Brief chapter summaries of 'Stereotypic Animal Behaviour – Fundamentals and Applications for Welfare' (2nd ed.) – eds. Georgia Mason and Jeff Rushen (CABI, 2006).

Chapter 1:

A Decade-or-More's Progress in Understanding Stereotypic Behaviour

Jeff RUSHEN and Georgia MASON

Repetitive, abnormal behaviour patterns are performed by tens, perhaps hundreds, of millions of animals worldwide: animals that live on farms and in laboratory animal facilities, stables, kennels, zoos, even in our homes. Our introductory chapter reviews the extent of research into this 'stereotypic behaviour' – traditionally defined as 'repetitive, unvarying, with no obvious goal or function' – since the book's first edition was published in 1993. We illustrate the growing number of papers on captive animals, contrasting them with the much greater number on human clinical subjects and on research animals invasively manipulated to produce abnormal behaviour. We report recent meta-analyses showing patterns in captive animals' stereotypic behaviour (e.g. systematic variation with taxon, and relationships with other signs of poor welfare). We also review the outstanding research questions raised by the first edition, and how they have been tackled in this one. Some contributed 'boxes' in this chapter further set the scene for the rest of the book: one summarises the motivational hypotheses typically advanced by ethologists, a second introduces explanations in terms of brain (dys)function, a third reviews how 'coping' might help account for stereotypic behaviours, while the last considers what is meant if they are labeled 'pathological'.

Section I: Normal animal, abnormal environment?

Chapter 2:

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

Renee BERGERON, Amanda BADNELL-WATERS, Sarah LAMBTON and Georgia MASON

Ungulates are the most prevalent mammalian stereotypers: millions of these animals are affected worldwide, and more stereotypic individuals (e.g. crib-biting horses, sham-chewing sows, tongue-rolling cattle and wall-licking giraffes) have been studied in this taxon than any other. Ungulates are united by being primarily herbivorous, and much evidence suggests that their oral stereotypic behaviours derive from natural foraging. Thus 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 how and why is diet important, exactly? Bergeron and colleagues review three principle hypotheses. The first is that captive ungulates' diets do not cause satiety or are deficient in other, specific ways (e.g. too low in salt, protein or fibre); stereotypic behaviours could then stem from innate, persistent attempts to find more food, or even from learnt behaviours that help redress these deficits (wood-chewing to gain fibre being a possible

example). A second hypothesis is that captive diets take so little time to find, chew or ruminate that animals are left with unfulfilled motivations to perform these foraging activities; oral stereotypic behaviour could then supply some of the motivational feedback normally supplied during natural foraging. A third hypothesis is that stereotypic behaviours are induced by the effects of artificial diets on gut function. Low-fibre, energy-rich foods have long been known to cause gastrointestinal dysfunction in ungulates, e.g. gastric ulcers in horses and pigs or ruminal acidosis in cattle. Abnormal chewing and similar could be a response to this, and could even have some benefits by generating saliva that then helps to rectify gastrointestinal acidity.

Further questions are posed by this chapter in contributed boxes; for example, how do ungulates resemble pandas, chickens and walruses? And is it ethical to physically prevent horses from stereotyping by means of 'cribbing-straps' or surgical interventions?

Chapter 3:
Locomotory Stereotypies in Carnivores: Does Pacing Stem from Hunting, Ranging or Frustrated Escape?

Ros CLUBB and Sophie VICKERY

Pacing in captive wild carnivores is the stereotypic behaviour most familiar to the general public; indeed in the Netherlands, the verb *'ijsberen'* – literally 'to polar bear' – is routinely applied to pacing, restless people! Carnivores are also a taxon in which fascinating case studies have been meticulously documented, many attempts have been made to reduce the behaviour, and perhaps most importantly, data now exist for 30+ separate species allowing the use of species comparisons to test hypotheses about the biological origins of pacing.

These three approaches differ in their support for the various hypotheses proposed concerning this behaviour's motivational basis. Observational studies often suggest a link between the pre-feeding pacing of carnivores and natural hunting behaviour, but other types of study do not. Indeed data collected when captive environments are altered often suggest instead that thwarted escape motivations are the cause. Cross-species comparisons cast further doubt on a central role for frustrated hunting: no aspect of natural foraging behaviour predicts the severity of this behaviour, and instead natural home range size emerges as the key. Possible explanations– and exciting directions for future research– include that carnivore pacing represents frustrated escape attempts (to forage, range, reach a mate, or for any one of a host of reasons); or that non-motivational factors render naturally wide-ranging species generally prone to persistent stereotypic behaviour (e.g. because they have been rendered more dysfunctional by captivity), with motivational factors then shaping the behaviour's timing and form.

This chapter also highlights the future role that species comparisons could play in understanding the stereotypic behaviours of all affected taxa, from the ungulates of the first chapter to the rodents of the next.

Chapter 4:
The Motivational Basis of Caged Rodents' Stereotypies

Hanno WÜRBEL

Rodents allow the type of controlled experiment that can be very challenging with, say, carnivores or ungulates. Würbel builds on the previous chapters to describe the motivational bases of rodent stereotypic behaviour, presenting some well-designed, hypothesis-led

ethological research investigating the causation of two examples: stereotypic digging in the gerbil and bar-mouthing in the laboratory mouse. These experiments carefully manipulated specific environmental stimuli to show the roles of motivations to escape from the cage and/or to seek appropriate shelter.

However, Würbel also shows convincingly that motivational explanations cannot be the full story: they can explain why animals repeat certain 'source behaviours', but not why these activities become so very time-consuming or ritualistic in appearance; for example, once rodent stereotypies develop, they can become astonishingly persistent, and even unresponsive to the types of environmental enrichment that would effectively prevent them appearing in younger animals. Würbel argues that other behavioural processes – perhaps even pathological ones – need to be invoked: a theme developed in the following chapters. A contributed box to this chapter also discusses the paradox of rodent wheel-running: is it a stereotypic behaviour or exercise, or even both?

Section II: Abnormal animals?

Chapter 5:
Perseveration and Stereotypy – Systems-level Insights from Clinical Psychology

Joe GARNER

Garner reviews how the brain's 'executive systems' organize and cause the performance of behaviour, and what happens when these systems malfunction. In particular, he focuses on the systems that sequence the specific motor patterns of any behavioural task, especially those comprising the dorsal striatum and its outputs. Dysfunction here potentially causes hyperactivity, rapid repetitions of and/or switches between different motor patterns, and stereotypic behaviour. Thus this brain region is the main site of action for stereotypy-inducing drugs (e.g. psycho-stimulants like amphetamine), and is often affected by abnormal rearing conditions (e.g. those reviewed in the following chapters).

In these cases, the changes implicated in stereotypic behaviour also result in forms of inappropriate repetition termed 'perseveration'. Garner describes a series of experiments that therefore ask, do captive animals with high levels of stereotypy also show strong tendencies to perseverate? The answer is yes: in every species looked at to date, from jumping bank voles to pacing sun bears, the most stereotypic individuals also show the most persistent, repetitive responding in tasks designed to assess their abilities to give up a learnt response in extinction or tendencies to spontaneously generate variable versus predictable responses. These results could have important implications. However, a major caveat (and important direction for future research) is that alone, these correlational studies alone are not enough to demonstrate that the perseveration of stereotypers is abnormal or even induced by captivity. To investigate this, we need the type of experimental manipulation discussed in the three following chapters.

Chapter 6:
Deprived Environments: Developmental insights from Primatology

Melinda NOVAK, Jerrold MEYER, Corinne LUTZ and Stefan TIEFENBACHER

For primates, being deprived of maternal care has major effects. Some accounts of maternal loss come from primates hand-reared in zoos, but most data stem from the research of Harlow and colleagues several decades ago. Here, work on social deprivation included the raising of rhesus infants for the first months of life without mothers or peers: these unfortunate animals grew up to spend spent much of their time in stereotypic behaviour. Some early forms seemed to mimic the mother-infant interactions these infants could not experience, e.g. self-clasping and digit-sucking apparently reflecting the loss of physical contact and diminished opportunities to suckle. However, frustrated motivations were not the whole story. As the monkeys matured, these behaviours were replaced by new abnormalities such as somersaults, head bobs and sometimes injurious behaviours like self-biting (disturbing activities which, paradoxically, may actually help these animals cope with acute stress). Furthermore, they showed additional changes including poor abilities to extinguish learnt responses (*cf.* the perseveration described in the previous chapter), heightened fearfulness, and long-lasting disturbances of forebrain serotinergic and dopaminergic function.

Early social deprivation is not the only cause of primate abnormal behaviour: isolating or otherwise stressing normally-reared animals can also induce it. However, it is clear that maternal separation has particularly profound and long-lasting effects. Two contributed boxes build on these findings to discuss findings on the appallingly deprived 'orphan' children discovered in Romania in the early 1990s, and the possible role of maternal deprivation elsewhere, such as in the stereotypic behaviours of farm animals.

Chapter 7:
The Neurobiology of Stereotypy I: Environmental Complexity

Mark LEWIS, Mark PRESTI, John LEWIS and Courtney TURNER

This chapter focuses on the physical environment: the predictability and restricted space typical of 'impoverished' captive conditions. Lewis and colleagues review evidence that the prolonged exposure to such environments can induce stereotypic behaviours that become increasingly hard to then abolish with enrichment. In contrast, the early exposure to enriched environments can sometimes ' protect' animals from the subsequent development of stereotypic behaviours, even if they are moved to barren environments. A contributed box reviews similar effects evident in the wild-caught and captive-born animals, the former seeming somewhat protected from stereotypic behaviour when brought into captivity.

Why do such effects occur? One way to address this question is to examine the CNS changes seen in stereotypy-inducing environments. Lewis and colleagues have conducted a series of experiments on this issue, rearing deer mice in barren or enriched environments and investigating the high and low stereotypers that emerge. Enriched animals with negligible stereotypic behaviour prove to be a distinctive group, with higher levels of neuronal metabolic activity, dendritic branching and the neurotrophin BNDF in the motor cortex and striatum. These data thus build on the previous chapter, in implicating specific changes in basal ganglia functioning, particularly in the circuits between motor cortex and dorsal striatum.

Chapter 8:
The Neurobiology of Stereotypy II: The Role of Stress

Simona CABIB

This chapter looks at the effects of stress on another region of the basal ganglia: the nucleus accumbens and its connections. Cabib does this by contrasting the well-characterized responses of two mouse strains – DBA/2 and C57BL/6 – to sustained stress, using them to argue that some genotypes respond to certain types of stress with a suite of neurobiological changes ('stress sensitization') whose consequences include stereotypic behaviour.

Repeated exposure to uncontrollable aversive situations can cause profound, long-term changes in brain organization. Such changes seem to fall into two classes. One type, readily seen in the C57 mice for instance, is that stressors come to elicit increasingly minimal dopamine response from the nucleus accumbens. This acts to increase learned helplessness (e.g. causes more passive floating in 'forced swim' tests); to reduce responsiveness (including stereotypy) to dopamine agonists like amphetamine; and to reduce the stereotypic behavior mice display in their cages: a powerful illustration of how low levels of stereotypic behaviour do not always guarentee good animal welfare. The second, alternative type of change, in contrast, causes stress-induced nucleus accumbens dopamine responses to become increasingly pronounced with repeated exposure. Isolated, food-deprived DBA mice illustrate this sensitization well, plus the behavioural changes that follow it: reduced susceptibility to 'behavioural despair' in situations like the forced swim test, enhanced susceptibility to the stereotypy-inducing effects of amphetamine, and increased stereotypic climbing within the home-cage.

Do these findings extent to other mice, or even to other species? Contributed boxes highlight some important future research areas by discussing the mixed support for this idea in other mouse strains; the possible role of opioid-mediated ventral tegmental effects in the stereotypic behaviours of a host of species; and the role of acute stress in primate abnormal behaviours.

<u>Section III: Treating stereotypic behaviours</u>

Chapter 9:
Environmental Enrichment as a Strategy for Mitigating Stereotypies in Zoo Animals: a Literature Review and Meta-analysis

Ron SWAISGOOD and David SHEPHERDSON

Zoo animals provided some of the earliest and best described cases of stereotypic behaviour, and zoos have taken the lead in finding practical ways to reduce it, usually through what is known as 'environmental enrichment' – alterations to the enclosure, or additions of particular objects or stimuli, made with the broad aim of increasing welfare. But how well does such enrichment work? Studies of enrichment and its effects on stereotyping zoo animals allowed these authors to pool and analyse around 20 papers dealing with about 100 individuals across multiple taxa. Their findings include that there is an impressive degree of success, enrichments typically reducing stereotypy-performance by half. However, not a single case eliminated the behaviour altogether, making it important in the future to really ascertain what 'works', what does not, and why.

Contributed boxes in this chapter discuss the role of enrichment in the captive breeding

of pandas; the practical realities of implementing enrichment programmes in zoos; and the effects of enrichment on laboratory primates. The chapter ends with suggestions as to how research on stereotypic behaviour in zoo animals could be improved – a topic potentially of great fundamental as well as practical value.

Chapter 10:
Veterinary and Pharmacological Approaches to Abnormal Repetitive Behaviour

Daniel MILLS and Andrew LUESCHER

Practicing veterinarians are often faced with the challenging job of 'curing' stereotypic behaviour. So, faced with a tail-chasing dog, a pet cat that has licked its belly bald or a much-loved horse that stubbornly crib-bites, what do vets do? The holistic approach described by Mills and Luescher offers some striking examples of complete treatment success. It also mirrors many of the themes reviewed in this volume. First, is the animal showing perfectly normal responses to an abnormal environment? For example, is it being exposed to motivationally conflicting situations that elicit perfectly relevant (if exaggerated and undesirable) species-typical responses? In such instances, educating the owner into changing their expectancies and/or the circumstances the animal is exposed to may be the only treatment needed. But what if the animal itself is psychologically abnormal? In such instances, any environmental change that reduces stress might be called for, as well as another approach available to veterinarians: the use of pharmacological compounds such as serotonin reuptake inhibitors. Mills and Luescher provide a detailed overview here of the use of many pharmacological compounds, along with some important warnings and caveats.

This chapter and its contributed boxes reiterate some questions that have been raised throughout the book: how heterogeneous is stereotypic behaviour? Are there fundamental sub-types that should be distinguished? And how might we recognise animal equivalents of obsessive–compulsive disorder? These and other questions are looked at anew in the final chapter.

<u>To end:</u>

Chapter 11:
Stereotypic behaviour in captive Animals – Fundamentals, and implications for welfare and beyond

Georgia MASON

I end with a synthesis. I show that there are three main causes of repetition: altered behavioural control by the forebrain (as implicated in perseveration); reinforcement (e.g. via 'coping' effects); and motivational effects – sustained elicitation by internal or external stimuli. There are also three main causes of predictability: environmental constancy; routine- (or habit-) formation; and the repeated elicitation of very specific action patterns. Finally, there are three main types of 'source behaviour' for repetition: escape attempts; actions that surrogate for natural behaviour patterns (such as foraging-like activities); and a third category of more puzzling, diverse, forms some of which probably reflect CNS dysfunction. Captivity induces stereotypic behaviour by causing frustration and/or by altering CNS functioning (via stress and/or through impeding normal development). Thus captive environments that induce

stereotypic behaviour typically also reduce animal welfare.

Stereotypic behaviour has traditionally been defined as 'repetitive, unvarying, with no obvious goal or function', but classifying behaviours solely according to ill-defined aspects of phenotype is obviously problematic. I suggest a new definition centred on the mechanisms underlying repetition: that stereotypic behaviours are repetitive behaviours induced by frustration, repeated attempts to cope, and/or CNS dysfunction. The former are maladaptive but readily reversible responses in normal animals to abnormal environments, while the latter represent a spectrum of pathological changes in the dorsal striatum and its connections, the nucleus accumbens and functionally related structures, and/or in the prefrontal cortex and its connections. The extent to which such pathologies explain what we see in millions of captive animals is just one of many outstanding issues which might be resolved by this book's next edition.