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The influence of roughage intake on the occurrence of oral disturbances in captive giraffids

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Abstract

Feeding behaviour of giraffe and okapi in captivity can differ significantly from the state in the wild. Duration and complexity of feeding and ruminating behaviour, and total amount of food ingested, are often reduced, while the energy content of the diet is increased compared to the wild. As known from domestic cattle in intensive keeping systems, oral disturbances like tongue-playing or licking of objects are reported to occur in captive giraffe and okapi. Oral disturbances are considered to be related to an intensive feeding system, e.g. characterised by a low intake of (physically) structured feeds like hay or fresh forage. We review evidence for this relation in domestic cattle and in giraffids in zoos, and add some own data on 6 giraffes and 3 okapis, which suggest an increasing influence of a high unstructured/structured feed ratio on oral disturbances. The causal and functional factors responsible for oral disturbances are understood only partly to date. It is unclear whether deprivation of feeding or of ruminating behaviour is more important, whether deprivation of behaviour itself or deviations of the normal physiology of the digestive process are responsible for a relation of oral disturbances with low roughage intake, and whether they can be interpreted as adaptive behaviour. Independent of a detailed explanation for the occurrence of oral disturbances, a higher roughage intake seems to reduce the occurrence of this behaviour. Suggestions are made as to which measures may be taken to achieve an adequate roughage intake in selective ruminants, and which kinds of roughage can be regarded as adequate for them. Further research is needed to be able to judge the suitability of different kinds of roughage for giraffe and okapi.

Key words:
oral disturbance, Giraffa camelopardalis, Okapia johnstoni, physical structure of feeds

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Introduction

Feeding behaviour of ruminants in the wild and in captivity

Ruminants typically feed on leafy plant material. Feeding and processing of such fibre-rich food distributed in small feeding units over a large area requires a high amount of effort. Daily grazing time under free ranging conditions has been estimated to be one third of the 24 h-cycle for herbivorous ungulates in general (Dürrsch 1976), 8–9 h/d (range: 4–12 h/d) for dairy cows, 9–10 h/d (range 5–15 h/d) for beef cattle and 8–9 h/d (range 3–13 h/d) for sheep (Arnold and Dudzinski 1978) and 11 h/d (range 9.5–13 h/d) for free ranging giraffes (Pellew 1984). Besides keeping the animal occupied for a lot of time, feeding behaviour in the wild is complex. Harvesting and ingesting fibrous leaves (grass, herbs or browse) involves a lot of particular tongue and chewing movements (e.g. Zeeb 1974, Kolter 1995). In addition to feeding behaviour, ruminants spend considerable time ruminating. Average values are 5–9 h/d of rumination for cattle (Arnold and Dudzinski 1978) and 7 h/d of rumination for giraffes (Pellew 1984). Total rumination time depends on the growth stage and fibre content of vegetation, more fibrous forages resulting in longer rumination.

While ruminants in the wild obviously have to rely predominantly on forage as food, diets in captivity can differ considerably from this. They include important amounts of feeds low in structured fibre. Such feeds can be called (physically) unstructured and are defined as having a small particle size, inducing few feeding and ruminating behaviours and thus few chewing and tongue movements. Feeds like all kinds of pellets or cubes, most produce and pure energy feeds like grains or bread belong to this group. In contrast to this, (physically) structured feeds have a large particle size and therefore cause a lot of chewing and tongue movements due to higher eating and ruminating activity. This feed group includes roughage like hay or browse. For cattle it has been shown that per kg dry matter (DM) of feedstuf, roughage induces considerably longer eating and rumination times compared to pelleted feeds (Balch 1971, Table 1; Piatkowski et al. 1990, Table 2). Graf (1991) compares activity budgets of cattle on pasture (feeding:

Table 1: Time spent with eating and ruminating by cows feeding on different feeds [min/kg DM] (from Balch 1971)

<table>
<thead>
<tr>
<th>Feedstuff</th>
<th>Eating</th>
<th>Ruminating</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oat straw</td>
<td>41–58</td>
<td>94–133</td>
<td>145–191</td>
</tr>
<tr>
<td>Good-quality hay</td>
<td>27–31</td>
<td>55–74</td>
<td>87–105</td>
</tr>
<tr>
<td>Grass silage</td>
<td>31–58</td>
<td>60–83</td>
<td>99–120</td>
</tr>
<tr>
<td>Finely ground hay</td>
<td>13</td>
<td>(0–6)(^1)</td>
<td>(13–19)(^1)</td>
</tr>
<tr>
<td>Pelleted concentrates</td>
<td>4–10</td>
<td>(0–25)(^1)</td>
<td>(4–29)(^1)</td>
</tr>
</tbody>
</table>

\(^1\) According to Balch (1971), these values show a high extent of irregular chewing (irregular reticulum contractions and jaw movements)
6–12 h/d; ruminating: 5–9 h/d) with those of fattening bulls on diet of concentrate and maize silage only (feeding: 2–5 h/d; ruminating: 3–6 h/d).

Additional deviations from the wild are that fermentation rate and energy content are typically lower in forage/structured feeds than in unstructured feeds (with high energy content = concentrates) (e.g. Hummel et al. 2003), and that distribution of food over the day is more aggregated in captivity than in the wild (for primates: Schwitzer and Kaumanns 2003).

**Oral disturbances**

For several, mainly herbivorous or omnivorous species, repetitive mouth or tongue movements, so-called oral disturbances, have been observed under restrictive captive conditions. Crib biting in horses (Waters et al. 2002a,b) and chewing on bars in pigs (Appleby and Lawrence 1987) are prominent examples for the occurrence of such behaviour. They fit with the definition of a stereotypy (Mason 1991) in being repetitive and apparently functionless, while another condition (invariance of motoric pattern) can be questioned (Stolze 1998). They are referred to as oral disturbances in the following.

Oral disturbances have been linked most often to the functional system (“Funktionskreis”, Immelmann and Beer 1989) of foraging, and have been associated with feeding practices of an intensive or restrictive kind (Rushen 1985). They are explained as a dysfunction in the regulation of feeding behaviour due to a lack of negative feedback in the captive situation (reduced feeding duration and quantity of chewing and tongue movements) (Kolter 1995).

**Oral disturbances in ruminants – with emphasis on giraffes and okapis**

In intensively kept domestic ruminants (predominantly cattle), oral disturbances typically manifest themselves as functionless movements of the tongue (e.g. Zeeb 1974, Sambraus 1991) called inner or outer tongue-playing (e.g. Redbo 1990), licking or nibbling on objects (e.g. Graf 1991), licking and sucking on pen mates (e.g. Sambraus and Gotthardt 1985), hair or
wool-eating (e.g. Sambraus 1985a), bar-biting (e.g. Redbo and Nordblad 1997) or pseudo rumination (e.g. Van Putten and Elshof 1978, Deswysen and Ehrlein 1981).

Tongue playing or excessive licking of objects are problems often mentioned for giraffes (*Giraffa camelopardalis*) and okapis (*Okapia johnstoni*) in captivity (e.g. Zeeb 1974, Sambraus 1991, Veasey *et al.* 1996, Bashaw *et al.* 2001, Tarou *et al.* 2003). Surveys on captive giraffids revealed a high occurrence of this behaviour in Japanese (almost 100% of the animals, based on behavioural observations; Sato pers. comm., cited in Koene and Visser 1997) and North American facilities (72% of all animals, based on a questionnaire sent to zoos; Bashaw *et al.* 2001). In these studies, some factors not related to diet have been proposed to influence this behaviour, like enclosure characteristics (paddock size and presence of other species, Sato and Takagaki 1991; time spent indoors, Bashaw *et al.* 2001) or social situation of the animals (kept alone or with penmates, Sato and Takagaki 1991; access to conspecifics overnight, Bashaw *et al.* 2001). Despite the fact that other factors have some influence on the occurrence of oral disturbances, most authors report diet related factors to have the most important influence on the occurrence of this behaviour. Examples are the amount of browse (Koene and Visser 1997, Stolze 1998), the amount of produce (Kolter 1995, Stolze 1998) or the kind of roughage in the diet (Koene 1999, Baxter and Plowman 2001).

In the past the amount of roughage in the diet has been reported or hypothesised to have a major influence on the occurrence of oral disturbances in ruminants (Papendieck 1979, Sambraus *et al.* 1984, Sambraus 1985a,b, Wierenga 1987, Fraser and Broom 1990, Sato *et al.* 1994). We review some quantitative or semi-quantitative data giving evidence for this relationship in domestic ruminants and giraffids.

**Influence of roughage intake on behaviour**

Table 3 summarises some of the available data relating oral disturbances and roughage intake in ruminants (mostly cattle). Graf (1991) found a negative correlation between abnormal oral activities (nibbling objects and coat nibbling) and access to hay in fattening bulls. The animals were fed a diet of maize silage plus concentrate, one group having additional access to hay. If the feeding regime was changed between the groups there was an according change in the amount of oral disturbances. For heifers on a diet of silage and concentrates, Redbo and Nordblad (1997) report levels of oral disturbances of 0.8 ×/observation period (period 1) and 4.5 ×/observation period (period 3) with access to additional straw, rising up to 20.1 ×/observation period without access to this roughage source (intermittent period 2). Feeding and rumination frequencies were considerably lower in the period without access to long straw.

Data of Stolze (1998) on giraffes suggest an influence of the amount of unstructured feeds on the occurrence of oral disturbances as well: Animals
Table 3: Review of some publications giving evidence for a correlation of roughage intake and the occurrence of oral disturbances (treatments A, B, C with increasing roughage content)

<table>
<thead>
<tr>
<th>Trial</th>
<th>Age, month</th>
<th>n</th>
<th>Feeding schedule</th>
<th>Oral disturbances</th>
<th>Feeding</th>
<th>Rumination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TP: 6.5 % (24 h)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.25-4</td>
<td>2</td>
<td>Milk replacer</td>
<td>LO: 15.8 % (24 h)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NO: 9.7 % (24 h)</td>
<td>-</td>
<td>1)</td>
</tr>
<tr>
<td>B</td>
<td>-</td>
<td>3</td>
<td>&quot; + 200 g straw</td>
<td>TP: 0.3 % (24 h)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.5-6</td>
<td>15</td>
<td>Milk replacer</td>
<td>LO: 9.7 % (24 h)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NO: 6.9 % (24 h)</td>
<td>-</td>
<td>2)</td>
</tr>
<tr>
<td>B</td>
<td>15</td>
<td>&quot; + 200 g straw pellets</td>
<td>TP: 2.6 % (24 h)</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>15</td>
<td>&quot; + 1 kg maize silage</td>
<td>TP: 0.6 % (24 h)</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>15</td>
<td>&quot; + 1 kg maize silage</td>
<td>TP: 0.8 % (24 h)</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>15</td>
<td>&quot; + hay ad libitum</td>
<td>TP: 0.5 % (24 h)</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>2.5-12</td>
<td>255</td>
<td>Maize silage, soybeans, grains</td>
<td>TP: 1.2 x/4.5 h 37.2 % of animals</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>6-13</td>
<td>93</td>
<td>&quot; + hay (100-150 g 3x a week)</td>
<td>TP: 0.3 x/4.5 h 24.8 % of animals</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Table 3: cont.

<table>
<thead>
<tr>
<th></th>
<th>6-9</th>
<th>~ 230</th>
<th>Maize silage, concentrates c)</th>
<th>NO: 15.7 x/6 h</th>
<th>21.1 % (6 h)</th>
<th>15.0 % (6 h)</th>
<th>4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>~ 230</td>
<td>“ + 1.5 kg hay</td>
<td>NC: 4.3 x/6 h</td>
<td>29.4 % (6 h)</td>
<td>21.4 % (6 h)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Heifers

<table>
<thead>
<tr>
<th></th>
<th>15-18</th>
<th>48</th>
<th>Silage + concentrate</th>
<th>OD: 20.1 x/week (4 h/d) b)</th>
<th>15.2 x/week (4 h/d)</th>
<th>24.8 x/week (4 h/d)</th>
<th>5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>48</td>
<td>“ + long straw</td>
<td>OD: 2.7 x/week (4 h/d) b)</td>
<td>38.7 x/week (4 h/d)</td>
<td>84.8 x/week (4 h/d)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Giraffe

<table>
<thead>
<tr>
<th></th>
<th>4</th>
<th>4.7 kg DM unstructured feeds/animal</th>
<th>TP: 1.7 % (4 h)</th>
<th>13.8 % (4 h) + FB 4.0 % (4 h)</th>
<th>39.9 % (4h)</th>
<th>6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>5</td>
<td>2.7 kg DM unstructured feeds/animal</td>
<td>TP: - LO: 0.1 % (4 h)</td>
<td>33.5 % (4 h) + FB 19.2 % (4 h)</td>
<td>29.4 % (4 h)</td>
<td></td>
</tr>
</tbody>
</table>

FB: feeding and nibbling on browse; LO: licking of objects; MO: Manipulating object; NC: coat nibbling; NO: nibbling object; OD: oral disturbance; TP: tongue playing.

d) given as % (of daily observation time) or frequency of occurrence/observation time 
b) data read and recalculated from graph
c) supplemented with grass silage, beet pulp, fodder beets, potatoes

offered unstructured feeds in amounts of estimated 2.7 kg DM per animal and ingesting higher amounts of alfalfa hay and browse showed no oral disturbances at all (morning) or on a very low level (0.2%; afternoon) (facility a; n = 5). In contrast, another herd (facility b; n = 4) offered unstructured feeds in amounts of 4.7 kg DM per animal and ingesting alfalfa hay and browse in smaller amounts had levels of oral disturbances of 14.4% (morning) and 9.8% (evening).

**Own data**

These data can be supplemented with some results emerging from own nutritional studies on giraffes and okapis (Clauss et al. 2003b, Hummel and Kolter 2003). Although the sample size of these studies is restricted, they give some additional information on the problem. Unstructured/structured feed ratio was used as unit. Absolute amounts would have had to be best related to body weights, which could only be estimated for all of the animals.

**Giraffes**

The keeping of the giraffes has been described in Clauss et al. (2003b). The observed giraffe group consisted of six animals, of which 3 adults were kept individually and 3 juveniles as a group (Table 4). They were fed a diet of alfalfa hay and a browser pellet (Mazuri Browser Breeder; Special Diets Services, Mazuri, Witham, Essex, UK), both *ad libitum*, and limited amounts of beech browse (*Fagus sylvatica*) (0.5 kg DM/adult; 0.7 kg DM for juvenile group), linseed extraction chips (Cargill Plc, Gladstone Dock, Bootle, UK) (0.9 kg DM/adult; 1.8 kg DM for juvenile group) and a vitamin E pellet (Ele-Vit-E, Special Diets Services, Mazuri, Witham, Essex, UK) (0.17 kg DM/animal).

**Table 4:** Study animals (body weights based on estimation)

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Sex</th>
<th>BW (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Giraffe 1</td>
<td>13</td>
<td>Female, lactating</td>
</tr>
<tr>
<td>Giraffe 2</td>
<td>11</td>
<td>Female, pregnant</td>
</tr>
<tr>
<td>Giraffe 3</td>
<td>11</td>
<td>Male</td>
</tr>
<tr>
<td>Giraffe 4</td>
<td>2.5</td>
<td>Female</td>
</tr>
<tr>
<td>Giraffe 5</td>
<td>1.5</td>
<td>Male</td>
</tr>
<tr>
<td>Giraffe 6</td>
<td>0.5</td>
<td>Male</td>
</tr>
<tr>
<td>Okapi 1</td>
<td>6</td>
<td>Female</td>
</tr>
<tr>
<td>Okapi 2</td>
<td>5</td>
<td>Male</td>
</tr>
<tr>
<td>Okapi 3</td>
<td>14</td>
<td>Male</td>
</tr>
</tbody>
</table>
During the day, beech browse was hand-fed to the animals. They had access to troughs and racks only during closing hours (intake had to be estimated on an individual level for the nutritional part of the study). Food intake and behaviour was recorded for 7 days. The measured ratios of unstructured/structured feed (in dry matter) were compared to the amount of oral disturbances observed in individual animals. For the three juvenile giraffes, according average values were calculated. Observation time was between 9:00 and 17:00, which sums up to a total duration of 56 h per animal. The animals were observed simultaneously and behaviour was recorded in 30 sec scans.

Feed intakes of the giraffes are given in Table 5. The unstructured/structured feed ratio of the ingested diet (in dry matter) varied between 2.3 and 3.7 in these animals. The giraffes showed behaviours like tongue playing or wall licking to varying degrees (average of 5–29 % of observation time), but the behaviour was documented for all animals (Table 5). The percentage of oral disturbances showed a tendency to increase (see animal 2 and 6) with an accompanying increase in unstructured/structured feed ratio. When regarding these results, it is important to remember that although the animals were fed some browse during observation hours, they had no access to other feeds during this time but only in their stables (in an earlier study with the same giraffe group, similar total dry matter intakes had been recorded when some animals had been allowed constant access to their food; Clauss et al. 2001). This explains the low values of feeding and is likely to have an increasing effect on oral disturbances. Yet, this does not change the general trend of an increase of the occurrence of oral disturbances in these giraffes, if unstructured/structured feed ratio is increased.

| Table 5: Occurrence of oral disturbances (% of observed time; 9:00–17:00), ratio of unstructured/structured feed and total feed intake in 6 captive giraffes (mean ± SD) |
|-----------------|---------|---------|---------|---------|---------|---------|
| Giraffe         | 1       | 2       | 3       | 4       | 5       | 6       |
| Feeding [%]     | 6.1     | 6.6     | 5.8     | 7.2     | 5.1     | 5.2     |
| ±1.8            | ±1.6    | ±2.8    | ±2.8    | ±2.9    | ±2.8    |
| Rumination [%]  | 25.2    | 28.3    | 21.4    | 16.2    | 23.6    | 15.4    |
| ±8.1            | ±5.7    | ±7.8    | ±6.8    | ±3.6    | ±6.1    |
| Oral disturbances [%] | 28.5    | 13.7    | 5.0     | 21.2    | 23.5    | 11.8    |
| ±24.1           | ±7.2    | ±2.7    | ±8.7    | ±6.9    | ±7.9    |
| Unstructured/structured feeds ratio | 3.7     | 2.5     | 2.3     | 3.3     |         | (mean animal 4–6) |
| Daily feed intake [kg DM/d] | 11.0    | 8.1     | 8.6     | 13.6    |         | (sum animal 4–6) |
Okapi

The keeping of the okapis has been described in Hummel and Kolter (2003). All three animals were housed separately during the night. Animal 1 and 2 were kept together during the day (Table 4). They were fed a diet of alfalfa hay *ad libitum* and limited amounts of different browse, a pelleted concentrate (Deer pellet; Brogården, Gentofte, Denmark), oats and some produce. Consumption of alfalfa hay during times when okapi 1 and 2 were kept together (~7h/day) was regarded to be equally distributed on both individuals. Concentrates and produce were offered in two meals (7:30 and 16:30). Animals had some limited access to vegetation growing in their enclosure. For these animals, food intake and behaviour was recorded for 7 days. Observation time was 9:00-17:00 (56 h total duration per animal). Observations were done using instantaneous sampling as recording rule (5 min intervals) and scan sampling on all 3 animals as sampling rule (Martin and Bateson 1993).

Unstructured/structured feed ratios of 0.9, 1.3, and 2.3 (in dry matter) were measured (Table 6). Two okapis showed almost no oral behaviour that could be considered to be abnormal. Only the animal with the highest proportion of unstructured feeds in the diet performed considerable amounts of such behaviour, mainly excessive licking of objects. The highest occurrence of disturbed behaviour in this animal was after the second concentrate meal. Our results agree with the trend in the reviewed publications. They indicate that a high roughage intake has a decreasing influence on the occurrence of oral disturbances.

<table>
<thead>
<tr>
<th>Okapi</th>
<th>Feeding [%]</th>
<th>±</th>
<th>Ruminating [%]</th>
<th>±</th>
<th>Oral disturbances [%]</th>
<th>±</th>
<th>Unstructured/structured feeds ratio</th>
<th>±</th>
<th>Daily feed intake [kg DM/d]</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>37.8</td>
<td>±11.7</td>
<td>12.2</td>
<td>±5.4</td>
<td>0.3</td>
<td>±0.1</td>
<td>1.3</td>
<td>±0.1</td>
<td>4.4</td>
</tr>
<tr>
<td>2</td>
<td>20.0</td>
<td>±7.3</td>
<td>5.1</td>
<td>±3.2</td>
<td>0.2</td>
<td>±0.2</td>
<td>0.9</td>
<td>±0.2</td>
<td>3.1</td>
</tr>
<tr>
<td>3</td>
<td>22.3</td>
<td>±5.3</td>
<td>11.7</td>
<td>±3.2</td>
<td>2.2</td>
<td>±1.8</td>
<td>2.3</td>
<td>±1.8</td>
<td>3.9</td>
</tr>
</tbody>
</table>

When comparing data of intensively managed domestic cattle and giraffids living in zoos, one has to be aware of some important differences in these studies. Calves of cattle are typically raised artificially. Suckling
motivation is very high in young calves, and a deprivation of suckling behaviour can result directly in the development of oral disturbances like tongue playing (Zeeb 1974). Sato et al. (1994) and Seo et al. (1998a) state that this does not only lead to high levels of oral disturbances at young ages, but to some predisposition for oral disturbances over the whole life span of the animal. Early weaning obviously is a very rare exception in zoo giraffes or okapis, only occurring in calves not accepted by the mother.

A second major difference is that in animals kept for economic purposes, roughage supply was artificially restricted. The fattening bulls in the cited publications had almost no access to adequate roughage sources. In recent attempts to quantify structural quality of feeds for cattle, De Brabander et al. (1999) quantified straw and hay to have more than twice the structural value than maize silage, which was offered in considerable amounts to most animals in the cited studies. While oral disturbances in calves and fattening bulls kept on slatted floors therefore simply reflect a lack of access to fibre sources like hay, fresh forage or straw, zoo animals typically have a far less limited or completely unlimited access to roughage sources. A smaller proportion of roughage in their diet therefore can be seen as result of their own selection.

Possible explanations for the occurrence of oral disturbances

Disturbed behaviour is generally considered to be multifactorially caused and to be influenced by several motivational systems (Mason 1991, Rushen et al. 1993, Sato et al. 1994). In a system as complex as mammals, many different biological functions influence its coping capacity against potentially aversive, stressful conditions. Individual differences in the proneness to oral disturbances seem to be the rule rather than an exception (e.g. Redbo and Nordblad 1997). Going beyond the evaluation of eliciting environmental factors like small roughage intake or time-limited food access is difficult. Some considerations on possible explanations for mechanisms at work in the animal are presented in this section.

It seems to be common sense that the development of oral disturbances is due to a deprivation of behaviour related to metabolism. While deprivation of feeding behaviour is the only possibility in non-ruminating animals, in ruminants a deprivation of ruminating behaviour may have as severe consequences. Therefore, besides the suppression of feeding behaviour, suppression of ruminating behaviour can be considered as eliciting factor for oral disturbances in ruminants, too (e.g. Baxter and Plowman 2001).

Explanations for the development of oral disturbances can either focus on ethological or on physiological factors. An ethological explanation is characterised by the fact that not only the consequences of a behaviour are considered to be of importance to the animal but also the behaviour itself. The majority of authors has related oral disturbances to a deprivation of feeding behaviour. The argumentation can have its priority on the quantity (e.g. not enough time spent feeding) or complexity (a lack of certain tongue
or chewing movements) of feeding behaviour. Toates (1986) reports feeding behaviour to have an effect on determination of satiety per se, irrespective of stomach load. Results of Lindström and Redbo (2000) give evidence for an effect of feeding behaviour on the occurrence of oral disturbances in dairy cows.

Explanations focusing more on physiological factors assume that a deviation from normal physiological processes involved in ingestion and digestion of food may cause oral disturbances. A lack of bulky feeds and therefore a lack of digestive tract (and rumen) fill may induce oral activities (Lindström and Redbo 2000), a relation which has been shown for pigs (Robert et al. 1993). A possible relation between feeding behaviour/oral disturbances and the balance of the fermentation chamber has been addressed in horses: Wood chewing and coprophagy (Willard et al. 1973, 1977) and eating bedding, grasping, wood chewing and stall licking (Johnson et al. 1998) was considered to be related to low pH in the caecum. Another possible connection may be a lack of rumination (Baxter and Plowman 2001) and the corresponding lack of physiological consequences of this behaviour (e.g. saliva production).

The statement of Hughes and Duncan (1988) still seems to be valid: Results pointing to a negative correlation of roughage intake and oral disturbances can be due to a physiological requirement for roughage, an ethological need for oral manipulation or a combination of both. Lindström and Redbo (2000) and Johnson et al. (1998) also mention this difficulty to separate effects of physiology and behaviour. Results of Lindström and Redbo (2000) working with fistulated cows indicate that both ethological (feeding and ruminating activity) and physiological factors (rumen fill) can be of importance in the prevention of oral disturbances. Oral disturbances were lowest in cows having high rumen fill and long feeding and ruminating time (0.3 % (24 h)/3.6 bouts/24 h), intermediate in animals with high rumen fill/short feeding and ruminating time (1.8 % (24 h)/14.0 bouts/24 h) or vice versa (0.3 % (24 h)/11.4 bouts/24 h) and highest in animals having low rumen fill and short feeding and ruminating times (8.6 % (24 h)/34.9 bouts/24 h).

Every disturbed behaviour can either be seen as adaptive or non-adaptive. The interpretation as non-adaptive looks at oral disturbances only as a sign of discomfort of the animal. Among those to challenge this view was Wiepkema et al. (1987) who report beneficial effects of tongue-rolling on abomasal ulcers and scars in veal calves. The authors interpret this result as a consequence of the potential stress-coping effects of oral disturbances. The hypothesis of a potentially beneficial role is supported by Seo et al. (1998b) who measured a reduction of heart beat frequency during tongue playing in calves. More recently, the presumably saliva-inducing effect of oral disturbances (due to chewing and tongue movements) has received some attention in cattle (estimation of 24–144 L of saliva due to tongue playing; Redbo 1992) and horses (Nicol et al. 2002). Saliva is of high importance for the digestive system of the animal, e.g. for keeping the rumen system
stable by buffering short chain fatty acids produced by regular fermentation in the rumen (Van Soest 1994). In theory, the saliva induced by oral disturbances might help to alleviate the drop in rumen pH caused by the fermentation of energy-dense concentrate feeds.

The conclusion of this section is that different causal and functional explanations seem to be possible concerning the occurrence of oral disturbances. Further research is necessary to give a closer insight in the development of this behaviour in ruminants.

**Practical consequences in the zoo**

It seems that the black box “animal” does not always have to be unraveled completely, if one wants to react when confronted with a group or individual animals showing oral disturbances. The existing data suggest that in some cases, the occurrence of this behaviour can be reduced significantly by guaranteeing an *adequate intake of adequate roughage* by the animals.

At this point one should remember that feeding schedules and keeping systems for domestic cattle and zoo giraffids can differ considerably in the availability of roughage for the animals. The advice of Redbo and Nordblad (1997) to offer roughage on an *ad libitum* basis to reduce oral disturbances in cattle is being put into practice more or less in most facilities keeping giraffes or okapis. The animals have constant *ad libitum* access to alfalfa hay and can, theoretically, adjust hay intake according to their physiological/behavioural needs. Nevertheless, low intake of physically structured feeds has been reported for giraffes (Foose 1982, Haet al. 2005) and for browsing ruminants in general (Clauss et al. 2003a). According to Kolter (1995), in zoo-kept bison and banteng fed roughage-rich diets, oral disturbances are rarely observed compared to giraffe and okapi. The fact that the latter species may not always adjust roughage intake to their needs raises some questions about dietary planning in these animals. Obviously, the selection of a diet high in unstructured feeds by the animals – in the presence of *ad libitum* roughage – can have two reasons: either the concentrate is offered in too high amounts, or the roughage is avoided by the animal.

Unstructured feeds (mostly concentrates) are routinely offered to giraffes and okapis in considerable amounts. While this practice is sometimes questioned from the point of view of domestic ruminant nutrition, it has to be stated that especially giraffes have been reported to have problems meeting their energy requirements in some facilities (Fowler 1978, Junge and Bradley 1993, Clauss et al. 2001, Ball et al. 2002). Suitable compromises between feeding a diet high in concentrates and energy (and therefore increasing the probability of oral disturbances) and feeding a high amount of roughage (and therefore lowering dietary energy content to some extent) have to be found. Recommendations for the amount of roughage in the diet have been > 50% (okapis; Crissey et al. 2000) and 60–70% (giraffe and okapi; Lintzenich and Ward 1997). These recommendations can be difficult
to meet in practice since e.g. giraffe can be reluctant to consume alfalfa (or any other) hay in such proportions (Clauss, pers. obs.; Hatt et al. 2005).

The right kind of structured feed for browsing ruminants has been a constant source of discussion. Most authors agree that high quality roughage should be fed and that fresh browse is the preferred roughage of these species (e.g. Crissey et al. 2000). There are several reports of a decreasing effect of browse on oral disturbances (Sato and Takagaki 1991, Koene and Visser 1997, Bashaw et al. 2001), which has been related to the high effort of tongue- and chewing movements while eating browse (Sato and Takagaki 1991, Koene and Visser 1997). This view is supported by the finding that when browse was supplied pre-cut as leaves only, requiring minimal effort for ingestion, Schaub et al. (2004) did not observe an effect on the frequency of oral disturbances. The routinely used roughage for browsing species in zoos, alfalfa hay, is considered to be nutritionally more comparable to browse leaves and to be of higher quality than grass hay. The high occurrence of oral disturbances, especially in giraffes, raises the question whether diets with alfalfa hay as the single roughage properly meet the various demands on an adequate roughage supply to giraffids.

Despite doubts on the suitability of grass hay as a suitable single roughage source for giraffes because of a low intake by the animals (Foose 1982), two publications on giraffe report a decreasing effect of grass hay on oral disturbances in comparison to alfalfa hay. While in one of these grass hay was added to an existing diet (Baxter and Plowman 2001), the other compared the occurrence of oral disturbances 5 h after food administration with roughage changing from day to day (alfalfa hay, grass hay or a mixture of both) (Koene 1999).

Considering roughage quality one should keep in mind that Owen-Smith (1988) reports the percentage of woody material in rumen contents of giraffes to be as high as 15% during the dry season and 5% during the rainy season. Woody material generally is poorly digestible, and it is probable that this material elicits more rumination than comparably soft and small leaves. Pellew (1984) reports that in the wild, giraffes are considered to ingest fibrous roughage by feeding on old, broad-leaf foliage. Baxter and Plowman (2001) report from their two study animals that oral disturbances were much more prominent in the older female than in the younger male. Besides spending less time on feeding, the female rarely stripped bark from browse and trees compared to the male. Little is known about the rumination capacity of giraffes and okapis. To some extent, the physical structure of roughage or effective fibre has to be seen as a body size- and species-specific characteristic, e.g. small grazing or intermediate ruminants (sheep and goats) requiring a smaller particle size (1 mm) than large grazing species (cattle; 2–4 mm) for rumination (Van Soest 1996).

Among other candidates to be considered as adequate browser roughage are dried browse (e.g. Mosig 1980), browse silage (Nijboer et al. 2003), fresh alfalfa, fresh meadow grass/hay mix (Dierenfeld 1996) and chopped grass or the according grass silage (Clauss et al. 2003a). Some of them
may fulfil more the ethological, others more the physiological needs of the animals, e.g. as chopping hay may lead to increased hay intake, but decreased feeding effort.

Measures that are likely to increase roughage intake in general may be offering several different kinds of roughage at the same time or offering roughage in several small rather than in few large batches (Heller and Potthast 1990). Offering roughage in a way that stimulates more complex feeding behaviour, like hay in closed-top feeders, had a reducing effect on oral disturbances in the study of Bashaw et al. (2001). It is felt that despite some evidence for a reducing effect of a high proportion of roughage on oral disturbances, little is known about the causal factors of this relation. Further studies including roughage preference trials and trials quantifying the influence of different roughage on feeding and ruminating behaviour would be very helpful. These studies should include a quantification of food and energy intake on a herd or preferably on individual level.

Conclusion

Oral disturbances are a common phenomenon in zoo giraffes and okapis. While several models can be used to explain the development of this behaviour in ruminants, the exact chain of cause and effect is still to be found. This may be in part due to the multifactorial nature of this behaviour. Nevertheless most authors see a somehow restricted feeding routine as the by far most important factor. Data for domestic ruminants, giraffes and okapis combining quantitative ethological (quantity of oral disturbances) and nutritional (food intake) data point into this direction. The frequency of oral disturbances is increased by a high content of physically unstructured feeds in the diet. Monitoring of adequate roughage intake seems warranted if oral disturbances occur in conspicuous quantity in a giraffe or okapi group.

References


