

## The effects of captivity on the morphology of captive, domesticated and feral mammals

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### ABSTRACT

1. The effects of captivity on the behaviour of wild and domestic animals have been relatively well studied, but little has been published on morphological changes in wild animals in captivity. We review the evidence for changes in a wide variety of mammalian taxa, with non-mammalian examples where relevant.

2. We consider the morphological effects of the process of domestication, and compare changes in both hard and soft tissues in captive and domestic animals with those in their wild counterparts. These include skull shape differences, brain size reduction, postcranial adaptations and digestive tract changes.

3. We also summarize studies that have looked at morphological change in feral animals in comparison with their wild and domestic ancestors, and consider their use as an analogue for morphological change in captive-bred animals that have been released into the wild.

4. We then discuss the importance of this work for the wider aims of conservation of endangered species and captive breeding over many generations, and emphasize the importance of studying these changes now, while for many species, the process is just beginning rather than many generations down the line, or immediately prior to release, where survival of captive-bred animals may be severely compromised.

*Keywords:* captive breeding, domestication, feral, morphological change, phenotypic plasticity, reintroduction

### INTRODUCTION

There is increasing awareness of the potential for 'domestication' to occur as a by-product of wild animals being kept and bred in captivity. Much of this work has been centred on behavioural changes, such as loss of response to predators and alteration of defensive and sexual behaviours (e.g. Price, 1999, 2002). However, it is also apparent that morphological and physiological changes can occur in captivity, which could have important implications for reintroductions and the management of wild and captive populations as a whole, but as yet these have received little attention. This may in part be because there is an essential difference between the aims of taxonomy/functional morphology and conservation; conservationists aim to preserve and propagate live animals, whereas skeletal morphologists rely on dead ones for their raw materials. Skeletons are also often viewed as rigid, genetically defined

entities; whereas in reality, they are entirely plastic, responding significantly to behavioural and environmental stimuli. There is also a perception that the remains of captive animals are 'atypical', and should therefore not be included in morphological or taxonomic studies (Hollister, 1917; Howell, 1925).

Studies of captive-bred animals provide a unique opportunity to assess the relative importance of environmental and genetic influences on morphology, which may have important taxonomic and evolutionary implications, and may affect the conservation and management of wild-living and captive populations. This latter point will become increasingly important as wild and captive populations for each species are managed together. Given that the current aim of zoos is to maintain self-sustaining, genetically diverse populations for up to 200 years (Soulé *et al.*, 1986), it is time that the consequences of morphological and physiological changes in captivity are quantified and addressed.

We review briefly the common changes that occur in the skeletal morphology of wild animals when domesticated, as these may provide important indicators of how we may expect morphological changes to occur in species removed from the wild for many generations and which have often survived severe population bottlenecks when brought into zoos. We then review the variety of morphological changes, from shape changes to decreasing brain size, which have been observed in captive wild animals. Studies of feral domestic animals may also prove of benefit, as they provide natural experiments to help us find out if the morphological changes that occur in multigenerational captive animals persist in the wild, or if they are simply individual responses to the captive environment. Suggestions are then given for areas where further investigation is necessary.

## DOMESTICATION

A variety of physical changes are thought to have occurred to wild mammals during domestication. These were listed by Clutton-Brock (1999) as changes in body and brain size, alteration of external appearance, the gaining of a fat layer beneath the skin and a reduction of the facial region. The majority of these changes are thought to result from increasing neoteny in domestic mammals, which is a form of paedomorphosis. The animals that we see today are the ultimate product of some 5000–15 000+ years of domestication, and the differences between them and their wild ancestors are likely to be marked, given the power of artificial selection to bring about rapid morphological changes. This subject has been a topic of interest since the mid-19th century (Darwin, 1868), and evidence is gathering to suggest that characteristics that are considered to be markers of domestication, such as floppy ears and shortened tails, can arise relatively quickly by selecting for behavioural characteristics conducive to captivity. In 1959, Dmitry Belyaev began a breeding programme for silver foxes *Vulpes vulpes* which had been bred in fur farms for over 50 years. In this experiment, the tamest animals from each generation were selected to be the founders of the next generation. After 30–35 generations, foxes were produced with floppy ears (0.23%), rolled (9.4%) or shortened tails (0.14%) and maloccluded teeth, although the latter were still at very low levels within the population (percentages based on occurrences per 100 000 foxes after 40 years) (Trut, 1999). Moreover, many coat colour mutations (e.g. non-agouti, white spotting), which are frequently seen in domestic mammals, also became more common (12.4%) in these domesticated foxes. After 40 years, 70–80% of the population was tame; animals actively solicited human contact by whining and licking the hands of their keepers (Trut, 1999). This experiment has shown that within 10–15 generations, significant morphological changes began to occur as a by-product of the selection of animals for tameness. We believe that domestication may be occurring inadvertently in captive wild mammals (albeit at a slower

rate than artificial selection) through passive selection for animals that are behaviourally more suited to captivity, thereby resulting in concomitant morphological changes over several generations, which may have severe consequences for the ability of the descendants of today's captive endangered species to be successfully reintroduced to the wild after 200 years.

### CAPTIVE BREEDING FOR CONSERVATION

Early efforts to consider the effects of captive breeding on wild mammals have concentrated on preserving the genetic variability of the population (e.g. Frankham *et al.*, 1986). While this is obviously important, it appears that captivity can also erode an animal's ability to function in the wild. There are numerous examples of captive-release programmes failing through poor foraging and lack of predator recognition or, in the case of the golden lion tamarin *Leontopithecus rosalia*, the loss of the ability for effective locomotion and orientation in their natural environment (reviewed by Menzel & Beck, 2000; Wallace, 2000). Trut (1999) observed that tamed silver foxes that had escaped from the breeding programme invariably returned to the farm, and suggested that they would have been unable to survive in the wild; similar behaviour has also been observed in escapee or released American mink *Mustela vison*. As Frankham *et al.* (1986, p. 136) commented, 'inadvertent selection for tameness and adaptation to the captive environment are inevitable. This reduces the chances of successful reintroduction of the population into the wild'. Populations of endangered species within zoos may have been subject to severe genetic bottlenecks, and are clearly self-selecting for those animals that can tolerate captivity. Only those animals that are able to adapt to captive life will survive, and a still smaller proportion of those will reproduce. For example, in an attempt to repeat the silver fox domestication programme with wild otters *Lutra lutra*, only 8 of 50 wild-caught otters reproduced successfully, while only 14% of wild brown rats *Rattus norvegicus* produced progeny that survived to adulthood (Trut, 1999). Therefore, it is not surprising that captive animals exhibit marked differences from their wild conspecifics relatively quickly, as they are founded from small populations and the selection pressures on captive animals are substantially different from those in the wild. We will now summarize the morphological and physiological changes, which have been observed in a wide variety of captive mammals, with the inclusion of some non-mammalian examples where relevant.

### CHANGES RESULTING FROM THE EFFECTS OF CAPTIVITY

#### Diet

Many of the early problems in captive animal husbandry were related to poor diet, and death rates were often high; Sutton (1884), for example, post-mortemed 130 carnivores from London Zoo between January 1882 and February 1884. Sutton's paper is one of the first to identify pathologies in captive wild mammals, including rickets and tuberculosis. He found individuals in which the 'teeth are large, defective in number and late in appearance' (Sutton, 1884, pp. 181–182), and also that paralysis of the hindquarters resulted from enlarged vertebral discs pressing on the spinal column (similar to that of spondyloarthritis, see below). His overall diagnosis was that these problems were all caused by the same factors: 'Bad hygienic conditions incident to the life of a captive' (Sutton, 1884, p. 181).

Diets lacking in necessary vitamins and minerals were a source of many pathological conditions, such as osteodystrophia fibrosa, which caused gross cranial thickening in three captive subadult baboons *Papio* sp. (Cordy, 1957). The long bones of these animals showed enlargements of the proximal and distal ends of the diaphyses, but the skull was most severely affected with only the basicranium remaining at normal size. It was suggested that an abnormal calcium : phosphorus ratio in the diet could be responsible (Cordy, 1957). du

Boulay & Crawford (1968) also looked at nutritional bone disease in a sample of 31 South American primates, of which 25 showed changes observable in radiographs, such as bowed limb bones and thickening of the skull vault, which were concluded to be due to a diet deficient in calcium and vitamin D<sub>3</sub>.

However, following extensive work on dietary nutrition in the 1960–70s, diseases such as these have largely been eradicated (see Kleiman *et al.*, 1996; section 2), although some animals such as big cats and callitrichids continue to cause concern. Baker & Lyon (1977) observed changes in eight lion cub *Panthera leo* skulls, including thickening of the cranial vault (especially the parietals), cranial asymmetry and herniation associated with increasing paralysis and eyesight loss. More recently, Chandra *et al.* (1999) provided more evidence for cranial thickening in lions, especially of the parietals and the tentorium cerebelli, and reviewed the evidence that vitamin A deficiency may cause this type of problem. Other possibilities included a genetic origin, but there is, as yet, no consensus on the cause of this malformation. Progressive limb paralysis and cerebellar degeneration has also been noted in captive-bred cheetahs *Acinonyx jubatus*, but it appears that no examination of the crania of these animals has been carried out and the cause remains unknown (Palmer *et al.*, 2001).

In addition to pathological changes, there are substantial differences related to body size and rate of maturity between wild and captive animals, and there is anecdotal evidence to suggest that better nutrition in captivity could be the cause. For example, Smuts, Anderson & Austin (1978) found that the cranial dimensions of a small sample of captive lion cubs were greater than those of their wild counterparts from the same geographical area. However, it is possible that the observed size differences were the result of faster maturation in the captive animals, as they only looked at specimens up to 36 months of age. Schaller (1972) also noted that wild Serengeti lion cubs were smaller than captive cubs of the same age, and thought this might be due to periodic starvation in the wild animals. A wild-caught, but captive-raised, cub was reported as being nearly twice the size of wild cubs of similar age (Schaller, 1972). Captive-bred chinchillas *Chinchilla laniger* have significantly longer and wider skulls with a greater degree of variation in skull profile in comparison with those of wild individuals (Crossley & del Mar Miguélez 2001). The authors suggested that the larger size of the captive specimens was probably due to an unrestricted diet with all nutrients available. In addition, some animals in captivity do appear to mature faster. A study of growth in wild and laboratory chimpanzees *Pan troglodytes* revealed that captive chimps grew bigger and faster than those from the wild (Kimura & Hamada, 1996). This difference occurred in the limb bones, which grew longer in laboratory chimpanzees, whereas skull measurements seemed to be unaffected. Kimura & Hamada (1996) concluded that a better, constant diet, coupled with health care in captivity, resulted in the observed size differences. In a study of dental eruption in yellow baboons *Papio cynocephalus* it was found that the eruption schedules, which had been based on laboratory animals, underestimated the age of wild baboons in Tanzania by up to 1.5 years (Phillips-Conroy & Jolly, 1988). It was concluded that the laboratory animals matured faster than those in the wild and, in particular, the captive males' canines and lower third premolars erupted much earlier than those of wild animals. In the same captive baboon population, menarche was also reached some 1.5 years earlier than in the wild animals (Altmann, Altmann & Hausfater, 1981), while in tamed silver foxes, reproductive age was reached 1 month earlier than in their wild conspecifics (Trut, 1999). There is anecdotal evidence to suggest that better nutrition in captivity has led to golden-headed lion tamarins *Leontopithecus chrysomelas* growing much larger in captivity (K. Leus, personal communication) and many callitrichids in captivity are tending to have litters of three rather than the normal two infants.

However, not all animals grow larger in captivity, and morphological changes need not be uniform. Groves (1982) described morphological differences between the skulls of captive and wild rhinoceroses, and found that captive male Indian rhinoceroses *Rhinoceros unicornis* had smaller skulls (even if originally wild-caught and brought into captivity before maturity) than those of wild animals. In contrast, a variety of changes were seen in five captive female Sumatran rhinos *Dicerorhinus sumatrensis*; two were very large, two were average-sized and one was a dwarf (Groves, 1982). A study of linear body and limb measurements of rhesus macaques *Macaca mulatta* from a free-ranging, but provisioned, population from Cayo Santiago, Puerto Rico, and a captive-bred group derived from the same locality, showed that captive-bred animals did not grow so large, possibly owing to a more restricted captive diet, which included lower total protein, although there may have also been some genetic influence, owing to a limited founding group in captivity (Gore, 1993). Unusually for captive mammals, few of the captive-bred macaques were overweight. An analysis of a small sample of equids (13 wild and 12 captive *Equus* spp.) showed that overall, captive animals had smaller crania than those of wild individuals, with the exception of palate breadth, which was of similar size in both groups (Groves, 1966). Poole, Carpenter & Simms (1980) found that grey kangaroos, *Macropus giganteus* and *M. fuliginosus*, that had been hand-reared, or were from captivity (or very extreme environments on the edge of the species' ranges), had different cranial shapes from those of their wild counterparts, and they suggested that skull size and shape were modified by early nutritional changes. Guthrie (1984) provided extra food for captive-raised Dall's sheep *Ovis dalli* and found that their horn and body size almost reached the larger sizes of those of their Pleistocene ancestors. A male captive-bred alpine ibex *Capra ibex* at Kolmården Zoo, Sweden, developed such large heavy horns owing to a plentiful and rich captive diet, that their weight resulted in arthroses to the cervical vertebrae, leading to constriction of the foramen magnum and spinal cord and the resultant loss of motor ability (B. Röken, personal communication). There has also been some experimental work on pheasant chicks *Phasianus colchicus* which confirms that bone morphology is permanently altered by early nutritional levels. Ohlsson & Smith (2001) found that the levels of protein in the diet in the first 3 weeks of life had a permanent effect on the length and asymmetry of the tarsometatarsus in captive birds, and that the effects on the skeleton were persistent, although the experimental animals caught up in terms of body weight with those chicks reared on a full protein diet.

### **Mechanical properties of food**

The mechanical properties of an animal's food may have a distinct effect on its cranial morphology and dental health, and there have been many studies on this subject in animals as diverse as caterpillars, squirrel monkeys and hyraxes (see Lieberman *et al.*, 2004 for a review of this area). The majority of these studies have involved feeding laboratory animals a diet that is either hard or soft to assess its impact on facial and cranial anatomy.

Corruccini & Beecher (1982) conducted experiments on squirrel monkeys *Saimiri sciureus* and found that animals fed on soft diets had crowded premolars, more displaced teeth and narrower muzzles, while those on hard diets had significantly broader maxillae. More recently, it has been shown that significant differences in the cranial shape of hyraxes *Procavia capensis* have resulted from eating different diets (Lieberman *et al.*, 2004). These studies indicate that there is a relationship between the mechanical properties of food and occlusal and morphological variation. Cheetahs inadvertently provided evidence for this in a non-experimental setting. Cats in zoological collections in North America are often fed on a pre-processed diet, which requires little or no chewing. It was thought that as a result of this soft diet cheetahs

developed 'focal palatine erosion' (FPE) (Fitch & Fagan, 1982), where the lower carnassials fail to occlude with the upper carnassials and impact instead upon the palate. In severe cases, this can lead to sinuses developing between the oral and nasal cavities (Fitch & Fagan, 1982). In the captive population, 15 out of 59 live cheetahs exhibited FPE, with 15 out of 20 fed soft diets being affected (Fitch & Fagan, 1982). Until 2004, this condition had only been noted in captive felids fed on pre-processed diets, but recent work by Marker & Dickman (2004) found some degree of palatine erosion in 144 of a sample of 208 live wild cheetahs in Namibia, with 85 of 208 showing severe erosion. However, only 13 of these animals had perforated palates (6.3% of the total sample) (Marker & Dickman, 2004), in comparison with eight (13.6%) of the North American captive cheetahs (Fitch & Fagan, 1982).

Many diets fed to captive animals have been formulated to provide the nutritional requirements for growth, but they often lack texture and interest (Lindburg, 1998). Also, in the wild food is often not as highly nutritious and contains abrasive particles such as grit or phytoliths. The lack of abrasion in captive diets, resulting in reduced or abnormal toothwear, has led to problems of malocclusion in herbivorous animals, such as rodents, lagomorphs and elephants, which have teeth designed to be worn down by chewing throughout their life.

Studies of both equids (Groves, 1966) and chinchillas (Crossley & Miguélez, 2001) have shown that an insufficiently abrasive diet can have serious consequences for an animal's oral health. In the case of the equids, the increasing height of the maxillary and mandibular molars led to the incisors being held apart, so that the animals were unable to graze effectively (Groves, 1966). Like the equids, the tooth crowns of captive chinchillas were found to be significantly higher than those of wild chinchillas, which led to difficulties in chewing and, in some cases, the tooth roots protruded into the nasal cavity (Crossley & Miguélez, 2001). A slightly different problem is seen in captive elephants (most commonly in the Asian elephant *Elephas maximus*) as they have a very specialized dentition. Each molar erupts in sequence, and there are usually only one or two molars present in any one quadrant of the mouth at any time. However, if the diet is not abrasive enough, the next molar may erupt before the preceding tooth is worn away, leading to impaction and malocclusion in the jaws (Fagan, Oosterhuis & Roocroft, 2001; A.C.K., personal observation). The most famous example of this problem was seen in 'Jumbo' the African elephant *Loxodonta africana* at London Zoo, whose bad temper as a result of this condition led to him being sold to Barnum and Bailey's Circus in 1882 (Jolly, 1976).

A comparative study of brown bear *Ursus arctos* skulls from the Berne bear pit and the wild found that the captive bears had increased levels of attrition to the canines, possibly as a result of chewing cage bars, and also had a high prevalence of dental caries and calculus formation, especially in bears over 10 years of age (Wenker *et al.*, 1999). It is thought that the diet of the Berne bears has contributed to the problems with their teeth, as they were fed on 'mostly low-fibre, paste-like food' (Wenker *et al.*, 1999, p. 217). However, some animals in the wild bear sample also had a large number of caries (up to 64% in one animal). Dental calculus may also be a problem in big cats, but providing whole carcasses to feed on and bones for them to chew on does appear to reduce its occurrence (Haberstroh *et al.*, 1984). However, in the feeding experiment on squirrel monkeys, it was found that the incidences of periodontal disease, dental caries and tooth loss were greater in the group fed on hard diets (Corruccini & Beecher, 1982), probably owing to the dentition being adapted for a softer frugivorous/insectivorous diet.

Tooth pathologies have also been noted in captive animals. These range from those caused by trauma to developmental defects such as dental enamel hypoplasia. In a study of wild and captive primates, Molnar & Ward (1975) found that all animals had some level of microstruc-

tural tooth defects, including hypoplasia, but their incidences were higher in captive individuals. Recently, Franz-Odenaal (2004) has studied the incidence of hypoplasia in the teeth of wild and captive giraffes *Giraffa camelopardalis* and found that those of wild giraffes lacked defects, while those of captive animals showed lines that corresponded with periods of stress such as weaning. Fagan *et al.* (2001) discussed the incidence of traumatic breakages of elephant *Loxodonta africana* and *Elephas maximus* tusks caused by the captive environment, and noted similar occurrences in walrus *Odobenus rosmarus* and babirusas *Babyrousa babyrussa*.

### Biomechanics of the skull

It appears that not all areas of the skull react equally to the circumstances of captivity. A variety of morphometric studies have found that the skulls of captive animals are significantly different from those of their wild conspecifics in some areas and yet other dimensions remain unchanged. Many of the areas that do appear different in captive animals are related to the feeding apparatus, and this is probably a result of the different mechanical properties of captive diets (see above). For example, Groves (1982) reported that the skulls of captive Indian rhinoceroses were smaller, yet had increased mastoid and zygomatic breadths and higher occipital crests than those of wild individuals. He suggested that it could have been due to badly placed feeding trays or the feeding of inappropriate foodstuffs. Duckler (1998) also found a thickening and change in shape of the sagittal crest in a series of captive tiger *Panthera tigris* skulls, and postulated that this might be a result of stereotypical behaviour, such as overgrooming.

Hollister (1917, 1918) described differences between the skulls of captive lions, which had been caught in the wild in East Africa, and those of wild lions from the same geographical area. These differences included increased breadth of the zygomatic arches, shortening of the skull, and reduced cranial volumes in the captive-reared animals. Hollister considered these changes to be due to a lack of exercise of the cranial muscles in captivity. Howell (1925) re-examined Hollister's specimens and concluded that these animals were pathological, and suggested a dietary deficiency as the cause of the observed differences that also included a general increase in the overall thickness of the skull and a reduction in the height of the foramen magnum. Despite the pathological nature of Hollister's lions, his observation of an increase in zygomatic breadth has been supported by O'Regan (2001). Further work on a larger sample of skulls found that the breadth of the muzzle was also significantly larger in both male and female captive lions and leopards *Panthera pardus* than in wild individuals (O'Regan & Turner, 2004). Finding this difference in two species of big cat suggests that there may be a biomechanical, age-related or behavioural reason for these changes, but without knowledge of the life history of the animals, it is difficult to be certain.

Captive crocodylians also exhibit cranial changes. In a study of American alligators *Alligator mississippiensis*, Meers (1996) found that the skulls of captive animals had broader maxillae and premaxillae, a flatter profile and less sculpting or rugosity on the cranial surface than those of wild individuals. These changes were all related to the biomechanics of the feeding apparatus. Captive reptiles are fed to ensure the maximum growth in the minimum amount of time, resulting in animals that have smaller skulls than those of wild alligators of similar body size, and suggesting that the cranium cannot match the growth rate of the body (Meers, 1996). There are concerns that animals with this morphology that have been bred for release into the wild could out-compete the wild animals, as their larger body size would give them an advantage over wild individuals when competing at carcasses (Meers, 1996). Their

smaller skulls may, however, place them at a disadvantage in holding onto carcasses and twisting off mouthfuls to swallow, especially when competing with others.

A study of the skulls of two wild and three captive populations of oldfield mice *Peromyscus polionotus subgriseus* found that there were significant differences between the wild and captive populations (McPhee, 2004). Each captive population had different founders, although they were all drawn from the same geographical area, and they had been bred in captivity for different lengths of time (2, 14 and 35 generations). McPhee (2004) found that each population had its own trajectory (i.e. that different populations had different morphological changes), and that these changes were not cumulative over time (i.e. increased palate breadth in one group did not lead to even wider palates in the next). This has important implications as it suggests that populations held in isolation will develop significantly different morphological traits, and so conversely, it is possible that captive populations managed as whole may all develop the same features. Most of the above studies have used morphometrics to look for differences between wild and captive specimens. However, other techniques can also be informative. Armitage (1983) used radiographs to determine whether or not an archaeological specimen came from a captive individual. This study of two wild and two captive weeper capuchin *Cebus olivaceus* monkey mandibles found that the wild animals had good cortical development and the medullary cavity contained few widely spaced and thick trabeculae, whereas the captive animals had a porous and 'poorly developed' cortical layer and the medullary cavity was completely infilled with a mass of cancellous bone, which was consistent with the archaeological specimen being from a captive individual (Armitage, 1983).

#### Changes to soft tissues and physiology

Rich, nutritious and easily digestible captive diets may have a significant effect on gut morphology and physiology, which could compromise the survival of captive-bred animals released into the wild, where diets will be poorer and less easy to digest. This phenomenon appears to have only been studied in birds, but we have no knowledge of the consequences of captive diets for mammals. For example, the concentration of the required nutrients in a highly nutritious artificial-formula diet means that captive capercaillies *Tetrao urogallus* develop shorter intestines and caecae, and lighter hearts, livers and gizzards than those of wild birds (Liukkonen-Anttila, Saartoala & Hissa, 2000). As a result, captive-reared birds are less able to digest their natural foodstuffs, such as pine needles, and deal with the toxins they contain (Liukkonen-Anttila *et al.*, 2000). In this case, therefore, the overly nutritious captive diet has actually caused physical changes to the birds' digestive systems and its physiological capacity to deal with wild diets. Similar changes in gut morphology have been recorded in red grouse *Lagopus lagopus scotica* (Moss, 1972), barnacle geese *Branta leucopsis* (Owen, 1975) and houbara bustards *Chlamydotis* spp. (J. Samour, personal communication). Studies on captive-bred Japanese quail *Coturnix japonica* showed that gut length is phenotypically labile. A laboratory group reared on a high-fibre diet had longer gut lengths than those on a low-fibre diet. However, when the diets were switched between groups, it only took 3–4 weeks for the gut length to increase in the new high-fibre group and to decrease in those on the low-fibre diet (Savory & Gentle, 1976). Wild birds may also show seasonal variation in gut length, which correlates with changing seasonal diets (e.g. spruce grouse *Canachites canadensis*, Pendergast & Boag, 1973). It is unclear whether there is similar phenotypic plasticity in mammals. Schauenberg (1977) distinguished between domestic cats *Felis catus*, and European wildcats *F. silvestris*, on the basis of relative and absolute gut length. It has been suggested that domestic cats have a longer gut length, in order to increase digestion times for a less carnivorous diet (Kitchener, 1998). However, despite a similar diet, wildcats

and feral domestic cats have significantly different gut lengths where sympatric in Scotland (Balharry & Daniels, 1998). There are insufficient gut length data from African and Asian wildcats to be certain whether the domestic cat's gut length has been determined by its direct ancestors, the African and Asian wildcats *F.s. lybica* and *F.s. ornata*, or whether it is an adaptation to captivity that may have become fixed within the population.

A study of wild ( $n = 10$ ) and captive-bred ( $n = 4$ ) marsupial feathertail gliders *Acrobates pygmaeus* found that captive-bred individuals differed both morphologically and physiologically from two wild populations (Geiser & Ferguson, 2001). The captive-bred individuals were from a lineage that had been in captivity for four generations. The captive animals had longer tails and snouts than those of the wild individuals, but most importantly, they differed in their ability to enter torpor. Feathertail gliders enter torpor for up to several days in any season during periods of low air temperature. The captive-bred animals were active for much longer periods, and entered torpor at lower temperatures (15 °C) than the wild animals (20 °C). In addition, captive-bred gliders became hypothermic and had to be warmed externally at lower temperatures, whereas the wild-caught animals were never hypothermic (Geiser & Ferguson, 2001). The captive-bred gliders' inability to keep body temperatures stable in ambient temperatures that they would encounter in the wild could threaten their survival, if they are not fully acclimatized to the local environment (Geiser & Ferguson, 2001).

Kitchener, Merryweather & Allchurch (1999) carried out a study to look at the differences between the flight musculo-skeletal systems of mainly Rodrigues fruit bats *Pteropus rodricensis*. They found that the wild-caught founders and captive-bred animals showed no differences in the development of the musculature associated with flight, but no wild-living animals were available for comparison to see if diminished flight levels in captivity have resulted in poorer development of flight musculature there. No significant difference was recorded between the body weights of captive and wild Rodrigues fruit bats. However, the captive bats accumulated subcutaneous fat steadily throughout their lives, until it comprised 30+% of body weight by the age of 20 years, which would probably have prevented or severely affected flight capability. This suggests that the proportion of body mass attributable to the flight musculature is far greater in wild-living bats.

### Age, activity levels and arthropathies

Many animals live longer in captivity than they do in the wild. For example, gorillas *Gorilla gorilla* survive for more than 50 years in captivity compared with 35 years in the wild (Nowak, 1999; Macdonald, 2001). What is not clear, however, is whether the changes such as arthropathies that have been observed in captive animals are normal age-related changes, the result of lack of activity, different nutrition, chronic infection or other environmental factors.

Rothschild, Rothschild & Woods (1998) found spondyloarthropathy in both wild and captive big cats, but osteoarthritis and calcium pyrophosphate deposition disease (CPPD) were only found in captive animals. Spondyloarthropathy is likely to result in a decrease in activity for the affected animals, and would eventually compromise survival in the wild. Kolmstetter, Munson & Ramsay (2000) found that degenerative spinal disease was present in eight of 37 big cat skeletons from Knoxville Zoo. All affected animals were recorded as having progressively decreased activity levels and weight loss prior to death/euthanasia. All vertebral columns showed narrowed or collapsed disc spaces or disc mineralization, and five had spondylosis. Age at onset of clinical signs varied from 10 to 19 years, with a median age of 18 years.

In a study of a variety of captive wild mammals ranging in size from the plains pocket gopher *Geomys bursanus* to the brown bear, Greer, Greer & Gillingham (1977) found osteoar-

thritis in 45 of 145 skeletons. These ranged from mild to severe cases, and included animals such as the giant anteater *Myrmecophaga tridactyla*, gemsbok *Oryx gazella* and Arabian camel *Camelus dromedarius*. None of the skeletons of 11 primates showed arthritic changes, nor the 28 small mammal skeletons (Greer *et al.*, 1977).

Kitchener, Kolter & Brownstein (2001; see also Kitchener, 2004) examined the incidences of various arthroses in captive bears. All bears over 15 years old had severe spondyloarthroses and osteoarthroses with incidences of particular skeletal pathologies reaching more than 96% in 27 individuals of seven species (Kitchener, 2004). Kompanje, Klaver & de Vries (2000) described spondyloarthropathies and osteoarthroses in three captive bears from South-East Asia, which were similar to those recorded by Kitchener (2004). Kompanje *et al.* (2000) distinguished between those which were caused by degeneration of the joints (osteoarthroses) and those which might be triggered by chronic infections (spondyloarthropathies), such as *Campylobacter*, *Chlamydia*, *Mycoplasma*, *Salmonella* and *Shigella*. In humans, these infections may result either from sexually transmitted diseases or gastroenteritis (Kompanje *et al.*, 2000). Roundworms *Ascaris* can also cause reactive arthritis in humans. As discussed by Kitchener (2004), there is suggestive evidence that the skeletal changes may in part be due to activity levels in the captive animals. Two Sumatran tigers *Panthera tigris sumatrae*, which were trained to climb telegraph poles for food each day, had skeletons that were unaffected by arthritis, in marked contrast to less active cats of a similar age.

### **Brain size and complexity**

Reduction in brain size is one of the key criteria for defining a domestic mammal (Clutton-Brock, 1999). However, brain size is not a fixed parameter, and work by Krech, Rosenweig & Bennett (1962) found that rats raised in an enriched environment had larger brains than those reared in a standard laboratory cage. The process of encouraging captive animals to display more of their normal behavioural repertoire, which often includes more activity and responding appropriately to environmental stimuli, is termed 'environmental enrichment' (Young, 2003). Empirical evidence for the importance of environmental enrichment has been seen in experiments, which found that house mice *Mus domesticus* exposed to an enriched environment developed significantly more neurones in the hippocampus (Kempermann, Kuhn & Gage, 1997), while those that had access to a running wheel showed a significantly increased ability to learn (van Praag *et al.*, 1999). These changes are not restricted to just laboratory rodents; studies have shown that London cab drivers (having learned the 'knowledge', Biegler *et al.*, 2001), polygynous male voles, female cowbirds and food-storing birds, all have relatively large hippocampi owing to their requirement for above-normal spatial learning and memory. Captive-bred mammals, which have had no opportunity to develop their spatial memory, may therefore be disadvantaged when released into the wild, as has been shown for golden lion tamarins (Menzel & Beck, 2000). Work by Marchetti & Nevitt (2003) has shown that hatchery-reared rainbow trout *Oncorhynchus mykiss* have significantly smaller brains than those of wild trout. They also found that the areas of the brain that showed the greatest differences were those linked to aggression, feeding behaviour and reproduction, a finding that supported previous work that found that these were the areas in which captive-reared fish are deficient (Marchetti & Nevitt, 2003). Ranchered American mink were found to have, on average, smaller brain sizes than wild mink, depending on whether they had been reared in cages or in open-air enclosures (Kruska, 1996). Moreover, the captive mink had much more variable brain sizes and parts of brains than those of wild animals. Several other studies have reported reduced brain sizes in captive-bred compared with wild individuals, including Mongolian gerbils *Meriones unguiculatus* (17.7% brain weight : carcass

weight; Stuermer *et al.*, 1997), pigs *Sus scrofa* (33% brain weight : carcass weight; Kruska & Röhrs, 1974), and llamas *Lama glama* (17% compared with guanacos, *L. guanicoe* of similar body weight; Kruska, 1982). Przewalski's wild horses *Equus ferus przewalskii* are now totally derived from captive-bred individuals. Despite a captive breeding programme to maintain genetic diversity and no attempt at deliberate domestication, these animals show a 16% decrease in brain weight or a 14% decrease in cranial volume, which is similar to that recorded for domestic horses *Equus caballus* (Röhrs & Ebinger, 1998). Now that Przewalski's horses have been successfully reintroduced to Mongolia and China, it will be interesting to see if their cranial volumes revert to those of their wild ancestors. This has not been the case for feral ferrets *Mustela furo* in Britain and feral domestic cats in Australia, which still retain much smaller cranial volumes than their wild ancestors despite living for many generations in the wild (Birks & Kitchener, 1999; Kitchener and Wagner, unpublished data; see below). Similar results have been recorded for feral dogs, goats and donkeys (Herre & Röhrs, 1990 in Hemmer, 1990), and also for feral domestic pigs in the Galapagos Islands, which are otherwise said to be similar in external appearance to the European wild boar, but with the colouration of the domestic pig (Kruska & Röhrs, 1974).

#### FERAL ANIMALS AS AN ANALOGUE FOR CAPTIVE RELEASE

It may be argued that many of the changes discussed above are simply the reaction of an individual to captivity, and that such changes will not be passed onto their offspring. If this is the case, then there should be no discernible difference between wild and feral individuals of the same species. With our growing knowledge of changes seen in captive animals, it is important to see if any of the observed changes will persist in the wild once animals have been released, as captive release programmes are expensive and time-consuming. Several studies have been undertaken to examine differences between wild, captive and feral animals, and these have produced some interesting results.

Pocock (1932) studied a sample of feral ferret skulls from the island of Mull, Scotland. He was unable to distinguish these from the skulls of wild polecats on the basis of their postorbital breadths and cranial volumes. He suggested that the poor development of the jaw muscles in captive ferrets resulted in their narrower postorbital breadth and lower cranial volume compared with wild polecats and feral ferrets. However, Birks & Kitchener (1999) found significant differences in cranial volume and postorbital breadths between polecats and feral ferrets, which suggested that these differences were not just the result of phenotypic plasticity. Lynch & Hayden (1995) reported differences between captive and feral American mink crania – captive mink have larger skulls, shorter palates and narrower postorbital constrictions. The skulls also displayed reduced sexual dimorphism, which suggested that there might be a relaxation of sexual selection, owing to selective breeding for larger animals and lack of competition for resources in captivity. Feral mink can adapt to different environments relatively quickly, as an examination of 15 populations of feral mink in Belarus found that there were substantial non-metric differences between the founder populations and the subsidiary populations after only 30–40 years in the wild (Ulevičius, Sidorovich & Lauzhel, 2001). Sexual dimorphism was also reduced in the domesticated foxes (Trut, 1999). In a comparison of wild and captive Coho salmon *Oncorhynchus kisutch*, Hard *et al.* (2000) found that captive fishes exhibited a reduction in sexual dimorphism and had smaller heads but larger bodies than the wild salmon. Male salmon, which had been reared in captivity, were also discriminated against by wild and captive female fishes, and were therefore less likely to reproduce than the wild males. These differences might be due to a lack of environmental stimuli such as sea water, migration or increased density in the captive populations. However,

although they are thought to be the result of environmental changes, a genetic difference between the populations could not be ruled out (Hard *et al.*, 2000).

## DISCUSSION

In this review, we have covered a very wide range of morphological changes in a variety of animals. Some of the morphological differences between wild and captive animals can be rectified with appropriate changes in husbandry (e.g. dietary nutrition and abrasion). However, others imply a much greater modification in captive animals than may previously have been expected (e.g. brain size in feral mink). It may prove difficult to release animals which have adapted to captivity for many generations, if changes in brain size, speed of development, etc., have taken place. The changes in internal physiology such as that seen in the shortening of bird's intestines are obviously of great importance, and it will be worth looking to see if similar modifications have occurred in captive mammals and whether they are reversible. Activity levels appear to have a great effect on captive animals, from pathology to increasing amounts of subcutaneous and deposited fat, and this is also something that needs to be addressed. Environmental enrichment in the form of hiding food, scratching and climbing posts, etc., may well lead to changes in the prevalence of these problems, and the next generation of captive animals will hopefully benefit from these changes. Kitchener (2004) has suggested that environmental enrichment will be deemed successful when we can no longer discern any morphological differences between wild and captive-bred animals.

The lessening of sexual dimorphism in a variety of animals (silver foxes, mink and salmon) is also a cause for concern. Sexual dimorphism is central to many reproductive strategies, with the largest males having access to the most females. If this is disrupted, then animals in a population who would not normally be chosen to mate with will have as much opportunity to breed as those who display these traits. If the intention of a captive release programme is for the wild animals to interbreed with the captive ones, then they may be at a disadvantage from the start. In addition, such breeding practices may result in captive populations diverging from the wild ones at a much faster rate. Accelerated maturity may be of benefit if the object is to breed as many animals as possible in a short time period, perhaps to restock habitat from which they have been extirpated but where the niche is still present. If, however, they are to be held in captivity for a number of generations, the faster they breed, the more space will be required to house them, and the process of morphological change from the wild to 'domestic' form may be speeded up. It is also possible that niche separation between different species, or between males and females of the same species, could be altered by a change in the size of captive animals, leading to potential competition between species or sexes owing to inevitable exploitation of similar-size prey.

It is time to think of these problems now, while most captive animals have only been in zoos for a few generations, rather than 200 years in the future. If behavioural abilities can be eroded in 20 years or so, for example, in golden lion tamarins, more effort needs to be put into enriching the environments of all zoo animals, not just those destined for captive-release. The chances are that most species will become endangered at some point and that without further work, the stocks that we are perpetuating may not be able to be released in 200-year time.

## CONCLUSION

A wide variety of animals show differences in captivity, but we are still a long way from understanding what these changes are and their causes. They are important for a variety of reasons, not just for the welfare of the animals, but also because they have the potential to

provide information on the wider issues of mammalian evolution and morphology, particularly with regards to domestication. It is important to understand the changes that occur in captive mammals, because for many species these are the only individuals available for study. The snow leopard *Panthera uncia* is a very rare cat, and there are few wild-caught individuals in museum collections. No one would suggest going out to collect more to feed the interests of taxonomists, but then what is the alternative? Either to refuse to study that species because there is no 'valid' (i.e. wild-caught) material available, or attempt to understand which structures may have been altered by captivity and quantify that change? Unfortunately, the former opinion often prevails.

There is also one very noticeable bias in these analyses – the majority have concentrated on crania, with very few studies looking at the rest of the skeleton. This is partly due to historical factors which have left museums filled with skulls, but very few postcranial skeletons. However, in terms of locomotion and age-related pathologies, the appendicular skeleton is very important and this is an area that needs to be studied.

The majority of the case studies presented in this paper have been small scale, involve small sample sizes or are mentioned in passing in papers written for other purposes. This is an area that urgently needs addressing, and requires focused and carefully thought-out projects to try and unravel the complexities of relating morphological change to diet, environment, lifestyle, etc. in a large number of animals. The ideal pilot projects would be based on animals that have a discrete geographical range in the wild, are readily available in museum collections, have been kept as captive populations at a similar latitude, and breed relatively quickly so that there is a good sample size (e.g. Lewis & Thomas, 2001; McPhee, 2004). Many rodents and other small mammals could offer ideal models, whereby manipulation of the captive environment would be possible over short time scales to see their effects on morphology and behaviour. However, we also take the longer-term view and urge zoos, wildlife managers and museums to work together to take advantage of specimens that become available to study the effects of captivity on larger and rarer species. The National Museums of Scotland has been building such a collection of captive-bred, known-age specimens of a wide variety of endangered species, in order to support long-term morphological studies as outlined above.

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Additionally, quantifying the morphological effects of captivity will help morphologists make decisions about specimen selection and address sources of sample based bias.

The Standard Zoo Diet. Most captive facilities provide felids with a diet of ground meat supplemented with vitamins.

Many studies have reported on the impact of captivity on specific pieces of anatomy in captive animals. For instance, cranial thickening has been documented in captive subadult baboons (*Papio* sp.; [23]) and lion cubs [24].

Other studies, however, have shown decreased skull sizes of some captive mammals including in Indian rhinos (*Rhinoceros unicornis*; [28]) and some equids (*Equus* spp.; [29]).

Animals in captivity experience drastically different selective pressures than their wild counterparts. This can cause evolutionary divergence in behavior.

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Diagram depicting the harsh effects of captivity | Courtesy of Ocean Futures Society.

Leading orca researchers agree that captivity is devastating to these marine mammals, who in the wild, engage in tight knit relationships with one another, travel over 100 miles daily, and work in pods to hunt and find food suited for their large diets. Many orcas have been captured and forced into captivity, which has denied them the opportunity to engage in their natural genetic behaviors.

This was a very powerful article! Although it is extremely saddening to learn about the effects of captivity on these animals, I think this is an important issue that must be addressed. With all of the stories we've seen, I am surprised yet disappointed that we are still fueling this devastating affair.

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