



Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures[☆]

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Abstract

In captivity, some species often seem to thrive, while others are often prone to breeding problems, poor health, and repetitive stereotypic behaviour. Within carnivores, for instance, the brown bear, American mink and snow leopard typically adapt well to captivity and show few signs of poor welfare, while the clouded leopard and polar bear are generally hard to breed successfully and/or to prevent from performing abnormal behaviour. Understanding the fundamental source of such differences could enable reproductive success and behavioural normalcy to be improved in zoos and breeding centres, by increasing the appropriateness of the enclosure designs and environmental enrichments offered particular species, and by allowing these to be offered pre-emptively instead of reactively. Here, we demonstrate that a significant proportion of the variation in apparent welfare between captive carnivore species stems from specific aspects of natural behaviour. We tested pre-existing hypotheses that species-typical welfare is predicted by natural hunting behaviour, general activity levels, ranging, or territorial patrolling (all activities that are constrained in captivity), by collating data on median stereotypy levels and infant mortality for multiple captive species, and then regressing these against median values for the relevant aspects of natural behavioural biology (e.g. hunts per day, proportion of flesh in the diet, home-range size, etc.). Our results revealed that instead of relating to foraging (e.g. hunting), as often assumed, carnivore stereotypy levels are significantly predicted by natural ranging behaviour (e.g. home-range size and typical daily travel distances). Furthermore, naturally wide-ranging lifestyles also predicted relatively high captive infant mortality rates. These results suggest that enclosure designs and enrichments focussing on carnivores' ranging tendencies (e.g. providing more space, multiple den sites, greater day-to-day environmental variability/novelty, and/or more control

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over exposure to aversive or rewarding stimuli) could be particularly effective means of improving welfare; and also, that targeting such enrichment programmes on wide-ranging species, before problems even emerge, might effectively pre-empt their development. Alternatively, species with relatively small ranges could instead be made the focus of future collections and breeding programmes, zoos phasing out wide-ranging carnivores in favour of those species inherently more suited to current or readily achievable enclosure sizes and enrichment regimes.

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1. Introduction

For many captive wild species, poor conception rates, high infant mortality rates, and/or poor adult survivorship are major impediments to attaining self-sustaining populations (e.g. reviewed by Snyder et al., 1996; Barnes et al., 2002; Clubb and Mason, 2002, 2004). Given that these animals receive veterinary care and are free from predation, drought and starvation, this is surprising and suggests a role of chronic, husbandry-related stress (see e.g. Broom and Johnson, 1993; Terio and Munson, 2000; Terio et al., 2004). Furthermore, abnormal, repetitive behaviours like pacing are rather prevalent (see Mason et al., 2007): these likely reflect inadequate environments, are perceived negatively by the public, and could even indicate psychological changes that would impede reintroduction success (e.g. Vickery and Mason, 2003; Mason et al., 2007). Together, these issues thus represent a real practical, welfare and ‘public relations’ concern, so often leading to sustained attempts to improve husbandry (see e.g. Schetini de Azevedo et al., 2007). Such attempts can be very valuable and no doubt often improve animal welfare. However, they are not always successful. Enrichments, for example, often reduce stereotypic behaviour, but very rarely abolish it (Swaigood and Shepherdson, 2005; Shyne, 2006); some individuals’ abnormal behaviours are extremely intransigent; and some species remain stubbornly problematic to breed. Together, such difficulties suggest either that the fundamental causes of welfare problems are not being targeted, or that enrichments are being utilised too late to prevent chronic stress or deprivation causing lasting changes to the animals’ brains and thence behaviour (as reviewed by Mason et al., 2007).

One way to identify the fundamental causes of these problems is to systematically compare susceptible species with those species which thrive in captivity, to analyse what it is about the natural behavioural biology of the latter that adapts them better to captive conditions. Fewer papers have been written about these more successful species, but examples as suggested by Taxon Advisory Group reports, ISIS database figures (<http://www.isis.org>) and various publications (e.g. Petter, 1975; Portugal and Asa, 1995; Primack, 1998) include ring-tail lemurs, rhesus monkeys, white-tailed deer and brown bears. In other branches of biology, comparing multiple diverse species has long been used to investigate relationships between variables and thence test ideas about niche effects, co-evolution, and factors predicting responses to evolutionarily new circumstances (see Clubb and Mason, 2004 for review). Conservation biology provides excellent examples, with ‘Comparative Methods’ being used to identify the traits that increase some species’ vulnerabilities to extinction in the wild (e.g. Purvis et al., 2000; Woodroffe and Ginsberg, 1998), or that decrease some species’ likelihood of surviving or breeding when introduced to new locations (e.g. Wolf et al., 1998a,b; Sol et al., 2002; see also Stamps and Swaigood, 2007). These methods are thus clearly relevant, and potentially

useful, for addressing questions about welfare differences across species (see Clubb and Mason, 2004 for review). Our aim was therefore to use them to investigate the primary biological sources of problems in certain captive carnivores. This work comprised Ph.D. research conducted between 1998 and 2001 (Clubb, 2001), many of the key findings of which have already been published (Clubb and Mason, 2003) but only in very brief form. Here we therefore present the rationale, methods and results in more detail; discuss the findings' practical implications *vis-a-vis* environmental enrichment and other aspects of captive husbandry; and consider avenues for future research.

We chose carnivores for several reasons. First, they are quite common in captivity: at the time this work was conducted, zoos held 159 species, with ca. 19,000 individuals being recorded in the ISIS database (probably representing a true global total of around 60,000; cf. e.g. IUDZG, 1993). Second, carnivores show unexplained species variance in captive breeding success and/or morbidity (e.g. Ginsberg and Macdonald, 1990; Nowell and Jackson, 1996; Mellen et al., 2000), and had also attracted much behavioural study (e.g. of stereotypic behaviour). Furthermore, carnivores in the wild show great ecological diversity (e.g. Bekoff et al., 1984); and a complete phylogeny existed for them (Bininda-Emonds et al., 1999)—an essential prerequisite for comparative work (see Clubb and Mason, 2004). Finally, some specific, but previously untested, hypotheses had been advanced as to the sources of their welfare problems, particularly as regards stereotypic behaviour. Perhaps unsurprisingly, given the importance of natural behaviour for good welfare, these all focussed on aspects of behaviour in the wild which are constrained by captivity.

The first such hypothesis is that natural foraging modes are key in carnivores' responses to captivity. Thus pacing, their most common stereotypic behaviour (see Mason et al., 2007), had been held to derive from the frustrated appetitive phases of hunting, i.e. prey search and/or pursuit (e.g. Terlouw et al., 1991; Mason and Mendl, 1997). Boorer (1972), in contrast, suggested more broadly that omnivores like raccoons adapt well to captivity, proposing that "in general the less specialised animals settle down most easily in zoos, and exhibit less disturbed behaviour once they have done so"; while Morris (1964) and Ormrod (1987) suggested quite the opposite, proposing opportunistic omnivorous animals to be more prone to 'boredom' and other problems when captive. Observational and enrichment studies provide evidence both for and against these ideas; for instance, foraging enrichments commonly reduce stereotypic pacing, but they rarely eliminate it and furthermore, such behaviours can be displayed at times or locations quite incompatible with foraging motivations (reviewed by Clubb and Vickery, *in press*). Some carnivores also find elements of foraging rewarding (e.g. Mason et al., 2001), although whether the locomotory aspects are is unknown. This left the status of these hypotheses rather uncertain. However, the hypotheses do make clear predictions concerning species differences, which enable them to be tested: for example, if the first is correct, then species naturally showing frequent or sustained hunting activity should systematically prove more vulnerable to problems in captivity than species which are not obligate hunters.

The second proposed risk factor is high natural activity levels. Small carnivores and bears had been suggested as particularly susceptible to the development of behavioural problems due to their highly active lifestyle, since they would naturally spend a considerable portion of the day actively foraging (e.g. Meyer-Holzappel, 1968; see also Hediger, 1950; Morris, 1964; Ormrod, 1987). Again, behavioural evidence from observations and enrichment studies provides evidence both for and against this idea (reviewed by Clubb and Vickery, *in press*); but again, comparative approaches could provide a resolution, since in terms of species differences, this hypothesis makes a clear prediction: a positive correlation between the proportion of time spent active (and/or foraging) in the wild, and the incidence or degree of stereotypy in captivity.

The third hypothesis is that welfare problems stem from restricting natural ranging and related behaviours. Thus [Forthman-Quick \(1984\)](#) suggested that the apparent tendency for species such as the coyote (*Canis latrans*) and wolf (*Canis lupus*) to develop pacing lies in the fact that they range widely in the wild (see also [Mellen, 1991](#); [Ormrod, 1987](#)). Lastly, [Morris \(1964\)](#) hypothesised that stereotypic pacing derives from territorial patrolling behaviour. Again, both suggestions have some partial support from behavioural studies of captive animals (reviewed in [Clubb and Vickery, in press](#)), but again, make clear, directional cross-species predictions: respectively, a positive correlation between species' stereotypic behaviour levels and the distances they typically travel in the wild and/or their natural home-range sizes; and that territorial carnivores will display more pacing than non-territorial species.

2. Methods

To quantify captive carnivore welfare fully, ideally one would use multiple measures that are sensitive to stress (e.g. hypothalamo-pituitary-adrenal axis functioning; conception rates; morbidity rates; the prevalence of self-mutilation; etc.; see e.g. [Morgan and Tromborg, 2007](#) and [Tarlow and Blumstein, 2007](#)). However, comprehensive, quantitative data on these are simply not available for most captive species (for instance, zoo 'studbooks', which could supply some of this information, only exist for a subset of animals). We therefore focussed on just two measures: (i) stereotypic behaviour, which typically reflects poor welfare and/or an environment different from that required for normal brain development (reviewed by [Mason and Latham, 2004](#); [Mason, in press](#); [Mason et al., 2007](#)); and (ii) infant mortality, which in carnivores is known to vary across sites (e.g. [Wielebnowski, 1996](#)), and often reportedly reflects poor maternal care (maternal neglect, rough handling of infants, or infanticide), in turn commonly a product of acute or chronic stress (e.g. [Bahr et al., 1998](#); see also references in [Tarlow and Blumstein, 2007](#)). For both these measures, reasonable amounts of data have been collected in zoos; these exist for multiple diverse species; and furthermore, infant mortality and stereotypic behaviours are both responses that zoos generally wish to understand and reduce. We restricted our analyses here to those species for which data on both these variables were available, to increase the reliability of our conclusions with respect to welfare; some results therefore differ slightly from those published elsewhere.

2.1. Stereotypy data collation

Stereotypy data were systematically collated from the following sources: all papers reviewed by [Mason \(1991\)](#); the proceedings of the International Society for Applied Ethology's annual congresses 1991–1999 inclusive; and all volumes of the two publications where most captive wild carnivore behavioural reports are published: the *International Zoo Yearbook* (1959–1999 inclusive) and *Zoo Biology* (1982–1999 inclusive). In addition, unpublished reports (e.g. by students) were collected from 14 zoos of the Federation of Zoological Gardens of Great Britain and Ireland (now BIAZA). Several prominent researchers in the field of zoo carnivore behaviour were contacted for unpublished data; and additional papers were also gleaned from other journals (e.g. *Applied Animal Behaviour Science*, *Animal Behaviour*, etc.) whenever encountered. Data from domesticated species (domestic dog, cat, ferret) were not used.

Using data from multiple sources requires care that only good quality, comparable, information is used (see e.g. [Gittleman, 1989b](#)). For inclusion here, studies had to involve a minimum of 1 week of data collection and were also excluded if judged of general poor quality

(e.g. using very infrequent behaviour sampling, and/or dubious definitions of stereotypic behaviour, e.g. ‘persistent inactivity’). Only data from adults were used, and data from animals experiencing food restriction, social isolation, changes in group structure or newly imposed environmental enrichments were also excluded to eliminate transient novelty effects. These criteria meant that some studies from fur farms were used; these supplied data for three species: *Alopex lagopus*, *Mustela vison*, and *Vulpes vulpes* (see Table 1). Sexes and sub-species were pooled to increase sample sizes. For final calculations, only stereotyping individuals were used, since we had little confidence that behavioural data were regularly or reliably collected from non-stereotyping animals (which would have caused estimates of species’ stereotypy prevalence or overall mean values to be inflated and inaccurate). Overall, these methods yielded data for 33 species. Note that it would have been ideal to eliminate those species for which very few individuals were sampled, but in practice this would have involved losing so many (see Table 1) that we did not do this, assuming that the resulting great loss of statistical power would have been more disadvantageous than the loss of accuracy this poor sampling represented.

For each species, values for stereotypic behaviour (% observation time) were thus averaged across the (non-independent) stereotyping individuals within each separate study, and a median then calculated across any replicate studies to derive final species estimates. Medians, rather than means, were used because data were frequently skewed, and we did not want very good or very poor sites to be overly influential. We firstly focused on repetitive locomotion, collectively described as ‘pacing’ from this point (and including repetitively walking back and forth; route-tracing; vertical circling and swimming) since this is the most prevalent stereotypy among carnivores (97% of reported stereotypies here: Clubb, 2001; see also Mason et al., 2007). This process was also repeated for all stereotypies.

2.2. Infant mortality

Fewer than 50% of our 33 species had studbooks. Infant mortality data were therefore all taken from the captive breeding records of the *International Zoo Yearbooks* (IZY): the only source of public, long-term captive breeding records that covers non-studbook as well as studbook species. These comprise voluntary ca. annual submissions from zoos on births per species in their collection, and on the number of infants dying before 30 days. For each of the 33 species, these figures were collated from 1988 to 2000 editions (a period coinciding with the publication of 85% of our stereotypy papers, thence controlling – to some degree – for any temporal changes in our two dependent variables). The infant mortality rate for each species was first calculated as the total number of deaths over births in this period at each site (individual dams were not identifiable in these data, so site had to be taken as the unit of replication), with the median value across sites then being calculated to derive a species average. Some fur farm data were available too—again for the three species listed above; in these instances, each farm was simply treated like an extra zoo when calculating the final cross-site median. As for stereotypic behaviour, medians were used to prevent figures being disproportionately skewed by extremely successful or unsuccessful zoos. A different method had to be applied to lions and leopards, however, since for these species individual zoo data were not published by site; here the global total number of births and deaths over the period were instead used to calculate the overall mortality rate (see Table 1). Note that sub-species were pooled, to increase the sample size per species and be consistent with our approach with stereotypic behaviour. However, because many more replicates were available for this variable than for stereotypy, here we could be more stringent about low sample sizes. Two species (the giant panda, *Ailuropoda melanoleuca* and brown hyaena, *Parahyaena brunnea*: see Table 1)

Table 1
Species for which data on stereotypic behaviour and infant mortality were obtained

Species	Number of sites yielding data on stereotypic behaviour (fur farms given in brackets)	Number of papers yielding data on stereotypic behaviour (papers on fur farms given in brackets)	Total number of stereotyping individuals ^a	Number of sites yielding data on infant mortality (subtotal from fur farms given in brackets)	Total number of births across all sites	Total number of deaths by 30 days across all sites
<i>Acinonyx jubatus</i> , cheetah	3	3	8	53	844	236
<i>Ailuropoda melanoleuca</i> ^b , giant panda	1	1	2	3	4	2
<i>Alopex lagopus</i> , Arctic fox	(1)	(1)	42	39 (4)	575	180
<i>Caracal caracal</i> , caracal	5	3	13	61	292	108
<i>Felis chaus</i> , jungle cat	2	2	3	46	395	147
<i>Felis margarita</i> , sand cat	2	2	9	13	121	40
<i>Felis silvestris</i> , wild cat	1	1	2	75	886	307
<i>Genetta tigrina</i> , large-spotted genet	1	1	1	5	36	8
<i>Leopardus pardalis</i> , ocelot	6	5	15	59	328	106
<i>Leopardus wiedii</i> , margay	1	1	2	13	51	16
<i>Leptailurus serval</i> , serval	3	2	6	101	773	301
<i>Lynx canadensis</i> , Canadian lynx	1	1	2	20	137	35
<i>Lynx lynx</i> , Eurasian lynx	1	2	7	110	904	288
<i>Melursus ursinus</i> , sloth bear	2	2	5	15	71	37
<i>Mustela vison</i> , American mink	(1)	(1)	154	12 (3)	269	45
<i>Oncifelis geoffroyi</i> , Geoffroy's cat	3	5	13	21	147	57
<i>Panthera leo</i> , lion	1	2	3	n/a ^c	2552	1076
<i>Panthera onca</i> , Jaguar	3	8	9	106	494	167
<i>Panthera pardus</i> , leopard	4	7	12	n/a ^c	580	164
<i>Panthera tigris</i> , tiger	7	4	18	161	2292	682

<i>Parahyaena brunnea</i> ^b , brown hyaena	1	1	1	1	2	0
<i>Potos flavus</i> , kinkajou	1	1	1	30	114	31
<i>Prionailurus bengalensis</i> , leopard cat	2	1	4	65	892	343
<i>Prionailurus viverrinus</i> , fishing cat	3	1	3	19	209	64
<i>Puma concolor</i> , mountain lion	1	1	1	102	586	222
<i>Suricata suricatta</i> , meerkat	1	1	5	111	1983	798
<i>Tremarctos ornatus</i> , spectacled bear	1	1	1	32	148	51
<i>Uncia uncia</i> , snow leopard	8	4	26	85	546	134
<i>Ursus americanus</i> , American black bear	1	3	1	33	281	75
<i>Ursus arctos</i> , brown bear	6	3	7	125	1005	200
<i>Ursus maritimus</i> , polar bear	6	7	20	63	263	173
<i>Ursus thibetanus</i> , Asiatic bear	2	2	19	54	250	84
<i>Vulpes vulpes</i> , red fox	(1)	(1)	11	70 (4)	599	234

^a Not all studies provided the number of individuals that showed stereotypic behaviour/pacing and therefore some of these figures represent the maximum number of stereotypic individuals.

^b Infant mortality data came from less than one birth a year.

^c Individual zoo data not provided (see Section 2).

stood out for their very low birth-rates – well under one birth a year, across very few sites – and so we excluded these data as unlikely to reflect population infant mortality rates accurately.

Details on the species with data for both variables, and the number of sites, etc. yielding figures, are given in [Table 1](#).

2.3. *Wild behavioural biology*

A group of 18 ecology journals containing most of the relevant information were first identified (see [Clubb, 2001](#) for details). To identify relevant papers, electronic databases were then used to search the abstracts of every paper published in these journals between 1981 and 1999, while the abstracts of papers published between 1960 and 1980 were searched by hand. In addition, papers published in other journals were occasionally used when encountered, and books written by field researchers on specific species were also consulted (e.g. [Schaller, 1972](#); [Bailey, 1993](#)).

Studies used to derive species estimates were, again, selected according to quality criteria. Those used to calculate home-range size, distance travelled daily, time spent active, foraging and travelling were primarily radio-tracking studies, conducted for a minimum of 10 months, but there were some exceptions when long-term, direct observation studies were also used (see [Clubb, 2001](#) for details). Data on provisioned populations were also excluded, since provisioning would likely affect behaviour greatly, and also only occurred in one of our 33 species. Data from juveniles, and sub-adults were also excluded, as were data from non-residents for home-range estimates. Species medians were calculated for the variables below. As for our zoo data on stereotypic behaviour, an average was taken across relevant individuals in each study for each sex, then across each sex to calculate a study average (some studies just provided an average value or a range of values, in which case the author's mean or the midpoint of the range was taken as the study average), and finally, a median was taken across all study averages to derive species averages. This was done for the following:

- (a) *Time spent foraging (% day)*. This was the median proportion of observation time or radio-locations during which foraging activity was detected. Some studies monitored study animals during active periods only, for example during daylight hours for diurnal species. In these situations, inactivity was assumed for the rest of the day, to derive estimates over 24 h.
- (b) *Proportion of live vertebrate flesh in the diet*. Data from studies quantifying the percent occurrence of individual food categories by stomach content or faecal analysis were used by summing all occurrences of vertebrate matter, excluding carrion, in the diet as a percentage of the sum of all occurrences of all food categories (for more details see [Clubb, 2001](#)).
- (c) *Chase distance (in m)*. Chase distance describes the distance travelled between the start of a chase until the prey was killed or the predator gave up (as defined by the author).
- (d) *Distance between kills (km)*. This refers to the distance travelled during the interval between kills. Data were derived from radio-tracking studies that measured the straight-line distance between locations.
- (e) *Hunt rate (hunts per 24 h)*. Hunt rate was quantified as the average number of hunts carried out during a 24-h period, including those not resulting in a kill.
- (f) *Kill rate (kills per 24 h)*. Kill rate described the average number of successful hunts during a 24-h period.
- (g) *Degree of dietary specialization*. Levin's standardised measure of trophic niche breadth was used to quantify dietary specialisation (see [Krebs, 1989](#)). The studies used to estimate the

proportion of flesh in the diet were used to calculate diet diversity for each species. In total 13 categories of food type were used, aiming to separate food types involving different foraging strategies: large mammals (>100 kg); medium-sized mammals (10–100 kg); small mammals (1–10 kg); very small mammals (<1 kg); fish; birds; eggs; cold-blooded vertebrates; terrestrial vertebrates; aquatic vertebrates; fruit and nuts; plant matter (browse, graze, etc.) and carrion.

- (h) *Time spent active (% day)*. Activity level was quantified as the median proportion of observations or radio-locations during which activity was detected. ‘Activity’ includes behaviours such as foraging, travelling, climbing, playing and fighting. As with foraging, inactivity was assumed outside observations periods for studies that only monitored animals during their ‘active period’.
- (i) *Home-range size (km²)*. When available, estimates derived from the ‘minimum convex polygon’ method were preferred, primarily because this was the most commonly used, and hence comparable, method. In addition, some long-term direct observation data were used. Since home range can vary by orders of magnitude with food availability (e.g. Gittleman and Harvey, 1982), the minimum range recorded was also extracted from each study, these then being used to generate a median minimum range.
- (j) *Distance travelled daily (km)*. The median distance travelled per day by adult individuals came from radio-tracking studies that gave the straight-line distance travelled over a defined period of time (e.g. 24 h apart). Again, 24 h estimates were derived by assuming that animals were stationary outside their active period. Since daily travel distances can also vary by orders of magnitude with food availability, again the minimum travel distance per study was used to calculate a median minimum value across studies.
- (k) *Territoriality*. Species were classed as territorial or non-territorial based on Grant et al. (1992). Species reported to employ both strategies were classed as territorial, due to sample size considerations.

2.4. Checks, balances and possible confounds considered in analyses

- (i) *Body weight (kg)*. Body weight correlates with a wide range of factors (e.g. Gittleman, 1985; Lindsedt et al., 1986), including range size. Body weight estimates were taken from Gittleman and Purvis (1998).
- (ii) *Captive activity levels*. The ‘stereotypic behaviour’ publications were used to obtain data on levels of non-stereotypic activity in captivity, to check that any observed effects were special to the abnormal behaviour, not to locomotion or activity *per se*. These came from all individuals observed, not just stereotypic ones.
- (iii) *Husbandry variables*. Information relating to husbandry likely to influence stereotypic behaviour was also recorded from the captive behaviour publications. This was to check that there were not systematic variations in husbandry that could explain apparent species differences. Species medians were calculated for the following: enclosure size (m²) and meal frequency (number of meals per normal day, including ‘snacks’, and excluding ‘starve days’; for details see Clubb, 2001). All other variables were categorical with two levels. Individuals were classed accordingly for each variable, a study estimate derived according to which was the most prevalent (i.e. > 50%), and species estimates calculated in the same way across all studies (in practice there was much consistency within species, and thus all individuals of the same species tended to fall within the same level for each category). These variables were: rearing history (captive-born or wild-caught); predominant substrate: ‘hard’ – concrete, rock and metal – or ‘manipulable’; availability of cover (could animals escape from the view of

visitors or from conspecifics?); access to elevated areas (availability of structures allowing climbing and/or providing a view); social grouping in captivity compared to the wild (captive individuals were classified as solitary-, pair- or group-housed; this was then scored as whether the same or different from the wild, as taken from Gittleman, 1989a); meal timing (morning or afternoon); presence of weekly starve days (yes/no); meal processing level (classified as consisting entirely of processed food, or including non-processed items such as whole carcasses); and feeding enrichment (individuals were categorised according to whether or not they received feeding enrichments) (for more details see Clubb, 2001).

- (iv) *Wild infant mortality.* To verify that any findings did not simply reflect natural inter-species variation in offspring mortality, data on the survival of young in the wild were provided by John Gittleman, e.g. as reported in Gittleman (1993) and since updated.
- (v) *Comparison of wild data with another database.* In order to check the validity of our dataset, estimates of home-range size were compared with those published by Creel and Macdonald (1995).
- (vi) *Study length/sampling period.* Possible effects of observation period/sampling regime were also checked to see that they did not affect results systematically (e.g. by correlating with recorded values, or with key variables of interest) (details in Clubb, 2001).
- (vii) *Effect of farmed species, extreme species, and omitted species.* Species with data from fur farms were excluded from repeat analyses, to check that findings were not skewed by these more intensively held species; in response to some informal criticisms/concerns, the polar bear, the most extreme species in most analyses, was also excluded – although never an actual statistical outlier – to check that findings were not overly reliant on this one animal; and finally, the two species for which we had particular concerns about the quality of infant mortality data (*A. melanoleuca* and *P. brunnea*) were added back to the database, to check that their prior removal had not altered our final findings.

2.5. Analysis

In comparative studies, data points (i.e. species averages) need to be checked for statistical independence by testing for ‘phylogenetic effects’, i.e. the danger that closely related species are inherently similar, leading to forms of pseudo-replication that violate the assumptions of most statistical tests (see Clubb and Mason, 2004 for details). Not all variables are influenced by phylogeny, so we first ran diagnostic tests to identify whether or not this was an issue for our variables. We used the complete phylogenetic tree published for carnivores by Bininda-Emonds et al. (1999), and tests for serial independence (TFSI) (Abouheif, 1999) which measure the autocorrelation between adjacent species, i.e. the degree of non-randomness in a trait between adjacent species, to reveal whether closely related species are more similar than expected by chance. Where such effects were found, simple cross-species tests (with individual species as the units of replication) were corroborated with analyses correcting for phylogenetic effects (Harvey and Rambaut, 2000). A range of modern comparative methods are available to solve this problem (see Clubb and Mason, 2003), and we used the comparative analysis of independent contrasts (CAIC) (Purvis and Rambaut, 1995).

The variables compiled for captive carnivores were then compared with the variables recorded in their wild counterparts, primarily using least squares regression on log-transformed data (the exceptions being investigation of categorical factors, e.g. territoriality). In cases when a significant correlation was found between dependent and any potential confounding variables (e.g. body weight), the effect of the confound was investigated in subsequent regression analyses:

Table 2

Species medians for stereotypic behaviour, pacing, infant mortality and all our wild variables

Species	SYA	SPP	CIM	FOR	FLE	CHD	KID	HUR	KIR	DDS	ACT	HRS	MHR	DTD	MDT	TER
<i>Acinonyx jubatus</i> , cheetah	24.60	24.60	25.00		100.00	206.91			0.80	0.024	16.67	106.30	60.00	4.00	4.00	T
<i>Ailuropoda melanoleuca</i> , giant panda ^a	6.50	6.50	0.00								57.65	7.30	7.10	0.60	0.60	NT
<i>Alopex lagopus</i> , Arctic fox	0.55	0.55	17.20		89.83			2.80	6.70	0.049	53.00	38.50	9.00			T
<i>Caracal caracal</i> , caracal	14.27	14.27	27.27		100.00					0.242	35.70	17.10	2.97	4.90	4.90	
<i>Felis chaus</i> , jungle cat	12.45	12.45	40.00		86.63					0.092						
<i>Felis margarita</i> , sand cat	12.68	12.68	20.00		80.81					0.158						
<i>Felis silvestris</i> , wild cat	1.50	1.50	28.57		93.16					0.061						
<i>Genetta tigrina</i> , large-spotted genet	8.30	8.30	21.05		28.53					0.114						
<i>Leopardus pardalis</i> , ocelot	16.80	16.80	28.57		92.70					0.14	43.60	4.40	1.15	4.19	3.29	
<i>Leopardus wiedii</i> , margay	12.25	12.25	25.00													
<i>Leptailurus serval</i> , serval	8.74	8.74	40.91	6.75	95.20		0.43	7.50		0.071	30.10	9.70		2.64	2.64	
<i>Lynx canadensis</i> , Canadian lynx	6.25	6.25	19.09		91.92	46.00	8.00		0.60	0.0849		140.30	41.00	8.21	8.21	
<i>Lynx lynx</i> , Eurasian lynx	6.76	6.76	24.04		98.65	40.00	7.14	1.63	0.40	0.072		120.20	2.70	2.17	2.16	
<i>Melursus ursinus</i> , sloth bear	17.29	15.49	33.33							0.045	48.88	10.90	1.60	1.05	1.05	
<i>Mustela vison</i> , American mink	17.30	10.20	3.71	29.00	87.90				0.20	0.187	32.00	0.20	0.05	0.63	0.63	
<i>Oncifelis geoffroyi</i> , Geoffroy's cat	15.65	15.65	33.33		100.00					0.089	38.03	6.40	2.33			
<i>Panthera leo</i> , lion	48.00	48.00	42.16	4.92	100.00	26.80	3.68	1.18	0.30	0.072	9.00	148.30	19.70	11.28	2.28	T
<i>Panthera onca</i> , Jaguar	20.80	20.80	20.00		100.00	18.50			0.10	0.064	54.30	89.70	28.00	4.58	2.40	NT
<i>Panthera pardus</i> , leopard	10.54	10.54	25.00	10.38	100.00	48.33	24.93	1.10	0.30	0.056	52.20	33.50	2.02	2.44	2.15	T
<i>Panthera tigris</i> , tiger	16.43	16.43	33.33		100.00	150.00			0.20	0.027	67.00	48.40	16.40	8.07	4.68	T
<i>Parahyaena brunnea</i> , brown hyaena ^a	24.70	24.70	0.00	1.18		80.00	8.97				35.70	228.10	31.90	14.44	12.50	T
<i>Potos flavus</i> , kinkajou	57.20	57.20	0.00													
<i>Prionailurus bengalensis</i> , leopard cat	11.00	11.00	33.33		59.520					0.234				0.90	0.90	

Table 2 (Continued)

Species	SYA	SPP	CIM	FOR	FLE	CHD	KID	HUR	KIR	DDS	ACT	HRS	MHR	DTD	MDT	TER
<i>Prionailurus viverrinus</i> , fishing cat	9.17	9.17	28.57													
<i>Puma concolor</i> , mountain lion	11.75	11.75	25.00		95.32				0.10	0.075	37.80	236.30	39.00	6.46	2.46	NT
<i>Suricata suricatta</i> , meerkat	10.00	10.00	36.84	19.94	25.29					0.019		3.50	2.00			
<i>Tremarctos ornatus</i> , spectacled bear	52.00	52.00	31.67							0.084						
<i>Uncia uncia</i> , snow leopard	7.43	7.43	14.29		99.30				0.10	0.114		38.90		1.35	1.35	
<i>Ursus americanus</i> , American black bear	16.13	16.13	11.11			8.63				0.165	55.75	39.10	1.37	1.63	1.30	NT
<i>Ursus arctos</i> , brown bear	11.65	10.90	0.00	41.47		45.00			1.10	0.12	46.20	182.50	0.50	1.55	1.35	NT
<i>Ursus maritimus</i> , polar bear	36.80	32.10	64.71	14.85						0.072	15.28	79472.6	1204.0	8.79	7.12	
<i>Ursus thibetanus</i> , Asiatic black bear	7.50	7.50	12.50				0.29			0.089	59.10	23.00	3.22			
<i>Vulpes vulpes</i> , red fox	0.16	0.16	22.20	22.50	77.29			44.40		0.254	27.83	2.20	0.29			T

Gaps indicate a lack of data. SYA, all stereotypic behaviour (% obs.); SPP, stereotypic pacing (% obs); CIM, captive infant mortality (% births); FOR, time spent foraging (% 24 h); FLE, proportion of vertebrate flesh in the diet (%); CHD, chase distance (m); KID, distance between kills (km); HUR, hunt rate (per 24 h); KIR, kill rate (per 24 h); DDS, degree dietary specialisation (Levin's trophic niche breadth); ACT, time spent active (% 24 h); HRS, home-range size (km²); MHR, minimum home-range size (km²); DTD, daily travel distance (km); MDT, minimum daily travel distance (km); TER, territoriality (T, territorial/intermediate; NT, non-territorial). N.B. estimates for stereotypic behaviour include data only from those individuals displaying that behaviour.

^a Species were left out of analyses due to sparse infant mortality data, but later added back in to check results (see Section 2).

both partialled out using General Linear Models, and included by running multiple regressions. Transformations were used where needed to normalise data. All tests were performed using Minitab Release 13.32. With one exception (the role of diet diversity, where opposing hypotheses had been advanced), comparisons between wild and captive variables were one-tailed, because we were testing clearly directional hypotheses (see Section 1); and CAIC was always used where appropriate. Sixteen regressions were run for each of the captive variables (see Table 2); previously we used an alpha cut-off of $p < 0.01$, due to concerns about multiple testing (Clubb and Mason, 2003), but this may have been too conservative (especially since our power was low in some analyses). Here we therefore show all results for which $p < 0.05$.

3. Results

Behavioural data were gleaned from around 940 captive individuals, 426 of whom showed stereotypic behaviour and were thence used in our final analyses; these came from over 42 sites (38 zoos, 4 fur farms) and ca. 100 studies (ca. 85% of which were dated 1990 or later, and over 90% of which came from Europe/North America). For infant mortality, data came from over 500 zoos (ca. 75% in the developed world) plus a handful of fur farms, and reflected over 20,000 births and 7000 infant deaths (see Table 1).

Information on aspects of wild behaviour was available on all these species, although not for all variables nor for all species. Degrees of freedom thus vary in subsequent analyses, due to missing data. Species median values for the captive and wild variables are given in Table 2.

3.1. Checks, balances, and potential confounds

Study length or observation method did not systematically vary with species, nor correlate with any of our independent or dependent variables (see Clubb, 2001 for details). The same was true for husbandry variables. The only exception was that large species were typically held in large enclosures ($F_{1,21} = 63.2$, $p < 0.0001$), but this aspect of housing did not predict species-typical stereotypic behaviour (pacing: $F_{1,19} = 0.25$, $p > 0.05$; all stereotypic behaviour: $F_{1,19} = 0.00$, $p > 0.05$) so, importantly, was not a systematic confound. Medians, etc. for these husbandry-related variables are given in Table 3.

Table 3
Species-typical husbandry variables

Species	ENC	FRQ	REA	SUB	COV	ELV	GRP	TIM	STV	PRO	ENR
<i>Acinonyx jubatus</i> , cheetah	950.4	1.5	C	S	Y	N		A	N	P	N
<i>Ailuropoda melanoleuca</i> , giant panda		2						M	N		
<i>Alopex lagopus</i> , Arctic fox			C	H	N					N	N
<i>Caracal caracal</i> , caracal	36.1	1	C	H	Y	Y	D	A	N		
<i>Felis chaus</i> , jungle cat	90.0	1				Y		M	N	P	Y
<i>Felis margarita</i> , sand cat	25.9	1	C	H		Y		M	Y	N	N
<i>Felis silvestris</i> , wild cat							D	A			
<i>Genetta tigrina</i> , large-spotted genet											
<i>Leopardus pardalis</i> , ocelot	40.5	1.8		S	Y	Y		A	N	P	N
<i>Leopardus wiedii</i> , margay	22.8	1.6		S	Y	Y		A	N	P	N
<i>Leptailurus serval</i> , serval		1				N	D	M	N		

Table 3 (Continued)

Species	ENC	FRQ	REA	SUB	COV	ELV	GRP	TIM	STV	PRO	ENR
<i>Lynx canadensis</i> , Canadian lynx			C	H	Y	N		A	N	N	N
<i>Lynx lynx</i> , Eurasian lynx	129.1	1	C	H	Y	Y	D	A	N	N	N
<i>Melursus ursinus</i> , sloth bear	100.0	2.25	C	S	Y	N		A	N	P	N
<i>Mustela vison</i> , American mink	1.1	1.5									
<i>Oncifelis geoffroyi</i> , Geoffroy's cat	23.7	1	C	H	Y	Y		A	N	P	N
<i>Panthera leo</i> , lion	1140.6	1	C			N		A	Y	P	Y
<i>Panthera onca</i> , Jaguar	196.8	1	C	S	Y	Y		A	Y	P	Y
<i>Panthera pardus</i> , leopard	144.0	1	C	S	N	Y	S	A	N	P	Y
<i>Panthera tigris</i> , tiger	901.2	1	C	S	Y	Y	D	A	Y	P	Y
<i>Parahyaena brunnea</i> , brown hyaena	2000.0	1		S	Y	N	D		Y	N	N
<i>Potos flavus</i> , kinkajou		2.58	C	H	Y	N	S	A	N	N	N
<i>Prionailurus bengalensis</i> , leopard cat	5.9	1	C	H	Y	N		A	N	N	N
<i>Prionailurus viverrinus</i> , fishing cat	25.6	1	C	H		N		M	N		
<i>Puma concolor</i> , mountain lion		1			N		S	M	N		
<i>Suricata suricatta</i> , meerkat	6.0	1		S	Y	N		A	N		
<i>Tremarctos ornatus</i> , spectacled bear			C	S	Y	N					
<i>Uncia uncia</i> , snow leopard	128.6	1	C			Y		A	Y	P	Y
<i>Ursus americanus</i> , American black bear	55.4	2	W	H	N	N	S	A	N	P	N
<i>Ursus arctos</i> , brown bear	1537.6	1	C	H	N	N	D	A	N	N	N
<i>Ursus maritimus</i> , polar bear	836.9	1	C	S	N	N	D	M	N	P	Y
<i>Ursus thibetanus</i> , Asiatic bear	686.0	1	C	H	N	N	S	M	N		
<i>Vulpes vulpes</i> , red fox			C	H			D			N	N

ENC, enclosure size (m²); FRQ, meal frequency (average number of meals per day); REA, rearing history (C = captive-born; W = wild-caught); SUB, substrate (H = predominantly 'Hard'; S = predominantly 'Soft'); COV, availability of cover (Y/N); ELV, access to elevated areas (Y/N); GRP, social grouping compared to the wild (S = same; D = different); TIM, meal timing (M = morning feeds; A = afternoon feed, or both morning and afternoon); STV, weekly starve days (Y/N); PRO, meal processing level (P = processed food; N = diet includes non-processed items); ENR, feeding enrichment (Y/N).

Creel and Macdonald's (1995) estimates of home-range size were strongly correlated with median home-range size as used in this paper ($F_{1,14} = 24.37$, $p < 0.0001$). Body weight was correlated with home-range size, diet diversity (only when controlling for phylogeny) and the proportion of flesh in the diet (cross-species plot analyses only), and so body weight was controlled for in analyses involving these variables (see also Clubb, 2001; Clubb and Mason, 2003). Infant mortality in the wild and in captivity did not co-vary (see Clubb and Mason, 2003 for details). Tests for serial independence revealed that most variables were not significantly affected by phylogeny, with the exception of body weight, the time spent foraging and the

Table 4

Relationship between wild variables and captive stereotypic behaviours; pacing *per se* and infant mortality from cross-species plots (see text for results controlling for phylogeny)

Hypothesis: stereotypic behaviour stems from ...	Wild variable	Stereotypic behaviour (all)	Stereotypic 'pacing'	Infant mortality
Natural foraging mode	Time spent foraging (% 24 h) ^a	$F_{1,6} = 1.46, p = 0.136, R^2 = 19.6\%$	$F_{1,6} = 2.30, p = 0.090, R^2 = 27.7\%$	$F_{1,6} = 4.15, \text{NS} (p = 0.088)^b, R^2 = 40.9\%$
	Prop. vertebrate flesh in diet (%) ^{a,c}	BWt included: $F_{2,19} = 2.94, \text{NS} (p = 0.077)^b, R^2 = 23.6\%$; BWt partialled out: $F_{1,19} = 0.44, p = 0.257$	BWt included: $F_{2,19} = 4.13, p = \text{NS} (p = 0.016)^b, R^2 = 30.3\%$; BWt partialled out: $F_{1,19} = 0.86, p = 0.183$	BWt included: $F_{2,19} = 1.05, p = 0.184, R^2 = 10.0\%$; BWt partialled out: $F_{1,19} = 1.33, p = 0.132$
	Chase distance (m)	$F_{1,7} = 0.02, p = 0.451, R^2 = 0.2\%$	$F_{1,7} = 0.12, p = 0.02, R^2 = 0.2\%$	$F_{1,7} = 0.65, p = 0.223, R^2 = 8.5\%$
	Distance between kills (km)	$F_{1,4} = 0.03, p = 0.439, R^2 = 0.7\%$	$F^{a,b} = 0.03, p = 0.438, R^2 = 0.7\%$	$F_{1,4} = 0.01, p = 0.468, R^2 = 0.2\%$
	Hunt rate (per 24 h)	$F_{1,4} = 2.32, p = 0.102, R^2 = 36.7\%$	$F_{1,4} = 2.32, p = 0.203, R^2 = 36.7\%$	$F_{1,4} = 0.10, p = 0.386, R^2 = 2.4\%$
	Kill rate (per 24 h)	$F_{1,10} = 2.12, \text{NS} (p = 0.088)^b, R^2 = 17.5\%$	$F_{1,10} = 1.88, p = 0.100, R^2 = 15.8\%$	$F_{1,10} = 0.36, p = 0.281, R^2 = 3.5\%$
	Degree dietary specialisation (Levin's trophic niche breadth) ^d	$F_{1,26} = 0.46, p = 0.505, R^2 = 1.7\%$	$F_{1,26} = 0.64, p = 0.431, R^2 = 2.4\%$	$F_{1,26} = 2.80, p = 0.106, R^2 = 9.7\%$
Naturally active lifestyle	Time spent active (% 24 h)	$F_{1,16} = 7.65, \text{NS} (p = 0.014)^b, R^2 = 32.3\%$	$F_{1,16} = 7.05, \text{NS} (p = 0.009)^b, R^2 = 30.6\%$	$F_{1,16} = 6.19, \text{NS} (p = 0.024)^b, R^2 = 27.9\%$
	Time spent foraging (% 24 h)	See above	See above	See above
Restricted ranging behaviour	Home-range size (km ²) ^{a,c}	BWt included: $F_{2,19} = 3.17, p = 0.033, R^2 = 25.0\%$; BWt partialled out: $F_{1,19} = 0.11, p = 0.371$	BWt included: $F_{2,19} = 3.94, p = 0.019, R^2 = 29.3\%$; BWt partialled out: $F_{1,19} = 0.14, p = 0.357$	BWt included: $F_{2,19} = 2.91, p = 0.039, R^2 = 23.4\%$; BWt partialled out: $F_{1,19} = 5.09, p = 0.013$
	Minimum home-range size (km ²) ^{a,c}	BWt included: $F_{2,17} = 3.41, p = 0.029, R^2 = 28.6\%$; BWt partialled out: $F_{1,17} = 0.85, p = 0.185$	BWt included: $F_{2,17} = 4.42, p = 0.014, R^2 = 34.2\%$; BWt partialled out: $F_{1,17} = 1.26, p = 0.139$	BWt included: $F_{2,17} = 6.19, p = 0.005, R^2 = 42.1\%$; BWt partialled out: $F_{1,17} = 11.11, p = 0.002$
	Daily travel distance (km)	$F_{1,16} = 3.74, p = 0.036, R^2 = 18.9\%$	$F_{1,16} = 6.03, p = 0.013, R^2 = 27.4\%$	$F_{1,16} = 5.95, p = 0.014, R^2 = 27.1\%$
	Minimum daily travel distance (km)	$F_{1,17} = 0.02, p = 0.446, R^2 = 0.1\%$	$F_{1,17} = 0.01, p = 0.456, R^2 = 0.1\%$	$F_{1,16} = 5.10, p = 0.019, R^2 = 24.2\%$
Territorial patrolling behaviour	Territoriality	$T = -0.33, p = 0.387, \text{d.f.} = 5$	$T = -0.30, p = 0.774, \text{d.f.} = 5$	$T = 2.04 (2\text{-tailed}), p = 0.048, \text{d.f.} = 5$

All *p*-values are one-tailed unless otherwise stated (see Section 2). Throughout: BWt = body weight.^a Results confirmed by CAIC analysis (see text and Clubb and Mason, 2003).^b Non-significant, as direction of relationship is in opposite direction to one-tailed predictions. *p*-values given are two-tailed.^c Correlated with body-weight, therefore BWt included in analyses.^d Two-tailed tests were performed on this variable due to the nature of the hypotheses being tested, cf. other variables (see Sections 1 and 2).

proportion of flesh in the diet. All analyses involving these three variables were therefore repeated using CAIC (e.g. all home-range analyses). The effects of ‘fur’ species, the polar bear, and the species omitted for sparse breeding records, are reported in the relevant sections below.

3.2. Stereotypic behaviour

No foraging variable significantly positively correlated with stereotypic behaviour (see Table 4), i.e. it was no more common in species with a great reliance on live vertebrate flesh, a narrow dietary niche, frequent hunts per day, frequent kills per day, long chase distances, nor great distances travelled between kills (see Table 4). Natural activity levels also did not predict high stereotypic behaviour frequencies (e.g. % stereotypic behaviour versus general activity levels in wild: see Table 4). (The fact that instead, results opposite to the hypotheses’ predictions sometimes emerged – see Table 4 – is considered in Section 4.) Furthermore, territoriality *per se* did not predict stereotypy frequency (see Table 4).

Body weight and home-range size (median and minimum) together predicted stereotypic behaviour (see Table 4 and Fig. 1). Home-range size with body weight partialled out had no effect on its own (see Table 4). All these results were confirmed by CAIC analyses. Median daily travel distances also significantly predicted pacing frequency (see Table 4 and Fig. 2), an effect unaffected by bodyweight. This home range/travel distance effect was specific to stereotypic behaviour: wide-rangers did not show more general activity in captivity (see Clubb and Mason, 2003).

Although not statistical outliers, we checked that the result did not rely on polar bears, or on fur farmed species. Removing polar bears made no major difference to the findings (e.g. pacing versus daily distance travelled: $F_{1,15} = 4.01$, $p = 0.034$, $R^2 = 21.1\%$), although only trends remained for relationships between stereotypic behaviour and minimum home-range size ($F_{2,16} = 1.86$, $p = 0.094$, $R^2 = 18.9\%$) and daily travel distance ($F_{1,15} = 2.07$, $p = 0.086$, $R^2 = 12.1\%$). The same was true when the three ‘fur animals’ were removed (e.g. stereotypic

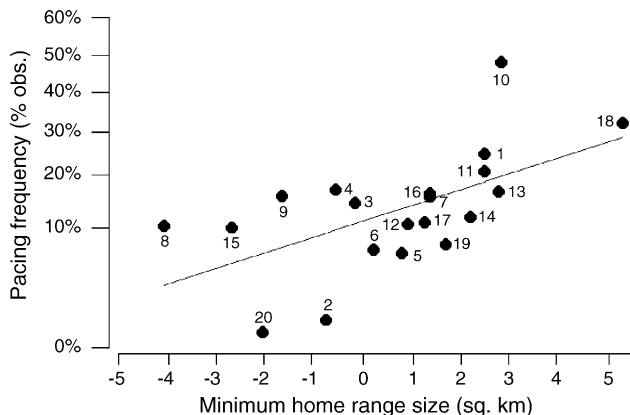


Fig. 1. Minimum home-range size (accounting for body size) and median % pacing frequency in affected individuals. Stereotypy data was arcsine transformed but units on the y-axis are given in the raw form for clarity. Species are labelled as follows: (1) *Acinonyx jubatus*; (2) *Alopex lagopus*; (3) *Caracal caracal*; (4) *Leopardus pardalis*; (5) *Lynx canadensis*; (6) *Lynx lynx*; (7) *Melursus ursinus*; (8) *Mustela vison*; (9) *Oncifelis geoffroyi*; (10) *Panthera leo*; (11) *Panthera onca* (12) *Panthera pardus*; (13) *Panthera tigris*; (14) *Puma concolor*; (15) *Suricata suricatta*; (16) *Ursus americanus*; (17) *Ursus arctos*; (18) *Ursus maritimus*; (19) *Ursus thibetanus*; (20) *Vulpes vulpes*.

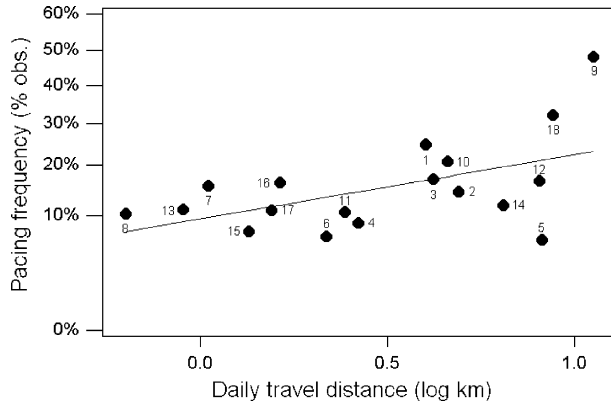


Fig. 2. Daily travel distance and median pacing frequency. Pacing data was arcsine transformed but y-axis units are given in the raw form for clarity. Species are labelled as follows: (1) *Acinonyx jubatus*; (2) *Caracal caracal*; (3) *Leopardus pardalis*; (4) *Leptailurus serval*; (5) *Lynx canadensis*; (6) *Lynx lynx*; (7) *Melurus ursinus*; (8) *Mustela vison*; (9) *Panthera leo*; (10) *Panthera onca* (11) *Panthera pardus*; (12) *Panthera tigris*; (13) *Prionailurus bengalensis*; (14) *Puma concolor*; (15) *Uncia uncia*; (16) *Ursus americanus*; (17) *Ursus arctos*; (18) *Ursus maritimus*.

behaviour versus minimum home range: $F_{1,15} = 5.14, p = 0.020, R^2 = 25.5\%$; stereotypy versus daily distance travelled: $F_{1,15} = 5.20, p = 0.019, R^2 = 25.7\%$), with the exception that the relationship between pacing and median home-range size was again reduced to a trend ($F_{2,16} = 2.24, p = 0.069, R^2 = 21.9\%$). Lastly, including the giant panda and brown hyaena in analyses (excluded here due to their sparse infant mortality data) had no major impact on the results (see Clubb and Mason, 2003).

3.3. Infant mortality

Natural foraging and general activity levels similarly did not positively correlate with captive infant mortality (see Table 4). However, natural home-range size again did predict this measure, mortality being higher in wider-ranging species (see Table 4 and Fig. 3), confirmed by CAIC

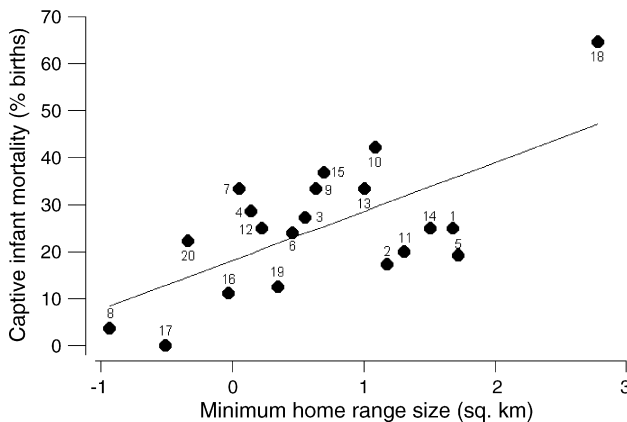


Fig. 3. Minimum home-range size (with body size partialled out) and median captive infant mortality rate over days 1–30. Species are labelled as in Fig. 1.

analyses (see Clubb and Mason, 2003). Median and minimum daily travel distances had similar effects (see Table 4). Territorial species also had higher infant mortality levels than non-territorial species, which just reached significance (see Table 4).

Infant mortality in the wild, in contrast, was not related to home-range size; and minimum home range predicted captive mortality even when wild mortality rates were controlled for (see Clubb and Mason, 2003 for details).

Again, we explored the impact of some of the species (although not statistical outliers). Experimentally removing the polar bear made no major difference to the findings (e.g. infant mortality versus daily distance travelled: $F_{1,15} = 3.66$, $p = 0.038$, $R^2 = 19.6\%$) although in the case of median home-range size the relationship was lost. Key findings also remained when ‘fur animals’ were removed (e.g. infant mortality versus minimum home range: $F_{1,14} = 9.50$, $p = 0.004$). Adding the giant panda and brown hyaena, with their very sparse infant mortality data, had no major impact on the results (e.g. infant mortality versus minimum home-range size: $F_{1,19} = 6.05$, $p = 0.012$).

4. Discussion

Zoos and animal-keepers have long known that some carnivores thrive in captivity, while others are often hard to keep without problems, and our study shows that biological principles underlie these species differences. However, although our hunch at the outset had been that hunting-based foraging modes would be the key (cf. e.g. Mason and Mendl, 1997), in fact, having a naturally wide-ranging, far-travelling lifestyle instead predicted more compromised captive welfare. Thus captive infant mortality was best predicted by minimum home-range size *per se* (regardless of whether body size was factored in), and slightly less strongly, by natural median daily travel distance; while the time devoted to pacing stereotypies, in individuals developing abnormal behaviour, was best predicted by large median daily travel distances in the wild, and by the combination of being both large and having a large range size. Since large range sizes are also a risk factor for local extinctions *in situ* (Woodroffe and Ginsberg, 1998), this suggests that wide-ranging carnivores are in double jeopardy.

Before considering the practical implications of this, let us first acknowledge three major uncertainties in this work. First, is natural ranging behaviour the only important aspect of natural lifestyle? Clearly not: it only predicted some of the variance in our captive variables. This was doubtless partly due to sampling issues (as evident in Section 3 and Table 1, sample sizes were minimal for some species and some variables, and thence unlikely to give accurate estimates of population medians); along with data quality issues too (for example, in the captive behavioural studies used, different authors probably used different implicit criteria for scoring stereotypic behaviour; while the published infant mortality figures used were self-reported by zoos, and unchecked for accuracy). That natural ranging only predicted some of the variance in captive welfare is also probably due to other, more biologically interesting, factors too. For example, it could be that further aspects of natural lifestyle (e.g. aspects of natural foraging behaviour) would have met predictions if we had had data from sufficient species; or that they might then explain the scatter around our key regressions (unfortunately, our dataset had too many gaps to allow the multivariate analyses needed to investigate this). Indeed, surprisingly some wild behaviour variables (namely, proportion of live vertebrate flesh in the diet and time spent active) did not just reject the hypotheses under test: they indicated correlations in the opposite directions (see Table 4). These results are strictly non-significant because we used one-tailed tests, but we mention them in case worthy

of future investigation. They could merely be Type II errors; or due to negative correlations between these wild behaviour variables and ranging—univariate analyses do suggest this to be a possibility (see Clubb, 2002). However, instead it could be something real is going on, whereby very active species and/or those highly dependent on live vertebrate prey do show less stereotypic behaviour than inactive, less carnivorous species. Future work is needed to see whether these counter-intuitive results are robust or merely artefacts (see Section 4.4).

The second uncertainty is: what exactly is the role of husbandry? Many aspects of rearing and husbandry are known to affect captive animals' behaviour and welfare (see e.g. Mason et al., 2007 and Morgan and Tromborg, 2007). Although we showed that these were not responsible for the 'home-range effects' themselves, such husbandry effects thus probably did cause some scatter around our key regressions (for instance, the relatively high stereotypic behaviour of the mink – at least for a small ranging species [see Fig. 1] – is likely because all this species' behavioural data came from a fur farm). Once more field and captive data have accrued in the future, it would be fascinating to investigate these likely contributions in detail (see also Section 4.4).

Our third and final unknown is: how are the 'home-range effects' mediated, and what, if any, is the role of stress? Some possible explanations for these effects do not invoke differential stress or welfare. For example, wide-ranging species could be better adapted to sustained locomotion (e.g. in terms of muscle physiology), and hence simply able to stereotype for longer periods (although this is perhaps belied by the lack of similar effects on non-stereotypic activity); and/or the offspring of wide-ranging species may, for some reason, be systematically more likely to be euthanised as surplus, creating the observed regression. However, alternative (and arguably more parsimonious) explanations for these effects are that captive environments are least adequate for welfare and/or normal functioning in naturally wide-ranging species. This could be because captive conditions represent deprived rearing environments for such species, the relatively large differences between natural and captive environments thence causing an abnormal development of brain and behaviour most marked in wide-rangers (in which case 'home-range effects' should be strongest in, or even unique to, captive-bred individuals, and accompanied by other generalized changes in behaviour and brain functioning; see e.g. Garner, *in press*; Lewis et al., *in press*). Alternatively, captive environments may cause the most stress to naturally wide-ranging species, via the prevention of natural, species-typical responses (in which case 'home-range effects' should be strongest in, or even unique to, wild-caught individuals, and accompanied by other signs of chronic stress such as adrenal hypertrophy, etc.). Again, these effects are currently hard to investigate (our dataset was insufficient even to look at the 'source effects' suggested above), but are very amenable to future research.

However, whatever the exact mechanism(s) (indeed, given the subtly different predictors of infant mortality and of stereotypic behaviour, more than one may be at work), and whatever other factors additionally affect captive carnivores, our general finding does give novel insights into what influences their success in captivity. These insights can potentially now be used to better understand – and perhaps address – abnormal behaviour and infant losses in this taxon. Our results have three main practical implications for carnivore housing and husbandry, discussed below.

4.1. Refining carnivore housing, husbandry and enrichment

The first practical implication of our findings is that considering what it means to be naturally wide-ranging might be a particularly fruitful, effective route to designing appropriate

future enclosures and environmental enrichments for captive carnivores. This is important because currently, environmental enrichments typically never abolish stereotypic behaviour in captive carnivores: they merely reduce these behaviours (see Section 1); and in some carnivore species, current average captive infant mortality rates seem unacceptably high (see below).

Perhaps the most obvious suggestion is that zoo enclosures should be made larger. After all, there is evidence that wild animals use far larger land areas than they are provided with in zoos, even when they are provisioned: thus for example, even with garbage to forage upon, grizzly bears still maintain ranges of over 15 km² (Craighead et al., 1995) (cf. their median zoo enclosure area in our dataset: 1538 m²). However, it might be more biologically relevant, and also suggest more practicable husbandry changes, to break down what moving around a large range actually involves for a wild animal, and to use this to suggest possible enrichments.

For the polar bear, to briefly consider one example, the median minimum home range across our studies was 1204 km², and the median average home range, 79,472 km². The median average travel distance was 8.8 km/day, not too dissimilar from the median minimum, 7.1 km/day. Daily travel distances are thus fairly large, and indeed these animals have the stamina to cover more impressive distances still (e.g. swimming tens of kilometres; Matthews, 1993), adaptations we suggest above might contribute to their abilities to pace for long periods in captivity. However, we suspect that the important thing to note is how small such daily travel distances are relative to the whole annual range: polar bears are effectively nomads within vast areas, regularly shifting from one location to another according to changing food supplies, the presence of conspecifics (either potential mates or sources of danger), and the availability of dens (e.g. Perry, 1966; Mauritzen et al., 2003). Such shifts in location involve very impressive navigational abilities, especially when moving ice passively displaces bears from desired routes (Mauritzen et al., 2003). The continually changing drift ice, and the animals' own movements, mean too that their surroundings change completely from one period to the next. This need in the wild for regular decision-making and navigation, and the animals' exposure to ever-changing environments, contrasts markedly to life in captivity: here, no such abilities are required, and the animal's surroundings (which, in our studies, were enclosures averaging 950 m²: about 1 millionth of the minimum home range) are essentially constant. Similar pictures emerge looking at the natural lifestyle of more terrestrial wide-ranging carnivores: African wild dogs, for example, rarely spend two consecutive nights in the same location before moving on to use other parts of their range (Creel and Creel, 2002), while wolves likewise remain in one sub-region of their territory for just a few days, before shifting to another (e.g. Peters, 1979). The lifestyle of this type of animal contrasts greatly with that of small-range species. The American mink in the wild, for example, often criss-crosses its entire territory in just one single day; will do so repeatedly, day after day, month after month (e.g. Dunstone, 1993); and sleeps in regularly used dens scattered within what must be an extremely familiar, intimately known patch of land. Likewise, a red fox may have a home range of less than 1 km²: an area it could cross entirely in a matter of minutes, and within which it may live for several years (Macdonald, 1987).

So how might such observations inform enclosure design and enrichment use? We suspect that it is not simply (thwarted) opportunities to move large distances that are important for captive wide-rangers. After all, stereotyping carnivores regularly travel further than they would do in the wild (e.g. a caged pacing mink can cover 40 km/day – de Jonge, unpublished – over four times the typical distance covered in the wild; Dunstone, 1993): thus even in small enclosures, movement *per se* is not necessarily constrained. It could be, however, that wide-rangers are more

motivated to perform particular types of locomotion that cannot occur in captivity, such as sustained running (e.g. as would naturally occur in hyaenas or cheetahs, for example; Terio and East, pers. comm.). Alternatively, the important ‘missing variables’ in captivity could actually be the stimuli and the challenges that are encountered when ranging widely in the wild: for example, it could be that regular or substantial variation in the visual, olfactory, auditory and tactile cues coming from the surroundings is important; or the cognitive challenges of decision-making, and/or of spatial learning and navigation (*sensu* Meehan and Mench, 2007). A final possibility is that abilities to respond facultatively to threat or to resource availability, i.e. to exert control (cf. e.g. Morgan and Tromborg, 2007), are particularly important to wide-ranging species. As we have seen, wide-ranging carnivores naturally make daily choices, moving towards desired resources and away from potential threats in a manner which determines where they move and what they are exposed to each day. Thwarting such opportunities for control may perhaps thus be particularly stressful for such animals, both in general, and perhaps also in particular, specific ways (spotted hyaenas, for example, naturally have a ‘fission–fusion’ social system which could be difficult to recreate in an enclosure [East, pers. comm.]).

Further research is clearly needed to determine exactly what it is about natural wide-ranging lifestyles that makes some carnivores more vulnerable in captivity (and indeed whether or not exactly the same aspects underlie the pacing and infant mortality effects). However, in the interim, we suggest that to improve their captive environments it could be beneficial to focus on: providing substantial increases in space; greater numbers of viewpoints (especially viewpoints that offer variety, or perhaps large vistas); greater numbers of resting places, potential den-sites and/or burrows; more variable and complex enclosure boundaries (e.g. with sections that are opened and closed at different times, perhaps under the control of the animals themselves); more spatial and/or stimulus complexity and less day-to-day environmental predictability—combined (importantly) with the ability of the animals to control their own access to such increased variability; and more scope to approach or retreat from the public, conspecifics, and other stimuli, at will. Comparing successful with unsuccessful enclosures in multi-zoo studies, hypothesis-directed enrichment experiments, and more detailed comparative work (see Section 4.4), should all help to test and refine these suggestions in the future. In the meantime, we do not advise abandoning the foraging enrichments that, in zoos, have rather dominated enrichment strategies to date, but we do suggest that they are supplemented with approaches arguably more likely to tackle the root causes of carnivores’ problems.

4.2. *Pre-empting problems by targetting captive wide-rangers*

The second practical implication of our findings is that zoos trying to pre-empt welfare problems before they emerge (a strategy with practical, as well as ethical, benefits, since there is evidence that impoverished environments can cause brain changes that are then hard to reverse—see e.g. Lewis et al., in press; Novak et al., in press; Mason et al., 2007) would be wise to focus first on species that range widely in the wild, allocating resources accordingly. Of those we used here, these include the polar bear, American black bear, and puma. Based on further home-range estimates (taken from Creel and Macdonald, 1995) controlling for body weight, some additional species that we predict would be susceptible in captivity are the side-striped jackal, European polecat, wolverine, and African wild dog. Such animals thus might sensibly be selected *a priori* for the most intensive enrichment programmes (see above) and other improvements to husbandry—even *before* individuals show any signs of problems. Alternatively, they might be deselected as zoo species, an idea we develop below.

4.3. Avoiding problems by phasing out captive wide-ranging species

The third practical implication of our findings is that that zoos could use this information to favour keeping those species inherently likely to fare well under current conditions, and phase out those that are not (e.g. replacing polar bears with brown/grizzly bears; brown hyaenas with spotted hyaenas; fishers or European polecats with American mink, and so on). After all, worldwide, zoos currently keep over 4000 species and sub-species of birds and mammals (<http://www.isis.org>, accessed November 2005), but arguably only have space for 600–1200 if captive populations are to be self-sustaining and genetically viable (Ebenhard, 1995; see also Balmford et al., 1996). This means that choices must be made, and the ease with which a species can be husbanded and bred in captivity is one important factor in such choices (e.g. EAZA, 2005; IUDZG, 1993; WAZA, 2005; see also Balmford et al., 1996). Furthermore, our widest-ranging species seemed to be faring far worse in zoos than one would expect given veterinary care, ample food, and the lack of predation. For wild carnivore infants, the biggest killers are predation and starvation (e.g. Bailey, 1993; Matthews, 1993; Laursen, 1994; Durant, 2000; Burrows, pers. comm.) — two threats that should be absent in good captive conditions. In the lion, for instance, according to the widely cited Schaller (1972), two thirds of wild cubs die in their first year; but only 30% die before the age of 6 months, starvation and predation being among the causes. Such data strongly suggest that in a good quality, protected environment, lion cub mortality in the first 30 days should thus be well under 30%, and yet the current zoo average is 42%.

We therefore suggest that it might be sensible – both more cost-effective and humane – for zoos to focus on those carnivores inherently best suited to current, or at least readily achievable, enclosure sizes and enrichment/husbandry regimes. Wide-ranging species instead could be conserved in specialized breeding centres (which may have additional advantages of range country climates and a lack of visitor disturbance; the De Wildt cheetah sanctuary in South Africa, for example, has infant mortality rates of just 16%, compared with the zoos' median of 25%; Strachan, unpublished data); or instead via the *in situ* approaches that many advocate as preferable (e.g. Balmford et al., 1996).

4.4. Further comparative research, on carnivores and on other taxa

As a final note, we would like to emphasise that our study shows how incredibly valuable are the data that zoos collect on infant mortality, and the often small-scale behavioural/enrichment studies run in zoos, especially when they are collated and analysed *en masse* (see also Schetini de Azevedo et al., 2007). Comparative approaches also allow us to use such data to investigate hypotheses that it would be difficult, unethical or plain impossible to tackle experimentally. Overall, there is therefore real scope for using this approach in the future. For a more in-depth understanding of the ecological bases of carnivore welfare issues, we probably need to wait at least another 5 years, for more publications and data to accumulate. However, once added to our databases, the information therein should improve the accuracy of estimation, via sampling more individuals and populations; and fill in missing cells so that all relationships could be investigated with more statistical power, and multivariate analyses conducted. With the addition of more detail, we could also perhaps ascertain what specific aspects of being wide-ranging explain captive responses; see if similar effects explain within-species variance (e.g. differences between sexes, age classes, and/or sub-species); and see if ranging also predicts stereotypy prevalence within populations, conception rates, and other

welfare-/husbandry-relevant dependent variables. In the interim, it would be fascinating to now collate and analyse past data for other taxa, to see if comparative approaches could similarly help give insights into the ecological factors important for welfare and housing issues in captive primates, ungulates, and other groups of animal.

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