The welfare of wild animals in travelling circuses

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Executive Summary

- We were asked to provide the Welsh Government with an impartial literature review and an analysis of the scientific evidence available as to whether captive wild animals in travelling circuses and other animal shows achieve their optimal welfare requirements as set out under the Animal Welfare Act 2006 and any other relevant legislation.
- The Animal Welfare Act 2006 makes it a criminal offence for any person responsible for an animal to fail to provide for the animal's welfare. Under the Act, the person responsible for an animal must take all reasonable steps to ensure the needs of the animal are met. These needs include -

  (a) its need for a suitable environment,

  (b) its need for a suitable diet,

  (c) its need to be able to exhibit normal behaviour patterns,

  (d) any need it has to be housed with, or apart from, other animals, and

  (e) its need to be protected from pain, suffering, injury and disease.

  However, there is considerable debate about the welfare of wild animals in travelling circuses, and views are polarised as to whether the specific conditions provided by circuses and other travelling shows that use wild animals can meet the welfare needs of wild animals.
- For this review, we considered the collective effect of all aspects of management and the environment on the welfare of wild animals in travelling circuses and mobile zoos since, while one aspect of management may be interpreted as promoting good welfare, the others may not, and so the cumulative effect may be poor welfare overall.
- We reviewed Welsh, UK and EU legislation affecting animals in circuses and provided an overview of countries that have banned the use of some or all wild animals in circuses. We identified 33 countries that have nationwide bans on the use or import/export of some or all wild animals in circuses, including 18 EU member states. In 19 of the 23 countries for which information was available, animal welfare/ protection was the sole or one of the reasons for banning the use of wild animals in circuses.
- There are also local bans in various semi-autonomous regions/counties/ municipalities in a number of countries, including Argentina, Australia, Brazil, Canada, Chile, Norway, Poland, Republic of Ireland, Spain, UK and USA. More than 200 local authorities in the UK, including nearly half of the local authorities in Wales, already have a ban on animals in circuses; of these, more than two thirds ban all animals, while the remainder ban wild animals.
- There is a lack of clarity as to what constitutes a domesticated animal, a wild species, a travelling circus, a mobile zoo, and performance. This leads to inconsistencies in which pieces of legislation apply to which species and in which circumstances.
- In England, in 2015 only 19 wild animals (seven reindeer, three snakes, three zebras, three camels, one ankole, one fox and one raccoon) were covered by licences issued to two circuses under the Welfare of Animals in Travelling Circuses (England) Regulations 2012. Substantially more individuals and a much greater range of species of wild animals are used in European circuses.
- In the UK, many more wild animals are used in a variety of other mobile entertainments (collectively referred to as "mobile zoos" for this report). A survey in 2016 found that there were around 188 mobile zoos, plus 7 mobile 'farms', with around 3570 wild animals between them. These are minimum estimates. The animals are used for a variety of purposes, including display, handling and performing tricks at a wide range of venues. The number of calls to the RSPCA's Cruelty and Advice Line in 2015 suggests that there is public concern about these shows.
- While the use of wild animals in interactive shows is likely to have greater impact than simple displays, the education and conservation role of travelling circuses and mobile zoos is likely to be marginal, and any potential educational and conservation benefits are likely to be outweighed by the negative impression generated by using wild animals for entertainment.
- We contacted 658 experts and organisations around the world to seek their views on the key welfare issues for wild animals in travelling circuses and mobile zoos. These experts were identified through scientific publications,

internet research and recommendations from other experts. They included 138 animal trainers and circuses, 206 lawyers and veterinarians with expertise in wild animal welfare, 107 people working for relevant NGOs, 144 scientists such as biologists, researchers, behavioural and species experts, and 58 zoo and wild animal sanctuary staff. Other contacts included relevant government officials and wildlife experts.

- For the first questionnaire, we asked 613 experts to list up to ten indicators of good and bad welfare and up to ten factors that could contribute to good and bad welfare of wild animals in circuses and the other travelling animal shows. We also asked them to list any issues they believed apply specifically to non-domesticated animals used in circuses and other travelling animal shows. We received 97 completed questionnaires, a response rate of 15.8%.
- For the second questionnaire, we used the 10 largest response categories for each question in the first questionnaire to form 42 statements about the welfare of wild animals in circuses and other travelling shows and asked 623 experts to indicate the extent to which they agreed with each statement, on a scale from 0% to 100% using a slider. We received 98 responses, a response rate of 15.7%.
- We analysed the answers to identify the significant areas of agreement and disagreement between different groups of experts. The greatest difference was between animal trainers and circuses and NGOs and the three groups of experts (lawyers and veterinarians, scientists, and zoo and wild animal sanctuary staff) that were considered to be impartial (i.e. were not directly involved with the issue). Animal trainers and circuses disagreed with the three groups of impartial experts on 11/42 questions (26%), and NGOs disagreed with the impartial experts on 8/42 questions (19%), whereas the impartial groups of experts only disagreed with each other on two questions (5%) each. So there was substantial agreement on welfare issues associated with wild animals in travelling circuses and other forms of animal entertainment between lawyers and veterinarians, scientists, and zoo and wild animal sanctuary staff. In the literature review, we discuss where the scientific evidence supports the views expressed by different groups of experts.
- The main areas where experts disagreed were the influence of different aspects of captive animal management on the welfare of wild animals in travelling circuses and mobile zoos, the potential impacts of handling and training on their welfare, and the impacts of transport and travel on their welfare. Having identified the main areas of disagreement between the different groups of experts, we looked for scientific evidence that would help assess the rationale for these differences of opinion.
- To identify relevant literature, we developed search terms based on the results of the first questionnaire survey. Of the 1430 sources of information we located from the database searches, 666 (46.6%) were published up to and including 2006, and 764 (53.4%) were published from 2007 onwards. We also identified 270 other records from other sources: of these 153 (56.7%) were published up to and including 2006, and 117 (43.3%) from 2007 onwards. Thus there has been a substantial increase in the amount of information available since the last review of the welfare of wild animals in travelling circuses.
- All sources of information were then assessed to decide whether they met the criteria for inclusion in a scientific review. It was impossible to define which species are used in circuses and mobile zoos, especially since the search for novelty and changing attitudes have led to a rapid expansion of the number of mobile zoos and of the species used in wild animal entertainment generally. So we did not exclude any species of wild animal from the literature review. Since very little research has been done on animals in travelling circuses and mobile zoos *per se*, we used studies on how wild animals respond to changes in environment, husbandry and/or transport in other captive situations to identify key indicators of good welfare, how particular experiences affect welfare, and whether travelling circuses and mobile zoos can fulfil the welfare requirements of wild animals.

- We were asked to consider *"What evidence is there that the welfare, both physical and mental, of wild and/or non-domesticated animals is sub-optimal in travelling and non-travelling circuses?"* Compared with static zoos, enclosures for animals in circuses and travelling animal shows are generally much smaller and less complex and the provision of environmental enrichment is likely to be extremely limited or non-existent due to the need to maintain portability, ease of handling of the animals and compliance during training sessions. Limitations of space and facilities mean that animals are often kept in inappropriate social conditions, such as isolation of social species, grouping of solitary species and/or proximity of incompatible species. It is more challenging for travelling circuses to provide species-typical and ecologically-relevant food and to source and store food appropriately. Normal behaviour of wild animals in circuses and travelling animal shows is frequently disturbed or thwarted by handling, training, performance, transport, restraint and an impoverished environment. Training methods commonly used in circuses do not facilitate the minimal use of negative reinforcement, coercion, force and aggression. Caging/tethering and the performance of unnatural movements contribute to physical deformities, injuries, lameness and psychological distress. Taken together, these factors indicate that the welfare of wild animals is sub-optimal in circuses and travelling animal shows.
- We were asked *"To review the issue of environmental enrichment and, in particular, whether the regular training and interaction with the animals provides enrichment"*. While training has the potential to enhance the psychological welfare of animals through offering mental stimulation, it is not an appropriate substitute for other methods of improving welfare such as environmental enrichment and general enclosure suitability, which have multiple indirect benefits.
- We were asked *"What evidence exists to demonstrate that travelling environments might induce behaviours that are not normally consistent for wild animals?"* Travelling environments are associated with restriction of normal behaviour patterns and high levels of stereotypical behaviour in captive wild animals and are unable to meet the specific climatic and environment needs of many species, thereby adversely affecting their behaviour.
- We were asked *"Does the evidence currently available support a ban on the use of such animals in travelling environments?"* We took into account the collective and cumulative effects of all aspects of management and the environment when considering the welfare of wild animals in travelling circuses and mobile zoos. The available scientific evidence indicates that captive wild animals in circuses and other travelling animal shows do not achieve their optimal welfare requirements, as set out under the Animal Welfare Act 2006, and the evidence would therefore support a ban on using wild animals in travelling circuses and mobile zoos on animal welfare grounds.

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Remit of the review

We were asked to provide the Welsh Government with an impartial literature review and an analysis of the scientific evidence available as to whether captive wild animals in travelling circuses and other travelling animal shows achieve their optimal welfare requirements as set out under the Animal Welfare Act 2006 and any other relevant legislation.

We were told that the questions which primarily needed to be considered were:-

- What evidence is there that the welfare, both physical and mental, of wild and/or non-domesticated animals is sub-optimal in travelling and non-travelling circuses?
- To review the issue of environmental enrichment and, in particular, whether the regular training and interaction with the animals provides enrichment.
- Does the evidence currently available support a ban on the use of such animals in travelling environments?
- What evidence exists to demonstrate that travelling environments might induce behaviours that are not normally consistent for wild animals?

The requirements of the contract were to provide:-

- The Welsh Government with an impartial literature review and an analysis of the scientific evidence that is available as to whether captive wild animals in travelling circuses achieve their optimal requirements as set out under the Animal Welfare Act 2006 and any other relevant legislation. We were told that this should also include their environment and enrichment of that environment and of the animals.
- A report that will enable a view to be taken by the Wales Animal Health and Welfare Framework Group on the concerns expressed by the Welsh Government as to whether it is appropriate for non-domesticated animals to be used in travelling entertainment.

We were given the following potential parameters for the review:-

- Contact all relevant persons that we consider appropriate, to ask them to advise us of any relevant evidence and scientific literature of which they are aware, and to record these representatives/organisations in our review.
- Summarise the existing scientific evidence of standards of animal welfare from the UK.
- Summarise the existing scientific evidence of standards of animal welfare from the rest of the world, using scientific polling to obtain international feedback.
- To include non-domesticated animals in the review; these were defined as a member of a species that is not normally domesticated in the British Islands i.e. a species whose collective behaviour, life cycle or physiology remains unaltered from the wild type despite their breeding and living conditions being under human control for multiple generations.
- Review the relevant legislation in other countries, their rationale for implementing a ban on wild animals in circuses, and whether there is appropriate evidence for a country not to implement a ban on the use of such animals.
- The welfare of animals in transport and any relevant European rules on travelling circuses.
- Whether there is any scope for circuses to carry out the ethical functions of licensed zoos, such as research, education and conservation, and what evidence, if any, is available to support that approach.
- The evidence presented in the contract report must be weighted to ensure that it is clear where research is published by groups with a vested interest e.g. circus unions or animal rights campaigners.
- To make it clear where evidence is not necessarily scientific, such as polls and petitions.
- To include the trade in circus animals, if known, and the sorts of animals that are traded.
- To consider any other evidence that may be relevant, such as: the Zoo Expert Committee's review of mobile zoos such as falconry displays, reptile/invertebrate shows and educational shows, which have many features in common with circuses; the Captive Animals' Protection Society's data on the number of mobile zoos in the UK and the animals used; and the RSPCA data on the number of complaints about these forms of animal entertainment.
- To consider whether any countries/ administrations have set proactive measures to safeguard animal welfare in circus operations.
- To review existing legislation that affects circuses.

Background

In March 2010 the UK Government published a summary of the responses to its consultation on whether wild animals in circuses should be banned, and on 13 May 2011 announced its decision to introduce a licensing system rather than a ban on wild animals in circuses[1]. Animal welfare groups expressed significant concerns about this decision. The Government cited concern over a legal challenge to a ban in Austria as one of the reasons for not pursuing a ban in England at that time. However, the case against the Austrian ban was later dropped[1].

The Animal Welfare Act 2006 makes it a criminal offence for any person responsible for an animal to fail to provide for the animal's welfare. However, there is considerable debate about the welfare of wild animals in travelling circuses, and views are polarised as to whether the specific conditions provided by circuses meet the welfare needs of wild animals. The Animal Welfare Act 2006 provides the Secretary of State with powers to introduce additional regulations, and on 23 June 2011 a back bench debate was held on the motion tabled by Mark Pritchard MP "That this House directs the Government to use its powers under section 12 of the Animal Welfare Act 2006 to introduce a regulation banning the use of all wild animals in circuses to take effect by 1 July 2012". The motion was passed unopposed.

The Government then published a consultation on its proposed licensing system in March 2012, and at the same time announced its intention to ban the use of wild animals in circuses in the longer term. It was said that the proposed licensing scheme would cover all aspects of life for a wild animal in a travelling circus environment including[1]:-

- Good accommodation and housing whilst being transported, at a performance, and in winter quarters;
- Full veterinary care;
- Controlling carefully who has access to the animals;
- Diet including food storage, preparation and provision;
- Environment such as noise and temperature; and
- Welfare during training and performance.

Regulations to bring in the licensing scheme were laid before Parliament on 12 July 2012. The draft Wild Animals in Circuses Bill which, if it had been adopted, would have banned the use of all wild animals in travelling circuses, was published on 16 April 2013. In Section 2, the Government stated that it does not believe it is appropriate to continue to use wild animals in travelling circuses because:-

- It is not necessary to use wild animals in travelling circuses to experience the circus;
- wild animals are just that and are not naturally suited to travelling circuses and may suffer as a result of being unable to fulfil their instinctive natural behaviour;
- we should feel duty-bound to recognise that wild animals have intrinsic value, and respect their inherent wildness and its implications for their treatment; and
- the practice adds nothing to the understanding and conservation of wild animals and the natural environment.

The draft Bill extended to England and Wales, but the offence of using a wild animal in a travelling circus in the draft Bill only applied to England. However, the Defra Minister Lord de Mauley wrote to his three counterparts in the Devolved Administrations to ask them to consider whether they would allow the Westminster Parliament to legislate for their countries.

However, the EFRA Select Committee Report[2] published on 9 July 2013 recommended that the Government revise its approach to the Bill so that a Schedule be attached that contained a proscribed list of animals which can no longer be used in travelling circuses; while this suggested that all big cats and elephants could be included on the list, species such as snakes, camels, zebras or raccoons would not be included. The Select Committee concluded "that there remains insufficient evidence, in line with the findings of the 2007 'Radford Report', for a ban on welfare grounds"[2].

The Government published its response on 22 October 2013[3]. It disagreed that a redraft of the Wild Animals in Circuses Bill would be effective or that a proscribed list of animal species was necessary, since it did not consider that it is still acceptable to use some species of wild animals in circuses but not others, and that the key issue was not the number of wild animals used in travelling circuses but that they are used at all[1].

There has been no further progress in England. Animal welfare is a devolved issue and, to date, legislation to prohibit the use of wild animals in circuses has not been put forward in Wales, Scotland or Northern Ireland.

Legislation relevant to circuses with animals in Wales

Animal welfare legislation

The Animal Welfare Act 2006 applies to the welfare of vertebrate animals. Sections 4 to 8 apply only to ‘protected animals’, which include those commonly domesticated in the British Isles, permanently or temporarily under the control of humans, or not living in a wild state, and Section 9 applies to animals for which a person is ‘responsible’. Animals used in circuses and other travelling shows are therefore covered by Sections 4 to 9. Key requirements of the Act include Section 4 regarding the prevention of unnecessary suffering and Section 9, which introduces a ‘duty of care’, making owners and keepers responsible for making sure the welfare needs of their animals are met. Section 9 states:-

9. Duty of person responsible for animal to ensure welfare

(1) A person commits an offence if he does not take such steps as are reasonable in all the circumstances to ensure that the needs of an animal for which he is responsible are met to the extent required by good practice.

(2) For the purposes of this Act, an animal’s needs shall be taken to include -

- (a) its need for a suitable environment,
- (b) its need for a suitable diet,
- (c) its need to be able to exhibit normal behaviour patterns,
- (d) any need it has to be housed with, or apart from, other animals, and
- (e) its need to be protected from pain, suffering, injury and disease.

(3) The circumstances to which it is relevant to have regard when applying subsection (1) include, in particular -

- (a) any lawful purpose for which the animal is kept, and
- (b) any lawful activity undertaken in relation to the animal.

(4) Nothing in this section applies to the destruction of an animal in an appropriate and humane manner.

Council Regulation (EC) 1/2005 applies to the welfare of animals during transport and related operations in the EU. Article 1 (1) states: “This Regulation shall apply to the transport of live vertebrate animals carried out within the Community, including the specific checks to be carried out by officials on consignments entering or leaving the customs territory of the Community.” This suggests that animals travelling with a circus should be covered by the Regulation. However, in 2008, the European Commission issued the following statement[4]: “In the opinion of the Commission it can be argued that, despite the wording of Council Regulation (EC) 1/2005, and in order to ensure the consistency of the Regulation with Art. 37 of the EC Treaty, circus animals do not fall within the scope of that Regulation”, although the Commission noted that “it is ultimately for the European Court of Justice to give binding legal interpretations of Community law.”

Council Regulation (EC) 1/2005 is implemented in Wales by the Welfare of Animals (Transport) (Wales) Order 2007. Individual Member States are permitted to introduce more stringent requirements so can include the transport of circus animals if they wish. Defra guidance on the Regulation and the implementing Orders in England, Wales, Scotland and Northern Ireland states: “It is our view that the transport of circus animals is not within the scope of the Regulation when the animals can be described as travelling in their permanent housing. This position has been adopted in order to ensure consistency with Article 37 of the EC treaty and has the support of the European Commission. The transport of circus animals not travelling in what can be described as their permanent place of housing is therefore within the scope of the Regulation”[5]. Defra indicates that, where circus animals fall outside the scope of the Regulation, the general provisions under Article 4 of the Orders and the Animal Welfare Act 2006 are applicable. Article 4 of the Orders applies to invertebrates as well as vertebrates that fall outside the scope of the Regulation.

Therefore, the full requirements of Regulation 1/2005 and the implementing Order apply for those animals in circuses that are transported in vehicles/containers that are separate from their usual accommodation. For those animals in circuses that are transported in the cages or other containers in which they are usually housed, only very basic legal requirements are applicable to their welfare during transport, as set out under Article 4 of The Welfare of Animals (Transport) (Wales) Order 2007, which states:-

General provision on the protection of animals during transport

4. (1) It is an offence to transport any animal in a way which causes, or is likely to cause, injury or unnecessary suffering to that animal.

(2) It is an offence to transport any animal except in such receptacles or means of transport, under conditions (in particular with regard to space, ventilation, temperature and security) and with such supply of liquid and oxygen, as are appropriate for the species concerned.

(3) This article applies to the transport of cold-blooded invertebrate animals.

(4) This article applies to the transport of vertebrate animals except those to which Council Regulation (EC) No 1/2005 applies.

Registration and licensing requirements

The exhibition and training of performing animals is regulated by the Performing Animals (Regulation) Act 1925 (as amended), which stipulates requirements for the registration of circuses with a local authority. Registration does not necessitate inspections. Under Section 5 of the Act, 'exhibit' is defined as meaning exhibit at any entertainment to which the public are admitted, whether on payment of money or otherwise and 'train' means to train for the purpose of any such exhibition. Section 7 of the Act excludes the training of animals for *bona fide* military, police, agricultural or sporting purposes, or the exhibition of any animals so trained.

The Zoo Licensing Act 1981 (as amended) sets out the local authority licensing requirements for zoos. The Act is not applicable to circuses, defined as "a place where animals are kept or introduced wholly or mainly for the purpose of performing tricks or manoeuvres at that place".

The Dangerous Wild Animals Act 1976 (as amended) sets out the local authority licensing requirements for keeping dangerous wild animals. There is an exemption for circuses, defined as "any place where animals are kept or introduced wholly or mainly for the purpose of performing tricks or manoeuvres". The latest version of the Schedule, containing the list of mammals, birds, reptiles and invertebrates covered by the Act, is given in The Dangerous Wild Animals Act 1976 (modification) (No. 2) Order 2007.

The Licensing Act 2003, as amended by the Legislative Reform (Entertainment Licensing) Order 2014, regulates the provision of entertainment. Entertainment that consists of or forms part of a performance by a travelling circus is not covered by the Act, provided certain conditions are met, as set out below. However, the Act may be applicable in circumstances where the specified conditions are not met:-

Circuses

12D. (1) The provision of any entertainment that consists of or forms part of a performance by a travelling circus is not to be regarded as the provision of regulated entertainment for the purposes of this Act if the conditions in sub-paragraphs (2) to (5) are satisfied.

(2) The first condition is that the entertainment is not of a description falling within paragraph 2(1)(b) (exhibition of a film) or paragraph 2(1)(d) (boxing or wrestling entertainment).

(3) The second condition is that the entertainment takes place between 8am and 11pm on the same day.

(4) The third condition is that -

(a) the entertainment takes place wholly within a moveable structure, and

(b) the audience present is accommodated wholly inside that moveable structure.

(5) The fourth condition is that the travelling circus has not been located on the same site for more than 28 consecutive days.

(6) In this paragraph, "travelling circus" means a circus which travels from site to site for the purpose of giving performances.

Animal movement and veterinary health checks

Commission Regulation 1739/2005 sets out the requirements for the movement of circus animals between EU Member States. The Regulation applies to travelling exhibitions, fairs or animal acts where animals are kept for the primary purpose of public exhibition or entertainment. The types of animal covered by the Regulation are listed in Annex A of Directive 92/65/EEC.

Regulation 1739/2005 has been introduced into Welsh law through an amendment to the Animals and Animal Products (Import and Export) (Wales) Regulations 2006. The amending Regulations are the Animals and Animal Products (Import and Export) (Wales) (Laboratories, Circuses and Avian Quarantine) Regulations 2007.

To be permitted to move to another Member State, a circus based in England or Wales must be registered with the Animal and Plant Health Agency (APHA) and the animals must have passports and meet testing and vaccination requirements. At least ten days prior to travel to another Member State, a circus must inform the Competent Authority (in the Member State where it is currently situated) of its intention to move.

Within the UK, animals in circuses may be subject to temporary movement restrictions and other requirements, as necessary for the control of disease outbreaks, in accordance with the Animal Health Act 1981 (as amended).

Wildlife trade restrictions

Trade in certain species is restricted under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). CITES is implemented in the EU through a set of Regulations known as the EU Wildlife Trade Regulations. Currently these are Council Regulation (EC) No. 338/97 (The Basic or Principle Regulation) (as amended), Commission Regulation (EC) No. 865/2006 (the Implementing Regulation) (as amended), and Commission Implementing Regulation (EU) No. 792/2012 (the Permit Regulation). In addition, Commission Implementing Regulation (EU) No. 2105/736 (a Suspensions Regulation) is in place to suspend the introduction into the EU of particular species from certain countries. The current version of the Annexes to Regulation 338/97, containing the lists of species covered, is in Commission Regulation (EU) No 1320/2014.

The EU Wildlife Trade Regulations are implemented in the UK by the Control of Trade in Endangered Species (Enforcement) Regulations 1997 (as amended) and the Control of Trade in Endangered Species (Fees) Regulations 2009.

Circuses must abide by these rules, which include a prohibition on the display to the public for commercial purposes of species listed in Annex A of Regulation 338/97 (as amended) unless an exemption is granted in accordance with Article 8 of Regulation 338/97, for example because the animals were captive born and bred or were acquired before the restrictions applied. Article 8 of The Control of Trade in Endangered Species (Enforcement) Regulations 1997 states:-

Purchase and sale etc

8. (1) Subject to paragraphs (3) and (4), a person who, contrary to Article 8 of the Principal Regulation, purchases, offers to purchase, acquires for commercial purposes, displays to the public for commercial purposes, uses for commercial gain, sells, keeps for sale, offers for sale or transports for sale any specimen of a species listed in Annex A to the Principal Regulation shall be guilty of an offence.

(2) Subject to paragraphs (4) and (5), any person who, contrary to Article 8 of the Principal Regulation, purchases, offers to purchase, acquires for commercial purposes, sells, keeps for sale, offers for sale or transports for sale any specimen of a species listed in Annex B to the Principal Regulation which has been imported or acquired unlawfully shall be guilty of an offence.

(3) Paragraph (1) does not apply to anything done under, and in accordance with the terms of, any certificate or general derogation granted pursuant to Article 8 of the Council Regulation.

(4) A person shall not be guilty of an offence under paragraph (1) or (2) if he proves to the satisfaction of the court that at the time the alleged offence was committed he had no reason to believe that the specimen was a specimen of a species listed in Annex A, or as the case may be Annex B.

(5) A person shall not be guilty of an offence under paragraph (2) if he proves to the satisfaction of the court-

(a) that at the time when the specimen first came into his possession he made such enquiries (if any) as in the circumstances were reasonable in order to ascertain whether it was imported or acquired unlawfully; and

(b) that at the time the alleged offence was committed, he had no reason to believe that the specimen was imported or acquired unlawfully.

(6) Without prejudice to the generality of paragraph (5) above, a person shall be taken to have made such enquiries as are mentioned there if he produces to the court a statement which was furnished by the person from whom he obtained possession of the specimen ("the supplier"), which was signed by the supplier or by a person authorised by him, and which states that-

(a) the supplier made enquiries at the time the specimen came into his possession in order to ascertain whether it was a specimen which had been imported or acquired unlawfully; and

   (b) the supplier had no reason to believe at the time he relinquished possession of the specimen to the accused that the article was at that time a specimen which had been imported or acquired unlawfully.

(7) A person who furnishes, for the purposes of regulation 6 above, a statement which he knows to be false in a material particular, or recklessly furnishes for those purposes a certificate which is false in a material particular, shall be guilty of an offence.

(8) A person guilty of an offence under paragraph (1), (2) or (7) above shall be liable-

   (a) on summary conviction, to a fine not exceeding level 5 on the standard scale, to a term of imprisonment not exceeding three months, or to both; and

   (b) on conviction on indictment, to a term of imprisonment not exceeding two years or a fine, or to both.

Article 8 of Regulation 338/97 states:-

Provisions relating to the control of commercial activities

1. The purchase, offer to purchase, acquisition for commercial purposes, display to the public for commercial purposes, use for commercial gain and sale, keeping for sale, offering for sale or transporting for sale of specimens of the species listed in Annex A shall be prohibited.

2. Member States may prohibit the holding of specimens, in particular live animals of the species listed in Annex A.

3. In accordance with the requirements of other Community legislation on the conservation of wild fauna and flora, exemption from the prohibitions referred to in paragraph 1 may be granted by issuance of a certificate to that effect by a management authority of the Member State in which the specimens are located, on a case-by-case basis where the specimens:-

   (a) were acquired in, or were introduced into, the Community before the provisions relating to species listed in Appendix I to the Convention or in Annex C1 to Regulation (EEC) No 3626/82 or in Annex A became applicable to the specimens; or

   (b) are worked specimens that were acquired more than 50 years previously; or

   (c) were introduced into the Community in compliance with the provisions of this Regulation and are to be used for purposes which are not detrimental to the survival of the species concerned; or

   (d) are captive-born and bred specimens of an animal species or artificially propagated specimens of a plant species or are parts or derivatives of such specimens; or

   (e) are required under exceptional circumstances for the advancement of science or for essential biomedical purposes pursuant to Council Directive 86/609/EEC of 24 November 1986 on the approximation of laws, regulations and administrative provisions of the Member States regarding the protection of animals used for experimental and other scientific purposes (6) where the species in question proves to be the only one suitable for those purposes and where there are no specimens of the species which have been born and bred in captivity; or

   (f) are intended for breeding or propagation purposes from which conservation benefits will accrue to the species concerned; or

   (g) are intended for research or education aimed at the preservation or conservation of the species; or

   (h) originate in a Member State and were taken from the wild in accordance with the legislation in force in that Member State.

Licensing of wild animals in circuses in the UK

In England the person responsible for the operation of a travelling circus that has wild animals must hold a licence in accordance with the Welfare of Animals in Travelling Circuses (England) Regulations 2012. The licensing requirements do not currently apply in Wales, Scotland or Northern Ireland. The licensing conditions include:-

- Giving the Secretary of State notice before acquiring a wild animal for use in a travelling circus, notification of the tour schedule, and records of each licensed animal
- Making care plans for each individual or social group of licensed animals, restricting access to the animals to people with appropriate qualifications or experience, and consultation with, and regular inspection of the animals by, a veterinary surgeon
- Responsibility of the operator to promote the welfare of licensed animals
- Specific welfare requirements for display, training and performance, for environment, and for transport

The licensing requirements are generally non-specific. For example, accommodation for the animals must be of "an appropriate size" and, where welfare standards are specified, these fall well below those for wild animals in zoos[6].

The current situation globally

Globally, we have identified 33 countries that have nationwide bans on the use or import/export of some or all wild animals in circuses, including 18 EU member states: details are summarised in Table 1. A ban was also announced in China but it does not, as yet, appear to have been fully implemented and it is not entirely clear whether this applies to animal performances at all circuses and zoos or only at state-owned zoos[7-9]. Due to time constraints, it was not possible to refer to primary sources for every country so secondary sources are referenced in some cases. Where possible, we have given information on the specific species covered by each ban as definitions of 'wild animals' vary.

Information on the rationale for the various bans is included where available. Where supplementary information was not available but the title of the legislation containing the ban has been identified, we have assumed that there is an element of animal protection in the rationale for bans enacted under animal protection/welfare/anti-cruelty legislation, an element of animal health in the rationale for bans enacted under animal health legislation, and an element of wildlife conservation in the rationale for bans applicable specifically to CITES-listed species. The most common reason identified for the bans is animal welfare/protection: in 19 out of 23 countries for which information on the rationale was found, animal welfare/protection was the sole reason, or one of multiple reasons, identified for the ban. In some cases, for example in Belgium and Denmark, the decision was based on the conclusions of a body or working group after considering the scientific evidence regarding whether the needs of various species of wild animals could be met in a circus environment. In Belgium, a 2011 report by the Council of Animal Welfare concluded that, by their very nature, circuses are unable to provide species of wild animals with conditions that meet their species-specific physical, psychological and behavioural needs[10]. In Denmark, a working group concluded that, for most wild animals, it was not possible to keep them in circuses in a way which would be acceptable from an animal welfare point of view. However, for elephants, sea lions and zebras, the majority of the working group considered that it would be possible to keep them in an acceptable way, provided that they were kept in accordance with certain welfare provisions[11]. Other reasons identified for the bans include animal health/disease transmission (four countries), public safety (three countries), wildlife conservation (three countries), investigative evidence or reports of animal abuse/mistreatment (two countries) and societal concern for animal welfare (one country).

Table 1. Summary of bans on the use of animals in circuses around the world

EU countries	Ban applies to:	Rationale
Austria[12]	*All wild animals*	*Animal protection*
Belgium[13]	*All wild animals* (only domesticated species listed in Annex 1 are permitted to be used in circuses; the list includes parrots, which arguably are not domesticated, and some exotic species: camels, lamas, and water buffalo)	*Animal welfare* The 2014 amendment lists permitted species based on a 2011 report by the Council of Animal Welfare, which concluded that by their very nature, circuses are unable to provide species of wild animals with conditions that meet their species-specific physical, psychological and behavioural needs[10]
Bulgaria[14]	*Most wild animals* (except dolphins)	*Animal protection*
Croatia[15]	*All wild animals*	*Animal protection*
Cyprus[16,17]	*All animals*	
Czech Republic[18]	*Some wild animals* (newborn primates, pinnipeds, Cetacea, excluding the Delphinidae family, rhinoceri, hippopotami and giraffes)	*Animal protection*
Denmark[19]	*Most wild animals* (except elephants, sea lions, zebras, foxes, mink and parrots)	*Animal welfare* Ban based on the findings of a working group regarding which species could be kept in an acceptable way from a welfare perspective[11]
Estonia[20]	*Wild-caught animals*	*Animal protection*
Finland[21]	*Some wild animals* (in Finland, only certain listed species can be used in circuses, including horses, ponies, cats, dogs and a few others; on the Åland Islands, apes, predators, wild ruminants, ungulates, marsupials, pinnipeds, rhinos, hippos, raptors, cone animals and crocodilians are explicitly prohibited in circuses but other species, including elephants, are allowed with permission)[22]	*Animal welfare* The Animal Protection Law indicates that the decision of the Ministry regarding which species are prohibited in circuses in Finland is based on whether there is available knowledge to provide acceptable humane conditions[21]

EU countries	Ban applies to:	Rationale
Greece[23]	*All animals*	
Hungary[24]	*Wild-caught animals, elephants, rhinos, primates and CITES (Appendix 1) listed species caught after 2010*	*Animal protection and wildlife conservation*
Malta[25]	*All animals*	*Animal protection*
Netherlands[26]	*All wild animals* (only domesticated species listed in Annex IV of the Decree are permitted to be used in circuses, which includes some exotic species – camels, alpacas and llamas)	*Animal health* Secretary Sharon Dijksma of the Ministry of Economic Affairs in The Hague: "The health of animals is more important than their use for parties or clinging to outdated traditions"[26]
Poland[27]	*Wild-caught animals* (and only animals for which it is possible to provide living conditions appropriate to the needs of the species may be used in training/ shows/entertainment)	*Animal protection*
Portugal[28]	*CITES-listed species and their hybrids*	*Wildlife conservation, animal welfare, animal health and public safety* The preamble of the Ordinance refers to species conservation, animal welfare and health, and danger to people[28]
Slovakia[29]	*CITES-listed species*	*Wildlife conservation*
Slovenia[30]	*All wild animals*	*Animal protection*
Sweden[31]	*Some wild animals* (monkeys, predators with the exception of domesticated dogs and cats, pinnipeds with the exception of sea-lions, rhinoceroses, hippopotamuses, deer with the exception of reindeer, giraffes, kangaroos, birds of prey, ratite birds and crocodilians)	*Animal protection*

Non-EU countries	Ban applies to:	Rationale
Bolivia [16,17,29,32]	*All animals*	*Animal abuse* Ban reportedly based on animal cruelty/findings of undercover investigations [32]
Bosnia & Herzegovina [16]	*All animals*	
Colombia [33]	*All wild animals*	
Costa Rica [34]	*All wild animals*	*Animal health*
Ecuador [16,17]	*Native wild animals* (and restrictions on the use of exotic animals and ban on imports of native and exotic wild animals with circuses)	
El Salvador [16]	*All wild animals*	
India [35]	*Some wild animals*	*Animal protection*
Israel [36]	*All wild animals* (training to perform unnatural acts)	*Animal protection*
Mexico [16,17]	*All wild animals*	
Panama [16,17]	*All wild animals*	
Paraguay [16,17]	*All wild animals*	
Peru [16,17]	*All wild animals*	
Serbia [37]	*All wild animals*	*Animal protection*
Singapore [38]	*All wild animals*	*Public safety, animal welfare, animal abuse and societal concern* The Agri-Food and Veterinary Office statement refers to increasing numbers of accidents and reports of abuse, growing public concern over welfare, and inadequate accommodation[38]
Taiwan [16,39]	*Protected wildlife* (import/export)	*Public safety, animal health and animal welfare* DPP Legislator Tien Chiu-chin states: “Whether we are talking from the point of view of public safety, disease prevention or animal welfare, this amendment to stop circus animals from being imported into Taiwan is necessary”[39]

Where the use of wild animals continues to be permitted in circuses, some countries have taken steps to protect their welfare by introducing legally-binding minimum standards or non-legally-binding guidelines for circus animal welfare in addition to any general requirements under generic animal protection/anti-cruelty legislation. For example, in New Zealand the Animal Circuses (Welfare) Code of Practice 2005[40] (issued under the Animal Welfare Act 1999) stipulates legal minimum standards and recommended best practice for the care of circus animals, covering obligations of owners and persons in charge of animals; circus operation; food and water; shelter, accommodation and housing; environmental and behavioural enrichment; animal training and performances; species-specific standards for elephants, lions and primates; disease and injury control; transport; and a quality assurance system. In Germany, the Guidelines for Entertainment, Training and Use of Animals in Circuses and Similar Establishments are not legally binding but assist owners, authorities and courts in deciding whether animal husbandry meets the requirements of the law[41]. In Australia, welfare codes for circus animals are legally-binding in some Territories e.g. South Australia[42] but not in others e.g. Victoria[43], and the draft proposed national standards for exhibited animals specifically exclude animals in circuses[44]. Legal requirements also vary between States in the USA[45], with some basic requirements stipulated under Federal law[46] applicable across all States.

There are also local bans in various semi-autonomous regions/counties/municipalities in a number of countries, including Argentina, Australia, Brazil, Canada, Chile, Norway, Poland, Republic of Ireland, Spain, UK and USA[16,17,47]. More than 200 local authorities in the UK already have a ban on animals in circuses (more than two thirds of these ban all animals, while the remainder ban wild animals)[16,48]. The known local authority bans in Wales are summarised in Table 2.

Table 2. Local authority bans in Wales collated in 2009 by the RSPCA and updated in 2016[6]

Council	Ban	Date	Notes
Blaenau Gwent	No	2016	
Bridgend	No	2009	Circuses treated in the same way as any other event with animals
Caerphilly	Yes	2009	Policy relates to pre 1996 councils; no formal policy exists relating directly to Caerphilly council
Cardiff	Yes	1985	Wild animals banned but not domesticated animals, which are monitored by offices and require a code of practice from the circus
Carmarthenshire	No	2009	
Ceredigion	No	2009	No plan to be revised
Conwy	No	2009	Allowed a circus in 2013
Denbighshire	Yes	1998	Circus on private land which they licence and is inspected by officers
Flintshire	No	2008	Would want widespread public consultation. Have not had a circus in 12 years
Gwynedd	No	2009	Estate Department does not allow circuses with animals but no formal ban
Merthyr Tydfil	Yes	1995	No formal ban but as a condition of hire do not allow wild animals
Monmouthshire	No	2008	
Neath Port Talbot	Unknown	2008	Letter sent but no reply
Newport	Yes	2008	
Pembrokeshire	Yes	1996	Circuses with animals on private land are subject to an inspection by Animal Health and Welfare Inspector
Powys	No	2016	
Rhondda Cynon Taff	Yes	2008	Inspection by Animal Health Officers if on private land
Swansea	Yes	2009	Pre-1996 policy
Torfaen	No	2008	
Vale of Glamorgan	Yes	2008	
Wrexham	Yes	2008	No formal policies in place to support a ban
Ynys Mon	No	2008	Each application reviewed on merit; no recent animal circuses allowed

Yes	10	45%	
No	11	50%	
Unknown	1	5%	

What is a non-domesticated animal?

For this review, we were told that non-domesticated animals were defined as "a member of a species that is not normally domesticated in the British Islands; that is to say, a species whose collective behaviour, life cycle or physiology remains unaltered from the wild type despite their breeding and living conditions being under human control for multiple generations". This definition derives from the Zoo Licensing Act 1981 and is the one used in an earlier review of *Wild animals in travelling circuses*[49]. However, the earlier review included camels, llamas and reindeer as non-domesticated animals, even though all have a long history of domestication (Appendix 1).

In its review of the wildlife legislation in England and Wales, the Law Commission recommended that a wild animal "should be defined as any animal which was not bred in captivity, or an animal that was bred in captivity which has been lawfully released into the wild as part of a re-population or re-introduction programme. Secondly, an animal should not be considered "captive-bred" unless it was bred in captivity using animals which were lawfully in captivity"[50]. This definition related to the legislation that was being reviewed by the Law Commission and is not helpful when considering which species currently used in travelling circuses and mobile zoos should be considered to be wild animals.

It is also unclear why some domesticated species require a licence under the Dangerous Wild Animals Act 1976. Many domesticated species pose a risk to human health and safety: 74 people were killed by cattle in the 15 years from 2000[51].

Wild animals used in circuses

While a limited range of species is currently used in traditional British circuses, a survey in 2006 listed the following species in European circuses, with the most common in italics: mammals - *African elephant, Asian elephant*, antelope, baboon, bison, black bear, *Bactrian camel*, chimpanzee, eland, European brown bear, fox, giraffe, *guanaco*, hippopotamus, hyaena, jaguar, kangaroo, leopard, liger, *lion, puma*, pygmy hippopotamus, reindeer, rhesus monkey, rhinoceros, *sea lion*, snow leopard, tapir, *tiger*, water buffalo, wolf and *zebra*; birds - emu, ostrich, parakeet, parrots and macaws, penguin, vulture; and reptiles - *alligator* and *pythons*. The numbers of some of these are substantial: there were 90 elephants in German circuses and 400 big cats in French circuses[52].

In 2015, 19 wild animals in England (seven reindeer, three snakes, three zebras, three camels, one ankole, one fox and one raccoon) were covered by licenses issued to two circuses under the Welfare of Animals in Travelling Circuses (England) Regulations 2012:-

Table 3. Animals licensed in circuses in England in 2015[6]

	Circus Mondao	Jolly's Circus	Total
Ankole	-	1	1
Camel	2	1	3
Fox	-	1	1
Raccoon	-	1	1
Reindeer	2	5	7
Snakes	-	3 (1 boa, 2 Burmese pythons)	3
Zebra	1	2	3
Tiger	-	-	-
Lion	-	-	-
Total	**5**	**14**	**19**

In 2014, 23 wild animals in England (six reindeer, three snakes, three zebras, three tigers, three camels, two lions, one ankole, one fox and one raccoon) were covered by licenses issued to the same two circuses under the Welfare of Animals in Travelling Circuses (England) Regulations 2012[6]:-

Table 4. Animals licensed in circuses in England in 2014[6]

	Circus Mondao	Jolly's Circus	Total
Ankole	-	1	1
Camel	2	1	3
Fox	-	1	1
Raccoon	-	1	1
Reindeer	2	4	6
Snakes	-	3 (1 boa, 2 Burmese pythons)	3
Zebra	1	2	3
Tiger	-	3	3
Lion	-	2	2
Total	**5**	**18**	**23**

Wild animals used in mobile zoos

In recent years there has been an increasing trend to use wild animals in a diversity of travelling animal shows. For convenience, hereafter we refer to these as "mobile zoos". In 2013 a survey by the Captive Animals' Protection Society (CAPS) found that 169 companies were hiring animals out for parties, events and school talks, with at least 3,000 animals held by these companies. This estimate was based on internet research and Freedom of Information requests to local authorities; since no stock lists were available, the number of species and individual animals were estimated from the available promotional information. So there were likely to be more businesses and animals involved. An updated list in 2016 found that 35 mobile zoos had closed but that 54 had started to operate, so that the number of mobile zoos was around 188, plus 7 mobile 'farms', with around 3570 animals between them[53,54].

A great range of wild animals is used in these mobile zoos. The most popular species in CAPS's 2016 survey were African land snails, bearded dragons, corn snakes, hedgehogs, hissing cockroaches, millipedes, royal pythons, scorpions and tarantulas. These animals are generally transported packed in dog/cat crates or plastic containers of varying kinds and used to give talks or other types of presentations, often referred to as 'experiences'. Typical events are school/educational establishment talks, party packages, corporate bookings, fêtes and other external events. Many of these companies also offer animal assisted therapy, claiming to assist healing or help overcome social issues[54]. However, while there is an extensive literature on the benefits of animal assisted therapy with companion animals, and some evidence for animal assisted therapy with cetaceans, there is virtually no scientific evidence of the benefits of animal assisted therapy with exotics[55,56].

While some animals are only handled by the mobile zoo operator or are kept in their carriers/ containers for people to observe, many are handled by children and/or adults. This can include activities such as simply holding animals, draping snakes around people's necks, and/or sitting birds and some mammals on someone's shoulder. Some birds are tethered for people to look at and many animals are walked on leads/harnesses. Many mobile zoos offer the chance to hand feed the animals as part of the experience, and some use wild animals in 'performances'. Some of the animals used in these displays are dressed in clothes. Some use birds of prey and parrots in flying displays, others make the animals perform certain behaviours on command, or complete a series of tricks, such as moving over obstacles and manipulating objects. Examples include a parrot riding on the back of a tortoise, animals being made to complete assault courses, and birds riding bicycles[54].

It is becoming increasingly popular to use wild animals at Christmas events. In 2015, at least 80 events used reindeer, penguins or camels; these animals were paraded, kept on show or interacted with humans. For example, penguins were used to parade through a town centre at a Christmas market, reindeer were paraded through a town pulling a sleigh, and reindeer were kept in pens for a number of days for people to look at. Venues for these Christmas events included schools, universities, town centres, shopping centres, garden centres, a hospital and a hospice[57].

The Zoo Licensing Act 1981 defines a zoo as "any establishment where animals of wild species are exhibited to the public"[58]. The Act stipulates that "all zoos that are open to the public, with or without charge on seven or more days in a twelve-month period need a licence from their local authority to operate"[58]. Circuses are specifically excluded from the Zoo Licensing Act 1981; they are defined as "a place where animals are kept or introduced wholly or mainly for the purpose of performing tricks or manoeuvres at that place". Circus winter quarters, which are static and may be open to the public, are included within the definition of a circus and so are not considered to be zoos[58].

The Zoo Licensing Act 1981 was introduced before mobile zoos were common, which seem to fall between zoos and circuses. Some Christmas events by "mobile zoos" are static and display animals, usually reindeer, at one site for more than seven days a year. Also, many if not most mobile zoos are displaying wild animals to the public for more than seven days a year, albeit generally in different locations. It is unclear why an "establishment" displaying wild animals to the public is required to be licenced under the Zoo Licencing Act 1981 if it is static but not if it is mobile. It is also hard to see how training wild animals to perform tricks in mobile zoos differs from wild animals performing tricks in travelling circuses, other than that the species involved are generally smaller.

The 2013 survey by CAPS found that 66% of the businesses they identified were not registered with a local authority under the Performing Animals (Regulation) Act 1925[53] and there appears to be a significant level of public concern about mobile zoos. In 2015, 44 calls to the RSPCA's Cruelty and Advice Line were about mobile zoos using wild animals, including bird of prey displays: 93% of these calls were from members of the public with concerns for animal welfare (the rest were queries from the businesses themselves). The species used in these businesses, from the calls logged, included aardvark, African pygmy hedgehog, arachnids, barn owl, bearded dragon, Bengal eagle owl, burrowing owl, camel, crocodiles, European badger, European eagle owl, European hedgehog, falcon, fox, Harris's hawk, kestrel, lizard, meerkat, penguins, raccoon, raccoon dog, reindeer, Richardson's ground squirrel, skunk, snake, tortoise and white-faced scops owl. Venues for these events included a conference centre, festival, high street, nightclub, outdoor fair, pop-up café, pub and a wedding[59].

In the time available to us, we were unable to find where or how the animals in mobile zoos are sourced, or the extent of the trade in the animals for mobile zoos. However, in view of the large number of mobile zoos that have opened (and closed) in recent years, there must be a significant turn-over in stock. It is unclear what happens to wild animals that are no longer used in mobile zoos. There is also an extensive trade in many of these species to the public. This is based on misconceptions about the animals, due both to mobile zoos and advertising, and is a particular problem for smaller species such as meerkats[60]. The perception that wild animals are "cute", "cuddly", "domesticated", "malleable", or that they are "pets" can be extremely damaging to their welfare.

It is also unclear whether some of the animals used in these shows (skunks, possibly foxes) have had their anal glands removed to enable them to be used for performances and/or handled by members of the public. Removing an animal's anal glands for public display could be considered a prohibited procedure under the Mutilations (Permitted Procedures) (England) Regulations 2007, where a 'prohibited procedure' is defined under Section 5(3) of the Act as one 'which involves interference with the sensitive tissues or bone structure of the animal, otherwise than for the purpose of its medical treatment'. Similar provisions apply in Wales (Mutilations (Permitted Procedures) (Wales) Regulations 2007) and Scotland (Animal Health & Welfare (Scotland) Act 2006 and subsequent Regulations). Any animals with their anal glands removed may have been obtained from a country that permits such mutilations.

Using wild animals for performances

Under the Wild Animals in Travelling Circuses (England) Regulations 2012, a licence is required to operate or manage "a travelling circus in England that uses wild animals"[61]. The guidelines issued by Defra state that "the word "circus" is well understood" but for clarity is defined to include "any place where wild animals are kept or introduced wholly or mainly for the purpose of performing tricks or manoeuvres" and "a "travelling circus" means a circus which gives performances in more than one place and includes winter quarters where a wild animal associated with the circus is based while not touring". It is unclear how this definition excludes mobile zoos such as bird of prey and parrot shows, where species of wild birds are used to perform various sorts of manoeuvres, or those mobile zoos where wild animals are trained to perform tricks.

Static zoos also use wild animals in different types of entertainment to increase visitor numbers[62]; these include photo sessions, a range of interactions with the public, and the performance of various types of acts[63]. Whipsnade Zoo, for instance, currently produces a show called Sealion Splash Live! **(https://www.zsl.org/zsl-whipsnade-zoo/news/sealion-splash-live)** in which sea lions have been trained to leap several feet out of the water to touch balloons suspended above their pool, feats of balancing and other tricks. This is comparable to the tricks that sea lions perform in circuses, and we could not see a clear distinction between training wild animals for entertainment in static zoos compared to training them for entertainment in travelling circuses and mobile zoos. Some static zoos also have their own mobile zoos. It was suggested to us that a key difference between static zoos and travelling circuses and mobile zoos is the primary role of the collection. In many static zoos, collection planning entails identifying the role of each animal in the collection. While the role of some of the animals may be to perform in encounters or shows, the overall role of the collection is conservation and education, so the performance role of some of their animals is purportedly to help fulfil the conservation and educational priorities of the collection as a whole[56]. However, this would still appear to be contrary to the Government's basic principle that "we should feel duty-bound to recognise that wild animals have intrinsic value, and respect their inherent wildness and its implications for their treatment".

It is also unclear what constitutes a performing animal. According to Defra, "there is a difference between the exhibition of an animal (or the training of an animal for an exhibition) and the exhibition of a performing animal (or the training of a performing animal for an exhibition)". It is their opinion that the former do not require a licence whereas the latter do and that where the "line is drawn between the two is a matter of interpretation" but that "there must be an 'aspect of performance' for a licence to be required" under the Performing Animals (Regulations) Act 1925[64]. In contrast, the RSPCA uses a wider definition, and refers to a 'performing animal' as one "that is taken away from, or disturbed in, its usual environment and/or social group, or trained/set up to perform specific desired behaviours for the purposes of public display" and that 'performance' includes productions such as circuses and mobile zoos, as well as film, TV, theatre, county fairs, art exhibits etc.[65]. This definition seems more relevant for wild animals, since the key issues are the welfare effects of being taken away from, or disturbed in, their usual environment and/or social group, and how the animals are trained to perform particular behaviours or to interact with the public, including simply being handled or 'petted'.

Contributions to conservation and education

We were also asked to consider whether travelling circuses and other animal entertainment shows could make a meaningful contribution to conservation/education. In his review, Radford said "It is acknowledged that some circuses claim to make a contribution to education and/or conservation, but these are unconvincing compared to the resources and expertise which zoos now devote to these activities"[49]. While the estimated 273 licensed zoos in Britain[66] have more resources available to them, the issue is whether circuses and travelling shows can make a meaningful contribution to conservation and education with the resources available to them.

There is no expectation that small zoos in Britain should undertake major conservation and educational projects[58]. As a guide, for a hypothetical zoo without conservation-sensitive species and 80,000 visitors per annum, putting up bird or bat boxes, maintaining hedgerows or a pond would be sufficient to comply with the conservation requirements of the Zoo Licensing Act 1981, provided that the public are informed of the work[67]. So any benchmarks for conservation and/or education activities undertaken by travelling circuses should, as with zoos, be commensurate with their size and resources.

As a guide to what might be expected from circuses and other travelling animal shows, section 1A(a) of the Zoo licensing Act 1981 requires zoos to participate in one or more of the following five optional *ex situ* conservation activities:-

a. participating in research from which conservation benefits accrue to the species, and/or training in relevant conservation skills, and/or the exchange of information relating to species conservation and/or, where appropriate, captive breeding, repopulation or reintroduction of species into the wild;

b. promoting public education and awareness in relation to the conservation of biodiversity, particularly by providing information about the species exhibited and their natural habitats;

c. accommodating their animals under conditions which aim to satisfy the biological and conservation requirements of the individual species, inter alia, by providing species specific enrichment of the enclosures; and maintaining a high standard of animal husbandry with a developed programme of preventive and curative veterinary care and nutrition;

d. preventing the escape of animals in order to avoid possible ecological threats to indigenous species and preventing intrusion of outside pests and vermin;

e. keeping of up-to-date records of the zoo's collection appropriate to the species recorded.

While it would be more challenging for circuses and other travelling animal shows to participate in activities (a) and (c), they could include signage and educational information in their presentations and, in theory, be considered to be promoting public education and the exchange of information comparable to the *ex situ* conservation activities undertaken by smaller zoos. They could also raise funds for *in situ* conservation via additional donations or a proportion of entrance fees, and/or by stimulating educational activities after the circus has moved to a new location. In this respect, travelling circuses and other animal shows could have a greater impact on individuals than zoos, although zoos generally have much larger numbers of visitors. Public animal training produced more positive visitor experiences and had more holding power compared to passive exhibit viewing[68], although what visitors learn is largely down to the knowledge of the presenter and how they present the information [69]. Visits to circuses are relatively short so visitors are less likely to lose interest over time than they are at larger institutions such as zoos[70]. Median visit time to one (large, immersive) zoo exhibit was 11 minutes, but only 50% of this time was spent looking at animals or engaged with interpretive elements[71]. Visitors viewed another enclosure for less than 10 seconds[72].

It has long been argued that interactive animal 'shows' have the potential to have greater educational value than traditional zoos[73], especially when supported by accurate factual information[62]. However, several studies have highlighted the negative educational consequences of wild animal shows. Using wild animals for demonstrations and rides may portray wild animals as pets, thereby nullifying conservation messages and encouraging the public to exploit wild animals for personal benefit[74]. The use of chimpanzees in the media for entertainment negatively distorted the public's perception of wild animals and may therefore hinder conservation efforts[75]. A recent discourse analysis revealed that circuses are not conducive to promoting conservation messages because: they typically justify their use of animals by asserting that captivity is preferable to the wild, which promotes the idea that humans care for animals better than they do themselves; they broaden the definition of natural behaviour to any movement an animal can physically complete, which misrepresents how animals actually behave in the wild and disguises the fact that training is required to produce the behaviour; and they minimise the differences between humans and animals, which portrays the idea that animals are willing performers and disguises the underlying human domination[76].

With the increasing diversity of interactive forms of education, the overall contribution of travelling circuses and mobile zoos to conservation and/or education is likely to be marginal, and any potential benefits are likely to be outweighed by the negative impressions generated by using wild animals for entertainment.

Questionnaire surveys

Because of the polarised nature of the issue, we contacted relevant experts to obtain their views on the key welfare issues for wild animals in travelling circuses. Judgmental information can be indispensable for identifying and prioritizing issues, particularly when provided by experts in the field[77]. We used a two-stage process; this helped us identify areas of agreement and disagreement, and identify and prioritise the key issues to consider in our review of the scientific literature. Relevant experts were identified through scientific publications, internet research and recommendations from other experts.

In total 658 people and organisations were contacted directly about the two questionnaires: these included 138 animal trainers and circuses (*ATCs*), 206 lawyers and veterinarians with expertise in wild animal welfare (*LVs*), 107 people working for a relevant NGO (*NGOs*), 144 scientists such as biologists, researchers, behavioural and species experts (*Scis*), and 58 zoo and wild animal sanctuary staff (*Zoos*). We based the classification on the responder's personal expertise. So, for instance, a scientist with a publication record who was currently working for an NGO was classified as a scientist. Other contacts included relevant government officials and wildlife experts. All contacts were free to forward our questionnaire to other relevant experts at their discretion, and many did, so it is likely that many more people than the 658 people in our contact list had the opportunity to participate. Respondents were asked whether they would agree to be identified in the report: those who agreed are listed in Appendix 2.

The first questionnaire

We sent the first questionnaire, which consisted of three questions, to 613 experts around the world. They were asked to list up to ten indicators of good and bad welfare (questions 1a and 1b), and up to ten factors that could contribute to good and bad welfare (questions 2a and 2b), of wild animals in circuses and other travelling animal shows. Question 3 asked participants to list any issues they believed apply specifically to non-domesticated animals used in circuses and other travelling animal shows (Appendix 3).

We received 97 completed questionnaires, a response rate of 15.8%: 19 were from *ATCs*, 18 from *LVs*, 12 from *NGOs*, 38 from *Scis*, and 10 from *Zoos*. Some questionnaires were filled in collectively by several members of the same organisation and submitted as a single response.

The responses to each question were then categorised into six broad categories: behaviour, environment, health, management, training and performance, and travel. Within each of these broad categories we further sorted the responses into 'response categories' which contained aspects of a similar issue; for example, the broad category *health* included the response categories *appetite/thirst* and *physical condition* and the response category *physical condition* included aspects such as *foot condition*, *coat condition* and *injuries*. We plotted graphs separately for each question to identify the welfare indicators, contributing factors and issues that were most commonly identified by experts. To avoid inflation when experts listed different aspects of a similar issue in the same question, we only counted each specific response category once per question, per participant, regardless of the number of different aspects of the issue that were listed. For example if one expert listed *coat condition* and *lack of injury* as indicators of good welfare for question 1a, these would be counted as a single mention of 'physical condition', within the broad category of 'heath' (Appendix 4). Common behavioural indicators of psychological health such as *stereotypical behaviour* and *response to handlers* were included in the broad category *behaviour*.

Some response categories appeared under multiple broad categories, e.g. *frequency/duration* was used to summarise issues related to the frequency and duration of training under the broad category *training and performance* and issues related to the *frequency/duration* of transportation under the broad category of *travel*. In Appendix 4, the different broad categories are colour-coded to help interpretation.

Unfortunately some participants misinterpreted questions 1a and 1b and listed factors that might contribute to good or bad welfare as indicators of welfare. This led to aspects of the environment appearing on the graphs as indicators, which clearly they are not. However these misinterpretations were few in number so were unlikely to affect the overall pattern of responses.

a. Responses to question 1a and b: indicators of good and poor welfare

The most common indicators of animal welfare in circuses and travelling shows identified by experts were aspects of health and behaviour, and therefore physical and psychological health. The top indicator of both good and poor welfare was physical condition, such as body weight, muscle mass or fitness, and the condition of the pelage or epidermis, eyes, hooves, antlers etc. The ability of animals to engage in normal or natural behaviour (defined as belonging to the behavioural repertoire of animals of the same species, age and sex in nature) was the second most popular indicator of good welfare, whereas a scarcity of natural behaviour or the presence of abnormal or stress-related behaviours such as stereotypies, aggression and fearfulness, were said to indicate poor welfare. Several experts suggested that some behavioural indicators of good or poor welfare could be observed in response to human contact, such as when being approached or handled. Psychological health was considered an important aspect of animal welfare and some experts suggested that this could be determined by an animal's alertness, responsiveness and interest in their surroundings, in addition to the presence or absence of abnormal/stereotypical behaviour. The presence or absence of injury and disease, and aspects of physiology such as endocrinology, reproduction and digestion, were also considered reliable welfare indicators.

b. Responses to question 2a and b: factors that contribute to good and poor welfare

The leading factor that experts considered likely to contribute to good welfare in captive wild animals in circuses and other travelling shows was the availability, suitability and quality of food and water. This was closely followed by aspects of animal housing, particularly the size, condition and suitability of enclosures for the particular species, including during transportation. Experts considered that housing was the leading factor contributing to poor welfare, ahead of food and water. In addition to environmental housing conditions, animal welfare was thought to be influenced by the provision of a species-appropriate social environment, i.e. housing solitary species alone and social species in appropriate groups.

Conversely, training by positive reinforcement and by encouraging natural behaviour or movements was thought to contribute to good welfare by offering mental and physical stimulation. The frequency and duration of training sessions and performances were a concern for some experts, since overwork or overstimulation could interfere with natural behavioural time budgets, deprive animals of rest and cause excessive disturbance and stress.

The availability and provision of professional health care and veterinary treatment was considered an important contributor to good animal welfare, while the lack of regular veterinary health checks or deprivation of timely treatment were said to have a negative effect on animal welfare. The knowledge, experience and attentiveness of staff such as carers, handlers, grooms, trainers, business owners/managers and veterinarians, were frequently mentioned as contributors to both good and poor animal welfare.

Additional factors thought to influence welfare were the importance of exercise, the extent of freedom, choice and control animals have over their activities, the condition and hygiene of transport facilities and housing, the amount of time spent under close confinement, and the effects of human contact.

c. Responses to question 3: factors that influence welfare in circuses that are not found in other captive environments

Many experts believed that the welfare of animals in circuses was influenced by the greater frequency and duration of travel and performance not experienced by animals in other captive environments. The limited size and complexity of temporary enclosures was also considered a factor likely to influence welfare. Views were mixed as to whether the impacts of frequent travel, performance and regular changes of scenery on animal welfare are positive, by offering mental and physical stimulation and reducing boredom, or negative, due to excessive disturbance, disruption and unpredictability.

Other factors thought to influence animal welfare more in circuses than permanent captive environments were frequent human contact and handling, limited opportunity to engage in natural behaviour in a natural social environment, and the training of animals to perform movements that were unnatural or uncomfortable. Training itself was judged either to enhance or impair welfare depending on the training methods used and the experience of the trainer.

The frequent change of scenery as a result of regular travel was considered likely to be enriching by presenting novel stimuli and potentially stressful due to a lack of predictability and familiarity.

The second questionnaire

For the second questionnaire, we used the 10 largest response categories for each question in the first questionnaire to form 42 statements about the welfare of wild animals in circuses and other travelling shows. We then contacted 623 experts, including some who had not been invited to respond to the first questionnaire, and asked them to indicate the extent to which they agreed with each statement, on a scale from 0% to 100% using a slider (Appendix 5). We received 95 responses from individuals, two collective responses on behalf of animal trainers and circuses and one collective response on behalf of the British Veterinary Zoological Society, giving 98 responses in total, a response rate of 15.7%. Eight were from *ATCs*, 25 from *LVs*, 17 from *NGOs*, 36 from *Scis*, and 12 from *Zoos*.

To analyse the differences in the opinions of different groups of experts, the responses to each question were recorded as a percentage agreement score. We then ran a one-way ANOVA to test for differences in percentage agreement scores between groups of experts. If a difference was detected, *post-hoc* tests were done using Tukey's Honest Significant Differences method; P-values were considered significant at the 0.05 level (Table 5).

Table 5. Differences in opinion by the five groups of experts. The questions (Q) are listed by number; the actual questions are shown in Appendix 5. The different groups of experts are: *ATC* = animal trainers and circuses, *LV* = lawyers and veterinarians with expertise in wild animal welfare, *NGO* = people working for a relevant NGO, *Sci* = scientists such as biologists, researchers, behavioural and species experts, and *Zoo* = zoo and wild animal sanctuary staff

Q	F	P	ATC-LV	ATC-NGO	ATC-Sci	ATC-Zoo	LV-NGO	LV-Sci	LV-Zoo	NGO-Sci	NGO-Zoo	Sci-Zoo
1	F(4,92)=1	0.412										
2	F(4,93)=2.993	**0.023**		0.017								
3	F(4,91)=0.796	0.531										
4	F(4,91)=0.978	0.423										
5	F(4,90)=16.73	**<0.001**	<0.001	<0.001	<0.001	<0.001					0.008	
6	F(4,93)=1.29	0.280										
7	F(4,88)=2.279	0.067										
8	F(4,93)=2.365	0.059										
9	F(4,89)=1.095	0.364										
10	F(4,91)=0.747	0.562										
11	F(4,91)=0.691	0.600										
12	F(4,92)=1.658	0.166										
13	F(4,91)=0.206	0.934										
14	F(4,91)=4.289	**0.003**		0.007	0.008							
15	F(4,90)=0.147	0.964										
16	F(4,91)=0.386	0.818										
17	F(4,91)=0.912	0.460										
18	F(4,93)=8.127	**<0.001**	0.008	<0.001	<0.001	0.044	0.023				0.048	
19	F(4,92)=5.97	**<0.001**						0.018	0.002		0.007	
20	F(4,93)=1.196	0.318										
21	F(4,93)=0.907	0.463										
22	F(4,93)=1.051	0.385										
23	F(4,93)=0.497	0.738										
24	F(4,92)=1.843	0.127										
25	F(4,91)=4.744	**0.002**		<0.001	0.015							
26	F(4,92)=5.684	**<0.001**		<0.001	0.001	0.048						
27	F(4,88)=8.438	**<0.001**	0.01	<0.001	<0.001		0.02				0.04	
28	F(4,86)=5.483	**<0.001**		0.002			0.05			0.003	0.005	
29	F(4,89)=1.221	0.308										
30	F(4,87)=0.812	0.521										
31	F(4,88)=0.756	0.556										
32	F(4,91)=10.96	**<0.001**	0.001	<0.001	<0.001	<0.001	0.004			0.003		
33	F(4,88)=1.482	0.214										
34	F(4,91)=11.39	**<0.001**		<0.001	0.002		<0.001			0.001	0.003	
35	F(4,88)=6.169	**<0.001**	0.001	<0.001	<0.001							
36	F(4,93)=8.639	**<0.001**	<0.001	<0.001	<0.001	0.002						
37	F(4,91)=8.569	**<0.001**	<0.001	<0.001	<0.001	<0.001						
38	F(4,92)=0.975	0.425										
39	F(4,90)=5.328	**<0.001**							0.025		<0.001	0.013
40	F(4,93)=11.6	**<0.001**	<0.001	<0.001	<0.001	0.001						
41	F(4,93)=11.78	**<0.001**	<0.001	<0.001	<0.001	0.001						
42	F(4,91)=4.848	**<0.001**	0.035	<0.001	0.01	0.03						

The differences between the five groups of experts are summarised in Table 6. In answering the questions, many participants expressed concerns regarding their wording, since most were context dependent and could not indicate 'good' welfare alone. This was unavoidable for this sort of exercise, and the questions may have been interpreted slightly differently by different respondents. If so, this will have added to the variation within each group of experts. However, the data were still robust enough to enable us to identify the significant areas of agreement and disagreement. Three groups of experts (*LVs*, *Scis* and *Zoos*) were not directly involved in the issue and considered to be impartial. *ATCs* disagreed with the three groups of impartial experts on 11/42 questions (26%), and *NGOs* disagreed with the impartial experts on 8/42 questions (19%), whereas the impartial groups of experts only disagreed with each other on two questions (5%) each. So there was substantial agreement on welfare issues associated with wild animals in travelling circuses and other forms of animal entertainment between *LVs*, *Scis* and *Zoos*. The specific areas of agreement and disagreement are discussed below.

Table 6. The number of answers to the 42 questions that were significantly different between the five groups of experts; *ATC* = animal trainers and circuses, *LV* = lawyers and veterinarians with expertise in wild animal welfare, *NGO* = people working for a relevant NGO, *Sci* = scientists such as biologists, researchers, behavioural and species experts, and *Zoo* = zoo and wild animal sanctuary staff. *LVs*, *Scis* and *Zoos* were considered to be impartial experts.

	ATC	*LV*	*NGO*	*Sci*	*Zoo*
ATC		10	16	14	11
LV	10		5	1	2
NGO	16	5		3	7
Sci	14	1	3		1
Zoo	11	2	7	1	
N questions disagreed with ≥1 other groups of experts	16	14	18	17	15
N questions disagreed with ≥1 *impartial* groups of experts	11	2	8	2	2

Questions 1-8 asked about the utility of different aspects of behaviour as welfare indicators (Appendix 6). Opinions were highly varied on whether reproductive success and the absence of fear, aggression and abnormal behaviour were useful indicators of good welfare, leading to a mean agreement of ~50%. All respondents agreed that the expression of natural behaviours and social interactions indicate better welfare. *ATCs* believed good appetite was an indicator of good welfare, but *NGOs* disagreed (P=0.017). Anticipatory behaviour prior to scheduled events such as feeding was not considered to indicate compromised welfare by all groups of experts, yet only *ATCs* believed anticipatory behaviour prior to performances indicates that the animals want to perform and enjoy performing (P<0.001). *Zoos* were slightly more open to this idea, but *NGOs* objected strongly (P=0.008).

Questions 9-13 asked about the impact of various aspects of the captive environment on animal welfare. There were no detectable differences between the different groups of experts for any of these questions. All participants agreed on the importance of adequate space, shelter, hiding places, lighting and climate to ensure good welfare, although some *ATCs* and *Zoos* considered species-appropriate lighting, temperature and humidity to be less important. Complex, stimulating and environmentally enriched environments were also considered to promote good welfare.

Questions 14-24 asked about aspects of captive animal management and their influence on welfare. All participants believed that having choices contributes to better welfare, particularly *NGOs* and *Scis*; this was significantly different to *ATCs* (P<0.05), who expressed more mixed views on the importance of choice. All participants agreed that captive wild animals require appropriate diets for good welfare and that food should be presented in a way that encourages foraging behaviour. A species-appropriate social environment was also recognised as a key contributor to good welfare. *ATCs* believed that human-animal interactions were a good substitute for socialisation with conspecifics and could contribute to good welfare; this was in marked contrast to all other groups of experts (P<0.05). *LVs* and *NGOs* strongly agreed (mean agreement >80%) that predators and prey should not be housed in close proximity; the views of *ATCs* and *Scis* were more mixed. *Zoos* agreed the least (mean agreement 44%), significantly less than *LVs* and *NGOs* (P<0.05). All groups of experts agreed on the positive influence of attentive staff, and *ATCs* were particularly supportive of this statement (mean agreement ± SE 97.1 ± 2.5%). Participants believed that keepers, managers and the government are all responsible for ensuring good animal welfare, but managers and the government were thought to hold slightly more responsibility than keepers and trainers (mean agreement 79% vs 70% across all participants). Regular veterinary health checks were considered important for good welfare, though *ATCs* had very varied views on this issue (SD 40.4).

Questions 25-35 asked about the potential impacts of handling and training on welfare. *ATCs* strongly believed that frequent handling improves animal welfare by facilitating less stressful veterinary treatment, in contrast to *Scis* (P=0.015) and particularly *NGOs* (P<0.001), whereas the opinions of *Zoos* were extremely varied (SD 44.5). *ATCs* also believed that frequent handling facilitates earlier detection of disease by staff, again in contrast to *Scis* (P=0.001), *NGOs* (P<0.001) and *Zoos* (P=0.048), although not *LVs*. When asked whether a strong human-animal bond might improve welfare for performing animals, *ATCs* expressed strong agreement (mean agreement ± SE 86.8 ± 5.6%) in contrast to all other groups except Zoos (P≤0.01); *NGOs* were particularly opposed to this idea compared to *LVs* and *Zoos* (P<0.05), who averaged a mean agreement of around 50%. *Zoos* and *ATCs* largely believed all species can be trained using only positive reinforcement, whereas *LVs* and *Scis* were slightly less convinced, and while *NGOs* showed a lot of variation in their responses (SD 41.0), they were significantly more opposed to this view (mean agreement ± SE 32.6 3 10.3%) than the other groups of experts (P≤0.05). All participants agreed that negative reinforcement should be avoided in training and that animals should only be trained to perform natural movements, though the opinions of *ATCs* and *Zoos* varied more widely (SD 42.1 and 38.2 respectively). Adequate resting opportunities away from humans were considered extremely important by all. *ATCs* did not believe that frequent training is stressful for animals, in contrast to all other groups of experts (P≤0.001); *NGOs* agreed particularly strongly with this statement (mean agreement ± SE 96.0 ± 2.1%). All participants agreed that animals should be allowed to participate voluntarily in performances and training, though *ATCs* agreed less strongly.

ATCs strongly believed that regular training improves mental health and physical fitness, in contrast to *Scis* (P=0.002); *NGOs* were more opposed to this view than all other groups of experts (P<0.05). *LVs*, *NGOs*, *Scis* and *Zoos* all considered husbandry training to be more beneficial to animal welfare than training for performance, whereas *ATCs* thought the opposite (*ATCs* vs *LVs*, *ATCs* vs *NGOs* and *ATCs* vs *Scis* all P<0.001).

Questions 36-42 asked about aspects of transport and travel and their impact on welfare. The views of *ATCs* were very different to the other groups of experts for several of these questions. *ATCs* believed that animal welfare was not compromised by frequent transport, whereas all other groups of experts did (P≤0.002). *ATCs* did not believe that the frequency and duration of transport should be minimised to avoid unnecessary stress, whereas all other groups of experts did (P<0.001). All participants agreed on the importance of species-appropriate transport conditions. Question 39 suggested that transportation deprives animals of behavioural opportunities and asked whether this deprivation should be avoided during transport. However feedback from participants implied this question was difficult to interpret, so the results should be viewed with caution. On visual inspection, there was very little variation between the views of *ATCs* and *NGOs*. Nor were there any statistically significant differences from the other groups of experts, probably due to outliers increasing the variance (*ATCs* SD 24.2, *NGOs* SD 32.1). Zoos mainly disagreed with the statement, in contrast to *LVs*, *NGOs* and *Scis*, who largely agreed (P<0.05). *ATCs* believed that regular travel between venues was mentally stimulating for animals and therefore contributed to good welfare, in marked contrast to all other groups of experts (P<0.001). *ATCs* were also alone in the belief that this mental stimulation outweighs the limited size and complexity of temporary enclosures (P<0.001). Finally, in comparison to all other expert groups, *ATCs* disagreed that the portable enclosures required for regular travel cannot meet the preconditions for good welfare (P<0.05).

Having identified the main areas of disagreement between the different groups of experts, we particularly looked for scientific evidence that would help assess the rationale for these differences of opinion.

Animal welfare – concepts and definitions

Much of the debate about travelling circuses has been about whether they can fulfil the welfare needs of wild animals. However, there is no single unified definition of animal welfare. So when considering the welfare of wild animals in travelling circuses, it is important to remember that welfare emerges from a complex combination of factors that renders it impossible to define by distinct requirements[78]: we need to take into account the collective effect of all aspects of management and the environment when considering the welfare of wild animals in travelling circuses and mobile zoos since, while one aspect of management may be interpreted as promoting good welfare, the others may not, and so the cumulative effect may be poor welfare overall. This is encapsulated in the concept of nutritional, environmental, health, behavioural and mental domains of welfare, with good welfare existing when an animal's needs in these interacting domains are largely being met[79].

We discuss the concepts and indicators of welfare in the literature review.

Literature review

It was impossible to define which species are used in circuses and mobile zoos, especially since the search for novelty and changing attitudes have led to a rapid expansion of the number of mobile zoos and the species used in wild animal entertainment generally. So we did not exclude any species of wild animal from the literature review, but as far as possible focussed on species currently held in European circuses and mobile zoos. Very little research has been done on animals in travelling circuses and mobile zoos *per se*, possibly due to inaccessibility or because regular travel renders experimental conditions impossible to control/standardise for long term sampling. However studying how wild animals respond to changes in environment, husbandry or transport in other captive situations can help identify key indicators of good welfare, how particular experiences affect welfare, and whether travelling circuses and mobile zoos can fulfil the welfare requirements of wild animals.

Literature selection

Our remit was to review the literature and analyse the scientific evidence available as to whether captive wild animal in travelling circuses and mobile zoos achieve their optimal welfare requirements. We used the welfare issues identified in the first questionnaire survey to help guide the literature search: the search terms we used are shown in Table 7.

Table 7. Search terms used for the literature review

We used various combinations of the following words in all of their different forms in Google Scholar, Scopus and the Web of Science:-

*Circus, zoo, exotic, animal, species, performance, display, demonstration, entertainment, welfare, well-being, wild, non-domesticated, captivity, housing, enclosure, exhibit, refuge, shelter, enrichment, husbandry, predictability, familiarity, food, feed, diet, nutrition, temperature, lighting, light-dark, day-night, circadian, daily rhythm, chronobiology, activity, noise, vibration, disturbance, handling, human contact, human-animal relationship/bond, visitor, spectator, audience, crowd, public, train, tame, training method, positive/negative reinforcement, operant conditioning, falconry, transport, travel, loading, frequency, duration, physical condition, health, disease, injury, psychological, pleasure, enjoy, emotion, choice, stress, mental/physical stimulation, exercise, normal/*natural *behaviour, play, stereotypy, reproduction, early weaning, infant-mother separation, social, predator-prey proximity*

We also combined these words with the names of the following species commonly used in circuses and other travelling animal shows:-

Bear, big cat, bird of prey, camel, crocodile, elephant, falcon, fox, giraffe, hippopotamus, lion, Panthera, *primate, raccoon, raptor, reindeer, reptile, rhinoceros, sea lion, tiger, wolf and zebra*

All articles we located were then assessed to decide whether they should be included in the review; the criteria for inclusion were:-

- Peer-reviewed papers (including those in refereed symposia and books) where the conclusions were supported by the data
- Peer-reviewed papers that were case studies and/or based on a limited sample size; where relevant, caveats are included in the review
- Unpublished research theses (Masters level and above) since they are peer-reviewed by independent examiners
- Reports written by three or more independent experts
- Peer-reviewed conference proceedings (not just an abstract) that contained original data

All the above sources were read and considered but only those deemed relevant to our remit were cited in the report. The following did not constitute robust scientific evidence but were included in the review if they contained relevant background information:-

- General books and book chapters that were not peer-reviewed
- Reports written by fewer than three experts
- Reviews and reports written by NGOs
- Press reports and magazine articles
- Official welfare or husbandry guidelines
- Conference abstracts that were not peer-reviewed

The following were excluded:-

- Peer-reviewed journal articles that used unreliable methods, or whose conclusions were not supported by the data, or were not relevant to our remit
- Conference abstracts or proceedings that were not peer-reviewed
- Opinions and statements
- Consultations, legislation and letters

The process is summarised in Figure 1. Of the 1430 sources of information we located from the database searches, 666 (46.6%) were published up to and including 2006, 764 (53.4%) were published from 2007 onwards. Comparable figures for the 270 records identified from other sources were 153 (56.7%) up to and including 2006, and 117 (43.3%) from 2007 onwards. Thus there has been a substantial increase in the amount of information available since the last review of the welfare of wild animals in travelling circuses[49].

We reviewed the publications and summarised the main findings for the aspects of captivity that affect animal welfare in Appendix 7; the key points that emerged are below.

Housing and husbandry: key welfare points

- A greater emphasis should be placed on a species' needs rather than the conditions it is able to tolerate; this is a key issue for all species, and is of particular concern for amphibians and reptiles.
- Regular travel means that **circuses** and **mobile zoos** have to compromise between maximising cage size and portability; they are limited in the space they can provide animals, and larger cages may be incompatible with the use of animals in public displays.
- Adequate space is particularly important for wide-ranging species such as large cats, bears and elephants, but also has a significant impact on the welfare of smaller species of mammal, birds and reptiles.
- Providing an opportunity to climb is particularly important for arboreal species.
- Enrichment is not a substitute for poor enclosure design and should be used in combination with appropriate enclosure size and furnishings.
- Restraint is often used in **circuses** and can cause injury and distress in both domestic and nondomestic animals and limits opportunities to perform species-typical behaviours such as socialising, which will impact psychological welfare in social species such as elephants, equids and camelids, and can cause health problems by limiting exercise opportunities.

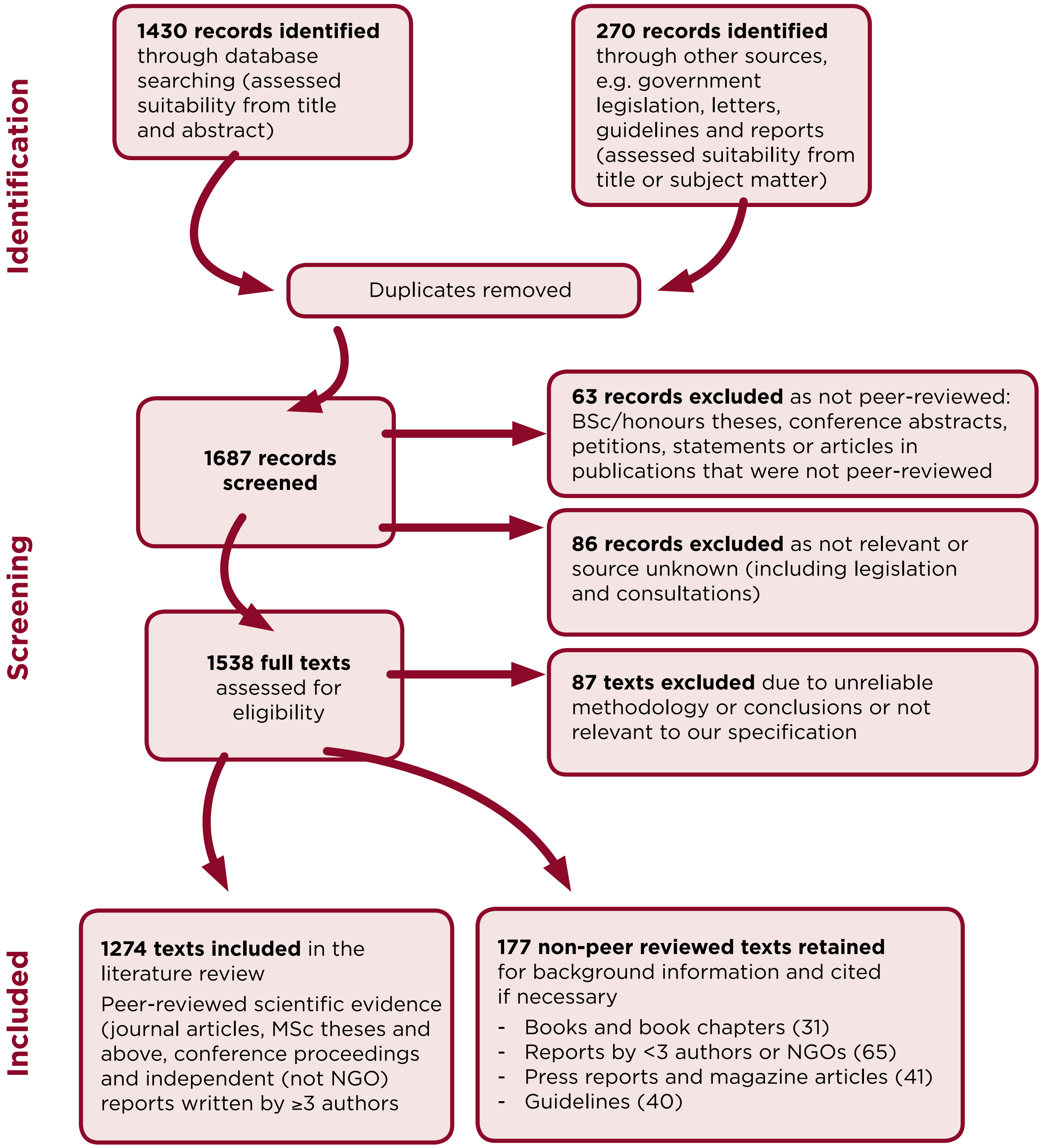

Figure 1. Process for selecting the literature to include in the review

- Additional space is not by itself sufficient to improve animal welfare significantly and enclosure quality (complexity and suitability) is more important than size, although of course adequate space is a prerequisite to provide complexity.
- Furnishing enclosures more appropriately and encouraging natural behaviour improves animal welfare and increases their educational value for visitors.
- Enclosure substrate is important to ensure good welfare by facilitating physical comfort and providing opportunities to exhibit natural behaviour.
- A choice of resting sites is important for thermoregulation in both heterotherms and homeotherms, and to prevent social stress in group-housed species and accommodate individual differences.
- Suitable lighting conditions are particularly important for the welfare of light-sensitive species such as reptiles, birds and sea lions.
- Access to water is important for the physical and mental health of species that bathe regularly such as birds of prey, tigers and elephants, and for semi-aquatic species such as otters, polar bears and sea lions.

Environmental enrichment: key welfare points

- Enrichment is used to increase environmental complexity, expand behavioural choices and/or encourage species-appropriate behaviour, with the aim of reducing stress and improving welfare. Enrichment techniques for wild animals usually involve either increasing the animal's control, cognitive challenge, fulfilling behavioural needs, facilitating socialisation or rewarding exploration with the acquisition of new, and useful, information.
- Enrichment is the preferred means of tackling the underlying causes of stereotypic or abnormal behavioural patterns since it gives animals the choice as to whether to participate, and the majority of studies on zoo animals showed a positive effect of enrichment on stereotypic behaviour. However, enrichment in zoos is usually targeted: particular enrichments are used to promote specific behaviours that the animal should be doing but is not, or to reduce behaviours that the animal is doing but should not be. It follows therefore that enrichment should be monitored and adjusted to the needs of each animal.
- Food-based enrichment is highly successful in stimulating foraging behaviour: in addition to increased foraging and feeding behaviour, it may cause other behavioural alterations, such as increased behavioural diversity and locomotion, or reduced abnormal behaviour. However, it is only effective while food is available.
- Auditory enrichment has had mixed effects; there are species-specific responses to auditory cues. **Circus** animals are presented with novel scents and auditory cues with each change in location: whether this is enriching or detrimental is unclear and probably depends on the species and the scent.
- **Circus** animals are often on display to the public during performances and in their home cages and exercise pens. The availability of a retreat space or a visual barrier improves the welfare of animals by allowing them some degree of control over their environment and may enable them to cope with aversive stimuli.
- Enrichments that give animals control may be more successful than offering increased environmental complexity. How individuals respond to enrichment, and captivity generally, depends on a variety of factors, including age, sex, individual history, personality and dominance status; providing choices can help accommodate individual differences.
- Habituation may be avoided by introducing enrichment on a randomised schedule; the regular transportation of **circus** animals means they do not have continuous access to exercise pens, enrichment objects or the same scents, so may have less opportunity to habituate and therefore respond more to/benefit more from enriching opportunities when they are available.

- Space limitations in transporters may limit the variety of potential enrichment items **circuses** can provide. Enrichment that offers extrinsic reinforcement, such as training with food rewards, may produce more significant behavioural changes that are attenuated less quickly than devices that rely on intrinsic reinforcement.
- Enrichment may reduce compliance during training and performance; life in relatively barren **circus** enclosures may cause animals to be more sensitive to reward and thus more compliant during training sessions.

Training: key welfare points

- There is a continuum between providing opportunities for animals to perform all of their motivated behaviours, and training them to perform behaviours outside their natural repertoire: "At one end is the chimpanzee's tea party and at the other is the food-burying acouchi"[80].
- Training using positive reinforcement can help animals cope with their environment through systematic desensitisation and counter-conditioning to potentially adverse stimuli, which enrichment cannot always do, but this depends on what is being trained and how the animal is trained.
- The free contact training of animals in travelling **circuses** and **mobile zoos** does not facilitate the minimal use of negative reinforcement and punishment required for good welfare since negative reinforcement is used more often when trainers are in direct contact with animals.
- Training that facilitates the use of positive reinforcement, i.e. distance training and especially protected contact, requires specialist facilities such as strong barriers that may not be transported easily or securely fastened at a **circus** site.
- Training animals to participate voluntarily in events reduces the need for enforced restraint, which is highly stressful; there is no scientific evidence that animals habituate to involuntary restraint.
- Aggression towards humans or conspecifics stems from fear, discomfort, uncertainty and/or apprehension, and training based on positive reinforcement can desensitise animals to potentially fear-inducing stimuli; pairing positive reinforcement with negative stimuli causes the fear to diminish over time.
- Desensitised animals are ultimately less fearful of events or procedures, which contributes to better psychological welfare. **Circus** animals are desensitised to the **circus** ring during initial training: the length of time taken for animals to be desensitised could indicate the level of stress inflicted by the experience.
- It is not known whether desensitisation training is used to prepare **circus** animals for regular transportation, or whether they eventually habituate to the experience without assistance.
- There is considerable variation in how individuals respond to training: some may show continued inexorable stress responses and ongoing attempts to train unsuitable animals, even by positive reinforcement, may impair welfare by causing unnecessary and prolonged stress.
- From the animal's perspective, there is probably little difference between performing a behaviour for public entertainment and performing a behaviour to facilitate a veterinary procedure, since both are performed in response to a cue and a reward is subsequently received. It is the motive behind the training and consequent direct benefits of learning and performing the trained behaviour that are different, as are the frequency that the actions are performed and, for some unnatural postures, the physical exertion on the animal and potential for injury.
- Traditional animal training methods are coercive and based on force and aggression, which most professional trainers have now discarded in favour of positive reinforcement techniques that empower the animal because the most productive human-animal relationships are built on trust: this is strengthened by positive interactions and weakened by negative ones. Some trainers are slow or reluctant to make this switch, particularly because punishment is a difficult habit to overcome, and many trainers in **circuses** are bound by tradition. For elephants and big cats, **circus** trainers can only use free contact training.
- Different trainers, even at the same establishment and following the same protocol, use slightly different techniques which may confuse and frustrate animals, and using multiple trainers limits the development of strong human-animal relationships and thus the efficiency of training sessions and resultant welfare benefits.

- When animals are worked by presenters rather than the original trainers, this can prevent efficient two-way communication during rehearsals and shows if the presenters are unable to understand and respond appropriately to the animals' body language: this can lead to confusion, frustration and potentially pain.
- Training based on positive reinforcement can give animals choices and some control, though not as much as enrichment. Progressive training affords learning opportunities that can be as challenging and rewarding as learning through problem solving with a complex enrichment device, but is only enriching while the animal is still learning, and not once the behaviour is learnt, i.e. when the animal performs the behaviour reliably on cue. The performance of the routine stops being enriching, and 'training sessions' offer no new learning opportunities.
- Training using positive reinforcement that teaches new behaviours can contribute to increased activity levels by expanding an animal's behavioural repertoire and can help teach it how to use enrichment devices. Training based on positive reinforcement can also have indirect benefits such as reducing stereotypical behaviour and aggression, or increasing affiliative behaviour.
- Positive reinforcement training allows animals to have greater choice and control than other training methods, and elephants in protected contact training exercised choice or control over their environment because there was no risk of negative consequences. Negative reinforcement may be required to achieve full cooperation for most individuals.
- In **circuses**, big cats performed with apparent willingness although not necessarily great enthusiasm and the mental and/or physical stimulus of more frequent performances did not appear to improve or impair their welfare, based on their behaviour after performance. This could be because the animals have learnt through training to modify their behaviour and perform 'willingly' to get the reinforcement but are still stressed by what they are required to do. **Circus** elephants and tigers perform significantly more stereotypic behaviour prior to performances.
- While progressive positive reinforcement training has the potential to enhance the psychological welfare of animals through offering mental stimulation, it is not an appropriate substitute for other methods of improving welfare such as environmental enrichment and general enclosure suitability, which have multiple indirect benefits.
- **Circus** trainers feel obliged to train animals to do 'what the audience likes': how animals are presented in a **circus** and **mobile zoo** has great potential to influence the audience's attitude towards the species in general. If travelling **circuses** and **mobile zoos** are to have an educational role to facilitate conservation, educational acts should showcase the animal's natural agility or intelligence, and explain this in the context of the animal's wild conspecifics. However, this will depend on the overall presentation: even if e.g. a meerkat in a **mobile zoo** is trained to perform natural behaviours, it is not educational if the meerkat is on its own, on a lead and being petted. However, most animal performances in travelling **circuses** and **mobile zoos** focus on tricks that do not reflect natural behaviours.

Handling: key welfare points

- While contact with live animals has beneficial effects on human health, and can be effective at influencing public perceptions, it is unclear whether animals also benefit from the experience. Human-animal interactions can be positive, neutral or negative, and have the potential to affect animal welfare.
- Handling effects on the physiology, health and emotions of animals depend on the individual, its temperament, past experiences, socialisation history and the nature of the contact.
- Interactions between animals and their keepers are an influential feature of a captive animal's life, and so it is important that they are positive, since human-animal relationships influence animal welfare.
- Staff with negative attitudes or insufficient experience will develop poorer quality relationships with animals, which may compromise their welfare by failing to reduce, or even enhancing, stress.

- Visitors are largely ignorant of animals' communication cues. Handling brings humans into close proximity with potentially dangerous animals and increases the risk of injury or death to both parties, particularly if animals are handled aversively. Many wild animals are capable of injuring their handlers so it is in the interest of keepers and trainers to handle animals in a positive way. However, non-domesticated animals are unpredictable and will attack even familiar keepers under unusual circumstances.
- Increasing the predictability of human-animal contact can facilitate coping. However, overly predictable routines, as occur in travelling **circuses** and **mobile zoos**, can themselves be stressful for some species.
- Working animals and those used in **circuses** and other forms of entertainment are often hand reared to facilitate easier handling and training. While hand rearing clearly benefits humans, it may have severe impacts on the welfare of the animals, especially later in life, when hand-reared animals may show abnormal behaviour and underdeveloped social skills.

Visitor presence: key welfare points

- Two-thirds of studies into the effects of human or visitor presence on a diversity of non-domesticated species, including a study of **circus** tigers, found evidence of visitor-induced stress.
- Visitor effects include changes in activity levels, changes in stress-related behaviour and avoidance. Some species show increased mortality in response to public viewing and changes in social behaviour caused by human disturbance are common.
- Housing conditions that offer limited opportunities to escape the gaze of visitors, as occurs in **circuses** and **mobile zoos**, may affect welfare if animals are unable to control the extent of human contact. More complex environments that offer greater behavioural and locational choice will help animals to cope with disturbance through distraction and opportunities to escape.
- The effects of visitors will generally be smaller for animals in enclosures that allow them greater choice and control of animal-visitor interactions.
- Larger enclosures allow animals to control visitor proximity and greater enclosure complexity provides opportunities for animals to escape from visitors and/or provide distraction.

Noise and disturbance: key welfare points

- Noise causes stress but the behavioural and physiological impacts vary widely.
- Many animals are capable of detecting sound outside of the range detectable by humans, and wild animals in travelling **circuses** and **mobile zoos** will be exposed to a wide spectrum of both ultrasonic and infrasonic sounds. Cars, heavy goods vehicles and buses produce high levels of infrasound, up to and over 100 dB, and road surface conditions can add to the levels of infrasound.
- Species sensitive to seismic vibrations such as snakes, kangaroos, elephants and some birds, or infrasound like alligators, elephants, giraffe, hippopotamus, okapi, prairie dogs, rhinoceros and tigers, may be distressed by excessive anthropogenic vibration and infrasound from diesel engines, wind turbines, fireworks and aircraft.
- Captive animals appear less affected by noise when exposure is predictable or they are able to control it. However, unlike visual stimuli, captive animals can do little to control their exposure to noise. Providing barriers and refuge areas may do little to reduce noise exposure.
- Animals have the capacity to learn to cope with noise, indicated by attenuated behavioural responses, though this may not signify a lack of stress, and exposure to chronic noise may have an additive effect in combination with other stressors in the captive environment, resulting in a more substantial impact on welfare.

The social environment: key welfare points

- All experts agreed that the expression of natural behaviours and social interactions indicate better welfare and that the lack of opportunity to exhibit natural social behaviours with conspecifics is likely to contribute to poor welfare.
- Inadequate social groupings have serious impacts on animal welfare, including stress, aggression, abnormal behaviour, reproductive failure and early mortality.
- While conspecifics may be a source of stimulation for some individuals, incompatibility between group-housed individuals can lead to adverse welfare.

- High social density can cause social stress and competition for access to resources, so it is important to provide multiple complexity in space-restricting enclosures to maximise behavioural opportunities available to all cohabitants and facilitate social avoidance.
- Long-lived species that live in complex societies can be severely affected by social perturbations, and even temporary separation, such as for **circus** performances, can cause distress.
- Space is limited in travelling **circuses** and **mobile zoos**, and housing conspecifics in neighbouring enclosures that are visible but not accessible for affiliative or agonistic interactions may cause frustration and lead to stress-related behaviours. Conversely, housing incompatible species in close proximity may be stressful.

Reproduction: key welfare points

- The limited social groupings available in travelling **circuses** and **mobile zoos**, and lack of enrichment in cages is likely to place severe limits on opportunities for animals to engage in natural behaviours.
- While **circuses**, and some **mobile zoos**, have bred a variety of species, it is questionable whether they make a significant contribution to captive breeding. For captive wild animals to have any conservation value, they need to be part of the entire captive 'metapopulation'. This requires engagement with studbooks, record-keeping, breeding loan and being part of a managed population.
- Breeding is a natural and highly motivated behaviour. Any breeding by **circus** animals is largely done in the winter quarters and, if cycling does not coincide with this period, the opportunity for breeding is minimal. Captivity can induce obesity, overproduction of sex steroids and other factors that reduce breeding success in **circuses** and **mobile zoos**.
- Prenatal stress causes long term damage, demonstrated by impaired motor and behavioural development and a reduced ability to cope with stress and conflict.
- Maternal deprivation caused by early weaning or termination of the mother-infant bond predisposes offspring to develop behavioural abnormalities such as stereotypic behaviour, social incompetence and increased fearfulness. Rearing environment greatly influences longevity and welfare, and is a particular problem where animals are hand-reared to facilitate training.
- While all the groups of experts agreed that expressing natural behaviours is a key welfare indicator in captive wild animals, their ability to do this is severely restricted in travelling **circuses** and **mobile zoos**.

Mortality and morbidity: key welfare points

- Though many species live longer in captivity than in the wild, increased length of life may not be associated with increased quality of life.
- Performing animals are exposed to new pathogens at each new venue and grazing on common land exposes **circus** animals to unknown pathogens. Frequent and close human contact propagates zoonotic disease, and limited or no quarantine facilities will increase the chance of disease transmission.
- Frequent travel within and between countries and importing animals of little-known origin has the potential to propagate disease widely and quickly; several diseases present in **circus** animals are of zoonotic importance.
- Many diseases have expanding host ranges and many potential hosts are unknown, so precautions against infection and transmission may not be taken. This enhances the risk that diseases may be spread without knowledge or intention
- High density social housing in small enclosures and close-proximity housing between different species facilitates the spread of disease both within and between species.
- The stress associated with frequent travel, performance, human contact and housing conditions can lead to immunosuppression, enhancing the risk of disease spread.
- Chronic lack of exercise caused by restrictive caging and tethering in travelling **circuses** and **mobile zoos** may contribute to obesity, bone disease and deformity, foot problems and psychological distress.
- Requiring captive wild animals to perform unnatural movements in **circuses** and other forms of animal entertainment can put unnecessary strain on the body, leading to deformities, lameness and injuries.
- Lack of knowledge of species-specific dietary requirements and/or the inability to source appropriate foods in travelling **circuses** and **mobile zoos** can lead to nutritional disorders.

Diet and nutrition: key welfare points

- Free access to food, particularly the concentrated foods commonly fed to captive animals, in combination with space restriction, can lead to health problems such as obesity, diabetes, cardiorespiratory disease, reproductive disorders, urinary disorders, lameness, thermal discomfort, tumours and mortality.
- The amount and frequency of feeding has an impact on animal welfare, and the optimal feeding amount and time is species specific. Grazers and browsers designed to spend large parts of the day feeding may suffer in **circuses** when feeding opportunities are limited due to performance, travel or inadequate feeding schedules. Inappropriate diets may not facilitate adequate rumination, which is physiologically essential for digestion in ruminants and takes up a significant proportion of the day.
- Many wild animals exhibit seasonal changes in nutritional requirements and may show seasonal inappetance; adapting feeding patterns poses a significant problem for wild animals in travelling **circuses** and **mobile zoos** where training and performance may involve feeding.
- Wild animals have specific nutritional requirements and changes in food sources associated with regular changes in location by travelling **circuses** and/or feeding by visitors can have a significant impact on an animal's health and welfare. This may be a significant problem for carnivores, where the quality of meat from local slaughterhouses cannot be guaranteed.
- Inappropriate diets can lead to nutritional deficiencies and diseases, and food can be a source of parasites and pathogens, depending on how it is sourced, stored and fed to animals; appropriate sourcing, storage and presentation is harder in travelling **circuses**.
- Species-typical and ecologically-relevant food presentation is important for captive wild animals; foraging in captivity typically requires only a fraction of the time and behavioural diversity seen in the wild, and these problems are exacerbated in **circuses** and **mobile zoos** when animals are used for performance and/or travel. Failure to provide food of the right type and consistency can lead to poor health and welfare.

Transport: key welfare points

- Habituation to frequent transport may reduce, but does not eliminate, the negative effects of transport on welfare. **Circus** animals may be subjected to further transport before they have fully recovered from the previous journey.
- Domesticated species that are transported regularly show a range of adverse welfare indicators, including lower reproductive rates, increased risk of disease and physiological traits indicative of stress.
- The effects of confinement in small barren enclosures during transport are of particular concern because, compared with most other animals, wild animals in travelling **circuses** and **mobile zoos** spend a substantially greater proportion of their time being transported. Transport causes disruption of eating, drinking, resting, rapid eye movement (REM) sleep and circadian activity patterns. These effects are likely to be exacerbated by irregular schedules and frequent journeys with insufficient recovery periods.
- Both **circus** elephants and **circus** tigers spend more time performing stereotypies during transport compared with when they are not being transported, including when elephants were picketed. Stereotypy-eliciting situations are generally associated with poor welfare.
- Continuous postural adjustments to maintain balance during transport are physically and mentally stressful for animals. Driving events, such as acceleration, braking, stopping, cornering, gear changes and uneven road surfaces, can have a major negative influence on the welfare of animals by affecting the risk of injury and disturbing the ability of the animals to rest during the journey.
- Transport in vehicles does not allow tigers access to the shade or pools they need for thermoregulation or the opportunity for elephants to perform at least some of their thermoregulatory behaviours; temperatures recorded during transport of **circus** tigers and **circus** elephants did not exceed the ability of the animals to thermoregulate but the vehicles generally lack monitoring systems to alert the driver to extreme temperatures.
- Reptiles are particularly unsuited to regular transport due to their sensitivity to noise and vibration and reliance on external factors for thermoregulation.

Translocation: key welfare points

- Although the regular translocation of wild animals in travelling **circuses** and **mobile zoos** to new environments may help prevent loss of novelty, habituation and boredom, frequent relocation may never allow enough time for an animal to settle completely.
- Wild animals can take an unexpectedly long time to acclimatise to new environments, even when they are not very different in terms of size and facilities. The duration and amount of disturbance caused by each relocation may influence acclimatisation.
- In the wild, animals are familiar with their home range so regular rotation between familiar areas (i.e. animal rotation management in zoos) may be less stressful than translocation to a completely novel place.
- Although animals in travelling **circuses** and **mobile zoos** are subject to frequent changes in location, consistency in use of the same travelling cage may reduce the stress of relocation.
- Animals in travelling **circuses** and **mobile zoos** have no control over when they change location, which they would have in the wild, and lack of choice and control is known to cause distress in captive animals.

Choice and control: key welfare points

- Captive animals are less able to control their exposure to environmental stimuli e.g. by moving, sheltering or adjusting activity patterns. In the prolonged absence of controllability, animals may enter a state of learned helplessness or seek to gain control through maladaptive behaviour such as stereotypies.
- Travelling **circuses** and **mobile zoos** control an animal's day-to-day activities and this can have a significant negative impact on their welfare by disrupting daily, seasonal and annual cycles of activity and inactivity.
- Allowing animals more control over their environment has proven welfare benefits. Where control is not possible, opportunities for choice create the illusion of control and contribute to a more positive affective state.
- Anything that undermines the perception of control will harm animal welfare, and this lack of perceived control may be the greatest stressor for animals in **circuses** and **mobile zoos** in small/barren enclosures and/or when tethered/chained.

Conclusions

- There is a lack of clarity as to what constitutes a wild species and a domesticated species. Reindeer, llamas, alpacas, dromedaries and Bactrian camels have been domesticated for several thousand years and they are genetically different from their wild progenitors. This is reflected in clear differences from their wild ancestors in their behaviour, life cycle and physiology. Whether these species are "not normally domesticated in the British Islands" only appears relevant if it is not possible to provide appropriate husbandry skills or environmental conditions. It is also unclear why some potentially dangerous domesticated species require a licence under the Dangerous Wild Animals Act 1976 whereas others do not.
- Large numbers of domesticated reindeer have been imported over the last decade for commercial purposes. Keeping domesticated reindeer requires considerable stockmanship skills and there are significant welfare concerns about domesticated reindeer that are not managed using traditional techniques and/or kept by inexperienced owners.
- For convenience, we have referred to travelling animal shows other than circuses as 'mobile zoos'. There is a lack of clarity as to what constitutes a circus and a mobile zoo, and there are comparable welfare concerns. Wild animals are used for entertainment in a diversity of ways by travelling circuses and mobile zoos that involve frequent transport and close contact with people. In mobile zoos some animals are only used for display, but a number are also used for a range of performances. Even the smaller species used in these shows are not suited to travelling and handling by members of the public, and their welfare is likely to be compromised by frequent handling, transport and long periods on display. There are also significant concerns about what happens to these animals once they are no longer used in the mobile zoo, and the fact that some may have had operations (such as removing their anal scent glands so that they can be handled by members of the public) that would be illegal in Britain.
- There are a large number of businesses in Britain that collectively use several thousand wild animals for entertainment. It appears to be easy to set up a mobile zoo business because of the lack of regulations. The Performing Animals (Regulation) Act 1925 (as amended) stipulates requirements for the registration of circuses with a local authority and the Welfare of Animals in Travelling Circuses (England) Regulations 2012 stipulate welfare standards and the need for care plans and inspections of wild animals in travelling circuses (these licensing requirements do not currently apply in Wales, Scotland or Northern Ireland). The Zoo Licensing Act 1981 (as amended) sets out the local authority licensing requirements for zoos. It seems anomalous that mobile zoos are not regulated, even when they have static displays for Christmas and other events that last more than seven days. Two-thirds are not registered with a local authority under the Performing Animals (Regulation) Act 1925. It is more challenging to meet the welfare needs of captive wild animals than domesticated animals, and there are also greater health and safety issues. There appear to be considerable public concerns over the welfare of the large number of wild animals currently used for entertainment.
- Any potential contribution by travelling circuses and mobile zoos to education and conservation activities is at best likely to be marginal. Although interactive animal shows hold public interest longer than traditional zoos, the use of wild animals in entertainment may have a negative impact on the public's perception of wild animals, especially children, and hinder conservation and education efforts. It is also contrary to the Government's 2013 position in the draft Wild Animals in Circuses Bill, that we should respect the "inherent wildness" of captive wild animals and that using them for entertainment "adds nothing to the understanding and conservation of wild animals and the natural environment". In this respect we could not see any difference between using wild animals for entertainment in travelling circuses and mobile and static zoos. There is a lack of clarity as to what constitutes a 'performance' by a wild animal and therefore requires a licence under the Performing Animals (Regulation) Act 1925.

- The use of wild animals in travelling circuses and other wild animal shows is contentious and has been the subject of governmental and public debate in the UK and in many other countries both in the EU and worldwide for at least a decade. When we asked a range of experts to comment on the welfare issues associated with wild animals in travelling circuses and mobile zoos, three groups (*LVs*, *Scis* and *Zoos*) showed substantial agreement. These are arguably the three most impartial groups of experts. The greatest disagreement was between *ATCs* and the other four groups of experts. Disagreements on the welfare aspects of behaviour were small, and there were no detectable differences about the welfare importance of the captive environment for wild animals in travelling circuses. The greatest differences between the different expert groups were on the issues of animal management, handling and training, and transport and travel.
- All the groups of experts agreed that a species-appropriate social environment was a key contributor to good welfare of captive wild animals. However, wild animals in travelling circuses and mobile zoos are often kept in inappropriate social conditions, such as isolating social species, grouping of solitary species and/or proximity of incompatible species. Inadequate social groupings can have serious impacts on animal welfare, including stress, aggression, abnormal behaviour, reproductive failure and early mortality. The lack of opportunity to exhibit normal social behaviours is a significant concern for circus animals and is likely to contribute to poor welfare.
- *LVs* and *NGOs* both agreed that predators and prey should not be housed in close proximity, whereas the views of other experts were more mixed. Housing incompatible species in close proximity can be stressful. Proving hiding places in enclosures, especially for prey species, may reduce adverse impacts. However, facilities are limited in travelling circuses and mobile zoos, and predators and prey are often, if not generally, housed within auditory and olfactory communication, and often within sight of each other.
- The experts' opinions were highly variable as to whether reproductive success was an indicator of good welfare. *ATCs* most strongly agreed that good welfare can be indicated by normal reproductive behaviour. However, breeding rates are low in circuses, and failure to breed in captivity can lead to a number of adverse welfare problems. Maternal deprivation caused by early weaning or termination of the mother-infant bond, due to demands for performance or hand-rearing to facilitate handling and training later in life, predisposes offspring to develop behavioural abnormalities such as stereotypic behaviour, social incompetence and increased fearfulness.
- All the groups of experts agreed that the absence of fear, aggression and abnormal behaviour were useful indicators of good welfare in captive wild animals. However, while they are not seen in undisturbed free-living wild animals, stereotypies are a major problem in captive wild animals and are often performed for a significant part of the day. Wild animals in travelling circuses and mobile zoos often exhibit higher rates of stereotypy than conspecifics in other captive environments. Most situations that cause/increase stereotypies also decrease welfare, suggesting that the welfare of wild animals is of greater concern in travelling circuses and mobile zoos than other captive environments. Space limitation is the most important inducer of stereotypic behaviour in wide-ranging carnivores.
- While all groups of experts agreed on the welfare importance of a diet that closely resembles what an animal would have in the wild, concentrated foods combined with a lack of space can lead to a diversity of health issues for captive wild animals. Regular changes in location and/or feeding by visitors can have a significant impact on the health and welfare of wild animals in travelling circuses and mobile zoos, as does failing to provide food of the right type and consistency. It is more challenging for travelling circuses to provide species-typical and ecologically-relevant food and to source and store food appropriately.

- Most experts agreed that having choices contributes to better welfare of captive wild animals, although *ATCs* expressed more mixed views on the issue, and all groups of experts agreed that adequate resting opportunities away from humans were extremely important for good welfare. All groups of experts agreed that wild animals should be allowed to participate voluntarily in performances and training, although *ATCs* agreed less strongly. It is, however, hard to assess whether wild animals engage in performances voluntarily. If the reward for performance is access to a resource that the animal wants or needs but is controlled by the trainer, the animal's participation is not necessarily voluntary even though it may appear to be. The choices available to animals in captivity are trivial compared to those in the wild and, in the prolonged absence of controllability, animals may enter a state of learned helplessness or seek to gain control through maladaptive behaviours such as stereotypies. The lack of perceived control over their environment and activities may be the greatest stressor for captive wild animals in travelling circuses and mobile zoos.
- All five groups of experts agreed on the importance of adequate space, shelter and hiding places to ensure good standards of welfare for captive wild animals. Space limitation is the most important indicator of stereotypic behaviour in wide-ranging carnivores, and wide-ranging species housed in larger enclosures are less stressed, move more, pace less and/or show more naturalistic behaviour. Smaller species also show a range of welfare benefits in larger enclosures. However, animals housed in larger enclosures may be more difficult to handle or show greater fear of humans, which is incompatible with their use in travelling circuses and mobile zoos. Despite the importance of both size and design to ensure good animal welfare, enclosures for wild animals are generally much smaller and less complex in travelling circuses than other captive environments.
- All five groups of experts agreed that complex, stimulating and environmentally enriched environments promote good welfare in captive wild animals, and the interaction between enclosure size and complexity leads to species-specific welfare benefits. Enrichment is the preferred means of tackling the underlying causes of abnormal behaviour patterns since it gives animals choice. However, in travelling circuses and mobile zoos, the provision of environmental enrichment, particularly control-orientated enrichment, is likely to be extremely limited or non-existent due to the need to maintain portability, ease of handling of the animals and compliance during training sessions.
- Some *ATCs* and *Zoos* considered that providing a species with appropriate lighting, temperature and humidity may be less important that other environmental conditions, but this was not the general view of experts. Climatic conditions, and a range of microclimates, are likely to be particularly important for heterothermic species and failure to meet their needs can have a significant impact on their welfare. Even when appropriate thermal conditions are maintained in their cages, exposing reptiles to the open air during public displays can lead to multiple health problems. Failure to provide appropriate lighting is likely to have an adverse impact on the welfare of heterotherms and birds. Providing an appropriate substrate for thermoregulation and camouflage is important for a whole range of species. The inability to provide, and maintain, appropriate climatic conditions in circuses and mobile zoos adversely affects animal welfare.
- Exposure to noise is a stressor for a diversity of wild animals, and has wide-ranging adverse impacts on their behaviour and physiology. Gates, vehicles, machinery, crowds and caretaking activities all increase sound pressure levels in captive environments beyond that normally experienced by wild animals and captive animals are frequently exposed to sound pressures that exceed the recommended limit for human well-being. Species sensitive to seismic vibrations or infrasound may be distressed by excessive anthropogenic vibration and infrasound. Circus animals will probably quickly acclimatise to music and applause during performances. Sudden or unexpected sounds are more likely to have adverse impacts, and the long-term effects of chronic noise exposure may have a more significant impact on animal welfare than acute exposure to individual short-term stimuli.

- Travelling circuses and mobile zoos bring animals into close contact with humans, and different species of animals into contact with each other. This poses a significant risk of disease transmission from animals to humans and between species of animals. Grazing on common land or farmland can expose circus animals to various parasites and pathogens, and the regular movement of animals between venues may facilitate the spread of nematodes such as lungworm and infections such as brucellosis, Johne's disease, bovine TB and ovine herpesvirus around Britain.
- Travel in small and/or temporary enclosures causes a range of health problems for wild animals in travelling circuses and mobile zoos, and facilitates the spread of parasites and diseases. Limited space can lead to injuries in reptiles and other species; standing for long periods on inappropriate perches causes problems such as bumblefoot in raptors and parrots; inappropriate substrates facilitate the spread of diseases and can cause serious foot pathologies and degenerative joint diseases in elephants.
- Circuses and mobile zoos bring visitors into close contact with the animals that are on display. Captive wild animals react to the presence, density, position and activity of visitors. Visitor-induced stress was reported in 63% of the studies we reviewed. Housing conditions are likely to influence an animal's ability to cope with visitors: the visitor effect will generally be smaller for animals in enclosures that allow them greater choice and control of their interactions with visitors. Larger enclosures control visitor proximity and complexity provides opportunities for escape and distraction. Circus animals and those used in mobile zoos have little or no control over their interactions with humans, and this has adverse effects on their welfare. We found no scientific evidence that the close contact between handlers/trainers and wild animals in circuses reduces stress caused by the proximity of visitors.
- Handling by members of the public can lead to significant welfare problems, both for the animals and humans. Visitors are largely ignorant of animals' communication cues. Circuses and mobile zoos bring humans into close proximity with potentially dangerous animals and this increases the risk of injury or death to both parties, particularly if animals are handled aversively. Handling and disturbance during physiological resting times interfere with activity patterns and time budgets, increasing stress levels, and can cause serious physical damage and stress to both invertebrates (which are generally more delicate) and a wide range of vertebrates.
- Training methods commonly used in circuses, where trainers are in direct contact with potentially dangerous animals, do not facilitate the minimal use of negative reinforcement, coercion, force and aggression required for good welfare. Training that facilitates the use of positive reinforcement, i.e. distance training and especially protected contact, requires specialist facilities such as strong barriers that are unlikely to be feasible in travelling environments. Also, participation cannot be voluntary in circuses and mobile zoos because animals have to perform on cue for each scheduled show.
- Positive reinforcement and protected contact training allows animals to have greater choice and control and could be considered enriching for animals. However, there are limits to what can be achieved with these methods. Unlike other groups of experts, *ATCs* strongly believed that regular training improves mental health and physical fitness, and affords learning opportunities that can be as challenging and rewarding as learning through problem solving with a complex enrichment device. Training is only enriching while the animal is still learning, not once the behaviour is learnt, i.e. when the animal performs the behaviour reliably on cue. Routine performances are likely to be less enriching because they offer no new learning opportunities. Training has the potential to enhance the psychological welfare of animals through offering mental stimulation but is not an appropriate substitute for other methods of improving welfare such as environmental enrichment and general enclosure suitability, which have multiple indirect benefits.

- Unlike the other groups of experts, *ATCs* did not believe that frequent training is stressful to animals. There was some disagreement between the five groups of experts on the importance of anticipatory behaviour prior to scheduled events such as performances, with *ATCs* most strongly disagreeing that the absence of anticipatory behaviour was an indicator of good animal welfare. Similarly, while *ATCs* were strongly of the view that anticipatory behaviour prior to performance indicates that the animal wants to, and enjoys, performing, the other four groups of experts disagreed. A predictable routine may help circus animals to cope and reduce the impact of limited control. Long-term unstimulated animals experience boredom, and anticipatory behaviour prior to performances (and other scheduled events such as feeding) may indicate an otherwise deficient environment in circus animals.
- *ATCs* believed that a strong human-animal bond might improve the welfare of performing animals, unlike all the other groups of experts except *Zoos*. Interactions between animals and their keepers are a permanent and influential feature of a captive animal's life, and so it is important that they are positive, since staff with negative attitudes or insufficient experience will develop poorer quality relationships with animals, which may compromise animal welfare by failing to reduce, or even enhancing, stress. Different trainers, even at the same establishment and following the same protocols, use slightly different techniques which may confuse and frustrate animals, and using multiple trainers limits the development of strong human-animal relationships. This can be a significant welfare concern in travelling circuses and mobile zoos, particularly when presenters are not the people who trained the animals and have limited experience in animal training.
- There are concerns over the welfare of animals that are no longer used in travelling circuses and mobile zoos. We could find no studies on the welfare effects of ceasing to use animals for entertainment, but rehabilitated/retired animals previously used in entertainment may show more stereotypical behaviour than other captive animals.
- Unlike the other groups of experts, *ATCs* believed that animal welfare was not compromised by frequent transport. However, while habituation to frequent transport may reduce the negative effects of transport on welfare, it does not eliminate them, and circus animals may be subjected to further transport when they have not fully recovered from the previous journey. Levels of stereotypy during transport indicate that the welfare of circus animals is likely to be compromised by frequent transport. Continuous postural adjustments to maintain balance during transport are physically and mentally stressful for animals and transport causes disruption of eating, drinking, resting, REM (rapid eye movement) sleep and circadian activity patterns. These effects are likely to be exacerbated by the irregular schedules of travelling circuses with frequent journeys and insufficient recovery periods, and probably also with mobile zoos. We could find no scientific evidence that wild animals fully adapt to frequent transport. Despite being transported frequently, many circus animals (those transported in their usual housing) do not have the same level of legal protection of their welfare during transport as other animals.
- Unlike other groups of experts, *ATCs* believed that regular transport between venues was mentally stimulating for the animals, and thereby contributed to good welfare, and that this mental stimulation outweighs the limited size and complexity of temporary enclosures. However, animals can take a long time to acclimatise to new environments, even when they are not very different in terms of size and facilities. The duration and amount of disturbance caused by each relocation may influence acclimatisation, and frequent movements may not allow enough time to settle completely
- We could find no scientific evidence to support the assertion that transporting wild animals in circuses is of greater welfare concern than in mobile zoos, which take their animals back to a fixed base. Even domesticated species that are transported regularly but returned to the same home base show a range of adverse welfare indicators, including lower reproductive rates, increased risk of disease and physiological traits indicative of stress. In addition, there are welfare concerns over the ability to provide the right environmental conditions for animals carried in temporary transports, particularly species such as reptiles and birds of prey.

- We should be aiming to provide the best possible welfare for captive wild animals. However, the facilities provided for wild animals in travelling circuses and mobile zoos are based on tolerances rather than needs; this has a significant negative effect on all aspects of their welfare. In our review of the needs of wild animals, we found that all five of the 'freedoms' are compromised in travelling circuses and mobile zoos.
- The European 'Welfare Quality' project used outcome-based measures to assess the welfare of farm animals. This provides a basis to assess the longer-term consequences of housing systems and husbandry practices. Most if not all of the twelve 'welfare criteria' used in the 'Welfare Quality' project are compromised for wild animals used in travelling circuses and mobile zoos.
- It is important to incorporate positive experiences into the assessment of animal welfare, and this is particularly relevant when considering the needs of wild animals in travelling shows. Welfare emerges from a complex combination of multiple factors. We considered the collective effect of all aspects of management and the environment of wild animals in travelling circuses and mobile zoos, and the positive experiences across the life of these wild animals. We could not find any evidence to suggest that the cumulative experience of periods performing, on display, and/or being petted and photographed balanced a lifetime of close confinement, regular disturbance and minimal choice and control. Life for wild animals in travelling circuses and mobile zoos does not appear to constitute either a 'good life' or a 'life worth living'.
- In 2013 the EFRA Select Committee recommended that the Government revise its approach to the draft Wild Animals in Circuses Bill to include a list of proscribed species that could no longer be used in travelling circuses, and suggested that all big cats and elephants be included on the list, whereas species such as snakes, zebras or raccoons would not. While the welfare concerns may be greater for larger species in travelling circuses, we could find no scientific evidence to suggest that some species of wild animals (vertebrates or invertebrates) are more suited to life in a travelling circus or mobile zoo. Furthermore, the scientific rationale for the Select Committee's selection of particular species that could be used in travelling circuses is unclear. Reptiles such as large snakes are particularly unsuited to regular transport due to their sensitivity to noise and vibration, their reliance on external factors for thermoregulation, and their need for specific environments for e.g. feeding and moulting.
- The Animal Welfare Act 2006 introduces a 'duty of care', making owners and keepers responsible for making sure the welfare needs of their animals are met. Under the Act, the person responsible for an animal must take all reasonable steps to ensure the needs of the animal are met. These needs include:-

  (a) its need for a suitable environment,

  (b) its need for a suitable diet,

  (c) its need to be able to exhibit normal behaviour patterns,

  (d) any need it has to be housed with, or apart from, other animals, and

  (e) its need to be protected from pain, suffering, injury and disease.

The scientific evidence indicates that captive wild animals in travelling circuses and mobile zoos do not achieve their optimal welfare requirements set out under the Animal Welfare Act 2006, for the reasons we have explained above.

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Appendices

Appendix 1

What is a non-domesticated animal?

We were told that non-domesticated animals were defined as "a member of a species that is not normally domesticated in the British Islands; that is to say, a species whose collective behaviour, life cycle or physiology remains unaltered from the wild type despite their breeding and living conditions being under human control for multiple generations". This definition derives from the Zoo Licensing Act 1981 and is the one used in an earlier review of *Wild animals in travelling circuses*[1]. However, the earlier review included camels, llamas and reindeer as non-domesticated animals; the rationale for this is unclear.

While it has been argued that reindeer are in the early stages of domestication[2,3], reindeer show features typical of other domesticated species, such as much greater colour variation than wild herds, a shorter muzzle and smaller body size. They also breed earlier and have a less strong urge to migrate. Reindeer were probably domesticated on at least two or three separate occasions in eastern Russia and Fenno-Scandia within the last two or three thousand years, and were the last species to be domesticated by humans[4], although selective breeding has not been as intense because both humans and reindeer continued their nomadic lifestyle[5]. A Dangerous Wild Animals Act 1976 licence is required to keep caribou and reindeer, but domesticated reindeer are exempt.

From 2005 to 2013, 90 consignments containing 1168 domesticated reindeer were imported, and there are an estimated 1500 reindeer in the UK[6]. However, the Veterinary Deer Society does not recommend holding small numbers of reindeer on farms or small holdings, and they require high levels of stockmanship if they are to thrive[6]. There are considerable welfare concerns for domesticated reindeer held in captive conditions that do not facilitate traditional husbandry techniques[7], particularly those kept by inexperienced owners for commercial reasons[8]. There appear to be few welfare concerns for the two free-ranging herds in the Cairngorms, numbering around 150 animals[9]. Of these, between 60 and 75 are available for Christmas events and displays, but only trained castrated males are used for pulling sleighs. These animals are used to human contact and receive extensive training prior to being used in shows[10].

Llamas and alpacas are both domesticated and, because they are so different from their wild ancestors, traditionally have been given different Latin names. The alpaca (*Lama pacos*) is the domesticated version of the vicuña (*Vicugna vicugna*), and the larger llama (*Lama glama*) is the domesticated form of the guanaco (*Lama guanicoe*); both alpacas and llamas have a long history of hybridization[11,12]. However, in the world list of mammal species, *Vicugna vicugna* is used for both the vicuña and alpaca and *Lama glama* for both the guanaco and llama[13]. Llamas were domesticated in the Peruvian Andes some 5000 to 3800 years before present (BP) and then moved to lower elevations; the alpaca was possibly domesticated a little earlier, some 6000 BP and moved to lower elevations by about 3800 BP[14]. There are over 2000 llamas[15] and around 50,000 alpacas[16] in Britain. Llamas are used in circuses and llama trekking is becoming increasingly popular in Britain; both llamas and alpacas are reared commercially on farms. No Dangerous Wild Animals Act 1976 licence is required to keep llamas and alpacas and no licence has been required to keep guanacos since 1 October 2007.

Dromedaries were first domesticated in southern Arabia around 4000 BP, and wild populations probably survived in Arabia to around 2000 BP. However, since dromedaries are now only known as domesticated animals or as feral populations, it is unclear how they differ from their wild ancestors. As with reindeer, after domestication dromedaries had to remain nomadic to be able to continue to live in desert environments[17]. While most of those in Britain are held in zoos and wildlife parks, some are used for trekking, racing, camel polo, Christmas events, weddings, and a variety of corporate events. Fewer than 30 are held in Britain outside zoos[18]. A Dangerous Wild Animals Act 1976 licence is required to keep dromedaries.

Bactrian camels were probably domesticated 5000 to 6000 BP, and show a number of morphological differences from wild Bactrian camels, which have relatively smaller humps, ears and hoof plates, relatively longer legs, and no *corpus callosum* on the fore legs[19]. Some authors assign wild camels subspecific status, and recent genetic studies have shown that the surviving population of wild Bactrian camels is not the direct ancestor of the domestic Bactrian camels, which may have originated from a single wild population that is now extinct[20]. The separation between the surviving wild population and the ancestors of domestic Bactrian camels is estimated to have occurred 700,000 years ago, long before domestication[21]. There are more Bactrian camels than dromedaries in Britain, and they are used for riding and trekking, corporate events and parties, as well as in circuses. Fewer than 65 are held in Britain outside zoos[18]. A Dangerous Wild Animals Act 1976 licence is required to keep both the domestic and wild forms of the Bactrian camel.

Thus the situation with these species is complex: reindeer, dromedaries and Bactrian camels have a long history of domestication, but all only show small morphological and physiological differences from their wild ancestors because all three retained their nomadic lifestyle in the environment to which they were adapted. However, they show clear genetic differences from their wild counterparts. Llamas and alpacas were not nomadic and selective breeding has led to greater morphological and physiological differences from their wild ancestors. However, the "collective behaviour, life cycle or physiology" of all these species is altered from the wild type. If a species is domesticated, whether it is "normally domesticated in the British Islands" is only relevant if a lack of husbandry expertise and/or unsuitable environmental conditions lead to inappropriate welfare and/or safety concerns.

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Appendix 2

People who contributed to one or both of the questionnaires

We received 17 responses from experts who asked to remain anonymous. The people who agreed to be named, and the affiliations they asked to be included, are below:-

Dr Simon Adams BSc BVMS MRCVS
Independent zoo and wildlife veterinary adviser

Thomas L. Albert
Vice President, Government Relations, Feld Entertainment, Inc. dba Ringling Bros and Barnum & Bailey®

Ms Brooke Aldrich
Wild Futures

D.V.M. Andrés Alejandro Castro
Universidad Nacional de Colombia

Thomas Althaus, PhD in biology (zoology/ethology)
Independent consultant for European Circus Association

Mr Jonathan Ames
Eagle Heights Wildlife Foundation

Libby Anderson
OneKind

Paloma Jimena de Andrés Gamazo, DVM, PhD
Head veterinarian at La Reserva del Castillo de las Guardas, Spain

Dr Rob Atkinson
Consultant

Dr Heather Bacon
Independent

Dr Tom Bailey, BSc, BVSc, MRCVS, CertZooMed, MSc, PhD, Dip ECZM, RCVS
Specialist in zoo and wildlife medicine, Origin Vets, Pembrokeshire, Wales, UK

Mr Chris Barltrop BA (Hons)
Circus professional, former Chair of Circus Sub-group of the Defra Circus Working Group towards the 'Radford Report'.

Miss Jennifer Barnes
Five years' experience in animal encounter businesses/exotic animal businesses working with non-domesticated animals

Carole Baskin
CEO of Big Cat Rescue

Professor Patrick Bateson
University of Cambridge

Professor emeritus Marc Bekoff
Ecology and Evolutionary Biology, University of Colorado, Boulder

Mr Neil Bemment
Paignton Zoo Environmental Park

Dr Cynthia Bennett
Associate editor, Journal of Applied Animal Welfare Science

Dr Brian Bertram
Retired zoologist

Cristina Biolatti, DVM, PhD
Regional Center for Exotic Animals, Istituto Zooprofilattico Sperimentale del Piemonte, Turin

Chris Biro
Executive Director of Bird Recovery International and owner of The Pirate's Parrot Show

Nancy Blaney
Senior Policy Advisor, Animal Welfare Institute (USA)

Dr M Bracke
Researcher of Animal Welfare, Wageningen University and Research Centre

Professor Donald Broom
Cambridge University

Mrs Rona Brown
Rona Brown's Movie Animals

Dr Bryan Carroll

Mr Jordi Casamitjana,
International Fund for Animal Welfare

Dr Julian Chantrey
University of Liverpool, Institute of Veterinary Science

Suzanne Chipperfield
Fossett's Circus, Lucan, Ireland

Mr Thomas Chipperfield
An Evening with Lions and Tigers

Pamela Clark, CPBC, CVT
Certified parrot behavior consultant and certified veterinary technician, Creekside Veterinary Clinic in Keizer, Oregon and the International Association of Animal Behavior Consultants

Mrs Anna Claxton MSc
University of Edinburgh

Dr Ros Clubb
RSPCA

Mr James S Clubb
Heythrop Zoological Gardens Ltd.

Mr Mike Collins
Site manager and wolf keeper,
UK Wolf Conservation Trust

Jan Creamer
President, Animal Defenders International

Mr Keith Cutler
veterinary surgeon

Mr John Dineley, BA Hons
Zoological consultant

Miss Christina Dodkin
Research Director, Animal Defenders International

Tobias Dornbusch Diplom Biologe (MSc Biologist)
European Elephant Group

Mr Chris Draper
Born Free Foundation/University of Bristol

Dr Julian Drewe
Royal Veterinary College,
University of London

David Duffy
Tom Duffy's Circus, Ireland/
Circus Guild of Great Britain

Dr Kate Evans
Elephants for Africa

Dr Elena Fedorovich
Senior researcher, Moscow State University,
Department of Psychology

Dr Eduardo J. Fernandez
Affiliate professor, Department of Psychology, Trinity Lutheran College

Dr Vicki Fishlock
Resident scientist,
Amboseli Trust for Elephants

Dr Neil A Forbes BVetMed DipECZM FRCVS
Great Western Exotic Vets

Emma Ford
Vice Chairman Scottish Hawk Board

Mr and Mrs Joseph and Rebecca Fossett
Joseph's Amazing Camels Ltd.

Mrs Daniela Freyer
Pro Wildlife

Dr Marion E. Garaï
Elephant Specialist Advisory Group SA,
Space for Elephants Foundation SA,
European Elephant Group

Mr Greg Glendell
Honorary director, BirdsFirst UK

Mrs Emma Goodman Milne BVSc MRCVS
Independent veterinary surgeon

Mr David Hancocks

Dr Moira Harris
Harper Adams University

Prof Dr Heribert Hofer DPhil
Leibniz Institute for Zoo & Wildlife Research Berlin, Germany

Bengt Holst
Scientific Director, Copenhagen Zoo

Dr H Hopster
Wageningen UR Livestock Research

Dr Geoff Hosey
Biology, University of Bolton

Mr Jolyon Jamieson
Retired circus artiste

Dr Kimberley Jayne
University of Exeter and Animal Defenders International

Dr Lance Jepson MA VetMB CBiol MSB MRCVS
Zoo and exotic animal veterinarian,
Origin Vets, Pembrokeshire, UK

Dr Mike Jessop BvetMed MRCVS

Mr Peter Jolly
Jolly's Circus, licensed under the Wild Animals in Travelling Circuses (England) Regulations 2012/President, Circus Guild of Great Britain

Mr Kenneth Kaemmerer,
Pittsburgh Zoo & PPG Aquarium

Lisa Kane
Attorney, Coalition for Captive Elephant WellBeing

Dr Andrew Kelly
Irish Society for the Prevention of Cruelty to Animals

Dr Winnie Kiiru
Conservation Kenya

Dr Marthe Kiley-Worthington
Centre d'eco-etho recherche et education, France

Dr Andrew Kitchener
National Museums Scotland

Dr John A Knight, BVetMed MRCVS, BVA, BVZS, EAZWV, WAZWV, MSB,
Chris Lawrence Vet of the Year 2015,
CEVA Animal Welfare Awards

Prof Dr Richard Kock
Royal Veterinary College

Dr Michael Kreger
Biologist

Mr Alexander Lacey
Big cat carer, breeder and trainer

Professor Phyllis C Lee
University of Stirling

Mr Guy Lichty
North Carolina Zoo

Dr Kati Loeffler
Veterinarian

Dr William Keith Lindsay
Member, Scientific Advisory Council,
Amboseli Trust for Elephants, Kenya

Mr Bruce Maclean
HerpVet Services

Miss C Macmanus
Circus Mondao, licensed under the
Wild Animals in Travelling Circuses
(England) Regulations 2012
& Circus Guild of Great Britain

Mr Philip Mansbridge
International Fund for Animal Welfare

Lori Marino
Executive Director, The Kimmela Center
for Animal Advocacy

Ken McCort
Four Paws Animal Behavior Services (Ohio)
and Wolf Park (Indiana)

Mr Nick Mertens,
researcher, Pachyderm/World of Zoology

Ms Carney Anne Nasser
Legislative counsel and captive exotic
specialist, Animal Legal Defense Fund

Dr Katarzyna Nowak
Anthropology, Durham University,
Durham UK

Miss Nicola O'Brien
Campaigns Director at the Captive Animals'
Protection Society

Xareni Pacheco
Veterinary professional, MSc in animal
behaviour and animal welfare, PhD in
animal behaviour, University of Exeter,
University of Edinburgh

Jemima Parry-Jones MBE
Director, International Centre for Birds of Prey

Mr Thomas Pietsch
Four Paws International

Dr Mark Pilgrim
Director General, North of England
Zoological Society, Chester Zoo

Alex Podturkin, PhD
Moscow Zoo, junior scientific researcher,
scientific research department

Mr Craig Redmond
Independent animal protection consultant

Dr Ian Robinson
International Fund for Animal Welfare

Johnny Rodrigues
Chairman, Zimbabwe Conservation Task Force

Dr (MRCVS) Stephanie Sanderson
EWS Partnership Ltd

Dennis L Schmitt DVM, PhD, Dipl. ACT
Chair of Veterinary Care, Research and
Conservation, Feld Entertainment,
Ringling Bros Center for Elephant
Conservation

Helen M. Schwantje
Fish and Wildlife Branch, British Columbia
Ministry of Forests, Lands and Natural
Resource Operations

Dr Graeme Shannon
Bangor University

Mr James Shaw & Mrs Sharon Shaw
Lakeview Monkey Sanctuary

Mrs Ilaria Di Silvestre
Eurogroup for Animals

Mr Mark Peter Simmonds
University of Bristol, School of
Veterinary Sciences

Mrs Elizabeth (Tilly) Smith BSc Hons Zoology
Director and Secretary of The Reindeer Company
Ltd, owner/manager of The Cairngorm Reindeer
Herd, Aviemore, Scotland

Ms Catrina Steedman BSc(Hons) MRSB
Emergent Disease Foundation

Dr Miranda Stevenson
UK zoo inspector

Mrs Georgie Stewart
Program Officer, Humane Society International (Australia)

Mr Peter Stroud
Independent zoological consultant, former zoo keeper, curator and director

Mr Olaf Töffels
European Elephant Group

Mr Simon Tonge
Whitley Wildlife Conservation Trust

Mr Terence Turkington
Falconer

Laura Van Der Meer
On behalf of Fédération Mondiale du Cirque

Mr Clifford Warwick PGDipMedSci CBiol CSci EurProBiol FOCAE FRSB
Emergent Disease Foundation

Dr Deborah Wells
Reader in Psychology, Queen's University Belfast

Professor Françoise Wemelsfelder
Scotland's Rural College

Mrs Isabel Wentzel
Manager, Wildlife Protection Unit, National Council for the Societies for the Prevention of Cruelty to Animals (NSPCA), South Africa

Greg Whittaker
Animal husbandry manager, Moody Gardens, Inc.

Mr Wilkinson
Noah's Ark Zoo Farm

Dr Kirsten Wimberger
Wild Bird Trust

Dr med vet Angelika Wimmer
European Elephant Group

Dr Lisa Yon
Lecturer in Zoo & Wildlife Medicine, University of Nottingham, School of Veterinary Medicine & Science

We also received four collective responses for the second questionnaire from the following groups:-

Laura van der Meer
On behalf of Federation Mondiale du Cirque

Thomas L. Albert
Vice President – Government Relations, *on behalf of* Feld Entertainment, Inc. dba Ringling Bros. and Barnum & Bailey®

Mark Stidworthy MA VetMB PhD FRCPath MRCVS, RCVS
Recognised specialist in veterinary pathology (Zoo and Wildlife), President, British Veterinary Zoological Society, *on behalf of* BVZS Council

Rona Brown
Government Liaison Officer Circus Guild of Great Britain *on behalf of* the Circus Guild of Great Britain, European Circus Association, Martin Lacey jr, ENC, CFA Italy, Jollys Circus (Licensed Circus England), Circus Mondao (Licensed Circus England), Duffys Circus Ireland, Chris Louth UK, Jim Clubb, Amazing Animals, Suzanne Chipperfield, Pawsi, Rona Brown's Movie Animals, Yvonne Kludsky Spanish Circuses, John le Mare Australia, Jolyon Jamieson

We are extremely grateful to all the people who responded to our requests for information and returned our questionnaires.

Appendix 3

The first questionnaire

We have been asked by the Welsh Government to review the science currently available on the use and behaviour of wild animals in circuses and travelling shows. The first part of this process is to seek the views of relevant experts around the world to identify the key issues we should consider. To this end, we are seeking advice and guidance from people with expertise on keeping captive wild animals, animal training, the circus industry, animal welfare generally and the behaviour of wild animals. As someone with relevant expertise, we would be grateful if you could assist us by completing the attached, short questionnaire. We are interested in your opinions only, and there are no 'right' or 'wrong' answers.

We would be grateful if you could answer three questions. The first question relates to indicators of welfare, which might include behavioural, health or physiological measures, though please do not feel limited to these. The second question relates to factors that affect welfare. These might include aspects of the environment, transport, housing or husbandry, though again please do not feel limited to these types of factors. The third question asks if there are any specific issues that you consider only apply to animals in circuses or other forms of animal entertainment. These may, of course, repeat some of the points you have already made.

For each of the questions, please list up to ten issues you think are important. You can of course suggest fewer issues. If you do not feel qualified to answer any of the questions, please leave them blank. Also, please do not try to rank the factors you consider to be important. We will compile a list of the key factors identified by all the experts and then ask everyone to score their importance.

Could we also ask you to think about *all* the species used in circuses and other types of travelling animal shows. While these are typically mammals, they also include birds, such as parrots and birds of prey, and some large reptiles, such as pythons and crocodilians. If you think that some of the factors you identify only apply to specific species or groups of species, please indicate this on the questionnaire.

The schedule for the review is tight, so please try to reply within two weeks of receipt.

Finally, for transparency, we have been asked to publish a list of the people who have contributed to this review in the report. We will not be making individual views or contributions public: these will remain confidential. So could you please put your title, name and affiliation at the end of the form so that we can acknowledge you correctly. If you do not want your name included in the report, please indicate this at the end of the questionnaire.

If you have any questions, please do not hesitate to contact us at **circuswelfarestudy@gmail.com**.

Your co-operation is key to the success of this study, and we would be extremely grateful if you could spare a few minutes to answer this questionnaire.

Many thanks for your help.

Yours

Jo Dorning
Stephen Harris
Heather Pickett

The welfare of wild animals in circuses and travelling shows

For all questions, please consider only the welfare of non-domesticated animal species that are, or could be, used in a circus and/or other forms of entertainment, including mammals, birds and reptiles. If your answer or area of expertise relates to a particular species or group of species, please specify where you are answering in relation to certain species only.

1. ***Indicators of welfare of wild animals in circuses***

Indicators of welfare might include (but are not restricted to) aspects of behaviour, health or physiology. Please supply up to ten indicators of good welfare and up to ten indicators of poor welfare. If some or all of your answers relate only to certain species, please specify.

a) In your opinion, what are the most important indicators of good welfare in circus animals?

1.	
2.	
3.	
4.	
5.	
6.	
7.	
8.	
9.	
10.	

b) In your opinion, what are the most important indicators of poor welfare in circus animals?

1.	
2.	
3.	
4.	
5.	
6.	
7.	
8.	
9.	
10.	

2. Factors that affect the welfare of wild animals in circuses

Factors that affect welfare might include (though are not restricted to) aspects of housing, social environment, husbandry, diet, veterinary care, transport, training and performance. Please supply up to ten factors contributing to good welfare and up to ten factors contributing to poor welfare. If some or all of your answers relate only to certain species, please specify.

a) In your opinion, what are the most important factors likely to contribute to good welfare in circus animals?

1.	
2.	
3.	
4.	
5.	
6.	
7.	
8.	
9.	
10.	

b) In your opinion, what are the most important factors likely to contribute to poor welfare in circus animals?

1.	
2.	
3.	
4.	
5.	
6.	
7.	
8.	
9.	
10.	

3. Factors unique to non-domesticated animals used in circuses/entertainment

Do you think there are specific factors that affect the welfare of non-domesticated animals used in circuses or other entertainment shows, which do not apply to other captive environments such as zoos and, if so, do you think that these factors are likely to enhance or impair welfare?

1.	
2.	
3.	
4.	
5.	
6.	
7.	
8.	
9.	
10.	

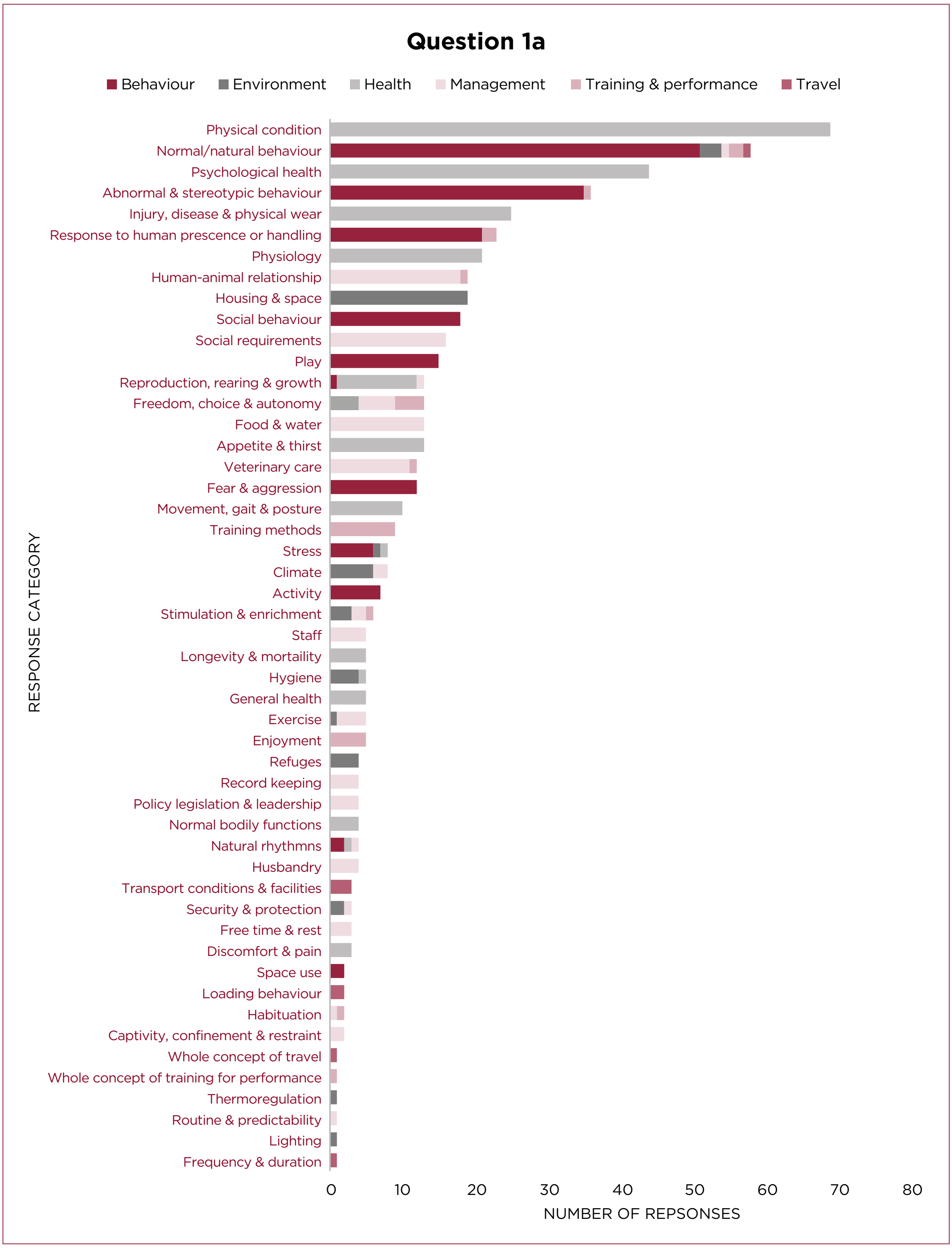
Please give your title, name and affiliation as you would like to see it appear in the report:-

If you do not want your name included in the report, please put an "X" in this box ☐

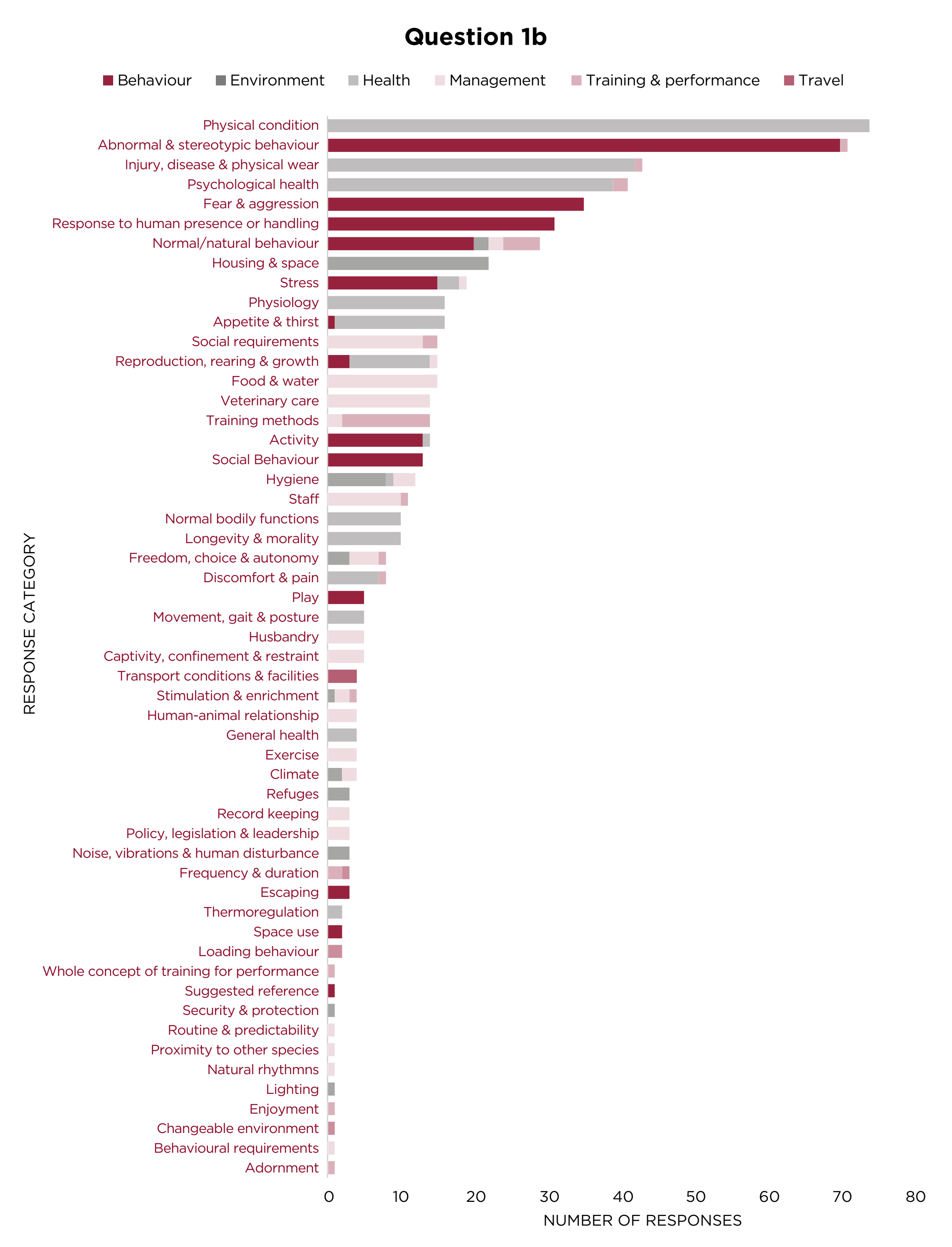
Appendix 4

The first questionnaire

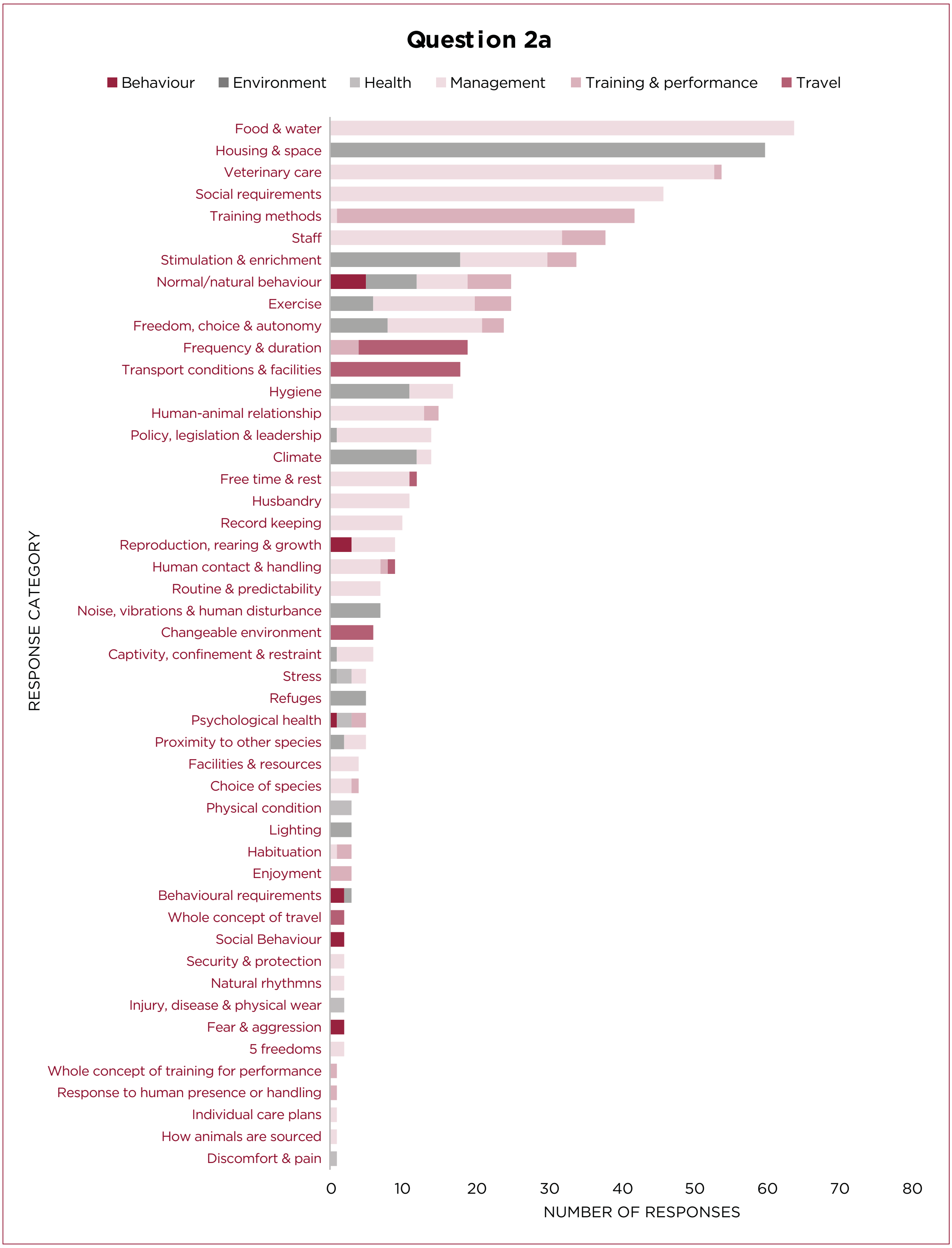
Responses to question 1a



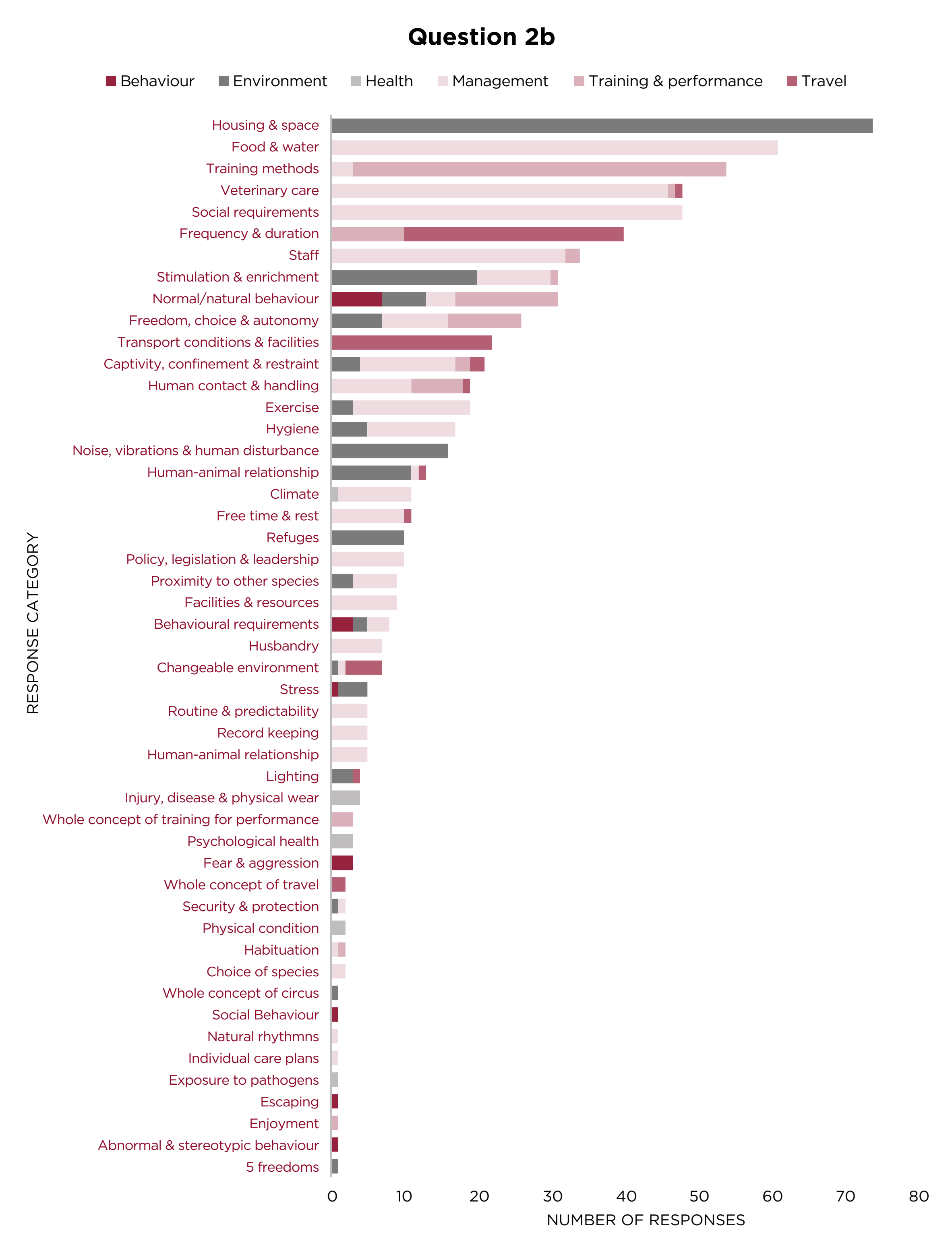
Responses to question 1b



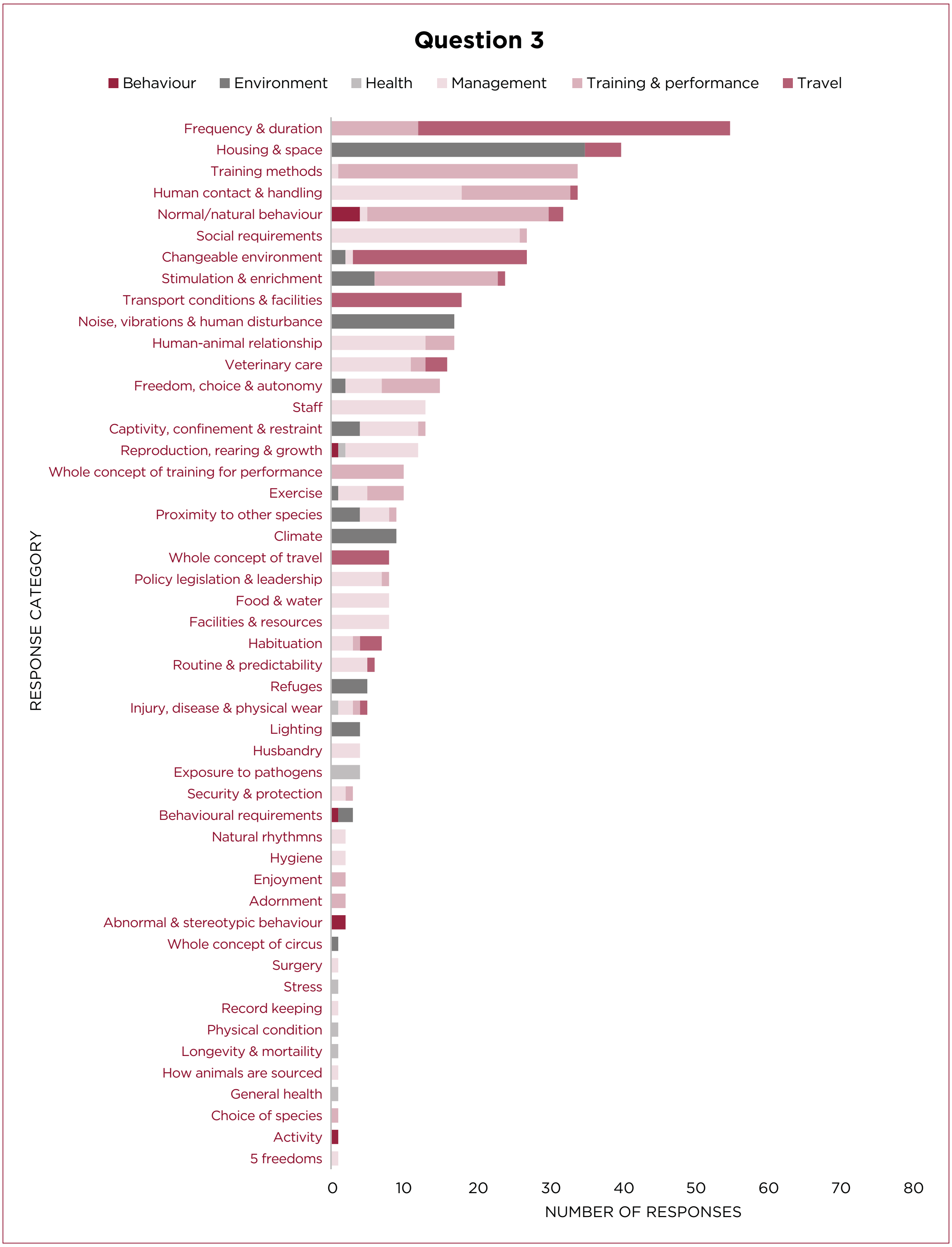
Responses to question 2a



Responses to question 2b



Responses to question 3



Appendix 5

The second questionnaire

Thank you for taking part in our review. We have been asked by the Welsh Government to review the science currently available on the use and welfare of wild and/or non-domesticated animals in circuses and other travelling shows around the world. Wild and/or non-domesticated animals are members of species that are not normally domesticated in the British Islands. At the beginning of this process we asked relevant experts from around the world to help identify the key issues to consider in our review (questionnaire round 1). We then combined the issues raised into a number of statements and are now asking experts to what extent they agree with each statement (questionnaire round 2).

Whether or not you contributed to the first questionnaire, we would be extremely grateful if you could find time to participate in round 2.

For each statement, all you have to do is use your cursor to click along a scale from 0-100% to indicate the extent to which you agree with each statement, with 0% indicating that you *strongly disagree* with the statement and 100% that you *strongly agree* with it. We are interested in your opinions only, and there are no 'right' or 'wrong' answers. If you feel unable to comment on some of the statements, please feel free to leave them unanswered by not clicking on the scale below that statement.

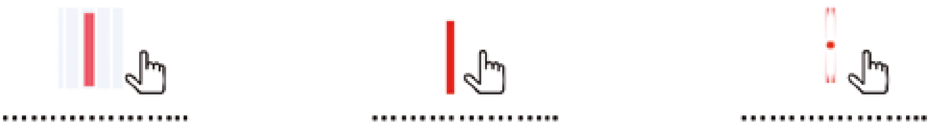
To view this questionnaire you need to open it in either Adobe Acrobat Reader or Preview.

Each statement looks something like this:

Q1. To what extent do you agree with the statement that "Good welfare can be indicated by normal sexual function/cycling and normal reproductive behaviour, in terms of mating, normal pregnancy/incubation and successfully rearing young"

0% 100%

To indicate the extent to which you agree with the statement, please click the cursor at your chosen point along the scale from 0% to 100% and a red marker will appear. The marker may vary in appearance depending on your computer system (shown below).



Note that each statement refers to the welfare of wild/non-domesticated animals. If your opinions (for any/all statements) relate to specific species or groups of species, please indicate this in your return email.

Please remember to 'Save' your changes before you return the form.

Thanks, your input is much appreciated.

Jo Dorning, Stephen Harris and Heather Pickett

The questions were:-

1 To what extent do you agree with the statement that "Good welfare can be indicated by normal sexual function/cycling and normal reproductive behaviour, in terms of mating, normal pregnancy/incubation and successfully rearing young"

2 To what extent do you agree with the statement that "Good welfare can be indicated by a normal appetite and thirst appropriate for wild animals of the same species, age and sex, and for that period in their annual cycle, e.g. reptiles typically do not eat during the reproductive or dormant periods"

3 To what extent do you agree with the statement that "Captive animals can be considered to have good welfare when they show no evidence of abnormal behaviour, such as pacing, weaving, bar-biting, head twists or self-harm such as feather plucking or over-grooming, or other repetitive movements that are not part of the species' normal behavioural repertoire"

4 To what extent do you agree with the statement that "Captive animals can be considered to have good welfare when they show no evidence of anticipatory behaviour, defined as abnormal, repetitive behaviour (movements that are not part of the species' normal behavioural repertoire in nature) linked to scheduled events, such as around feeding time"

5 To what extent do you agree with the statement that "If a captive animal shows anticipatory or stereotypic behaviour prior to performances, this is a positive sign that the animal wants to perform, and that they enjoy performing"

6 To what extent do you agree with the statement that "A captive animal can be considered to have good welfare if it displays a full/complete repertoire of natural behaviours (such as foraging, grooming/preening, bathing, digging, climbing, flying, nesting, socialising) in the proper context and as frequently as shown by animals of the same species, age and sex in the wild"

7 To what extent do you agree with the statement that "A captive animal can be considered to have good welfare if it does not show fear or aggressive behaviour towards humans or conspecifics", where fear or aggressive behaviour might include a prolonged submissive posture, hiding, avoidance or reluctance, immobility, sweating, panting, shaking, uncontrolled defecation, repeated vocalisations, threatening postures, spitting, kicking and/or biting

8 To what extent do you agree with the statement that "Captive animals of social species can be considered to have good welfare if they display a diversity of appropriate, positive social interactions with their conspecifics, such as play, grooming and/or cooperation"

9 To what extent do you agree with the statement that "To ensure good welfare of captive animals, enclosure size should be proportional to the species' body size and ranging behaviour"

10 To what extent do you agree with the statement that "To ensure good welfare of captive animals, enclosures should provide refuges where animals can hide/retreat/escape from spectators or conspecifics and shelter from adverse weather conditions"

11 To what extent do you agree with the statement that "To ensure good welfare of captive animals, enclosures should be complex, interactive environments for mental and physical stimulation"

12 To what extent do you agree with the statement that "To ensure good welfare, captive animals should be housed in conditions that provide lighting, thermal and humidity conditions that replicate the species' natural habitat"

13 To what extent do you agree with the statement that "To ensure good welfare, captive animals need access to a variety of environmental enrichments to stimulate natural behaviours"

14 To what extent do you agree with the statement that "Having choices, such as choice of food, choice of location, choice of activity and/or choice of social partners, contributes to good animal welfare"

15 To what extent do you agree with the statement that "To ensure good welfare, captive animals require a diet that closely resembles what they have in the wild, in terms of variety, quality, quantity and presentation"

16 To what extent do you agree with the statement that "To ensure good welfare, captive animals should be presented with food in such a way as to encourage natural foraging/feeding behaviour"; this might, for instance, include searching, chasing, bark-stripping, digging and/or grazing

17 To what extent do you agree with the statement that "To ensure good welfare, captive animals should always be housed/kept in a species-appropriate social environment, i.e. solitary species should be housed alone and social species in groups of a similar size and composition (age range, sex ratio, relatedness) to animals of the same species, age and sex in nature"

18 To what extent do you agree with the statement that "For captive wild animals, socialisation with human handlers/trainers is a good substitute for socialisation with conspecifics and therefore contributes to good welfare"

19 To what extent do you agree with the statement that "To ensure good welfare, it is important that prey species are never housed in close proximity to predators, and *vice versa*"

20 To what extent do you agree with the statement that "Welfare of captive animals is positively influenced by caring, attentive and dedicated staff that respect their animals, pay close attention to their individual needs and monitor how individuals respond to different situations"

21 To what extent do you agree with the statement that "It is primarily the responsibility of the care staff and trainers to ensure good standards of animal welfare"

22 To what extent do you agree with the statement that "It is primarily the responsibility of the managers and business owners/proprietors to ensure good standards of animal welfare"

23 To what extent do you agree with the statement that "It is primarily the responsibility of the government to ensure good standards of animal welfare through the production and enforcement of welfare guidelines, policy and legislation"

24 To what extent do you agree with the statement that "To ensure good welfare, animals require regular health checks (at least every 3 months and not just when there is a problem) by a qualified professional with species-specific knowledge"

25. To what extent do you agree with the statement that "The frequent handling and training of performing animals makes veterinary procedures less stressful for the animals, thereby contributing to good welfare"

26 To what extent do you agree with the statement that "The frequent handling and training of circus and other performing animals facilitates the early detection of sickness, thereby contributing to good welfare"

27 To what extent do you agree with the statement that "Circus and other performing animals develop a strong and positive bond with their trainers/keepers/handlers, which contributes to good welfare"

28 To what extent do you agree with the statement that "All species can be successfully trained by only using reward-based training or positive reinforcement, including dangerous or unpredictable animals such as big cats and elephants"

29 To what extent do you agree with the statement that "To ensure good animal welfare, training should never involve negative reinforcement, coercion or punishment"

30 To what extent do you agree with the statement that "To ensure good welfare, animals should only be trained to perform natural movements or behaviours that they would normally show in the wild"

31 To what extent do you agree with the statement that "To ensure good welfare, the training and performance schedule should allow adequate time away from humans (excluding travel time) when animals are free to engage in natural behaviours and rest undisturbed"

32 To what extent do you agree with the statement that "Frequent training and performances are stressful for animals and contribute to poor welfare"

33 To what extent do you agree with the statement that "To ensure good welfare, animals should be allowed to choose whether or not to perform or participate in training"

34 To what extent do you agree with the statement that "The stimulation of regular training and performances improves both mental health and physical fitness and therefore contributes to good welfare"

35 To what extent do you agree with the statement that "Training animals to cooperate during veterinary or husbandry procedures is more beneficial to animal welfare than training animals to perform for the entertainment of paying audiences"

36 To what extent do you agree with the statement that "Good animal welfare is not compromised by frequent transport, loading and unloading"

37 To what extent do you agree with the statement that "To ensure good welfare, animals should only be transported when absolutely necessary and for the shortest times possible to avoid unnecessary stress"

38 To what extent do you agree with the statement that "To ensure good welfare, transporters should contain species-appropriate holding facilities that reflect the species' biological needs, in terms of space, substrate and climate"

39 To what extent do you agree with the statement that "To ensure good welfare, animals must not be deprived of opportunities to perform natural behaviours during transportation"

40 To what extent do you agree with the statement that "The unpredictable and variable environments with different sights, smells and sounds that are experienced through frequent travel to new locations are a great source of mental stimulation and therefore contribute to good animal welfare"

41 To what extent do you agree with the statement that "The welfare benefits of the varied, stimulating environments experienced by travelling animals outweigh the disadvantages of the limited size and complexity of temporary enclosures"

42 To what extent do you agree with the statement that "The nature of circuses and other mobile animal entertainment necessitates small and simple animal enclosures that are easy to assemble/ disassemble and transport between venues and that the preconditions for good welfare can only be met in the complex environments made possible by stationary/permanent housing"

Please give your title, name and affiliation as you would like to see it appear in the report:-

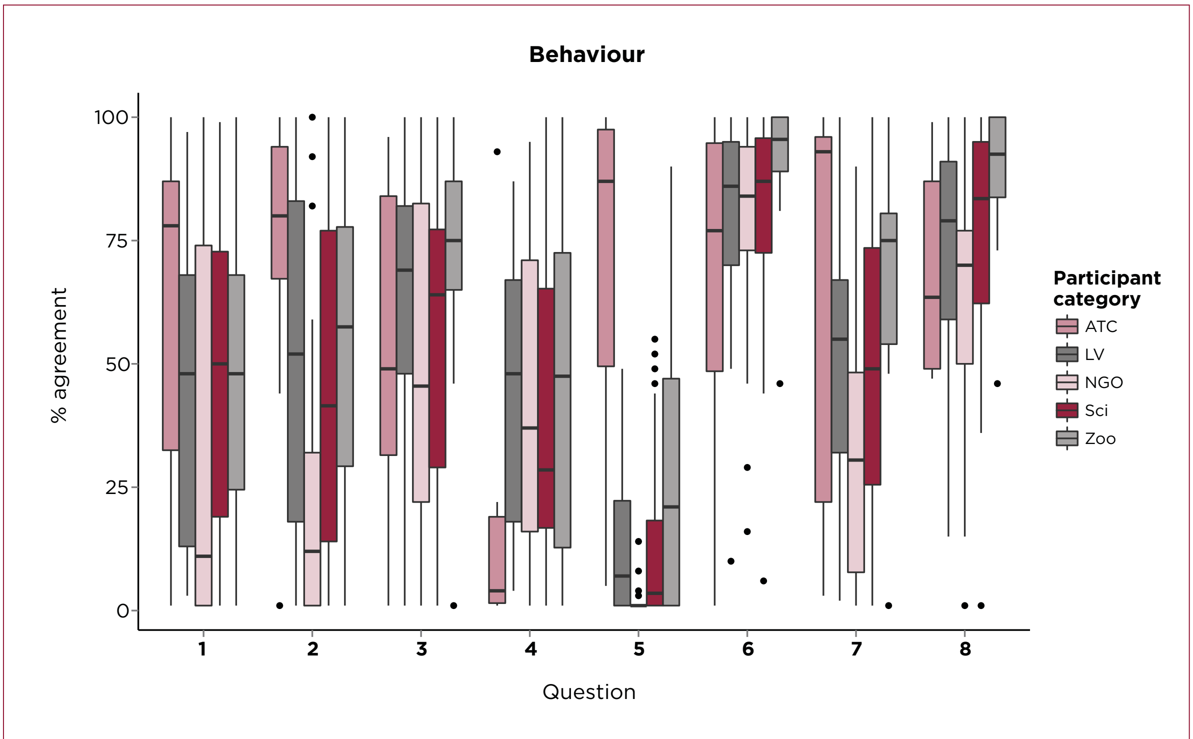
If you do not want your name included in the report, please put an "X" in this box ☐

Appendix 6

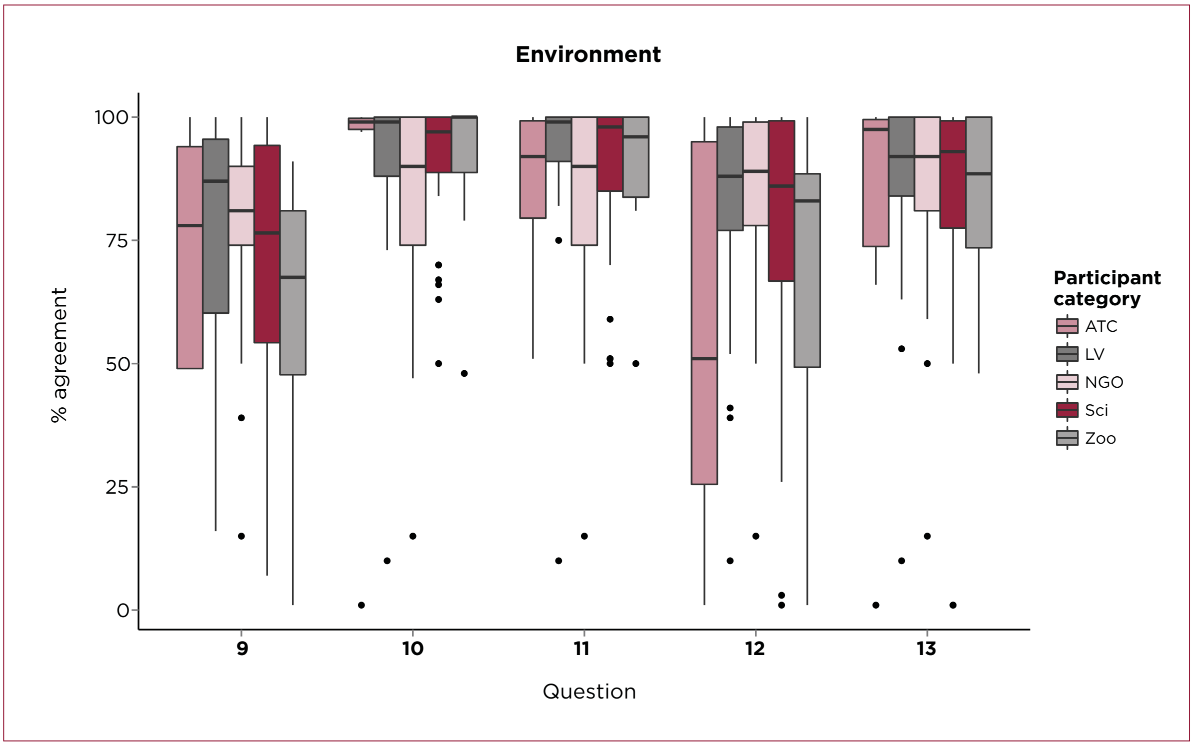
Responses to the second questionnaire

The numbers refer to the questions in Appendix 5 and are grouped by welfare issue and the type of respondent: *ATC* = animal trainers and circuses, *LV* = attorneys and veterinarians with expertise in wild animal welfare, *NGO* = people working for a relevant NGO, *Sci* = scientists with relevant expertise and *Zoo* = zoo and wild animal sanctuary staff. The horizontal lines denote the median score, the coloured boxes the upper and lower quartiles, the vertical lines the 95% confidence intervals, and dots mark outliers. 98 questionnaires were included in the analyses, but some people did not answer all the questions.

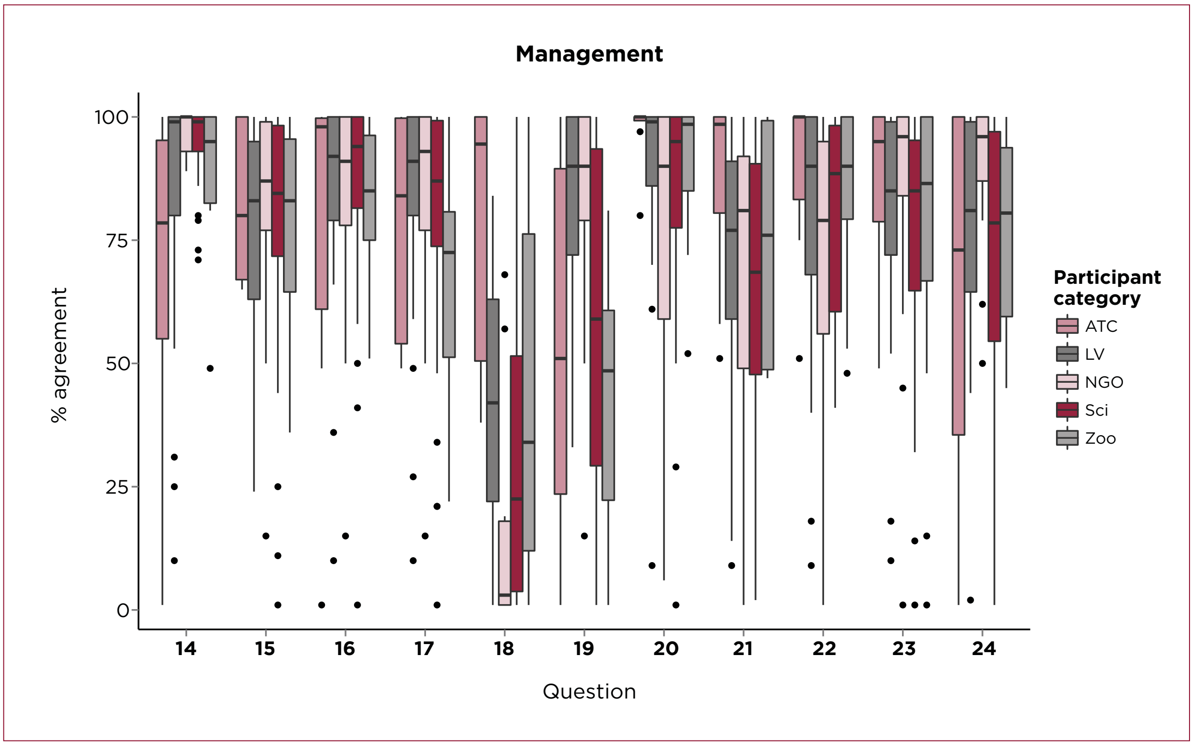
Responses to questions 1 to 8



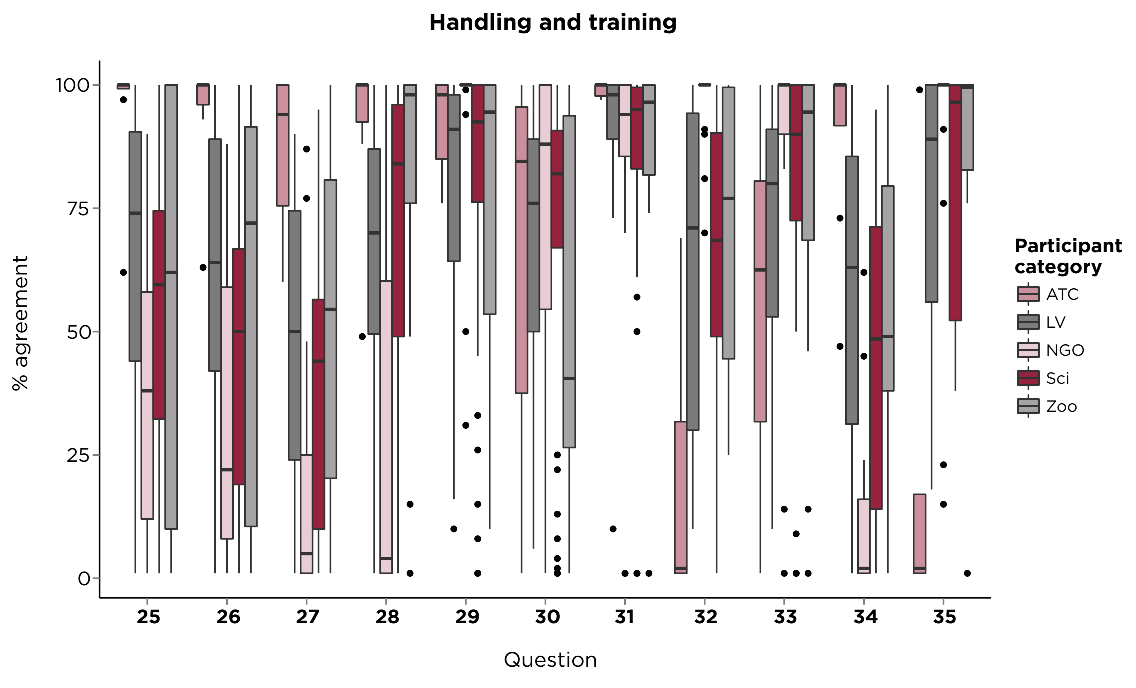
Responses to questions 9 to 13



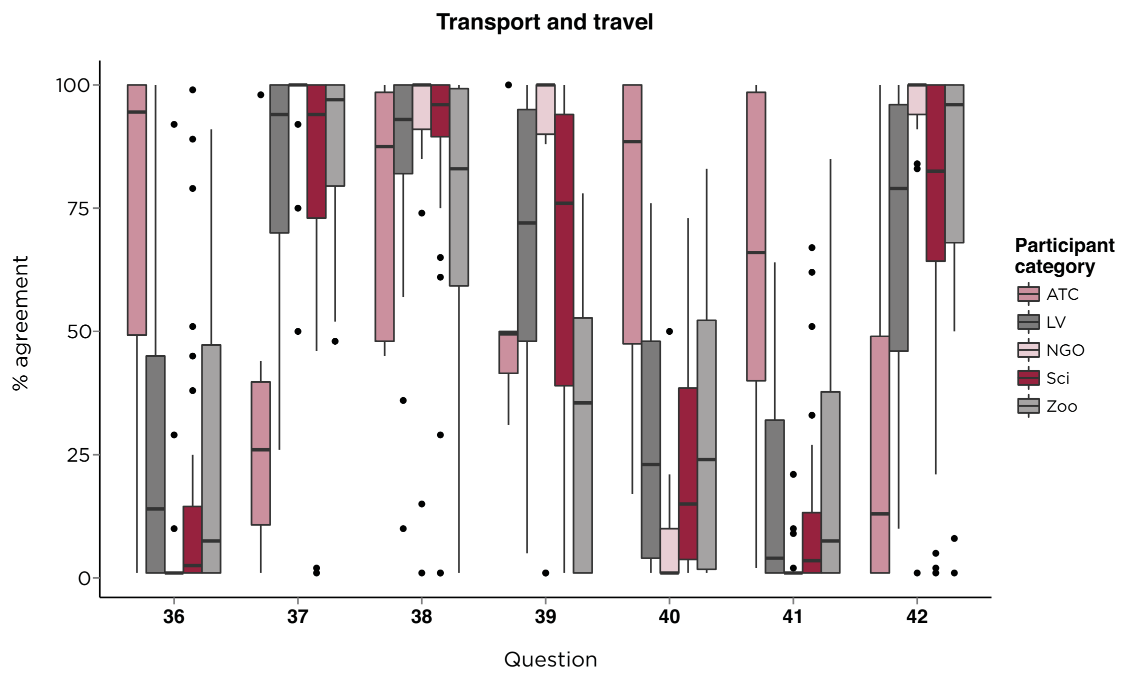
Responses to questions 14 to 24



Responses to questions 25 to 35



Responses to questions 36 to 42



Appendix 7

Review of the literature

Animal welfare – concepts and definitions

Different welfare scientists give greater or lesser importance to various aspects of welfare: some emphasise the biological functioning of the animal in terms of health, growth and reproduction; some emphasise the affective (emotional) state of the animal in terms of positive and negative experiences; and others emphasise the degree to which the animal is able to behave 'naturally'[1].

In the 'biological functioning' approach, welfare is considered to be compromised when normal biological functioning is impaired, as reflected by, for example, increased mortality or morbidity, reduced growth or reproduction, or behavioural abnormalities such as stereotypies (repetitive behaviour patterns with no obvious function) or self-inflicted injuries. With this approach, "The welfare of an individual animal is its state as regards its attempts to cope with its environment"[2].

While animals may grow, reproduce and appear healthy, they will have poor welfare if they experience subjective suffering such as prolonged frustration from having little space in which to move[3]. Negative emotional states, like frustration, may be reflected in behavioural and/or physiological changes, indicating that an animal is having difficulty coping. Some experts argue that this is not always the case and that the animal's feelings are what matter, irrespective of whether biological functioning is impaired. So "Welfare is not simply health, lack of stress or fitness and there will usually be a close relationship between welfare and each of these. However, there will also be enough exceptions to preclude equating welfare with any of them. Thus, neither health, nor lack of stress, nor fitness is necessary and/or sufficient to conclude that an animal has good welfare. Welfare is dependent on what animals feel"[4].

Yet focusing exclusively on feelings may also be problematic. Things that make animals feel good in the short term may ultimately compromise their welfare if, for example, they have a negative impact on health, and *vice versa*. This can be addressed by combining both the 'biological functioning' and 'affective state' approaches into a succinct definition of animal welfare; thus welfare is good when an animal is "fit and happy" (or "fit and feeling good" for anyone uncomfortable with the word 'happy')[5].

Welfare can be defined as the balance between positive and negative experiences or transient affective states[6] and assessed by asking two fundamental questions: "Are the animals healthy?" and "Do the animals have what they want?"[7]. The question then arises of how we know what animals want. Some welfare scientists consider that providing animals with an environment similar to that in which their wild ancestors lived is necessary for good welfare and that animal welfare is likely to be compromised if the conditions in which animals are kept are substantially different from the conditions in which they evolved i.e. animals have a right "to live their lives in accordance with the physical, behavioural, and psychological interests that have been programmed into them in the course of their evolutionary development and that constitute their telos (i.e. intrinsic nature)" and "to be responsible guardians of animals, we must look to biology and ethology to help us arrive at an understanding of these needs"[8]. This is likely to be particularly important for wild animals held in captivity.

However, 'naturalness' is no guarantee of good welfare. Being chased by a predator may be 'natural' but it does not necessarily follow that it is necessary for good welfare. "It is not the 'naturalness' of the behaviour that should be our criterion for whether an animal suffers but what the animal's own behaviour has shown us it finds reinforcing (i.e. the animal will work to obtain or avoid it) or not"[9]. So scientific methods have been developed that allow researchers to 'ask' animals which conditions they prefer when given a choice and how much they are motivated (in terms of how hard they are willing to work) to obtain or avoid particular conditions or resources[9].

Assessing animal welfare

An enquiry into the welfare of animals kept under intensive livestock husbandry systems in 1965 concluded that animals should have the freedom "to stand up, lie down, turn around, groom themselves and stretch their limbs"[10]. This list was subsequently developed by the then Farm Animal Welfare Council, the British Government's advisory body on farm animal welfare, into the 'Five Freedoms'[11]:-

- Freedom from hunger and thirst (by ready access to fresh water and a diet to maintain full health and vigour);
- Freedom from discomfort (by providing an appropriate environment including shelter and a comfortable resting area);
- Freedom from pain, injury and disease (by prevention or rapid diagnosis and treatment);

- Freedom to express normal behaviour (by providing sufficient space, proper facilities and company of the animal's own kind);
- Freedom from fear and distress (by ensuring conditions and treatment which avoid mental suffering).

The 'Five Freedoms' are widely used internationally as a framework for animal welfare assessment, legislation and assurance standards. They describe aspects of an animal's welfare state (e.g. freedom from discomfort) and the 'inputs' (e.g. a comfortable resting area) considered necessary to achieve this state. More recently, scientists have started to develop welfare assessment criteria based on direct measurements of the 'outcomes' for the animals, such as levels of injuries and expression of various behaviours. For example, this approach was used as far as possible in the European 'Welfare Quality' project (2004-2009) which assessed cattle, pig and poultry welfare according to four 'Welfare Principles' and twelve 'Welfare Criteria', defined as follows[12]:-

- **Good feeding**
  1 Absence of prolonged hunger
  2 Absence of prolonged thirst
- **Good housing**
  3 Comfort around resting
  4 Thermal comfort
  5 Ease of movement
- **Good health**
  6 Absence of injuries
  7 Absence of disease
  8 Absence of pain induced by management procedures
- **Appropriate behaviour**
  9 Expression of social behaviours
  10 Expression of other behaviours
  11 Good human-animal relationship
  12 Positive emotional state

Using outcome measures to assess welfare has a number of advantages. Measures such as body condition and chronic injuries can provide evidence of the long-term consequences of housing systems and husbandry practices, whereas input measures tend to give a 'snapshot' of conditions at a point in time e.g. during a welfare inspection visit, which is usually arranged in advance so conditions could potentially be altered, such as by providing additional bedding or enrichment material. However, there are also risks associated with relying on measuring welfare outcomes. Animals with the worst injuries or health problems may be culled, and so excluded from measurements, and behavioural problems may not be evident during the time animals are being observed, especially if measurements are taken over a short time frame, as is usually the case with welfare inspection visits.

The use of outcome measures avoids making *a priori* judgements regarding the welfare impact of any particular housing system or practice but this does not mean that the use of outcome measures removes the need to stipulate adequate input standards. Rather, the assessment of appropriate and validated welfare outcome measures should provide a powerful tool to evaluate housing systems and husbandry practices, and inform decisions as to which systems and practices are able to provide acceptable welfare standards. Welfare can be poor in any housing system if management practices are poor. However, systems vary in their potential to provide good welfare. Even if management is good, welfare is likely to be poor in barren, cramped conditions that severely limit opportunities to perform highly motivated behaviours.

It is also important to consider welfare over the whole life of an animal. The Farm Animal Welfare Council proposed that the welfare of animals should be considered in terms of an animal's quality of life over its lifetime, including the manner of its death[13], and that this quality of life can be classified as:-

- A 'life not worth living';
- A 'life worth living';
- A 'good life'.

This approach gives greater emphasis to the importance of positive experiences to animal welfare and reflects an ongoing shift in animal welfare science towards attempts to incorporate positive aspects of welfare into welfare assessment. However, welfare is a property of individual animals, and while it is possible to make general observations about what would constitute good welfare for a particular species, implementation of measures to ensure good welfare should be tailored to the needs of individual animals.

To determine whether the welfare requirements of captive wild animals can be fulfilled by circuses and mobile zoos, we conducted a comprehensive review of the scientific literature on the welfare impacts of different aspects of captivity on wild animals. It is important to consider the impacts of all aspects of the captive environment in combination (i.e. visitors, space limitation, management), as well as assessing them individually[14] since absence of poor welfare in one aspect of living does not always equate to good welfare overall[15]. First we describe common indicators of welfare and then discuss evidence of the effects of different captive environments and aspects of management in nondomesticated animals. The limited scientific research done specifically in circuses and mobile zoos is supplemented with evidence from zoos and animals in the wild.

Indicators of welfare

The impacts of captive conditions and management practices on animal welfare can be measured behaviourally or physiologically. Behavioural stress indicators include increased vigilance, hiding, freezing, aggression and abnormal behaviour, or reduced activity, exploration, behavioural diversity or reproductive/maternal behaviour[16]. Physiological welfare indices include heart rate, hormonal activity, immune function and growth. These measures are used to make inferences about animal feelings and estimate how well animals have adapted to their environments and whether they are coping[17]. The strengths and limitations of some common welfare indicators referred to in this review are discussed below. Ideally a wide range of welfare indicators should be considered because different individuals cope using different methods and therefore respond to circumstances in different ways[2,18,19].

Normal behavioural repertoires and time budgets

'Natural' behaviour can be defined as "behaviour animals have a tendency to perform under natural conditions because these behaviours are pleasurable and because they promote biological functioning"[20]. Behavioural observations help identify imbalances in activity levels or abnormal patterns of behaviour and the degree of similarity between captive and wild animals' behavioural time budgets provides a good indication of welfare[21]. However, comparing wild and captive behaviour is far from perfect since animals need not perform the entire wild repertoire to have good welfare[21]. It is also important to consider individual behaviours in the context of the entire animal's interaction with its surroundings to prevent misinterpretation[22].

The notion of 'behavioural need' describes behaviour that is largely motivated by internal stimuli, such as sleeping, nesting or foraging, and behaviour that occurs in contexts that are inappropriate or unrelated to environmental stimuli often indicate frustration of a behavioural need[23]. Animals will work hard to gain opportunities to fulfil behavioural needs[24], e.g. to gain material for nest building[25]. Therefore welfare may be adversely affected if the environment does not allow animals to perform internally-driven behaviours once motivation rises above some threshold[23]. Though some behaviours are not necessary in captivity, their non-performance leaves a void in an animal's day that may lead to boredom or abnormal behaviour[21] and potentially physical or psychological suffering[24].

Naturalistic time budgets are highly species-specific. For instance, large felids spend most of their time resting in the wild and in captivity[26-31], so if a captive felid spent most of its time eating, this would signify a welfare issue. But if a captive elephant spends most of its time eating, this is a good sign, since feeding is its primary activity in the wild[32,33]. General activity levels are often used as a welfare indicator and the high levels of inactivity common in captive animals can be interpreted as a welfare problem[34]. However, different forms of inactivity can indicate affective state and inactivity such as basking may be a positive sign[34].

Some captive animals have very similar behavioural repertoires to their free-living counterparts, e.g. zebra[35] and rats and mice[36], but the needs of some species may be impossible to satisfy in captivity. For instance, birds that spend large amounts of time airborne such as albatrosses or swallows are likely to suffer if confined in cages[37]. Captive and wild coyotes had similar time budgets, but only captive coyotes exhibited stereotypic behaviour[38]. Similarly, most chimpanzees display behaviours seen in the wild but, unlike their wild counterparts, abnormal behaviour is endemic in the captive population[39]. Oncillas exhibit similar activity patterns to wild peers, but were more sedentary and exhibited stereotypic pacing[40]. So many captive animals retain the same behavioural repertoires as their wild counterparts but perform them to different extents.

Play

Play is repeated, incompletely functional behaviour differing from more serious versions structurally, contextually, or ontogenetically and can be categorised as social, object or locomotor play[41-43]. Play is energetically expensive so rarely occurs in unfavourable environmental conditions or animals with a negative affective state (see *Animal emotions and affective state* on page 78), so is a useful indicator of both the absence of bad welfare and the presence of good welfare[42,44]. Playing is a self-reinforcing pleasurable experience that rewards interaction with the environment, and is thought to help animals acquire information and develop skills and behavioural versatility to facilitate coping[42,44,45]. Social play also builds social competence and can enhance both current and future welfare of individuals[42,44] and, since play is socially contagious, it can also spread good, or bad, welfare in groups[42].

Play has been observed in some invertebrates[46], fish, possibly some amphibians and reptiles[47,48] and birds[45,49], but is most common in mammals[41,42,44,50,51]. Play is most often seen in juveniles due to its role in behavioural development[42,44,45,51,52], but in some species adults also play[44,51,53-55], suggesting that play also has immediate benefits such as gaining information about the environment, objects or conspecifics or reinforcing social relationships[42]. So play deprivation during the juvenile period due to inadequate housing or social environment[56] may impair an animal's social competence and coping ability as an adult[44], and play deprivation during adulthood denies animals of pleasurable experiences and the opportunity to gain information, which may compromise psychological welfare[42].

Coping behaviour

Animals exhibit coping behaviour in response to aversive situations[57], and this can be used to indicate stress and welfare. Coping strategies are used interchangeably and include escape[58,59] or attack[60] for aversive stimuli, and appetitive searching (i.e. locomotion and exploration) for absent desirable stimuli [61-63]. If none of escape, attack or searching works, animals may simply 'wait' for a spontaneous change in the aversive situation, i.e. hypoactivity or lethargy[57,61]. In unsuitable environments poor welfare results from animals struggling or failing to cope[64]. Prolonged 'waiting' may develop into apathy or learned helplessness and repeated appetitive searching and displacement behaviour is associated with the development of stereotypic behaviour[57,65].

Physiological stress responses

Most animal welfare studies use cortisol to measure stress. The pituitary releases adrenocorticotrophic hormone (ACTH) in response to short term acute stressors, which stimulates the adrenal gland to secrete glucocorticoid hormones (GCs)[16]. GCs prompt changes in metabolism and redirect resources away from non-essential biological functions such as growth or reproduction in preparation for fight or flight [25,66]. GCs interact with virtually all biological processes, including the metabolic, neurological, cardiorespiratory, immune, digestive and reproductive systems, and ultimately influence health, fitness and survival[67,68]. GCs are usually sampled from blood, saliva, urine or faeces, and glucocorticoids in feathers[69] and hair[70,71] can be used to measure long term variation in adrenocortical activity.

Differences in rates of steroid biosynthesis may lead to different conclusions being drawn, depending on the substrate used and the stage of the stress response that samples are collected[72-74].

The extent and duration of a rise in GCs is a useful measure of stress in response to adverse events, and circulating GCs may be elevated for longer in stressed animals that have difficulty coping[72]. Baseline GCs are also used to infer overall stress levels, although baseline GC concentration is not an ideal welfare indicator because it can increase or decrease with poor welfare[75,76]. For instance, one experiment with wolves showed no correlation between behavioural responses to enrichment and faecal glucocorticoid metabolite concentrations (FGMs)[77], whereas a different study on wolves found a positive correlation between FGMs and pacing[78]. Another wolf study found no correlation between FGMs and heterophil to lymphocyte ratio, indicative of immune function, which is suppressed by stress[79]. Baseline FGMs can also vary between individuals under the same conditions[77].

Acute stress is adaptive and allows animals to avoid danger or harm[25], but relentless exposure to repeated stressors leads to chronic stress, and prolonged elevation of GCs can lead to long-term problems including suppressed growth and immune function[25,68,80], reproductive acyclicity or reduced fertility[68,81-83], and impaired maternal behaviour[16]. To reduce these damaging effects, chronic stress can suppress GC production[84]. Therefore an uncharacteristically low stress response may not indicate lack of stress but a reduced ability to respond to stress[77,79,85,86]. Instability in hormone levels may be a better indicator of chronic stress[78,82,87].

Aversive situations may only trigger a stress response if they are perceived as aversive[88] and this depends on the individual[74,89-92], their species[17,93,94], sex[95-99], dominance status[71,100,101], physical condition[102-104], developmental stage[104,105] and personality[100,106-111], as well as the context of the stressor[100,112]. Seasonal differences have been reported in adrenal activity and usually correlate with reproductive status[72,99,103,113,114] but may be related to seasonal differences in captive management[115]. Circadian variation in GCs is also reported[116].

This multitude of influencing factors severely complicate the interpretation of GC levels, so while we cite a number of studies that used GCs as measures of stress, these should be interpreted with caution and ideally alongside behavioural indicators to determine how severely the stressor disrupts normal functioning[75,88,117,118].

Abnormal and stereotypic behaviour

Stereotypies have been defined as repetitive, invariant behaviour patterns with no obvious goal or function that seem to arise in response to sub-optimal environmental conditions or unavoidable stress[119,120]. Stereotypies are common in captivity but not seen in undisturbed free-living wild animals, although they occasionally occur in animals in tourist areas[121]. While they have no obvious goal, their persistence implies they serve some function for the animal[122]. They are thought to facilitate coping, as in several species they have been associated with a fall in GCs and a reduction in behaviour associated with distress, anxiety or aggression[120].

Proximate causes of stereotypic behaviour involve the frustration of specific highly-motivated behaviour patterns[123], along with perseveration (a tendency to repeat actions inappropriately), which may be associated with central nervous system (CNS) malfunction[124,125]. The characteristics of stereotypic movements are different from natural goal-directed behaviours, and seem to allow an animal to disengage from their environment[126] and lower their awareness of external events[120]. This may explain why animals that perform stereotypies have a reduced ability to adapt their behaviour to a change in circumstances[126].

Where data exist, most situations that cause/increase stereotypies also decrease welfare[127], so stereotypies are useful to help identify poor welfare conditions[128], though not necessarily to identify the individuals that are suffering the most. In a suboptimal environment, animals that perform fewer or no stereotypies may actually be faring worse than those that perform more, since the act of performing stereotypic behaviour can itself be soothing and help to reduce stress[127,129,130]. However, injurious stereotypies such as self-mutilation are unlikely to facilitate coping[131].

Common stereotypies include pacing[63,126,132-134], swaying[135-137], head bobbing[138-140], overgrooming[141-143], feather pecking[144,145], regurgitation and reingestion[122,146,147], self-mutilation[131,143,148] and pattern swimming[149,150]. Some behaviour may not fit the description of stereotypical but is considered abnormal, e.g. hyperactivity or interaction with transparent boundaries in reptiles[61] or flashing in fish[151].

Stereotypies are a major problem in captive animals and are performed for a significant part of the day, which suggests many captive environments are suboptimal. In a survey of 257 captive giraffe and okapi, 80% showed stereotypic behaviour, most commonly licking or pacing[152]. In a study of 55 polar bears, 51 displayed stereotypic pacing[153] for up to 14% of the day[154]. In farmed mink, all females developed stereotypies before seven months of age, regardless of social environment, weaning age or housing[155]. Stereotypies were exhibited during 14% (range 6-21%) of the day in zoo wombats[133], 17.8% (range 0.5-88%) of observation time in zoo bears in Poland[156], 18% (range 0-51%) in zoo bears in Thailand[126], and 23% in zoo tigers[157].

Circus animals often exhibit higher rates of stereotypy than conspecifics in other captive environments. Stereotypic behaviour occurred in 60% of zoo elephants[16], but in several studies of circus elephants, all individuals exhibited some form of stereotypic behaviour for up to 46% of the time[26,137,158-161]. Primates from circuses and mobile zoos exhibited higher levels of stereotypic behaviour than animals reared in fixed-site zoos[162,163]. The high levels of stereotypy seen in circus animals have even been misinterpreted by some staff members as normal behaviour[164].

Pacing may indicate a frustrated motivation for travel, exploration or mate searching[132]. Carnivore stereotypies are primarily predicted by daily travel distances rather than foraging or overall activity levels[165,166]. In several species males hold larger home ranges than females, and may experience an unfulfilled motivation to travel or explore when confined to small or simplistic environments. There is evidence for this in okapi and wombats, where males pace more than females[133,134]. Stereotypic behaviour may also be anticipatory, e.g. circus elephants[160] and tigers[167]. Stereotypy in elephants has also been associated with locomotor opportunities[160,168] and social deprivation[140]. Rocking and self-sucking were more common in hand-reared chimpanzees, suggestive of frustrated suckling and comfort from their mother[169]. Self-directed stereotypies may stem from the desire for control, since in captivity an animal's own body and its products are among the few things it can autonomously manipulate and control, and are a source of stimulation in deprived environments[170]. Captivity itself may be the fundamental causal factor, e.g. characteristics of abnormal behaviours seen in chimpanzees are suggestive of compromised mental health[39,171].

Many stereotypies are food-motivated, since foraging is essential for survival and thus a highly motivated behaviour among all animals. Free-ranging animals spend a significant part of their day locating, acquiring and processing food, e.g. 90% of the daytime in coatis[172], whereas foraging behaviour is largely redundant in captivity. Pre-feeding stereotypies are anticipatory, e.g. pre-feeding pacing in an American black bear was motivated by frustrated foraging, since food-hiding enrichment eliminated this behaviour[132], and elephants' stereotypy increased in the lead up to feeding[159,173] and after depletion of foraging material[174]. Big cats also paced more prior to feeding[175]. Post-feeding oral stereotypies such as regurgitation and reingestion may indicate lack of satiation[122,146,176], and frequent regurgitation of stomach acid may cause clinical problems[147]. Oral stereotypies are commonly related to food type or presentation method in species that manipulate food orally, e.g. stereotypic licking in giraffe and okapi[152,177].

Some species are more prone to developing stereotypies. In a review of 21 publications, felids, giraffes and seals spent the highest percentages of their time performing stereotypical behaviour[178]. Sometimes even closely-related taxa differ in their ability to cope with captivity, e.g. Bengal tigers paced less than Siberian tigers[28]. Prosimian monkeys were most likely to exhibit stereotypic behaviour if they belonged to the genera *Microcebus* and *Varecia*[142], and brown bears stereotyped more than Asiatic black bears[156].

Some individuals cope better than others in captivity. Considerable individual variation in the characteristics and frequencies of stereotypical behaviour have been observed in a number of species, which precludes the identification of trends[143] e.g. elephants[161,179-181], polar bears[182], sea lions[183] and wombats[184]. Sometimes individual differences in stereotypies are related to personality[154,181,185]. Sex differences in stereotypies may reflect differences in life history and thus different frustrations, e.g. elephants[186], macaques[135,185] and sloth bears[187].

Stereotypic behaviour is widespread among captive animals and a useful indicator of suboptimal environments. Animals may develop stereotypies in response to a variety of frustrated behaviours or environmental inadequacies. Stereotypies may facilitate coping and once established these behaviour patterns can be difficult to stop.

Psychological wellbeing

What is psychological wellbeing?

Good welfare depends on both physical and psychological wellbeing[188]. While psychological *health* is characterised by adequate adaptation to the environment and an absence of mental disorders, psychological *wellbeing* encompasses positive experiences, happiness and contentment[189] *coupled with* the absence of negative experiences[190]. Some authors believe that welfare in sentient animals depends exclusively on cognitive needs, since animals 'know what they need' and, if these needs are fulfilled, then so too will the animals' physical needs[191].

Animal emotions and affective state

Psychological state, or affect, describes an individual's subjective experience or emotion[192]. There is widespread evidence that both vertebrates and some invertebrates can experience emotions of varying complexity[193,194] from pain[195-199] to empathy[194,200,201]. Emotions such as pleasure and pain are adaptive products of evolution that guide sentient animals toward and away from positive and negative experiences that may influence survival[36].

Positive emotional experiences such as pleasure are reinforcing and contribute to positive affect. Positive emotions are more difficult to assess behaviourally and physiologically compared to negative emotions[108], but there is evidence that animals experience pleasure during play, nursing and feeding, maternal care, sexual activity, socialisation, touch and comfort through exploring and interacting with their environments and conspecifics[36,193,202]. As positive emotions are important for animal welfare, restrictive captive environments that deny animals the freedom to access these experiences will impair their quality of life[36]. Emotional contagion has also been reported in a variety of captive animals, whereby a fearful, or playful, animal can influence the emotions of their conspecifics, and such empathy has implications for animal welfare in socially-housed species[194].

Negative experiences are aversive and can manifest as fear, aggression, or even physical symptoms, e.g. psycho-physiological disorders in cetaceans[203]. Negative emotions following traumatic experiences in exceptionally intelligent species such as chimpanzees and elephants[204] may result in psychiatric disorders, e.g. depression and post-traumatic stress disorder (PTSD)[205-207]. Chronic psychiatric disorders may not be detectable in physiological measures of stress[76]. Pain is the sensory and emotional experience of actual or potential tissue damage[208]. Different species and individuals have different pain tolerance thresholds and therefore express external signs of pain at different stages of severity. Prey species such as bovines and cervids may have particularly high pain tolerance thresholds, below which symptoms are subtle, e.g. changes in eye expression or activity patterns[192,195].

Engaging in certain activities such as play or affiliative behaviour indicates a positive affect and happiness in animals, at least in that moment[190], but if these behaviours are only displayed infrequently the positive emotional state may only be brief[209]. Likewise, momentary resistance to handling may indicate a brief negative state. There are multiple good and bad moments in an animal's day which promote positive and negative affective states, and it is important to examine the balance between these over time to determine their overall psychological welfare[189,202,209]. For instance farmed game will experience pain and distress at slaughter, but may still have a 'life worth living' if they experience significant pleasure and limited pain throughout their life up to that point[210]. Circuses are a sink for unwanted zoo animals, particularly males, which are often more spectacular in appearance than females, that would otherwise be euthanased[26]. But the mere fact that these animals are allowed to live is not sufficient evidence of a life worth living. Captive animals can only have a life worth living when positive experiences outweigh the negative ones for the major part of their life.

Anticipatory behaviour and sensitivity to reward

Mental stimulation is emotionally rewarding and many animals are motivated to seek complex environments and novel stimuli, and acquire information[189]. Several experimental studies have used preference tests to show that animals will exert greater effort to obtain more valuable rewards, and that the perceived reward value depends on the animal's affective state[36,108,211]. Long-term unstimulated animals experience boredom, indicated by heightened responses to rewards, e.g. mink in unenriched cages showed more interest to novel stimuli or rewards than mink in enriched cages[212].

Anticipatory behaviour is a goal-directed increase in activity and alertness in the appetitive phase prior to an expected reward, such as food or mating opportunities, and commonly develops in captive environments with predictable schedules[209]. Anticipatory behaviour is a real-time indicator of an animal's perception of an event, and thus its affective state in that moment[209]. Anticipation stimulates the release of the neurotransmitter dopamine, which reinforces anticipatory behaviour prior to positive events, but sensitivity to dopamine is influenced by the animal's needs and past experiences[213], e.g. hungry or under-stimulated animals may respond more strongly to food or enrichment[190]. Therefore the intensity of anticipatory behaviour reflects the perceived importance of the event, and rare positive events will elicit higher intensity anticipatory behaviour in animals that experience a lower ratio of positive: negative events, and have consequently become more sensitive to reward[209].

Many captive animals show anticipatory behaviour prior to feeding, training or gaining access to outdoor space because these are rare positive events[25,133,134,136,150,159,174,214-221]. Anticipatory behaviour is also shown prior to expected aversive events, but may involve a different pattern, posture or location, e.g. pacing at the back of the cage instead of the front[218].

Housing and husbandry

Enclosure size

Captive wild animals are frequently housed in enclosures that constitute a minute fraction of their natural home ranges[165]. Minimum recommended enclosure sizes for animals in circuses are on average 26.3% of the recommended enclosure size for animals in zoos[222], which are themselves 100 times smaller than their minimum home range in the wild[223]. Over the last two centuries there has been a trend for zoos to move away from close confinement towards larger, more open spaces, and a greater emphasis has been placed on a species' needs rather than tolerances[224]. However, circuses have to compromise between maximising cage size and portability[179]. Enclosure sizes are typically much smaller in circuses than in other captive environments such as zoos[222] because circuses are limited in their ability to provide animals with extra space, and animals housed in larger enclosures may be more difficult to handle and/or show greater fear of humans[225,226], which is incompatible with the use of animals in public displays.

Space limitation is the most important inducer of stereotypic behaviour in wide-ranging carnivores[165,166]. A review found that stereotypic pacing is also positively correlated with natural day journey length in primates[227]. Several zoo-based studies have reported that wide-ranging species move more, pace less and/or generally show more naturalistic behaviour and are less stressed in larger enclosures[28,214,228-231].

Wide-ranging species, particularly lions and tigers, are among the most common species in European circuses[232]. However, they are often housed in cages with between 2.2 and 24.4 m^2 floor space[167,233], occasionally with additional access to an exercise pen up to 10 m in diameter on a rotational basis with conspecifics[180]. Under the Welfare of Wild Animals in Travelling Circuses (England) Regulations 2012, the minimum indoor space requirement is 12 m^2 per big cat, and outdoors 50 m^2 for up to two cats, with an extra 25 m^2 per additional animal[234]. Circus tigers spent less time pacing in exercise pens than inside cages on transport vehicles (beast wagons)[26]. Yet the effect of limited access (40 minutes) to an exercise pen on total time spent pacing seemed to depend on distance travelled (i.e. number of paces taken) while in the pen[179]. Wild tigers have large home ranges[166,235,236] but tend to be active in short bursts[237]. In larger zoo enclosures some tigers covered similar distances to their wild counterparts[231]. For circus tigers, short periods of access to a small pen may not allow (or motivate) them to cover sufficient distances to satisfy their behavioural needs. When given longer access to an exercise pen, circus tigers spent 40% of their time in the pen in the day and 29% in the night, and spent most of this time lying down[180]. The distance travelled and whether extended access to the pen reduced the total time spent pacing were not recorded, but half the tigers spent more than 10% of their time pacing and one individual up to 77.5%. Since performing stereotypies for more than 10% of an animal's waking life has been suggested as a baseline measure that its welfare has been unacceptably compromised[238], the welfare of circus tigers appears to be compromised even with almost unlimited access to an exercise pen.

Space is also important for other species. Pregnancy loss was lower in macaques housed in larger cages[239]. Female zoo elephants walked more in larger enclosures[240]. Black rhinos housed in larger enclosures had more births[241]. Male dromedaries exhibited less frequent stereotypical behaviour when allowed an hour of access to a paddock compared to when they were confined to single stalls all day[242]. Larger enclosures were associated with lower levels of stereotypical behaviour in zoo bears[156,243], cheetahs[244], giraffes and okapi[134,152], mink[155] and red deer[245], and reduced FGMs in zoo-housed armadillos[246]. Elephants with more outdoor space spent less time performing stereotypic behaviour[217,247] and had lower FGMs[248]. Dominant zoo elephants used a greater percentage of available space than subordinates, suggesting that larger spaces allow more natural social functioning[249], and translocated wild elephants chose large over small paddocks[250].

Reptiles are often considered sedentary but still require space: home ranges of skinks are approximately 1 ha, box turtles 40 ha and indigo snakes 158 ha, and arboreal monitors may travel more than 180 metres in a day[251]. Greater space can enhance physical health: lizards are prone to obesity in captivity[252] and may become overweight due to lack of exercise in small enclosures[253]. Smaller reptile enclosures are cheaper to maintain and more easily transported, but space limitation can lead to obesity, increased parasitic load and skin abrasions from stereotypical behaviour[252].

Captive animals are usually confined to indoor enclosures at night and for nocturnal or crepuscular species this severely restricts activity and impacts on their welfare. Three zoo elephants engaged in different behaviours including foraging and socialising throughout the 24 hour period[254] and were most active between 18:00 and 24:00 and 06:00 and 07:00[255], suggesting that nocturnal restraint or confinement is a major limitation on opportunities for activity. This is supported by increased stereotypy prior to being moved inside in the evening[136,174] and during winter when more time is spent indoors[173]. Bears exhibited more stereotypical behaviour if kept indoors at night[243]. Circus tigers paced twice as much (in an exercise pen) at night (19.6%) as in the day (10% day)[180], and felids in general appear to pace more at night[180,256,257]. This may stem from a frustrated motivation to travel since wild tigers are most active at dawn, dusk and night[235,258,259], Leopards are slightly more diurnal than tigers but are still crepuscular and active at night[216,259].

Vertical space

Vertical space may be just as, if not more, important than floor area for species that climb[260-267]. In two-tiered cages, the lower level is often darker[268], but rhesus and long-tailed macaques still preferred the top tier of their cage after light levels were reversed so that lighting conditions became more desirable in the bottom tier; this suggests that cage preference was due to elevation rather than lighting conditions[263]. However, elevation alone may not ensure good welfare, since rhesus macaque behaviour was the same regardless of cage tier[268]. For zoo-housed clouded leopards, FGMs were not affected by enclosure size but were significantly lower in enclosures with more accessible vertical space[107], suggesting that enclosure height has a greater impact on their welfare than floor area. There are features of some species' natural habitat that seem essential for their well-being in captivity. Adding wooden branches to cages increased activity levels, reduced aggression and eliminated stereotypic behaviour in marmosets[225]. Free-living urban marmosets use artificial structures for travelling but always rested in trees[266].

Restraint

Restraint is stressful in both domestic[129,270] and nondomestic animals[271,272]. Pythons restrained in a PVC tube had higher plasma corticosterone levels than those restrained manually, probably due to the substantial force required to extract the animal from the tube[273]. Young birds of prey unaccustomed to tethering may suffer tibiotarsal fractures if they try to fly[274]. Shackling and tethering severely restricts movement[26,275,276] and limits comfort, opportunities for exercise and environmental hygiene. This may affect physical condition, since standing on unclean ground[277,278] and lack of exercise[269] both impair foot health in elephants. Chaining and shackling elephants is associated with pale mucous membranes indicative of compromised health[279]. Camels are obligate nasal breathers so a poorly fitting nose piece on a halter may cause suffocation if it slips when the camel pulls back[280].

Restraint limits opportunities to perform species-typical behaviours such as socialising[158], which will impact psychological welfare. Elephants always associated with a wider variety of social partners in paddocks than when shackled[158], suggesting they suffered social deprivation when restrained. Paddocks were also associated with increased comfort behaviour (grooming, bathing) and play[158] and eating[278] in elephants. The behavioural and social limitations imposed by close confinement clearly affect welfare because all circus elephants perform more abnormal behaviour when shacked than when loose[160,278,281]. However two-thirds of elephants still exhibited stereotypic behaviour when unshackled[160,278], suggesting that lack of restraint is not sufficient to prevent abnormal behaviour.

Lack of enclosure complexity

Most studies conclude that additional space is not sufficient to improve animal welfare by itself [31,282] e.g. primates[283,284], felids[31,84,214], elephants[285,286], okapi[134], coyotes[38] and bears[287]. This suggests that enclosure quality (complexity and suitability) is more important than size[31]. In leopard cats[256] and leopards[288], enhanced enclosure complexity (variety of structures, substrates and behavioural opportunities) may be an effective substitute for limited space, but studies on other species have found that increased enclosure quality has no effect without increased space. After translocation to smaller, barren enclosures, cage enrichment reduced the FGMs of oncillas but increased those of margays, suggesting that enrichment could not counterbalance the detrimental impact of space-restriction in margays[257]. Enrichment is not a substitute for poor enclosure design, and should be used in combination with appropriate enclosure size and furnishings[289].

Heterogeneous space use, i.e. concentrated activity in a small proportion of the space available, is an indicator of poor welfare and increasing enclosure complexity using structural enrichment may diversify space use[290]. Larger spaces typically provide more opportunities to increase complexity. Increased enclosure size coupled with increased complexity improves welfare, e.g. moving two baboons from a small unenriched cage to a large enriched enclosure reduced the frequency of stereotypic behaviour[291]; zoo pandas performed less stereotyped behaviour and played more in larger enclosures with a wider variety of terrain, substrates and vegetation types[292]; zoo-housed sun bears in barren, indoor enclosures performed stereotypical behaviour more frequently than conspecifics housed in larger, relatively enriched outdoor enclosures[287]; daily temporary relocation of zoo-housed chimpanzees from their main enclosure to a smaller, barren holding area elicited increased aggression and anxious self-directed behaviour[293]; relocating five laboratory-housed opossums from a barren cage to a larger, enriched pen eliminated stereotypical behaviour from all individuals and elicited natural behaviours not seen in the barren cage[294].

Adding structures such as logs, platforms and pools to enclosures increases environmental complexity and can improve animal welfare through providing shelter and behavioural choices. Geckos favoured areas of their enclosures that contained hides or furnishings such as logs[295]. Zoo-housed red foxes favoured areas of their enclosures containing structures (e.g. hides or hedges) over open space[296]. Zoo-housed lion-tailed macaques performed more autogrooming, foraging and social behaviours in areas of their enclosure enriched with trees, platforms or water bodies[265].

Enclosure substrate

Stakeholders identified enclosure substrate as the most important welfare concern for captive elephants[297]. Most zoos that house elephants have replaced concrete flooring with rubberized flooring and sand to reduce foot problems[298]. The installation of rubber flooring also increases diurnal locomotion and standing rest in zoo elephants[299,300]. Wild Asian elephants typically spend more time in standing sleep than laying down[301], so rubber flooring encouraged more natural sleeping positions. There was also a (non-significant) reduction in foot-lifting behaviour indicative of discomfort in the feet and joints, a common ailment in elephants housed on hard surfaces[299]. Circus elephants picketed on macadam performed more stereotypic behaviour than when penned on turf, but it is unclear whether this was due to a more appropriate substrate or the lack of restraint[160].

Zoo tigers had abrasions from laying down on concrete floors that were not seen on tigers housed on a natural substrate[28]. It may be important to provide a substrate that provides camouflage for prey species e.g. leopard cats preferred mulch over other substrates when hiding, which provided better camouflage[256]. Substrates that provide digging opportunities may improve the welfare of burrowing animals: deep substrates were associated with reduced FGMs, reduced stereotypy and increased exploratory behaviour in armadillos and hedgehogs in a petting zoo[246]. Dust-bathing is important for skin care and thought to provide protection from biting flies and ectoparasites, so loose substrates such as dirt and dust will allow elephants[160,202] and zebra[35] to exhibit this important comfort behaviour. Varied and suitable nest building materials for orangutans will benefit welfare because they promote species-typical behaviour and more comfortable nests promote better sleep[303].

Tigers in enclosures with vegetation and a natural substrate explored more and paced less[28]. By providing shade and cover, and possibly attracting birds and insects into the enclosure, vegetation may provide animals with more choices in their environment, which will improve their mental state and encourage more species-typical behaviours. Furnishing enclosures more appropriately and encouraging natural behaviour improves animal welfare and increases their educational value for visitors[304].

Lighting conditions

Captive animals often live under unnatural light conditions: different species may adjust to human schedules by becoming more diurnal or may be kept under artificial rather than natural light. Housing animals under inappropriate lighting may be detrimental to their welfare. In laboratory-housed marmosets, light levels below 200 lux during the light phase were associated with increased FGMs and reduced autogrooming[305]. Iguanas were vitamin D deficient without sufficient exposure to natural sunlight[306] and geckos oriented towards natural sunlight when given the opportunity[295]. Insufficient exposure to UV-B radiation can lead to nutritional secondary hyperparathyroidism in reptiles[307].

Birds rely on vision for foraging, nesting and mate selection: ultraviolet light is used in normal avian colour perception and lighting conditions may affect their welfare. Domestic chickens reared under UV-deficient light had consistently higher basal plasma GCs and showed a nonsignificant trend for less exploratory behaviour than chicks reared under full-spectrum lights[308]. A similar pattern was seen in European starlings[309], and a preference test with 17 species of zoo-housed birds showed that their choice of UV-light conditions depended on their natural habitats[310]. Some birds can also detect flicker in artificial lights: starlings kept under low light flicker frequency (LF) showed increased involuntary muscle spasms, increased preening, reduced eating and lower basal GC levels, all indicative of chronic stress[311]. Starlings favoured high flicker frequency over LF light[312] and female starlings show inconsistent mate choice under LF light[313]. Wild birds exposed to light at night also develop their reproductive system earlier and moult earlier[314]. Lighting conditions influence many aspects of bird physiology and behaviour, and consequently welfare.

In laboratory-housed marmosets, light levels below 200 lux during the light phase were associated with increased FGMs and reduced autogrooming, suggesting that light intensity affects their welfare[305]. Sea lions are adapted to low light conditions, so in circuses they are at risk of eye problems, such as corneal disease and cataracts, due to overexposure to UV light as a result of insufficient absorption of UV-radiation in light-coloured pools with shallow, clear water and a lack of shade[315].

Forcing animals to follow human daily rhythms may have a detrimental impact on nocturnal animals adapted to low light conditions, e.g. owls should not be flown in the brightest part of the day[275]. Indoor-housed koalas with no access to natural sunlight showed unstructured activity patterns atypical of their wild counterparts[316]. Nocturnal marsupials may suffer in European institutions because seasonal variation in day length is wider in Europe than in Australia and the shorter summer nights interfere with natural rhythms and allow less time for activity such as foraging[316].

Temperature conditions

Some circuses and travelling animal shows exhibit animals that have evolved to survive in different, often highly specific climates. Reptiles are ectothermic (i.e. rely on the eternal environment to regulate their internal body temperature) and will select microenvironments where they can gain or lose heat to maintain their temperature[317]. So thermal gradients in enclosures are important because they add choice of microclimate for reptiles[295]. Temperature requirements of different species of reptile vary considerably and may even fluctuate in the same species at different times of the year[317]. If reptiles are kept in temperatures that are too warm or too cold, this places stress on their immune system and can lead to problems such as dehydration[317].

Temperature can also be important for homeotherms, since many have specific temperature requirements. Mammals with a low metabolic rate struggle to thermoregulate at extreme temperatures, e.g. marsupials[318] and kinkajous[319]. On cold days giraffe showed more stereotypical behaviour and were less attentive during training[320]. Temperature was positively correlated with self-directed behaviour (scratching and biting) in squirrel monkeys[321].

Duikers are sensitive to climatic conditions and a heated shelter reduced infant mortality from hypothermia and maternal neglect[322]. While tolerance of suboptimal temperature and humidity may vary with species, inappropriate conditions that fail to meet the needs of individual species contribute to health and welfare problems in primates[323]. Dromedaries are sensitive to cold and humidity[324]. A speckled bear's stereotypic behaviour increased, and resting decreased, at temperature extremes (below 5°C or above 17°C), probably due to an absence of resting sites with appropriate thermal properties[62]. Thus a choice of resting sites is important for both heterotherms and homeotherms to thermoregulate.

In temperate countries the upper critical temperature of polar bears and the thermal neutral zone of sun bears may be exceeded throughout most of the year[325]. In these bears, thermoregulation behaviours such as changes in activity, posture and substrate preference appear prior to panting and heat dissipation[325], suggesting that thermal discomfort may not be easy to recognise outside temperature extremes. Different surfaces have different thermal inertia, and unsuitable substrates can impair thermoregulation[25]. Substrate preferences in polar and sun bears depended on ambient temperature[325], and the limited range of substrates available in semi- or non-permanent enclosures may limit the thermoregulatory abilities of some species and lead to thermal stress.

Elephants are temperature-sensitive: they cannot sweat, and regulate their body temperature by storing heat during the day and cooling during the night[326]. Female zoo elephants walked more as temperature increased[240]. Elephants also spent an increasing amount of time dust bathing once maximum daily temperature exceeded 13°C, below which dusting was rarely observed[302]. Dust bathing may have a role in maintaining social cohesion as well as skin care; so cool conditions may impair normal social and comfort behaviours. Asian elephants also performed more stereotypical behaviour in cold weather, possibly due to increased hunger and/or the inability to return to indoor accommodation[186], although another study found no temperature effect[286]. Wild African elephants select landscapes based on ambient temperature stability i.e. areas where temperature changed more slowly[327]. Not having the freedom of choice when held under close confinement may impair elephants' ability to thermoregulate and so have welfare consequences. Equally, the sensitivity of elephants to cold requires captive animals to be confined in heated barns during the colder months, which itself can contribute to poor welfare[328,329].

Tigers evolved in temperate climates with cold winters, whereas lions live in hotter climates, and so zoo tigers displayed more cooling behaviours than lions on warm days[330] and spent 90% of their time in shaded areas[28]. This suggests it is important to provide tigers with sufficient shade to help them to thermoregulate. The need for shade is also often overlooked in bear enclosures[331]. Some circuses have air conditioning[167] and circus transporters may provide shade at certain times of day, but unshaded exercise pens may be undesirable for temperate species such as tigers, particularly on hot days, and limit their motivation to use them.

Environmental enrichment

Environmental enrichment can be broadly defined as "an improvement in the biological functioning of captive animals resulting from modifications to their environment"[332]. Enrichment is used to increase environmental complexity, expand behavioural choices and/or encourage species-appropriate behaviour, with the aim of reducing stress and improving welfare. A better outcome is an animal with "improved animal health, increased lifetime reproductive success or increased inclusive fitness"[332] and/or a behavioural time budget that approximates that of their wild conspecifics[333]. Enrichment is common in zoos: 95% of the institutions accredited with the Association of Zoos and Aquariums had a structured enrichment program for elephants[269]. Some circuses do not use enrichment[160] and in those that do, objects may not be provided to animals when they are unsupervised in case they are used to aid escape[334].

Enrichment may be social (biologically appropriate social groupings), structural (platforms, climbing apparatus), sensory (sound, scent), cognitive (problem solving, training), food-based (hidden food, foraging tasks) or involve novel objects. Enrichment techniques in zoos usually involve either increasing the animal's control, cognitive challenge, fulfilling behavioural needs, facilitating socialisation or rewarding exploration with the acquisition of new, and useful, information[335]. Besides improving welfare, enrichment may also help conserve the natural behaviour and cognitive abilities of animals destined for reintroduction and aid subsequent survival[336]. However, environmental enrichment studies have focussed on a limited range of species: of 744 papers, over 90% were on mammals (mostly rodents and primates), 8.2% on birds and <1% on reptiles, amphibians, fish and invertebrates[337]. The need for complexity is based on the fact that animals experience consciousness and therefore pain and suffering. This is widely recognised in mammals and birds, but an awareness of pain and emotion has been deemed implausible for animals such as fish and invertebrates that lack a neocortex, the brain region necessary for consciousness[338]. However several studies of various aquatic animals contradict this theory and report physiological and behavioural responses (beyond reflexive withdrawal) to noxious stimuli such as capture, restraint, electric shocks and social stress from the presence of dominant conspecifics[197,198]. Even more primitive animals seem capable of experiencing suffering in an unsuitable environment, so it is important to consider the consequences of captivity for the welfare of all species.

The 'success' of enrichment is mainly evaluated using the extent or nature of behavioural changes or behavioural tests (54% studies) and fewer than 3% of enrichment studies have used a combination of behaviour and physiology[337]. While 65% of studies reported that enrichment improved animal welfare, this should be interpreted with caution. Most zoo studies involve fewer than six experimental animals, which is widely considered to be the minimum sample size to generate a statistically significant result and account for individual differences[337]. Additionally, experimental conditions are less easily controlled in zoos and circuses compared to farms and laboratories, so the underlying cause of any change is often unspecifiable. Finally, researchers are often less inclined to publish negative results[178] so the true success rate for enrichment attempts may be lower.

Enrichment studies that measure behaviour often use the incidence of stereotypy as a key indicator of welfare[339]. Many animals exhibit stereotypic or abnormal behavioural patterns in captivity and enrichment is the preferred means of tackling the underlying cause since, unlike alternative methods such as punishment or physical prevention, enrichment gives animals a choice of whether or not to participate in the treatment[128]. In a review of 54 studies, 90% of the 63 effect sizes showed a positive effect of enrichment on stereotypic behaviour in zoo animals[340]; another review (25 studies) reported a 53% success rate[178]. Yet no enrichment study has abolished stereotypy in all subjects, which suggests that enrichment alone, at least in the short term, is rarely enough to end the perseverative dysfunctions that underlie stereotypical behaviour[128]. Enrichment may take time to induce significant improvements or require additional complexity or alternative stimuli[341].

Enrichment may also affect sexual behaviour. Male mink in enriched cages performed less stereotypic behaviour, had higher androgen levels, had better developed *os penises* (bacula) and gained more copulations[342]. In another study, enriched male mink copulated for longer, while enriched females weaned more offspring[343]. Bobcats in one zoo only reproduced successfully after the implementation of an extensive enrichment program[344]. Environments enhanced by enrichment may promote normal development: infant marmosets raised in enriched cages developed faster than those in non-enriched cages, which could improve spatial cognition and motor skills and enable better coping with different situations later in life[345].

A possible outcome of enrichment is reduced compliance during training and performance. In a novelty test, enriched parrots were less fearful than barren-housed parrots toward novel objects and unfamiliar handlers, but were more aggressive and less interactive during handling[346]. Parrots from barren cages were more motivated to interact with familiar humans as a source of stimulation than those in more complex cages[346].

Social enrichment

In social species such as primates, interaction with a conspecific may elicit more beneficial changes in behaviour than any other form of enrichment. Rhesus macaques showed increased species-typical behaviour and reduced abnormal behaviour when they were pair- and group-housed rather than singly housed, whereas unenriched individuals did not differ behaviourally from food- and object-enriched animals, suggesting that social partners were more beneficial to welfare than 'inanimate' enrichment[347-349].

Structural enrichment

Enrichment for amphibians and reptiles is often considered to be of little importance, possibly because their specific climatic and dietary requirements already necessitate a 'naturalistic' enclosure. However, many amphibians and reptiles have sophisticated communication systems, complex social behaviours, behavioural plasticity and remarkable cognitive abilities[43,350,351], and environmental complexity appears to be important for their welfare. Adding pipes as refuges reduced bite wounds and eliminated cannibalism in tanks of South African clawed frogs[352]. Adding retreat spaces to wolf enclosures reduced social aggression[353]. Eastern box turtles showed a strong preference for enriched enclosures over barren ones, and barren-housed turtles showed more escape behaviour and had a higher heterophil:lymphocyte ratio, possibly indicative of stress-induced immunosuppression[79].

While many birds and mammals have fewer 'essential' requirements, being able to tolerate more variation is not an assurance that they have everything they need[224]. Lack of retreat space is a significant stressor for captive wild animals in public view[25]. Circus animals are often on display to the public both during performances and in their home cages and exercise pens. The availability of a retreat space or a visual barrier improves the welfare of animals by allowing them some degree of control over their environment and may enable them to cope with aversive stimuli. Sheep and goats in a petting zoo showed the lowest amount of undesirable behaviour when a full retreat space was available[354]. Adding more hiding places reduced FGMs in clouded leopards[130]. Farmed foxes had lower urinary glucocorticoid metabolite concentrations (UGMs) after concealment screens were added to their cages[355]. After the addition of a visual barrier to the visitor viewing window, zoo-housed primates[356-358] showed less aggression and less abnormal behaviour, and polar bears swam more and rested less[359]. However, a visual barrier had no effect on the behaviour or space use of orangutans, gorillas, lions or tigers[359].

Optional retreat spaces can improve welfare, but adding permanent visual barriers (such as blocking a window) can be detrimental if they do not allow any choice or control. Adding a solid fence to a tiger enclosure as a visual barrier from keepers and conspecifics increased the frequency of pacing by a female tiger[228], and farmed blue foxes avoided cage areas where their view was obstructed by concealment screens[355]. Welfare may be more affected by the ability to control access to stimuli than the stimuli *per se*.

Platforms, elevated areas and edge zones (the enclosure periphery nearest to visitors) give animals a better view of their surroundings and many animals may benefit from being able to see what is going on. Platform use by farmed blue foxes increased at times of elevated disturbance during working hours[360]. The addition of platforms to enclosures that were already fairly complex reduced pacing in zoo-housed felids[361]. Zoo chimpanzees and gorillas both showed space-use preferences for corners in their enclosure, which were thought to offer security, and areas with views of the keeper's food preparation area[262,264]. Some animals spend the majority of their time on platforms[355], or in the edge zone, particularly when pacing, e.g. circus tigers[167] and in less complex enclosures[265], where the 'view' may provide mental stimulation or allow the animals to see keepers approach. Some animals perform more abnormal behaviours such as pacing in the edge zone[214,265,288].

Daily access to pools of a suitable size, depth and water quality are essential for some species to allow species-typical behaviour. Broad-snouted caiman require a pool with plenty of shallow margins, where they choose to spend most of the day[362]; birds of prey rarely drink but require water for bathing[363]; hippopotamuses require a pool and, in zoos they spend >99% of awake time in water[364]. In a cross-institutional study, tigers with access to a pool filled with clean water, regardless of its size, showed significantly more behaviour associated with 'enhanced welfare'[28,31].

Sensory enrichment

Appropriate olfactory enrichment can improve animal welfare, but has had limited success at improving the welfare of birds, which are most reliant on visual perception[337]. Olfactory enrichment has also been unsuccessful in several species of mammals: gibbons showed the least interest in sensory enrichment (scented mats) when presented with a choice of enrichment devices[365], and scented cloths had no effect on the behaviour of gorillas[366] or meerkats[367].

Olfactory enrichment does not always elicit a positive response. Inappropriate olfactory stimuli such as predator scents can elicit anxiety-related behaviour in prey species[368,369] even when captive born[370], although this is not invariably the case[371]. This may have implications for the close-proximity housing between predators and prey.

However, olfactory enrichment has been beneficial for most species of mammals studied. Scented pine cones increased homogeneity of space use in armadillos, bush babies and sloths[372]; domestic cat semiochemicals (pheromones) stimulated play and affiliative behaviour in lions[30]; and the scent of natural prey stimulated increased activity and social behaviour in lions[373,374] and wild dogs[375], and increased exploration in cheetahs[221]. Blood-impregnated logs elicited investigatory behaviours including sniffing, licking and pawing in wild dogs, bush dogs and tigers, and they all responded more to prey odours than non-prey odours[376]. Less 'natural' scents, such as cinnamon and other kitchen spices, may also initiate positive responses in large felids[374,377-380]. Some species show no preference for either natural or non-natural scents; both were associated with reduced pattern swimming in sea lions[290]. Scent suitability may be less important than the regular rotation of different odours to prevent habituation[381]: while black-footed cats responded more to catnip and prey odour than nutmeg, nutmeg still elicited a significant change in their time budget[381], and Amur leopards showed a greater response to nutmeg over predator and prey odours[382].

Since circus animals are presented with novel scents with each change in location; this may have an enriching effect for some species, despite the lack of species-relevance of most of the odours they are likely to encounter. Conversely, moving to new sites may have a detrimental effect on species reliant on olfactory cues. The disruption of familiar scent marks by regular cage cleaning has been associated with increased cannibalism and reduced handleability in rats[383,384].

Auditory enrichment has had mixed effects. Adding auditory stimuli to an already noisy environment may increase stress, particularly if animals have no opportunity to escape[332]. Playing rainforest sounds was linked to a significant decrease in species-typical behaviour in bush babies and two-toed sloths[372] and increased agitation in a pair of gorillas[385], yet decreased stereotypic behaviour in another trio[386]. Music, both classical and rock, was associated with increased stereotypic behaviour in the same trio of gorillas[386], while classical music had no significant effect overall on gibbons, although one individual increased self-scratching, a displacement behaviour indicative of stress[387]. Asian elephants exhibited significantly less stereotypic behaviour when exposed to classical music[388]. Animals are clearly sensitive to their auditory environment and there are species-specific responses to auditory cues.

Cognitive enrichment

Captive animals benefit from devices or tasks that are cognitively challenging and require problem solving or tool use to obtain a reward. Contrafree-loading (a preference for food that requires effort) in response to foraging enrichment has been observed in several species including parrots[389], rhesus macaques[390] and cheetahs[391]. Puzzle feeders are one of the most effective types of food-based enrichment for increasing foraging activity in primates[392]. The behavioural time budget of captive chimpanzees that participated in a voluntary cognitive experiment with food rewards was more similar to their wild counterparts than captive chimpanzees with no access to cognitive enrichment and so did not have to work for their food[393]. An enrichment device containing honey that elicited tool use in chimpanzees also reduced inactivity, particularly in dominant animals who had more access to the device, though there was no reduction in abnormal behaviour[394].

Food-based enrichment

Food-based enrichment is used to stimulate foraging behaviour and is highly successful in most species. In addition to increasing foraging and feeding behaviour in African harrier hawks[395] and tigers[396], food-based enrichment sometimes causes other behavioural alterations, such as increased behavioural diversity[372] and locomotion[397] or reduced abnormal behaviour[398]. A meta-analysis of 54 studies showed that food-based enrichment is more effective than scent, which was more effective than structural enrichment at reducing stereotypical behaviour[340].

Food-motivated species or individuals may respond more to enrichment when it contains a food element. Seals explored enrichment devices more when they contained food[149]; hidden food was more effective than enrichment objects at promoting nonstereotypic activity in wolves[77,78]; foraging enrichments occupied a greater amount of time than object enrichments in parrots[399], squirrel monkeys[400], African wild dogs[401], gibbons[365], chimpanzees and gorillas[397]; and only food-based enrichment stimulated increased activity in Goeldi's monkeys[402]. When given food-based enrichment, macaques showed more species-typical activity and also used the feeding enrichment devices for non-feeding activity such as play[348]. Multiple feedings of hidden food increased food-searching and exploration by nearly three-fold, and halved stereotypic pacing in leopard cats [403]. However, not all species prefer food-based enrichment, e.g. sea lions[183]. Automated box feeders filled with meat to vary spatiotemporal food availability in two snow leopards' enclosures did not reduce stereotypic behaviour, possibly because boxes do not stimulate natural hunting behaviour [63].

Enrichment appears to be most successful when it targets species-specific behaviours. Hiding peanuts to stimulate food-searching in elephants was inappropriate for a species that naturally forages on browse and grass[404]. However, replacing their hay with browse, which has a longer handling time and stimulated natural food-handling behaviour, was associated with a substantial increase in feeding and general activity in elephants[405]. For elephants, food-based enrichment should increase handling time but not nutrient acquisition[335] since obesity is a problem for captive elephants[247]. Species such as giraffe that exhibit oral stereotypies associated with feeding motivation may benefit from enrichment such as complex feeders that encourage oral manipulation[341].

Encouraging natural hunting and foraging behaviour may help satisfy the behavioural needs of captive animals. Rat snakes housed in enriched enclosures and fed on live prey had higher growth rates and were more behaviourally adaptive in cognitive tests than snakes housed under standard laboratory conditions and fed dead prey[406], and blue-tongued skinks were more active when fed live prey[253]. The welfare of captive carnivores may be improved by creating an environment where the reward of eating is contingent upon achieving goals through hunting behaviour[407].

Live prey can be simulated, although large or fast species may require considerable space for acceleration and deceleration, and the effort animals exert to catch simulated prey depends on reward [391,408]. Prey on a bungee cord reduced pacing in two cougars but there was no change in FGMs[409]. Moving bait stimulated hunting behaviour in captive cheetahs, such as chasing and striking, and increased the time they spent looking at hoof stock in adjacent enclosures[410]. While cheetahs show increased vigilance in response to the sight of prey species[221], enrichment promoting increased prey observation may increase stress in nearby prey species.

Partial or whole carcasses stimulate natural food-processing behaviours and increase non-stereotypic activity in lions[396] and off-exhibit stereotypy in large felids, but did not influence on-exhibit behaviour, suggesting the motivation for on-exhibit pacing was not food-related[411]. However, captive-bred animals are often accustomed to a particular diet and may show neophobia to the sudden appearance of an unfamiliar carcass[411].

However, feeding enrichment only lasts as long as food is available[62]. Prolonging the benefits of feeding enrichment by providing more food increases the risk of obesity. Food can be provided at a slower rate, such as a drip-feeder for chimpanzees[412], although more tortuous enrichments have the potential to raise frustration levels[413]. Feeding enrichment may stimulate foraging and reduce inactivity temporarily, and reduce food-motivated stereotypies, but had little effect on stress-related behaviour caused by environmental deficits in squirrel monkeys[400], wolves[77,78], coyotes[38] and wombats[184].

Novel object enrichment

Novel objects such as balls work better as enrichment for some species than others. They reduced self-mutilation in a turtle[47] and stimulated increased activity and play in peccaries[54]. However, human infant toys had no effect on activity budgets of several species of new world primates[414], wild dogs showed little interest in balls[401], and traffic cones did not reduce stereotypical behaviour in bears, whereas a cow hide reduced stereotypical behaviour by >50%[415]. Adding objects to an enclosure may increase environmental complexity but will have little benefit if they are not relevant to the target species.

Giving animals choices

Enrichments that give animals control may be more successful than offering increased environmental complexity[416]. Chimpanzees favoured enrichment items that allowed the highest degree of control[417], and zoo-housed red foxes had the highest behavioural diversity during feeding enrichment that allowed animals control over access to food compared to unpredictable feeding enrichments[418]. However, enrichments that allow animals control usually involve technology and can become quite complex, e.g. a computerised acoustic 'prey' system[419]. Complex control-oriented enrichment may not be possible in travelling and semi-permanent exhibits.

While enrichment often reduces undesirable behaviour because it gives animals choices[128], sometimes welfare is only improved by having multiple choices. Eastern blue-tongue skinks in larger enclosures had an increased tendency to hide, so multiple retreat spaces are required to avoid heterogeneous space use in large enclosures[253]. Chimpanzees chose to employ all available methods to obtain juice from a feeder[420]. Adding multiple hiding places to their enclosure reduced stereotypic behaviour and increased hiding in leopard cats, apparently helping them cope with aversive stimuli [256]. Pacing in small felids varied with the number of visual barriers and was reduced or absent in enclosures with more than six visual barriers[421]. The number of enrichment objects was negatively correlated with pacing in zoo tigers[28], and captive Canadian lynx had significantly lower FGMs when more hiding places were available[230].

Unsuccessful enrichment may be improved by incorporating additional choices. Animals appear to benefit from having multiple options. So the addition of a raised basking platform to facilitate climbing had no effect on behavioural or physiological parameters in eastern fence lizards[422], and adding a single platform to farmed fox cages did not decrease UGMs[355]. Different types of enrichment will initiate different changes in behaviour, so providing a choice of enrichment options to stimulate different behaviours may be more effective[339,377]. While too much choice may be overstimulating and lead to displacement behaviour such as inactivity[401], animals appear to benefit from having multiple options.

How individuals of the same species respond to enrichment, and captivity generally, depends on a variety of factors, including age, sex, individual history, personality and dominance status[282]. Providing choices can help accommodate individual differences. For example, when given a choice, most spotted pythons preferred elevated refuge shelters, but some chose surface or submerged sites[423]. Individual differences in responses to different enrichment stimuli have been reported in almost all published enrichment studies in species as diverse as marine turtles[339], bears[415,424,425], gibbons[387], giraffe[341], leopards[411], lions[374], peccaries[54], seals[149], squirrel monkeys[426], walrus[427], wild dogs[375] and wolves[77,78,336].

Age effects on enrichment have been reported in a diversity of species. Feeding enrichment elicited a greater reduction in feeding anticipation behaviour among subadult than adult giant pandas, and adults displayed a preference for feeding enrichment whereas subadults showed no preferences[428]. Juvenile chimpanzees[417] and gorillas[429] interacted with enrichment objects more than adults, and adult peccaries showed stronger preferences for specific enrichment objects than juveniles[54].

Some ursids show high sexual dimorphism and clear gender differences in activity levels and behavioural diversity[424], so may benefit from sex-specific enrichment such as strength-challenging enrichment for males[289]. Sex differences were also reported in the hormonal (FGM) responses to different enrichment types in wolves, which may arise from differences in reproductive strategies[78].

Dominant animals may block or displace subordinates from enrichment devices and subordinates may increase stereotypic behaviour when enrichment is present, perhaps due to competition for access[149,394,415]; this may reduce the effectiveness of enrichment for subordinate animals. Additionally, competition for food-based enrichment in group housing could result in unequal feeding and consequently obesity or malnourishment[392].

In group-housed animals, poorly distributed enrichment may promote competition, which can be neutral, playful[415], or aggressive[282]. Intraspecific aggression may not necessarily indicate poor welfare, particularly in species such as peccaries that regularly reinforce their social status[54]. However, husbandry practices that increase aggression may be detrimental to welfare. Potentially injurious or stressful competition could be avoided by supplying several widely spaced enrichment devices[420], including vertically for arboreal species[430], or by temporarily separating individuals during enrichment[391,409].

Habituation to enrichment

While longer-term use of enrichment can lead to a greater reduction in stereotypic behaviour[431], animals can quickly become habituated to enrichment items[294,360]. So short term enrichment studies cannot record the longevity of any apparent effectiveness and may fail to detect habituation[187]. While elephants were reported not to habituate to classical music, they were only tested for six days[388]. Olfactory stimuli may only serve as enrichment when the scents are novel. Black-footed cats habituated to scent-impregnated cloths over the course of five days[381] and the response of Amur leopards to novel scents attenuated within four days[382], both despite daily scent replenishment. Animals also habituate to novel objects: chimpanzees showed more abnormal and rest/idle behaviour when enrichment items were just one day old compared to when they were new[432], and their use of enrichment items over three weeks stabilized at a mean of 2.5% of the subjects' time[433]. While chimpanzees still used enrichment objects (balls) after 4.5 years of exposure, this was only for 1% of the time[434]. Peccaries interacted with novel objects most within the first week of exposure[54]. Animals will even habituate to food-based enrichment; small felids showed attenuated responses to hidden food packets over the course of just one week[435].

Habituation may be avoided by introducing enrichment on a randomised schedule, as seen in cheetahs[29,221]. Allowing animals intermittent rather than constant access to enrichment devices, as in sloth bears[187], or presenting different types of enrichment on a rotation to large felids[378], giant pandas[428] and gibbons[365] may also prevent the attenuation of enrichment benefits. Some zoos have strict rules on the number of times per week an enrichment device can be used[436]. The regular transportation of circus animals means they do not have continuous access to exercise pens or enrichment objects, so may have less opportunity to habituate and therefore benefit more from enriching opportunities when they are available. Conversely, space limitations in transporters may limit the variety of potential enrichment items circuses can provide. Enrichment such as food or social opportunity that offers extrinsic reinforcement may produce more significant behavioural changes that are attenuated less quickly than devices that rely on intrinsic reinforcement, i.e. the behaviour itself is reinforcing[437].

Enrichment can never cause a permanent change in behaviour: it must continue to be provided or any benefits will revert[435]; and a period of enrichment followed by deprivation may be more damaging to animal welfare than never having enrichment[123].

Training

Training is used to facilitate learning and modify animal behaviour[438]. It is argued that training provides mental and physical stimulation and that interacting with humans through training and husbandry can be enriching for captive animals[439].

Training methods

Classical conditioning is used to train an association between a primary reinforcer (reward) and a secondary reinforcer (signal). Food is the most common primary reinforcer for veterinary and husbandry training because it is powerful and effective in a short space of time[440]. Trainers also use verbal praise or physical contact such as stroking because it works better than food for some species[440]. A secondary reinforcer (bridging stimulus), such as a whistle or clicker, is used to signal that the correct behaviour has been performed and the delivery of a reward is imminent[438]. The bridge-reward delay must be short to prevent confusion or frustration[441], and virtually all animal trainers use some variant of clicker training[440]. Operant conditioning, i.e. behaviour changing as a function of consequence[442], can be used in training once this association has been learnt.

Operant conditioning is based on positive and negative reinforcement and/or punishment. In positive reinforcement training, the frequency of a behaviour is increased by rewarding its performance with food or social contact. With negative reinforcement, a negative stimulus is removed when the animal performs the required behaviour[443,444]. Positive punishment decreases the frequency of a behaviour by introducing something negative when it is performed, such as the verbal command “No!” Negative punishment decreases the frequency of a behaviour by removing something positive on its performance, such as the opportunity to work for food[445]. Punishment has short term benefits for the trainer but in the long term impairs the welfare of the animal through fear, unresponsiveness, escape/avoidance, aggression and apathy[446]. Birds in particular do not respond well to negative reinforcement and punishment[447,448]. It is not in the interest of falconers to rough-handle hawks as broken wing feathers will not be replaced until the next annual moult[363], and free-flying birds cannot be stopped from flying away in response to negative treatment[449]. So punishment can encourage cooperation but does not induce good welfare[450].

Positive reinforcement is considered to be the most humane training method and so is most beneficial to an animal’s psychological welfare[451,452]. It is also more effective than punishment-based training because it results in more obedient animals that exhibit fewer problematic behaviours[453]. A variety of animals can be trained successfully by only using positive reinforcement e.g. tortoises[454], macaws[455], chimpanzees[456,457], marmosets[458], mangabeys[459], macaques[460] and vervet monkeys[461].

It is generally agreed that negative reinforcement should only be used in a life threatening situation[451] or when positive alternatives are exhausted[445]. However, the line between negative reinforcement and positive punishment is blurred[440,462], so spraying a cat with water until it enters its indoor enclosure is negative reinforcement, whereas spraying a cat because it would not enter its indoor enclosure is positive punishment. Training that relies on positive reinforcement and uses no physical punishment avoids confusing scenarios. Shouting (in reprimand) also constitutes punishment[453] and a study of 15 circuses found “too much unnecessary shouting” by animal staff[26].

While a study of circus animal training sessions found no evidence of physical cruelty or excessive stress[26], all observed sessions were reinforcement training and rehearsal rather than initial training. Negative reinforcement may be used in circuses more than trainers admit, particularly since training takes time and tight schedules may lead to more forceful training[164]. Animals remember bad experiences: one bad experience can teach an animal to mistrust a handler for a long time[450], and one instance of harsh punishment may be enough to attain long-term control using intimidation[463]. So training based on fear or pain would damage the human-animal relationship.

Free contact and protected contact

Elephants and other large animals are trained using ‘free’ or ‘protected contact’. The elephant and handler interact directly in free contact (FC) training but this can be extremely dangerous, particularly with mature bulls: humans are most often injured by elephants when in direct contact[464]. So FC training necessitates the use of protective tools such as a ‘guide’ (a wooden, metal or plastic staff with a metal hook, also known as a bull hook or ankus) to cue the elephant’s behaviour[465]. Elephants may also be tethered by one front and one hind foot during FC for certain husbandry procedures. Although spoken commands typically replace physical cues over time, FC inevitably begins with physical cues and, as the safety of the handler depends on complete compliance by the elephant, physical punishment may be necessary to discourage dangerous behaviours[465]. While a researcher successfully trained four juvenile elephants in FC to participate in a trunk wash for tuberculosis testing using only positive reinforcement[466], trainers of wild elephants believe there is no substitute for a guide when 'breaking' a frightened and dangerous wild elephant, but once 'broken' vocal reprimand can be used with positive reinforcement[467].

Protected contact (PC) was developed in 1989 at San Diego Zoo for safer husbandry training that does not require punishment or restraint of elephants[468]. In PC the elephant and handler interact through a secure barrier. This is safer and training can be done without guides, using only spoken or visual commands (targets) and positive reinforcement (a whistle or clicker, and food rewards). The only discipline used in PC is 'time out', the temporary withdrawal of the trainer's attention[468]. Elephants also have a choice whether or not to approach the barrier and so participate in training voluntarily[469]. Animals will be more comfortable and confident when trained or approached in spaces where they have room to escape[444,446]. Some circus trainers use PC for safety in the initial stages of training when building trust with young or new animals but then progress to FC[470]. A survey of zookeepers revealed that PC is also the most frequently used handling method for big cats in zoos and is considered the most beneficial handling method for both animals and visitors in terms of safety, welfare and educational value[471]. Keeper-animal relationships were more favourable, i.e. the animal showed greater affinity toward the keeper, if they interacted with the animal through a barrier rather than entering the enclosure[472].

A study of the training of three elephants in a zoo found that positive reinforcement was delivered on average eight times more often in PC than in FC, and in FC positive (food) and negative (guide) reinforcers were used at the same rate[473]. This suggests that the FC training used in circuses does not facilitate the minimal use of negative reinforcement required for good welfare during training, especially since negative reinforcement is more often used when trainers are in direct contact with animals[462].

Animals trained at a distance are generally trained using positive reinforcement[462]. Distance training is also used for aggressive animals, such as Steller's sea lions: rather than being taught specific 'tricks', they are rewarded when they display a particular behaviour at liberty. This is slowly conditioned using food rewards until it can be performed on cue[474]. Behaviours can still be directed by modifying the environment, such as by setting up a hanging ball for a sea lion to touch.

Training that facilitates the use of positive reinforcement, i.e. distance training and especially protected contact, requires specialist facilities such as strong barriers that may not be easily transported or securely fastened at a circus site.

Maximising motivation for reinforcers

Training will be most effective when the animal is most receptive to reinforcers, such as food when they are hungry or those times of the day when they are naturally most active[438,475]. This can limit the frequency of training sessions for reptiles, which only eat occasionally[475]. Hunger is essential when training birds of prey to ensure they are motivated to return for food; daily weighing can help avoid health-damaging weight loss from withholding food[447]. Species such as bears that hibernate may be less food-motivated during the winter[476] and some training methods involve withholding of food, such as when taming wild reindeer[477].

Individual differences in the rate of learning

The amount of time required to train each animal is influenced by their prior experiences, stress level and motivation, in combination with the strength of the reward, the skills and experience of the trainer and any concurrent distractions[446,466]. Many trained birds are unsuitable for demonstration work due to temperament[275]. Yet personality does not always affect learning ability or compliance with training[478], which may be better explained by sex[456] or species differences[478,479]. This implies that not all individuals or species can be trained for the same task: birds of prey show considerable species differences in temperament, behaviour and flying adaptations, and so species should be chosen specifically for the task in mind. While accipiters (true hawks) make excellent falconry birds, they are probably too highly strung for demonstrations[275].

Individual differences in learning rate have been reported in primates[457,479], eland[272], alpacas[480] and bears[415], and some individuals may show continued inexorable stress responses to training. Circus animals that do not perform well or habituate to the ring are culled, but only as a last resort because euthanasia is expensive[26]. Ongoing attempts to train unsuitable animals may impair welfare by causing unnecessary and prolonged stress. However, animal trainers argue that they are well attuned to the individual personalities and abilities of their animals and can tailor routines accordingly[26,470].

As with enrichment, the effectiveness of training may depend on dominance rank. Husbandry training had a greater positive effect on the behaviour of low-ranking than high-ranking chimpanzees[481]. Dominance rank affected compliance with voluntary shift-training in group-housed sooty mangabeys: low-ranking individuals were less compliant[459]. When training individual animals in a group, conspecifics may obstruct or distract the subject and interfere with training[482] and dominant individuals may displace subordinates[272].

Purpose of training

Training can contribute to better welfare by reducing stress during husbandry and veterinary treatment, providing mental and physical stimulation, and facilitating socialisation and reproduction.

a. Voluntary participation and desensitisation

A single experience of capture or some other unpleasant procedure is often enough for an untrained animal to learn to avoid the areas or people involved for an extended period[450]. The objections of easily-manipulated animals such as small reptiles are easily ignored[475], but non-compliance in large or aggressive animals impedes even routine care. Training animals to cooperate with husbandry and veterinary procedures such as weighing, blood tests, scans, x-rays, treatment and medication before their first experience of such interventions will prevent animals from considering these experiences unpleasant. Training an animal to present a certain part of their body for inspection, or to 'station' (stay) in a certain place/position, is used to gain locomotor control. This can reduce or eliminate the need for restraint and enable less stressful, and quicker, separation from conspecifics, movement between enclosures and transportation[440,443,454,456,459]. Training animals to accept treatment when sick can also improve their physical condition and reduce the time spent in isolation due to illness[482]. Husbandry training has been achieved in a diversity of wild species[447,483], such as reptiles[454,475,482], birds[455], primates[458.479,484], ungulates[272], marine mammals[485], and bears[486]. Laboratory animals can also be conditioned to participate voluntarily in tests that require temporary restraint[271,487,488]. This results in improved welfare because enforced restraint is stressful and there is no scientific evidence that animals habituate to involuntary restraint[271].

Aggression towards humans or conspecifics stems from fear, discomfort, uncertainty and/or apprehension, and training can desensitise animals to stimuli that are potentially fear-inducing[489]. Pairing positive reinforcement with negative stimuli causes fear to diminish over time[443]. Training animals to participate voluntarily in procedures or events desensitises them to potentially frightening or painful procedures, eliminates the need for chemical immobilisation or enforced restraint, and consequently reduces stress[271,452,484,487,490,491]. Procedures using trained animals are also much faster[457,458], further reducing any disturbance caused by the procedure. Desensitised animals are ultimately less fearful of events or procedures, which contributes to better psychological welfare[451]. During initial training circus animals are desensitised to the circus ring, which can take months or years[26]. The amount of time taken for animals to become desensitised could indicate the level of stress inflicted by the experience. It is not known whether desensitisation training is used to prepare circus animals for regular transportation.

b. Socialisation, reproduction and exercise

Socialisation training can be used to strengthen social bonds in group-housed animals. Training animals to touch targets gently facilitates proximity and affiliative behaviours and may aid smoother, less stressful or aggressive introductions of new individuals[492]. Dominant animals that monopolise food can be trained to allow subordinates to feed by reinforcing cooperative rather than aggressive behaviour[443]. Training animals to feed cooperatively reduces fearfulness in subordinates[443], which may make them more receptive to environmental enrichment. Shared goal-directed training (rewarding collaborative efforts) can be used to create social ties and has led to the formation of alliances in dolphins[443]. Training can also be a useful tool for teaching animals that lack maternal skills how to care for their young[493,494], and trained zoo elephants can go out for walks, which provide exercise and mental stimulation[447].

c. Human use or entertainment

Besides husbandry training, which may or not be presented in public demonstrations, animals may also be trained to perform behaviours exclusively for human benefit, either as working animals or for public entertainment. Dogs and horses have been trained for work, sport and leisure for thousands of years. Placing a rider on the back of a horse has no analogue in the natural repertoire of horses[495] and may resemble a potentially lethal threat under natural conditions. This also applies to other ridden animals, such as camelids, cattle and elephants. In immature camels the weight of a rider can cause irreparable damage to the animal's back[496]. Even though horses have been domesticated for over 5500 years[497], they still show an increase in heart rate and heart rate variability (indicative of psychological stress) in response to being mounted by a rider[498]. However, the extent of this increase can be moderated using more appropriate training methods: horses trained using natural horsemanship showed less evidence of stress during early training and mounting than horses trained using conventional methods[499].

Birds of prey can be trained to hunt and catch wild prey (falconry), disperse birds from buildings, airfields or other sites (bird-hazing), or for public demonstrations[500,501]. Circus animals are trained to participate in spectacular performances, sometimes involving elaborate props, costumes and exaggerated movements. While husbandry training does not always involve 'natural' behaviours, such as holding a foot to accept an injection, they are safe and usually relatively comfortable. In contrast, some circus acts are potentially injurious. Rare behaviours exhibited by wild animals in extreme situations are often misinterpreted and blown out of proportion, e.g. an elephant reaching into a well to drink during drought looks like a 'hand stand', likewise an elephant standing on hind legs to reach high branches, but such behaviours are very rarely exhibited in the wild because they place excessive strain on the body. Misinterpretation reassures trainers that such movements are 'natural behaviours' that can be used in daily performances[502]. Certain postures are particularly dangerous: because elephants do not have a pleural cavity around their lungs[503], the sternal recumbency (sitting) posture can cause suffocation, particularly if they are tired[277]. Sitting also places excessive pressure on the diaphragm and can cause a hernia; circuses that recognise this risk train their elephants to defecate before the performance to minimise the chance of a prolapse occurring in the ring[504]. The positions and movements of elephants during circus performances places additional strain on their bodies[505], and may accelerate the decline in their welfare compared to zoo elephants. While zoo elephants generally perform a more limited range of activities, their welfare scores still declined with age[247]. Training animals, particularly sensitive species like elephants, to stand in postures that represent aggression or submission in intraspecific interactions may influence their emotional state[181].

Circus animals may undertake one or several performances per day. Animals will spend approximately 10-15 minutes performing their act in addition to some time (minutes or hours) confined or restrained prior to performance, possibly within public view and petting distance[159,179,506]. Animals that are used to give rides to the public spend additional time in the ring[159], although the amount of time spent performing is relatively little compared to the time spent confined to cages, waiting to perform or in transit between venues. Some circus animals never perform: in one circus only three of four tigers were used for performance[167].

Animals in performances are not necessarily voluntary participants, since the animals are expected to perform when the show begins. In circuses, big cats were reported to need 'encouraging' (with a broom handle) to go to the ring[26]. This sort of training will be less beneficial to welfare than that which allows animals to choose not to participate. However, from the animal's perspective, if movements and positions are not likely to be uncomfortable or harmful, there is probably little difference between performing a behaviour for public entertainment and performing a behaviour to facilitate a veterinary procedure, since both are performed in response to a cue and a reward is subsequently received[440]. Yet the motive behind the training and consequent direct benefits of learning and performing the trained behaviour are quite different.

The trainer

The principles of animal training are relatively simple to learn but not everyone has the right personality to be a good trainer, which includes patience, empathy, flexibility, consistency and a calm demeanour[440,452]. Trainers require a good understanding of both the species and individual to interpret their body language: they need to observe the often subtle reactions of animals and respond to them immediately and appropriately to reduce fear, anxiety, discomfort or confusion, which could potentially manifest as aggression[438]. Inexperienced trainers may also not realise when animals start to train them and this is dangerous: dolphins and apes have shaped their trainers gradually to lean further out over a pool or come within grabbing range[440].

Traditional animal training methods are coercive and based on force and aggression, which most professional trainers have now discarded in favour of positive reinforcement techniques that empower the animal[446,450]. This comes after the realisation that the most productive human-animal relationships are built on trust, which is strengthened by positive interactions and weakened by negative ones[446]. Some trainers are slow or reluctant to make this switch, particularly because punishment is a difficult habit to overcome[446]. Many trainers in traditional circuses that feature animal acts are 'not prepared to learn and bound by tradition[26], so may be less willing to adopt contemporary training practices that go against generations of tradition. For instance most circus elephant trainers have adopted traditional Asian elephant training techniques[507]. Circus trainers have few or no recognised qualifications or valid formal training[164], and can become impatient and angry with their animals[26]. Good knowledge of the species and their reflexes eliminates the need for cruelty and violence in training[449]. However, presenters may have limited knowledge of animals and sometimes are only interested in 'cutting a dash'[26,508]. Circus animals are not always handled by knowledgeable, experienced professionals with an appropriate temperament.

Consistency of both trainer and training protocol is important for successful training. In zoos, trainers that are also involved in husbandry and veterinary procedures have better control of the animals than staff not actively involved in the initial training[440]. Inconsistency in the training process in both zoos and circuses has led to animals quickly becoming unresponsive or aggressive and consequently requiring a considerable amount of retraining[26,440]. Animals such as macaws have learnt tasks faster with multiple trainers[455], whereas rhesus macaques learn faster when trained by the same person[460]. Different trainers, even at the same establishment and following the same protocol, use slightly different techniques. This may confuse and frustrate animals, and using multiple trainers limits the development of strong human-animal relationships and thus the efficiency of training sessions and resultant welfare benefits[494]. Some circuses commission trainers to teach animals a particular act, which is then exhibited by a presenter rather than the original trainer. When animals are worked by presenters rather than the original trainers, this can prevent efficient two-way communication during rehearsals and shows if the presenters are unable to understand and respond appropriately to the animals' body language: this can lead to confusion, frustration and potentially pain.

A personal licensing system or mandatory proficiency test would ensure animal trainers and handlers/presenters have adequate knowledge: the better qualified the trainer and handler, the better the welfare of the animal[275]. A permit is required to become a falconer in the USA and, in some states, this can only be obtained after passing a written exam with 80% accuracy[501].

Welfare benefits of training

a. Training reduces fear

Fear and anxiety are emotional states characterised as a feeling of insecurity and induced by the perception of potential or actual danger[509], and can manifest as behavioural and/or physiological changes such as increased heart rate, glucocorticoid release and/or suppressed appetite[510]. Fearfulness is a personality trait defining an individual's predisposition to react to potentially threatening situations[509]. Desensitisation training using positive reinforcement reduced fearfulness towards humans and in laboratory-housed rhesus macaques[511]. Untrained elephants or those previously trained using free-contact became less aggressive and/or less fearful of novel stimuli when trained using protected-contact[468]. In some circuses large felids are conditioned to return to a pedestal if confused about what to do or where to go, or to avoid fear or panic[26].

b. Training reduces abnormal behaviour

Training that teaches new behaviours can contribute to increased activity levels by expanding an animal's behavioural repertoires and, when used alongside environmental enrichment, can help teach animals how to use enrichment devices[451]. When animals perform abnormal behaviour such as stereotypy or self-mutilation, training can be used to reinforce alternative behaviour[512,513]. Targeted training can condition animals to perform specific behaviours such as parental care[493] and play[514]. Training can also have indirect benefits on behaviour, such as reducing stereotypical behaviour[152,341,461,481,515,516] and aggression[460,479,515], or increase affiliative behaviour[461,481,514]. Husbandry training was associated with a decline in monkey-initiated interactions with visitors and keepers, possibly because training introduced predictable cues for food acquisition, or led to habituation to human presence[517].

c. Training provides learning opportunities

Learning is a beneficial experience since knowledge is required for survival in nature[518] and many captive animals actively seek the opportunity to learn e.g. parrots[389] and wolves[519]. Some animals show positive emotional responses to learning[415,520]. Training affords learning opportunities that can be as challenging and rewarding as learning through problem solving with a complex enrichment device[451]. However, training can only be considered enriching while the animal is still learning, not once the behaviour is learnt, i.e. when the animal performs the behaviour reliably on cue[521]. Many circus animals are trained to perform a particular act and repeat the same routine all season and sometimes for many years[26]. Once circus animals have been taught the act, they stop learning and the performance of the routine stops being an enriching experience. The 'training sessions' on tour simply rehearse the learned act and offer no new learning opportunities.

d. Training gives animals more choice and control

Controllability and predictability reduce stress and consequently will improve psychological welfare[88]. Captive animals have little control over their lives, so allowing animals to choose whether to participate in training, and training them to participate in events and procedures voluntarily, gives them more choice and control[485]. Animals must be willing participants in training[452], and trainers can empower them by being attentive to their body language and backing off if the animal shows signs that it does not want to participate in training[446,450]. Positive reinforcement training allows animals greater choice and control than other training methods, since they are free to 'experiment with a broader range of behavioural responses' without negative consequences[451]. This is evident in elephants, where the latency to perform a behaviour following a cue (cue-response latency) was longer in elephants trained in PC than FC, and rate of refusal was also higher in PC[473]. This may indicate that elephants in PC were exercising choice or control over their environment because there was no risk of negative consequence. This was also the case in rhesus macaques, where only individuals trained using a combination of positive and negative reinforcement would move to a confinement cage on cue; no macaque trained using only positive reinforcement would move voluntarily into a confinement cage[522]. In another study rhesus macaques could only be trained up to a certain point using positive reinforcement alone, beyond which negative reinforcement was required for most individuals to achieve full cooperation with pole-and-collar assisted transfer to a chair restraint[523]. This is not surprising: confinement is probably not worth a small food reward. While some alpacas could be trained to accept confinement by only using positive reinforcement, possibly because they are a domesticated species, it was still not possible to train every individual[480].

Do animals enjoy training/performance?

In circuses, big cats performed with apparent willingness, although not necessarily great enthusiasm: 40% of the cats observed were reluctant to enter the ring and some were keen to leave the ring at the end of the performance[26]. Circus tigers almost never paced after performances and showed no difference in post-performance behaviour (lying or pacing) whether they performed once or three times per day[167], suggesting that the added mental and/or physical stimulus of more frequent performances did not improve or impair their welfare.

Stereotypic behaviour can be induced by positive stimuli such as food and water [159,476] or release from indoor housing[136]. Positive reinforcement training involves access to desired reinforcers, so animals can show anticipatory behaviours prior to training sessions[393,415,438]. Circus elephants[159] and tigers[167] perform significantly more stereotypic behaviour prior to performances, although it is unclear whether this is due to anticipation or in response to disturbance from increased human activity. Zoo elephants did not show anticipatory behaviour prior to trained painting sessions and painting did not reduce stereotypy. However, elephants that were not chosen to paint on a given day showed higher levels of non-interactive behaviour, such as standing awake separate from conspecifics[181]. Painting was not enriching because it did not reduce stereotypy and may have contributed to increased stress in individuals not chosen to paint[181].

Whether the training is in itself stressful probably depends on the likelihood that the task and training method will make the animal become frightened, confused or frustrated. Orangutans and bonobos showed no significant change in salivary cortisol during positive reinforcement training for medical procedures[524]. However, during circus training species such as camelids frequently displayed behaviours associated with aggression and frustration, and occasionally fear, whereas some other species showed little/no adverse response[26].

Is training more beneficial than environmental enrichment?

Training has the potential to enhance the psychological welfare of animals through offering mental stimulation, allowing them to work for food, and giving them choice and control[451]. Training such as desensitisation or socialisation may enable an animal to cope with its environment better than environmental enrichment[518]. However, training is not an appropriate substitute for other methods of improving welfare such as environmental enrichment and general enclosure suitability[440,521]. For example, positive reinforcement training only reduced stereotypies in singly housed macaques that performed ‘high’ levels of abnormal behaviour compared to their conspecifics[525]. Another study on macaques showed that husbandry training reduced stereotypic behaviour, but only for the first month[526]. Training combined with environmental enrichment can achieve higher welfare than either one alone[518]. Training and enrichment achieve the same outcomes in terms of increasing choice and control, and stimulating targeted behaviours, although animals have less flexibility and control over the timing and nature of their responses to stimuli in a human-controlled training situation than with environmental enrichment[527]. Also, training may not promote increased species-typical behaviour beyond the food-seeking instinct triggered by food rewards[518], unless the training programme is specifically designed to do this, while environmental enrichment commonly has multiple indirect benefits.

Grizzly bears trained for a cognitive bias task in PC showed anticipatory pacing prior to training, which was positively correlated with an increase in ‘optimistic’ response bias in the cognitive test[415]. The bears’ cognitive bias was unaffected by time spent with a puzzle feeder in their enclosure, suggesting that bears respond better to interactive cognitive enrichment than object cognitive enrichment. The benefit of training may vary between species. In a preference test, individual wolves showed preferences for different types of enrichment: two preferred training, one preferred environmental enrichment, and the other showed no significant preference[528]. That some individuals actively chose training suggests it offers benefit to some, but not all, animals, which reiterates the need for the provision of choice to accommodate individual preferences.

Educational benefits of training and performance

Circus trainers feel obliged to train animals to do 'what the audience likes', perhaps in keeping with tradition, or due to lack of imagination[26]. Reptiles used in animal shows or demonstrations are rarely shown being trained to exhibit natural or active behaviours and are generally just carried or held[475]. For other species, chosen acts might be fictitious 'attacks' on the presenter, bipedal walking, or balancing on pedestals. How animals are presented in a circus has great potential to influence the audience's attitude towards the species in general. A study that compared visitor experiences of tiger exhibits at a traditional zoo and a tourist theme park concluded that the theme park had more holding power: visitors spent longer at exhibits and learned and retained more factual information[529]. This suggests that animal 'shows' have the potential to have educational value when accurate factual information is presented.

However, acts which humans find degrading may decrease their respect for the animals[26]. If circuses are to have an educational role to facilitate conservation, educational acts should showcase the animal's natural agility or intelligence, and explain this in the context of the animal's wild conspecifics. For instance, walruses forage at depths of 100m where light cannot penetrate so they must rely on their sensitive vibrissae to identify prey: a blindfolded object discrimination test in a zoo display demonstrates the sensitivity of this species' vibrissae and its importance for survival in their natural habitat[474]. However, most circus entertainments focus on tricks that do not reflect natural behaviours.

Handling

Human contact can have both beneficial and adverse effects[530]. Captive wild animals are frequently touched and handled by keepers and caregivers[60,531,532], and by unfamiliar and inexperienced people during public demonstrations and educational programs[273,463,533]. Birds of prey used in public photo sessions may be passed repeatedly between the arms of inexperienced people[534]. Animals used in petting zoos and 'open house' in circuses may be touched and petted by hundreds of unfamiliar visitors. Elephants are often used for rides before and after circus performances[159,160], and one tethered circus camel was touched by 200 people in just one hour[26]. Contact with live animals has beneficial effects on human health[535-538] and is highly effective at educating the public and changing attitudes[273,539,540]. The impacts on the animals are less clear. Human-animal interactions can be positive, neutral or negative, and have the potential to affect animal welfare[60]. Handling effects on the physiology, health and emotions of animals depend on the individual, its temperament, past experiences, socialisation history and the nature of the contact[530,541].

Positive effects

Several reviews[530,542-544] report that gentle handling can reduce stress and fear in domestic animals such as dogs[545], donkeys and horses[546,547], and livestock[531,548,549]. There is also some evidence that nondomestic animals also benefit from human contact. Zoo-housed felids that spent more time with keepers had lower FGMs[107] and were more likely to reproduce successfully[550]. Leopard cats paced less when keepers were present[256], and chimpanzees exposed to ten minutes of positive interaction with a familiar keeper showed reduced abnormal behaviour and increased social grooming[551]. A similar trend was observed in marmosets that increased play and grooming when they spent more time with a familiar caretaker[552]. 'Play therapy' benefitted gorillas by increasing intraspecific social play and reducing abnormal behaviour[514]. Dolphins played more after participating in a dolphin-interaction programme that allowed petting by visitors, although it is unclear whether this was due to the petting or training aspect of the event[553].

Some nondomestic animals appear to enjoy or find comfort in human contact, e.g. rhinos and tapirs showed pleasure by laying down when being scratched[447], and birds of prey shook their feathers, a sign of comfort[554], at the sight of their familiar handler[449]. Some primates[555,556], koalas[316] and dolphins[553] actively initiated human contact, although in some cases this is food-motivated[60,530,533,544,557,558]: while this may make human contact a positive experience, begging may not contribute to good welfare.

Interactions between animals and their keepers are a permanent and influential feature of a captive animal's life[559,560]. Therefore it is important that they are positive, since human-animal relationships (HARs) influence animal welfare[561]. HARs form when a number of repeated interactions occur between the same animal and human, and each interaction builds on the positive or negative valence of the previous one, allowing each party to make predictions about the other's behaviour[562]. Zoo professionals commonly form HARs with zoo animals and these bonds are generally welfare-enhancing[563]. Some laboratory primates find routine human presence distressing[564] but those with more 'friendly' HARs with caretakers were more willing to approach humans and coped better with routine husbandry[559]. So positive HARs can be beneficial by facilitating coping[561].

The keeper-animal dyads formed in zoos are influenced by stockmanship style[560], and the relationship between stockmanship and productivity/welfare is well-documented in livestock[531,542]. Positive zookeeper attitudes towards animals, along with their knowledge and experience, has been associated with more positive HARs in various exotic species[472,478,560]. Caregivers that understood and employed species-specific interactions with chimpanzees had more friendly interactions with the animals[565], illustrating the significance of good species knowledge, and one study reported that animals were less fearful when cared for by keepers with high job satisfaction[472]. This supports the idea that the emotional state of animals and their keepers might be reciprocal and that this reciprocity might contribute to good animal (and keeper) welfare[472]. Interactions between tigers and keepers were related to the personality of the keeper, not the tiger[566]. Human behaviour is the factor that influences animal welfare and this is determined by our personality[537]. Evidently HARs are strongly influenced by the human participant, and staff with negative attitudes or insufficient education and experience will develop poorer quality HARs, which may compromise animal welfare by failing to reduce, or even enhance, stress. However, staff that form very strong and positive HARs can still compromise animal welfare if sentiment prevents humane medical treatment or euthanasia[537], or results in overfeeding[567].

Neutral effects

While a positive HAR with familiar caregivers can improve welfare, the HAR between animals and visitors is usually neutral or negative[60]. Visitors are largely ignorant of the communication cues used by animals, so a positive bidirectional HAR is highly unlikely to develop[521]. Wild animals such as birds of prey and elephants are able to differentiate between people[449,560,568]. Stimulus discrimination is a well-established phenomenon given the behavioural and physiological costs of inappropriate fear responses[543,569], and relationships with familiar caregivers are the most beneficial for animal welfare.

Handling may have no apparent effect on animals. Giving rides had no effect on salivary cortisol levels in dromedaries[570]. Ten minutes of gentle handling, the typical handling period for captive reptiles, had no effect on the behaviour or heterophil/lymphocyte ratios in ball pythons and blue-tongued skinks[273]. Gentle handling also had no effect on frog heart rates, although they were only handled for one minute[571]. Even more extensive and invasive procedures coupled with temporary (eight hour) captivity had no effect on plasma corticosterone concentrations or movement patterns of wild gopher tortoises[572]. Finally, swim-with-dolphin sessions had no significant effect on dolphin behaviour, possibly because there was a 'refuge area' at one end of the pool, which the dolphins used twice as much while visitors were in the pool[573].

Negative effects

When circus animals have developed a positive HAR with their handler or trainer, the sudden lack of interaction with familiar humans in the winter quarters may have a significant welfare impact. In winter, circus animals are not touring with their usual handlers and trainers, and may work abroad. Circus lions and tigers separated from their regular handler over the winter lost condition and became listless despite no change in diet, but rapidly regained condition following reunion with their familiar handler three months later[574]. The absence of an owner for a period of time (e.g. a holiday) also causes stress to pet parrots and contributes to feather plucking[575].

Handling can have significant negative effects on animal welfare. Capture is stressful for free-living wild animals[576], and physical capture is more stressful than chemical immobilisation[577]. Several species of wild caught birds showed a significant increase in plasma cortisol following capture and handling (placed in a cloth bag and blood sampled at regular intervals) that continued to rise for 60 minutes until release[578]. Wild-caught screech owls showed elevated plasma cortisol for up to 30 minutes[579]. Wild-caught tree lizards showed a rapid response to acute stress (four hours restraint in a bag) with a six-fold increase in plasma corticosterone in the first ten minutes that continued to rise over a four hour period[580]. Plasma corticosterone concentrations were initially undetectable in wild caught frogs, but rose six fold after a 24-hour period in captivity[581].

Handling also causes stress in long-term captive animals. Baseline FGM levels of male koalas handled and used for public photo sessions were 200% higher than unhandled males[582]. One minute of gentle handling caused an immediate increase in the heart rates of green iguanas, which took 10 minutes to return to baseline[571]. The same pattern of tachycardia has been observed in wood turtles, who also showed signs of stress fever[583]. So reptiles are capable of experiencing an emotional response to stress. Stress handling can also cause physical damage if done inappropriately, e.g. birds have fragile bones and incorrect handling procedures can damage wings and legs, or compromise breathing[584].

The reactions of animals to humans can be compared with their reactions to environmental enrichment to determine whether they perceive human contact as enriching[561]. Cognitive bias testing revealed that rhesus macaques had a more negative affective state after a veterinary assessment compared to after food-based enrichment that did not involve human contact[390], demonstrating that the monkeys considered the husbandry procedure to be a negative experience, affecting their emotions and thus psychological welfare. Early handling in blue fox cubs had an initial positive effect on growth, but this was short-lived because early-handled foxes showed higher physiological stress when adult than unhandled conspecifics[585].

Fear in wild animals is thought to be primarily species dependent, but is also influenced by past experiences including interactions with humans[586]. Handling that is perceived as aversive is stressful for animals and increases fear in livestock[543,548,549] and eland[272]. Repeated handling of birds of prey, such as in public photo sessions, can cause stress and damage the waterproofing of the plumage[534]. The timing of handling is important, both within the animal's life cycle and its physiological cycle. Handling at a particular stage of metamorphosis was associated with mortality in frogs[587]. Morning is the physiological resting time for koalas in captivity and the wild[316], and when visitor density is highest in zoos[588]. Handling and disturbance during physiological resting times interferes with activity patterns and time budgets[316] and can lead to higher stress levels[579,589].

Handling can cause serious damage to delicate animals such as those used in aquarium 'touch tanks': 51% of the UK's public aquaria have touch pool exhibits[151]. Handling stress can cause physical damage such as bruising, scale loss and skin abrasions, either directly through rough handling, or indirectly though stress, e.g. tissue regression in sponges[590], claw shedding in crabs[591], immunodeficiency in frogs and rays, escape behaviour in dogfish[592], stereotypies[151,591] and mortality in starfish[151,592]. Zoonotic diseases caused by pathogens introduced on human skin are also a potential danger[151,592,593]. Some touch tank animals, such as starfish, move too slowly to have any control over being touched, so aquaria rotate the individuals used in touch tanks to moderate handling stress[591,593].

Handling brings humans into close proximity with potentially dangerous animals and increases the risk of injury or death to both parties, particularly if animals are handled aversively[543]. Good knowledge of the species and personality of individual animals can help avert attack[280,464]. However, non-domesticated animals are unpredictable and will even attack familiar keepers under unusual circumstances, suggesting that HARs are not always as strong as people perceive[60]. Camels can bite, spit, kick, stamp and inflict serious and/or fatal injuries[280]. Males in rut are particularly dangerous and children have had their necks fractured by being lifted by the head and shaken[280]. Elephants can cause lethal injury and elephant keepers are more vulnerable to attack during FC handling and when adding or removing chains[464]. The behavioural patterns of nondomestic animals can cause their reactions to be unpredictable and there have been many reported attacks and injuries to both keepers and visitors[60,454,594]. Fear of mortality in humans influences our attitudes towards animals and contributes to exploitative and tempestuous HARs[595].

Ways to alleviate handling stress

Blindfolding, hooding and darkness can alleviate handling stress. Hoods used to calm birds of prey seem to disengage birds from their environment to some extent: hooded birds remain inactive and motionless[596] and hooding reduces stress caused by negative stimuli[449]. This helps keep birds calm in potentially stressful situations such as busy showgrounds or during transport[534]. Likewise, Adelie penguins showed a lower stress response when hooded and held by their legs than penguins restrained in a mesh bag inside a cardboard box[597]. However in farmed ostriches, time spent hooded and restrained in a holding pen prior to transportation was positively correlated with physiological stress pre- and post-transport, and some birds that were restrained for longer displayed immobile sitting behaviour, which was considered a tonic immobility response associated with stress[598].

Environmental unpredictability is defined as a single event that disrupts ‘normal’ ongoing activities[561]. Events, such as the density and behaviour of unfamiliar visitors may cause an animal stress[219,561,599]. While some stress is natural and acceptable, the ability to cope and adapt behaviourally, emotionally and physiologically, determines the welfare impact of a threatening situation[561,600]. Coping ability is affected by behavioural choices, which are often limited in captivity: in the wild animals can control the amount of stimulation they receive by approaching, attacking or hiding. High stimulus predictability and controllability causes the least behavioural or physiological disruption[219]. Increased predictability may reduce the impact of limited control, since learning to predict significant events and how to respond to them appropriately can help captive animals adapt to their environment and facilitate coping[600].

Ensuring that aversive events are temporally predictable and reliably signalled will alleviate some of the stress associated with lack of control by providing reliable ‘safety periods’ when the animals can relax[219]. For instance, a reliable signal prior to disturbance reduced the stress effects of construction noise in macaques[601], and brown capuchins showed less anxiety-related behaviour when keepers entered the enclosure if they knocked first[602]. Parrots[144] and rhesus macaques[185] housed further from the door had more pre-warning of human approach and therefore exhibited less abnormal behaviour than conspecifics near the door, which were subject to more unpredictable human disturbance. Cheetahs[603] and polar bears[594] also appeared less stressed when enclosure design allowed a view of the surroundings.

However, overly predictable routines can themselves be stressful for some species. Felids pace more when fed on a temporally predictable regime[244], particularly prior to anticipated feeding times[214,257], and pacing was reduced in cheetahs by varying feeding times[29]. Bears[243], otters[150] and chimpanzees[604] also showed more stereotypical behaviour when food was not predictably signalled. Signalled predictability may be more important than temporal predictability[219].

When not travelling, circus animals have a well-structured day, with regular training sessions and shows. Circus tigers that increase pacing before performances[167] may recognise the increased activity of handlers and influx of visitors as indicators that a performance is approaching. Stereotypic pacing can be a coping mechanism[127], and so these familiar and predictable cues appeared to trigger a learned coping response.

The value of predictability also applies to HARs in terms of familiarity. Being cared for by a higher number of different keepers impairs the development of a strong HAR[60]: the ensuing lack of familiarity caused stress in okapis[134] and clouded leopards[107], and increases the risk of attack[60]. Stereotypic licking is less common in giraffe and okapi fed at predictable times by familiar staff than conspecifics fed at unpredictable times by visitors[152]. Where circus animals have a small number of handlers, familiarity may aid the development of a positive HAR and subsequently facilitate coping.

Habituation

Although handling can cause stress for naïve animals[580,581], chronic exposure to an aversive stimulus can lessen the stress effect in some species[605]. Wild adult and juvenile kestrels habituated to repeated capture and restraint, as indicated by reduced corticosterone levels[606]. Wild-caught monkeys showed diminishing stress responses over time to routine husbandry such as room changes and tethering[284]. Captive koalas showed less resistance to capture if accustomed to daily rather than monthly handling[316], although lack of resistance may not represent lack of stress. In wombats, daily handling reduced human avoidance but not the physiological stress response, indicating that the wombats had entered into a state of learned helplessness[607]. However there is no evidence that animals habituate fully to involuntary restraint[271] or extreme or painful procedures[541,608]. Training should be used to encourage voluntary participation by animals rather than relying on habituation: this gives animals more choice and control and reduces the welfare impact of handling.

Hand rearing

Hand rearing is sometimes necessary when captive animals lack the skills or motivation to raise their own young; this can be a particular problem in some species[609]. However, working animals and those used in entertainment are often hand reared to facilitate easier handling and training in later life, such as birds of prey[275]. While hand rearing clearly benefits humans, it may have severe impacts on the animals. Hand-reared and captive-born animals develop a stronger affinity for keepers than parent-reared or wild-born counterparts, as seen in wolves and black rhinos, but they did not have less fear of humans[472]. Fearfulness reduces an animal's ability to cope with their environment, so although positive HARs with familiar keepers may be beneficial under specific circumstances they do not beget good welfare in general.

Early rearing experiences can have profound consequences on animals when adult, such as leading to abnormal behaviour and undeveloped social skills[120]. Hand-reared animals may be unable to communicate efficiently with conspecifics, e.g. human-imprinted raptors cannot be housed with conspecifics because they will attack them[448]. However, leaving owls with their parents for the first few weeks of life makes them more likely to breed successfully when adult[275]. Of four captive maned wolves, only the hand-reared wolf displayed stereotypic pacing[77]. Hand-reared chimpanzees have less developed social skills and often show increased aggression when housed at high social densities; socially experienced naturally-reared chimpanzees perform less agonistic behaviour at high social densities because they have learned not to accelerate aggression[171]. However, with proper management, some hand-reared zoo animals have been successfully integrated into social groups, e.g. acouchi and gorillas[447].

Visitor presence

Animals react to the presence, density, position and activity of visitors. Human observers have been associated with both adverse and, occasionally, enriching changes in animal behaviour and physiology[605]. Animals are aware of visual attention: apes can discriminate between face and body orientation[557], horses are sensitive to human gaze[610], and elephants recognise visual attention from human face orientation[611]. Regardless of any response, animals are clearly aware that they are being watched and this may cause distress if they are unable to escape[216].

Our review of the literature on the effects of human or visitor presence on a diversity of non-domesticated species showed visitor-induced stress in 63% of cases; 23% of studies reported no visitor effect and 3.5% reported that visitors had a positive effect on animal welfare (Table 1). The remaining studies were inconclusive. Species and individual differences in responses to human disturbance were common[182,286,291,612-614]. Sex differences were also reported, perhaps due to sexual dimorphism in perceived threat[612,614-617]. Visitor-induced stress was apparent in circus tigers when animal holding areas were open to the public prior to performances[167], suggesting that the regular handling/training of animals in circuses does not make them less sensitive to the effects of visitors than animals in other captive environments.

Table 1. The effects of visitor presence on non-domesticated animals

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Birds						
African penguin	54	Zoom Torino, Italy	Structurally enriched: vegetation and pool directly adjacent to human swimming pool	Visitor density did not affect adrenocortical activity	None	618
African penguin	54	Zoom Torino, Italy	Structurally enriched: vegetation and pool directly adjacent to human swimming pool	Visitor presence reduced pool use by penguins, especially at high visitor density, but only during May-July, at beginning and peak of visitor swimming season. By August visitors had no effect on penguin pool use, suggesting habituation	Stress, followed by habituation	619
Greater rhea	5	Belo Horizonte Zoo, Brazil	Wire-fenced, otherwise not described	Visitor presence increased vigilance but also behaviours indicative of relaxation such as stretching and nest building	None	620
Long-billed corella	1	Adelaide Zoo, Australia	Not described	Interacted more with humans on quiet than busy days. Spent 90-100% time at the front of the enclosure during human -bird interactions. When high visitor density spent less time at front of cage, suggesting a stimulus threshold. Some behaviours only performed if visitors present	Positive	621
Canids						
Bush dog	4	Belo Horizonte Zoo, Brazil	Paddock	Increased visitor density associated with increased activity	Ambivalent	617
Mexican wolf	12	Africam Safari Park, Chapultepec Zoo, San Juan de Aragon Zoo, Mexico	Naturalistic substrates and vegetation	Higher FGMs and spent less time eating and resting on days with more visitors	Stress	622
Elephants						
African elephant	4	Belo Horizonte Zoo, Brazil	Paddock	Females (n=3) showed reduced activity as visitor numbers increased	Stress	617

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
African elephant	10	Mabula Game Reserve, South Africa	Wild	In presence of game vehicles, increased clustering, vocalisation, temporal gland secretion and behaviour associated with disturbance or distress. Higher FGMs in elephants in part of reserve with highest human activity	Stress	90
African elephant	116	Serengeti National Park, Grumeti Game Reserve, Ikoma Open Area, Tanzania	Wild	FGMs lower in protected area (Serengeti National Park) than two partially protected areas where human disturbance higher	Possibly stress	623
Asian elephant	9	St Louis Zoo, USA	Structurally enriched: trees, stumps, rocks, pond	All elephants spent less time at front of enclosure closest to visitors. Some (n=3) exhibited less stereotypy at high visitor density, whereas visitors had no effect on others (n=2)	Stress	286
Asian elephant	6	Terra Natura Zoological Park, Spain	Internal courtyards before opening, dry meadows thereafter	Salivary cortisol higher in month zoo first opened to public than month prior to opening or second month after opening; could be due to habituation or end of construction work	Unclear due to con-founding factors	91
Felids						
Cheetah	4 adults, 11 cubs	Fota Wildlife Park, Ireland	Trees, dens	Activity and space use not influenced by visitor presence or noise. More likely to react to visitors that stood in front of, rather than behind, boundary rail	Probably none	624
Cheetah	15	12 zoos, USA	Not described	FGMs increased in cheetahs moved to on-exhibit enclosures, decreased in cheetahs moved to off-exhibit enclosures	Stress	85
Clouded leopard	72	12 zoos, USA	Various	FGMs higher in clouded leopards housed on-exhibit than conspecifics housed off-exhibit	Stress	107

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Indian leopard	16	Thiruvananthapuram Zoo, Arignar Anna Zoological Park, Shri Chamarajendra Zoological Gardens, Guindy Children's Park, India		Visitor presence associated with lower activity levels and increased use of the centre and back of enclosure. Presence/absence of visitors did not influence stereotypic pacing, but on days with unusually high visitor density stereotypic pacing increased greatly. Resting said to be visitor-avoidance motivated, pacing was visitor-escape motivated	Stress	216
Jaguar	2	Belo Horizonte Zoo, Brazil	Pit	Increased visitor density no effect on behaviour	None	617
Jaguar	2	Woodland Park Zoo, USA	Structurally enriched: pool, trees, platforms	One paced less when visitor noise high, the other did not exhibit pacing. At higher visitor densities, length of nonvisible bouts shorter, possibly due to visibility attracting more visitors	Ambivalent	613
Lion	4	Toronto Zoo, Canada	Structurally enriched: naturalistic, scratching posts	No effect of visitor density; increased looking at visitor area with higher visitor noise levels	None	359
Lion	4	Oakland Zoo, Canada	Not described	Visitor density correlated with less frequent social contact with conspecifics	Stress	359
Lion, Amur leopard, Siberian tiger, snow leopard, clouded leopard, fishing cat	14	Brookfield Zoo, USA	Not described	Visitor presence no effect on activity levels	None	27
Ocelot	5	Belo Horizonte Zoo, Brazil	Pit/cage	Increased visitor density associated with increased activity (n=1) and increased vigilance (n=2)	Possibly stress	617
Tiger	1	Toronto Zoo, Canada	Structurally enriched: trees, logs	Spent less time close to visitor area at high visitor density and high visitor noise	Possibly stress	359

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Tiger	4	Oakland Zoo, Canada	Structurally enriched: trees, logs, pools	No effect of visitor density on behaviour	None	359
Tiger	4	Ringling Brothers and Barnum and Bailey Circus	Cage	Increase in pacing during 'open house' prior to performances when animal holding areas open to public	Stress	167
Marsupials						
Kangaroo Island kangaroo	11	Melbourne Zoo, Healesville Sanctuary, Australia	Naturalistic free-range exhibits with trees, logs and grass	Visitor density positively correlated with visitor-directed vigilance, locomotion and decreased resting. Visitors no effect on distance from path or FGM concentration	Probably none	625
Koala	13	Koala Conservation Centre, Australia	Naturalistic: eucalyptus trees with boardwalk	Increased visitor noise and higher visitor density at close proximity (<5m) associated with increased vigilance, up to 25% of time awake - main activity usually resting, foraging; vigilance not previously reported. Total daily visitors had no effect on behaviour	Stress	626
Red kangaroo	4	Healesville Sanctuary, Australia	Naturalistic free-range exhibit with trees, logs and grass	Visitor density positively correlated with visitor-directed vigilance; had no effect on distance from path or FGM concentration	Probably none	625
Mongooses						
Meerkat	10	Melbourne Zoo, Werribee Zoo, Australia	Structurally enriched: digging substrates, climbing structures and naturalistic furniture	Visitor intensity (noise, attempted interaction) no effect on vigilance, distance to visitors or time spent looking at visitors	None	627
Pinnipeds						
Harbour seal	8	Antwerp Zoo, Belgium	Pool, beach and enrichment objects	At high visitor density seals spent more time swimming under water, less time resting or vigilant	Stress	58

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Primates						
Ring-tailed lemur, Mayotte lemur, black spider monkey, white-fronted capuchin, patas monkey, de Brazza monkey, Sykes monkey, talapoin, Barbary macaque, lion-tailed macaque, Celebes crested macaque, hamadryas baboon	61	Chester Zoo, UK	Structurally enriched: climbing structures	Animals tried to interact with visitors, particularly large (>5) and active audiences that tried to interact with an animal; also increased locomotion and time in edge zone. Social behaviour unaffected	Positive	555
Baboon	19	Southwest National Primate Research Center, USA	Individual cages with some small enrichment items	When human observer present, animals showed reduced appetitive behaviour but no other behavioural change	Stress	615
Black-capped capuchin	10	Melbourne Zoo, Australia	Structurally enriched: trees, logs and climbing structures	Avoided visitor viewing area - spent less time at height of visitor area	Stress	358
Bornean orangutan, Sumatran orangutan	12	Chester Zoo, UK	Structurally enriched: climbing frames, ropes, platform	High visitor density correlated with increased clinging by infants, adults covering heads with paper sacks. Responded more to increased visitor noise than visitor density	Stress	628

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Bornean orangutan, Sumatran orangutan, hybrid orangutan	11	Singapore Zoo, Singapore	Free-ranging enclosures: high canopy with real trees, vines, hammocks and platforms	Responded more negatively to close proximity visitors (<10m) where visitors at eye level: increased regurgitation, begging, looking at visitors; less play/social/ feeding behaviour. Only affected by visitor density when >40, suggesting proxim- ity more important than density. Where visitors below eye level, visitor density no effect, while close proximity visitors (<10m) increased feeding, begging and decreased regurgitation	Stress but also lack of fear	533
Brown howler monkey	4	Belo Horizonte Zoo, Brazil	Cage	Increased visitor density associated with increased vigilance	Stress	617
Chimpanzee	24	Chester Zoo, UK	Structurally enriched: climbing frames, ropes, logs	Humans and chimpanzees motivated to communicate with each other: chimpanzees do this mainly to obtain food	Positive	556
Chimpanzee	6	Oakland Zoo, Canada	Structurally enriched: climbing structures	No effect of visitor density on behaviour; slight increase in time spent in edge zone	None	359
Chimpanzee	88	Laboratory chimpanzee rehabilitation facility, USA	Structurally enriched: climbing structures, visual barriers, manipulable objects	Increased rates of wounding suggested increased aggression on weekdays when human activity higher	Stress	564
Chimpanzee	4	Belo Horizonte Zoo, Brazil	Pit	Increased visitor density associated with increased vigilance only in the two males	Stress	617
Chimpanzee	11	Los Angeles Zoo, USA	Sparsely furnished: tree stumps and hammock	On days of high visitor density, less foraging, grooming, play and interaction with enrichment objects	Stress	432

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Cotton -top tamarin, Diana monkey, ring-tailed lemur	12	Edinburgh Zoo, UK	Structurally enriched: ledges and dead trees	Reduced affiliation, increased activity and aggression when visitors present, especially in arboreal monkeys. Visitor effect reduced by 50% after lowering height of visitors	Stress	629
Cotton -topped tamarins	29	Rotterdam Zoological and Botanical Gardens, Netherlands	Structurally enriched: branches and nest boxes	Visitor density positively correlated with agonistic behaviour and negatively correlated with affiliative behaviour. Frequency of parent-offspring interactions lower in on-exhibit enclosures	Stress	630
Diana monkey	6	Edinburgh Zoo, UK	Structurally enriched: ropes, branches and climbing structures	Visitor density positively correlated with active behaviours (feeding, playing), negatively correlated with grooming, resting. Vigilance not affected	None	631
Golden lion tamarin	1	Toronto Zoo, Canada	Structurally enriched: naturalistic, climbing structures, mixed-species exhibit	Less grooming at high visitor density; no effect of visitor noise	Possibly stress	359
Golden-bellied capuchin	4	Belo Horizonte Zoo, Brazil	Island	Increased visitor density associated with increased vigilance and decreased abnormal behaviour	Ambivalent	617
Golden-bellied mangabey	10	Sacramento Zoo, USA	Sparsely enriched: three branches	Animals moved to cages with higher visitor density showed increased aggression toward visitors and cage mates	Stress	632
Golden-bellied mangabey	10	Sacramento Zoo, USA	Sparsely enriched: three branches	Human-directed threats more often towards visitors than keepers or observers. Visitors viewed as interlopers	Stress	633
Golden-headed lion tamarin	4	Belo Horizonte Zoo, Brazil	Cage	Increased visitor density associated with increased vigilance, activity	Stress	617

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Hamadryas baboon	2	Sapucaia do Sul Zoological Park, Brazil	Structurally enriched: climbing structures and tree	Male increased stress-related faeces-throwing when visitors present; no effect on female	Stress	291
Hamadryas baboon	5	Oakland Zoo, Canada	Structurally enriched: climbing structures	Visitor density correlated with increased foraging and decreased social grooming	None	359
Lion-tailed macaque	30	Arignar Anna Zoological Park, Jaipur Zoo, Mahendra Chaudhury Zoological Park, Maitri Baagh Zoo, National Zoological Park, Patna Zoo, State Museum and Zoo, Thiruvananthapuram Zoo, India	Enclosures of varying size and complexity	Visitor presence associated with 20% increase in abnormal behaviour and 3% increase in social, mating and aggressive behaviours. Used enriched areas of enclosure more on days with no visitors. Displayed aggression towards visitors 5.6 times per hour	Stress	558
Mandrill	3	Zoological Garden of Vienna, Austria	Sparsely furnished	Visitor density positively correlated with activity, stereotypical behaviour and attention to visitors	Stress	629
Mandrill	3	Parken Zoo, Sweden	Structurally enriched: climbing structures	Visitor density positively correlated with agonistic and abnormal behaviour, negatively correlated with rest and affiliative behaviour	Stress	634
Pileated gibbon	1	Blackpool Zoo, UK	Structurally enriched: branches, ropes and shelves	Visitor density positively correlated with self-biting but not chewing orality	Stress	635
Rhesus macaque	20	Southwest National Primate Research Center, USA	Individual cages with some small enrichment items	When human observer present, animals showed reduced appetitive and manipulative behaviour and increased rest, particularly in females	Stress	615

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Ring-tailed lemur, mongoose lemur, red-ruffed lemur, squirrel monkey, Francois langur, spot-nosed monkey, De Brazza's monkey, golden-bellied mangabey, gibbon, orangutan, chimpanzee	39	Sacramento Zoo, USA	Structurally enriched: climbing structures, ropes, trees/ branches	Locomotion increased when visitors present, as did time spent in edge zone. Active audiences elicited more visitor-directed behaviour than passive audiences, particularly large audiences. Visitors no effect on intragroup social behaviour	Stress but also lack of fear	636
Siamang	6	Adelaide Zoo, Australia		Visitor presence caused no change in activity but siamangs more hostile when visitors mimicked agonistic siamang behaviour such as yawning, staring	Some stress	621
Siamang, white-cheeked gibbon	5	Disney's Animal Kingdom, USA	Structurally enriched: trees, ropes, climbing structures	Spent more time out of sight or in areas far from visitors on days of high visitor density; visitors no other effect on behaviour	Stress	637
Spider monkey	7	Chester Zoo, UK	Structurally enriched: climbing frames, ropes, logs	Increased visitor density associated with increased urinary glucocorticoid metabolite concentrations UGMs	Stress	638
Squirrel monkey	5	Oakland Zoo, Canada	Structurally enriched: naturalistic, climbing structures	Visitor density correlated with increased locomotion and vigilance, decreased time out of sight	Ambivalent	359

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Sumatran orangutan	6	Toronto Zoo, Canada	Structurally enriched: naturalistic, climbing structures	No significant effect of visitor density on behaviour but slight increase in looking at visitors; higher visitor noise associated with increased social grooming	None	359
Western lowland gorilla	12	Port Lympne Zoo, UK	Structurally enriched: climbing frames, ropes, movable objects	Visitor numbers correlated with self-scratching and visual monitoring, but only in absence of feeding enrichment	Stress	639
Western lowland gorilla	8	Chessington Zoo, UK	Structurally enriched: climbing frames, ropes, movable objects	Visitor numbers not correlated with self-scratching or visual monitoring, regardless of enrichment	None	639
Western lowland gorilla	5	Toronto Zoo, Canada	Structurally enriched: naturalistic, climbing structures	No effect of visitor density on behaviour; social play decreased as visitor noise increased	Some stress	359
Western lowland gorilla	13	Bai Hokou study site, Republic of Congo	Wild (habituated to humans)	Tourist density no significant effect on activity budgets or human-directed aggression, but researcher density negatively correlated with feeding rate. For silverback, visitor proximity positively correlated with human-monitoring (vigilance); he directed less aggression towards observers >10m away	Some stress	616
Western lowland gorilla	10	Disney's Animal Kingdom, USA	Structurally enriched: dense plant material, rocks, visual barriers	On days with high visitor numbers, spent more time out of sight; individuals in bachelor groups showed increased aggression but those in family groups no change in aggression with visitor density	Stress	640
Western lowland gorilla	1	Belo Horizonte Zoo, Brazil	Pit	Increased visitor density associated with increased vigilance	Stress	617

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Western lowland gorilla	18	Zoo Atlanta, USA	Structurally enriched: vegetation, rocks, climbing structures	Abnormal behaviour increased in response to high visitor density in two groups, decreased in other two groups. Visitors no effect on behaviour, suggestive of good welfare. Males tend towards increased aggression at high visitor density	Ambiva-lent	614
Western lowland gorilla	6	Belfast Zoological Gardens, Ireland	Structurally enriched: climbing structures	Rested more at low visitor density; increased aggression, autogrooming and stereotypical behaviour at high visitor density	Stress	641
White-faced capuchin	7	Barro Colorado Island, USA	Wild (habituated to humans)	Visitor presence no effect on activity or movements (speed/stopping frequency) of radio-collared monkeys	None	642
Ungulates						
Zulu suni, slender-horn gazelle, Dorcas gazelle, impala, yellow-backed duiker, Mhorr's gazelle, lowland nyala, Nile lechwe, Arabian oryx, bongo, sable, greater kudu	46	San Diego Zoo, USA	Paddocks with shelter	When keepers entered enclosure, animals vocalised more and fed and drank less, but no increase in defecation, indicating the event was more distracting (interrupted spatial cohesiveness) than stressful. Females showed less vigilance when visitors present; showed more vigilance overall than males towards visitors and keepers	Probably none	612

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Black rhinoceros	26	10 zoos, USA	Various	Higher FGMs in enclosures exposed to public on greater portion of perimeter	Stress	82
Black rhinoceros	60	19 zoos, USA	Various	Mortality positively correlated with percentage of the enclosure perimeter that allowed visitors unobstructed view	Stress	241
Chinese goral	63	Omkoi Wildlife Sanctuary and Chiang Mai Night Safari, Thailand	Structurally enriched: rocks	Higher FGMs on-exhibit than conspecifics off-exhibit; on-exhibit animals also housed at higher density	Stress	99
Giraffe	2	Belo Horizonte Zoo, Brazil	Paddock	Increased visitor density associated with increased activity	Ambivalent	617
Indian blackbuck	8	Arignar Anna Zoological Park, India	Trees and shelters	Visitor density positively correlated with intergroup aggression, locomotion and higher FGMs; rested more at low visitor density	Stress	643
Indian gaur	4	Arignar Anna Zoological Park, India	Paddock with trees and platform	Higher levels of intragroup aggression and locomotion on days when visitors present; increased resting when no visitors	Stress	644
Indian rhinoceros	2	Terra Natura Zoological Park, Spain	Internal courtyards before opening, dry meadows thereafter	Salivary cortisol higher in month when zoo first opened to public than in month prior to opening or second month after opening; could be due to habituation or end of construction work	Unclear due to con-founding factors	91
Pampas deer	189	Emas National Park, Brazil	Wild	Deer from areas with frequent human disturbance higher FGMs and flight distances than in areas with low human activity	Stress	103
Red deer	40	Agricultural and Pastoral Research Institute, New Zealand	Fenced pasture	Increased vigilance during, and increased aggression after approach and presence of human in paddock	Stress	645
Red deer	3	Belo Horizonte Zoo, Brazil	Paddock	Increased visitor density associated with increased vigilance	Stress	617

Species	*N*	Institution	Enclosure type	Response	Visitor effect	Source
Sika deer	21	Zhu-Yu-Wan Park, China	Fenced paddock with trees	Increased visitor density associated with increased vigilance and resting at expense of time foraging	Stress	646
Waterbuck	3	Belo Horizonte Zoo, Brazil	Paddock	Increased visitor density no effect on behaviour	None	617
Ursids						
Polar bear	3	Toronto Zoo, Canada	Structurally enriched: pool, rocks, barrels	No significant effect of visitor density on behaviour but slight increase in looking at visitors; less investigatory behaviour with higher visitor noise	None	359
Polar bear	3	Toronto Zoo, Canada	Structurally enriched: pool, rocks, barrels	Higher visitor density associated with increased stereotypical behaviour in one but reduced stereotypy in other two	Ambivalent	182

Visitor effects include changes in activity levels[216,617,629], changes in stress-related behaviour[216,629,635,639,641] and avoidance[359]. Some species show increased mortality in response to public viewing[241]. Changes in social behaviour caused by human disturbance are common[163,359,533,629,630,634] and may contribute to low reproductive success[630].

The most common response to human presence is increased vigilance, which may have an impact on welfare if it is prolonged and at the expense of self-maintaining activities such as rest or foraging[646]. Vigilance is thought to be associated with perceived threat or stressful excitement[621,629]: smaller species may be more likely to perceive humans as a threat and so may be more likely to be adversely affected by visitors[27,605,629]. Vigilance could also be in anticipation of food, e.g. tigers became vigilant when they saw their keeper[28]. Some species associate visitors with food acquisition opportunities[533,556]; food solicitation suggests a lack of fear and begging animals may find visitors enriching if they throw food[605].

Visitor density, proximity and noise are often discrete variables[359] and may have specific effects on different animals. Some animals appear to be more strongly affected by visitor noise than density[359,628]. Others are more sensitive to visitor proximity[533,616,624]. The visitor effect is influenced by a multitude of factors, including individual history, species, housing conditions and the behaviour of the human audience. The most negative aspect of visitors may be the nature of the interaction, rather than density or proximity, combined with the animal's inability to escape[647]. Visitor interest in zoo exhibits is higher when the animals are active[27], so visitors may attempt to stimulate activity. Active audiences that attempt to interact with the animals are likely to cause behavioural changes[555,605,636]. Interacting with visitors can be a source of stimulation for some species or individuals, which may actively seek human contact[555,556,621]. However, zoo visitors that initiate interactions with animals are likely to be ignorant of an animal's communication cues and how to respond to them appropriately[521], and this lack of bidirectional communication allows animals little control over the interaction. This is likely to be a particular problem for circus animals due to the small size and relatively barren nature of many circus animal enclosures. Some animals respond differently to familiar and unfamiliar humans[612]. Mangabeys displayed significantly more threats towards unfamiliar zoo visitors than keepers or researchers, and appeared to treat visitors as 'interlopers'[633].

Housing conditions are likely to influence an animal's ability to cope with visitors. Cotton-top tamarins showed less affiliative, and more agonistic, behaviour towards conspecifics when housed in glass-fronted than mesh-fronted cages[630], and mandrills showed less agonistic and stereotypic behaviour after a glass viewing panel was covered with a visual barrier[357]. Housing conditions that offer limited opportunity to escape the gaze of visitors may affect welfare if animals are unable to control the extent of human contact[605]. Some wild-habituated species show very little response to human observers[616,642], possibly due to having adequate escape distance and more control over the situation. Chimpanzees and gorillas spent less time watching visitors after translocation to a more enriched exhibit with access to outside space[648]. More complex environments that offer greater behavioural and locational choice will help animals to cope with disturbance through distraction and opportunity to escape. So the visitor effect will generally be smaller for animals in enclosures that allow them greater choice and control of animal-visitor interaction[647]: larger enclosures control visitor proximity and complexity provides opportunities for escape and distraction[588,605].

Noise and disturbance

Gates, vehicles, machinery, crowds and caretaking activities all increase sound pressure levels in captive environments beyond that in nature[25,649], where most noise arises from wind and animal vocalisations, and sound pressure rarely exceeds 40 dB[650]. Routine husbandry activities emit sounds between 60-80 dB, reversing trucks exceed 90 dB, and average noise levels in cities range between 50-80 dB[651]. Zoo noise averages 60-80 dB[113,627,652], but can climb to 130 dB on busy days[617], and 65 dB is considered a quiet day for a zoo[113]. Higher intensity sounds include firework displays (120 dB)[25] and jet aircraft (80-120 dB)[649,653,654], and captive animals are frequently exposed to sound pressures that exceed the recommended limit for human well-being (<70 dB)[655].

How animals perceive and respond to different sounds will depend on the characteristics of the stimulus and the context in which it is presented[656] (Table 2). Noise responses also depend on an animal's audible range[657]: this varies widely between species[649]. Many animals are capable of detecting sound outside the range detectable by humans, and animals used in travelling circuses and mobile zoos will be exposed to a wide spectrum of both ultrasonic and infrasonic sounds. Snake auditory systems are not particularly sensitive to sound but they are remarkably sensitive to vibration of the head and body[658]. Both African and Asian elephants produce and detect infrasonic calls[659,660], and can recognise calls from familiar conspecifics over distances of up to 2.5 km[661]. Cars, heavy goods vehicles and buses produce high levels of infrasound, up to and over 100 dB, and road surface conditions can add to the levels of infrasound[662]. Species sensitive to seismic vibrations such as snakes[663], kangaroos[664], elephants[665] and some birds, or infrasound like alligators, elephants, giraffe, hippopotamus, okapi, prairie dogs, rhinoceros and tigers[25], may be distressed by excessive anthropogenic vibration and infrasound from diesel engines, wind turbines, fireworks and aircraft. Species sensitive to ultrasound such as prairie dogs and ground squirrels may respond to the high frequency sounds emitted from computer monitors and fluorescent lights[25].

Table 2. Effects of noise and disturbance on wild animals

Species	*N*	Location	Type of disturbance	Sound pressure	Response to noise or disturbance	Noise effect	Authors
Reptiles							
Desert tortoise	14	Laboratory	Simulated sonic and subsonic aircraft noise	Subsonic (94-114 dB), supersonic (0.25-6 psf)	Subsonic booms induced defensive responses including freezing, head withdrawals and vigilance which resulted in reduced activity and consequently reduced mean heart rate. Freezing duration decreased rapidly with subsequent exposure. Sonic booms induced brief bouts of vigilance. No hearing loss was caused.	Stress and habituation	654
Birds							
Bald eagle	≥ 127	Wild	Firearms	82-116 dB	Most birds showed tonic immobility and sometimes a head turn. Nesting birds were less likely to be active after firing than roosting birds. No impact on nest success	Mild stress	666
California spotted owl	9	Wild	1 hour of chainsaw sound 100m away	50-60 dB	No detectable increase in FGMs	None	667
Ferruginous hawk, northern harrier, burrowing owl, short-eared owl	200+	Wild	Military training including artillery firing	Not measured	No effect on nest distribution or success	None	668
Hawaiian honeycreepers	10	Zoo	Music concerts and machinery noise	Subjective	Decreased FGMs, foraging, general activity levels and courtship	Stress	130
Northern spotted owl	36	Wild	Proximity to major logging road	Not measured	Higher FGMs in males whose home ranges were within 400m of the road compared to males further away. No effect in females	Mild stress	96
Prairie falcon	333	Wild	Military activity	Not measured	Fewer falcons observed during constant military activity than during intermittent activity, and lower abundance in closer proximity to military training areas	Mild stress	669

Species	*N*	Location	Type of disturbance	Sound pressure	Response to noise or disturbance	Noise effect	Authors
Mammals							
Common marmoset	9	Laboratory	Human activity: Cage building and loud talking	Subjective	Elevated saliva cortisol	Stress	670
Black-tufted marmoset	-	Wild - city centre park	Urban noise	50-80 dB	Avoided noisy areas (>55dB) of the park, regardless of food availability, suggesting space use was based on noise minimisation rather than foraging efficiency	Mild stress	651
Black and white ruffed lemur	10	Zoo	Visitor noise	61-75 dB	Reduced grooming and locomotion; increased feeding (this possibly attracted visitors and led to increased noise rather than being caused by noise)	Mild stress	652
Cynomolgus macaque	16	Laboratory	10 days of recorded detonations	92 dB(A)	Eight animals received a signal before playback and eight did not. The signal group showed no behavioural or physiological response to playback, but the control group had elevated immunoreactive cortisol metabolites	Stress and habituation	601
Diana monkey	2	Zoo	Visitor noise	61-75 dB	No behavioural effect	None	652
Emperor tamarin	3	Zoo	Visitor noise	61-75 dB	Decreased resting	Mild stress	652
Golden lion tamarin	1	Zoo	Visitor noise	Not reported	No behavioural effect	None	359
Javan leaf monkey	5	Zoo	Visitor noise	61-75 dB	Decreased locomotion; increased feeding (this possibly attracted visitors and led to increased noise rather than being caused by noise)	Mild stress	652
Orangutan		Zoo	Visitor noise	Subjective	Increased clinging by infants and looking at the visitor area	Mild stress	628
Orangutan	6	Zoo	Visitor noise	67-83 dB	Increased social grooming	Probably none	359

Species	*N*	Location	Type of disturbance	Sound pressure	Response to noise or disturbance	Noise effect	Authors
Rhesus macaque	24	Laboratory	White noise	100 dB	Higher plasma cortisol and less social contact behaviour, but only if no control over the noise: monkeys that could control noise levels were not significantly different from peers not exposed to noise	Stress and habituation	671
Silvery marmoset	3	Zoo	Visitor noise	61-75 dB	Decreased resting.	Mild stress	652
Variegated Columbian spider monkey	4	Zoo	Visitor noise	61-75 dB	Increased aggression	Stress	652
Western lowland gorilla	5	Zoo	Visitor noise	63-80 dB	Decreased social play	Mild stress	359
Western lowland gorilla	4	Zoo	Simulated caretaker sounds	60-80 dB	Increased clinging by infants, increased activ-ity and displays (signs of arousal) in adults	Stress	385
African nocturnal primates, small ungulates and mam-malian carnivores	N/A	Wild	Proximity to roads	Not measured	Biodiversity declined steeply closer (<30m) to roads	Stress	672
Caribou (female only)	10	Wild	Low-altitude aircraft	46-127 dB	Responses were mild in late winter (disturbed sleep and consequently increased resting bouts) and strongest during post-calving (increased activity and locomotion)	Stress	653
Maghrebi dromedary	8	Farm - milking parlour	Unusual sounds	Subjective	Inhibition or disruption of milk removal and increased vigilance and escape attempts	Stress	59
Mule deer	45	Wild	Oil and gas development	Not measured	Space use changed: Selected habitats further away from the development that were not favoured before	Stress	673

Species	*N*	Location	Type of disturbance	Sound pressure	Response to noise or disturbance	Noise effect	Authors
Red deer	40	Paddock	ACDC song 'Thunder-struck'	90 dB	Increased aggression during song and remained more vigilant afterwards, though only for 10-15 minutes. The presence of a shelter did not lessen this response	Stress	645
Elephant	3	Zoo	Enclosure renovations	Not measured	One female showed an increase in serum cortisol during and after renovations but the other two elephants showed no change	Ambiguous	300
Giant panda	2	Zoo	Ambient noise	60-84 dB	On loud days pandas showed increased locomotion, scratching, agitated vocalisations, UGMs and door-directed behaviour. Brief loud noise induced behavioural distress and chronic low-amplitude noise elevated UGMs. The female was especially sensitive to noise during oestrus and lactation	Stress	113
Giant panda	2	Zoo	Construction noise	30-110 dB	Increased activity, door-directed behaviour, and stereotypic and stress-related behaviour. Increased UGMs may have been due to seasonal effects and they did not avoid noisier areas	Stress	674
Black leopard, serval, Afghan leopard, snow leopard	5	Zoo	Exhibit construction	Subjective	Decreased activity, decreased pacing, decreased time spent visible and elevated FGMs	Mild stress	675
Cheetah	15	Zoo	Visitor noise	Subjective	No effect on activity or space use	None	624
Coyote	6	Zoo	Noise, fireworks and music from a festival	Subjective	5 individuals showed a 5-fold increase in FGMs compared to baseline, and the extent of the stress response was greater in individuals housed closer to the noise	Stress	676

Species	*N*	Location	Type of disturbance	Sound pressure	Response to noise or disturbance	Noise effect	Authors
Chipmunk	23	Wild	Logging area vs. undisturbed area	Not measured	Higher FGMs in logging area	Stress	73
Koala	13	Zoo	Visitor noise	Subjective	Increased vigilance (up to 25% awake time)	Mild stress	626
Jaguar	2	Zoo	Visitor noise	Subjective	One individual paced less when visitor noise was high (the other did not exhibit pacing behaviour)	Unclear	613
Lion	4	Zoo	Visitor noise	55-80 dB	Increased looking at the visitor area	Mild stress	359
Meerkat	10	Zoo	Visitor noise	51-55 dB	No effect on vigilance, distance to visitors or time spent looking at visitors	None	627
Polar bear	3	Zoo	Visitor noise	57-78 dB	Less investigatory (sniff object) behaviour at higher visitor noise	Probably none	359
Tiger	4	Zoo	Visitor noise	62-78 dB	Spent less time close to the visitor area	Mild stress	359

Exposure to noise is a potential stressor in a range of species and systems. In farmed animals noise is associated with impaired maternal behaviour, altered time budgets and reduced growth, feeding efficiency, milk yield and reproductive output[59,649]. Terrestrial wildlife species start to respond to noise levels above 40 dB and welfare impacts have been documented below 50 dB, while 50% of aquatic studies detected a biological response at or below 125 dB (63.5 dB after accounting for the pressure difference)[677]. For wildlife, acoustic masking can impair reproductive efforts in species such as frogs and birds that rely on acoustic communication[678,679], or foraging in species such as some birds of prey and lemurs that use sound to hunt[678]. In marine mammals noise is associated with accelerated ageing, reproductive suppression and symptoms of sickness[680]. Some zoo animals showed greater stress responses to visitor noise than visitor density, e.g. orangutans[628], jaguars[613], lions and gorillas[359] and koalas[626].

Noise can impair social behaviour[359,645,652,671], interfere with activity and sleeping patterns[113,385,652-654,674,675], or alter space use by triggering avoidance[359], particularly in free-living wild animals[651,669,672,673]. Animals often show increased vigilance[59,359,626,628,645,654,678] and sometimes escape behaviour[59,113,674] in response to noise. Tonic immobility, a sign of fear characterised by freezing or death feigning[192], was triggered by aircraft noise in tortoises[654] and by gunfire in bald eagles[666].

Noise can lead to DNA damage and alter gene expression, which has implications for developmental, physiological and immunological processes[681]. Cell damage is not always reversible if perturbations occur at key developmental stages, e.g. young animals that are still developing may be especially sensitive[656]. Increases in plasma GCs may be related to noise intensity[682], and elevated cortisol in response to noise has been observed in a variety of captive and wild animals[96,113,300,602,671,675,676]. This general stress reaction will influence most organs, leading to short-term and potentially long-term physiological and behavioural alterations[649]. There may be age[385,628,656], sex[96] and individual[113,300,613,674] differences in response to noise. Animals may be more sensitive to noise during certain parts of the reproductive cycle[113], and the effects of noise may depend on lifestyle[679]. Providing barriers and refuge areas may do little to reduce noise expose: noise levels inside glass-fronted zoo enclosures were just 4 dB quieter than in the visitor area outside[359], and providing a shelter did not reduce the behavioural response to loud music in red deer[645].

However, several studies found no detrimental effect of noise on animals[359,624,627,652,667,668]. The absence of a physiological response may be due to experimental design, such as if the noise intensity did not exceed the threshold to elicit a detectable response, e.g. 85 dB for rats[682]. Increased vigilance or looking to locate the source of sound was common but will only have a serious effect on welfare if self-maintaining behaviours are inhibited, such as foraging in koalas[626]. Fear caused by noise only seems to last as long as the stimulus; red deer returned to normal activity within 15 minutes[645]. Despite showing increased agitated behaviour on louder days, pandas did not avoid noisier areas of their enclosure[674].

A lack of avoidance may indicate habituation i.e. animals 'getting used to' a stimulus, whereas acclimatisation means the stimulus no longer evokes a physiological stress response[656]. Some animals appear to show rapid behavioural acclimatisation to noise[602,649,654,671]. The rate of acclimatisation depends on a balance between the regularity of exposure to the stimulus and the perceived level of threat it presents. Animals will acclimatise faster to stimuli that are similar, repeated regularly and perceived as small threats[656]. Macaques that received a signal prior to noise playback[602] or had control over the noise levels[671] showed no evidence of a stress response to the noise. However, a reduced behavioural response to noise may indicate a learned tolerance rather than acclimatisation, e.g. if the energetic cost of a response is too high[657,680]. While behavioural acclimatisation is often seen in wildlife[678,679], physiological acclimatisation to noise is uncommon in wild animals, suggesting that noise still elicits a stress response under apparent habituation[656].

Gradual-onset, repetitive or chronic background noise may be less distressing and easier to habituate to than unpredictable, irregular or high amplitude noise[25,649]. The sound of visitors viewing captive animals is discontinuous with occasional loud peaks[617,652]. Perching hawks are easily disturbed by sudden human noise or inappropriate movements[596]. Sudden loud noise from low-flying jets during a training exercise was associated with an extreme case of mass-cannibalism in farmed mink[683], although a review on responses to intermittent sonic booms reported that startling was the most common response among mink and the noise did not impair reproductive success[684]. However, the same review also detailed several compensation claims by farmers and pet owners whose animals had been injured or killed in fear responses to sonic booms.

An observed response does not necessarily reflect the magnitude of the impact experienced by the animal[656]. Many studies on the effects of noise on animals are not under controlled conditions. Where animals showed no response, it may be that the baseline noise level was not significantly less aversive than the elevated noise level[627]. Where hormonal stress indicators are used, detected levels may have been confounded by circadian or seasonal variation, or general dysregulated hormonal function due to chronic stress[76]. Behavioural responses are influenced by the psychological state of the individual, which is the product of multiple factors including physical condition and past experiences[656].

Context may be the single most important factor in mediating the stress response, particularly in terms of predictability and the available choice of behavioural responses, so it is impossible to determine the physiological and psychological effects of noise on an animal based on behaviour alone and without contextual information[656]. The contexts of animals in zoos and laboratories will differ widely from wild conspecifics. Likewise noise effect studies are frequently confounded by a multitude of interacting variables that render it almost impossible to isolate the primary driving influence behind any detected response[677,681].

Few studies have considered the possible long-term effects of chronic noise exposure, which is widespread[678]. Cumulative effects from repeated long-term exposure to aversive stimuli may have a more significant impact on animal welfare than acute exposure to individual short-term stimuli[656,677,681,685], and the additive effects of noise, human disturbance, lack of choice and inappropriate housing conditions may all act synergistically (or obstructively) to produce a more damaging effect than any single factor in isolation[681].

The social environment

The availability of appropriate social contacts and protection from aggression were among the most important welfare issues identified in our circus questionnaire and in an earlier survey[686]. Lack of opportunity to exhibit natural social behaviours with conspecifics may contribute to poor psychological welfare in both wild and domesticated species: domestic horses still exhibit the same repertoire of social behaviours as their wild counterparts[687]. Inadequate social groupings have serious impacts on animal welfare, including stress, aggression, abnormal behaviour, reproductive failure and early mortality[688].

Solitary species

Solitary species can suffer when housed in groups. When housed in groups of five or more, duikers had stress-related jaw abscesses and a 50% shorter life expectancy than those housed in groups of three or fewer[322]. Canadian lynx housed alone had the lowest FGMs and mixed-sex groups of three or more had the highest FGM levels[230]. Okapis paced more as the number of neighbouring conspecifics increased[134]. Two pair-housed polar bears continuously maximised the inter-individual distance and rarely occupied the same enclosure zone[689]. This reiterates the importance of multiple complexity in space-restricting enclosures to maximise behavioural opportunities available to all cohabitants and facilitate social avoidance.

In the wild, sociality is determined by a multitude of factors including predation risk, foraging efficiency, parasite reduction and parental care. Captive animals are not at risk from the same environmental pressures and their optimal group size may be more flexible[688]. While primarily solitary in the wild, tigers explored more and paced less when housed in sibling pairs as opposed to alone, possibly owing to increased opportunity for play and stalking behaviour[28]. Separating group-housed tigers into individual enclosures at night had no significant effect on behaviour[690]. The activity levels of snow leopards, also primarily solitary, were not significantly different when housed alone or in a group, but group-housed animals displayed a wider behavioural diversity, including social play, allogrooming and vocalisations[691]. Similarly, three polar bears exhibited more stereotypical behaviour when conspecifics were inactive and less when they were all active concurrently, and one female exhibited more stereotypical behaviour when conspecifics were out of sight[182]. One spectacled bear's stereotypic behaviour was negatively correlated with frequency of intraspecific interaction with cage mates[62], even though spectacled bears are solitary in the wild. So conspecifics may be a source of stimulation for some individuals that are normally considered to be solitary.

Social species

Depriving animals of opportunities to perform motivated social behaviours such as allogrooming and mating can result in chronic stress, abnormal behaviour, impaired development and social and reproductive incompetence[688]. Housing social species singly is stressful, e.g. 57% of young parrots housed alone developed stereotypical behaviour within a year, whereas no pair-housed parrots did[692]. Marmosets showed a rise in saliva cortisol in response to social isolation[670]. Caged parrots exhibited less stereotypy when they were housed with more neighbours[144]. Stereotypic hair-pulling behaviour in primates is positively correlated with natural group size, suggesting that highly social primates housed in small groups or alone may experience frustrated motivation for allogrooming, indicative of poor psychological welfare: this may manifest as over-grooming and hair-pulling, leading to poor physical welfare[227]. Rhesus macaques[347] and squirrel monkeys[693] showed more species-typical behaviour and less abnormal behaviour when group-housed than when housed singly. Social partners were more effective at improving welfare than 'inanimate' object enrichment[347]. Young pair-housed parrots showed increased activity and exploratory behaviour, and spent less time preening and screaming, than singly housed conspecifics[692].

Solitary cheetahs paced more than group-housed conspecifics[244]. Though the study did not report a sex effect, group-housed male cheetahs commonly form stable coalitions[694,695], as they do in the wild[696], suggesting that solitary housing may cause social deprivation. Female cheetahs however are typically solitary in the wild[696] and pair housing can cause significant stress, manifesting as aggression and prolonged anoestrus[84], although one of the six pairs in that study developed a strong bond, characterised by allogrooming, lack of agonism and uninterrupted oestrus cycling. This indicates the importance of compatibility in socially-housed animals.

Access to members of the opposite sex can also improve welfare in captivity. Allowing male dromedaries just 30 minutes exposure to females per day significantly reduced plasma cortisol and increased walking, reduced the time spent feeding and ruminating[697], and increased sexual behaviour[698].

Group composition

Both group size and composition are important. African and Asian elephants have complex societies that differ between the sexes. Females live in largely related, hierarchical groups centred on the offspring and led by a matriarch[329]. Average group size ranges from 12-18 individuals, although groups of up to 52 have been reported in African elephants[138,329,699]. Females typically stay with their natal group their whole lives[699] but may encounter hundreds of other individuals from other families in the population, suggesting that elephants have an extensive social network[329]. In contrast, the social networks of captive elephants are extremely limited. At least 75% of captive (zoo) female elephants are housed in groups of four or less primarily unrelated individuals, and sometimes completely alone[138]. Elephants are expensive to feed and manage, and this may limit group sizes in circuses and other private businesses. Stress due to social deprivation is clear in singly housed elephants. One solitary female spent 24-52% of the day performing stereotypic behaviour[217], another 31%[599], and social isolation was correlated with increased stereotypy[700]. Merging two small groups of Asian elephants led to an increase in social behaviour in all individuals and a reduction in stereotypical behaviour in all but one, although there was some initial stress and behavioural patterns took longer than six months to return to baseline[701].

Optimal group composition may vary seasonally or as animals mature. In farmed silver foxes, group housing had a more beneficial effect on cubs than vixens[226] and group-housed foxes showed increased aggression in late autumn coinciding with the onset of dispersal in wild foxes[585]. Similarly, wolves and wolf-dog crosses showed increased aggression during winter compared to autumn and spring, though most aggression was noncontact [702]. The presence of playful juveniles can weaken social bonds between adults and produce chronic cortisol increases, e.g. in squirrel monkeys[703], and housing female mink with their kits beyond weaning age led to increased plasma cortisol levels and bite wounds in the mothers[704]. In the wild, mothers spend less time with their young over weaning, but this is generally not possible in captivity. Family groups will require additional space and, where possible, playmates to reduce stress from overcrowding and unreciprocated infant-adult play attempts. Wild male elephants disperse when they reach adolescence at 10 to 20 years and join bachelor groups[705]. Adolescence is a time of learning and social development and is arguably the most important life stage for male elephants[705]. The importance of sex-appropriate social housing during adolescence has also been reported in male guinea pigs[101]. Depriving animals of appropriate social opportunities during this critical period may impair normal development, leading to severe social deprivation and significant welfare problems later in life. However, bull elephants are far less common than females in captivity[138]: they are extremely dangerous and difficult to handle during musth and so require specialist safety equipment[706]. Consequently zoos that house males for breeding purposes often only keep one, although group housing is slowly becoming more common in zoos[706].

Captive animals have fewer opportunities to make social adjustments to alleviate social stress or locate compatible breeding partners[688]. Reproductive failure in captivity is often attributable to restricted mate choice, e.g. ostriches[707]. Social species are often less fearful when group-housed, e.g. parrots[692] and bears[708]. Social partners can help buffer responses to stress[703] and may aid habituation, which is partially acquired by social learning[709]. Allogrooming is thought to function as a stress-reducer in zebra, since it occurs most often in small enclosures when animals are at high density[35].

However, incompatibility with housing partners can lead to increased aggression, injury and psychological trauma[707]. This can be alleviated by increasing the choice of social partners by group housing, but housing social species at densities that are too high may lead to social stress[707]. Overcrowding has led to: lower nesting success in alligators[95]; cannibalism by larger conspecifics in South African clawed frogs[352]; increased aggression in red deer[710] and zebra[35]; increased stereotypic licking in giraffe and okapi[152]; alopecia in rhesus macaques[711]; and elevated FGMs in goral[99] and pampas deer stags[103]. Dominant individuals may block subordinates from accessing food, as seen in blue foxes[585], and social housing may lead to increased risk of injury in parrots[692] and blue foxes[585].

Small exotic felids are less likely to reproduce when housed in groups larger than a pair[550], brown bears showed more agonistic behaviour when housed with more than one conspecific[243], and female sun bears housed with a male partner had higher FGMs and showed more agonistic behaviour when another female was also present[712]. Stress at high social densities is not always displayed as increased aggression: no change[713] or reduced aggression suggests a conflict avoidance strategy[171]. Group-housed tigers also showed reduced aggression in response to space restriction during enclosure renovations, but affiliative behaviour also declined, and this reduction in social behaviour continued for a year after returning to their original housing conditions[121]. The tigers exhibited social rather than conflict avoidance, which may have led to a deterioration of the social bonds within the group, suggesting that even temporary changes in housing can have a lasting impact on social cohesion. Similar problems may also apply to mixed species exhibits. Interspecific interactions, particularly displacement and aggression, were more frequent between group-housed zebra and eland in smaller exhibits with higher social density[52], although mixed-species housing can be successful at appropriate social densities[702].

Effects of social disruption

Long-lived species such as elephants and primates that live in complex societies can be severely affected by social perturbations. Social disruption in wild elephants can have repercussions that last for decades[714]. Abnormal behaviour including hyper-aggression and infant neglect has been observed in several populations of wild elephants following anthropogenic alterations to social contexts, such as culls, translocation and premature weaning[715]. A herd of captive elephants showed variable adrenal hormone responses to overnight separation from the matriarch[83]; even short-term social disruption had a clear physiological effect that may have been mediated by the presence of other conspecifics.

Translocation caused changes in the social proximity networks of capuchins and squirrel monkeys: in capuchins, younger individuals became more central, possibly indicating that they were more stressed by the move and sought reassurance or comfort from social contact[716]. Laboratory-housed rhesus macaques showed increased stereotypic behaviour and self-biting after being permanently separated from their social partner[185]. After the removal of a resident male, two female giraffe showed an increased rate and diversity of stereotypical behaviour and increased social contact behaviour[717]. Loss of a social partner was clearly distressing and the increased social contact may have had a comforting function. Loss of a social partner may be less detrimental for animals if other conspecifics are still present, e.g. a cheetah that lost his preferred social partner was soon incorporated into another coalition[695]. However, problems may arise for animals housed alone. One elephant showed extended periods of inactivity following the death of her only companion[599], and a male brown bear spent more time alert-inactive and less time sleeping, particularly in the more vulnerable lateral lying posture, compared to when his mate was still alive[708].

Separation for performance

Circuses and animal exhibitions may not always use all individuals in performances, particularly if they are ill, injured, or pregnant. Temporary separation from conspecifics may be distressing for some social species. Cortisol increased significantly in common marmosets when isolated from conspecifics for just 15 minutes, although isolation stress was alleviated by playback of calls from a familiar conspecific[718]. Another study isolated marmosets for four hours, and observed the same pattern: only playback calls from familiar, not unfamiliar, conspecifics could reduce the stress response[719]. Male cheetahs form strong psychological attachments and the separation of coalitions for just 10 minutes can cause significant distress[694]. Circus elephants showed signs of distress when separated from their conspecifics who were taken to the ring to perform, and performed parts of their acts to musical cues heard from the main tent[159]. While the author interpreted this as anxiety to join the performance, the reaction could be anxiety due to social separation. Elephants are capable of empathy[200], show concern and compassion to conspecifics in distress and helping behaviour, regardless of kinship[699,720]. This was observed during a circus performance when an elephant fell from a tower of pedestals and its conspecifics rushed over[721].

The wider social environment

It is important to consider the influence of every aspect of the environment within the animal's sensory range[332] and this may include adjacent enclosures. Housing conspecifics in neighbouring enclosures that are visible but not accessible for affiliative or agonistic interactions may cause frustration and lead to stress-related behaviours such as pacing[722]. Separation from visible conspecifics led to increased pacing in two cheetahs and a snow leopard[214]. Singly-housed cheetahs paced more when able to view other cheetahs in adjacent enclosures[244]. Tigers paced less when the view of neighbouring conspecifics was obstructed by a visual barrier[722]. Pacing was more frequent when tigers were housed with neighbouring conspecifics than with no neighbours[723]; in this study all the tigers that paced regularly had neighbours that also paced regularly, and it was unclear whether this was due to all animals responding to the same stimuli or to each other.

Space is limited in captive environments, and particularly in circuses, and this may necessitate incompatible species being housed in close proximity. This may be stressful: when penned adjacent to cattle or pigs rather than unfamiliar peers, red deer spent more time in areas furthest away from the alternate species: they showed increased vigilance and intraspecific aggression and rested less[724]. Deer penned next to pigs had higher heart rates than deer penned next to an empty pen[724]. FGMs were higher in clouded leopards housed in visual contact with potential predators (leopards, lions, tigers) than those not visually exposed to predators[107].

Exposure to predator scents is a significant source of stress in many prey species[25], although prey species may not necessarily be distressed by close proximity to predators. There is some evidence that predator-naïve animals such as those born in captivity lack the ability to respond to predator stimuli such as scents or sounds, and have to learn predator recognition[725]. However captive-born red-bellied tamarins responded to predator scents with sniffing, avoidance and alarm calls[726], and anecdotal evidence suggests that captive-bred elephants can still recognize the scent of predators[298]. Yet even if they can recognise predators, captive prey species may learn that they are safe: zoo ungulates showed little response to playback of lion roars beyond orienting to the source of the sound[727]. However, this may take time: leopard cats suffered chronic elevated glucocorticoid levels (lasting 10 weeks) and suppressed exploratory behaviour after translocation to a cage within olfactory and auditory (but not visual) range of lions and tigers[256]. This suggests that they found being housed in close proximity to potential predators threatening. However the addition of hiding structures to the enclosure appeared to facilitate coping: an increase in hiding behaviour coincided with a reduction in UGMs. This highlights the importance of providing hiding places in enclosures, particularly for prey species, and the importance of considering predator-prey housing proximities.

Reproduction

Circuses have bred a variety of species[26] and the first captive-bred elephants in the western hemisphere were born in circuses[334,728]. However it is questionable whether they make a significant contribution to captive breeding: while British circuses were breeding 41% of their animals 25 years ago[26], the numbers bred today are low and, without collaboration with other captive establishments, the limited genetic diversity of the remaining circus stock, and mixed species breeding, restricts the animals suitable for breeding.

Greater institutional experience improves breeding success in captive tigers, and zoos that breed regularly have greater knowledge and facilities for successful breeding and hand rearing[729]. Maintaining a studbook may contribute to better dispersion of species-specific knowledge, encourage adherence to husbandry guidelines and appropriate breeding. Ruminant species with studbooks have longer life expectancies in captivity than those without a studbook[730,731].

Circuses do not seem to monitor reproductive cycling in their animals, at least not in elephants[334], which is often important for successful conception in captivity[732]. Circuses may be reluctant to relinquish trained, revenue-generating elephants to zoos to participate in breeding programmes[334], and circus elephants have entered temporary acyclicity in response to sudden changes in their social environment when on breeding loan to zoos[733]. Any breeding by circus animals is largely done in the winter quarters[26] and, if cycling does not coincide with this period, the opportunity for breeding is minimal. However, this is not invariably the case: Feld Entertainment's Center for Elephant Conservation has had great success breeding Asian elephants (**https://www.ringlingelephantcenter.com/meet-our-herd/elephant-calves/**).

Elephant fecundity is much lower in captivity than the wild, and European zoo populations are declining at approximately 10% per annum, sometimes requiring zoos to supplement their collections with wild imports[734]. Elephant populations have even shown a low rate of growth in some traditional forest camps, which may be the only situations where captive populations have been sustained through breeding[224]. For many species, the captive environment does not promote successful breeding: 42% of exotic felid pairings[550] and 68% of sun bear pairings failed to produce live offspring[712].

In addition to animals that do not breed well, captive breeding programs for some species may not bring any net benefit to wild populations compared to *in situ* conservation, because successful breeding requires genetic diversity and advocates the collection of wild specimens[735]. It is also unclear how many captive breeding programmes actually contribute to conservation. Reduced genetic variability due to small breeding populations reduces the ability of animals to respond to environmental change[736], so captive-bred animals may suffer impaired coping ability. Captive-bred animals generally do worse in the wild than wild-born conspecifics[737,738].

The 'need' to breed

Breeding is a natural and usually highly motivated behaviour. Wild female elephants can breed from 15 years up until 60 years old, and spend most of their reproductive life pregnant or raising young; however, many captive females never breed[733,739] or cease to breed prematurely[734]. Prolonged nulliparity or long non-reproductive periods in captive female rhinoceroses and elephants induce the development of reproductive tumours and cystic hyperplasia, leading to asymmetric reproductive aging and gradual loss of fertility[733,739]. These conditions are rarely seen in undisturbed, free-living elephants[733].

The importance of early breeding has also been shown in captive tigers: breeding success of female tigers increases with age up to five years and declines thereafter, though cycling does not decrease[729]. This pattern is partly explained by the fact that reproductive success is lower among the youngest and oldest sexually mature animals due to maternal inexperience and senescence[740]. Many circus animals are old and potentially past breeding age. Older female cheetahs produce smaller litters[741,742]. So earlier breeding is important to increase breeding success[729]. Postponement of reproduction in zoo felids has been associated with the higher prevalence of mammary gland cancers[743].

Free-ranging female cheetahs breed every two years from approximately three years old until death at eight to 12 years[740,744], whereas captive cheetahs show an early cessation of breeding due to an increased incidence of diseases such as gastritis and renal failure[742] or endometrial hyperplasia and severe pathologies[740]. One study reported that 87% of older (over eight years) female cheetahs in captivity experienced endometrial hyperplasia and 56% severe pathologies, which were attributed to prolonged reproductive cycling without pregnancy [740].

Captive breeding

Since healthy adult elephant bulls come into musth once a year for two to three months and become aggressive and difficult to handle[745], captive establishments try to control or suppress musth for safety and to reduce the time spent in confinement[732]. This can be done through hormonal injections, which may have a long term effect on fertility[745], or food restriction to reduce body condition and shorten musth[746]: both have welfare implications. The rutting season in male dromedaries also lasts two to three months and rutting males are more aggressive[747].

Obesity and chronic stress, which can lead to obesity by increasing fat deposition, are believed to contribute to the high stillbirth rates and reduced longevity in captive elephants[734]. Captive female Asian elephants are heavier in circuses and zoos than free-living peers, and have longer gestation periods and heavier neonates, which are more often stillborn than in wild elephants[748]. Stillborn calves weigh more than those born alive[728,748]. Even live-born calves weigh more than their wild counterparts[734]. Obesity in mother elephants reduces the chance of live births and reduces postnatal offspring survivorship[734].

Captivity may induce overproduction of sex steroids. Captive male Canadian lynx had around seven times higher faecal androgens than wild males[749] and captive females had higher faecal oestrogen and progestogen[750]. Wild-caught lynx held in pens showed similar faecal oestrogen and progestogen to captive lynx, but after release hormone levels decreased to baseline[750]. This steroid over-production may be related to metabolic dysfunction due to chronic stress causing generalised adrenal stimulation[749], since captive lynx also have higher FGMs than wild lynx[751], or due to body weight, since captive lynx are twice as heavy as wild lynx and obesity is associated with changes in steroid production[749]. Captive cheetahs had higher baseline FGMs and larger adrenal cortices than wild cheetahs, evidence of a persistent adrenocortical response to captivity that appeared to suppress testosterone in males, though not oestradiol in females[81]. This could be down to sex differences in physiology, since another study also found that FGMs were unrelated to ovarian hormone patterns in female cheetahs, despite aggression indicating possible social stress[89].

Black rhinoceros male:female pairs housed together year-round had more variable FGMs, which were correlated with increased fighting, compared to pairs only housed together during oestrus[82]. Wild black rhino are also sensitive to their social environment, since females living in areas with more tourism, predators and elephants had longer inter-calving intervals and were less likely to be pregnant[752].

Social stress-induced suppression of olfactory behaviours in white rhinos was associated with cessation of ovarian activity in all but one (dominant) female at each institution[82]. Social factors and stress have been associated with temporary acyclicity in captive elephants[83]. Ovarian suppression has also been reported in pair-housed female Canadian lynx[750] and sun bears[712].

Maternal steroids play a pivotal role in foetal brain development and therefore prenatal stress has a long term impact on offspring[753]. In laboratory and farm animals, offspring that experience prenatal stress have: delayed motor development; impaired learning ability due to neophobia and fear; impaired social, sexual and maternal behaviour; reduced exploration and play; and generally cope less well with stress and conflict[754]. The effects of prenatal stress can continue to the second generation. In rodents, prenatal social stress tends to result in masculinisation in daughters and less-pronounced male-typical behaviour in sons[753]. In elk and mule deer maternal condition during gestation and lactation was positively correlated with antler size in male offspring; since antlers are a sexually selected trait, poor maternal condition could reduce the reproductive fitness of her offspring[755].

Maternal experience

Postpartum stress is related to maternal behaviour and higher stress increased maternal failure in captive gorillas[756]. Experienced female cheetahs and tigers have greater breeding success[729,742]. In wild elephants, maternal inexperience causes slower growth in sons and higher mortality for both sexes[757], and 15.7% of zoo-born Asian elephants are killed or refused by their mothers[748]. In wild elephant populations, 20% of females are usually greater than 30 years old, whereas around 60% of captive females are over 30 years old[739]. Young females make better mothers if they can learn from older females: calf mortality in semi-captive Asian timber elephants has been linked to the importance of having social relationships with older females for successful mothering[758], and mothers are less likely to kill or reject their offspring if they grew up with an older female[748].

Effects of early separation

The separation of parent and offspring is a natural event at the onset of independence. It is generally a gradual process for free-living animals and occurs when offspring are capable of living independently. Among free-living large-bodied mammals, the natural time of weaning is once the neonate has reached four times its birth weight, and the duration of lactation depends on ecological and therefore maternal condition, rather than offspring age *per se*[759]. Parent-offspring bonds may also be severed by morbidity and mortality[760], or inadequate maternal care. But the timing and nature of maternal separation in captivity is largely under human control. Early weaning in farm animals increases productivity and profit[761]. In circuses, carnivores should be handled and trained before they are 10 months old because they are more amenable to new experiences[470]. Hand-rearing animals allows the development of a closer human-animal bond and facilitates training. It is popular among trainers of working and performing animals such as raptors, which cannot be trained fully as adults, and so must come into human care at least before the first moult[94]. Even separation later in infancy takes its toll. In the wild female elephants typically stay with their natal herd their entire lives, yet captive elephants are frequently shipped between zoos for captive breeding programs. The median age of separation from their mother is 8.3 years for captive Asian females and 16.3 years for African females[734]. Losing a mother before they are nine years old leads to reduced survivorship in wild African elephants, and early weaning has a similar effect in captive Asian elephants[762].

Separation from the mother is a significant cause of stereotypic behaviour stemming from escape or redirected sucking which, coupled with frequent vocalisations in some species, suggests maternal loss and the inability to suck are aversive[761]. Early-weaned mink were more likely to develop stereotypical tail biting[763]. Self-sucking was more likely in hand-reared chimpanzees[169]. Suckling strengthens the mother-offspring bond and premature separation while the young are still sucking can trigger bouts of reinstatement behaviour in both mother and young, such as searching and calling: these behaviours lead to reunion in the wild but are futile in captivity[760]. When separated from their mothers, captive infant gorillas showed signs similar to anaclitic depression in children, followed by despair[764]. Protest and despair were also observed in infant rhesus macaques when separated from their mothers for a three week period: both mothers and infants displayed emotional disturbance, but this was most intense and enduring in the infants[765]. Weaning stress in juvenile giraffe causes ameloblast (enamel cell) disruption and leads to enamel hypoplasia (molar defects)[105], and rhesus macaques single housed from an early age were more likely to exhibit stereotypies as adults than peers single-housed when older[135].

Longer-term effects of maternal deprivation include a decreased ability to cope with aversive situations due to heightened fearfulness and less adaptive stress response, which can also lead to stereotypic behaviour[761]. Wild-born chimpanzees from the pet and performance industry were less easy to rehabilitate than captive-born peers, since they had experienced more social upheaval early in their lives[766]. The effects of maternal deprivation can be mediated by having a more enriched environment[761], e.g. mink weaned into larger, multi-compartmental cages with all their littermates exhibited less stereotypic behaviour than those in smaller cages with a single cage mate[155].

Hand rearing

The decision to hand rear should be based on five factors: environmental, social, health, conditioning, and preventative medicine[767,768], and a lack of knowledge when hand-rearing animals can lead to serious welfare problems[769]. In some captive situations hand-rearing is necessary for the welfare of the offspring[609,770], but it is often done for commercial reasons and/or to facilitate handling when adult. Exposing hand-reared animals to older conspecifics from an early age, such as through protected contact, can aid successful reintegration into social groups[768,771]. Some animals do just as well[772] or even better when hand-reared compared to parent-reared. Hand-reared duikers showed normal social behaviour and were less easily stressed than parent-reared duikers[322]. However hand-reared whooping cranes showed less predator avoidance behaviour following wild release than parent-reared peers[773], and hand-reared chimpanzees were less socially competent[774], suggesting some behaviours can only be learnt from natural rearing. Hand-reared animals may also be more susceptible to infection when not suckled[775]. Ostrich chicks do better when reared by foster parents than when hand-reared[707]. To maximise offspring survival and welfare, hand-rearing should be a last resort[776]; hand-reared animals are often aggressive when adult, particularly males[777], and hand-reared parrots can become sexually imprinted on their owners and are prone to a stereotypies and self-harming[778].

Effects of early experience

During different stages of normal infant development, genes interact with the environment to produce rises and falls in fearfulness, so disruption of the environment during sensitive stages of development can alter fear behaviour later in life[779,780]. Similarly, disruption such as social deprivation or trauma during sensitive periods of attachment formation often leads to animals being less socially competent. Adult behaviour is often associated with early life experiences and animals exposed to more human-centric environments as infants may show behavioural problems later in life[781], such as impaired maternal behaviour[754,782], stereotypies[761], or social incompetence[781,783-785] (Table 3).

Captive-born elephants have lower survivorship than wild-born elephants that are subsequently imported to captivity, suggesting that birth origin is the most significant predictor of adult survivorship, and since imported wild-born elephants are usually less than four years old, this suggests early experience plays a key role in early mortality[762]. In humans, trauma during juvenile development creates a vulnerability to post traumatic stress disorder (PTSD) and a predisposition to violence in adulthood, and there is also evidence for this in wild elephants[205]: calves that experience trauma such as culls and social breakdown, or are raised by inexperienced mothers, are less able to regulate stress-reactive hyperaggression as adolescents and adults.

Table 3. Examples of the impact of early experiences

Species	*N*	Experience	Effect	Authors
Reptiles				
Veiled chameleon		Isolation or group housing during first two months	Isolation-reared chameleons were more submissive and adopted darker, duller colours when introduced to unfamiliar conspecifics, and performed less well in a foraging task	785
Birds				
Aplomado falcon	216	Captive-born or wild-born	Captive-born juveniles survived and recruited at lower rates than wild-born juveniles	737
Ostrich	206	Different rearing conditions with different amounts of human contact	Yearling chicks that received more human contact during their first three months of life were more docile and less fearful of humans, but there was no difference between human-imprinted chicks and chicks that only encountered humans during routine husbandry	786
Mammals				
African and Asian elephant	4500	Early separation from mother (captive Asian) or losing a mother before nine years old (wild African)	Reduced survivorship	762
Asian elephant	4500	Captive-born or wild-born	Captive-born elephants have lower survivorship than wild-born elephants that are subsequently imported to captivity	762
Chimpanzee	60	Exposure to other chimpanzees during infancy	Rehabilitated pet and performer chimpanzees that had experienced less conspecific exposure during infancy displayed less frequent grooming and sexual behaviour as adults, which has implications for social bonds within groups. Zoo-bred chimpanzees with more conspecific exposure exhibited more coprophagy, potentially a socially-learned behaviour	781
Chimpanzee	18	16-27 years of solitary confinement in a laboratory	When resocialised after ~20 years of solitary confinement, early deprived (mean 1.2 years) chimpanzees engaged in less social behaviour such as allogrooming and were less tolerant of passive close proximity than late deprived (mean 3.6 years) chimpanzees	783,784

Species	N	Experience	Effect	Authors
Mink	141	1:1 sibling housing vs. group housing after weaning at either six, eight or ten weeks of age	Early weaned solitary females exhibited more stereotypical behaviour than later weaned females	155
Mink	202	Weaned at seven vs. eleven weeks	Early-weaned mink had a greater propensity to chew and were more likely to develop tail biting behaviour	763
Rhesus macaque	8	Repeated maternal separations up to eight months from birth	Increased fearfulness and coo vocalisations, an infant-parent contact call, that still persisted one year after the final separation	787
Rhesus macaque	29	13 day period of separation from mother when infants were 30 weeks old	Infants that experienced separation spent more time sitting unoccupied than controls both as yearlings and at 2.5 years old	779

Mortality and morbidity

In general, wild animals do not show symptoms of illness until they are extremely unwell, as evidenced by 'sudden death' in reindeer[788] and dromedaries that do not show signs of suffering until they are completely exhausted[324]. So non-domesticated species require close monitoring and prompt veterinary attention on detection of any problem[789]. Lack of attention to ill health is especially dangerous for animals with fast metabolic rates, such as birds, which progress rapidly from ill to demise[789].

Mortality and survivorship

Survival in captivity can exceed that of animals in the wild due to protection from environmental stressors, including predation and food shortage. This trend was observed in first-year survival of five species used for falconry[790]. Mean life expectancy in captive reindeer and red deer is largely equal or longer than their free-ranging counterparts[730]. Captive wild mammals such as bears, big cats, zebra, raccoons and raccoon dogs have outlived their wild counterparts by up to 300% [791-793]. Orangutan survival in zoos used to be lower than in the wild but survivorship is now comparable to the wild due to improved captive management practices[794].

However, other species fail to thrive in captivity: the life expectancy of roe deer is 20-30% lower in captivity[730]. Captive giraffe only reach half the age of their wild counterparts[795]. Survivorship of captive elephants has increased over time[796], yet the median life expectancy of captive-born African elephants is just 16.9 years, compared to 56 years in undisturbed wild populations[762]. A study of 42 African elephants in German circuses found that most died between the ages of 17 and 32[797]; this is older than zoo elephants, but still far younger than in the wild. The median life-expectancy for captive-born Asian elephants is 18.9 years in zoos; while no data are available for wild Asian populations, 41.7 years is the norm in a large (>5000) population of semi-captive timber elephants[762]. Although these working elephants haul up to 400 tonnes of logs per year, they are able to forage in the forest at night in large family groups and maintain a wide social network[758], which may contribute to better welfare and longevity.

Ailments and diseases in captive animals

Captive animals suffer from ailments and diseases that are either not present in wild populations or much less common. All aspects of management have the capacity to act in combination with the animal's natural physiology to influence their physical and mental health.

Though many species live longer in captivity than in the wild, length of life may not equate with quality of life[793]. Animals with extended lifespans in captivity can suffer from health problems caused by physical and mental deterioration seldom experienced by their wild counterparts[798]. The average age of circus animals is high compared to other captive populations, probably for both sentimental and economic reasons: significant time, effort and expense goes in to acquiring and training circus animals and circuses may be reluctant to retire or euthanase old animals[26]. Veterinary records from 70 geriatric zoo mammals showed that many had outlived their wild counter-parts but 79% were suffering from 'mild to severe pain, discomfort and a significantly reduced quality of life' due to neoplasia or pathological dysfunction of the musculoskeletal system[791].

There is a high incidence of dental and skeletal pathologies in old zoo mammals[798]. Bone and joint-related diseases are common in geriatric animals and are usually associated with osteoarthritis and degenerative joint disease, e.g. birds of prey[799], raccoon dogs[793] and elephants[269,800,801]. Arthritis seems particularly common in large species with a high body mass, such as bears, bovines, elephants and gorillas, compared to lighter animals such as foxes and small rodents[802]. In birds of prey, osteoarthritis in the lower limbs induces redistribution of weight onto the less affected foot, which may lead to pododermatitis, or 'bumblefoot'[799]. Geriatric birds of prey have been diagnosed with heart disease [799,803], hepatic and renal disease, neoplasia, ophthalmic conditions and senility[799].

These conditions all suggest that long-term captive animals will experience significant chronic pain as they get older, particularly if husbandry and management do not meet their species-specific requirements.

Contact with humans

61% of known human diseases are zoonotic[804], so close proximity between humans and animals in circuses and other forms of live animal entertainment leaves both animals and humans vulnerable to zoonotic infection[805]. Even if disease is not caught from humans directly, they can still facilitate disease spread, e.g. keepers that clean multiple enclosures with the same equipment or visitors that pet different animals without washing their hands. The danger of zoonotic disease transmission is recognised in wild animal tourism, e.g. the seven metre rule for gorillas[616,806], although such rules are rarely applied in captivity. In addition, travelling circuses are likely to have limited or no quarantine capability for animals (or staff) once infected: it is important to maintain good human health in keepers and trainers that are in regular close contact with animals. *Mycobacterium tuberculosis* (TB) has been transmitted between elephants and bidirectionally between elephants and humans in several zoos and circuses[328,807-813]. In 2011, 5.1% of captive elephants in the USA were estimated to be infected with TB and cases seem to be rising[814]. TB appears to be more common in elephants that experience greater amounts of human contact, e.g. in temples[809], and the disease has the potential to spread to wild elephants and other species[812]. Humans have also infected mongooses and baboons with TB[815].

Mycoplasma bacteria can cause arthritis and is transmitted between humans and animals, or by cross-grazing on contaminated land[816]. *Mycoplasma*-associated arthritis has been reported in giraffes[816] and circus elephants, sometimes without symptoms of lameness[817]. This condition is not easily treated[817] and increased joint strain during performances will add to the pain of inflamed arthritic joints. *Mycoplasma* species are also associated with infertility and respiratory disorders such as tuberculosis and pneumonia in birds and crocodilians[818,819].

Grazing on common land and interactions with wildlife

Travelling animals may be put out to graze on common land or farmland, where cross-grazing or contaminated food and water can expose circus animals to various parasites and pathogens from other animals, and facilitate the spread of these pathogens around the country to other wildlife, livestock, pets and humans. Many non-domesticated grazers such as bison, camelids and cervids are susceptible to diseases associated with grazing livestock[820,821]. These include nematode infections such as lungworm or bacterial infections such as bovine TB (*Mycobacterium bovis*), brucellosis, Johne's disease and ovine herpesvirus[820,822,823]. The tick-borne disease babesiosis has been associated with poor maternal condition and calf mortality in reindeer[824]. Bovine TB infects a wider range of hosts than *M. tuberculosis*[825], and circus animals may become infected by grazing on land contaminated by livestock or wildlife carriers such as deer or badgers. Camelids are incidental, spillover hosts of *M. bovis* and become infected through contact with badgers and cattle, or environment contaminated by their secretions and excreta; they can transmit the disease between camelid herds, other animals with which they come into contact, and close human in-contacts[826].

Circus animals can contract cowpox virus from wild small rodents: one circus elephant was infected by rats in its stable[827]. Cowpox is also transmissible between animals and humans, and carers without knowledge of cowpox symptoms may not wear gloves[827] or have the facilities to quarantine infected animals. Many diseases have expanding host ranges, such as canine distemper virus, which has been transmitted from wild raccoon dogs to wild bears and zoo tigers and lions[828]. Big cats such as captive lions are susceptible to helminth infections such as (*Toxocaris leonine*)[829], and infection could occur by eating infected rodents attracted to the litter and animal feed at circus sites. Captive apes including chimpanzees and bonobos interact aggressively with local wildlife and sometimes kill and eat it, e.g.

waterfowl, small mammals and frogs, which poses a risk of infection with leptospirosis, *Salmonella*, toxoplasmosis and other diseases[830]. Ratites can contract helminth infections from the faeces of wild (or captive) raccoons and skunks[831]. Rheas can die from infection with *Chlamydia psittaci* contracted from sharing water troughs or dusty substrates with wild birds, and emus and ostriches are susceptible to *Mycobacterium avium* from faeces of wild birds[831]. Rodent-contaminated fruit and vegetables can harbour bacteria including *Leptospira, Listeria* and *Salmonella*[832].

Staff may also not be aware of any potentially poisonous plants at each new venue, which may be dangerous for species put out to browse and graze[833]. Injuries of the oral mucosa from grazing amongst thistles and foreign objects can lead to bacterial infections such as leptospirosis or necrobacillosis in the mouths and throats of ruminants, and cold, wet conditions (particularly if they have foot abrasions) leaves them vulnerable to foot infections[822].

Effects of housing and husbandry

Inadequate housing in terms of climate, space and substrate can affect both mental health and physical condition. Unsuitable housing conditions and management may be due to lack of facilities or inadequate knowledge, and can have a negative impact on animal welfare. Pinnipeds have higher survival rates at institutions with more days of species-specific experience[834]. Circus animals are extremely valuable to their owners economically and emotionally, so they are likely given the best possible care[315]. In fact many animal keepers believe they are providing the best possible care for their animals, yet have little or no knowledge of what their animals actually require[331].

With limited space, active lizards such as Asian water dragons and green iguanas, and large snakes such as boas, can develop skin abrasions from coming into contact with the sides of their enclosure[835]. Snakes in enclosures with wire tops develop rostral abrasions from escape attempts[835]. Small, crowded travelling enclosures facilitate continuous reinfestation with intestinal parasites such as roundworm or toxascarosis, a regular problem with lions and tigers in circuses and zoos[829,836].

Bumblefoot is an inflammatory infection in the avian foot common in captive raptors and parrots, but not seen in wild birds[274]; the main cause is prolonged use of perches of an inappropriate size, shape or texture, but is also caused by obesity or malnutrition[769,837]. For good welfare it is essential to provide a variety of perching surfaces that encourage differential weight bearing to prevent foot lesions[274,799]. Regular exercise and appropriate diet is also important for the prevention of bumblefoot: wild-caught falcons required twice-daily training and a high-energy diet to have a significant impact on the incidence of bumblefoot. However, training frequency had no effect on the disease in captive-bred falcons, which did better on a low-energy diet; this was attributed to reduced 'circulatory condition' and lower metabolism in captive falcons due to long-term lack of exercise and a low-energy diet[838]. This suggests captive falcons have poorer body condition and physical fitness than their wild counterparts and reiterates the importance of considering a species' needs above tolerances. Crocodilians abrade their skin when crawling out of concrete ponds, especially those without a sloping entry point, leading to infections not dissimilar to bumblefoot in birds[839].

Bumblefoot and other long-term inflammatory diseases such as gout can lead to Amyloid A (AA) amyloidosis[840], a progressive disease in captive birds and mammals[841], and a major cause of liver failure and death in hunting falcons[840]. The incidence of AA amyloidosis in captive birds increases with age and is more common in exotic species, suggesting a stress effect on disease prevalence caused by lack of adaptation to an unsuitable environment[803,841]. Clinical symptoms can also be preceded by subtle weakness or abnormal behaviour, which could make affected birds vulnerable to bullying in group housing[803]; ultimately the disease is fatal.

Certain substrates may attract and harbour insect vectors and facilitate disease propagation, e.g. captive falcons in the Middle East were infected with the nematode *Serratospiculoides seurati* by ingesting beetles while tethered on sandy substrates[842]. Non-sterile wood chip and bark substrates or damp organic matter such as hay can harbour *Aspergillus* spores in aviaries[843,844].

Lameness has been reported in zoo elephants due to osteoarthritis and limited locomotion[599]. Limited exercise is associated with foot pathology in captive elephants[269], and stakeholders identified substrate as the most important of 15 welfare issues for captive elephants[845]. Elephants are prone to foot problems if housed on sand and/or concrete[139]. The elephant knee is uniquely adapted to support an enormous compressive load and in captivity unsuitable conditions, such as restricted movement and cold, hard or damp flooring, interfere with this adaptation and accelerate the development of osteoarthritis and degenerative joint disease[800,801]. A survey of 81 captive Asian elephants reported that 43% had hyperkeratosis, and skin condition was especially poor in temples or tourist camps where the elephants were kept in unsuitable conditions without regular access to water[279]. Most of these elephants had wounds, abscesses, foot cracks and eye problems that were rarely seen in forest camps or zoos. Many circuses fail to provide suitable skin care for their elephants including daily bathing, and opportunities to dust-bathe or scratch[846] and bathing seem particularly rare during winter when elephants are housed in their winter quarters[797].

Keeping animal facilities clean and handler personal hygiene are essential biosecurity measures for breaking disease transmission cycles[847]. Parasitic infestations can accumulate in unsanitary enclosures, including the cage furniture[835]. Naturalistic enclosures with textured or loose substrates, cage furniture, ground-level pools and communal feeding areas are more difficult to sanitise and thus contribute to disease spread more than simpler enclosures[832]. Proteinaceous food remains in enclosures can cause outbreaks of red-leg disease in amphibians[848]. High parasite burden or infection can result in dysecdysis (abnormal skin shedding) in snakes and lizards[835]. Unmonitored water conditions in tanks and pools can cause algae overgrowth and subsequent superficial algae infections in aquatic or semi-aquatic reptiles[835]. Build-up of debris in water can predispose crocodilians to fungal infections[839]. Water that runs between multiple enclosures or terraria can spread bacterial infections such as salmonellosis and tuberculosis in amphibians and reptiles[848], and the parasite *Entamoeba invadens* which causes necrotic enterohepatitis in snakes and lizards[849].

Long-term inhalation of cleaning product residues such as bleach in small or poorly-ventilated enclosures can irritate the respiratory tract in reptiles[835]. Pathogens such as amoebae can be transferred between enclosures that are cleaned using the same utensils[848]. In homing pigeons, poor sanitation is associated with *Escherichia coli* and *Salmonella* infections, ascarid parasite and pigeon fly infestations, and dust is a key factor increasing propagation of *Chlamydia*[818] and mycoplasmosis[819] in captive birds.

Effects of climate

Too-low temperature or humidity can lengthen or impair the shedding cycle in snakes and lizards, which can result in bacterial and fungal infections[835]. Reptiles require species-specific climates that vary at different stages of the moult cycle, so good species knowledge and enclosures that offer a choice of different climatic conditions, including suitable substrates which can moderate humidity, are essential[835]. Unsuitable climates or substrates can also lead to blisters, burns, cracks or lesions in the skin of reptiles, which are then vulnerable to bacterial or fungal dermatoses, particularly when they are handled by humans or housed in unsanitary conditions[819,835]. Even when temperatures in enclosures are spot on, exposing reptiles to the open air during public displays can cause significant thermal distress and contributed to multiple health problems and death in a circus python[850].

Pathogens generally have specific temperature requirements. Maintaining reptiles under atypical climatic conditions can aid the proliferation of locally adapted pathogens that animals would not encounter in their natural environments and thus may not be equipped to resist. Fungal pulmonary lesions have been reported in crocodilians maintained under temperatures that were too low for the crocodilians but perfect for the pathogens[839].

Captive birds can develop dermatological conditions when exposed to unsuitable climates, such as avascular necrosis of distal extremities, wing tip oedema or frostbite[274,769]. Frostbite injuries occur in tropical raptors and raptors housed with insufficient thermal protection, and can cause loss of digits vital for prehension and balance[837]. Cold tissue damage is also seen on the ears of some circus elephants[797].

Effects of social conditions

Human contact can pose significant threats to animals that are unable to avoid or control the extent of human contact, so it is particularly important in restrictive environments to house animals with compatible social partners and provide species-specific husbandry. Disease threats are greater at events like circuses, fairs and shows, where multiple species (including humans) from different sources and each under various forms of stress comingle[851].

Unsuitable housing companions or too-high social densities can result in fight and other wounds in caimans and birds[849]. Bite wounds in turtles and lizards can lead to fungal or bacterial infections, abscesses that require anaesthesia to remove or viral infections, e.g. papillomavirus, which has no effective treatment[835]. The leathery shells of soft shell turtles are easily scratched in overcrowded conditions, leaving them prone to fungal infections[835]. Fight wounds or cuts and scrapes acquired in overcrowded conditions will facilitate infection by some viruses such as pigeon pox that require a break in the skin for penetration[852]. Overcrowding facilitates the spread of bacterial diseases including *Chlamydia* and *E. coli* in homing pigeons[818], and was thought to contribute to continuous parasitic reinfestation in a circus that housed 11 lions in one enclosure measuring 9 x 2 metres[836]. Beak injuries from fighting in captive birds may lead to feeding difficulty[769], and birds fed on soft food (due to beak deformity) may develop frustrated motivation for feeding behaviour. Blackleg and malignant oedema infections are associated with wounds in deer and can be fatal[822,823]. Trauma, including lameness and wing damage, was the leading cause of mortality and morbidity in zoo-housed kori bustards: it was caused by hostile exhibit mates, unsuitable diet and stress associated with human contact[853].

Higher social densities in enclosures and during transport may accelerate disease transmission, e.g. herpes virus is spread by the faecal-oral route in turtles and tortoises[835]; the parasitic mite *Knemidokoptes pilae* can be spread between birds that share perches[769]; pigeon paramyxovirus-1 is transmitted by direct contact between crowded homing pigeons[852] and can cause Newcastle disease in ratites and psittacines[831]. Similarly, housing animals in mixed-species groups may expose them to pathogens to which they have no natural resistance. Amphibians are susceptible to fish parasites such as protozoa and copepods[848]. Turtles can be latent carriers of amoebae that infect snakes and lizards and cause amoebic dysentery, which is almost always fatal[848]. Several species of reptiles and monkeys have been infected with TB (of unknown origin) in Japanese zoos[825]. In zoos, TB has spread from elephants to other species housed nearby including black rhino[808] and chimpanzees[811]. *Mycobacterium pinnipedii* (pinniped tuberculosis) has spread from a sea lion to a camel, crested porcupine and tapirs[854,855]. Tapirs are particularly susceptible to TB[849].

Quarantine is probably the most important management practice to prevent disease outbreak[832]. Lack of quarantine facilities can lead to transmission of viruses and infections, particularly from new animals from other facilities or the wild. Examples in reptiles include herpes virus, often fatal in tortoises and turtles[835], parasitic infestations[835] and amoebic dysentery, which is almost always fatal and most commonly sourced from un-quarantined imports[848]. Failing to quarantine imported birds may also lead to outbreaks of avian influenza[831].

Effects of performance

Animals used for demonstrations may be trained to perform physically challenging movements with the potential to cause injury. Due to economic pressure, circuses may be reluctant to give animals adequate time to recover from such injuries, which may mean they never fully heal[856]. An Indian python used in a circus had repeated health problems throughout its life, despite regular veterinary treatment, and was eventually euthanized for secondary septicaemia originating from stomatitis (infected oral lesions)[850]. Performance stress coupled with underlying poor husbandry was believed to have led to immunosuppression and predisposed the snake to infection.

Birds used for public display are sometimes deflighted to prevent escape. Although deflighting reduces the need for close confinement, the procedure also causes discomfort and pain, distress, risk of haemorrhage, infection or injury, and deprives birds of the opportunity to exhibit natural flying behaviour, ultimately violating four of the five freedoms[584].

Animals forced to work when they are too young, too old, pregnant or lactating may be at increased risk of work-related injury. Camels do not mature before they are six years old and repeatedly putting a heavy (adult) jockey on a young camel's back can damage their spine; unlike horses, it is not possible to put stirrups on camel saddles to facilitate even weight distribution[496]. Old elephants were more likely to get back lesions when giving tourist rides[857]. Calf mortality in semi-captive Asian timber elephants has been linked to nutritional deficiency in their mother due to workload[758].

Muscle weakness observed in circus elephants indicates that the lack of free movement and exercise caused by space limitation and shackling is not compensated for by training[797], and performing unnatural movements can put unnecessary strain on the body. Circus acts such as repeated kneeling, crawling and standing on two legs all lead to premature wear on tendons, muscles and joints even in young elephants[856], and can lead to leg deformities, as seen in 40% of African circus elephants[797]. Lameness is common in circus elephants[817]. Perineal hernias result from excessive force on the diaphragm, as occurs when elephants are made to 'mount' each other in performances[505]. Elephants can get back and girth lesions when giving rides without suitable padding material[857].

Effects of stress

Increased stress can suppress the immune system and facilitate infection and disease transmission[847]. Stress can occur due to handling, transportation or an inappropriate diet or environment, including climate, housing and social conditions. In amphibians and reptiles, environmental or handling stress, or a combination of the two, such as transport in winter, can provoke outbreaks of latent infection[819,839,848].

Stress-induced immunosuppression is associated with aspergillosis, a respiratory disease, in raptors[789].

Bison and deer suffering stress from overcrowding are more susceptible to necrobacillosis infection[822]. Several veterinarians consider that stress is the condition to which reindeer are most susceptible[821], since they are adapted to roaming and browsing in an arctic climate[788], a completely different lifestyle to that in captivity. Reindeer naturally lose weight over the winter but should regain condition in the spring: failure to notice when body condition does not recover can lead to death by fatal inanition, which is becoming increasingly common in 'Christmas reindeer' with naïve owners[788]. In wild-caught reindeer, handling and transport stress has been associated with gastrointestinal problems, such as abomasal ulceration[823]. Stress from pasture that is too rich is a common concern for captive reindeer, which naturally feed on low quality food[788,821].

Periparturient females such as camelids and cervids experience immunosuppression due to the redistribution of circulating immunoglobulins to the colostrum, so may be particularly susceptible to infection at this time[847]. Vesicular and ulcerative dermatopathy in 40 captive black rhinoceroses was associated with stress due to maladaptation and poor diet[858]. This condition has not been seen in wild rhinoceroses: no pathogens were isolated from the lesions and episodes coincided with stress events such as transportation, cold temperatures, intraspecific harassment, oestrus and advanced pregnancy, or concurrent diseases. This suggests the epidermis of black rhinoceroses is acutely sensitive to suboptimal conditions and disruption. Asian elephants translocated between institutions have a lower life expectancy[762], suggesting frequent transport between venues elicits stress responses that negatively impact welfare in the short and long term[762].

Stress can lead to abnormal behaviour. Self-mutilation of the feet in Amazon parrots leads to dry, flaky skin and sometimes secondary infections[769]. Repetitive abnormal behaviour can lead to skeletal abnormalities. Dental pathology is almost ubiquitous in captive bears either from high sugar diets, trauma or stereotypical bar-biting, which erodes the tooth enamel and weakened teeth are prone to fractures and infection[775]. One study of African elephants in German circuses reported that all 42 individuals exhibited stereotypical weaving behaviour and many had deformed legs or backs[797]. Elephants that exhibit stereotypical behaviour are also more likely to have foot problems[139].

Diet and nutrition

The literature on the diet and nutrition of captive wild animals is extensive: here we consider some of the key issues.

Free access to food, particularly the concentrated foods commonly fed to captive animals, in combination with space restriction, can lead to health problems such as obesity, diabetes, cardiorespiratory disease, reproductive disorders, urinary disorders, lameness, thermal discomfort, tumours and mortality[84]. Obesity is a common and significant problem in captive animals due to their relative inactivity and high calorific intake[318]. Obesity increases the likelihood of arthritis, diabetes mellitus, pancreatitis and cardiovascular disease[319] and may contribute to increased risk of mammary gland cancer in zoo carnivores[743]. The risk of obesity can be reduced by restricting the quantity or quality of diets, though a balance must be struck to avoid violating the 'Freedom from hunger'[84].

High-fat seed and nut-based diets are the most common cause of nutritional problems for large psittacines and may lead to obesity and secondary deficiencies in protein, iodine, calcium and vitamin A[859,860]. Obesity is common in captive coatis, is the most common nutrition-related disease in captive raccoons[172], and is a common nutritional problem in captive elephants[861] and llamas and alpacas[833]. Animals with low metabolic rates such as reptiles, kinkajous[319] and marsupials[318] are particularly prone to obesity in captivity. Obesity in reptiles may lead to fat deposits in the organs, e.g. fatty liver syndrome[307]. Wild alligators only feed at temperatures above 25°C and their appetites diminish below 29°C, possibly because digestion slows at low temperatures, so they are adapted to spend between four and seven months of the year fasting[862]: this must be recognised in captivity. Animals used to daily torpor or seasonal hibernation, such as some marsupials[318] and raccoon dogs[863], may become obese if fed during periods of lowered metabolism.

Captive animals cannot be depended on to select a healthy diet: when presented with a choice of foods animals may choose the more palatable, leading to nutritional imbalance[864]. For instance sugar gliders readily accept fruit but this is not a substantial part of their natural diet[318], and captive elephants only ate more roughage when fewer concentrates were fed[865]. Wild elephants depend on high-fibre browse and do not consume high proportions of concentrated food such as seeds and cereals[866], whereas captive elephants may be fed supplementary, calorie-dense concentrates or low-fibre grass hay that contribute to obesity[861,865]. One study found that 75% of UK zoo elephants were overweight[247]. Roughage has lower digestibility than concentrated food so will increase feeding time without the risk of obesity[865]. Therefore high-fibre roughage such as branches and alfalfa or oat hay is the recommended staple for elephants, and concentrates should only be fed to address vitamin or mineral deficiencies[861].

Feeding frequency and amount

The amount and frequency of feeds has an impact on animal welfare and optimal feeding is species specific. Giraffe and okapi fed more often during the day are more likely to exhibit stereotypic behaviour than those given fewer larger feeds[134,152]. Similarly, elephants spend more time feeding when fed with one large feed rather than several smaller feeds per day[867], whereas chimpanzees spend more time feeding when feeds are dispersed over the course of the day compared to a single bulk feed[867].

Grazers and browsers designed to spend large parts of the day feeding may suffer when feeding opportunities are limited. For instance, giraffes in captivity spend 60% less time feeding than their wild counterparts[21]. Over-winter indoor confinement of farmed red deer was associated with increased stereotypical wall-chewing indicative of limited foraging opportunity, which was reduced by providing additional forage[710]. In zebras parent-offspring conflict was lower, shown by a reduced rate of suckling bout termination, when mothers were fed while suckling, suggesting that feeding lactating zebras *ad libitum* improved the welfare of both mother and foal[868].

Elephants have fast passage rates and have low absolute digestibility coefficients for their body size[866], and therefore need to spend a lot of time feeding. Zoo elephants consume up to 300 lb of hay daily[869]. In the wild elephants can spend up to 75% of the day feeding[32,33]: in zoos this takes up 20-50% of their time[247,254,300,869], 25-33% of the time of picketed circus elephants[159,160] and 40-49% of penned circus elephants[160,278]. The penned elephants also tended to increase stereotypic behaviour when the hay ran out, although the total time spent stereotyping was unrelated to the time spent feeding[278], and elephants performed stereotypic behaviour during >15% observations even with continuous access to hay[160]. In zoo stereotypic behaviour in elephants has also been linked to food availability[186] and feeding frequency[599]. Several studies have found that abnormal behaviour reflects feeding rather than housing problems[152,242,341,870]. To replicate wild elephant feeding ecology, low quality bulk feeds should be spread throughout the day and night to reduce feeding anticipation[871]. Equally, low quality bulk food that requires manipulation increases food handling time, so total foraging time can still be high without leading to obesity[871].

Species such as cougars, lions, pinnipeds, polar bears and wolves have evolved to have a feast-or-famine lifestyle[872]. Wolves may endure several days without eating and, after a successful hunt, can consume up to 10 kg in the initial feeding bout[873], around 30% of their body weight[874], whereas in captivity wolves may be fed daily[336]. Similarly, lions hunt every two to three days[875] and eat 10 to 20 kg of meat in one bout[876], while most captive felids are fed five to seven times per week[382,396,875,877]. Overweight captive lions switched from daily feeding to a gorge-fast diet, where they were fed every three days, benefited from improved nutritional status and increased activity, without losing condition[875]. The natural digestive physiology of captive wild animals is key to ensuring good welfare.

Captive animals commonly show anticipative behaviour around predictable feeding times, e.g. increased activity in coyotes[220] and increased self-directed and abnormal behaviour in macaques[215]. However predictable feeding times are not truly predictable without a reliable signal and may cause additional stress, e.g. macaques increased rates of abnormal behaviour when predictable feeds were delayed[215]. Temporally unpredictable feeding is recommended for some species, though reliable signals are required to reduce false anticipation[219]. Coyotes fed on a temporally unpredictable regime scent marked and howled more than nearby conspecifics fed on a predicable regime, since feeding cues for predictably-fed coyotes were still detectable by unpredictably-fed coyotes and probably resulted in confusion[220].

Dietary requirements vary with health status and life cycle[864]. Animals require different diets according to age and growth stage, e.g. crocodiles[878], camelids[879], elephants[865], kinkajous[319], raccoons[172] and Virginia opossums[318]. 76% of African circus elephants were smaller than age-matched wild conspecifics, potentially attributable to early weaning or inadequate diet during the early growth phase[797]. In German circuses at least, all elephants are imported, usually as juveniles when they are easier to handle and thus train: there are detrimental impacts of early separation from the mother for elephants[762].

More active animals require more biological antioxidants, such as vitamin E, to repair their muscles[880]. Pregnant or lactating animals require increased calorific intake, e.g. kangaroos[881] and coatis[172], though increased eating also increases the risk of gastrointestinal parasite infection from forage[881], and female raptors must not be fed excessive casting material near to the breeding season, as the swollen oviduct may impair regurgitation[843].

The timing of food provision may be important to ensure efficient digestion in some species. In free-ranging koalas foraging activity peaks in the afternoon and captive koalas responded more to browse provided in the afternoon[316]. Seasonal voluntary inappetence in reindeer causes rapid weight loss over winter and 60% of mass reduction is from the digesta, viscera and blood, with no significant difference in carcass mass[882]. Leptin (an indicator of satiety), adrenaline, noradrenaline and plasma cortisol concentrations remained stable throughout winter fasting in raccoon dogs, demonstrating that this natural physiological process is not stressful and raccoon dogs do not need to feed during the winter[863].

Importance of a species-typical diet

Raptors must be fed daily with fresh meat from small mammals such as mice and rabbits, since digesting the connective tissue of large mammals such as cattle or horses stresses the kidneys of most raptors[501]. Crocodilians obtain energy from protein rather than fat: fatty food led to increased fat storage and impaired protein metabolism (and consequently growth) in captive estuarine crocodiles[878]. Captive crocodiles are fed a diet of fish, poultry and red meat, which is roughly twice as high in saturated fat than their natural diet of invertebrates and fish[883]. Consequently captive crocodile plasma contains a higher proportion of saturated fatty acids[884] and up to 15 times more cholesterol[883] than wild crocodiles. Imbalances in the ratio of unsaturated:saturated fatty acids can lead to metabolic disturbances, dermatitis, fatty liver, infertility and impaired growth[883,884]. High-fat fish diets that are low in vitamin E (due to rancid fish oils from poor storage) can also cause fat necrosis, pansteatitis and steatitis in crocodilians [819,839], which may be outwardly asymptomatic[885].

Two extensive studies reported that life expectancy in captive deer[730] and other ruminants[731] was correlated with the proportion of grass in their natural diet. Species adapted to grass diets, such as red deer and zebra, had higher survival rates, and thus appear to be easier to accommodate in captivity, than browsers such as roe deer and giraffe. Browse requires specific processing behaviours such as complex manipulation with the trunk[861] or tongue[177]. Providing fresh browse increased foraging and reduced inactivity in zoo-housed chimpanzees[628]. Black rhinoceroses are browsers, yet captive diets are based on hay, and poor diet has been associated with the development of cutaneous skin lesions in captive animals[858]. Vicugna are grazers and two captive animals exhibited increased stereotypic behaviour when browse was added to their enclosure, probably due to low species relevance[886]. The nutrient content and quality of browse and other plant-based food varies by season and supplier[864], so quality cannot be guaranteed.

Rumination, the regurgitation and mastication of rumen contents, is physiologically essential for digestion in ruminants[887], and rumination is also related to non-REM sleep, whereby if one is disrupted then so is the other[888]. Wild giraffe spend three to five hours per day ruminating[888], so this behaviour is a key component of their behavioural repertoire and is likely to be highly motivated. Giraffe prefer browse that supports good rumen function[21], and increasing dietary fibre stimulated increased rumination in two captive giraffes, which subsequently reduced oral stereotypy[887].

Captive cheetahs have fewer gastrointestinal health problems when their diets are based on raw meat, and including more skeletal components such as long bones and ribs reduces the likelihood of vomiting and diarrhoea[889]. However, cheetahs showed little interest in chewing bones unless meat was still attached[890]. Horse meat or commercially prepared diets increase the chance of gastrointestinal health problems[889].

Importance of species-typical food presentation

It is important to consider the non-nutritive aspects of diet[876], such as species-typical and ecologically-relevant food presentation. For carnivores, foraging is a lengthy process and involves locating, capturing, killing and processing prey, often followed by food caching and continuing vigilance to protect the carcass from scavengers[876]. Foraging in captivity requires only a fraction of this time and behavioural diversity.

Depending on their natural foraging behaviour, some species may benefit from food that is more widely distributed in space. Marmosets had more species-typical time budgets when food was scattered rather than in bowls[891]. Bears spent more time feeding when food was scattered rather than in a pile and started to show natural rhythms of alternation between feeding and sleeping[867]. Automated scatter feeders reduced stereotypy and increased activity and space use in grizzly bears[892]. However scattered food did not reduce stereotypical hair eating behaviour in captive baboons, suggesting the motivation was related to food processing rather than consumption[893].

Commercial diets or soft-textured packaged diets are popular because they are nutritionally complete, cheap, make for easier cleaning and are easier to store[894]. However, they can contribute to poor health. Commercial diets containing phytoestrogens from soya and equid oestrogens from horsemeat was associated with testosterone suppression in captive male cheetahs[81]. Soft foods also fail to wear the teeth to allow molar progression in macropods[318] and are associated with a higher incidence of tartar and gingivitis in kinkajous[319].

Wild carnivores feed primarily on whole carcasses which require specialist behaviours to process, from catching, killing and dragging to the feeding site, to ripping, pulling, tearing and shearing off flesh that is swallowed with minimal mastication[876]. Carcass feeding thus encompasses a broad range of oral behaviours that are not required for captive animals fed on soft diets. Food texture is important for both gastrointestinal[889] and dental health in carnivores. Soft textured diets weaken the masticatory muscles[895,896] and lead to gingival health problems, plaque formation and focal palatine erosion in captive carnivores[876,890].

Psychological aspects of feeding

One of the most common signs of poor adaptation to captivity in snakes is starvation: this may be because snakes have poor perception of prey objects in captivity and live prey that are too small may not elicit foraging behaviour[897]. Captive snakes fed on dead prey may need to be force-fed, since non-moving prey do not stimulate hunting behaviour, but force feeding may be stressful for the animal[898]. Allowing predators such as snakes to display natural hunting and foraging behaviour is desirable and could be achieved by feeding live prey. However, the feeding of live prey is a contentious issue, since the welfare of the prey animal must also be considered. Death can take up to two minutes and will be painful and highly stressful[898], and live prey can injure the predator[835].

Parrots showed a clear preference for oversized food pellets, which required more manipulation and therefore increased feeding duration[899]. Parrots fed on both oversized and regular-sized food pellets still ate some regular pellets, showing they exploited both options[899]. Parrots fed on oversized food pellets gnawed on wooden blocks less, suggesting they were less frustrated when given opportunities for foraging manipulation[899].

Unlike carcasses, consuming a commercial meat diet does not engage all the senses, e.g. felids process prey by smell and touch[894,900]. Cheetahs displayed more species-typical appetitive behaviour when on a carcass diet compared to a commercial processed meat diet, which has minimal handling time and does not engage natural food processing behaviours such as slicing and shearing[900]. Scavengers live on large carcasses almost exclusively in nature and captive vultures are more motivated to feed on large carcasses than small ones, bones or a commercial diet: large carcasses encouraged species-typical food handling behaviour and longer feeding times[901]. Wild tigers prefer large prey, specifically animals weighing between 60 and 250 kg[902], while cheetahs prefer prey up to 20 kg[876]. One disadvantage of carcass feeding is that animals may selectively eat only part of the carcass, which could lead to nutritional imbalance[894].

Live prey is sometimes used to stimulate hunting behaviour, e.g. Melbourne Zoo provide live crayfish and fish to otters and fishing cats, and insects for coatis, meerkats, fennec foxes, badgers and red pandas[877]. Live fish stimulated previously unseen hunting behaviours in fishing cats, increased space use and reduced sleeping, and the effects continued for two to eight days after food presentation[403]. Even species not intentionally fed live prey may catch animals that enter their enclosures in zoos[830,877].

In reptiles, more dominant individuals tend to over-eat and outcompete submissive animals who will receive less food[475]. In zebras, social aggression at feeders was caused by intolerance of neighbour proximity rather than food competition, suggesting the need for more widely-distributed food piles to alleviate social stress[903]. Increasing the number of ‘foraging patches’ by spreading food piles out reduced stereotypic behaviour in two vicugnas[886].

Nutritional disorders

Animal diets are formulated based on species-specific nutritional requirements, animal health status, management protocols and available food items, and around 64 possible nutrients may need to be considered[864]. Lack of knowledge on the digestive physiology of many wild animals means that the diets of captive wild animals are often based on domestic species perceived to be similar, e.g. horses are the model for rhinoceroses and elephants, but the validity of such ‘model species’ is questionable[866] and mistaken assumptions could easily lead to nutritional imbalance[864]. For instance, marsupials have a 30% lower metabolic rate than other eutherian mammals and hence have lower energy requirements than a eutherian model species[318].

Inappropriate diets can lead to nutritional deficiencies and diseases. Inadequate nutrition can lead to early mortality in kori bustards[853]. Poor diet in bears can cause chronic diarrhoea[156]. Vitamin and mineral imbalances and unsuitable amounts of protein can lead to softening of the beak in young birds and subsequent beak deformities or beak overgrowth that requires regular trimming[769]. Malnutrition in raptors contributes to respiratory fungal infections[904] and can lead to stomatitis in snakes[849]. Calcium and vitamin D deficiencies can cause nutritional secondary hyperparathyroidism, the most important nutritional disorder in reptiles[307].

Both invertebrates and vertebrates feed selectively according to macronutrient composition[905]. Wild grey kangaroos use natural salt licks as a source of sodium[906]. Wild elephants utilised all 88 vegetation types available to them[301]. After a kill wolves consume the internal organs first, particularly the liver which contains vitamin A and glycogen[872,873]; both captive and wild brown bears balance their intake of salmon with fruit to maintain a diet of 17 to 19% protein that maximises growth rate[907,908]. European badgers maintain a consistent protein intake across different habitats[909]. However animals do not necessarily select adequate diets nutritionally so it is important to provide a balanced diet[860].

Due to cost and convenience, falconers may supplement the diets of captive falcons with pieces of lean muscle, which has a lower calcium:phosphorus ratio and thus less absorbable calcium, so red meat diets (as opposed to whole prey diets) can lead to the common metabolic bone disease (MBD) nutritional secondary hyper-parathyroidism[910]. MBD as a result of low calcium to phosphorous ratios has been reported in a wide range of species including amphibians[587], crocodilians[819,839], coatis[172], primates[911,912] and camelids[913], especially camelids between three and six months of age[833]. Low calcium to phosphorous ratios are also associated with urolithiasis in male camelids and ruminants[833].

Whole prey items are often considered a nutritionally complete diet for carnivores[880], of which many feed almost exclusively on whole prey in the wild, e.g. falcons[910]. However peregrine falcons fed only on whole quail had lower vitamin E values to wild conspecifics, and showed increased reproductive success after supplementation[880]. Vitamin E functions as a biological antioxidant and deficiency has contributed to chronic muscle disease and degeneration in various captive exotics[880]. Captive animals are exposed to air pollution, particularly during transport, and air pollution causes increased oxidative stress; antioxidants in the diet, such as vitamin E, may moderate the impacts of oxidative stress on respiratory and cardiovascular health[880,914]. However vitamin E deficiency is widely reported in captive birds that consume high levels of polyunsaturated fatty acids (PUFA), such as seed diets, fish and meat, since PUFA reduces vitamin E absorption[880].

Vitamin A deficiency, or hypovitaminosis A, is a common result of poor diet in amphibians[915], chelonians and insectivorous lizards[252,307], birds[859] and mammals[172]. Hypovitaminosis A is associated with compromised vision and respiratory, reproductive and digestive infections caused by dry mucous membranes[307]. Reptiles can suffer from dysecdysis or bacterial and fungal dermatoses as a result of nutritional imbalance, particularly vitamin A deficiency in chameleons and chelonians, high fat diets in monitors and other large sedentary lizards, and vitamin C deficiency in snakes[835]. The MBD nutritional secondary hypothyroidism can also be induced by iodine deficiency in herbivorous lizards and chelonians if they consume too many goitrogenic plants (such as broccoli, cabbage, cress and kale) which interfere with iodine uptake[307]. Excess protein or water imbalance can cause gout in reptiles and birds[802,819,839]. Wild coati diets consist of insects and fruit, but captive coatis are often fed on commercial dog and cat food high in heme iron, which may lead to iron storage disease[172]. Zinc deficiency increases the risk of skin lesions in camelids[833].

Food as a source of disease and ill-health

Food can be a source of parasites and pathogens, depending on how it is sourced, stored and fed. Crocodilians can contract mycobacteriosis and salmonellosis from raw meat[819], particularly if fed chicken since avian-derived food carries a greater risk of food-borne infection, including *Salmonella* and falcon herpes virus, than mammal-derived food[843]. Reptiles are often bitten by live prey[897] and these bite wounds can become infected[835]. Raptors fed fresh (warm) pigeons can contract viral enteritis (inflammation of the intestine) or *Trichomonas gallinae* infections[789]. Overfeeding can lead to sour crop in raptors, which causes toxaemia and death if left untreated[910]. Aflatoxins in mouldy cereals can predispose sloth bears to hepatic neoplasia[775]. Circuses and travelling animal shows may not always be able to feed animals fresh meat: raptors fed on meat that is old or has been stored at room temperature can contract bacterial enteritis[789]. Most zoo felids are fed on raw horsemeat-based diets, which harbour disease-causing microorganisms[916]. Kinkajous do not need animal-based foods and, when fed meat in captivity, can develop salmonellosis, coliform enteritis, nutritional secondary hyperparathyroidism and intestinal parasites[319]. Macropods are susceptible to toxoplasmosis from barn hay contaminated with cat faeces[318], suggesting the importance of off-the-ground food storage and reliable suppliers.

Circuses may buy meat from local slaughterhouses to feed carnivores and cannot guarantee its quality. Five out of eight bears in a circus were killed by Aujeszky's disease after being fed pigs' heads[917]. All clinical cases of Aujeszky's disease in bears have been in captive animals, suggesting that they rarely encounter the virus in the wild; this may explain its rapid fatality[917].

Changes in diet can have adverse effects on captive wild animals. Psittacines may be neophobic and initially reject a new diet if it is not changed gradually[859,860]. Ruminants and camelids such as dromedaries[324] adapt slowly to new plant species in their diet, so a rapid change in diet from high forage to high concentrate grain or pellets can alter ruminal pH and microbial flora and lead to the metabolic disorder polioencephalomalacia[833]. Grain ferments rapidly and grain overload can also cause lactic acidosis and urolithiasis in camelids and ruminants[833]. Cervids such as reindeer are sensitive to sudden changes in diet and can contract gastrointestinal disease if feed is changed too quickly, particularly sudden increases in grain, protein or grass[788,822,823]. Captive reindeer may be handfed grain by visitors in Christmas grottos[788]: sudden grain overload can lead to necrobacillosis in bison and deer[822].

Transport

Few peer-reviewed studies have investigated the effects of transport on the welfare of wild animals in circuses. Some research has been conducted into the movement of zoo animals. Although these are similar to wild animals in circuses, in that they are not domesticated, they are unlikely to be transported on more than a few occasions and will not have been subjected to regular transport.

Most research on the welfare effects of transport involves livestock. Farmed animals are domesticated and are rarely transported more than a few times in their lifetime, so the findings may not always be applicable to wild animals in circuses, which are transported frequently. Some issues that contribute to welfare problems in livestock transported to slaughter, such as mixing of unfamiliar animals in crowded conditions, are less likely to be issues for circus animals, which are often transported in individual cages or compartments or in groups of familiar individuals.

Most studies of animals that are transported regularly involve horses. The results are still not necessarily directly applicable to wild animals in circuses, but the negative effects of transport on non-domesticated animals in circuses are likely to be at least as significant as for domesticated horses that are transported regularly.

Frequency of transport and habituation to transport

Animals in circuses may be transported weekly or even daily in some cases[222,233,918]. Physiological and behavioural measures indicate a reduced stress response to transport with repeated exposure in birds of prey[919], tigers[920], cattle[921], sheep[922] and horses[923]. However, there are still significant negative effects on health and welfare in animals that are habituated to frequent transport. For example, in horses, transport is generally associated with lower reproductive rates, increased disease incidence, a temporary reduction in athletic performance and the alteration of many other physiological traits indicative of stress[924].

Tigers naïve to transport showed a greater increase in respiration rate (230 ± 84% above baseline during transport and 394 ± 36% above baseline after transport) than tigers transported at least twice before (166 ± 57% above baseline during transport and 195 ± 56% above baseline after transport)[920]. Unlike the experienced tigers, naïve tigers had their ears oriented back and low most of the time during transport. FGMs peaked at 482% above baseline for naïve tigers, compared with 158% above baseline for experienced tigers, and raised levels persisted for nine to twelve days after transport in naïve tigers compared with six to nine days in experienced tigers. These data suggest that physiological disturbances associated with transport stress may not return to baseline levels before circus animals are subjected to further transport.

Loading and unloading

Loading and, to a lesser extent, unloading are the most stressful parts of transport for livestock[925]. This may also be true for circus tigers, in which body temperature may increase by 1-2°C as a result of the activity and excitement associated with loading[233]. Before transport, many cages and trailers require preparation and loading, which often involves work crews shouting to each other trying to co-ordinate efforts, or loud tractors to load cages into trailers or onto flatbed trucks[926]. Circus tigers may react to the presence of work crews or tractors by growling or swiping with their paws[233,926]. Circus tigers transported in cages built into the trailers were noticeably calmer during transport and did not show such a high transport-related increase in body temperature[233].

Since circus elephants load without difficulty[918,927], it has been suggested that they may view the transport container as 'home' since circus animals often spend much of their time in transport containers even when not being transported[927].

Effects of transport on behaviour

The effects of confinement in small barren enclosures during transport are of particular concern because, compared with most other animals, circus animals spend a substantially greater proportion of their time being transported. Transport causes disruption of eating, drinking, resting, REM (rapid eye movement) sleep and circadian activity patterns[923,928]. These effects are likely to be exacerbated by irregular schedules and frequent journeys with insufficient recovery periods.

The movement of circus elephants is very restricted during transport because they are typically chained diagonally by a front and rear leg[918]. Transported circus elephants spent on average 40.5% of observed time engaged in stereotypical weaving[927]. The average time spent weaving was 48.3% for elephants transported in a trailer and 35.2% for elephants transported in a rail car. In contrast, picketed circus elephants spent on average 15.9% of their time weaving one season and 14.3% the following season[159]. Elephants that were never observed to weave when outside the transport vehicle commenced weaving shortly after entering the trailer or rail car[927]. Confinement to transporters without a view outside may also cause distress. Elephants exhibited more nervous behaviour when confined to pens with a restricted view outside[250].

On two journeys of around four hours duration, circus tigers spent on average 27.2% and 22.8% of observed time engaged in stereotypical pacing[926]. On another journey of similar duration, two tigers that had performed just prior to transport were more inactive, with lower levels of pacing and this was mostly in the latter half of the journey, when it averaged 10.8% of observed time[926]. These levels of stereotypical pacing are higher than reported for circus tigers in their home cage when not being transported: this averaged 4.9% of observed time for tigers with or without short periods of access to an exercise pen[179]. Stereotypy-eliciting situations are likely to be poor for welfare[127], and so increased levels of stereotypy in circus elephants and tigers during transport suggest that their welfare is impaired by transport, although it has been argued that, since the elephants did not appear to be in a “trance-like state”, the stereotypy may not have been indicative of poor welfare[927].

Vehicle movement and vibration

Continuous postural adjustments to maintain balance during transport are physically and mentally stressful for animals[929]. Red deer were more likely to lose balance when they had more space, and they preferred to travel either parallel or perpendicular, rather than diagonally, to the direction of travel[930]. For road journeys, road type markedly affects the frequency with which transported animals experience losses of balance, with smoother travel on motorways and dual carriageways resulting in fewer falls and causing less disturbance to resting behaviour compared with other road types[931,932]. Driving events, such as acceleration, braking, stopping, cornering, gear changes and uneven road surfaces, can have a major negative influence on the welfare of animals by affecting the risk of injury and disturbing the ability of the animals to rest during the journey[933].

Vibration in animal transport vehicles is stressful for animals[934-936]. Reptiles are particularly sensitive to acoustic noise (airborne stimuli) and to vibratory noise (substrate-borne stimuli)[317,658] and are therefore particularly unsuited to regular transport.

Environmental conditions

The environmental conditions within transport vehicles are a major factor affecting animal welfare during transport[933]. Maintenance of appropriate temperature and humidity is particularly important when transporting reptiles, which are reliant on external factors for thermoregulation[317]. Temperatures recorded ranged from -1.1°C to 37.3°C inside trailers during transport of circus tigers in North America. All of the vehicles relied on natural ventilation for cooling and were not equipped to provide supplemental heating[233]. While the temperatures were within the range experienced by tigers in the wild, transport in vehicles does not allow them access to the shade or pools they need for thermoregulation[28,330]. Nevertheless, the tigers were able to maintain their body temperature during the surveyed journeys[233].

Similarly, the temperature inside elephant transport vehicles in North America was generally maintained between 10°C and 38°C[918]. While this is within the range of temperatures experienced by elephants in the wild and did not appear to exceed the ability of the elephants to thermoregulate, they would be unable to perform at least some of their thermoregulatory behaviours, and there were no monitoring systems to alert the driver to extreme temperatures. Most of the trailers used to transport circus elephants were not insulated and it is important to monitor internal temperatures, which can increase rapidly when a non-insulated trailer is stationary during hot weather[918].

Translocation

Animals exhibited in public demonstrations and entertainment shows are transported regularly between locations. Frequent changes in environment may influence the psychological welfare of animals and, depending on how individuals respond and how quickly they acclimatise to novelty, it may be positive by providing mental stimulation, or negative by causing distress due to disturbance, unsuitability or simply lack of familiarity.

Effects of translocation

Translocation has been associated with stress responses in a variety of captive animals when moved between different enclosures within the same facility. Lab-housed macaques that experienced more room moves displayed more stereotypic behaviour[185]. Leopard cats showed increased UGMs and hiding behaviour following translocation to novel enclosures[256]. Margays and tigrinas showed increased stereotypic pacing (70% of observation time as opposed to 35% before translocation) for the first three days after translocation from a large enriched enclosure to a smaller, barren enclosure, while FGMs remained elevated for several months and reproductive cycling was disrupted[257]. In cheetahs, some individuals showed elevated FGMs for over 30 days when moved between facilities, particularly if the new enclosure was in public view rather than off-exhibit, irrespective of pre-movement exhibit type[85]. Capuchins and squirrel monkeys rested more, had shorter inter-individual distances and spent more time at high (i.e. safer) elevations immediately after relocation to a new enriched enclosure[716]. Persian onager took up to 30 days to acclimatise (defined as having a mean FGM similar to baseline) after translocation to a smaller enclosure with increased human exposure, and one individual failed to acclimatise[114].

In translocation studies where animals are moved between different facilities or locations, the effects of translocation are coupled with the effects of a change in social environment. In cheetahs, some individuals showed elevated FGMs for over 30 days when moved between facilities, particularly if the new enclosure was in public view rather than off-exhibit[937]. Elephants showed an increase in FGMs after translocation[72,938] and a bull Asian elephant displayed a 400% increase in stereotypical behaviour and disturbed sleep patterns[938].

Besides moving animals between institutions or to newly built enclosures, some zoos move animals between enclosures as part of their routine husbandry. Animal rotation is a zoo management technique used to increase the spatial and behavioural opportunities of animals[939]. Rotation management is based on the idea that wild animals rotate between different but familiar areas of their home range, such as to exploit seasonal foraging patches or den sites. Cheetahs rotated between conspecifics' enclosures showed increased exploratory behaviour, suggestive of olfactory enrichment[603]. Rotating gorillas between two naturalistic exhibits on a regular basis appeared to be beneficial as they showed no change in abnormal behaviour, were more active, and utilised a greater proportion of each exhibit[940]. These gorillas were more active in their familiar 'home' enclosure than the less familiar 'away' enclosure[940], which may suggest they were more comfortable in the familiar environment. Another study of different species rotated between four exhibits showed no clear positive effect on behaviour or activity levels and the lingering scent of previous residents was associated with increased scent marking and pacing in tapirs and tigers[941]. While scents of other animals may provide some olfactory stimulation, these reactions indicate stress. So the regular rotation between different enclosures has the potential to offer some mental stimulation through maintaining novelty, but the positive effects seem to be minimal and habituation still occurs eventually[941]. Rotation also offers animals no control over when they change location.

Habituation to translocation

Animals can take an unexpectedly long time to acclimatise to new environments. In one long term study chimpanzees and gorillas took over a year to acclimatise to a new enclosure following translocation even though it was not very different in terms of size and facilities[648]. The duration and amount of disturbance caused by each relocation may also influence acclimatisation. Canadian lynx FGMs remained elevated for less time in an individual translocated within the same institution than a conspecific translocated 450 miles[230]. A group of black rhinos showed elevated FGMs for up to nine weeks after translocation between zoos, though individuals recovered faster if previously trained to crate[92]. This exemplifies the potential for training to alleviate transport stress and illustrates the importance of minimising travelling distances. While circus animals are subject to frequent changes in location, journeys between venues are already relatively short in Britain[942] and the beast wagon remains their primary enclosure: this consistency may reduce the stress of relocation.

Choice and control

It was put to us by the British Veterinary Zoological Society that the majority (if not all) animals used in performances generally in the UK are captive-bred and reared and thus habituated to their environment[943]. However, animals need to be able to make choices, and the choices available to animals in captivity are trivial in comparison to those available to them in the wild, where choices vary seasonally if not daily[448], and their very survival depends on the choices they make[600]. Unlike their wild counterparts, captive animals cannot control their exposure to environmental stimuli e.g. by moving, sheltering or adjusting activity patterns[25]. In the prolonged absence of controllability, animals may enter into a state of learned helplessness in response to aversive experiences[944] or seek to gain control through maladaptive behaviour, i.e. stereotypies[25]. Both scenarios are evidence of a failure to adapt. The desire for control is innate rather than learned, and since perceived control helps regulate stress responses, this desire seems to be biologically motivated and thus important for survival[945]. Therefore anything that undermines the perception of control will harm animal welfare, and this lack of perceived control may be the greatest stressor for captive animals[416].

Allowing animals more control over their environment has proven welfare benefits. Rats given control over a light stimulus performed better in a cognitive discrimination task than conspecifics with no control[946]. Allowing marmosets control over supplementary light evoked reductions in agitated behaviour and increased calm locomotion and rest, compared to conspecifics with no control[947]. The effect of control has also been shown in reverse: allowing monkeys control over a noise stimulus and then withdrawing it induced increased levels of aggression[671].

Where control is not possible, opportunities for choice create the illusion of control and contribute to a more positive affective state[945]. Animals and humans show a preference for choice[945], e.g. in an experiment pigeons preferred free over forced choice[948].

Protected contact training allows animals to choose whether or not to participate[451,473,485]. Visual barriers and retreat spaces allow animals to moderate their contact with humans[130,354-359]. Greater enclosure size and complexity offers a wider variety of behavioural opportunities[256,265,287,288,291,292,294]. When given free access to both on- and off-exhibit areas, giant pandas showed less agitated behaviour and reduced cortisol[949], polar bears showed increased social play and reduced stereotypical behaviour[950], and chimpanzees showed increased activity and social behaviour[951].

Having choices over locations appears to contribute to better welfare. However whether animals utilise available choices depends on individual experience and context[945] and environmental stimuli *per se* are less important that the opportunities they offer to the animal[952].

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