of large predators and fenced, most adults survived the study period (excepting two) and none left the reserve such as can occur where migration is an option. By the end of the study, nursery groups had increased in number from three to seven and all-male groups had increased from one to eight. The mean number of individuals in the focal nursery group was 10.4 (range 8 to 12) with a mean for all nursery groups of 7.1 (ranges 3 to 14).

At the conclusion of the study, the numbers of zebra had increased from 32 to 87. Females gave birth to more sons than daughters so that the female: male ratio of the adult population altered substantially from 4:1 to 0.56:1. The focal group produced eight sons and three daughters.

Social structure of nursery groups

In each of the nursery groups, two or three adult females remained together throughout the study or, in the case of nursery groups that formed during the period, from the time they first emerged to the end of the study. Each group had one female leader and leadership was stable in that it was retained by these females across all groups throughout the period. During the five-year study period, nursery groups were variously unaccompanied by resident males or accompanied by either one or two resident males. The first observation of a group without a resident male occurred at the beginning of the second year of study; the second at the beginning of the third year and the last during the last three months of the study. The mean residency time for males was 31.6 months (range 11–60 months). Three out of seven groups were without resident males for a mean time of eight months (range 5–14 months). The focal nursery group was accompanied by one resident male for 59% of the time, by two or more resident males for 18% of the time and by no males for 23% time.

Offspring of both sexes dispersed between approximately two and three years of age. Fillies left the group only if their father was still the attendant, reproducing male with three (15%) remaining in their original group to reproduce with a new male.

When colts dispersed, not all joined male-only groups with five (18%) moving initially to a second nursery group for a period before finally joining other males.

Mortality rates of foals averaged 22.5% per annum with foals typically dying within three days of birth (except for the January to April 2007 birthing season where 80% of foals died across all groups). Six foals were subjected to post-mortem investigation where all were found to be male and free of disease and parasites. Some mothers lost foals for several years in a row whilst others lost only one during the study period or none at all (not all females became pregnant every year). As expected in an environment free of large predators and with generally abundant resources, overall mortality rates of adults were low at 2.3%.

Activities of focal nursery group

The number of sessions in which resident males were present or absent during activity observations is shown in Table 1. Significance of each factor was tested using z-tests, as shown in Table 2. The coefficients presented in Table 2 give the change in the duration (s) of each activity (and the s.e.) in comparison with the arbitrary reference category for that variable. No significant variation in zebra activity occurred at the block level. Rather, for all activities, the majority of variation in occurred at the observation period level, with the zebra being much more active in some 30 min observation periods than others. There were a number of significant effects of role (male, female, foal) but once this had been accounted for, individual zebras within roles differed only in their vigilance, grazing, walking and flehmen behaviour (Table 2).

The mean time spent in vigilance activity was significantly greater for adult males than for adult females or foals at 41% for males and 12% for females during periods when males accompanied nursery groups. Table 2 shows that on average females spent 543.8 s less time being vigilant in each observation period than males. In addition, there was a pronounced effect of male presence on the amount of time that females spent in vigilance activity. Although there was no overall effect of male presence or absence on levels of vigilance activity, this was because of significant interactions between the responses of the different groups. When absent from the group, males showed little change in vigilance activity, foals showed a slight decrease but females showed a substantial increase to 19% (Table 2).

Having allocated less time to vigilance, females were able to use this time in additional grazing behaviour, spending 577.9 s more than males in this activity in each observation period (Table 2). Overall, it is apparent that females spent 70% of the time grazing and males just 36% overall. Foals also spent significantly more time grazing than males (Table 2).

When males were absent, there was a tendency for female grazing to decrease by nearly 3 minutes in each 30 min. observation period but this did not reach significance.

There was no difference in the time spent stand resting by males, females or foals but there was a very strong significant effect of male presence. This was also the case for self-grooming behaviour. Males, females and foals all performed more resting and self-grooming behaviour during periods of male absence from the nursery group. However, this effect was most pronounced for the males themselves who seemed to use periods of absence from the nursery group as a time of rest and self-care. The significant interactions show that the increase in resting behaviour during periods of male absence was lower for females than males, and the increase in self-grooming during periods of male absence was less for foals than for males (Table 2).

Males performed more social play than females but males and foals did not differ from each other in the amount of social play performed (Table 2). Foals performed significantly more object play than males. Although foals did not trot significantly more than males (Table 2), a separate factorial analysis showed that they spent significantly more time trotting than females ($p < 0.005$). Foals also cantered more than males (Table 2).

Flehmen behaviour took up relatively little actual time but males performed this activity significantly more than females (Table 2). For other activities that comprised a small proportion of the time budget (drink, nuzzle, chin, lie rest, suckle, pandiculation, defecation), there were no significant differences between males, females and foals and no effects of male presence or absence (Table 3).

There was a complete absence of aggression by males towards females or foals nor was any demonstrated by females to males or foals. Stable social relationships were evident in the occurrence of nuzzling (Table 2) and mutual grooming behaviours but there were no significant differences between males, females and foals or effects of male presence or absence.

The dusk temperature throughout the study was relatively stable at 23.2 °C (s.d. 5.1) and no effects of temperature variation on activity were detected.

DISCUSSION

All nursery groups were characterised by long-term stability in female membership regardless of whether resident males were present or absent from the group. Such findings contrast with other studies that suggest bonds between females are weak (Rubenstein 1994; Rubenstein and Hack 2004). Stability of female bonds have been noted in captive zebras (Ford and Stroud 1993; Schilder 1992) and for up to two years in wild zebra (Klingel 1969a) so as far as we are aware, this study is the first to follow individually identified females within their groupings in the wild for a long-term period.

The development of stable female groups may serve a number of functions. In primates reduced aggression in the utilisation of clumped resources may be one function (Isbell and Young 2002). But in animals where food is dispersed, the shared protection of juveniles may be more important (as proposed for elephants in (Archie et al. 2006). Although stable female bonds in captive zebras have been noted (Ford and Stroud 1993; Schilder, 1992), the function of such bonding in wild zebra has not been previously explored, nor are we aware of any previous recording of the exact membership of specific nursery groups over an extended period because such groupings can only be monitored when the identity of all individuals in the population are positively known. The protection of juveniles may lie behind stable zebra female affiliations not least because male residence within a nursery group is often either temporary or missing so that zebra females, like elephants, may need to rely on each other most of all for successful rearing of young. Our observations of females in all nursery groups also showed that like elephants, leadership was retained by one female per group throughout the period (or from the point a nursery group emerged to the end of the period). Such stability of leadership contrasts with other studies that found leadership varied with lactation state (Fischhoff et al. 2007a) and it is likely that year-round abundance of food and water resources influenced our findings.

Although the social structure of zebras has been reported as one male-to-many-females (Klingel 1967; Rubenstein & Hack 2004), we found more variable configurations. Three out of seven nursery groups had extended periods where they were not accompanied by resident males or were accompanied by two or more (absence of males has been reported in captive zebras, Schilder 1992). All males left after extended, stable periods of accompaniment of a group so it is unlikely that the biased sex ratio was a major factor. Our study suggested that social structure and group residency is more complex than previously thought.

Females gave birth to more males and, although it is more costly to give birth to males than females (Clutton-Brock 1991), females may have been assisted by the abundance of food resources which helped them maintain body condition. Heavy rain resulting in muddy conditions may have played a role in foal mortality as inclement weather and not lack of food appeared to be associated with some deaths, particularly in 2007. Although we saw no direct evidence of infanticide, in captive populations high levels of abortion, feticide and the infanticide of foals less than two months of age occur when a new resident male joins a nursery group (Pluhacek and Bartos, 2000; 2006). We cannot rule out this possible influence on the mortality rate of late-term and newborn foals.

Most foals remained in their nursery group for two to three years. Some studies suggest offspring of both sexes leave their nursery group at either the point they reach critical body-mass (horses: Berger 1986) or approximately between one to four-and-a-half years of age (wild zebras: Klingel 1969). Rubenstein (1994) found that young males dispersed at two years of age to join male-only groups but in our focal group, some sons stayed with their mothers for up to three years and not all joined male-only groups immediately. Our initial findings suggest choice of the second nursery group may be influenced by the presence of a full sibling of either sex in that second group although this requires further investigation.

We expected that young females would leave the focal group in their second year also (Klingel 1967; Rubenstein and Hack 2004) but they did so only if their father was still the resident male. If a new male was resident, fillies stayed and reproduced with him. Similar behaviour was found in Cape mountain zebras (Penzhorn 1984) and in Camargue horses where females remained with their familiar female group unless their father was resident at the time of their first oestrous when avoidance of inbreeding became necessary (Monard and Duncan 1996).

Surprisingly, we observed no male aggression towards adult females, offspring or between adult males or females. In equids generally, there is contradictory evidence for nursery male aggression towards dispersal of sons and daughters with some studies suggesting offspring are chased out of the nursery group by their fathers (wild zebra: Klingel 1969; captive zebra: Schilder 1992) and others finding no support for this (Cape mountain zebras: Penzhorn 1984; horses: Berger 1986). We observed no aggression towards offspring either at dispersal or at any other time. Similarly, despite previous reports of adult inter-male aggression in equids (Berger 1986; Klingel 1967; Rubenstein and Hack 2004), we saw no inter-male aggression during periods of resident male change-over, or when two or more males accompanied the same nursery groups. Our males knew each other and in Camargue horses who also knew each other, aggression was reduced, though not completely absent (Duncan et al. 1992). We also observed no aggression by adult females, whether pregnant or lactating, despite other studies showing that females can be aggressive to protect their offspring (Berger 1986). These findings are very different from that found in this species in other contexts (Rubenstein and Hack, 2004; Schilder 1992) and to our knowledge, we are the first to report the absence of this behaviour over a long-term period.

Play was a regular feature for the foals of this particular nursery group as they manipulated twigs or stones with their mouths or by pawing them and also by showing advancing-and-retreating patterns with respect to the object as has been previously described in horse object play (Waring 2003). Social play has been widely observed in horses (Fraser 1992; McDonnell and Poulin 2002) but less commonly in plains zebras (but see Andersen 1992; Penzhorn 1984; Schilder and Boer 1987).

Despite the reserve being free of large predators, vigilance was a common activity during our observations taken at dusk. Vigilance has both a predatory and social component but the contribution of each may depend on context. Zebra are a favourite prey choice of lions (Funston et al. 2001) with foals frequently targeted (Mills and Shenk, 1992). Thus zebra are sensitive to lion presence and modify their habitat use to avoid meeting lions (Valeix et al. 2009) not least because such encounters can result in a 75% chance of turning into hunts (Mills and Shenk 1992). Thus it is unsurprising that zebras are highly vigilant in areas where large predators occur.

It is, however, less clear how zebra might respond to environments where large predators are absent. Potentially, it would be advantageous to reduce the time allocated to this costly behaviour (Blumstein 2002) but in the early years of this study, the biased sex ratio may have been a factor in high vigilance levels. Further, the presence of small to medium-sized predators on the reserve (and

the residual influence of the 'ghost of predators past'; Byers 1998) may have contributed to ongoing vigilance activity.

Although our zebras were not being directly hunted, they were frequently observed watching the hunting of other mammals from higher ground in mountain foothills into which they had moved to avoid hunting vehicles. Because no data exists regarding whether the introduced population had been subjected to hunting previously we were not able to measure whether vigilance had been held over from previous experiences. However, it is possible that the practice of trophy hunting of other mammals may have influenced the maintenance of vigilance in our zebras (as has been shown in other ungulates subjected to hunting, Stankowich 2008).

The adult male zebras in the focal group were significantly more vigilant than females so that feeding time was reduced during our dusk observation periods. It is possible that at other times of day, vigilance activity might have been differently distributed between the sexes and this should be examined in future studies.

Our interesting findings on aggression and vigilance derive from just one group of zebra and we recognise that further studies are needed to establish the generality of these findings in other groups and populations. By studying individuals over a long-term period, we have established a possible base line for plains zebra activity that may have particular relevance for future efforts in conserving zebras, particularly with respect to potentially costly activities such as vigilance. Where we can better appreciate the factors influencing vigilance, aggression-free interactions across all zebra categories as well as the residual and direct impact of trophy hunting activities, then such findings could lead to managing and sustaining healthier populations.

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Table 1 Study Structure. On study days general information on zebra identity, social structure, residency and environment was collected. Focal animal behaviour observations were taken in 30 minute sessions on behaviour observations days. The proportion of these sessions when a resident male accompanied the nursery group is given in the last column.

Block	Dates	Number of Study days	Number of Behaviour Observation days	Number of Behaviour Observation Sessions	Number of Observation Sessions when male present
1	Oct 2004	16	/	/	/
2	Jan-Feb 2005	52	21	126	116
3	Apr 2005	25	10	75	67
4	Sept-Oct 2005	9	2	21	0
5	Nov 2005	28	8	28	0
6	Jan-Feb 2006	43	16	122	0
7	Apr-May 2006	26	10	75	2
8	Oct-Nov 2006	40	19	143	143
9	Feb 2007	7	/	/	/
10	Mar-Apr 2007	25	/	/	/
11	Aug-Sept 2007	32	/	/	/
12	Oct-Nov 2007	40	/	/	/
13	Oct 2008	26	/	/	/
14	Dec 2008-Jan 2009	44	10	120	26
15	May-July 2009	56	15	99	0
16	Aug – Oct 2009	72	5	20	0

Table 2 Sources of variation in activity duration and the modelled effects of role and male presence

	<i>Variation in activity between blocks</i>	<i>Variation in activity between individual zebra</i>	<i>Variation in activity between observation periods</i>	<i>Female activity relative to reference category of male activity</i>	<i>Foal activity relative to reference category of male activity</i>	<i>Male absence relative to reference category of male presence</i>	<i>Interaction female*male absence</i>	<i>Interaction foal*male absence</i>
Vigilance	z = 0.88	z = 3.67 *	z = 19.6**	-543.8 (58.6) z = 9.28**	-463.5 (59.3) z = 7.81**	-60.0 (93.4) z = 0.64 NS	+214.1 (100.8) z = 2.12*	-19.6 (105.0) z = 0.19 NS
Graze	z = 1.75	z = 3.10*	z = 19.6**	+577.9 (72.4) z = 7.98**	+432.7 (72.7) z = 5.95**	-119.4 (131.2) z = 0.91 NS	-169.7 (138.7) z = 1.22 NS	-46.1 (143.8) z = 0.32 NS
Stand Rest	z = 0.87	z = 1.79	z = 19.8**	+19.8 (31.5) z = 0.62 NS	+17.04 (31.2) z = 0.55 NS	+190.8 9 (63.1) z = 3.02**	-156.0 (68.1) z = 2.29*	-119.8 (69.3) z = 1.73 NS
Walk	z = 1.91	z = 2.26*	z = 19.7**	-26.4 (29.9) z = 0.88 NS	-32.7 (29.7) z = 1.10 NS	-0.85 (61.2) z = 0.01 NS	+60.3 (63.8) z = 0.94 NS	+19.1 (65.8) z = 0.29 NS
Trot	z = 0.80	z = 0.0	z = 20.3**	-4.93 (3.35) z = 1.47 NS	+6.13 (3.28) z = 1.87 NS	-3.31 (7.62) z = 0.43 NS	+3.16 (8.17) z = 0.39 NS	+7.97 (5.34) z = 1.49 NS
Canter	z = 1.36	z = 0.83	z = 19.8**	+1.74 (2.27) z = 0.77 NS	+5.01 (2.23) z = 2.25*	-2.54 (4.99) z = 0.51 NS	+3.63 (5.31) z = 0.68 NS	+1.41 (5.40) z = 0.26 NS
Social Play	z = 0.62	z = 0.82	z = 19.9**	-29.8 (14.3) z = 2.08*	12.6 (14.0) z = 0.90 NS	+17.12 (32.9) z = 0.52 NS	17.1 (32.9) z = 0.52 NS	28.2 (33.2) z = 0.85 NS
Urination	z = 0.58	z = 0.0	z = 20.1**	+0.34 (0.43) z = 0.79 NS	-0.43 (0.43) z = 1.00 NS	-1.37 (0.98) z = 1.40 NS	+0.71 (1.06) z = 0.67 NS	+0.92 (1.06) z = 0.87 NS
Self groom	z = 1.29	z = 0.0	z = 20.3**	0.02 (1.89) z = 0.01 NS	-0.63 (1.84) z = 0.34 NS	+11.34 (4.36) z = 2.60**	-8.8 (4.6) z = 1.91 NS	-9.2 (4.7) z = 1.96*
Object play	z = 0.0	z = 0.0	z = 20.6**	+0.14 (2.3) z = 0.06 NS	+4.9 (2.3) z = 2.13*	+0.01 (5.3) z = 0.00 NS	2.3 (5.7) z = 0.40 NS	-3.5 (5.7) z = 0.61 NS
Flehmen	z = 0.0	z = 2.85**	z = 19.7**	-0.72 (0.27) z = 2.68**	-0.65 (0.27) z = 2.44*	+0.43 (4.3) z = 0.10 NS	-0.57 (0.53) z = 1.07 NS	-0.66 (0.55) z = 1.20 NS

The coefficients presented give the average change in the duration (s) of each activity for a 1800s observation period in comparison with the arbitrary reference category for that variable. The standard error for each coefficient is shown in brackets.

*An effect significant at $p < 0.05$; **an effect significant at $p < 0.01$

Table 3 Overall mean duration of activities (s in 1800s observation period) that comprised a small proportion of the time budget. Standard errors shown in brackets.

	<i>Drink</i>	<i>Nuzzle</i>	<i>Chin</i>	<i>Lie rest</i>	<i>Suckle</i>	<i>Pandiculation</i>	Defecation
Males	1 (1) ³	10 (1)	2 (1)	7 (18)	-	<0.05 (0.5)	2 (1)
Females	0.6 (0.4)	3 (0.5)	<0.05 (<0.05)	10 (7)	6 (1)	<0.05 (0.2)	1 (0.4)
Foals	1 (0.4)	3 (0.5)	1 (0.3)	41 (7)	4 (1)	0.5 (0.2)	1 (0.4)