ENCLOSURE SIZE IN CAPTIVE WILD MAMMALS: A comparison between UK zoological collections and the wild.

JORDI CASAMITJANA[1]

Abstract

A comparison was made between the average enclosure size of a random sample of mammals kept during the years 2000-2001 in a random sample of UK zoological collections and the minimum home range of these taxa in the wild. Allometric laws were used to estimate the home range area, while direct observation from videotaped visits to the collections was used to estimate enclosure size area. The results showed that, as an average, the average enclosure size had an area 100 times smaller than the minimum home range.

Key words: mammal, zoo, enclosure size, allometric, megafauna, captivity, home range

Introduction

The zoo debate

Nowadays, many people choose not to go to zoos because they consider that either it is wrong to keep wild animals in captivity as a matter of principle, or the conditions the animals are kept in zoos are unacceptable. The zoo community, and its supporters, think otherwise, and this difference of opinion is what constitute the so called 'zoo debate'.

It is not unusual that people engaged in such debate try to prove their points either by quoting 'expert' opinion or by referring to facts, evidence and reports about zoo's activities. However, many of these 'facts' are missing because no objective research has ever been developed to find them.

One of the most common arguments used in the zoo debate refers to the space available to captive animals kept in zoos. The anti-zoo side of the debate often criticises enclosures for being too small, while zoo advocates tend to respond that they are big enough, or that size 'does not matter'. Who is right? Is there any fact that supports either side of this issue?

We set ourselves the task to answer this question by focusing in captive wild animals kept in UK zoological collections during the years 2000-2001, and this reports summarises the methods and results of the research undertaken for that purpose.

Captive, domestic and wild animals

It is obvious that wild animals did not evolve in captivity, and since many zoo animals are 'exotic', most of them live in conditions quite different than the ones their species naturally evolved in. Temperature, humidity, substrate, light, sound, diseases, predators, vegetation, space, smell, etc. all are factors that are likely to be different in the captive environment compared with the wild one. Doers this matter?

Many think, including me, that it does matter, independently if the wild animal in question has been born in the wild or not.

[1] *Independent Animal Welfare Consultant, jordi@casamitjana.freeserve.co.uk*

The fundamental difference between a wild animal and a domestic one is that the former has acquired its genetic makeup through natural selection, while the latter through artificial selection. Domestic animals exist because the selective breeding organised by human beings in order to modify the 'wild' genetic makeup in favor of 'useful' characters have changed their appearance, physiology and/or behaviour significantly enough so they are now distinctively different from their wild counterparts.

By definition, then, natural selection, in the evolutionary sense, is no longer the main drive that 'shapes' domestic animal's characteristics. Thus, a domestic animal may have adapted to environments that the wild animal from which it was bred from may have not. However, zoos, also by definition, are composed mainly of wild animals, not domestic animals, and since the difference does not reside on whether or not the animals are tamed –or where they live or were born– but how different is their genetic makeup from the 'natural' one, wild animals in zoos are still adapted to the habitat where their species evolved, and may never be adapted to the zoo's environment. Again, does this matter? Is 'adaptation' important?

Evolutionary speaking 'adaptation' has a reproductive meaning linked both to the concept of 'fitness' and to the concept of 'habitat'. A better-adapted individual is better 'fit' to reproduce than a worse adapted one. This 'fitness', though, can manifest itself in many ways: the ability to live longer, find more mates, take better care of offspring, be more efficient in fighting diseases, etc. Each and every of these 'fitness' expressions are modulated by environmental factors, and a more or less constant range of these factors will define a particular 'habitat'. In other words, wild animals are like they are because they evolved in a particular habitat, and if they are placed in other habitats their evolutionary 'fitness' is likely to change. Adaptation is important, because a non-adapted animal population is 'at odds' with its environment, and this situation would either force it to change (if there is room for natural selection) or become extinct.

Both 'adaptation' and 'fitness' have, though, other meanings besides the evolutionary one. In relation to individuals we use the term 'adapted' as synonymous of 'accustomed to', and we use the word 'fit' as synonymous of 'healthy'. These are the meanings used in the so called 'zoo debate', but in fact they are not too detached from the evolutionary meanings.

Since the 'health' of an animals and its ability of 'getting used to' a situation depends on a combination of its genetic makeup –which defines physical and psychological 'hard wired' characteristics –and the animal's experience with its environment, this individual 'adaptation' is also shaped, in part, by the 'habitat' where the animal acquired this genetic makeup. Thus, an animal placed in a habitat significantly different to the one its species evolved in is likely to be 'unfit' both form the evolutionary and welfare point of view. Furthermore, since it is the zoo's interest to keep the animal genetically as wild as possible (for commercial or conservation reasons), this 'unfitness' is likely to remain unchanged after generations.

If that were the case, you would expect to find specific welfare problems in captive wild animals, problems not normally encountered in the wild. In fact, this is exactly what we find if we observe the animals' behaviour. Many animals in captivity show a variety of so called abnormal behaviours (Odberg, 1978, Broom, 1981, 1983, Dantzer 1986, Fraser and Broom, 1990, Mason 1991a, Casamitjana & Turner, 2001) not observed in the wild, and which are likely to have an influence on their reproductive abilities (affecting their evolutionary 'fitness') as well as their health (affecting their welfare 'fitness'). Therefore, there is evidence that 'adaptation' does matter.

Captivity and available space

Is there, though, any particular difference between wild and captive habitats that better explains this 'unfitness' mentioned above? Is there anything in common among all captive animal habitats that is not normally found in the wild? One of the most basic differences is available space. By definition, a captive environment restricts the animal's movements by keeping it into an enclosed space (hence the term 'enclosure'), and this is applicable to all species in all collections.

Several studies have already shown the effect of enclosure size in the behaviour of captive animals (Fisher at al, 1980, Estep et al. 1978, Innis et al. 1985, Hogan et al. 1988, Jensvold et al. 2001), but there are no studies specifically designed to compare, in a quantitative way and across a range of different species, available habitat space between the wild and captivity. This is what we attempted in this study.

The term 'home range' describes the area where, under normal circumstances, a wild animal spends most of its life. Since animals in zoological collections spend their whole life in captivity, comparing enclosure size with home range size would inform us about how different life in captivity is from life in the wild, as far as spatial area is concerned. To emphasise this difference, if we compare the natural minimum home range size of species (as oppose to the average one) with the average enclosure size (as oppose to the minimum one) of the same species in captivity we would be able to qualify the difference in relation to factors of 'availability' that have more bearing in the present zoo debate about this issue.

Each taxon, with their specific biological needs, have a characteristic home range which tends to be the same in the same habitat independently of the individuals involved. This can be measured directly by observing the animals' behaviour, but it can also be deduced from particular biological traits using allometric laws. Allometric scaling laws describe how different body parts and characteristics of living organisms vary (or 'scale) in proportion to changes in body size (Norris, 1998).

Many animals' characteristics, including basal metabolic rate, brain size, size of offspring at birth, heartbeat duration, time of food passage through the gut, etc. scale linearly over most body sizes when plotted on logarithmic axes (Peters 1983, Blueweiss et al. 1978). Ecological and behavioural characteristics, not just physiological, also follow allometric laws. The clearest and best known ecological patterns occur in mammals, where home range sizes vary with body size and are influenced by energetic requirements (McNab, 1963, Harestand and Bunnell 1979, Lindstedt et al. 1986, Swihart et al. 1988).

Because the most accepted allometric laws that relate ecological factors refer only to mammals, we concentrated this study on this group. We used the modern (2000-2001) UK zoological collection population as a source of captive animal data, and the 'minimum home range size' as the variable for wild populations. Since information on body size, in particular if expressed in body mass, is much easier to find than information on home range size (which requires long term studies of many wild populations), the minimum home range was deduced from the body mass (using the allometric laws mentioned). The enclosure size was estimated from direct observation.

Methods

We selected a random sample of 103 UK zoological collections (which represents about 25% of the population). Using the Casamitjana & Turner (2001) method all collections where visited once during the high season of the years 2000-2001, and an electronic list with information obtained viewing the videotapes of these visits was compiled. From this list, a filtered spreadsheet was created which only contained the taxa present in the collections. This spreadsheet was ordered alphabetically per collection code, and in within the collection per 'time of entry' when the animal or its enclosure was seen during the visit.

Using a random number function 50 taxa from the list were selected. If one taxon selected belonged to a non-mammal, an animal normally domesticated in the UK following the legal definition (see Zoo Licensing Act 1981 and DEFRA) an animal whose taxon could not be determined (i.e. cat), or a taxon already selected, the next suitable taxon in the following rows of the list was selected instead. As a result of following this method the list of 50 different mammals not normally domesticated in the UK was a random sample. Using the initial list, the zoological collections visited that had entries for any of the 50 mammal taxa were also selected.

To estimate body size we used an average of the values of body mass published in Silva & Downing (1995), which are results of several estimations of body mass given in several studies per each particular species. We used the average value of the 10 first estimations (if available) of average body mass given per each taxon.

Due to the recent discovery that the relationship between body size and home range size in mammals is not totally linear when expressed logarithmically, and because we did not distinguish which trophic group the taxa belonged to, we used Kelt and Van Vuren (1999) method to estimate home range size. Brown et al. (1993) provided a model to explain non-linear constraints involving body size in relation to geographical range size, and they argued that there is an optimal mammal body size of about 100gr. Kelt & Van Vuren (1999) also use this concept of 100gr optimal body mass, and they showed that very large and very small species are energetically constrained to use larger foraging areas. We used the same formulas that Kelt & Van Vuren used to regress minimal home range size depending whether the animal is bigger or smaller than approximately 100gr:

(a) If taxon Body Mass is smaller than 100gr $R = 10^{((-1.01B) + 0.720)}$

(b) If taxon Body mass is bigger or equal than 100gr $R = 10^{((1.31B) - 4.06)}$

R = Home Range Size in hectares; B = Body mass in grams.

Kelt & Van Vuren used values of <u>minimal</u> home range, as oppose to average home range, and because we applied both formulas to the list of selected taxa according the estimated body mass we could then estimate the Minimal Home Range Size in hectares per taxon.

Using the entries from the initial list with the collections keeping the selected 50 mammal taxa, we viewed the videotapes corresponding to those entries to determine the average enclosure size per taxon. We used the following factor of 10 categorisation:

1. Less than, or equal to, 0.01 hectares (less than 1 metre x 1 metre)
2. Between 0.01 and 0.1 hectares (up to 10 metres x 10 metres)
3. Between 0.1 and 1 hectares (up to 100 metres x 100 metres)
4. Between 1 and 10 hectares (up to1 Km x 1 Km)
5. Between 10 and 100 hectares (up to 10 Km x 10 Km)
6. More than 100 hectares (more than 10 Km x 10 Km)

Since the categorisations are quite broad, and the tapes showed enough of each enclosure to roughly estimate their size, most enclosure sizes could be easily categorised by just viewing the tapes. If a collection showed different enclosure sizes for the same taxon, we used the biggest one. For each taxon an average category was assigned by calculating the average category number of all the selected collections keeping the taxon, and rounding the average to the closest integral.

Once each taxon had assigned a Minimum Home Range Size we categorised each size in within the categories we used to estimate enclosure size. ‘Average Enclosure Size’ could now be compared with ‘Minimum Home Range Size’ in the same categorised groups.

An average value for the difference between Minimum Home Rage Size and Average Enclosure Size was calculated, and the differences were expressed in times the former was bigger than the latter. Body mass groups of less than 300gr, between 300gr and 1Kgr, between 1 Kg and 10 Kgr, between 10Kgr and 100 Kgr, and more than 100 Kgr were created for further comparison.

Results

The 50 randomly selected mammal taxa, and the number of collections from the 103 UK zoological collection sample where each taxon was seen, follows:

Common name	Scientific name	Collections
Addax	Addax nasomaculatus	1
African buffalo	Syncerus caffer	1
African lion	Panthera leo	5
African crested porcupine	Hystrix africaeaustralis	4
African pygmy hedgehog	Atelerix albiventris	1
Arabian spiny mouse	Acomys cahirinus dimidiatus	1
Asian elephants	Elephas maximus	3
Black lemurs	Eulemur macaco macaco	2
Black tailed silvery marmoset	Callithrix argentata melanura	1
Brazilian agouti	Dasyprocta leporina	4
Brown rat	Rattus rattus	4
Californian sea lion	Zalophus californianus	3
Capybara	Hydrochoerus hydrochaeris	5
Chimpanzee	Pan troglodytes	5
Common marmoset	Callithrix jacchus	6
Cotton top tamarin	Saguinus oedipus	6
Damara zebra	Equus burchellii	1
Degu	Octodon degus	6
Fallow deer	Dama dama	9
Flying fox	Pteropus giganteus	1
Gerbil	Meriones meridianus	4
Giant anteater	Myrmecophaga tridactyla	1
Giraffe	Giraffa camelopardalis	3
Golden headed lion tamarin	Leontopithecus rosalia	3
Greater bushbaby	Galago crassicaudatus	1
Guenther's vole	Microtus guentheri	1
Harvest mouse	Micromys minutus	1
Lar gibbon	Hylobates lar	2
Llamas	Lama glama	12
Maned wolf	Chrysocyon brachyurus	1
Maras	Dolichotis patagonum	10
Meerkat	Suricata suricata	11
Naked mole rat	Heterocephalus glaber	1
Night monkey	Aotus trivirgatus	1
Parma wallaby	Macropus parma	5
Persian leopard	Panthera pardus saxicolor	3
Raccoon	Procyon lotor	6
Red deer	Cervus elaphus	14
Red necked wallaby	Macropus rufogriseus	11
Red panda	Ailurus fulgens	3
Red squirrel	Scireus vulgaris	10
Rock squirrels	Spermophilus variegatus	1
Scotish wild cat	Felis sylvestris	3
Seba's short tailed bat	Mystacina tuberculata	1
Serval	Leptailurus serval	1
Siberian chipmunks	Tamias sibiricus	21

Slender loris	Loris tardigradus	1
Squirrel monkey	Saimiri scireus	7
Woolly monkey	Lagothrix lagothricha	1
Yak	Bos grunniens grunniens	2

Table 1. List of mammal taxa selected with the number of collections of the selection where the taxa was found in 2000-2001

These taxa were kept in 51 of the 103 zoological collections selected, which, as can be seen in figure 1, represent most types of zoological collections (with the exception of aquaria) as defined by Casamitjana & Turner (2001).

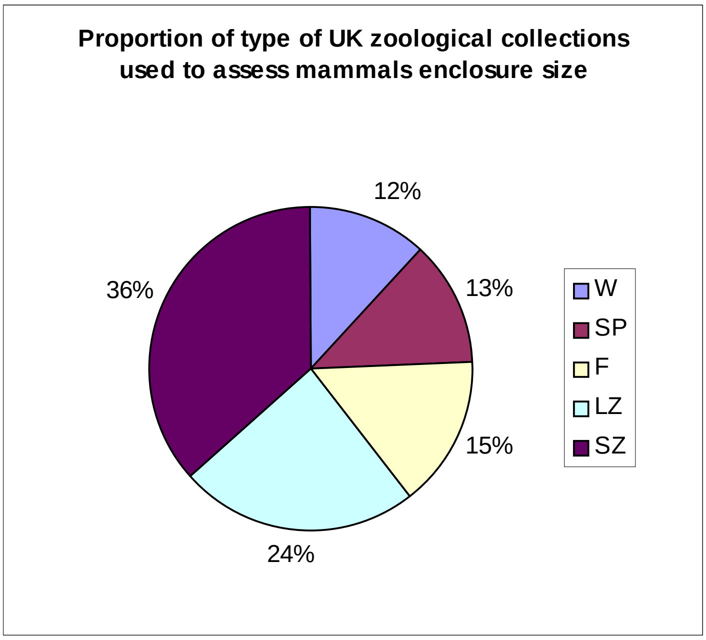

Figure 8. Proportions of type of UK zoological collections used to assess mammal's enclosure size (N=209 entries of selected taxa). AP= Amusement Parks, F= Farm, LZ= Large Zoo, SZ= Small zoo, S= Sanctuary, SP= Specialised Collection, SZ= Small Zoo, W= Wildlife/Safari Park. Definitions from Casamitjana & Turner (2001)

Table 2 shows the estimated body mass of each selected taxon.

Scientific name	**Estimations of body mass in Kg** (Silva & Downing,1995)										**Average Body Mass (Kg)**
Micromys minutus	0.0074	0.004									0.0057
Mystacina tuberculata	0.0123	0.00116									0.0067
Heterocephalus glaber	0.025	0.07									0.0475
Microtus guentheri	0.0516	0.0613	0.035								0.0493
Acomys cahirinus dimidiatus	0.011	0.09									0.0505
Meriones meridianus	0.054	0.032	0.098	0.077							0.0653
Tamias sibiricus	0.078	0.0957	0.0958								0.0898
Rattus rattus	0.115	0.145	0.142	0.116	0.11	0.28	0.07	0.173			0.1439
Atelerix albiventris	0.207										0.2070
Octodon degus	0.21										0.2100
Callithrix jacchus	0.354	0.369	0.225	0.292	0.118						0.2716

Loris tardigradus	0.322										0.3220
Scireus vulgaris	0.357	0.355	0.343	0.349	0.363						0.3534
Callithrix argentata melanura	0.35	0.439	0.32	0.32							0.3574
Saguinus oedipus	0.8	0.417	0.37	0.225	0.293	0.272	0.394				0.3959
Leontopithecus chrysomelas	0.48	0.7									0.5900
Suricata suricata	0.72	0.731	0.734	0.788	0.74						0.7426
Saimiri scireus	0.7	0.7	0.94	0.8	0.95	0.54	0.8	0.7			0.7663
Spermophilus variegatus	0.681	0.817	0.75	0.85							0.7745
Aotus trivirgatus	0.8	0.8	0.8	1.2							0.9000
Galago crassicaudatus	0.95	0.74	1.27	1.8	1.22	1.13					1.1850
Pteropus giganteus	0.9	1.3	1.6								1.2667
Eulemur macaco macaco	2.04										2.0400
Dasyprocta leporina	2	3.42	3.83	2.4	2	2					2.6083
Macropus parma	3.76	4.79									4.2750
Felis sylvestris	5.2	4.4									4.8000
Hylobates lar	4	5.8	4.6	4.5	5.31	5.05	5.7	4.5	6		5.0511
Ailurus fulgens	5.4	5.4	5								5.2667
Lagothrix lagothricha	7.5	7.5	7.5	7.5	5.9	6.7	7	6			6.9500
Procyon lotor	4.43	2.78	5.62	6.26	8.6	11.8	6.9	7.95	12.3	8.64	7.5280
Dolichotis patagonum	8										8.0000
Leptailurus serval	8.8	10.7	10.6	11.7	10.9	9.67	11.1				10.4957
Hystrix africaeaustralis	20.7	14.1	12.5	12.3	13	12.7					14.2167
Macropus rufogriseus	20	12	16	18.6	13.8	20	12.4	16.7			16.1875
Myrmecophaga tridactyla	20	20	21.4	27							22.1000
Chrysocyon brachyurus	23	23	22.7	23.8							23.1250
Panthera pardus saxicolor	32	30	20								27.3333
Hydrochoerus hydrochaeris	30	30	50	45	42.7	42.2	43.1	30			39.1250
Pan troglodytes	40	45	40	50	80	48.9	40.6				49.2143
Dama dama	59	38	43.4	69.5							52.4750
Addax nasomaculatus	70										70.0000
Zalophus californianus	75										75.0000
Lama glama	90										90.0000
Cervus elaphus	148	154	76.2	139	195	128					140.03333
Panthera leo	160	199	150	260	135	248	117	180			181.12500
Equus burchellii	391	239	290	239	239	239	290	313	174	240	265.40000
Bos grunniens grunniens	360										360.00000
Syncerus caffer	792	743	700	670							726.25000
Giraffa camelopardalis	1190	1350	795	1901	547	1170	1890	765			1201.00000
Elephas maximus	2190	1810	3020	1810	1810						2128.00000

Table 2. Estimated body mass in Kgr (from Silva & Downing, 1995) of each selected mammal taxon, with the average body mass in the last column (in red, average body mass inferior to 100 gr.)

Applying Kelt and Van Vuren (1999) formulas with the estimated body mass, the estimate Minimum Home Range Size of each selected taxon, categorised in six intervals, can be seen in table 3. Formula (a) above was applied on the taxa with body mass inferior to 100gr, represented in the table in red, while formula (b) was used for applied on rest.

Scientific name	**Average Body Mass (gr.)**	**Minimum Home Range Size (hectares)**					
		R< 0.01	**0.01<R<0.1**	**0.1<R<1**	**1<R<10**	**10<R<100**	**100 <R**
Micromys minutus	5.70			0.9048			
Mystacina tuberculata	6.73			0.7651			
Heterocephalus glaber	47.5			0.1063			
Microtus guentheri	49.3			0.1024			
Acomys cahirinus dimidiatus	50.5		0.0999				
Meriones meridianus	65.25		0.0771				
Tamias sibiricus	89.83		0.0559				
Rattus rattus	143.87		0.0585				
Atelerix albiventris	207.00		0.0942				
Octodon degus	210.00		0.0960				
Callithrix jacchus	271.60			0.1344			
Loris tardigradus	322.00			0.1680			
Scireus vulgaris	353.40			0.1898			
Callithrix argentata melanura	357.25			0.1925			
Saguinus oedipus	395.85			0.2202			
Leontopithecus chrysomelas	590.00			0.3714			
Suricata suricata	742.60			0.5020			
Saimiri scireus	766.25			0.5230			
Spermophilus variegatus	774.50			0.5304			
Aotus trivirgatus	900.00			0.6457			
Galago crassicaudatus	1185.00			0.9259			
Pteropus giganteus	1266.66				1.0104		
Eulemur macaco macaco	2040.00				1.8863		
Dasyprocta leporina	2608.33				2.6028		
Macropus parma	4275.00				4.9719		
Felis sylvestris	4800.00				5.7866		
Hylobates lar	5051.11				6.1864		
Ailurus fulgens	5266.66				6.5345		
Lagothrix lagothricha	6950.00				9.3972		
Procyon lotor	7528.00					10.4340	
Dolichotis patagonum	8000.00					11.2992	
Leptailurus serval	10495.71					16.1260	
Hystrix africaeaustralis	14216.66					23.9974	
Macropus rufogriseus	16187.50					28.4463	
Myrmecophaga tridactyla	22100.00					42.7714	

Chrysocyon brachyurus	23125.00					45.3886	
Panthera pardus saxicolor	27333.33					56.5025	
Hydrochoerus hydrochaeris	39125.00					90.3889	
Pan troglodytes	49214.28						122.078
Dama dama	52475.00						132.781
Addax nasomaculatus	70000.00						193.677
Zalophus californianus	75000.00						211.997
Lama glama	90000.00						269.189
Cervus elaphus	140033.33						480.355
Panthera leo	181125.00						672.901
Equus burchellii	265400.00						1109.967
Bos grunniens grunniens	360000.00						1654.841
Syncerus caffer	726250.00						4149.758
Giraffa camelopardalis	1201000.00						8020.498
Elephas maximus	2128000.00						16968.475

Table 3., Estimate Minimum Home Range Size (in hectares) of each selected mammal taxon, categorised in six intervals, calculated using the estimated body mass (in grams), and applying Kelt and Van Vuren (1999) formulas. In red the taxa with body mass inferior to 100gr. R= Minimum Home Range Size in hectares.

Table 4 shows the average enclosure size of the selected taxon estimated from the videotapes.

		Average Enclosure Size by category						
Taxa	**n**	**1 0.01ha**	**2 0.1ha**	**3 1ha**	**4 10ha**	**5 100ha**	**6 1000ha**	**Rounded category**
Addax	1				4.00			**4**
African Buffalo	1		2.00					**2**
African crested porcupine	4		2.00					**2**
African lion	5			3.40				**3**
African pygmy hedgehog	1		2.00					**2**
Arabian spiny mouse	1	1.00						**1**
Asiatic elephant	3			3.00				**3**
Black lemur	2			3.00				**3**
Black tailed silvery marmoset	1		2.00					**2**
Brazilian agouti	4							**3**
Brown rat	4		1.75					**2**
Californian sea lion	3			3.00				**3**
Capybara	5			3.00				**3**
Chimpanzee	5			3.00				**3**
Common marmoset	6		2.17					**2**
Cotton-top tamarin	6		2.00					**2**
Damara zebra	1			3.00				**3**
Degu	6		1.67					**2**
Fallow deer	9			3.44				**3**
Flying fox	1			3.00				**3**
Gerbil	4	1.00						**1**

Giant anteater	1			3.00				**3**
Giraffe	3				3.67			**4**
Golden headed lion tamarin	3		2.00					**2**
Greater bushbaby	1		2.00					**2**
Guenners vole	1	1.00						**1**
Harvest mouse	1	1.00						**1**
Lar gibbon	2							**3**
Llama	12			3.08				**3**
Maned wolf	1			3.00				**3**
Mara	10			3.00				**3**
Meerkat	11		2.27					**2**
Naked mole rat	1	1.00						**1**
Night monkey	1		2.00					**2**
Parma Wallaby	5			3.20				**3**
Persian leopard	3			2.67				**3**
Racoon	6		2.17					**2**
Red deer	14				3.57			**4**
Red panda	3		2.33					**2**
Red squirrel	10		2.30					**2**
Red-necked wallaby	11			2.91				**3**
Rock squirrels	1		2.00					**2**
Scottish wild cat	3			2.67				**3**
Seba's short tailed bat	1			3.00				**3**
Serval	1			3.00				**3**
Siberian chipmunks	21		1.90					**2**
Slender loris	1		2.00					**2**
Squirrel monkey	7		2.43					**2**
Woolly monkey	1			3.00				**3**
Yak	2			3.50				**4**

Table 4., Estimate average enclosure size of the selected mammal taxon expressed by category of size. The last common shows the rounded value of the number shown in the category of the same row. 'n'= the number of enclosures from which the averages have been calculated (ha = hectares).

We estimated the differences between captivity and wild per taxon, per group of body sizes, and as a whole (calculating the average for all differences). The comparisons were between estimated home ranges and enclosure size were made by calculating the difference between the size category number in home range and the size category number in enclosure size. The results of these calculations are shown in table 5, and each integer of the differences should be interpreted as a factor of 10 (i.e. number 1 would be 10 times the size, number 2 would be 100 times the size, etc.).

	Average Enclosure Size (AES) category	**Minimum Home Range Size (MHR) category**	**MHR-AES**	**MHR-AES Group averages**
Harvest mouse	1	3	2	
Seba's short tailed bat	3	3	0	
Naked mole rat	1	3	2	
Guenther's vole	1	3	2	
Arabian spiny mouse	1	2	1	
Gerbil	1	2	1	
Siberian chipmunks	2	2	0	
Brown rat	2	2	0	

African pygmy hedgehog	2	2	0	
Degu	2	2	0	
Common marmoset	2	3	1	0.8
Slender loris	2	3	1	
Red squirrel	2	3	1	
Black tailed silvery marmoset	2	3	1	
Cotton top tamarin	2	3	1	
Golden headed lion tamarin	2	3	1	
Meerkat	2	3	1	
Squirrel monkey	2	3	1	
Rock squirrels	2	3	1	
Night monkey	2	3	1	1.0
Greater bushbaby	2	3	1	
Flying fox	3	4	1	
Black lemurs	3	4	1	
Brazilian agouti	3	4	2	
Parma wallaby	3	4	1	
Scottish wild cat	3	4	1	
Lar gibbon	3	4	2	
Red panda	2	4	2	
Woolly monkey	3	4	1	
Raccoon	2	5	3	
Mara	3	5	2	1.5
Serval	3	5	2	
Cape crested porcupine	2	5	3	
Red necked wallaby	3	5	2	
Giant anteater	3	5	2	
Maned wolf	3	5	2	
Persian leopard	3	5	2	
Capybara	3	5	2	
Chimpanzee	3	6	3	
Fallow deer	3	6	3	
Addax	4	6	2	
Californian sea lion	3	6	3	
Llamas	3	6	3	2.4
Red deer	4	6	2	
African lion	3	6	3	
Zebra	3	6	3	
Yak	4	6	3	
African buffalo	2	6	4	
Giraffe	4	6	3	
Asian elephants	3	6	3	3.0
ALL (average)	**2**	**4**	**2**	

Table 5. Differences between Minimum Home Range Size category and Estimated Enclosure Size category in UK zoological collections per mammal taxon, per group of body sizes (last column, see methods), and as a whole (last row). The differences have been calculated using the size categorisation of table 4 and 5 (see text). The taxa is ordered by ascending body mass, so the values of the last column correspond to averages of values of the rows above them. AES= Average Enclosure Size, MHR= Minimum

Discussion

Due to the fact the zoological collections investigated were a random sample that represented about a quarter of all collections in the UK, and also the fact that the mammal taxa was selected randomly, the mammal enclosures investigated also constituted a random sample. As a consequence of this the results of this study are representative of the way captive wild mammals are presently kept in the UK zoological collections.

This results show that the bigger the animal the bigger the difference between its enclosure size and its natural home range. As can be seen in figure 2, megafauna (animals weighing more than 100Kg) are kept in UK zoological collections in enclosures an average 1,000 times smaller than their minimum home range.

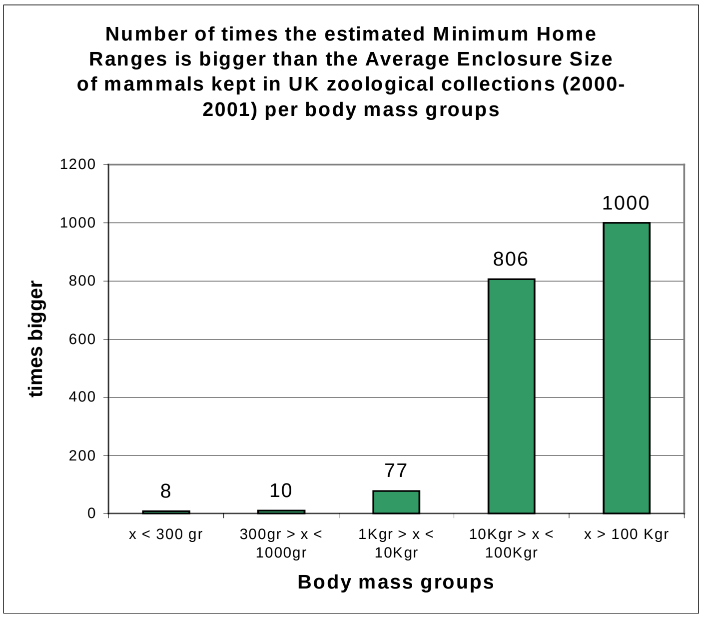

Figure 2. Number of times the Minimum Home Range Size is bigger than the Estimated Enclosure Size in mammals kept in UK zoological collections per body mass groups.

The average difference for all the mammals study suggest that mammals in the UK zoological collections are kept in enclosures about 100 times smaller than their minimum home range.

Considering these values, and applying it to human beings, a person that has lived in a village of 1 Km^2 most of his/her life would be in the same spatial situation than a captive zoo animal if this person was confined for life to live in a telephone box.

Looking at the taxa separately, Table 6 shows that only 10 % of the taxa show enclosure sizes similar than the minimum home ranges, more than a third of the taxa have enclosures 10 smaller, more than a fifth 100 times smaller and 2% 10,000 smaller. There are no cases, though, where average enclosure size was bigger than minimum home range.

	Num. Taxa	percentage
Same	5	10%
10 x smaller	18	36%
100 x smaller	15	30%
1,000 x smaller	11	22%
10,000 x smaller	1	2%

Table 6. Number of mammal taxa studied categorised by number of times the Average Enclosure Size is smaller than the Minimum Home Range Size. Same = no significant difference in categorisation between the two variables.

It is important to notice that these results only take in consideration area, not volume. Many species live in habitats where the third spatial dimension is very important (tree dwelling, for example), so although they might be living in an enclosure of roughly the same size as their Minimum Home Range (like the 10% of the taxa of this study), they may lack the third dimension, and therefore they may still be restricted. The opposite effect, an animal living in the wild with less access to one spatial dimension than in captivity, is unlikely, due to the fact that in the wild the animal is free to seek for an optimum habitat.

These results give support to the idea that one of the reasons for which many animals of many species show abnormal behaviours when kept in captivity is the restriction of space, although other factors, like the lack of proper stimulation, are likely to be also important. We should not conclude, then, that by merely increasing enclosure size we will be solving the problems captivity generates.

The magnitude of the difference between area in the wild and in captivity is indeed quite noticeable, and this new 'fact' certainly supports more the position of the anti-zoo side on the so called 'zoo debate'. Furthermore, it justifies and increasing concern in relation to megafauna, which the results show 'suffer' a much bigger space restriction in captivity than other animals. This may be an intuitive concept, but this study has provided now data that allows us to introduce it as a 'fact'.

The case of elephants is probably the best example to illustrate this problem, since elephants are the biggest land animal, and therefore the animal that, following our hypothesis, should show more welfare problems when living in captivity. Indeed, in a study about the welfare of elephants in zoos in Europe, Club & Mason (2002) have concluded that elephants do suffer many welfare problems in captivity they do not suffer in the wild, including high mortality, low breeding, illness and abnormal behaviour. These authors identify the restriction of space as one factor of the poor welfare found in elephants in captivity.

In relation to enclosure size, Club & Mason (2002) state "The EAZA recommends outdoor enclosures measure at least of 400m^2 for three animals, with another 100m^2 for each additional animal. The AZA recommends at least 167.2m^2 per elephant, with an additional 83.6m^2 for each additional elephant. These recommendations are not based on hard data and are likely affected by what is physically feasible in zoos, rather than from the viewpoint of maximal welfare (...) Wild elephants roam over considerable distances in the wild, the minimum being between 60 to over 100 times larger than these recommended enclosure sizes." Our results show that the actual elephant enclosure sizes in the UK, as opposed to the recommended by zoo organizations, are in fact an average of 1,000 times smaller.

Conclusions

1. In UK zoological collections of the period 2000-2001, the heavier the mammal kept the bigger the difference between the size of its enclosure and the size of its minimum home range.

2. Mammals kept in UK zoological collections during the period 2000-2001 are confined in enclosures that, as an average, have an area 100 times smaller than their minimum home range.

3. Mammals with a body mass bigger than 100 Kg (Megafauna) kept in UK zoological collections during the period 2000-2001 are confined to enclosures that have an average area 1,000 times smaller than their minimum home range.

4. The results of this study suggest that if a human being naturally living most of his/her life in a small village of about 1Km^2 was confined in a space with the same spatial restrictions that wild mammals kept in captivity have in today's UK zoological collections, this human would be living in a space approximately of the size of a telephone box.

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