2

Stereotypic Oral Behaviour in Captive Ungulates: Foraging, Diet and Gastrointestinal Function

R. Bergeron,[1] A.J. Badnell-Waters,[2] S. Lambton[3] and G. Mason[4]

[1]Département des Sciences Animales, Faculté des sciences de l'agriculture et de l'alimentation, Pavillon Paul-Comtois, Bureau 4131, Université Laval, Québec, G1K 7P4, Canada; [2]Equine Consultancy Services, Bridge Cottages, How Caple, Hereford, HR1 4SS, UK; formerly at the University of Bristol, Langford House, Langford, North Somerset, BS40 5DU, UK; [3]University of Bristol, Langford House, Langford, North Somerset, BS40 5DU, UK; [4]Department of Animal and Poultry Sciences, University of Guelph, Guelph, Ontario, N1G 2W1, Canada

Editorial Introduction

With millions of affected animals worldwide, ungulates are the most prevalent mammalian stereotypers. Agricultural ungulate stereotypies were also the first to attract serious scientific study. They therefore dominated the first edition of this book, and it seems probable that more individuals with stereotypies have now been studied in this taxon than in any other. Examples of the behaviours that Bergeron and co-authors consider here include crib-biting by horses, sham-chewing by sows and tongue-rolling by cattle and giraffes. Concerns about animal welfare and economic issues (e.g. stock value or productivity) have meant that many studies aimed to reduce these behaviours, rather than understand the niceties of their underlying mechanisms. Nevertheless, motivational explanations for ungulates' oral stereotypic behaviours have been developed, and to some extent tested. Ungulates are primarily herbivorous, and much evidence supports the hypotheses that their oral stereotypic behaviours derive from natural foraging. The forms of the movements are often similar, with some abnormal behaviours even involving ingestion (e.g. wood-chewing by horses); they typically peak with the delivery of food or end of a meal; and, like natural foraging, they are often reduced by factors increasing satiety. Thus, in practice, replacing captive ungulates' typically low-fibre, high-concentrate provisions with more naturalistic foodstuffs successfully reduces oral abnormal behaviour across a wide range of species. But what exactly is the link between natural foraging and oral stereotypic behaviour? This is less certain, and Bergeron and her colleagues review three principal hypotheses.

The first is that captive ungulates' diets do not fully satisfy them, because they give too little gut fill, are deficient in specific ways (e.g. too low in salt, protein or fibre), or supply too little energy (pregnant sows, for instance, are routinely fed a

fraction of what they would eat *ad libitum*). Stereotypic behaviours are then proposed either to stem from unlearnt, persistent attempts to find more food, or to be learnt behaviours that help redress the animals' underlying deficits (wood-chewing to gain fibre being one possible example). The second hypothesis is that captive diets take too little time to find, chew or ruminate, leaving animals with unfulfilled motivations to perform these natural foraging activities. If natural foraging is re-inforcing *per se*, quite independent of nutrient gain, then oral stereotypies can be seen as vacuum or redirected behaviours supplying at least some of the feedback normally provided by natural foraging. The third hypothesis is that oral stereotypic behaviour is not caused directly by diet quality or the minimal foraging that it requires, but instead by its consequences for gut function. Low-fibre, carbohydrate-rich foods have long been known to cause gastrointestinal dysfunction in ungulates, including gastric ulcers in horses and pigs and ruminal acidosis in cattle. More recently, experimental manipulations of both stereotypy performance and of gastrointestinal acidity have led to suggestions that oral stereotypic behaviours are a response to gut health, and perhaps even have some beneficial effects, for instance generating saliva that, if swallowed, helps to rectify gastrointestinal pH.

There is, however, evidence both for and against each of these hypotheses, and the next few years clearly need to see less *post hoc* explanation (valuable though such ideas have been) and more hypothesis-driven research, ideally combining a good physiological understanding of how various diets affect satiety and gastro-intestinal function, a better understanding of the aetiology of pathologies like ulcers, and a cross-species appreciation of the different modes of ungulate foraging behaviour. Indeed different forms of oral stereotypic behaviour may well prove to have different underlying aetiologies. Some further questions posed by this chapter are as follows: How do ungulates resemble pandas, chickens and walruses? Is it ethical to physically prevent horses from stereotyping, without first tackling the underlying causes of the behaviour? And last but not least, which of the many behaviours discussed here should we actually call 'stereotypies'?

GM

2.1. Introduction

Repetitive, seemingly functionless oral and oro-nasal activities are prevalent in captive ungulates. Indeed in contrast to other taxa, they are this group's typical abnormal behaviour (see Fig. 1.2, Chapter 1, this volume). Common examples include bar-biting and sham-chewing by sows, tongue-rolling by cows and crib-biting by stabled horses. Similar behaviours also occur in exotic ungulates in zoos, for instance object-licking by bongo antelopes (Ganslosser and Brunner, 1997), dirt-eating by Przwalski's horses (e.g. Hintz *et al.*, 1976) and tongue-rolling by giraffes and okapi (e.g. Koene, 1999; Bashaw *et al.*, 2001a). These behaviours have long caused concern, for both practical and welfare reasons. Crib-biting in horses, for example, increases energy expenditure and causes tooth wear (e.g. McGreevy and Nicol, 1998a), while oral stereotypies in sows similarly increase energy-use (Cronin *et al.*, 1986), reduce weight gain (Bergeron and Gonyou, 1997) and perhaps exacerbate the effects of food restriction on hunger levels (Rushen, 2003).

The occurrence of these behaviours has also prompted more funda-
mental questions about their ethological origins and putative functions.
Across multiple species, captive ungulates' oral behaviours often resemble
species-typical feeding movements, tend to be performed at high rates
around feeding and are usually affected by diet and the way that animals
are fed. This suggests they share a broadly common cause relating to
foraging behaviour. This chapter therefore reviews how similarities in
the feeding and foraging of free-living ungulates, and in the ways they are
fed in captivity, underlie these phenomena. We discuss the natural for-
aging biology of ungulates in Section 2.3, then review the various effects of
captive diet (especially fibre levels, calorific restriction, foraging time and
effects on gastrointestinal function) in Section 2.4. In Section 2.5, we
consider the possible functions of these behaviours. Because of their
strange appearance and apparent lack of function, stereotypic oral behav-
iours are often described as 'abnormal', even as 'vices' in horses (although
many dislike this term, e.g. Houpt, 1993). But are ungulate stereotypies
really malfunctional (in the sense of Box 1.4, Chapter 1, this volume), or are
they merely maladaptive – or even adaptive? In Section 2.6, we briefly
consider the possible contributory roles played by early experience (e.g.
early weaning), and the physical environment (e.g. restraint), before con-
cluding with a summary of the likely bases of ungulates' abnormal oral
behaviours, a discussion of their welfare significance, and suggestions for
further research. First, we look at the basics: what forms occur, how preva-
lent are they and why does their basic aetiology implicate foraging?

2.2. Prevalence, Nature and Possible Behavioural Origins of Stereotypic Oral Behaviour

The most common stereotypic oral behaviours in captive adult ungulates
are listed in Table 2.1 and shown on this book's website. Some of these are
unambiguously 'stereotypies', being repetitive, fixed in form and serving
no obvious function (*cf.* e.g. Ödberg, 1978; Mason, 1991). Others, how-
ever, are less clear cut: wool-chewing by sheep and wood-chewing in
horses, for instance, are relatively variable in form, have apparent goals,
and so are generally not classified as stereotypies (e.g. Nicol, 1999). To
reflect this diversity, here we use the term 'stereotypic behaviour' as a
broad descriptive term, encompassing all repetitive unexplained behav-
iours, even if not highly predictable from one movement to the next
(Chapter 10, this volume). Weaned infant ungulates also show oral stereo-
typies, but we generally do not discuss these in this chapter because they
seem to relate to frustrated suckling rather than adult foraging behaviours,
and their relationship with adult stereotypic behaviour is unclear.
Oral stereotypic behaviour can be very prevalent, i.e. occur in much of
the population. Prevalence figures often vary between studies, but neverthe-
less do help give a general idea of the scale of this issue. In horses, the
prevalence reported in six questionnaire surveys ranged from 0% to 8.3%
for crib-biting/wind-sucking, and 5% to 20% for wood-chewing (Canali and

Table 2.1. Common abnormal oral/oro-nasal behaviours in adult domesticated ungulates.

Stereotypic behaviour	Species	Description
Crib-biting or cribbing	Horses	Grasping the edge of a horizontal surface with the incisor teeth and pulling back, while drawing air into the cranial oesophagus and emitting a characteristic grunt (e.g. McGreevy et al., 1995c; Simpson, 1998). Air is not actually swallowed during cribbing, although the short column of air that remains in the upper part of the oesophagus after cribbing could be swallowed along with food (McGreevy et al., 1995c)
Wind-sucking	Horses	Same characteristic posture and grunt as crib-biting, but without grasping a fixed object (McGreevy et al., 1995c)
Wood-chewing	Horses	Grasping wood, and at least briefly chewing it (Johnson et al., 1998). Not generally considered a stereotypy, but may precede stereotypy development (Nicol, 1999)
Tongue-rolling or tongue-playing	Cows	Swinging of the tongue outside the mouth, from one side to the other, or repetitively rolling the tongue inside the mouth (Sambraus, 1985). Tongue-playing may also occur in their water-bowls (B. McBride; personal communication, Guelph, 2005).
Object-licking	Cattle, sows, sheep	Repetitive licking of non-food objects (e.g. Bashaw et al., 2001a). Tongue movements with contact, such as licking or biting at fences, walls or the food trough, have sometimes also been termed 'para-tongue-playing' (Seo et al., 1998)
Bar-biting	Sows, sheep, cows	Taking a bar (generally a pen fixture) in the mouth and biting on it (Sambraus, 1985)
Wool-biting	Sheep	Biting off and ingesting portions of fleece (e.g. Cooper et al., 1994). Not usually termed a stereotypy
Slat-chewing	Sheep	Nibbling at edges of slats and apparent ingestion of slithers of wood and/or faecal material (e.g. Cooper and Jackson, 1996)
Sham-chewing or vacuum-chewing	Sows	Chewing with nothing in the mouth. Often accompanied by gaping, and salivary foaming from the chewing motion (Sambraus, 1985). Tongue-sucking (Whittaker et al., 1999) may also be observed
Chain-chewing or chain manipulation	Sows	Chewing on a chain that has been installed experimentally as a focus for oral activities (so that they can be logged automatically; see Terlouw et al., 1991a). Sequences vary in their degree of stereotypy
Excessive drinking (polydipsia)	Sows	Drinking or manipulation of the drinker that exceeds physiological needs (Terlouw et al., 1991a; Robert et al., 1993). Drinker activities are often performed in a ritualistic way and incorporated into sequences of stereotypic activities, such as chain-chewing or bar-biting

Borroni, 1994; McGreevy *et al.*, 1995a,b; Luescher *et al.*, 1998; Redbo *et al.*, 1998; Bachmann and Stauffacher, 2002). Waters (2002) summarized such studies to yield a median prevalence of 3.1% for cribbing/wind-sucking, and 12% for wood-chewing, figures which translate into well over a million affected individuals, given ca. 15 million horses in the developed world alone (e.g. Mason and Latham, 2004). One study of cows reported that 40 out of 95 stabled dairy cows (42%) showed stereotypies (Redbo *et al.*, 1992), mostly tongue-rolling (although this figure is probably higher than the norm; J. Rushen, personal communication; Agassiz, 2005). A survey of giraffids reported higher prevalence rates still, with 72.4% zoo animals (214 giraffes, 29 okapis and 14 unspecified individuals) showing repetitive object-licking (Bashaw *et al.*, 2001a). A few studies also report prevalence for pregnant sows. Although often based on small populations, they suggest high rates, ranging from 28% (7/25 sows; Rushen, 1984) to 100% (117/117 sows; Cronin, 1985). Mason and Latham (2004) used such papers to generate a median prevalence of 91.5%, from which they estimated that over 15 million sows across Europe and North/Central America show these behaviours.

As well as being prevalent, oral stereotypic behaviour may be time-consuming. For example, horses can spend up to 8 h crib-biting each day, performing around 8000 bites (e.g. McGreevy and Nicol, 1998b; McGreevy *et al.*, 2001a), while in other species, even the average animal may spend several hours daily in such behaviours. Thus on one site, tethered cows spent 1% to 38% of a 24-h period stereotyping (Redbo, 1990; see also Redbo, 1992), although another study put the figure far lower, at 1–2% (Bolinger *et al.*, 1997). Likewise, pregnant sows spent from 7% (Broom and Potter, 1984) to 55% (Von Borell and Hurnik, 1990) of an 8-h observation period in oral stereotypies; while one female giraffe spent more than 40% of the night-time hours licking and tongue-playing (Baxter and Plowman, 2001).

So what are the origins of such behaviours? Perhaps tellingly, forms of dietary manipulation that reduce such levels of stereotypy in farmed pigs (increased fibre and/or increased calories, as we review later), do likewise for more natural foraging behaviours directed at grass, soil and stones in sows outdoors (see Braund *et al.*, 1998; Horrell, 2000). This suggests that oral stereotypic behaviour might be related to natural foraging. Its form and timing further implicate frustrated natural foraging. It often physically re-sembles natural foraging movements, with species feeding with tongue-sweeps, such as cattle or giraffes, developing stereotypic tongue movements (e.g. Bashaw *et al.*, 2001a), but sheep, goats, horses and pigs instead showing biting/chewing behaviours (e.g. Terlouw *et al.*, 1991a; Waters *et al.*, 2002). In cattle, abnormal oral behaviours even show developmental changes that parallel natural changes in foraging mode, with young calves sucking their tongues in a manner akin to normal suckling, but adults showing the curling and uncurling tongue movements typical of grazing (Fraser and Broom, 1990). Furthermore, as we have seen, some forms of oral stereotypic behaviour involve ingestion, e.g. of non-food solids or of water.

These behaviours also often have a close temporal association with feeding. In horses it may intersperse with food-ingestion (e.g. Kennedy

et al., 1993), and in many species, when food is presented in meals, stereotypic behaviour peaks around the time of delivery. However, typically it is then displayed most frequently after the food has been consumed (e.g. reviewed by Mason and Mendl, 1997). Post-feeding peaks have thus been observed in pigs (reviewed by Mason and Mendl, 1997; also Robert *et al.*, 1993, 1997; Spoolder *et al.*, 1995); giraffes (e.g. Veasey *et al.*, 1996; Tarou *et al.*, 2001); horses (e.g. Kusenose, 1992; Kennedy *et al.*, 1993; Gillham *et al.*, 1994); cattle (e.g. Sambraus, 1985; also see Fig. 2.1a); and sheep (see Fig. 2.1b). The stereotypies may be prompted by food-ingestion itself (see Terlouw *et al.*, 1993), although ingestion is not essential (see Mason and Mendl, 1997). Interestingly, in the wild, free-living giraffes also briefly show tongue-playing after feeding or drinking (Veasey *et al.*, 1996); while in wild boar housed in semi-natural enclosures, food-ingestion is also followed by rooting, and chewing at vegetation (Horrell, 2000). In Fig. 2.1b, also note the contrast in timing to the locomotor stereotypies seen pre-feeding (see Chapter 3, this volume for similar pre-feeding behaviour in captive carnivores).

Next, we discuss the experimental and epidemiological evidence for a role of frustrated foraging. We begin by discussing the natural biology of ungulates, to identify what is constrained in captivity. After all, when naturalistic foraging is impossible for caged primates or carnivores, they seldom show the extensive sham-chewing or tongue movements so typical of ungulates (e.g. Mason and Mendl, 1997; Mason, in press), suggesting that biological predispositions do play an important role.

2.3. The Natural Foraging Biology of Ungulates and How Captivity Affects It

2.3.1. The natural foraging biology of ungulates

The obvious foraging characteristic shared by ungulates is herbivory (although pigs are more correctly omnivores). Although different species vary in their relative use of grass, broad-leaved plants and/or other types of plant material (e.g. roots), and vary too in attributes like their selectivity (e.g. Van Soest, 1994), in general herbivory has several broad implications for how they naturally find and process food. The first is that because vegetation typically needs bulk-ingestion for nutrient gain, ungulates naturally spend many hours foraging. For instance, dairy cows on pasture spend nine or more hours grazing daily, and, pooling this 'prehension' with rumination, take over 72,000 bites a day (Linnane *et al.*, 2004; Newman, in press), while horses may graze for up to 16 h (e.g. Fraser and Broom, 1990). In the wild, giraffes spend 40–80% of the day browsing (Veasey *et al.*, 1996; Ginnett and Demment, 1997). In semi-natural environments, wild boars spend a quarter to a third of the day foraging and rooting (Blasetti *et al.*, 1988; Horrell, 2000); while domesticated pigs spend 22% to 28% of the day foraging, or 50% of their active time (Stolba and Wood-Gush, 1989; Buckner *et al.*, 1998).
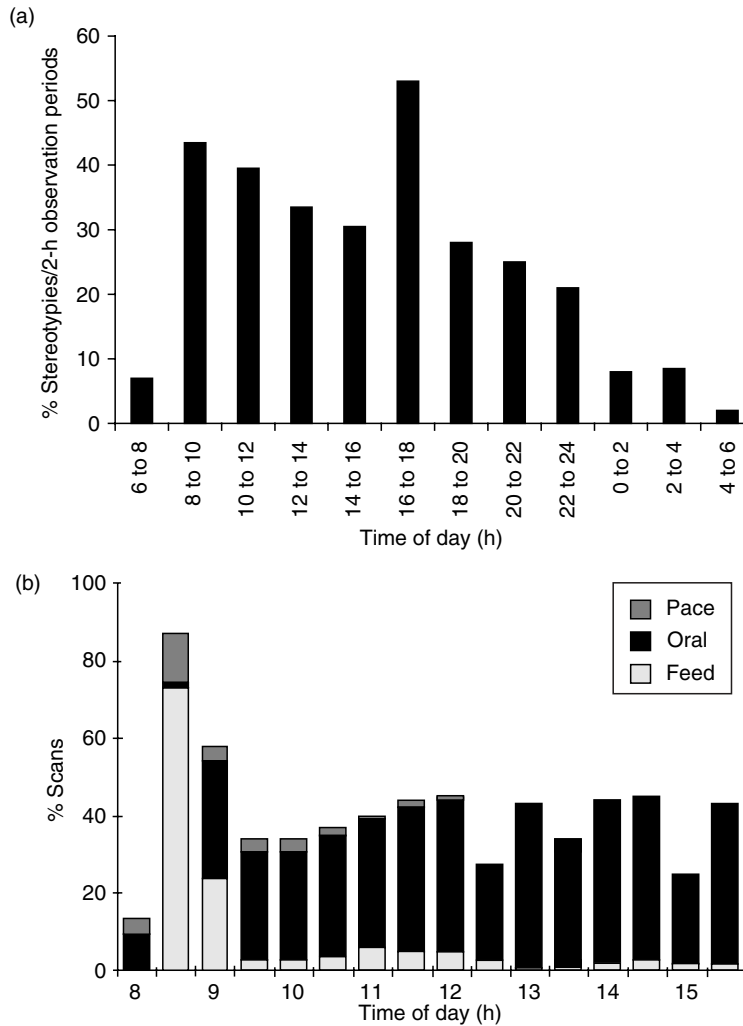
Fig. 2.1. (a) Average percentages of time spent in stereotypies by cows during 2-h observation periods across the day. Animals were fed at 06:00 and 13:30 h, and thus stereotypies increased within 2–4 h after feeding (adapted from Redbo, 1990). (b) The percentage of scans engaged in locomotor stereotypy (pacing), feeding and oral stereotypic behaviour (bar-biting, slat-chewing, wool-pulling) over the day. Data came from 30 restrictively fed lambs at 25 weeks of age. The lambs were singly housed, and received a low fibre pelleted feed at approximately 08:30 h each day and no supplementary forage. Most lambs consumed this ration within 45 min of delivery (from Cooper *et al.*, 1994). Thus oral stereotypic behaviour was relatively low pre-feeding, but pacing was relatively high.

The second implication of herbivory is that natural food is typically found in small, bite-sized portions, which may occur in clusters, e.g. one bush may be rich with leaf buds, another not. This may lead to local food-search being stimulated by ingestion: particulate food that occurs in

Box 2.1. Ungulate Ingestion and Digestion: Anatomical and Physiological Adaptations for Herbivory and their Behavioural Implications

S. LAMBTON and G. MASON

Ungulate digestion relies on cellulose digestion by micro-organisms in the gut. Ungulates are either pre-gastric fermenters (ruminants, e.g. cattle, sheep, goats, giraffes and camels), or post-gastric fermenters (e.g. horses, tapirs, rhinoceroses and to a lesser extent pigs). Adult ruminants are polygastric, with a three- or four-chambered stomach. In the latter species (e.g. the cow) these are the rumen, reticulum, omasum and abomasum (or true stomach), while camelids lack the omasum (e.g. Robbins, 1993; Van Soest, 1994). The rumen is the first chamber, and is a fermentation 'vat' of active bacteria, protozoa and fungi. Digesta is processed further in the reticulum, from which it is regurgitated as 'cuds'. After rumination, food passes back to the rumen for additional fermentation, before passing to the omasum for further mechanical processing, and then to the 'true stomach' or abomasum, where ruminal microorganisms are digested (e.g. Schmidt-Nielson, 1997). This type of digestive apparatus has several behavioural implications. First, non-foraging mouth movements in the form of rumination are a key part of the behavioural repertoire; e.g. occupying 6–8 h/day in cattle (Phillips, 2002); interestingly, such rumination can be accompanied by non-REM sleep (reviewed by Tobler and Schweirin, 1996). Second, the types of food selected and its intake rate affect ruminal microbial action: constraints which help shape ruminant foraging behaviour (e.g. Newman, in press). Third, because fermentation generates organic acids, ruminal pH must be controlled to protect the stomach and sustain microbial fermentation. This is largely achieved via salivation, which peaks during chewing and rumination (e.g. Meot *et al.*, 1997), the salivary bicarbonates and phosphates acting as buffers when swallowed (e.g. Sauvant *et al.*, 1999). Fourth, stomach development is itself shaped by the food ingested. In calves, for example, the digestive tract only fully develops post-weaning, the rumen not beginning to function until animals begin consuming solids (Van Soest, 1994). Thus if fed non-naturalistic foodstuffs, rumino-reticulum development is altered, e.g. zoo giraffes can show grazer-like reduced ruminal surface areas and very well-developed reticula, compared with wild, naturally browsing conspecifics (Hofmann and Matern, 1988).

Post-gastric fermenters have a simple stomach, and most mechanical processing of plant cell walls takes place in the mouth. Digestion is also initiated through chewing, by enzymes in the saliva (Pough *et al.*, 1989). Digesta then undergoes microbial fermentation in the caecum, which is enlarged to create a fermentation chamber and in horses comprises, together with the colon, around 60% of the alimentary canal (Frape, 1998). This type of digestive apparatus has two main behavioural implications: chewing the ingested food is an important part of processing, and thus these ungulates typically spend more time foraging than ruminants (e.g. Fraser and Broom, 1990) (if one excludes rumination from foraging time); and food intake rate – and passage rate – is relatively fast. Thus, in both ruminants and post-gastric fermenters, chewing-type oral movements are an important part of the behavioural repertoire.

Saliva is thus important in ungulate feeding. As well as the buffering and enzymatic functions described above, in some ungulates (notably browsers) it contains proteins that bind to plant tannins that would otherwise be detrimental (e.g. Fickel *et al.*, 1999; Clauss *et al.*, 2005). Browsers specializing in tanniferous plants also have much salivary urea recycling (Van Soest, 1994). Small wonder then that vast amounts of saliva are secreted during normal foraging: sheep may produce 6–16 l a day, and cattle, up to 100–190 l (Schmidt-Nielson, 1997). Horses also produce fairly large amounts, up to 10–12 l a day, which even in these non-ruminants helps buffer stomach acidity (Frape, 1998; reviewed by Nicol *et al.*, 2002). Finally, ungulate teeth are also adapted for herbivory, cheek teeth being high-crowned so that deep peaks and folds of enamel and the softer dentine wear differentially with use,

Continued

Box 2.1. *Continued*

forming effective grinding ridges. In some ungulates, e.g. the horse, cheek teeth are also 'open-rooted' and continuously growing (e.g. Young, 1981; Pough *et al.*, 1989), while in a few (e.g. the vicuna; Bonacic, 2005) even incisors show continual growth. Behaviourally, this means that chewing plays important roles in maintaining tooth function. Some authors even suggest that certain specialized chewing movements occur specifically to facilitate appropriate tooth wear, e.g. in sheep (Every *et al.*, 1998), although this idea is controversial (Murray and Sanson, 1998). Overall, these oral and gastrointestinal adaptations broadly mean that for ungulates, foraging movements often have functions beyond direct nutrient intake, acting also to maintain the ideal functioning of the teeth and/or gut.

patches often stimulates local search, especially if it is also rather cryptic and unlikely to flee while being searched for (Bell, 1991). Thus in wild boars, for example, stomach content analysis shows that they typically consume a lot of just one single food type at once, even though over time they eat a very diverse array of food items; and ingesting a small amount of food does promote further feeding and foraging (reviewed by Mason and Mendl, 1997; see also Horrell, 2000). To some extent, this dietary 'patchiness' may even hold for what look to us like uniform swards, because a third implication of herbivory is that ungulates are selective, responding to both specific nutrient deficits and gut functioning by carefully choosing the items they eat on the basis of fibre, sugar, mineral and/or nitrogen content (e.g. Newman, in press). Thus grazing sheep, for example, preferentially select either clover or grass at different times (Newman, in press; *cf*. Rutter *et al.*, 2004 on cattle). The fourth implication of herbivory is that ungulates have sophisticated adaptations for dealing with cellulose, tannins, silicates and other plant defences, especially specialized teeth, salivary glands and gastrointestinal tracts. These, and their behavioural implications, are reviewed in Box 2.1.

Together, it seems likely that these aspects of natural foraging are what make captive ungulates' abnormal behaviours so distinctive. Cross-species comparisons give further support to this idea (see Box 2.2). As yet, we know little about the relative roles played by ungulates' anatomical, physiological and behavioural adaptations, and indeed this may differ between species. We can, however, analyse how together these shape the likely impact of captive feeding regimes.

### 2.3.2. Effects of captivity on ungulate feeding, foraging and gut function

The precise feeding regime of captive ungulates varies with their natural food preferences or habits, the availability of natural foods, and economic constraints (see e.g. Henderson and Waran, 2001). In agricultural animals, it is also affected by their stage in the production cycle (e.g. pregnant sows are fed differently from lactating sows). However,

Box 2.2. Do Ungulate-like Natural Foraging Styles Lead to Ungulate-like Stereotypies in Other Animals?

G. MASON

If oral post-feeding stereotypies stem from naturally time-consuming foraging styles, from feeding on small, static, clustered food items, or even from herbivory *per se*, then they are unlikely to be unique to ungulates. We might expect them in any animal whose natural foraging behaviour has one or more of these traits, if it is fed non-naturalistically in captivity. So far, every post-feeding oral stereotypy reported outside of the ungulates does fit this pattern. Intensively farmed, trough-fed chickens thus display post-feeding spot-pecking, especially when food-deprived (reviewed by Mason and Mendl, 1997, who also review similar post-feeding spot-pecking in pigeons). Their less stereotyped, but still abnormal, 'feather-pecking' has also been reported after feeding (Blokhuis, 1986). Naturally, their wild equivalents spend much time foraging for seeds, invertebrates and vegetation (e.g. devoting 60% of their activity to ground-pecking) (reviewed by Mason and Mendl, 1997). Post-feeding oral stereotypies like paw-sucking and tongue-flicking are also fairly common in captive giant pandas, Asiatic black bears and sun bears, especially if fed non-naturalistic meals based on rice, bread or milk (Vickery and Mason, 2004; Swaisgood *et al.*, a,b in press). In the wild, giant pandas naturally spend a large proportion of their time (e.g. 14 h a day) seeking and eating shoots and leaves, while Asiatic black bears and sun bears do likewise for fruits and other vegetation, sun bears additionally consume small invertebrates (e.g. reviewed by Schaller *et al.*, 1989; Vickery and Mason, 2004). Our last case is the walrus. For decades, captive walruses have been reported performing repetitive oral behaviours like flipper-sucking, or repetitively rooting and sucking at the concrete of their pools (sometimes wearing their tusks down to stumps; e.g. Coates, 1962; Hagenbeck, 1962; Kastelein and Wiepkema, 1989; Kastelein *et al.*, 1991; see image on website); and a recent study reveals that these oral behaviours, too, peak post-feeding (D. Reiss, personal communication, New Orleans, 2004; Reiss *et al.*, in preparation; see figure).

Pre- and post-feeding oral stereotypies in four adult walruses in an aquarium setting
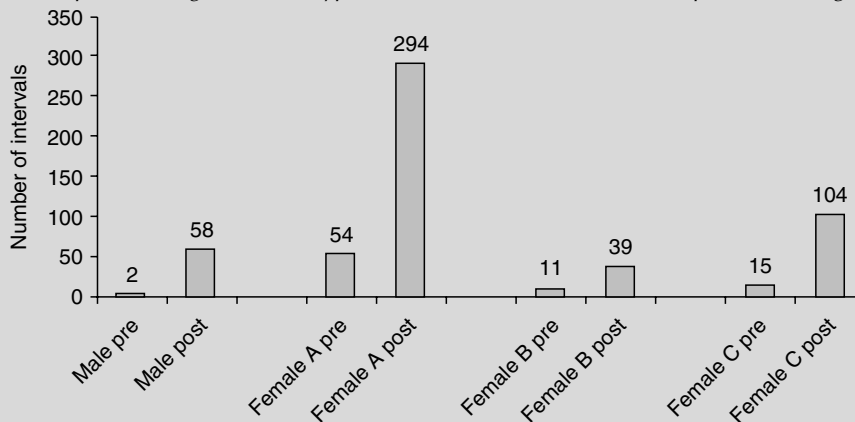
Although far from herbivorous, sure enough the walrus's natural foraging style is ungulate-like, with animals 'grazing' on patches of marine invertebrates rooted up from the seabed. This takes several hours a day, with many hundreds of small items being processed and eaten (e.g. Fisher and Stewart, 1997; Born *et al.*, 2003), and contrasts greatly with the rapidly eaten fish-based meals typical of captivity (e.g. Kastelein *et al.*, 1991).

Continued

Box 2.2. *Continued*

Adding these six species to our 'ungulate foraging story' is of course a long way from properly testing the hypothesis (*cf.* Box 3.2, Chapter 3 on cross-species comparisons), but it is intriguing. Further data are now needed (perhaps from manatees? aardwolves? rodents? the marsupials?) to see how consistently such stereotypies really do relate to natural foraging style, and to pinpoint what aspects of feeding motivation, behavioural time-budgets or even gastro-intestinal physiology are the specific predictors.

feeding and foraging in captivity typically differ in three ways from naturalistic situations.

2.3.2.1. Dietary preferences and/or needs may be unfulfilled, leaving the animal motivated to feed

Captivity often constrains the amount or composition of food that can be ingested. An extreme case is the pregnant sow, which is routinely food-restricted (to control weight gain, and maximize food intake when lactating; e.g. Cole, 1982; Mroz *et al.*, 1986). These animals are usually given just 2.5 kg of food daily: half or even a third of what they would eat *ad libitum* (Ramonet *et al.*, 1999; Bergeron *et al.*, 2000), resulting in prolonged high levels of frustrated feeding motivation (e.g. Lawrence and Illius, 1989). Brief periods of food restriction are also imposed on other captive ungulates (e.g. horses before a race; e.g. Murray, 1999; Merial, 2004), constraining natural meal patterning. Captivity often thwarts specific motivations for particular food-stuffs too. For example, both sheep and cattle select different diets (e.g. ones containing more fibre) during sub-acute ruminal acidosis (e.g. Keunen *et al.*, 2002), while free-ranging horses voluntarily select soils high in copper and iron for geophagia (e.g. McGreevy *et al.*, 2001b), and pigs with a choice select dietary protein levels in a state-dependent manner (reviewed by Lawrence *et al.*, 1993). Intensive housing conditions, however, generally prevent animals from expressing or satisfying such preferences.

2.3.2.2. Fewer behavioural demands are made on the animal, affecting the foraging time-budget

On farms and in zoos, homogeneous foodstuffs such as hay, browse or man-made diets (e.g. milled, low-fibre mash or pellets) are typically presented directly to the animal, in a single manger or trough. Thus food-search, and even consummatory behaviours like chewing, take a fraction of the time they would naturally. This effect is even more marked if food is restricted in quantity. Thus pregnant sows consume their daily meal of concentrate (a low-fibre food made of grain and protein-rich ingredients) in under 20 min (Ramonet *et al.*, 1999, 2000a); while concentrate-fed stabled horses may spend just 2 h feeding (Kiley-Worthington, 1983), or even as little as 20–30 minutes (Henderson and Waran, 2001). For ruminants, the situation differs further in that less time is also spent on rumination when fed concentrates, compared with diets high in natural forage (e.g. Abijaoude *et al.*, 2000;

Lindström and Redbo, 2000; Baxter and Plowman, 2001). This could be important because natural foraging activities can be intrinsically rein-forcing, regardless of nutrient gain (e.g. Wood-Gush and Beilharz, 1983; Hutson and Haskell, 1990; Mason *et al.*, 2001).

2.3.2.3. Captive diets may detrimentally affect gastrointestinal function

Low fibre, high carbohydrate concentrate diets can cause gastrointestinal acidity, and thence potentially mucosal damage (especially in mono-gastrics' stomachs) and/or acidosis (especially in ruminants, where ruminal contents become overly acidic, impairing proper fermentation). Sub-acute acidosis seems very prevalent (e.g. 20% of dairy cows; Oetzel, 2003), and such processes are well understood for ruminants. Here, dietary concentrates decrease ruminal pH by increasing fermentation (e.g. Sauvant *et al.*, 1999; Schwartzkopf-Genswein *et al.*, 2003) and reducing chewing and rumination (e.g. Abijaoude *et al.*, 2000) thence decreasing salivation (e.g. in cattle, to around two-thirds the levels secreted when grazing; Bauman *et al.*, 1971; see also Hibbard *et al.*, 1995; Meot *et al.*, 1997). Processed, low-fibre diets also cause gastrointestinal acidity in horses and pigs. Thus in horses, grain feeding can cause hindgut acidosis (e.g. Rowe *et al.*, 1994; Johnson *et al.*, 1998), while both concentrate feeding (Rowe *et al.*, 1994; Murray, 1999) and periods of food deprivation (Murray and Eichorn, 1996) increase gastric acid secretion and can cause foregut ulcers (e.g. reviewed by Nicol, 2000; Nicol *et al.*, 2002). Such lesions are very prevalent: in some breed/management groups (e.g. racehorses) they occur in the majority of individuals (e.g. reviewed by Murray, 1999; Merial, 2004). Like-wise, stomach ulceration is common in commercially kept pigs; for example, in sows, O'Sullivan *et al.* (1996) reported a mucosal lesion preva-lence of 60%, and Hessing *et al.* (1992) 63%; whereas in young slaughter pigs, Ayles *et al.* (1999) report gastric ulceration in 32–100% of animals, and Hessing *et al.* (1992) 36%. Again these problems are associated with a lack of fibre, small dietary particle sizes, pellet feeding and restricted feeding (e.g. Wondra *et al.*, 1995; and reviewed by Blood and Radostits, 1989).

2.4. What Aspects of Captive Feeding Regimes Cause Oral Stereotypic Behaviour?

In the following sections, we analyse which of these aspects of captive diets underlie abnormal behaviour. We begin with a caveat: many data come from non-experimental studies, e.g. those reliant on cross-site comparisons; and even when they do come from experiments, the research goals were often practical (e.g. aiming to reduce stereotypy, or improve welfare) rather than hypothesis-testing. Furthermore, much of this work predates recent sugges-tions about the role of gut dysfunction. Thus it is often unclear exactly *how* effects are mediated. Consequently, we start by simply illustrating the effects

of the typical high-concentrate, low-bulk diets on ungulate oral abnormal behaviour (see Section 2.4.1). We then lead on with three sections that try and tease apart the roles of: dietary deficits that leave the animal with unfulfilled motivations to ingest (*cf.* Section 2.3.2.1, above); altered time-budgets, especially, reduced foraging and rumination times (*cf.* Section 2.3.2.2) and gastrointestinal dysfunction (*cf.* Section 2.3.2.3). We do this partly by analysing the 'high-fibre diet' research in more detail, but also by drawing on further evidence from other types of manipulation.

2.4.1. The effects of high concentrate, low-fibre diets

Many authors have shown that ungulate stereotypies increase with the proportion of concentrated food in the diet. For example, lambs fed a concentrate-based diet perform more bar-biting, licking and wool-eating, than those receiving lucerne (Cooper *et al.*, 1995); in heifers, decreasing the proportion of forage, and increasing concentrates (while maintaining the energy content constant) increases the frequency of tongue-rolling, bar-biting and chain-chewing (Redbo and Nordblad, 1997); and in giraffes, feeding more fibrous forms of hay and/or adding forage (Koene, 1999; Bashaw *et al.*, 2001a; Baxter and Plowman, 2001) reduces tongue-playing.

Turning to non-ruminants, surveys of horses show that feeding forage in large or frequent amounts, rather than more concentrated diets, is associated with a reduced prevalence of abnormal behaviours including crib-biting and wood-chewing (McGreevy *et al.*, 1995a; Redbo *et al.*, 1998). A more recent study also reveals that foals receiving concentrates are four times more likely to develop crib-biting than other foals, while the feeding of hay replacers (fermented forages that are energy dense, so fed in relatively low quantities) instead of bulkier, higher-fibre hay, significantly increases wood-chewing (Waters *et al.*, 2002). Further-more, the behaviours emerge soon after weaning, a process typically involving a switch to concentrate foods, with crib-biting initiated at a median age of 4.6 months, and wood-chewing, 7 months (see Fig. 2.2).

In experimental studies, Dodman *et al.* (1987) also found that feeding horses grain or sweetened grain rations increased crib-biting, whereas lucerne pelleted hay had no such effect on the behaviour.

Pigs, especially pregnant sows, have received even more attention. High-fibre diets such as those based on oat hulls reduce chain-manipulating (Robert *et al.*, 1993, 1997, 2002); pre- and post-feeding stereotypies like sham-chewing and head-waving (Ramonet *et al.*, 1999); and post-feeding vacuum-chewing and the stereotypic rubbing or biting of stall fittings (Robert *et al.*, 2002). Post-feeding chain-chewing was reduced by an oat bran diet even if lower in energy than a concentrate-based control diet (though pre-feeding chain-directed stereotypies were only reduced by an oat bran, full calorie diet) (Robert *et al.*, 1997). Furthermore, feeding gilts a restricted diet with sugarbeet pulp not only
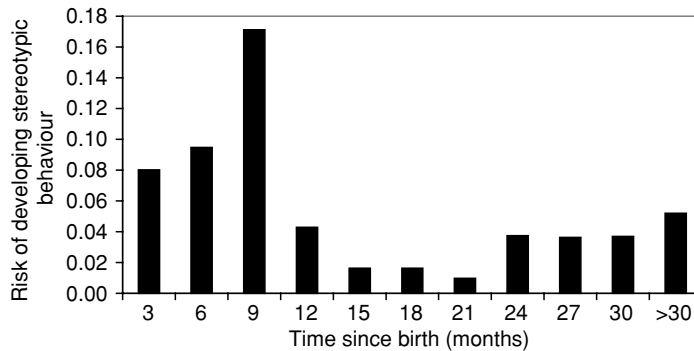
Fig. 2.2. The risk of developing a new form of stereotypic behaviour in horses at different ages. Most foals were weaned between 4 and 6 months of age (adapted from Waters *et al.*, 2002). On a finer timescale than can be seen from the figure, weaning (with its associated husbandry changes, including dietary ones), occurred at 15–35 weeks, and the emergence of new stereotypies peaked at 40 weeks. Note that the fall in risk evident from 12 months onwards thus does not indicate a decrease in the performance of existing stereotypies, merely a decline in the emergence of new ones.

reduced the incidence of post-feeding oral stereotypic licking, bar-biting and sham-chewing, but also rendered these behaviours less fixed in form (Brouns *et al.*, 1994). Figure 2.3 gives some illustrative data. Next, we move on to discuss the possible reasons as to why these low-fibre diets – and other types of dietary divergence from naturalistic foraging – promote stereotypic behaviour.
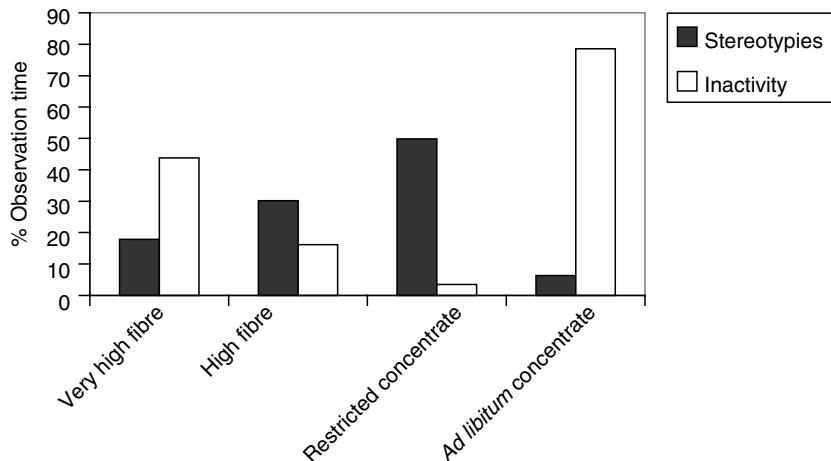
Fig. 2.3. Effect of fibrous and concentrate (restricted or *ad libitum*) diets on the percentage of time spent in stereotypic behaviours and inactive by pregnant sows in the 2-h post-feeding period. The crude fibre content was 23%, 18.2% and 5.3% for Very high fibre, High fibre and Control diets, respectively. Behaviours are expressed in median percentage of time remaining once feeding time has been removed (adapted from Bergeron *et al.*, 2000).

2.4.2. What are the roles of dietary deficits, or unfulfilled preferences, that leave animals motivated to feed?

Concentrate-based diets may fail to induce satiety, even when they meet nutritional needs, due to insufficient gut fill; thus animals fed such diets might remain motivated to eat. It is also possible that in these examples, and elsewhere too, specific appetites or food preferences are not met, playing a further role in stereotypy. Yet other cases still suggest that simple calorific deficits are also important.

2.4.2.1. Unfulfilled feeding motivations due to low satiety in low-fibre fed animals

Nicol (1999) hypothesized that in horses, hay reduces the risk of developing abnormal oral behaviour by reducing the feeding motivations via gut fill. Certainly for pigs, we know that stereotypy-reducing high-fibre diets promote short-term satiety. This is due to stomach distension (e.g. Lepionka *et al.*, 1997) plus altered nutrient absorption rates and post-meal blood concentrations of glucose, insulin and acetate (Rushen *et al.*, 1999; Ramonet *et al.*, 2000a). This satiety is often manifest in fewer postural changes, increased resting time around mealtime and reduced rooting-/foraging-like behaviours, e.g. to straw (e.g. Brouns *et al.*, 1994; Whittaker *et al.*, 1998). A negative relationship between diet bulk and feeding motivation in the post-feeding period has also been measured (Day *et al.*, 1996). In one study, high fibre fed sows even put on more weight, even though calorie intake was the same as on a control, concentrated, diet, perhaps because animals were less active (Ramonet *et al.*, 1999; though *cf.* Whittaker *et al.*, 1998). The stereotypy-reducing sugarbeet pulp, for example, causes a rapid satiety still present 2 h after the meal (Brouns *et al.*, 1997). Using operant conditioning tests for feeding motivation, Robert *et al.* (2002) also reported a lower feeding motivation both before the morning meal and after the afternoon meal, in gilts fed oat hull and lucerne diets compared to concentrate. Despite the general positive effects of high-fibre diets, however, some authors failed to find that they reduced feeding motivations (Bergeron *et al.*, 2000; Ramonet *et al.*, 2000b). Apparent discrepancies between studies may be explained by differences in the age of animals, methods of assessing hunger or the timing of measurement. For instance, reduced feeding motivations with high-fibre diets are often present only in the few hours after eating (e.g. Day *et al.*, 1996; Robert *et al.*, 1997; though *cf.* Robert *et al.*, 2002). This could explain why some high-fibre diets only reduce post-feeding stereotypies but not those that appear before the next meal.

Overall, the 'dietary fibre' studies of pigs thus suggest that hunger-reduction does correlate with stereotypy-reduction, but that fibre alone is often insufficient to achieve this around the clock: in the longer term, it seems that energy level is more important. They also suggest that motivations to ingest more nutrients are indeed important in stereotypy. Thus despite their high gut fill, high-fibre diets are less effective at reducing oral

behaviour than are conventional diets served *ad libitum* (Bergeron *et al.*, 2000; see Fig. 2.3). In Section 2.4.2.2, we therefore ask – are calories the key?

2.4.2.2. *Unfulfilled feeding motivations due to energy-restriction*

The most striking evidence for a role of energy-restriction comes from pregnant sows: energy-deficits play a major role in these animals' oral stereotypies (e.g. Appleby and Lawrence, 1987; Terlouw *et al.*, 1991a). Thus their stereotypies are usually greatly reduced when their daily food allowance of concentrate is increased (Appleby and Lawrence, 1987; Terlouw and Lawrence, 1993; Bergeron *et al.*, 2000). Furthermore, providing sows with 1.7 times as much digestible energy – despite no more dietary bulk – significantly reduced vacuum-chewing (Bergeron and Gonyou, 1997). Restricted feeding also increases stereotypies even when time spent foraging is statistically corrected for, suggesting that hunger, not just feeding time, really is important for sows (Spoolder *et al.*, 1995). The role of food restriction in stereotypies has also been investigated in ruminants. The restricted feeding of a total mixed ration (i.e. mix of concentrate and forage) compared to *ad libitum* feeding, increased the level and prevalence of oral stereotypies in dairy cattle (Redbo *et al.*, 1996; Lindström and Redbo, 2000). Similarly, food-restricted lambs performed more slat-chewing, wool-biting and repetitive-licking (Cooper *et al.*, 1994).

2.4.2.3. *Unfulfilled feeding preferences due to specific dietary deficits*

Specific deficits are also implicated in some abnormal behaviour. Bar-biting and slat-chewing by lambs was specifically increased by protein restriction (e.g. Whybrow *et al.*, 1995). Anecdotally, deficits of copper, manganese or cobalt can likewise induce tongue-rolling in cattle (Sambraus, 1985). Salt blocks also anecdotally reduce crib-biting in horses (Fraser and Broom, 1990), while in dairy cows, experimentally increasing the salt (NaCl) levels in concentrate diets reduced oral stereotypies (Phillips *et al.*, 1999).

2.4.2.4. *Frustrated ingestion in animals fed small amounts of motivating food*

Feeding motivations can be stimulated not just by baseline internal state but also by external stimuli associated with food delivery. Although infants are not the focus of our review, this issue has been best explored in calves, where the ingestion of a small amount of milk enhances suckling motivations, and in the absence of a teat, promotes object-sucking (e.g. De Passillé *et al.*, 1993). Thus Dodman *et al.* (1987) and Gillham *et al.* (1994) proposed that sweetened grain triggered oral stereotypies in horses because it is so highly palatable (although their proposed mechanism for the link was molecular rather than motivational). A related idea was proposed by Lawrence and Terlouw (1993), who suggested that the small amount of food offered to pregnant sows is not only insufficient to reduce hunger, but actually *increases* short-term feeding motivations.

This hypothesis was inspired by findings that feeding facilitates itself by positive feedback (Wiepkema, 1971), and that food-ingestion specifically prompts stereotypies (see Terlouw *et al.*, 1993). Interestingly, as low-fibre diets are less palatable to sows (Bergeron *et al.*, 2002), this could be an additional reason why they reduce post-feeding stereotypies.

2.4.2.5. Summary and potential explanations

Nutrient deficits and feeding motivations clearly potentiate ungulate oral stereotypies. This has led to hypotheses that the behaviours represent state-dependent foraging attempts, driven by dietary deficiency and/or insufficient gut fill (e.g. Terlouw *et al.*, 1993; Cooper *et al.*, 1994; Whybrow *et al.*, 1995; Nicol, 2000; McBride and Cuddeford, 2001).

But why, then, should such behaviours be sustained hour after hour, day after day? In some instances, the behaviour may actually redress underlying deficits and so be reinforced. For example, horses' wood-chewing could be a functional response to a lack of dietary fibre (Redbo *et al.*, 1998); and the chewing of urine-soaked wood slats by sheep may even be a way of gaining nitrogenous urea when protein-deficient (e.g. Whybrow *et al.*, 1995). This last could perhaps also explain wool-chewing by sheep, since soiled wool from animals' rear ends is preferred (Sambraus, 1985), although the rectifying of salt deficiencies could be another possibility. Alternatively, it may be that it is evolutionarily adaptive to food-search until successful (Mason, in press), and that such responses are relatively hard-wired and resistant to extinction (though *cf.* e.g. Haskell *et al.*, 1996). Or such persistence may instead result from some effect of the barren environment, or abnormal early-rearing conditions, as we discuss in Section 2.6.

However, the importance of nutrient deficits in all ungulate oral stereotypic behaviour is uncertain. After all, most stereotyping ungulates are not food-restricted, so this seems unlikely to be a general explanation. Furthermore, in sows, high-fibre diets can reduce stereotypies even if they do not reduce feeding motivation any more than control diets (Bergeron *et al.*, 2000). This suggests that other factors are important too. Restrictive diets and low-fibre diets do have other features in common that represent alternative causal factors for stereotypy – they make food take less time and effort to find and process; and they can also lead to gastrointestinal dysfunction. We therefore consider these next.

2.4.3. What is the role of decreased foraging or ruminating time?

The time spent foraging and/or ruminating falls considerably when concentrated diets are offered. This may frustrate some need to perform oral behaviours and/or give ungulates 'spare time' to fill with stereotypies. But how important for stereotypies are these changes in the behavioural time-budget?

2.4.3.1. Increased foraging/rumination time and high-fibre diets

Many authors have suggested that fibrous diets act to reduce stereotypies through encouraging more naturalistic oral behaviour (e.g. Rushen *et al.*, 1993). Thus in many studies of sows, high-fibre diets double or more the time spent feeding (e.g. Robert *et al.*, 1993; Brouns *et al.*, 1994; Ramonet *et al.*, 1999), and using multiple regression, Robert *et al.* (1997) found that this increased feeding time accounted for much of the differences in stereotypy level between diets. Thus across several diets identical in calories and major nutrient levels, but different in fibre level, low chewing time *per se* emerged as the key statistical predictor of stereotypic chain-chewing post-feeding. Similarly, in giraffes, feeding hay instead of lucerne prolonged feeding time in one study (as well as reducing tongue-playing; e.g. Koene, 1999), and prolonged the time spent ruminating (Baxter and Plowman, 2001) in another, these last authors hypothesizing that opportunities to ruminate are specifically important for stereotypy-reduction. Likewise, in cattle, increasing dietary forage results in longer feeding duration, along with reduced stereotypies (Redbo and Nordblad, 1997).

Studies where foraging/rumination times are manipulated via diet quality are clearly rather hard to interpret, however, so let us look at other types of study too.

2.4.3.2. Effect of providing straw bedding or other foraging opportunities

Straw has low nutritional value and is often used as bedding. However, it can serve as a foraging substrate, since animals may manipulate, chew and even consume some of it. Correspondingly, straw also has an effect on oral stereotypies. For example, in sows, experimentally providing straw bedding or loose straw also reduces the incidence of oral stereotyped activities (e.g. Fraser, 1975). Lambton and Mason (in preparation) also found that amongst barn-housed beef cattle, individuals with tongue-playing stereotypies spent the least time manipulating their straw bedding, even though they had the same access to it as did non-stereotyping individuals. The amount of straw actually consumed was not reported in these studies, so its potential effect on gut fill cannot be assessed. However, adding straw directly to the diet itself does *not* decrease stereotypies (Fraser, 1975) or feeding motivation (Lawrence *et al.*, 1989). Thus it seems that straw as a substrate on the ground is important, perhaps because it allows naturalistic foraging (e.g. Spoolder *et al.*, 1995; Whittaker *et al.*, 1998, 1999). Conversely, reducing naturalistic foraging opportunities can induce stereotypy-like behaviour, seemingly independent of nutrient-intake. Thus when the natural rooting and stone-chewing behaviour of food-restricted outdoor sows is impaired with nose-rings which make pressing the snout against the ground painful, animals instead perform more grass-chewing, and straw- or vacuum-chewing (Horrell *et al.*, 2001).

2.4.3.3. Effects of changing the foraging behaviours required to ingest food

Other research efforts have been made to specifically manipulate time spent foraging and feeding, without adding straw, or changing the quality and/or quantity of food in any way. For example, when mesh feeders were used to force giraffes to work harder to obtain their food, this successfully decreased stereotypic licking from 13% to 2% (Bashaw *et al.*, 2001b; see also Bashaw *et al.*, 2001a). Similarly, sows fed a conventional diet in a mash form instead of pellets, which increased their feeding time, showed decreased chain-chewing after eating (Bergeron *et al.*, 2002). This latter manipulation did not reduce feeding motivation in the post-feeding period (Brouns *et al.*, 1997), perhaps unsurprisingly since it was no more calorific or bulky, and yet it still clearly had an effect on stereotypic behaviour. Finally, Lindström and Redbo (2000) used invasive techniques on cattle to dissociate the behavioural components of feeding from the nutritional consequences. They found that a 50% reduction in food allowance increased cow stereotypies (see Section 2.4.2). However, they also found that this effect vanished if the animals either received compensatory rumen content (delivered direct to the rumen), enabling a high rumination level; or if they received a high food allowance, and thus could have a long feeding time, even if their rumen content was then maintained artificially low. Together these results suggest a generally beneficial effect of oral manipulation *per se*, through feeding and/or ruminating, on stereotypy.

However, increasing the foraging behaviours required to ingest food does not always reduce stereotypic behaviour. For example, a chain-based device inside the trough that increased the time food-restricted sows spent foraging, did not have great effects on their stereotypy: it decreased post-feeding vacuum-chewing, but chain-chewing and manipulation remained high (Bergeron and Gonyou, 1997).

2.4.3.4. Summary and possible explanations

These studies suggest that expressing foraging behaviour, particularly in a complex and variable way, can *per se* reduce stereotypies, regardless of nutrient intake. This has led to hypotheses that ungulates cannot or will not completely abandon naturalistic levels of foraging, even when captivity renders this redundant. If correct, this could indicate that complete flexibility in ungulate foraging time has not been selected for by evolution, leaving ungulates unable to reduce foraging behaviour to the low level required by captivity (Mason, in press), especially if concomitantly nutrient-restricted. Alternatively, defending a certain minimum level of daily foraging could have brought with it evolutionary benefits (independent of nutrient intake) such as information gain, appropriate tooth wear and/or maintaining digestive tract function (*cf.* Box 2.1). Indeed the potential role of these last factors as *proximate* drivers of stereotypy, not just ultimate ones, has recently been suggested, as we discuss below. Furthermore, because stereotypies were typically reduced but not abolished by the treatments described above, this further suggests that issues other than foraging time do need to be considered.

2.4.4. What is the role of gastrointestinal dysfunction?

2.4.4.1. Individual differences in gastrointestinal pH and lesions, and their relationships with stereotypy

In low fibre-fed animals, individual differences in gastrointestinal acidity may predict individual differences in stereotypy. Relationships between concentrate feeding, hindgut acidity and oral activities such as grasping and wood-chewing have long been observed in horses (Willard *et al.*, 1977; Johnson *et al.*, 1998), and tooth-grinding and crib-biting have also been associated, at least anecdotally, with gastritis in these animals (Rebhun *et al.*, 1982; Blood and Radostits, 1989). A recent study by Nicol *et al.* (2002) investigated these links in more detail. Foals that had recently started to crib-bite were compared with non-stereotypic foals, their stomachs being examined via video endoscopy. The crib-biters had significantly more in-flamed, dry and ulcerated stomachs, along with lower faecal pH. Similar associations have been suggested for pigs: in concentrate-fed pregnant sows, Marchant-Forde and Pajor (2003) report that a weak link between oral abnormal behaviour and gastric ulceration has been established, probably based on the findings of Dybkjær *et al.* (1994).

A different picture seems to emerge in cattle, however. Wiepkema *et al.* (1987) found that 67% of veal calves bucket-fed on milk replacer showed abomasal ulcers, the scars of past ulcers, or erosions (NB at this stage calves' stomachs are not fully developed, and thus the abomasum or 'true stomach' is their only functioning chamber). However, of those animals which developed tongue-playing, none had ulcers or scars, while those animals that did not, all had ulcers or scars. The same was not true for stereotypic biting of the crate, nor for erosions which appeared in different areas of the omasum. Canali *et al.* (2001) also found that veal calves with more abnormal oral behaviour in total had fewer abomasal ulcers, although this was not true if only strict stereotypies were looked at. Furthermore, in adult cattle, Sato *et al.* (1992) found that tongue-rolling was more common in individuals which later, at slaughter, proved not to be suffering from internal organs lesions, such as enteritis (gut inflammation) or hepatitis (liver inflammation). This finding could reflect a low incidence of ruminal acidosis, because this condition can have a range of deleterious effects throughout the body, including liver abscesses (e.g. see references cited by Keunen *et al.*, 2002, and by Hanstock *et al.*, 2004).

2.4.4.2. Individual differences in gastrointestinal motility

Crib-biting has been associated with altered gut transit time in the horse (McGreevy and Nicol, 1998a; McGreevy *et al.*, 2001a). Thus longer total gut transit times were found in crib-biters compared to control horses, al-though oro-caecal transit times did not differ significantly (McGreevy *et al.*, 2001a). This shows that crib-biters have reduced hindgut (but not foregut) motility. Their relative hindgut stasis suggests that the oro-caecal digestion of crib-biters is less efficient than that of non-crib-biters, perhaps

because they have poor mastication and/or emulsification of food in the foregut (meaning that fibre has to be retained in their hindguts for longer), or because they have some imbalance in hindgut flora (e.g. as a result of acidosis) (Nicol, 1999). Indeed, as we will see below, the crib-biting of these individuals may actually help to reduce their gut transit times from levels which otherwise would be even slower (with the cribbing behaviour thus seeming more efficacious for foregut motility than for hindgut).

2.4.4.3. Experimental alterations of gut acidity: do these affect stereotypy?

Four studies have investigated whether altering gut pH alters oral stereotypy. Johnson *et al.* (1998) focused on hindgut acidosis in horses. They found that antibiotics controlling lactate-producing bacteria (and thence increasing faecal pH) do reduce abnormal oral behaviours (though normal eating was reduced too, making interpretation a little tricky). Turning to foregut acidity, crib-biting in horses was also reduced by oral antacids (Mills and MacLeod, 2002; Nicol *et al.*, 2002). Thus in the latter study, crib-biting foals were allocated to a control or an antacid diet for 3 months. Crib-biting foals receiving the antacid diet tended to reduce their crib-biting duration to a greater extent than foals on the control diet; and foals showing the greatest reduction in ulcer severity score with the diet also tended to show the greatest reductions in crib-biting. Finally, working with pregnant sows, Marchant-Forde and Pajor (2003) have preliminary findings suggesting that adding a bicarbonate buffer to the diet may reduce bar-biting, though not all stereotypies were affected.

2.4.4.4. Summary and possible explanations

The results above have led to suggestions that stereotypy is not a response to nutrient deficits or reduced foraging time *per se*, but instead to their gastrointestinal consequences. Many of these studies are merely correlational, but the more recent experimental work does indicate that gastrointestinal acidity can play a causal role in stereotypies. Why might this be so? One possible explanation is that gastrointestinal discomfort exacerbates stereotypies by being stressful (see Chapter 8, this volume), but another is that stereotypies are an attempt to alleviate such problems via the production of buffering saliva (see Box 2.1). This idea was first suggested by Wiepkema *et al.* (1987) for calves, and broadened to horses by Nicol (1999). The apparent differences between horses and calves/adult cattle – i.e. that oral stereotypic behaviour seems to correlate positively with problems in the former, but negatively in the latter – may be because cattle produce enormous quantities of saliva (see Box 2.1): thus perhaps saliva generation has more effective results in bovids. Intriguingly, amongst crib-biting foals, those without ulcers had been cribbing for longer than those with gastric lesions (Nicol *et al.*, 2002), which would be consistent with beneficial consequences. This 'salivation hypothesis' could account for some of the discrepancies in the fibre/deficit/foraging time studies reviewed earlier, with gastrointestinal effects being the missing explanatory variable. However,

the idea clearly still needs to be properly experimentally tested. Furthermore, the aetiology of ulcers needs to be more fully understood, since in calves, for example, the lack of dietary fibre does not seem to play a causal role (indeed if anything the opposite is true for these young animals with their as yet undeveloped rumens; e.g. Mattiello *et al.*, 2002) and stress may be the more important factor (e.g. Dybkjær *et al.*, 1994).

2.5. The Biological Significance of Oral Stereotypic Behaviour: Is It Functional?

Above we have seen how ungulate oral stereotypic behaviour may have beneficial consequences (e.g. via nutrient ingestion or saliva generation), and other researchers have further suggested that it may increase feelings of satiety (e.g. Robert *et al.*, 1993 on polydipsia) and/or be generally calming (e.g. Rushen, 1984). The idea that ungulate oral stereotypic behaviour has some benefits has been supported by two further types of study, looking at within-individual changes during stereotypy-performance, or at the effects of stereotypy-prevention. (Other research has utilized individual difference within populations to compare stereotypers with non-stereotypers, but it has yielded confusing results, not least as such cross-sectional studies cannot distinguish individual differences *predisposing to* stereotypy from those *resulting from* stereotypy.)

Intriguingly in very young calves, during the performance of post-feeding non-nutritive sucking directed to objects like artificial teats, increases in plasma insulin and cholecystokinin are seen, which are thought to aid digestion (de Passillé *et al.*, 1993). Unfortunately, no study has looked at these hormones, or at any other gastrointestinal changes during oral stereotypy in adult ungulates, but variables related to stress have been measured. In horses, plasma cortisol levels are lower after a bout of crib-biting than before (McBride and Cuddeford, 2001), and heart rates also decrease during these bouts (Lebelt *et al.*, 1998; Minero *et al.*, 1999). Similar analyses show that in tethered gilts, switches from non-stereotyped to stereotypic behaviour are likewise accompanied by decreases in heart rate (and vice versa) (Schouten *et al.*, 2000); and the same seems true for tongue-playing heifers (Seo *et al.*, 1998). These data are correlational rather than indicating cause and effect, but they are nevertheless intriguing.

Stereotypy-prevention may be attempted either to abolish an undesired behaviour (see Box 2.3), or to collect research data, and when abolition is successful, consequences sometimes ensue. For example, in the calves mentioned above, reducing their non-nutritive sucking by removing a rubber teat resulted in a decrease in their post-meal hormone release (de Passillé *et al.*, 1993). In sows, in contrast, removing a chain that is stereotypically chewed did not increase heart rate or cortisol (Schouten *et al.*, 1991; Terlouw *et al.*, 1991b), but interpretation is hard here because the subjects did develop alternative oral behaviours, e.g. drinker-manipulation. Preventing horses crib-biting has had mixed stress physiology effects, some studies finding

Box 2.3. Is it Ethical to Physically Prevent Horses Performing Oral Stereotypies?

F.O. ÖDBERG

Oral stereotypies are unpopular with horse owners. They can cause incisor wear; there are beliefs – though ill founded (McGreevy *et al.*, 1995c) and based solely on correlations (e.g. Archer *et al.*, 2004; Hillyer *et al.*, 2002; Traub-Dargatz *et al.*, 2001) – that they cause colic; and overall, they can reduce a horse's commercial value (McBride and Long, 2001; Mills and McDonnell, 2005). People therefore often physically try to prevent crib-biting and wind-sucking. A horse may be fitted with a neck-strap that inflicts pressure or pain during stereotypy, an electric collar that delivers a shock during the behaviour, or a muzzle that prevents biting on to hard surfaces. Horses can also be discouraged from resting their teeth on a surface by placing sharp objects, electric wires and/or unpleasant-tasting substances there. Additionally, there are surgical approaches such as buccostomy (the creation of buccal fistulae), and various myectomies (i.e. the sectioning of specific muscles to stop the motor pattern, e.g. 'Forsell's operation').

There are several reasons to be concerned about such measures. One study (McBride and Cuddeford, 2001) showed that 'crib-straps' cause stress to both windsuckers and normal controls. Electric collars are inherently painful; and automatically triggered ones can react to non-stereotypic behaviours as well as stereotypies, thence potentially inducing learned help-lessness. Furthermore, physically preventing stereotypies could make things worse, if these behaviours actually help the animal. For instance, if oral stereotypies increase stomach pH through salivation, then surely they should not be prevented. Thus in some cases, at least, there does seem to be a decrease in arousal linked with wind-sucking, and an increase when performance is thwarted (e.g. McBride and Cuddeford, 2001; see also other studies discussed in this chapter). McGreevy and Nicol (1998a) did not find such effects, but their horses were moved from the home stable to an experimental one. Mills (personal communication, Lincoln, 2005) also found an increase in heart rate when deterrent bars were placed in the stables of weavers. Even if the link found in foals between crib-biting and gastric acidity is merely correlational (e.g. nervous individuals develop both stereotypies and gastritis/ulcers), or causal in the other direction (e.g. ulcers induce discomfort), which somehow – perhaps via the mechanisms discussed in Chapter 8 – enhances stereotypies, it still seems contra-indicated to merely prevent the stereotypy physically. As this chapter argues, ungulate oral stereotypies probably indicate thwarted foraging, and merely abolishing the symptoms does not cure this underlying problem.

Despite such concerns, when I screened seven reports on surgical responses to oral stereotypy published since 1990, all evaluated success solely or mainly by the degree of stereotypy-inhibition, and none used measurable welfare or stress parameters (Hakansson *et al.*, 1992; De Mello Nicoletti *et al.*, 1996; Jansson, 2000; Delacalle *et al.*, 2002; Fjeldborg, 1993). Only one briefly mentions that stereotypy elimination may increase stress (Schofield and Mulville, 1998), and only one enquired whether aspects of horse health improved (Brouckaert *et al.*, 2002). This probably reflects a medical education that, unfortunately, tends to focus on treating symptoms instead of understanding the underlying processes (though see Chapter 10, this volume for a more holistic veterinary view). Further, objective work is therefore needed to compare the health, condition, feed intake rates and stress levels of horses exposed to such techniques (using blind observers, and with appropriate controls such as normal horses and sham-operated windsuckers). In the interim, the ethics of such approaches remain highly questionable, especially when fundamental alternatives exist, namely improving husbandry.

nothing (e.g. McGreevy and Nicol, 1998a), others finding effects of the manipulations *per se* (e.g. cribbing collars) regardless of whether the stereo-typy was prevented (McBride and Cuddeford, 2001). However, when crib-bing is prevented, it is performed at higher levels the following day once collars are removed (McGreevy and Nicol, 1998b), a 'rebound' consistent with motivational effects. Crib-biters also eat more when deprived of crib-bing, and furthermore, their slow gut transits are reduced further (especially oro-caecal motility) if they are deprived of the opportunity to both crib-bite *and* eat hay (McGreevy and Nicol, 1998a; McGreevy *et al.*, 2001a). Relatively normal oro-caecal transit times in these animals thus seem to depend on them being able to eat fibrous food or to crib-bite.

Overall, more work is clearly needed here, but these intriguing find-ings could help explain why these activities are so time-consuming and persistent day after day. They could also perhaps explain why attempts to prevent stereotypy sometimes fail, e.g. horses may persevere with crib-biting despite preventative collars or surgery (reviewed e.g. McGreevy and Nicol, 1998a,b), while in giraffes, an attempt to reduce fence-licking by coating it with bitter substances just shifted the behaviour to new locations (Tarou *et al.*, 2003). Most importantly, they also raise concerns about the physical prevention of stereotypies that is routine in some stables (see Box 2.3) – partly since such approaches ignore the underlying problems, but partly also since they could decrease animals' welfare yet further, if these behaviours do indeed have beneficial consequences.

2.6. Other Factors Associated with Stereotypies in Captive Ungulates: Barren Environments and Early Weaning

So far we have discussed oral stereotypic behaviour as though simply strange-looking manifestations of adaptive foraging: the products of pla-cing normal animals in abnormal foraging environments. But are other aspects of husbandry important too?

2.6.1. A role for early weaning?

Agricultural ungulates are often removed from their mothers long before natural weaning age. For example, natural weaning age in pigs is esti-mated to be between 2 and 4.5 months (Newberry and Wood-Gush, 1985; Jensen and Recen, 1989), yet on farms, piglets are routinely weaned between 21 and 28 days, sometimes even earlier (Robert *et al.*, 1999; CARC, 2003). Likewise, cattle naturally wean their calves at 8–11 months (Veissier *et al.*, 1990; Reinhardt, 2002) – yet beef calves are generally taken from their mothers at around 5 months (CARC, 1991), and dairy calves are routinely separated on their first day of life, with female calves reared as replacement stock for the dairy herd then also weaned off milk at between

4 and 12 weeks (e.g. USDA, 2002). In other taxa, early maternal separation can have lasting effects on brain function and on tendencies to stereotype (Chapter 6, this volume); and within ungulates, the quality of the mother–foal relationship is a risk factor in the later development of equine stereotypies (Waters *et al.*, 2002; Nicol and Badnell-Waters, 2005). So could the early loss of the mother, or other aspects of mother–infant relationships that are constrained by captivity, help to explain the stereotypies of adult ungulates?

The belly-nosing of early-weaned piglets anecdotally can occasionally persist into adulthood (see Box 6.2, Chapter 6, this volume); and the offspring of restrained sows have been reported as more stereotypic in adulthood (reviewed by Bøe, 1997). However, we simply do not know whether the quantity or quality of early maternal care influences the later persistent bar-biting and sham-chewing shown by adult pigs. Furthermore, in calves, the cross-sucking common when artificially reared calves are group-housed away from the dam (e.g. Jensen, 2003) seems to increase the later risks of inter-sucking (the sucking of the teat of another animal) when young heifers, which in turn then increases the later risk of inter-sucking as adult cows (Lidfors and Isberg, 2003). However, again, whether early weaning creates a lasting predisposition towards true stereotypies in adult cattle (e.g. tongue-rolling) is unknown. Mason (Chapter 11, this volume) revisits this issue at the end of the book.

2.6.2. The physical environment

Stereotyping captive ungulates are typically physically restricted by enclosure and/or tethering. For instance, when cows are moved off pasture, they are not just prevented from grazing, but also kept in small stalls that prevent locomotion (e.g. Redbo, 1992). This contrasts greatly with the ranging they would show naturally: grazing cattle may travel up to 24 km daily (Fraser and Broom, 1990); while Sato *et al.* (2001) report home ranges of 2–6 km^2 for beef cattle in semi-wild conditions and Hernandez *et al.* (1999) report ranges of 14 and 47 km^2 for domestic and feral cattle, respectively.

So, could this type of physical restriction contribute to stereotypy? Some studies suggest not. When horse and giraffe stereotypies were investigated in cross-site studies, enclosure size and exercise allowance often has relatively little effect on oral behaviour (instead affecting locomotor stereotypies, e.g. pacing by giraffes and weaving by horses; Luescher *et al.*, 1998; Bashaw *et al.*, 2001a). Furthermore, in pigs, Terlouw and Lawrence (1993) experimentally investigated the interactive effect of food allowance and restraint. They found that sows receiving a higher food allowance (4 kg food/day) performed less drinking and chain manipulation than sows on a low food allowance (2.5 kg/day), regardless of whether loose-housed or tethered. Indeed, they even observed loose-housed sows performing *more* chain manipulation than the tethered sows (see Fig. 2.4).
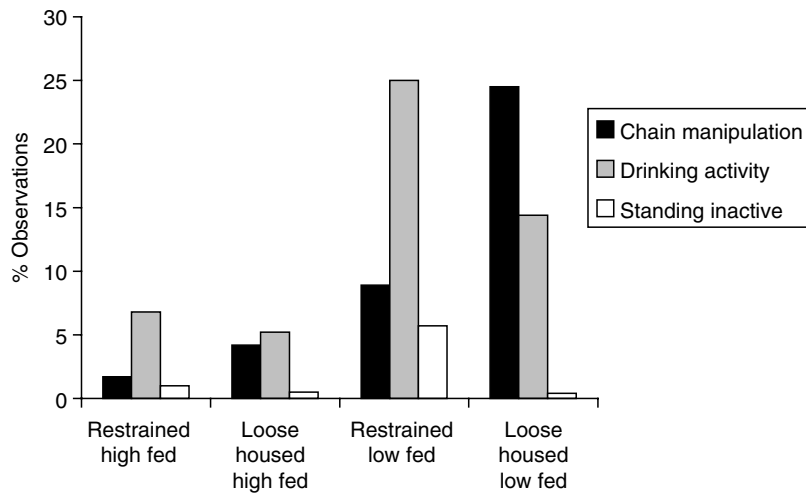
Fig. 2.4. Effect of degree of confinement and feed level on stereotypic behaviour. The figure shows the average percentage of observations spent standing/sitting, chain-manipulating (a putative stereotypy) and drinking, in sows exposed to two levels of two different aspects of husbandry (in a 2 × 2 design): diet significantly affected oral behaviours, but the type of housing did not (adapted from Terlouw and Lawrence, 1993). Many other studies suggest that the degree of confinement does affect oral stereotypic behaviour, however (see text for discussion).

However, other work shows that oral stereotypies *are* affected by factors other than diet alone. For instance, several studies indicate that they are more frequent in pregnant sows that are confined in individual stalls or cages, compared with loose-housed females: Vieuille-Thomas *et al.* (1995) reported prevalence rates of 66% in group-housed sows, but 93% in individually stalled animals (and see also Blackshaw and McVeigh, 1984; Jensen, 1988; Broom *et al.*, 1995; Jensen *et al.*, 1995; Soede *et al.*, 1997; Pol *et al.*, 2000). Similar results are seen in cattle, with time spent in stereotypies falling greatly when animals are group-housed indoors rather than kept in small individual stalls, despite no change in feeding regime (Redbo, 1992). Likewise, when stabled horses were exercised, they showed reduced wood-chewing compared to when kept full-time in stalls (Krzak *et al.*, 1991), and other studies suggest that environmental enrichment in the form of visual contact between stabled horses also reduces this behaviour (McGreevy *et al.*, 1995a).

One possible reason for such variable findings (see Chapter 11, this volume, for an alternative) is that the treatments under comparison differ in the degree of physical restriction or freedom that they offer, which in turn might have threshold effects on behaviour. For example, Lawrence and colleagues (Terlouw *et al.*, 1991a; Lawrence and Terlouw, 1993; Haskell *et al.*, 1996) argue that high arousal and barren unvarying environments together render post-feeding foraging attempts more persistent than they would be in more naturalistic situations, and also 'channel' them into a

few, repeatedly expressed behaviour patterns. In some instances, this may mean that oral or oro-nasal behaviours simply become more stereotyped in physically restrictive conditions, but not necessarily more frequent. Several studies suggest that the physical environment does not affect the total amount of oral behaviour, but does influence its form, and especially its degree of stereotypy. Thus food-restricted sows given straw on the floor manipulate this as much as they would pen fittings if straw is absent (e.g. Whittaker *et al.*, 1998), and similarly, sows held via tethers or stalls spend approximately the same amount of time chain-manipulating or bar-chewing as they would spend rooting on straw if loose housed, or chewing rocks and soil if kept outdoors (Schouten and Rushen, 1992; Dailey and McGlone, 1997). Furthermore, similarly fed outdoor sows spend roughly the same time chewing at things regardless of paddock type, but what they chew at depends on the availability of natural versus other substrates, with roots and branches being chewed if available, stones being chewed if not (Horrell, 2000). Studies comparing such conditions would thus draw different conclusions as to the effect of physical restriction or complexity, depending on how strict is their definition of stereotypy.

2.7. Conclusion and Perspectives

Overall, we have shown that in captive adult ungulates, the greater the difference between artificial and natural foraging regimes, the more abnormal behaviour is shown. Thus the greater the gap between what is possible in captivity and *ad libitum* feeding levels, and/or naturalistic fibre levels, and/or naturalistic, preferred foraging modes, the greater the degree of oral stereotypy. For instance, across a range of species, animals fed high concentrate low-fibre diets are reliably more prone to stereotypy development than animals on pasture or fed a large quantity of forage. This has clear relevance for welfare, since hunger and being unable to express preferred natural behaviour patterns are both causes of stress, while gastric or hindgut acidosis or ulceration probably causes discomfort, even pain. Management conditions that elicit oral stereotypies in ungulates are thus very likely to be sub-optimal. Such welfare considerations are particularly pertinent considering the many millions of ungulates that are fed low-fibre concentrates, and that perform stereotypic oral behaviour. More research is needed to assess the magnitude of these welfare problems, and, as we discuss further below, the best ways to alleviate them.

We have also shown that in some cases, within a given sub-optimal housing condition highly stereotypic animals may sometimes fare better than their less stereotypic conspecifics (Chapter 1, this volume); and that even where this is not known to be the case, performing bouts of stereotypy is still apparently associated with immediate benefits that are manifest as brief reductions in heart rate. This highlights how counter-productive it may be to prevent oral stereotypic behaviour physically, i.e. to merely abolish its expression without tackling its underlying

causes. However, again more research is needed as to the true welfare costs of different ways of tackling these behaviours (a theme also picked up towards the end of this volume, in Chapter 10). For example, food-restricted animals may perform fewer stereotypies when given more opportunity to perform natural foraging behaviour, and thus appear to fare better, but they could still remain chronically hungry levels of food-restriction stay the same.

Overall, we thus understand fairly well the general causes of stereotypic oral behaviour in ungulates: unnatural foraging regimes, with effects possibly exacerbated by physically restrictive environments and/or early weaning (Chapter 11, this volume). However, the precise underlying causes, and the extent to which these differ between animals of different ages, species, housing systems and preferred forms of oral stereotypy, are still the subject for much research. As we have seen, oral behaviours in captive ungulates share similarities with feeding behaviour, in their appearance, temporal distribution, and most likely in their underlying motivation. However, there are three specific means by which 'frustrated natural foraging' could give rise to stereotypies.

One such means is by leaving the animal in a state of thwarted motivation to ingest more food than is available; thus dietary deficits leave the animal with unfulfilled feeding motivations. Our food-deprived pregnant sow is one likely case in point. Furthermore, as we discussed, diet selection is naturally the principal means of modulating gastro-intestinal acidity, and herbivores also have excellent abilities to detect specific nutrient deficits and respond to them behaviourally (see e.g. Newman, in press). In captivity, in contrast, ungulates' diet selection is greatly constrained, again potentially leaving them in a state of unfulfilled feeding motivation for specific foodstuffs. However, even where such effects are demonstrably important in stereotypic behaviour, we still do not understand why deficits should result in sustained food-search hour after hour, day after day. Possible reasons include immediate consequences (such as nutrient ingestion from non-food sources); species-typical adaptations for patch-feeding (e.g. Box 2.2; Mason, in press) or even non-functional persistence resulting from stress sensitization (Chapters 8 and 11, this volume), but these issues remain unexplored. Furthermore, nor do we even always fully understand what dietary factors are needed for true satiety, or what complement of internal cues mediate this (see also Ingvartsen and Andersen, 2000). For example, a better understanding of the mechanisms by which fibrous ingredients affect digestive and metabolic processes is clearly necessary (as is assessment of the differential digestibility, net energy value, and other properties of different high-fibre diets). More consistent research across species might also help, because currently most attempts to assess hunger are done with sows; we thus know little as to whether other species are hungry when fed a large proportion of concentrate, and we also know little about polydipsia in species other than pigs, nor its possible relationship with hunger.

An alternative possibility is that ungulates have an inherent need (possibly state-dependent) to perform some foraging behaviours. Thus providing a foraging substrate such as straw, or increasing feeding time by making ingestion harder, can sometimes help to reduce stereotypies. This idea is consistent with observations that some foraging behaviours are inherently reinforcing. However, sometimes such approaches succeed in reducing stereotypic behaviour, and sometimes they do not. Does this depend on the underlying hunger levels of the animal? Or the degree to which the foraging opportunities offered are preferred and motivationally satisfying? Or instead, on the degree to which they have some beneficial physiological consequences? Or are yet other factors intervening, such as older stereotypies perhaps being harder to reverse than newly developed ones? Again we do not know. More hypothesis-driven research would help here, as currently many experiments have been designed to investigate the efficacy of methods of preventing stereotypies, without trying to understand why and how they work (or fail to). Furthermore, many studies of different species also differ in other variables too (e.g. horse studies often seem to deal with adult animals with well-developed stereotypies, while sow studies often look at young females with 'developing' stereotypies) which could be rectified in future work. Variation between species in their natural foraging biology could also be used to test hypotheses, as we see in Chapter 3, this volume. For example, perhaps browsers have a greater post-food stereotypy peak than grazers, because their food is naturally more patchy, so making ingestion-stimulated food-search more adaptive.

The third possible reason for sustained oral behaviours in captive ungulates is not because performing the behaviours is inherently important, but instead because it has useful consequences, for example, gastrointestinal health. The recent evidence linking stereotypies with gastrointestinal acidity/function opens a whole new array of research avenues. The causal relationships between dietary fibre, saliva production and gut acidity should therefore be investigated further, via hypothesis-driven experiment across a range of species. If this hypothesis *is* correct, and abnormal oral behaviours do effectively generate saliva which helps to alleviate abnormal gut pH, it also raises several further questions (e.g. Mason, in press). How do ungulates monitor their digestive tracts' pH, and does this vary with foraging niche? Do some or all ungulates monitor saliva production levels? If so, are they learned or innate responses to internal cues – or does this vary with dietary niche? How does diet interact with other factors, such as stress, in the aetiology of stomach lesions? And are other aspects of salivation important too, e.g. could adaptations for tannin-binding (see Box 2.1) play a role in some browsers' stereotypies?

Answering these questions could help to improve the fundamental understanding of ungulates, and also our abilities to husband them with good welfare. They may also apply to other taxa with somewhat similar foraging regimes, such as poultry. However, some of the questions raised by our review have even wider applicability to the other taxa discussed in the following chapters. Why do some individuals develop stereotypies,

while others in the environment do not – what genetic and experiential factors are involved? How do the various forms of stereotypic behaviour interrelate? Although some attempts have been made to objectively quantify repetition and fixation (see Stolba *et al.*, 1983), most authors use subjective judgements to classify ungulate oral behaviours as stereotypic or otherwise (see e.g. Terlouw *et al.*, 1991a,b; Robert *et al.*, 1993; Bergeron and Gonyou, 1997). How should we improve this? Do we need to? Is there a real, qualitative difference between 'unambiguous' stereotypies like bar-biting and 'abnormal-but-not-stereotypic' behaviours like cross-sucking or wood-chewing (e.g. as suggested by Garner in Chapter 5, this volume)? Or do they merely represent behaviours differing in their stages of development (Chapter 10, this volume), or degrees of functionality? And, last but not least, if some ungulate oral stereotypies *do* prove to be functional, then they are no longer stereotypies?

Acknowledgements

References

Abijaoude, J.A., Morand-Fehr, P., Tessier, J., Schmidely, P. and Sauvant, D. (2000) Diet effect on the daily feeding behaviour, frequency and characteristics of males in dairy goats. *Livestock Production Science* 64, 29–37.

Appleby, M.C. and Lawrence, A.B. (1987) Food restriction as a cause of stereotypic behaviour in tethered gilts. *Animal Production* 45, 103–110.

Archer, D.C., Freeman, D.E., Doyle, A.J., Proudman, C.J. and Edwards, G.B. (2004) Association between cribbing and entrapment of the small intestine in the epiploic foramen in horses: 68 cases (1991–2002). *Journal of American Veterinary Medical Association* 224, 562–564.

Ayles, H.L., Friendship, R.M., Bubenik, G.A. and Ball, R.O. (1999) Effect of feed particle size and dietary melatonin supplementation of gastric ulcers in swine. *Canadian Journal of Animal Science* 79, 179–185.

Bachmann, I. and Stauffacher, M. (2002) Prevalence of behavioural disorders in the Swiss horse population. *Schweizer Archiv fur Tierheilkunde* 144, 356–368.

Bashaw, M.J., Tarou, L.R., Maki, T.S. and Maple, T.L. (2001a) A survey assessment of variables relating to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science* 73, 235–247.

Bashaw, M.J., Tarou, L.R., Sartor, R., Bouwens, N., Maki, T. and Maple, T.L. (2001b) Stereotypic behavior in giraffe: concerns and contingencies. In: *Proceedings of the 2001 American Zoo and Aquarium Association Conference*, St Louis, Missouri.

Bauman, D.E., Davis, C.L. and Bucholtz, H.F. (1971) Propionate production in the rumen of cows fed either a control or high-grain, low-fiber diet. *Journal of Dairy Science* 54, 1282–1287.

Baxter, E. and Plowman, A.B. (2001) The effect of increasing dietary fibre on feed-

ing, rumination and oral stereotypies in captive giraffes (*Giraffa camelopardalis*). *Animal Welfare* 10, 281–290.

Bell, W.J. (1991) *Searching Behaviour: The Behavioural Ecology of Finding Resources.* Chapman & Hall, London.

Bergeron, R. and Gonyou, H.W. (1997) Effects of increasing energy intake and foraging behaviours on the development of stereotypies in pregnant sows. *Applied Animal Behaviour Science* 53, 259–270.

Bergeron, R., Bolduc, J., Ramonet, Y., Robert, S. and Meunier-Salaün, M.-C. (2000) Feeding motivation and stereotypies in pregnant sows fed increasing levels of fibre and/or food. *Applied Animal Behaviour Science* 70, 27–40.

Bergeron, R., Meunier-Salaün, M.-C. and Robert, S. (2002) Effects of food texture on meal duration and behaviour of sows fed high-fibre or concentrate diets. *Canadian Journal of Animal Science* 82, 587–589.

Blackshaw, J.K. and McVeigh, J.F. (1984) Stereotype behaviour in sows and gilts housed in stalls, tethers, and groups. In: Fox, M.W. and Mickley, L.D. (eds) *Advances in Animal Welfare Science.* Martinus Nijhoff Publishers, Dordrecht, pp. 163–174.

Blasetti, A., Boitani, L., Riviello, M.C. and Visalberghi, E. (1988) Activity budgets and use of enclosed space by wild boars (*Sus scrofa*) in captivity. *Zoo Biology* 7, 69–79.

Blokhuis, H.J. (1986) Feather-pecking in poultry and its relation with ground-pecking. *Applied Animal Behaviour Science* 16, 63–67.

Blood, D.C. and Radostits, O.M. (1989) *Veterinary Medicine: A Text Book of the Diseases of Cattle, Sheep, Pigs, Goats and Horses*, 7th edn. Bailliere Tindall, London.

Bøe, K. (1997) The effect of age at weaning and post-weaning environment on the behaviour of pigs. *Acta Agriculturae Scandinavica Section A* 43, 173–180.

Bolinger, D.J., Albright, J.L., MorrowTesch, J., Kenyon, S.J. and Cunningham, M.D. (1997) The effects of restraint using self-locking stanchions on dairy cows in relation to behavior, feed intake, physio-logical parameters, health, and milk yield. *Journal of Dairy Science* 80, 2411–2417.

Bonacic, C. (2005) Vicuña ecology and management. *Ecology Info* 27. Available at: http://www.ecology.info/vicugna.htm

Born, E.W., Rysgaard, S., Ehlmé, G., Sejr, M., Acquarone, M. and Levermann, N. (2003) Underwater observations of free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biology* 26, 348–357.

Braund, J.P., Edwards, S.A., Riddoch, I. and Buckner, L.J. (1998) Modification of foraging behaviour and pasture damage by dietary manipulation in outdoor sows. *Applied Animal Behaviour Science* 56, 173–186.

Broom, D.M. and Potter, M.J. (1984) Factors affecting the occurrence of stereotypies in stall-housed dry sows. In: Unshelm, J. and van Putten, G. (eds) *Proceedings of the International Congress on Applied Ethology in Farm Animals.* KTBL, Darmstadt, pp. 229–231.

Broom, D.M., Mendl, M.T. and Zanella, A.J. (1995) A comparison of the welfare of sows in different housing conditions. *Animal Science* 61, 369–385.

Brouckaert, K., Steenhaut, M., Martens, A., Vlaminck, L., Pille, F., Arnaerts, L. and Gasthuys, F. (2002) Windsucking in the horse: results after surgical treatment – a retrospective study (1990–2000). *Vlamms Diergeneeskundig Tijdschrift* 71, 249–255 (in Dutch).

Brouns, F., Edwards, S.A. and English, P.R. (1994) Effect of dietary fibre and feeding system on activity and oral behaviour of group housed gilts. *Applied Animal Behaviour Science* 39, 215–223.

Brouns, F., Edwards, S.A. and English, P.R. (1997) The effects of dietary inclusion of sugar-beet pulp on the feeding behaviour of dry sows. *Animal Science* 65, 129–133.

Buckner, L.J., Edwards, S.A. and Bruce, J.M. (1998) Behaviour and shelter use by outdoor sows. *Applied Animal Behaviour Science* 57, 69–80.

Canadian Agri-Food Research Council (CARC) (1991) *Recommended Code of*

Practice for the Care and Handling of Beef Cattle. Agriculture Canada Publication 1870/F.

Canadian Agri-Food Research Council (CARC) (2003) *Recommended Code of Practice for the Care and Handling of Farm Animals: Pigs. Addendum Early Weaned Pigs.*

Canali, E. and Borroni, A. (1994) Behavioural problems in thoroughbred horses reared in Italy. *Applied Animal Behaviour Science* 40, 74.

Canali, E., Ferrante, V., Mattiello, S., Gottardo, F. and Verga, M. (2001) Are oral stereotypies and abomasal lesions correlated in veal calves? In: *Proceedings of the 35th International Congress of the ISAE*. Davis, California, p. 103.

Clauss, M., Gehrke, J., Hatt, J.M., Dierenfeld, E.S., Flach, E.J., Hermes, R., Castell, J., Streich, W.J. and Fickel, J. (2005) Tannin-binding salivary proteins in three captive rhinoceros species. *Comparative Biochemistry and Physiology A – Molecular and Integrative Physiology* 140, 67–72.

Coates, C.W. (1962) Walruses and whales in the New York aquarium. *International Zoo Yearbook* 4, 10–12.

Cole, D.J.A. (1982) Nutrition and reproduction. In: Cole, D.J.A. and Foxcroft, G.R. (eds) *Control of Pig Reproduction*. Butterworths, London.

Cooper, J. and Jackson, R. (1996) A comparison of the feeding behaviour of sheep in straw yards and on slats. *Applied Animal Behaviour Science* 49, 99.

Cooper, J.J., Emmans, G.A. and Friggens, N.C. (1994) Effect of diet on behaviour of individually penned sheep. *Animal Production* 58, 441.

Cooper, J.J., McCullam, J. and Shanks, M. (1995) Effective fibre and abnormal behaviour in stall housed lambs. *Animal Production* 60, 567–568.

Cronin, G.M. (1985) The development and significance of abnormal stereotyped behaviours in tethered sows. PhD thesis, Agricultural University of Wageningen, The Netherlands.

Cronin, G.M., van Tartwijk, J.M.F.M., van der Hel, W. and Verstegen, M.W.A. (1986) The influence of degree of adaptation to tether-housing by sows in relation to behaviour and energy metabolism. *Animal Production* 42, 257–268.

Dailey, J.W. and McGlone, J.J. (1997) Oral/ nasal/facial and other behaviors of sows kept individually outdoors on pasture, soil or indoors in gestation crates. *Applied Animal Behaviour Science* 52, 25–43.

Day, J.E.L., Kyriazakis, I. and Lawrence, A.B. (1996) The use of a second-order schedule to assess the effect of food bulk on the feeding motivation of growing pigs. *Animal Science* 63, 447–455.

De Mello Nicoletti, J.L., Hussni, C.A., Thomassian, A., Gandolfi, W. and Pereira Leme, D. (1996) Estudo retrospectivo de 11 casos de aerofagia em eqüinos operados pela técnica de miectomia de Forssell modificada. *Ciência Rural* 26, 431–434.

De Passillé, A.M.B., Christopherson, R. and Rushen, J. (1993) Non-nutritive sucking by the calf and postprandial secretion of insulin, CCK and gastrin. *Physiology and Behavior* 54, 1069–1073.

Delacalle, J., Burba, D.J., Tetens, J. and Moore, R.M. (2002) Nd: YAG laser-assisted modified Forssell's procedure for treatment of cribbing (crib-biting) in horses. *Veterinary Surgery* 31, 111–116.

Dodman, N.H., Shuster, L., Court, M.H. and Dixon, R. (1987) Investigation into the use of narcotic antagonists in the treatment of a stereotypic behaviour pattern (crib-biting) in the horse. *American Journal of Veterinary Research* 48, 311–319.

Dybkjær, L., Vraa-Andersen, L., Pailey, L.G., Møller, K., Christensen, G. and Agger, J.F. (1994) Associations between behaviour and stomach lesions in slaughter pigs. *Preventative Veterinary Medicine* 19, 101–112.

Every, D., Tunnicliffe, G.A. and Every, R.G. (1998) Tooth-sharpening behaviour thegosis) and other causes of wear on sheep teeth in relation to mastication and grazing mechanisms. *Journal of the Royal Society of New Zealand* 28, 169–184.

Fickel, J., Pitra, C., Joest, B.A. and Hofmann, R.R. (1999) A novel method to evaluate the tannin-binding capacities of salivary

proteins. *Comparative Biochemistry and Physiology A – Molecular and Integrative Physiology* 122, 225–229.

Fisher, K.I. and Stewart, R.E.A. (1997) Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. *Canadian Journal of Zoology* 75, 1166–1175.

Fjeldborg, J. (1993) Results of surgical treatment of cribbing by neurectomy and myectomy. *Equine Practice* 7, 34–36.

Frape, D. (1998) *Equine Nutrition and Feeding*, 2nd edn. Longman Scientific and Technical, Harlow, Essex.

Fraser, D. (1975) The effect of straw on the behaviour of sows in tether stalls. *Animal Production* 21, 59–68.

Fraser, A.F. and Broom, D.M. (1990) *Farm Animal Behaviour and Welfare*, 3rd edn. Baillière Tindall, London.

Ganslosser, U. and Brunner, C. (1997) Influence of food distribution on behaviour in captive bongos, *Taurotragus euryceros*: an experimental investigation. *Zoo Biology* 16, 237–245.

Gillham, S.B., Dodman, N.H., Shuster, L., Kream, R. and Rand, W. (1994) The effect of diet on cribbing behaviour and plasma B-endorphin in horses. *Applied Animal Behaviour Science* 41, 147–153.

Ginnett, T.F. and Demment, M.W. (1997) Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* 110, 291–300.

Hagenbeck, C.-H. (1962) Notes on walruses *Odobenus rosmarus* in captivity. *International Zoo Yearbook* 4, 24–25.

Hakansson, A., Franzen, P. and Pettersson, H. (1992) Comparison of two surgical methods for treatment of crib-biting in horses. *Equine Veterinary Journal* 24, 494–496.

Hanstock, T.L., Clayton, E.H., Li, K.M. and Mallet, P.E. (2004) Anxiety and aggression associated with the fermentation of carbohydrates in the hindgut of rats. *Physiology and Behavior* 82, 357–368.

Haskell, M.J., Terlouw, E.M.C., Lawrence, A.B. and Erhard, H.W. (1996) The relationship between food consumption and persistence of post-feeding foraging behaviour in sows. *Applied Animal Behaviour Science* 48, 249–262.

Henderson, J.V. and Waran, N.K. (2001) Reducing equine stereotypies using an Equiball™. *Animal Welfare* 10, 73–80.

Hernandez, L., Barral, H., Halffter, G. and Colon, S.S. (1999) A note on the behaviour of feral cattle in the Chihuahuan Desert of Mexico. *Applied Animal Behaviour Science* 63, 259–267.

Hessing, M.J.C., Geudeke, M.J., Scheepens, C.J.M., Tielen, M.J.M., Schouten, W.G.P. and Wiepkema, P.R. (1992) Mucosal lesions in the pars oesophaga in pigs – prevalence and influence of stress. *Tijdschrift voor Diergeneeskunde* 117, 445–450.

Hibbard, B., Peters, J.P., Chester, S.T., Robinson, J.A., Kotarski, S.F., Croom, W.J. and Hagler, W.M. (1995) The effect of slaframine on salivary output and subacute and acute acidosis in growing beef steers. *Journal of Animal Science* 73, 516–525.

Hillyer, M.H., Taylor, F.G.R., Proudman, C.J., Edwards, G.B., Smith, J.E. and French, N.P. (2002) Case control study to identify risk factors for simple colonic obstruction and distension colic in horses. *Equine Veterinary Journal* 34, 455–463.

Hintz, H.F., Sedgewick, C.J. and Schryver, H.F. (1976) Some observations on digestion of a pelleted diet by ruminants and non-ruminants. *International Zoo Yearbook* 16, 54–62.

Hofmann, R.R. and Matern, B. (1988) Changes in gastrointestinal morphology related to nutrition in giraffes. *International Zoo Yearbook* 27, 168–176.

Horrell, R.I. (2000) Stone-chewing in outdoor pigs. Grant research report presented to the Universities Federation of Animal Welfare, UK.

Horrell, R.I., A'Ness, P.J., Edwards, S.A. and Eddison, J.C. (2001) The use of nose-rings in pigs: consequences for rooting, other functional activities, and welfare. *Animal Welfare* 10, 3–22.

Houpt, K.A. (1993) Equine stereotypies. *The Compendium* 15, 1265–1271.

Hutson, G.D. and Haskell, M.J. (1990) The behaviour of farrowing sows with free and operant access to an earth floor. *Applied Animal Behaviour Science* 26, 363–372.

Ingvartsen, K.L. and Andersen, J.B. (2000) Integration of metabolism and intake regulation: a review focusing on periparturient animals. *Journal of Dairy Science* 83, 1573–1597.

Jansson, N. (2000) Surgical treatment of windsucking in two horses younger than one year of age. *Ippologia* 11, 5–9.

Jensen, P. (1988) Diurnal rhythm of barbiting in relation to other behaviour in pregnant sows. *Applied Animal Behaviour Science* 21, 337–346.

Jensen, M.B. (2003) The effects of feeding method, milk allowance and social factors on milk feeding behaviour and cross-sucking in group housed dairy calves. *Applied Animal Behaviour Science* 80, 191–206.

Jensen, P. and Recen, B. (1989) When to wean – observations from free-ranging domestic pigs. *Applied Animal Behaviour Science* 23, 49–60.

Jensen, K.H., Pedersen, B.K., Pedersen, L.J. and Jørgensen, E. (1995) Well-being in pregnant sows: confinement versus group housing with electronic sow feeding. *Acta Agriculturae Scandinavica Section A Animal Science* 45, 266–275.

Johnson, K.G., Tyrrell, J., Rowe, J.B. and Pethick, D.W. (1998) Behavioural changes in stabled horses given nontherapeutic levels of virginiamycin. *Equine Veterinary Journal* 30, 139–143.

Kastelein, R.A. and Wiepkema, P.R. (1989) A digging trough as occupational therapy for Pacific walruses *Odobenus rosmarus* in human care. *Aquatic Mammals* 15, 9–17.

Kastelein, R.A., Paasse, M., Klinkjhammer, P. and Wiepkema, P.R. (1991) Food dispensers as occupational therapy for the walrus *Odobenus rosmarus divergens* at the Harderwijk Marine Mammal Park. *International Zoo Yearbook* 30, 201–212.

Kennedy, M.J., Schwabe, A.E. and Broom, D.M. (1993) Crib-sucking and windsucking stereotypies in the horse. *Equine Veterinary Education* 5, 142–154.

Keunen, J.E., Plaizner, J.C., Kyriazakis, L., Duffield, T.F., Widowski, T.M., Lindinger, M.I. and McBride, B.W. (2002) Effects of a subacute ruminal acidosis model on the diet selection of dairy cows. *Journal of Dairy Science* 85, 3304–3313.

Kiley-Worthington, M. (1983) Stereotypes in horses. *Equine Practice* 5, 34–40.

Koene, P. (1999) When feeding is just eating: how do farm and zoo animals use their spare time? In: van der Heide, D., Huisman, E.A., Kanis, E., Osse, J.W.M. and Verstegen, M.W.A. (eds) *Regulation of Feed Intake*. CAB International, Wallingford, UK, pp. 13–19.

Krzak, W.E., Gonyou, H.W. and Lawrence, L.M. (1991) Wood chewing by stalled horses: diurnal pattern and effects of exercise. *Journal of Animal Science* 69, 1053–1058.

Kusenose, R. (1992) Diurnal patterns of cribbing in stabled horses. *Japanese Journal of Equine Science* 3, 173–176.

Lawrence, A.B. and Illius, A.W. (1989) Methodology for measuring hunger and food needs using operant conditioning in the pig. *Applied Animal Behaviour Science* 24, 273–285.

Lawrence, A.B. and Terlouw, E.M.C. (1993) A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. *Journal of Animal Science* 71, 2815–2825.

Lawrence, A.B., Appleby, M.C., Illius, A.W. and Macleod, H.A. (1989) Measuring hunger in the pig using operant conditioning: the effect of dietary bulk. *Animal Production* 48, 213–220.

Lawrence, A.B., Terlouw, E.M.C. and Kyriazakis, I. (1993) The behavioural effects of undernutrition in confined farm animals. *Proceedings of the Nutrition Society* 52, 219–229.

Lebelt, D., Zanella, A.J. and Unshelm, J. (1998) Physiological correlates associated with cribbing behaviour in horses: changes in thermal threshold, heart rate, plasma beta-endorphin and serotonin. *Equine Veterinary Journal Supplement* 27, 21–27.

Lepionka, L., Malbert, C.H. and Laplace, J.P. (1997) Proximal gastric distension modifies ingestion rate in pigs. *Reproduction Nutrition Development* 37, 449–457.

Lidfors, L. and Isberg, L. (2003) Intersucking in dairy calves – review and questionnaire. *Applied Animal Behaviour Science* 80, 207–231.

Lindström, T. and Redbo, I. (2000) Effect of feeding duration and rumen fill on be-

haviour in dairy cows. *Applied Animal Behaviour Science* 70, 83–97.

Linnane, M., Horan, B., Connolly, J., O'Connor, P., Buckley, F. and Dillon, P. (2004) The effect of strain of Holstein–Friesan and feeding system on grazing behaviour, herbage intake and productivity in the first lactation. *Animal Science* 78, 169–178.

Luescher, U.A., McKeown, D.B. and Dean, H. (1998) A cross-sectional study on compulsive behaviour (stable vices) in horses. *Equine Veterinary Journal Supplement* 27, 14–18.

Marchant-Forde, J.N. and Pajor, E.A. (2003) The effect of dietary sodium bicarbonate on abnormal behavior and heart rate in sows. *Journal of Animal Science* 81 (Suppl. 1), 158.

Mason, G.J. (1991) Stereotypies: a critical review. *Animal Behaviour* 41, 1015–1037.

Mason, G.J. (in press). Animal farm: food provisioning and abnormal oral behaviours in captive ungulates. In: Stephens, D.W., Ydenberg, R.C. and Brown, J.C. (eds) *Foraging*. University of Chicago Press, Chicago.

Mason, G. and Mendl, M. (1997) Do the stereotypies of pigs, chickens and mink reflect adaptive species differences in the control of foraging? *Applied Animal Behaviour Science* 53, 45–58.

Mason, G.J. and Latham, N.R. (2004) Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, S57–S69.

Mason, G., Cooper, J. and Clarebrough, C. (2001) The welfare of fur-farmed mink. *Nature* 410, 35–36.

Mattiello, S., Canali, E., Ferrante, V., Caniatti, M., Gottardo, F., Cozzi, G., Andrighetto, I. and Verga, M. (2002) The provision of solid feeds to veal calves: II. Behaviour, physiology and abomasal damage. *Journal of Animal Science* 80, 367–375.

McBride, S.D. and Cuddeford, D. (2001) The putative welfare-reducing effects of preventing equine stereotypic behaviour. *Animal Welfare* 10, 173–189.

McBride, S.D. and Long, L. (2001) Management of horses showing stereotypic behaviour, owner perception and the implication for welfare. *The Veterinary Record* 148, 799–802.

McGreevy, P.D. and Nicol, C.J. (1998a) Physiological and behavioural consequences associated with short-term prevention of crib-biting in horses. *Physiology and Behaviour* 65, 15–23.

McGreevy, P.D. and Nicol, C.J. (1998b) Prevention of crib-biting: a review. *Equine Veterinary Journal Supplement* 27, 35–38.

McGreevy, P.D., Cripps, P.J., French, N.P., Green, L.E. and Nicol, C.J. (1995a) Management factors associated with stereotypic and redirected behaviour in the thoroughbred horse. *Equine Veterinary Journal* 27, 86–91.

McGreevy, P.D., French, N.P. and Nicol, C.J. (1995b) The prevalence of abnormal behaviours in dressage, eventing and endurance horses in relation to stabling. *The Veterinary Record* 137, 36–37.

McGreevy, P., Richardson, J.D., Nicol, C.J. and Lane, J.G. (1995c) Radiographic and endoscopic study of horses performing an oral based stereotypy. *Equine Veterinary Journal* 27, 92–95.

McGreevy, P.D., Webster, A.J.F. and Nicol, C.J. (2001a) Study of the behaviour, digestive efficiency and gut transit times of crib-biting horses. *The Veterinary Record* 148, 592–596.

McGreevy, P.D., Hawson, L.A., Habermann, T.C. and Cattle, S.R. (2001b) Geophagia in horses: a short note on 13 cases. *Applied Animal Behaviour Science* 71, 119–125.

Meot, F., Cirio, A. and Boivin, R. (1997) Parotid secretion daily patterns and measurement with ultrasonic flow probes in conscious sheep. *Experimental Physiology* 82, 905–923.

Merial (2004) Equine ulcers. Available at: http://gastrogard.us.merial.com/equine_ulcers.asp

Mills, D.S. and MacLeod, C.A. (2002) The response of crib-biting and windsucking in horses to dietary supplementation with an antacid mixture. *Ippologia* 13, 33–41.

Mills, D.S. and McDonnell, S.M. (2005) *The Domestic Horse: The Origins, Development and Management of its Behaviour*. Cambridge University Press, Cambridge, UK.

Minero, M., Canali, E., Ferrante, V., Verga, M. and Ödberg, F.O. (1999) Heart rate and behavioural responses of crib-biting horses to two acute stressors. *The Veterinary Record* 145, 430–433.

Mroz, Z., Partridge, I.G., Mitchell, G. and Keal, H.D. (1986) The effect of oat hulls, added to the basal ration for pregnant sows, on reproductive performance, apparent digestibility, rate of passage and plasma parameters. *Journal of the Science of Food and Agriculture* 37, 239–247.

Murray, M.J. (1999) Pathophysiology of peptic disorders in foals and horses: a review. *Equine Veterinary Journal Supplement* 29, 14–18.

Murray, M.J. and Eichorn, E.S. (1996) Effects of intermittent feed deprivation, intermittent feed deprivation with ranitidine administration, and stall confinement with ad libitum access to hay on gastric ulceration in horses. *American Journal of Veterinary Research* 57, 1599–1603.

Murray, C.G. and Sanson, G.D. (1998) Thegosis – a critical review. *Australian Dental Journal* 43, 192–198.

Newberry, R.C. and Wood-Gush, D.G.M. (1985) The suckling behaviour of domestic pigs in a semi-natural environment. *Behaviour* 95, 11–25.

Newman, J. (in press) Herbivory. In: Stephens, D.W., Ydenberg, R.C. and Brown, J.C. (eds) *Foraging*. University of Chicago Press, Chicago.

Nicol, C.J. (1999) Understanding equine stereotypies. *Equine Veterinary Journal Supplement* 28, 20–25.

Nicol, C.J. (2000) Equine stereotypies. In: Houpt, K.A. (ed.) *Recent Advances in Companion Animal Behavior Problems*. International Veterinary Information Service, Ithaca, New York.

Nicol, C.J. and Badnell-Waters, A.J. (2005) Suckling behaviour in domestic foals and the development of abnormal oral behaviour. *Animal Behaviour* 70, 21–29.

Nicol, C.J., Davidson, H.P.B., Harris, P.A., Waters, A.J. and Wilson, A.D. (2002) Study of crib-biting and gastric inflammation and ulceration in young horses. *The Veterinary Record* 151, 658–662.

Ödberg, F.O. (1978) Abnormal behaviours (stereotypies). In: *Proceedings of the First World Congress on Ethology Applied to Zootechnics*. Industrias Graficas Espana, Madrid, pp. 475–480.

Oetzel, G.R. (2003) Nutritional management and subacute ruminal acidosis in dairy herds. In: *Proceedings of the American Association of Bovine Practitioners 36th Annual Conference*, Columbus, Ohio.

O'Sullivan, T., Friendship, R.M., Ball, R. and Ayles, H. (1996) Prevalence of lesions of the pars oesophageal region of the stomach of sows at slaughter. In: *Proceedings of the American Association of Swine Practitioners*, pp. 151–153.

Phillips, C. (2002) *Cattle Behaviour and Welfare*. Blackwell Publishing, Oxford, UK.

Phillips, C.J.C., Youssef, M.Y.I., Chiy, P.C. and Arney, D.R. (1999) Sodium chloride supplements increase the salt appetite and reduce stereotypies in confined cattle. *Animal Science* 68, 741–747.

Pol, F., Courboulay, V., Cotte, J.P. and Lechaux, S. (2000) Logement en cases collectives ou en stalles individuelles en première gestation. Impact sur le bien-être des truies nullipares. *Journées de Recherche Porcine en France* 32, 97–104.

Pough, F.H., Heiser, J.B. and McFarland, W.N. (1989) *Vertebrate Life*, 3rd edn. Macmillan Publishing Company, New York.

Ramonet, Y., Meunier-Salaün, M.C. and Dourmad, J.Y. (1999) High-fiber diets in pregnant sows: digestive utilization and effects on the behavior of the animals. *Journal of Animal Science* 77, 591–599.

Ramonet, Y., Robert, S., Aumaître, A., Dourmad, J.Y. and Meunier-Salaün, M.C. (2000a) Influence of dietary fibre on digestive utilization, metabolite profiles and the behaviour of pregnant sows. *Animal Science* 70, 275–286.

Ramonet, Y., Bolduc, J., Bergeron, R., Robert, S. and Meunier-Salaün, M.C. (2000b) Feeding motivation in pregnant sows: effect of fibrous diets in operant conditioning procedure. *Applied Animal Behaviour Science* 66, 21–29.

Rebhun, W.C., Dill, S.G. and Power, H.T. (1982) Gastric ulcers in foals. *Journal of the American Veterinary Medical Association* 180, 404–407.

Redbo, I. (1990) Changes in duration and frequency of stereotypies and their adjoining behaviours in heifers, before, during and after the grazing period. *Applied Animal Behaviour Science* 26, 57–67.

Redbo, I. (1992) The influence of restraint on the occurrence of oral stereotypies in dairy cows. *Applied Animal Behaviour Science* 35, 115–123.

Redbo, I. and Nordblad, A. (1997) Stereotypies in heifers are affected by feeding regime. *Applied Animal Behaviour Science* 53, 193–202.

Redbo, I., Jacobson, K.G., van Doorn, C. and Petterson, G. (1992) A note on the relations between oral stereotypies in dairy cows and milk production, health and age. *Animal Production* 54, 166–168.

Redbo, I., Emanuelson, M., Lundberg, K. and Oredsson, N. (1996) Feeding level and oral stereotypies in dairy cows. *Animal Science* 62, 199–206.

Redbo, I., Redbo-Torstensson, P., Ödberg, F.O., Hedendahl, A. and Holm, J. (1998) Factors affecting behavioural disturbances in race-horses. *Animal Science* 66, 475–481.

Reinhardt, V. (2002) Artificial weaning of calves: benefits and costs. *Journal of Applied Animal Welfare Science* 5, 251–255.

Robbins, C.T. (1993) *Wildlife Feeding and Nutrition*, 2nd edn. Academic Press, New York.

Robert, S., Matte, J.J., Farmer, C., Girard, C.L. and Martineau, G.P. (1993) High-fibre diets for sows: effects on stereotypies and adjunctive drinking. *Applied Animal Behaviour Science* 37, 297–309.

Robert, S., Rushen, J. and Farmer, C. (1997) Both energy content and bulk of feed affect stereotypic behaviour, heart rate and feeding motivation of female pigs. *Applied Animal Behaviour Science* 54, 161–171.

Robert, S., Weary, D. and Gonyou, H.W. (1999) Segregated early weaning and welfare of piglets. *Journal of Applied Animal Welfare Science* 2, 31–40.

Robert, S., Bergeron, R., Farmer, C. and Meunier-Salaün, M.C. (2002) Does the number of daily meals affect feeding motivation and behaviour of gilts fed high-fibre diets. *Applied Animal Behaviour Science* 76, 105–117.

Rowe, J.B., Pethick, D.W. and Lees, M.J. (1994) Prevention of acidosis and laminitis associated with grain feeding in horses. *Journal of Nutrition* 124, 2742–2744.

Rushen, J. (1984) Stereotyped behaviour, adjunctive drinking and the feeding periods of tethered sows. *Animal Behaviour* 32, 1059–1067.

Rushen, J. (2003) Changing concepts of farm animal welfare: bridging the gap between applied and basic research. *Applied Animal Behaviour Science* 81, 199–214.

Rushen, J., Lawrence, A.B. and Terlouw, E.M.C. (1993) The motivational basis of stereotypies. In: Lawrence, A.B. and Rushen, J. (eds) *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. CAB International, Wallingford, UK, pp. 41–64.

Rushen, J., Robert, S. and Farmer, C. (1999) Effects of an oat-based high-fibre diet on insulin, glucose, cortisol and free fatty acid concentrations in gilts. *Animal Science* 69, 395–401.

Rutter, S.M., Orr, J.R., Yarrow, N.H. and Champion, R.A. (2004) Dietary preference of dairy heifers grazing ryegrass and white clover, with and without an anti-bloat treatment. *Applied Animal Behaviour Science* 85, 1–10.

Sambraus, H.H. (1985) Mouth-based anomalous syndromes. In: Fraser, A.F. (ed.) *Ethology of Farm Animals*. Elsevier, Amsterdam, pp. 391–422.

Sato, S., Kubo, T. and Abe, M. (1992) Factors influencing tongue-rolling and the relationship between tongue-rolling and production traits in fattening cattle. *Journal of Animal Science* 70 (Suppl. 1), 157.

Sato, S., Sugiyama, M., Yasue, T., Deguchi, Y. and Suyama, T. (2001) Seasonal change of land use strategy of free-ranging cattle in an agroforest setting without fencing. *Proceedings of the 35th Congress of the ISAE*, Davis, California, p. 152.

Sauvant, D., Meschy, F. and Mertens, D. (1999) Components of ruminal acidosis and acidogenic effects of diets. *INRA Productions Animales* 12, 49–60.

Schaller, G.B., Qitao, T., Johnson, K.G., Xiaoming, W., Hemind, S. and Jinchu, H. (1989) The feeding ecology of giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. In: Gittleman, J.L. (ed.) *Carnivore Conservation and Evolution*. Chapman & Hall, London, pp. 212–241.

Schmidt-Nielson, K. (1997) *Animal Physiology: Adaptation and Environment*, 5th edn. Cambridge University Press, Cambridge, UK.

Schofield, W.L. and Mulville, J.P. (1998) Assessment of the modified Forssell's procedure for the treatment of oral stereotypies in 10 horses. *The Veterinary Record* 142, 572–575.

Schouten, W. and Rushen, J. (1992) Effects of naloxone on stereotypic and normal behaviour of tethered and loose-housed sows. *Applied Animal Behaviour Science* 33, 17–26.

Schouten, W., Rushen, J. and De Passillé, A.M.B (1991) Stereo-typic behavior and heart rate in pigs. *Physiology and Behavior* 50, 617–624.

Schouten, W.G.P., Lensink, J., Lakwijk, N. and Wiegant, V.M. (2000) De-arousal effect of stereotypies in tethered sows. In: *Proceedings of the 34th International Congress of the International Society for Applied Ethology*, Florianopolis, Brazil, p. 46.

Schwartzkopf-Genswein, K.S., Beauchemin, K.A., Gibb, D.J., Crews, D.H., Hickman, D.D., Streeter, M. and McAllister, T.A. (2003) Effect of bunk management on feeding behavior, ruminal acidosis and performance of feedlot cattle: a review. *Journal of Animal Science* 81 (Suppl.), E149–E158.

Seo, T., Sato, S., Kosaka, K., Sakamoto, N. and Tokumoto, K. (1998) Tongue-playing and heart rate in calves. *Applied Animal Behaviour Science* 58, 179–182.

Simpson, B.S. (1998) Behavior problems in horses: cribbing and wood chewing. *Veterinary Medicine* November 1998, 999–1004.

Soede, N.M., Helmond, F.A., Schouten, W.G.P. and Kemp, B. (1997) Oestrus and peri-ovulatory hormone profiles in tethered and loose-housed sows. *Animal Reproduction Science* 46, 133–148.

Spoolder, H.A.M., Burbidge, J.A., Edwards, S.A., Simmins, P.H. and Lawrence, A.B. (1995) Provision of straw as a foraging substrate reduces the development of excessive chain and bar manipulation in food restricted sows. *Applied Animal Behaviour Science* 43, 249–262.

Stolba, A. and Wood-Gush, D.G.M. (1989) The behaviour of pigs in a semi-natural environment. *Animal Production* 48, 419–425.

Stolba, A., Baker, N. and Wood-Gush, D.G.M. (1983) The characterisation of stereotyped behaviour in stalled sows by informational redundancy. *Behaviour* 87, 157–181.

Tarou, L.R., Bashaw, M.J., Sartor, R., Maki, T.S., Liu, S.C. and Maple, T.L. (2001) When we're not looking: nocturnal behavior of giraffe. In: *Proceedings of the 2001 American Zoo and Aquarium Association Conference*, St. Louis, Missouri.

Tarou, L.R., Bashaw, M.J. and Maple, T.L. (2003) Failure of a chemical spray to significantly reduce stereotypic licking in a captive giraffe. *Zoo Biology* 22, 601–607.

Terlouw, E.M.C. and Lawrence, A.B. (1993) Long-term effects of food allowance and housing on development of stereotypies in pigs. *Applied Animal Behaviour Science* 38, 103–126.

Terlouw, E.M.C., Lawrence, A.B. and Illius, A.W. (1991a) Influences of feeding level and physical restriction on development of stereotypies in sows. *Animal Behaviour* 42, 981–991.

Terlouw, E.M.C., Lawrence, A.B., Ladewig, J., De Passillé, A.M.B., Rushen, J. and Schouten, W.G.P. (1991b) Relationship between plasma cortisol and stereotypic activities in pigs. *Behavioural Processes* 25, 133–153.

Terlouw, E.M.C., Wiersma, A., Lawrence, A.B. and Macleod, H.A. (1993) Ingestion of food facilitates the performance of stereotypies in sows. *Animal Behaviour* 46, 939–950.

Tobler, I. and Schweirin, B. (1996) Behavioural sleep in the giraffe (*Giraffa cameleopardalis*) in a zoological garden. *Journal of Sleep Research* 5, 21–32.

Traub-Dargatz, J.L., Kopral, C.A., Hillberg Seitzinger, A., Garbes, L.P., Forde, K. and White, N.A. (2001) Estimate of the national incidence of an operation-level risk factor for colic among horses in the United Sates, Spring (1998–1999). *Journal of American Veterinary Medical Association* 219, 67–71.

United States Department of Agriculture (USDA) (2002) Dairy 2002. Part I: Reference of Dairy Health and Management in the United States. National Animal Health Monitoring System.

Van Soest, P.J. (1994) *Nutritional Ecology of the Ruminant*, 2nd edn. Cornell University Press, Ithaca, New York.

Veasey, J.S., Waran, N.K. and Young, R.J. (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare* 5, 139–153.

Veissier, I., Lamy, D. and Le Neindre, P. (1990) Social behaviour in domestic beef cattle when yearling calves are left with the cows for the next calving. *Applied Animal Behaviour Science*, 27, 193–200.

Vickery, S.S. and Mason, G.J. (2004) Stereotypic behaviour in Asiatic black and Malayan sun bears. *Zoo Biology* 23, 409–430.

Vieuille-Thomas, C., Le Pape, G. and Signoret, J.P. (1995) Stereotypies in pregnant sows: indications of influence of the housing system on the patterns expressed by the animals. *Applied Animal Behaviour Science* 44, 19–27.

Von Borell, E. and Hurnik, J.F. (1990) Stereotypic behavior and productivity of sows. *Canadian Journal of Animal Science* 70, 953–956.

Waters, A.J. (2002) Factors influencing the development of stereotypic and redirected behaviours in young horses. PhD thesis, The University of Bristol, UK.

Waters, A.J., Nicol, C.J. and French, N.P. (2002) Factors influencing the development of stereotypic and redirected behaviours in young horses: the findings of a four year prospective epidemiological study. *Equine Veterinary Journal* 34, 572–579.

Whittaker, X., Spoolder, H.A.M., Edwards, S.A., Lawrence, A.B. and Corning, S. (1998) The influence of dietary fibre and the provision on straw on the development of stereotypic behaviour in food-restricted pregnant gilts. *Applied Animal Behaviour Science* 61, 89–102.

Whittaker, X., Edwards, S.A., Spoolder, H.A.M., Lawrence, A.B. and Corning, S. (1999) Effects of straw bedding and high fibre diets on the behaviour of floor fed group-housed sows. *Applied Animal Behaviour Science* 63, 25–39.

Whybrow, J., Cooper, J., Haskell, M. and Lewis, R. (1995) Feed quality and abnormal oral behaviour in lambs housed individually on unbedded slats. In: (eds) Rutter, S.M., Rushen, J., Randle, H.D. and Eddison, J.C. *Proceedings of the 29th Congress for the ISAE.* UFAW, Potters Bar, UK pp. 251–252.

Wiepkema, P.R. (1971) Positive feedbacks at work during feeding. *Behaviour* 39, 266–273.

Wiepkema, P.R., van Hellemond, K.K., Roessingh, P. and Rombery, H. (1987) Behaviour and abomasal damage in veal calves. *Applied Animal Behaviour Science* 18, 257–268.

Willard, J.G., Willard, J.C., Wolfram, S.A. and Baker, J.P. (1977) Effect of diet on cecal pH and feeding behavior of horses. *Journal of Animal Science* 77, 87–93.

Wondra, K.J., Hancock, J.D., Behnke, K.C., Hines, R.H. and Stark, C.R. (1995) Effects of particle size and pelleting on growth performance, nutrient digestibility, and stomach morphology in finishing pigs. *Journal of Animal Science* 73, 757–763.

Wood-Gush, D.G.M. and Beilharz, R.G. (1983) The enrichment of a bare environment for animals in confined conditions. *Applied Animal Ethology* 10, 209–217.

Young, J.Z. (1981) *The Life of Vertebrates*, 3rd edn. Oxford University Press, Oxford, UK.