The link between sexual dimorphism, activity budgets, and group cohesion: the case of the plains zebra (Equus burchelli)

P. Neuhaus and K.E. Ruckstuhl

Abstract: Animals that differ in reproductive status and body size have different needs in terms of foraging and resting. In most social ungulates this leads to sexual segregation, probably because of incompatibilities between the activity budgets of males and females. Since most studies on behavioural differences between the sexes have been done on sexually dimorphic species, we decided to look at a system in which males and females are similar in body size. We studied time budgets, synchrony of behaviour, and bite rates of plains zebras (Equus burchelli) to evaluate the factors that enable these extremely social ungulates to stay in stable mixed-sex family groups throughout the year. As we predicted, time budgets were similar among males, lactating females, pregnant females, and non-reproductive females. Furthermore, we observed close synchronization of behaviours between females that differed in reproductive status and males. Lactating females, however, did take more bites per minute when foraging than either pregnant or non-reproductive females or males. We assume that the higher bite rates of lactating females were due to the extra costs of producing milk for their foal. We concluded that the special harem mating system, and for females the year-round possibility of conceiving, force the animals to synchronize their time budgets, which might be a major reason for the lack of difference in body size between males and females.

Résumé : Des animaux de statuts reproducteurs et de tailles différents ont des besoins différents pour leur quête de nourriture et pour leur repos. Chez la plupart des ongulés sociaux, ces différences entraînent la ségrégation entre les mâles et les femelles, probablement à cause de l’incompatibilité entre leurs bilans temporels respectifs. La plupart des études sur les différences de comportement entre les sexes ont comme sujets des espèces à dimorphisme sexuel; nous avons décidé d’examiner un système dans lequel mâles et femelles sont de tailles semblables. Nous avons étudié les bilans temporels, le synchronisme des comportements et la fréquence des mastications chez des zèbres (Equus burchelli) dans le but de déterminer ce qui permet à ces animaux extrêmement sociaux de maintenir stables pendant toute l’année leurs groupes familiaux formés de mâles et de femelles. Tel que prévu, les budgets temporels sont semblables chez tous les mâles, toutes les femelles nourricières, toutes les femelles enceintes et toutes les femelles non reproductrices. De plus, il y a un synchronisme important des comportements chez les femelles de tous les statuts et chez les mâles. Cependant, lors des périodes d’alimentation, les femelles nourricières font plus de mastications à la minute que les femelles enceintes ou les femelles non reproductrices. Nous croyons que la fréquence plus grande des mastications chez les femelles nourricières est attribuable aux coûts reliés à la production de lait pour les poulains. Ce système particulier de reproduction en harems et la possibilité pour les femelles de concevoir en tout temps de l’année forcent probablement les animaux à synchroniser leurs bilans temporels respectifs, une situation qui peut, à son tour, expliquer l’absence de différences de taille entre mâles et femelles.

[Intaduit par la Rédaction]

Introduction

A variety of grass-eating animal species have evolved in the vast plains of southern and eastern Africa (Owen-Smith 1997). Most are ruminants, chewing the cud to enhance conversion of cellulose and fiber into digestible carbohydrates by microsymbionts (Demment and Van Soest 1985; Van Soest 1994). However, some very successful non-ruminant hind-gut fermenters, such as rhinoceroses (Rhinocerotidae) and zebras (Equidae), share the ruminants’ habitat. The plains zebra (Equus burchelli) is considered one of Africa’s most adaptable and successful grazers (Estes 1991). An interesting trait of plains zebras is their social system; they live in very stable harems (Klingel 1974, 1977).

Living in a group confers not only advantages, such as an increased likelihood of finding food or water or a decrease in predation risk through predator detection and dilution effects (Alexander 1974; Wrangham and Rubenstein 1986; Debn 1990), but also disadvantages, such as an increase in the risk of parasite transmission (Møller et al. 1993), in competition for food (Vasquez and Kacelnik 2000), and possibly in the costs of behavioural synchronization (Ruckstuhl 1999). While females in these groups are usually either...
lactating or pregnant (and quite often both; Estes 1991), the only adult male (stallion) in the group is responsible for keeping the group of up to 6 adult males and their offspring together (Klingel 1977).

It has been suggested that in red deer (*Cervus elaphus*) and Rocky Mountain bighorn sheep (*Ovis canadensis*), males and females have such different activity budgets that it would be energetically difficult for them to stay in the same group, and indeed, both species show sexual segregation (Conradt 1998; Ruckstuhl 1999). Further, in Alpine ibex (*Capra ibex*), it has been shown that feeding behaviour itself differs greatly, not only between females and males but also between lactating females and females without offspring (Neuhaus and Ruckstuhl 1998; Ruckstuhl 1999). Male African buffalo (*Syncerus caffer*) switch back and forth between female and bachelor groups (Prins 1989), probably because the bigger males can only synchronize their behaviour with that of smaller females during a certain time (Ruckstuhl and Neuhaus 2002). All these species are ruminants with a relatively high degree of sexual size dimorphism. Ruckstuhl and Neuhaus (2000, 2002) argued that the ability of animals to live in a group depends on their having similar body sizes, and hence similar needs, thus minimizing the possible costs of synchrony. In this study on zebras, we studied this prediction by choosing a non-ruminant species in which females and males are similar in body size. One of the main factors that force females and males into mixed-sex groups seems to be their mating system (Jarman 1983; Weckerly 1998), including the fact that males have the opportunity to mate year-round. Hence, males need to stay close to these females to maximize their reproductive success. The harem system of the plains zebra is a very specialized mating system in which females and males live together in family groups for many years (Klingel 1977; Estes 1991). We predicted that because of the specialized mating system and the high degree of stability of family groups, time budgets would not vary among group members, and the degree of synchronization of activities would be equally high for adults of both sexes and regardless of reproductive status. If there were any differences in feeding behaviour between females that differed in reproductive status and males, owing to differences in energetic needs, we expected to find them in the bite rate (the rate at which they crop forage per unit time). For example, higher bite rates for lactating females than for nonlactating females and males were reported for Alpine ibex and Rocky Mountain bighorn sheep (Ruckstuhl and Festa-Bianchet 1998; Neuhaus and Ruckstuhl 1998). While it has been argued that bite size can be an important factor influencing rates of food intake by mammalian herbivores (Gross et al. 1993a, 1993b), we can assume that bite sizes are similar, owing to the almost identical body sizes of male and female zebras; therefore, the main factor determining food-intake rate would be the cropping or bite rate.

**Methods**

We observed plains zebras in Etosha National Park, Namibia, from December 1999 to February 2000. During the observations most individuals were distinguishable through differences in stripe pattern. When this was not the case, observations on a specific group were averaged for animals of the same sex and reproductive status and used as one data point. Because plains zebras can breed year-round (Estes 1991), there were usually lactating females as well as pregnant females within a focal group. The reproductive status of females was determined by direct observation. Females were considered to be lactating when they nursed a foal. Pregnant females were defined as females with obvious signs of late pregnancy, such as an inflated belly or intermediate-sized teats. Nonlactating females without any signs of pregnancy were classified as females without young. The possibility that females whom we classified as without young were in an early stage of pregnancy cannot be excluded. We only once observed a bachelor group containing 7 males. Since we collected data on such a group only once, we calculated the average behaviour of those 7 males, but we did not analyse the data; however, the data are shown in Table 1 for comparison only.

We looked at the activity budgets of adult females and males and of females that differed in reproductive status. We also compared the proportions of time during which animals of different sex and age classes synchronized their activity budgets with those of the majority of the other group members (see below for the method of calculating synchrony). We also collected data on males’ and females’ bite rates, distinguishing between the females according to their reproductive status.

For observations on time budgets we observed a focal group for 5–10 h using the scan-sampling method (Altman 1974), with 5-min intervals. We noted the activity of each group member every 5 min, distinguishing between four behaviours: lying, standing, grazing, and walking. When observations had to be stopped because the animals went out of sight before we had observed them for at least 5 h, the data were dropped from the analyses. The remaining data were used to calculate the proportion of time the animals spent in each activity. The observations were carried out from a car with binoculars (10 × 40) and spotting scopes (25–40 × 60) during all daylight hours, from sunrise to sunset, evenly distributed for data sampling.

We then used the activity-budget data to calculate the extent to which individual animals synchronized their behaviour with that of other group members by calculating a synchronization factor ($S_f$) for each 5-min scan, using a similar method to that described by Ruckstuhl (1999) but adjusting for the 5-min scan-sampling method we used. The first animal was taken as the reference individual and its behaviour was assigned a value based on its degree of synchrony with the behaviour of other group members, as follows: if the behaviour of the reference individual differed from that of more than half of the group members, $S_f$ for that individual during that 5-min scan was 0; if it exhibited the same activity as most (>50%) of the other group members, its $S_f$ for that 5-min interval was 1. If half of the group members were exhibiting the same activity as the reference animal while the other half were exhibiting another behaviour, we assigned a $S_f$ of 0.5.

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Table 1. Percentages of time spent in different activities by plains zebras (*Equus burchelli*) that differed in sex and reproductive status.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Lactating females (N = 14)</th>
<th>Highly pregnant females (N = 8)</th>
<th>Nonlactating females (N = 10)</th>
<th>Males (N = 12)</th>
<th>Bachelor group (N = 7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lying</td>
<td>0.8 (0.59)</td>
<td>3.0 (1.06)</td>
<td>6.3 (2.04)</td>
<td>0.3 (0.19)</td>
<td>0.001</td>
</tr>
<tr>
<td>Grazing</td>
<td>63.3 (4.91)</td>
<td>60.2 (8.62)</td>
<td>54.3 (6.86)</td>
<td>63.5 (4.40)</td>
<td>ns</td>
</tr>
<tr>
<td>Standing</td>
<td>26.1 (5.73)</td>
<td>19.6 (3.12)</td>
<td>26.6 (3.78)</td>
<td>25.3 (2.97)</td>
<td>ns</td>
</tr>
<tr>
<td>Walking</td>
<td>9.9 (1.31)</td>
<td>17.2 (6.18)</td>
<td>12.7 (1.97)</td>
<td>11.0 (1.69)</td>
<td>ns</td>
</tr>
</tbody>
</table>

Note: Values are given as the mean, with the standard error in parentheses; ns, not significant. *N* is the number of different individuals.

*Subadult females 77 12 5 ns
Subadult males 78 12 7 ns
Adults 76 9 50 ns
Subadults 78 11 12 ns

Table 2. Percentages of time during which the behaviour of individual plains zebras was synchronized with that of the rest of their group in different age and sex classes.

<table>
<thead>
<tr>
<th>Synchronization index (%)</th>
<th>Mean SD N p (GLM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>73 10 14 ns</td>
</tr>
<tr>
<td>Adult females</td>
<td>77 11 36</td>
</tr>
<tr>
<td>Subadult males</td>
<td>78 7 7 ns</td>
</tr>
<tr>
<td>Subadult females</td>
<td>77 12 5</td>
</tr>
<tr>
<td>Adults</td>
<td>76 9 50 ns</td>
</tr>
<tr>
<td>Subadults</td>
<td>78 11 12</td>
</tr>
</tbody>
</table>

Note: *N* is the number of different individuals; ns, not significant.

After all *S*<sub>f</sub> values for all 5-min scans were calculated for the entire activity budget of the reference individual, a mean individual synchronization index (*S*<sub>index</sub>) was calculated:

\[
S_{\text{index}} = \frac{1}{n} \sum_{i=1}^{n} S_f
\]

where *n* is the number of 5-min scans.

This procedure was repeated for each group member. Individual *S*<sub>index</sub> values basically represent the percentage of time during which each individual’s activity was in synchrony with that of the other group members. If we were not able to distinguish between individuals in the group, we used the average *S*<sub>index</sub> value for all age and sex classes in the group for the final analysis. We excluded the activity data from newborn foals, since their behaviour differs from that of adults and subadults in that they do not graze. Further, two groups for which we had time budgets were excluded because we could not distinguish between all individuals.

To measure bite, step, and vigilance rates for an individual zebra, we observed it during a feeding bout. Bites, steps, and vigilance postures were counted for 10 × 1 min. Bites were easily recognised through repeated movements of the head. A step was counted as a single forward movement by one of the front legs, and a vigilance posture was defined as raising the head above shoulder height (Frid 1997). For the analyses we averaged bite, step, and vigilance rates over the 10-min sampling periods.

To compare the time animals of different sex and age classes spent in different activities we used general linear models (GLM). For multiple comparisons we used Scheffé’s post-hoc test to evaluate significant differences in behaviour.

Table 3. Numbers of bites, steps, and vigilance postures per minute for lactating and nonlactating female and male plains zebras.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Lactating females (N = 16)</th>
<th>Nonlactating females (N = 9)</th>
<th>Males (N = 17)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bites/min</td>
<td>46.27 (1.14)</td>
<td>41.92 (0.55)</td>
<td>42.93 (0.88)</td>
<td>0.01</td>
</tr>
<tr>
<td>Steps/min</td>
<td>9.57 (0.86)</td>
<td>8.97 (1.30)</td>
<td>6.98 (0.68)</td>
<td>ns</td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.28 (0.06)</td>
<td>0.36 (0.10)</td>
<td>0.38 (0.07)</td>
<td>ns</td>
</tr>
</tbody>
</table>

Note: Values are given as the mean, with the standard error in parentheses; ns, not significant. *N* is the number of different individuals.

Results

There was no difference in the percentages of time spent grazing, standing, or walking between male and female zebras of different reproductive classes (GLM, grazing: *F* = 0.472, *p* = 0.703; standing: *F* = 0.43, *p* = 0.733; walking: *F* = 0.919, *p* = 0.44; Table 1). However, there were significant differences in time spent lying (GLM, *F* = 6.882, *p* = 0.001). This difference was significant between females without young and lactating females, as well as between males and females without young (Scheffé’s post-hoc test, *p* = 0.007 for females without young versus lactating females; *p* = 0.004 for females without young versus males; Table 1). Interestingly, the 7 males in the bachelor group seemed to spend much more time lying and less time grazing than females or harem males (Table 1).

We found no difference in *S*<sub>index</sub> values for animals of different sex and age classes (GLM, adult females versus males: *F* = 1.153, *p* = 0.288; subadult females versus males: *F* = 0.043, *p* = 0.840; adults versus subadults: *F* = 0.376, *p* = 0.542; Table 2).

There was also no difference in numbers of steps taken per minute or vigilance rates between adult males, lactating females, and nonlactating females (GLM, step rate: *F* = 2.697, *p* = 0.08; vigilance rate: *F* = 0.528, *p* = 0.594; Table 3). There was, however, a significant difference in number of bites taken per minute. Lactating females had a higher bite rate than both nonlactating females and males (GLM, *F* = 5.03, *p* = 0.01; Table 3; Scheffé’s post-hoc test, *p* < 0.03 for
lactating females versus nonlactating females; \( p < 0.05 \) for lactating females versus males).

**Discussion**

In this study we compared activity budgets, synchrony of activity, and bite rates of male and female plains zebras living in a harem system. The goal was to test the hypothesis that differences in activity should be minimized and synchronization of behaviour between individuals within a family unit should be high, to ensure the stability of the harem. While most sexually segregating ungulates show a high degree of sexual dimorphism in body size (Weckerly 1998; Pérez-Barberia and Gordon 1999), there is commonly little body-mass dimorphism in species that live in mixed-sex groups (Ruckstuhl and Neuhaus 2002). Plains zebras, for example, do not show strong dimorphism in body mass, since males weigh around 250 kg, only slightly more than females, who weigh about 220 kg (Owen-Smith 1988; Estes 1991). As Ruckstuhl and Neuhaus (2000) suggested, similarity in body size may be a prerequisite for species living in stable mixed-sex groups.

As expected, there was no difference in activity budgets between males and females when grazing, standing, or walking. These results are similar to the findings for Camargue feral horses (*Equus caballus*), where time budgets of weaned individuals varied by less than 10% regardless of age, gender, or reproductive status (Duncan 1992). However, female zebras without young differed significantly from males and reproducing females in time spent lying: males and lactating females spent virtually no time lying, and in all cases considerably less than females without young. Males may be on the lookout for competing rival males, but by spending time standing instead of lying, males and lactating females are also less vulnerable to predators. It has been shown that bedded zebras are much more likely to be taken by lions (their main predator) than standing ones (Estes 1991).

A number of studies on ungulates have confirmed that lactating females often have a higher vigilance rate than nonlactating individuals (Haviernick 1996; Friid 1997; Toïgo 1999); however, this was not the case with our zebras. The equally high vigilance rates of stallions and mares with and without foals likely reflect the important role played by the stallion in keeping the social unit together; apart from defending the harem against intruding males, he also herds straying females back into the group should they venture too far from it (Klingel 1977; Kingdon 1997). In this context, it is interesting to note the high percentage of time the males in the bachelor group spent lying compared with the harem males. This result is consistent with results obtained from bachelor groups of feral horses, whose time budgets were characterized by large amounts of time spent lying (Duncan 1980; Berger 1986).

Also noteworthy is the similarity in the amounts of time males and females spent walking, likely a requirement for or a consequence of group stability. The comparable times that animals spent feeding indicate that male and female zebras either have similar needs in terms of intake, perhaps because of similarities in their body sizes, or because they adjusted their behaviour closely to each other’s as predicted. The activity of zebras within harems was highly synchronized with that of other group members, even when they differed in sex and body size, which supports our second line of argument above. A mean \( S_{\text{index}} \) value between 73 and 78% seems high, considering that we only distinguished between four different activities. It is comparable to the \( S_{\text{index}} \) values reported by Ruckstuhl (1999) for bighorn sheep groups of the same sex and same body size, but considerably higher than those found for bighorn sheep groups of mixed sexes and ages. Penzhorn (1984) also reported a high degree of synchronization of activities in the Cape mountain zebra (*Equus zebra zebra*).

The main behavioural difference we found in this study was in the number of bites taken per minute. As predicted, lactating females took more bites per minute than either nonlactating females or males. We interpret this result as representing compensatory behaviour by lactating females to cope with the increased energetic costs of lactation without concomitantly increasing their time spent grazing. Since grazing and walking are the two main behaviours that could affect synchrony of behaviour and group cohesion, we conclude that increasing the bite rate may be the only option for lactating females to meet their higher energetic and nutritional needs while synchronizing their behaviour and movements with those of the rest of the group.

To live year-round in the same group, animals have to synchronize their behaviour with that of other group members. We argue that the similarity in body sizes of male and female zebras is a critically important characteristic without which synchrony would be too costly. We suggest that zebras might have evolved to have similar body sizes in order to minimize the costs of synchrony and allow them to live in stable harem groups. The lack of body-size dimorphism is most obvious in species in which females can come into oestrus year-round, or in monogamous territorial species such as the Kirk’s dik-dik (*Madoqua kirkii*) or steenbok (*Raphicerus campestris*). In species in which oestrus is restricted to a few weeks per year, males compete for access to females, and sexual selection therefore favours large-bodied males with strong fighting skills, better storage of energy reserves, and secondary sexual characters such as large horns or antlers, which are used in male–male competition (Weckerly 1998).

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