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Stereotypic route-tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles

Abstract

In captive conditions (e.g. zoos), some Carnivora species typically show negligible stereotypic behaviour (SB) and reproduce successfully, while others tend to reproduce poorly and be very stereotypic. We used comparative methods to identify species-level risk factors for SB and captive infant mortality (CIM). Candidate predictor variables were natural ranging behaviour, territoriality, aspects of natural foraging, wild activity levels, cranial volume, and IUCN Red List status. Previous research had identified naturally long daily travel distances, and being large-bodied and wide-ranging, as SB risk factors. We nearly doubled the size of this original SB database, and then imposed stricter quality controls (e.g. on minimum sample sizes for inclusion). Analysing the resulting 23-species dataset confirmed naturally large ranges and travel distances as risk factors. It also showed that the range size effect: is independent of body mass (although body mass and range size together predicted SB most strongly); is stronger for stereotypic route-tracing (e.g. pacing) than for all SB forms combined; and explains the apparent daily travel distance effect (which vanished when range size was controlled for). Furthermore, a new finding emerged: that naturally long chase distances during hunts also predicted more severe route-tracing. Turning to CIM, previous research had also identified naturally long travel distances and large home ranges as risk factors. We failed to replicate this, or to confidently identify any species-level risk factor (despite CIM significantly varying between related species, at least for Canidae and Ursidae). Understanding what underlies high species-typical CIM thus requires more current data, and further research. Overall, naturally wide-ranging Carnivora with long chase distances are thus most prone to extensive stereotypic route-tracing in captivity. This suggests that captive carnivores cannot relinquish aspects of ranging and pursuit hunting, even

29 when their homeostatic needs are met; and also suggests new strategies for
30 environmentally enriching their enclosures more effectively.

31

32

33 **Keywords**

34 Behavioural needs, captive breeding, ethological needs, infant mortality, pacing,
35 stereotypic behaviour, stereotypy stress, welfare, well-being.

36

37

Introduction

Billions of wild and semi-wild animals, spanning over 10,000 species, live in captive conditions very different from their ancestral environments, being farmed, kept as pets, bred in zoos and conservation captive breeding centres, or used in research (Mason et al., 2013). Some species adjust readily to these conditions, largely thriving thanks to veterinary care, food provision, and protection from predators. Other species, however, appear to find confinement more challenging, being prone to abnormal behaviours (e.g. self-harm; stereotypic pacing), high rates of morbidity and mortality, and breeding problems (Mason et al., 2013; Mason, 2010). Comparative methods (e.g. Felsenstein, 1985) are ideal ways to reveal the reasons for these patterns, identifying traits that confer vulnerability to stress in captivity (Clubb & Mason, 2004). These methods test hypotheses by exploiting the variation between species. Often used to investigate patterns of co-evolution (e.g. Healy, McNally, Ruxton, Cooper, & Jackson, 2013) and test hypotheses about adaptation (e.g. Montgomery, 2014), they have an emerging role in addressing applied problems. The last two decades have thus seen conservation biologists using them to better understand invasiveness and extinction risk, by identifying traits that predict 'weed' species or confer vulnerability to anthropogenic effects (e.g. Cassey, Blackburn, Russell, Jones, & Lockwood, 2004; Fisher & Owens, 2004; Jeschke & Strayer, 2006; Sol, Backer, Reader, & Lefebvre, 2008). Recently, comparative methods have been used to investigate why species vary in their responses to captivity (e.g. Clubb & Mason, 2003; Mueller et al., 2011; Pomerantz, Meiri, & Terkel, 2013). Results can help identify species a priori well- or poorly-suited for ex situ conservation or use in research laboratories, and pinpoint the changes in captive husbandry most likely to improve animal well-being. Such research can even raise new fundamental research questions (e.g. Mason et al., 2013; Sih, 2013).

Here we apply comparative methods to investigate why Carnivora differ so greatly in their responses to captivity. For example, they vary in susceptibility to abnormal behaviours such as stereotypic pacing. Within the Ursidae for instance, pacing is rare in brown bears (*Ursus arctos*), yet prevalent and often time-consuming in polar bears (*Ursus maritimus*) (Clubb & Mason, 2007). Furthermore, while some captive Carnivora reproduce readily (e.g. American mink, *Mustela vison*; brown bears [Joergensen, 1985; Malmkvist, Gade, & Damm, 2007]), others are prone to breeding problems including high rates of acyclicity (e.g. black-footed cats, *Felis nigripes*) and infant mortality (e.g. black-footed ferrets, *Mustela nigripes*; giant pandas, *Ailuropoda melanoleuca*) (reviewed Diez-Leon et al., 2013, Diez-Leon & Mason 2016; Curry, Safayi, Meyerson, & Roth, 2015). These responses are all affected by stress (reviewed e.g. Clubb et al., 2009, Mason & Veasey 2010), suggesting species differences in typical welfare (where welfare means well-being or affective state; Dawkins, 1990; Mason & Mendl, 1993). The Carnivora is an ideal group to apply comparative methods to because all of its 286 species (Nyakatura & Bininda-Emonds, 2012) are held in zoos (Conde, Flesness, Colchero, Jones, & Scheuerlein, 2011); this is important because species are the units of replication in such analyses. Furthermore, they are well studied in the wild, where they exhibit great diversity in natural ecology and life history (Gittleman, 1986a, 1986b) (including varying in diet, from herbivory [e.g. giant pandas; kinkajous, *Potos flavus*] through to relying on live prey [e.g. tigers, *Panthera tigris*]): variation that facilitates testing hypotheses about risk factors.

Our research updates work conducted over a decade ago. Clubb and Mason (2003) used a dataset on 33 species that was finalised in 1999, to identify species-typical risk factors predicting levels of stereotypic behaviour (SB) and infant mortality in captive Carnivora. They found that the extent to which species ranged in the wild predicted their captive welfare: naturally long daily travel distances, and the

combination of being large-bodied and wide-ranging, were risk factors for SB; while naturally long daily travel distances, large home ranges and also being territorial were risk factors for elevated infant mortality. No aspect of natural foraging behaviour, in contrast, appeared to predict welfare. The three principle reasons to now replicate and expand upon this research are described below.

First, several recent developments allowed inclusion of more species, potentially giving new analyses greater power. For example, a previous culture of excluding Pinnipeds had become outdated (Bininda-Emonds & Gittleman, 2000; Bininda-Emonds, Gittleman, & Kelly, 2001), allowing these to be included. Many additional publications on captive carnivores had also accumulated since 1999, while an expanded International Species Information System (www.isis.com) run by the zoo community potentially enabled greater access to quality zoo data on reproductive issues. Furthermore, a comprehensive source of data on natural ecology and behaviour variables now existed: the 'PanTHERIA' database (Jones et al., 2009). Secondly, some hypotheses previously rejected by the original study nevertheless seemed supported by growing experimental evidence, making it worth re-testing them with a more powerful dataset. In particular, stereotypic route-tracing (e.g. pacing) had long been hypothesised to derive from frustrated hunting (Clubb & Vickery, 2006; Hoenig & Gusset, 2010; Jenny & Schmid, 2002; Mason & Mendl, 1997), an idea persistently supported by its timing (a marked pre-feeding peak) and successful reduction with foraging-based enrichment (e.g. Clubb & Vickery, 2006; Hoenig & Gusset, 2010).

Finally, the third reason to update the original work was that three new, testable hypotheses had been advanced since Clubb & Mason (2003). One was that species at risk to anthropogenic changes in the wild are more vulnerable in captivity (Mason, 2010b; Mason et al., 2013; Martin, Lurbiecki, Joy, & Mooers, 2014). Consistent with this, as well as being prone to welfare issues in captivity, wide-

ranging carnivores are more susceptible to local extinctions in the wild (Woodroffe & Ginsberg, 1998); and endangered Canidae had been reported to have elevated captive infant mortality (Ginsberg & Macdonald, 1990). The second new hypothesis was that intelligence is a risk factor, with high intelligence potentially rendering species vulnerable thanks to 'boredom' and frustration, or low intelligence instead acting as a risk factor by reducing the behavioural plasticity and flexibility essential for adjusting to captivity (Mason et al., 2013). The third new hypothesis focussed on the potential mechanisms by which species-typical wild behaviours, like ranging, could predict captive welfare (Clubb & Mason, 2007). One proposed mechanism is that captive Carnivora are motivationally frustrated by being unable to range. This predicts that home range effects on welfare will be weak or absent in captive-bred individuals, but strongest in subjects caught as adults from the wild: animals whose prior experience of natural ranging should enhance frustration via negative contrast (Davies, Nicol, & Radford, 2015; Zeaman, 1949). Alternatively, captivity could compromise brain development (captive-raised individuals often having smaller brains, poorer learning abilities, and more perseverative tendencies than wild-caught conspecifics; e.g. Burns, Saravanan, & Rodd, 2009; Morimura & Mori, 2010), with wide-ranging Carnivora being developmentally impaired by constrained ranging. This hypothesised mechanism makes an alternate prediction: that home range effects on stereotypic behaviour and infant mortality will be strongest in captive-raised individuals (and weaker or absent in wild-caught conspecifics). This paper therefore re-examines the potential species-level risk factors for poor welfare in captive Carnivora, expanding upon previous work by incorporating additional species, including new data not previously available, and tackling three new hypotheses.

Methods

We updated the three databases compiled by Clubb & Mason (2003): a Captive Carnivore Stereotypic Behaviour Database, and, for the species listed within this, a Captive Infant Mortality and 'Potential Risk Factors' Database.

Updating the Captive Carnivore Stereotypic Behaviour Database

Data from 2000-2010 inclusive were added from Zoo Biology and International Zoo Yearbooks, following Clubb and Mason (2003; 2007)'s methods. Additionally, all issues, from the first to 2010 inclusive, of the publication Shape of Enrichment, and all International Conference on Environmental Enrichment abstracts were systematically searched, as were abstracts in three further journals: Animal Welfare, Applied Animal Behaviour Science, and Journal of Applied Animal Welfare Science (which publish many relevant studies; Shyne, 2006; Walker, Diez-Leon, & Mason, 2014). As previously, studies were included only if meeting certain criteria: the observation period was at least one day; subjects were adults, and not food restricted or – to avoid transient novelty effects – affected by recent changes in group structure or husbandry. Studies were also excluded if deemed poor quality (e.g. using inconsistent data recording), or – a new criterion not used by Clubb and Mason – if individuals had been selectively bred for high or low stereotypic behaviour (relevant for American mink, *Neovison vison*). About 60 additional new studies met all these criteria. In addition, individual information such as each animal's ISIS 'accession number' (an identity code), name, birthdate and sex, was used to identify recurring observations of the same subjects (common for zoos where repeated studies were conducted by undergraduates). Such duplicates affected ~24% of studies; when found, a mean value for stereotypic behaviour was calculated for relevant individuals, to ensure the final database had only one entry per subject.

This first update yielded 18 new species (Table A1). This resulting set of 51 species became the focus of the two subsequent databases. However, like Clubb and Mason, for this first database we focussed on stereotypic individuals only, because study biases towards stereotypers would inflate population-level estimates of prevalence or average time budgets, rendering them unreliable. Subsequent analyses thus investigate average time budgets for stereotypic individuals only, since these values could be well-estimated. Data on this measure, henceforth called the ‘severity’ of stereotypic behaviour (defined as the average % observation time spent in SB), were available for 42 species (Table A1). Of these, species were only included in final analyses if data were available for at least five stereotypic individuals: a stricter criterion than that used by Clubb and Mason. This new cut-off criterion follows precedents set by Thorpe, Black, & Malhotra (1996), Clubb and Mason for their infant mortality studies, and a recent comparative analysis of parrot welfare (McDonald Kinkaid, 2015); and was applied to enhance the accuracy of species estimates, while also allowing retention of a fair number of species (23). For each of these 23 species, median values of stereotypic behaviour (SB) were calculated (study means being calculated from individual means, and these used to calculate species medians). Wherever possible, SB was also categorized as to whether it involved route-tracing (e.g. circling, linear pacing, or the following of any fixed, repeated path); or instead was ‘stationary’ (i.e. performed in one spot, for example: digging, rocking, head-rolling) or ‘oral’ (i.e. involving jaws, tongue and/or lips, e.g. sucking, fur chewing, regurgitation). The aim was to calculate median values for each sub-type, but in practice, forms other than route-tracing were so rare that a median was only calculated for this one sub-type (Table A1).

Where possible, each subject’s birth origin (wild-caught versus captive-bred) was recorded, to investigate how such effects interacted with birth origin, for testing hypotheses about underlying mechanism. This was published for fewer than 15% of

individuals, and so the authors of each study and institutions housing the individuals were contacted. Eighty-eight percent of zoos and 67% of authors contacted supplied information on rearing history. However, birth origin was again only known for a small fraction of these subjects (~15%): only twelve species contained five or more stereotypic subjects of known birth origin. We also requested information as to whether individuals were mother- or hand-reared (which could act as a confound; Mason 1994, Latham & Mason, 2008), and the age at which wild-caught individuals entered captivity (since subjects caught from the wild in infancy can resemble captive-bred animals in adulthood, becoming highly stereotypic: Jones, Mason, & Pillay, 2011). However, this was known for only ~40% of the fraction for whom birth origin was known: a lack of information that greatly compromised data quality. Consequently, the aim of investigating how birth origin interacted with species-level risk potential factors was abandoned, due to concerns about low power and poor data quality.

Finally, data on aspects of husbandry were also extracted from all studies, to check for relationships between husbandry and wild behaviour (see below).

Housing and husbandry data

Some aspects of housing and husbandry conditions could both affect SB and vary systematically across species, potentially being confounds (c.f. Mason, 2010a; Pomerantz et al., 2013). We therefore gleaned data from the publications used to compile the SB database on all variables that could potentially affect SB (Clubb & Vickery, 2006; Morgan & Tromborg, 2007; Shyne, 2006; Swaisgood & Shepherdson, 2005), using these to calculate species medians for: enclosure size (controlling for body mass), daily meal frequency (excluding starve days), and diet diversity (sum of different food types in the diet). The remaining variables were either categorical or ranked. For categorical variables, each species was given a summary value

reflecting the proportion of animals in one of the two categories (Table A2). These variables were social grouping (similar to or different from the wild); meal timing (morning [or morning and afternoon] or afternoon only); presence of weekly starve day (yes/no); meal processing level (entirely processed or with non-processed components like carcasses); and presence of foraging enrichment, as defined by the authors (yes/no or unknown). Ordinal variables were ranked from 1 to 4 (1 being poorest, 4 being best) and were: availability of cover (allowing escape from the view of visitors); and vertical complexity of enclosure (provision of elevated platforms, trees and/or rocks to climb) (Table A2). Species-level summary statistics for each husbandry/housing variable were then analysed for correlations with the potential risk factors using phylogenetic independent contrasts (see Methods). For those found to correlate, the relevant SB analyses were rerun including it as a covariate (see Methods).

Updating the Captive Infant Mortality Database

The original database contained data from the International Zoo Yearbook (1988-2000 editions, 1988 being the lower cut-off because 95% of the SB data came from 1988 or later), and from fur farms, for Clubb and Mason's 33 species. Two little-breeding species (giant pandas; brown hyaenas, *Parahyaena brunnea*) were excluded to leave 31. The International Zoo Yearbook stopped publishing captive infant mortality data in 2000, so could not be used to update values for these 31 species. However, data from the same sources were used to generate values for our 18 new species. Using Clubb and Mason's methods, births and deaths by 30 days of age were recorded. The ratio of deaths over total births for each was calculated for each site (except for leopards and lions, *Panthera pardus* and *P. leo*, for which data were not reported by site due to their large populations). These were used to

calculate species medians (Table A3). Again, species were only included in final analyses if data were available for at least five subjects (here five births, individual mothers or litters being unidentifiable). We also applied to ISIS to obtain fuller, more up-to-date infant mortality data for each species, along with information regarding each mother's birth origin in hope of investigating how birth origin interacted with potential species-typical predispositions (like range size) to influence infant mortality. However we were unsuccessful.

Updating the 'Potential Risk Factors' Database

This originally contained information from a literature search of 18 journals for 1960-1999 inclusive, for the 33 focal species. The aims were to test the ranging, hunting and territoriality hypotheses already mentioned, as well as two further hypotheses: that omnivory could either predict successful adjustment to captivity, or instead put species at risk of 'boredom' (see competing ideas from Boorer, 1972; Morris, 1964; and Ormrod, 1987); and that naturally more active species may be particularly susceptible to SB (Hediger, 1950; McDougall, Reale, Sol, & Reader, 2006; Meyer-Holzapfel, 1968; Morris, 1964; Ormrod, 1987). To retest these hypotheses, wherever possible (in practice for home-range size, trophic level and diet breadth), revised species medians for natural behaviour in the wild were obtained from PanTHERIA (Jones et al. 2009). Territoriality data for our additional 18 species came from Grant (1992). For other variables (kill frequency per 24hrs; hunt frequency per 24hrs; chase distance; distance between kills; daily activity levels; daily foraging time budgets; daily travel distance; minimum home range size), Clubb and Mason's database was updated with new data were obtained by searching all articles in each of the 18 journals used previously, for the past/present scientific names and all common names of our 51 target species. We did this for 1960-2010 for the 18 new species,

and for recent literature only (2000-2010, inclusive) for the 33 original ones. For inclusion, each study had to be at least 10 months long, span multiple seasons, and focus on non-provisioned adults. For estimates of hunting and kill rate a new criterion was added: studies were excluded if estimates did not include observed kills or hunts for *all* prey species (for example, some studies looked at reindeer kills only, omitting other prey). One final modification from the previous Clubb and Mason study was excluding “% vertebrate flesh” as an index of hunting, since distinguishing carrion from live-caught prey in stomach contents was judged too difficult.

To test the new hypotheses about intelligence, we used brain volume as a proxy (Deaner, Isler, Burkart, & van Schaik, 2007; Lefebvre, 2011; Reader, Hager, & Laland, 2011; Schuck-Paim, Alonso, & Ottoni, 2008), obtaining cranial volumes from Finarelli and Flynn (2009) and Swanson, Holekamp, Lundrigan, Arsznov, and Sakai (2012). To test the new hypothesis about vulnerability in the wild as a risk factor, information was obtained from the IUCN Red List (www.iucnredlist.org; Nov 2013). Each IUCN Red List category was given a rank for analysis (1, least concern; 2, near threatened; 3, vulnerable; 4, endangered; 5, critically endangered).

Table A4 lists all variables recorded and the species medians for each, along with the number of species that had data for each variable (Kroshko 2015 gives more details as to how each was calculated). Note that because data for many variables were not available for certain species, final sample sizes were greatly reduced in many analyses.

Statistical Analyses used in Hypothesis-testing

Phylogenetically independent contrasts (Felsenstein, 1985) were calculated using the PDAP module in Mesquite version 2.75 (Maddison & Madisson, 2006), using a recent Carnivora super-tree (Nyakatura & Bininda-Emonds, 2012) that is so well

resolved that no adjustments for polytomies (Garland & Diaz-Uriarte, 1999) were required. Least squares regressions were then run to investigate relationships between each wild variable and SB (total, plus route-tracing only) and captive infant mortality. To do this, contrasts were exported into JMP 10.0, with all regressions forced through the origin (necessary because the signs of each x and y value for contrasts are arbitrary; the regression line must therefore go through the origin because the absolute distance of each contrast from the origin is important [Garland, Harvey, & Ives, 1992]).

Appropriate transformations were used to normalise residuals. Results were also graphed and visually inspected for potential outliers, while for models with multiple independent variables, residuals were examined to identify potential outliers. Potential outliers were then confirmed/rejected using Grubbs' test (<http://graphpad.com>) with alpha set at 0.05 (two-tailed). If confirmed, outliers were removed and data reanalyzed. Results are given as T or F-values depending on JMP's output. Tests were one-tailed in almost all cases, due to clearly directional predictions (see Introduction; Levine & Banas, 2002; Rice & Gaines, 1994). Consequently, trends are typically not reported.

Analyses were typically simple univariate regressions (missing values precluding more complex model-building). The three main exceptions were as follows. First, because many aspects of natural behaviour and biology covary with body mass (Gittleman, 1985), body mass was an important potential confound. Before hypothesis-testing analyses were run, relationships between all potential risk factors and body mass (obtained from PanTHERIA) were therefore determined, three variables being found to correlate positively with body mass: home-range size, daily activity levels, cranial volume and IUCN Red List status. In analyses using these, body mass was therefore included as a covariate in each General Linear Model (GLM), using a sequential sums of squares procedure with the term of interest – the

potential risk factor – placed last, and body mass first (c.f. Doncaster & Davey, 2007). The second set of analyses to use GLMs rather than simple univariate regressions occurred when more than one wild variable proved predictive, and there were biological reasons to believe that these variables might inter-relate. In practice these involved hunting and ranging because the two may inter-relate: compared to herbivorous Carnivora, carnivorous species typically have larger home-ranges (Hendriks, Willers, Lenders, & Leuven, 2009; Kelt & Van Vuren, 2001) and greater daily travel distances (Carbone, Teacher, & Rowcliffe, 2005). Where we wanted to disentangle their relative effects, we therefore ran GLMs with both variables included, to assess which was the main driver of observed effects. Twice, however, these tests would not run as planned due to small sample sizes. To overcome this, these analyses were rerun using *all* species, even those for which data came from four or fewer individuals. These two analyses are clearly indicated in the text (see Results). A third set of GLMs was run when species-typical husbandry covaried with a potential risk factor. Diet breadth, time spent foraging, home-range size, trophic level and territoriality all significantly correlated with at least one value for species-typical husbandry (Table A4). Here, relevant SB analyses were therefore rerun with this husbandry variable included as a covariate (again using sequential sums of squares with the variable of interest as the last term).

Results

Descriptive findings for captive SB and infant mortality

Our literature search increased the number of individuals observed from around 800 (Clubb & Mason, 2007) to over 1,300, and the number of stereotypers from about 270 (Clubb & Mason, 2007) to 450. These spanned all families of the Carnivora,

though data from Felidae predominated (Table A1), with a median study date of 1997. Most SB involved route-tracing: this sub-type occurred in 45 of the 50 stereotypic species, and 78% of the stereotypic individuals performed it. In contrast, only 22% of individuals and 10 species exhibited the other sub-types (stationary or oral SB). In the 23 species with data on five or more stereotypers (representing 417 individual animals), median daily time budgets devoted to SB (of all sub-types) showed great variation, ranging from under 1% to c.55%. In the 21 species with data on five or more individual route-tracers, median daily time budgets devoted to route-tracing were similar, reflecting its status as the main sub-type of SB in Carnivora. The number of births included in the updated Captive Infant Mortality (CIM) Database increased from c. 18,000 (Clubb & Mason, 2007) to over 25,000 through the inclusion of additional species, with more than 8,900 of these infants dying before 30 days (Table A3). For the 49 species with data on five or more births, median CIM values also showed great variation, ranging from 0% (e.g. North American river otter, *Lontra canadensis*) to more than 90% (e.g. Pallas's cat, *Felis manul*).

Predictors of Stereotypic Behaviour

Relationships between each potential risk factor and the severity of total stereotypic behaviour, route-tracing, and captive infant mortality are presented in Table 1. Initially there seemed to be no significant correlations between total stereotypic behaviour and any potential risk factor (Table 1), but once relevant husbandry variables were statistically controlled for (the availability of cover), median home-range size emerged as a predictor (Table 2). The severity of the route-tracing sub-type of SB was, however, far more clearly related to natural behaviour than total SB was: route-tracing was significantly predicted by median home-range size (Figure

1a), daily distance travelled (Figure 1b), and chase distance (Figure 1c) in both initial analyses and those controlling for husbandry variables (Table 2).

*** Tables 1 and 2 about here ***

Were these correlations between stereotypic route-tracing and chase distance, home-range size and daily distance travelled in the wild, three independent effects or an inter-related cluster? To tease apart their relative influence, each variable was regressed against route-tracing while controlling for one of the others (and body mass where appropriate), with the following results. Home-range size remained a predictor of route-tracing when daily travel distance was controlled for ($t_{1,7} = 2.20$, $P = 0.032$). However, daily distance travelled no longer predicted route-tracing when home-range size was controlled for ($t_{1,7} = -1.71$, $P = 0.065$ -- the apparent trend being in the opposite direction to predicted). Planned tests for relationships between route-tracing and chase distance controlling for home-range size, or home-range size controlling for chase distance, could not be run due to lack of data. The same held for models investigating the relative importance of chase distance and daily distance travelled. Therefore data from stereotypic individuals of *all* species, regardless of the number of individuals contributing to the species median, were now included and these three sets of analyses rerun. Sample sizes were still very small, and so here we do present trends. Chase distance remained a predictor of route-tracing after controlling for home-range size ($t_{1,4} = 2.18$, $P = 0.048$), and home-range size still tended to predict route-tracing after controlling for chase distance ($t_{1,4} = 1.90$, $P = 0.065$). Chase distance also tended to still predict route-tracing when daily travel distance was controlled for ($t_{1,3} = 1.73$, $P = 0.091$). However, daily travel distance stopped predicting route-tracing when chase distance was controlled for ($t_{1,3} = -0.11$, $P = 0.460$). Finally, following Clubb and Mason (2003;

2007), we investigated the relationship between route-tracing and home-range size and body mass together, to determine if being heavy with a large home-range size is a greater risk factor than just being wide-ranging. This combination was highly significant ($F_{2,13} = 19.13$, $P < 0.0001$): far more so than effects of home-range partialling out body mass (Tables 1 and 2), and despite body mass alone (i.e. independent of its effects on range size) not predicting route-tracing ($F_{2,13} = 0.427$, $p > 0.1$).

Predictors of Captive Infant Mortality

There were no significant correlations between the potential risk factors and CIM (Table 1). To replicate Clubb and Mason, and mirror the analyses conducted for SB, we assessed whether home-range size and body mass together predict infant mortality. This model was significant ($F_{2,26} = 3.633$, $P = 0.021$), with large, wide-ranging carnivores having higher CIM. However, unlike the case for SB, within this model the relationship between infant mortality and body mass was highly significant ($t_{1,26} = 2.70$, $P = 0.006$, one-tailed) and appeared to be the sole variable driving this relationship. Minimum home-range sizes gleaned from the literature were also assessed as predictors (Table A4), since these had a particularly strong relationship with CIM in the previous research (Clubb & Mason 2003). However this was still not significant ($t_{1,20} = -1.10$, $P = 0.143$). Various measures of infant development (e.g. altriciality) at birth were investigated as potential confounds, but still no effects were observed (see Kroshko 2015 for details).

To then investigate whether related species actually varied in CIM (an underlying assumption of our approach), data were split by family, and species effects on CIM (site being used as the unit of replication; *P. leo* and *P. pardus* were therefore excluded) were analysed with Kruskal Wallis tests (since data could not be

normalized). There were no significant effects within Phocidae or Mustelidae, but species differed in CIM within Ursidae ($\chi^2_{1,7} = 24.54$, $P = 0.0009$) and Canidae ($\chi^2_{1,4} = 12.09$, $P = 0.0167$) (with a weak potential tendency within Felidae: $\chi^2_{1,21} = 30.03$, $P = 0.091$).

Discussion

Before discussing our significant findings, we review the non-significant ones, and consider some limitations in our analyses. Mirroring the previous study (Clubb & Mason, 2003; Clubb & Mason 2007), territoriality and being highly active in the wild did not seem to predict SB, and the same held for many aspects of foraging (chase distance being the one new exception). Furthermore, two new hypotheses, that IUCN Red List status would predict welfare problems, as would being of high or low intelligence (estimated from cranial volume), also appeared to have no predictive value. In some instances, these non-significant results could just reflect low statistical power (e.g. for distance between kills, we had data for just five stereotypic species). Data quality issues could also have obscured effects. For example, although we eliminated species whose data came from four or fewer subjects, this criterion far from guarantees accurate values for species-typical SB. Furthermore, despite controlling for husbandry as best we could in SB analyses, we were often hampered by insufficient details in published papers. So, before confidently rejecting the various unsupported hypotheses, it might be wise to retest them once more data have accumulated in the literature. The ideal future dataset would contain fuller information on husbandry, SB data for far more species, and larger sample sizes per species. Future research could also refine the predictor variables when re-testing some hypothesised risk factors. For example, the idea that IUCN Red List status predicts captive welfare arose from suggestions that high timidity and low behavioural

plasticity predict both poor abilities to cope with anthropogenic threat in the wild and poor abilities to adapt to captivity (Mason et al., 2013). Gleaning data on habitat breadth and other proxies of behavioural plasticity, as well as flight distance (cf. Møller, 2008) or other measures of timidity, might therefore be more fruitful (since measures of overall threat status will reflect both intrinsic risk factors -- the interest here -- *and* extrinsic ones that are less likely to be relevant to captive animals).

Re-thinking which aspects of natural biology may act as risk factors is even more important for understanding captive infant mortality. Home-range size, daily distance travelled and territoriality, previously shown to predict captive infant mortality, now did not. Unfortunately we cannot tell whether the original published effects were Type I errors, or the new non-significant findings are Type II errors. Furthermore, no other variable tested predicted CIM, save, unexpectedly, body mass. Whether this unexpected relationship between species-typical body mass and CIM is robust, or merely an artifact of these infants being easier to count and monitor, will need more research. Pending this future work, being unable to confidently identify predictors of CIM has two frustrating implications. The first is that we cannot shed light on the fundamental causes of species differences in captive infant mortality, despite great variation, at least within Ursidae and Canidae. This is problematic: infant mortality levels were high (at least up to 2000), and likely greater than one would expect in the wild or captive breeding centres (Clubb & Mason 2007, Curry et al. 2015, Diez-Leon & Mason 2016). We therefore suggest this as an urgent topic for future work, one best addressed using both a broader range of species-typical potential risk factors, and ISIS data on infant mortality (more current and comprehensive than International Zoo Yearbook values). The second implication is that this makes it difficult to interpret our significant SB results -- the predictive effects of ranging and hunting behaviour, as discussed below -- in terms of overall welfare. Ample evidence shows that SB reflects poor lifetime well-being (e.g. Gottlieb,

Captanio, & McCown, 2013; Mason & Rushen, 2006), but SB can be insensitive as a welfare indicator because not all individuals or species develop it when stressed, some displaying inactivity instead (e.g. Cabib, 2006; Fureix & Meagher, 2015; Mellor, Hunt, & Gusset, 2015; Fureix et al. 2016). Thus while the presence of SB indicates poor welfare (here, as we show, linked to certain life-history traits of species in the wild), the absence of SB does not guarantee good welfare. To therefore assess whether species with small ranges and negligible chase distances have better overall captive welfare, not just lower SB, analyses that regress these species-level risk factors against other potential welfare indicators are needed, ideally run by researchers with access to ISIS data. Such indicators might include infant mortality again, but repeated using better quality data; fertility (cf. Janczak, Pedersen, Rydhmer, & Bakken, 2003; Wingfield & Sapolsky, 2003); and/or measures reflecting how likely zoo Carnivora are to survive into old age (cf. Clubb et al., 2008; Mueller et al., 2011).

Turning to our significant results, we successfully replicated previous findings that species like polar bears, grizzly bears, caracals and others with naturally long daily travel distances and large home ranges (combined with body mass) are at risk of SB. These variables predicted how severely affected stereotypic individuals were (a measure that, in primates, co-varies with true population-level average SB time-budgets: Pomerantz et al., 2013). Our results also now revealed that this effect is independent of body mass, and stronger for stereotypic route-tracing than for all SBs combined. Furthermore, the daily travel distance effect proved to be just a side-effect of the home range effect (vanishing when range size was statistically controlled for) – suggesting that relevant aspects of wide-ranging lifestyles that predict SB do not include active travelling: a topic revisited below. Our findings join some new, broadly concordant results from other taxa. In several species where males have larger home ranges than females, males also show more route-tracing in captivity (Bennett,

et al. 2015); and in comparative analyses of zoo primates, how far a species typically travels each day in the wild tended to predict the time budgets they spent route-tracing, though, in this taxon, irrespective of range size (Pomerantz et al., 2013).

In addition, we newly found that species with long average chase distances in the wild (e.g. cheetahs, and canids like the coyote) are also vulnerable to more severe route-tracing: the first comparative evidence implicating hunting behaviour in pacing and similar SBs. As far as we could ascertain, the chase distance and home range effects on route-tracing were independent. These results do need treating with caution, being based on few species and thence few contrasts. However, the importance of aspects of hunting is further indicated by strong circumstantial evidence from our analyses: the significance of the overall model combining body mass and home range size was very high (far higher than for range size alone, or any other risk factor). This is relevant because, as a rule, carnivore body mass predicts hunting strategy (independently of its relationship with home-range size; Hendriks, Willers, Lenders, & Leuven, 2009; Nilsen & Linnell, 2006), with larger, heavier species feeding on larger prey, and expending more energy on the hunting of each (Carbone et al., 2007). Thus, although further research is needed here, together this does suggest that attributes of natural foraging niche relating to hunting help determine the severity of route-tracing. If hunting style does indeed complement ranging by being a second risk factor, then one possibility is that these two risk factors predict two distinct types of SB within the route-tracing category. Detailed data on the precise morphologies, locations and timings of SB (e.g. Cless, 2015; Dixon, Duncan, & Mason, 2008) would be needed to test this idea. Instead, another possibility is that chase distance and home-range size have additive effects on a common behavioural outcome, both predicting the same types of route-tracing. The explanations for such additive effects could be motivational, with both aspects of natural behaviour combining to elevate motivations to escape the enclosure (cf.

Clubb & Vickery 2006); or instead neurological, with both forms of deprivation combining to cause impaired brain function. Seeing how species-typical risk factors interact with birth origin (as presented earlier) could be one way to investigate this in the future.

Overall however, regardless of such mechanistic details, these two species-typical predictors of stereotypic route-tracing do suggest that within Carnivora, aspects of being naturally wide-ranging and a pursuit predator cannot readily be relinquished, even when humans address an animal's homeostatic needs. These may therefore be 'behavioural needs': "activities that animals have instinctive, intrinsic propensities to perform ... even when the physiological needs that the behaviour serves are fulfilled, and even when these behaviours are not [now] necessary for fitness" (Mason & Burn, 2011). More precisely identifying the nature of these needs is fundamentally interesting; important for animal welfare; and useful for any zoo wanting to reduce SB by replacing it with more naturalistic activities (e.g. Mellor et al. 2015). The best approach for both identifying what these specific behavioural needs are, and creating effective 'environmental enrichments' (sources of stimulation and outlets for highly motivated behaviour that improve captive welfare and reduce SB) will be to now combine further comparative studies with experimental work in zoos. For example, our data suggest that the relationship between home-range size and SB is mediated by aspects of a wide-ranging lifestyle other than active locomotion. These might include, for example, needs for novelty (since wide-ranging animals are often semi-nomadic, covering only a tiny fraction of their annual ranges each day); for control (since wide-ranging carnivores often facultatively shift location in response to resource availability); or for multiple different denning sites (Clubb & Mason, 2003; Clubb & Mason, 2007). The further use of comparative methods could thus help assess whether these aspects of ranging confer risk, by exploring the predictive power of species' ratios of day range to annual range, the

annual numbers of denning sites used, how often animals completely shift location per year, and measures of the habitat diversity experienced by individuals. In parallel, experimental, enrichment-oriented studies in zoos could investigate whether captive carnivores with naturally large home ranges particularly benefit from having multiple denning sites; being able to explore; gaining access to novel environments; viewing novel/variable vistas; or being able to control/modify their own enclosures. Turning to chase distance, to better understand *this* predictive trait and use it to design better ways to enrich enclosures, future comparative studies should investigate the predictive roles of the gaits that different species typically use when hunting; the peak speeds they attain during chases; and the killing methods typically used in the wild. Complementary experimental, enrichment-oriented research in zoos could likewise explore whether carnivores with long chase times are particularly motivated to express sustained appetitive pre-feeding behaviour (e.g. via opportunities to chase moving objects; Quirke, O'Riordan, & Davenport, 2013), or to perform particular forms of consummatory behaviour (perhaps as allowed by feeding large whole carcasses). Thus, inspired by our comparative findings, we hope such ideas for experiments could ultimately result in feasible, imaginative, evidence-based enrichments that tackle route-tracing effectively.

Conclusions

Our comparative evidence supports the hypotheses that aspects of wild hunting behaviour (long prey chase distances) and ranging behaviour (large home range sizes) are independent risk factors for stereotypic route-tracing in captive Carnivora. Further research should now pinpoint the specific components of hunting or ranging that are the key, partly to reveal which have evolved to be 'behavioural needs', and partly for practical reasons, to help create the best captive environments and most

effective enrichments for these animals. Further research is also needed to explain why captive Carnivora vary so greatly in their infant mortality levels.

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864 Table 1. Relationships between species-level potential risk factors and stereotypic
865 behaviour (total, plus route-tracing only), and captive infant mortality.

Hypothesis: Problems in captivity stem from ...	Species-level potential risk factor	Total stereotypic behaviour	Stereotypic route-tracing	Captive infant mortality
Natural foraging behaviour	Time spent foraging in the wild (% 24 hour)	$t_{1,5}=-0.46, P=0.334^c$	$t_{1,5}=-0.35, P=0.370^c$	$t_{1,8}=-1.02, P=0.168^c$
	Trophic level	$t_{1,20}=0.67, P=0.255$	$t_{1,17}=0.43, P=0.338^c$	$t_{1,44}=0.12, P=0.453$
	Chase distance (m)	<i>Only data for route-tracing</i>	$t_{1,3}=4.21, P=0.012 (+)$	$t_{1,6}=0.10, P=0.463$
	Distance between kills (km)	$t_{1,3}=1.96, P=0.145$	$t_{1,3}=1.31, P=0.283$	$t_{1,4}=-1.35, P=0.248$
	Hunt frequency (per 24 h)	<i>Only data for route-tracing</i>	$t_{1,4}=1.19, P=0.149^c$	$t_{1,5}=0.31, P=0.383^c$
	Kill frequency (per 24 h)	$t_{1,5}=1.56, P=0.089$	$t_{1,4}=1.32, P=0.129$	$t_{1,8}=0.44, P=0.336$
	Diet breadth (number of diet categories consumed)	$t_{1,19}=0.43, P=0.668^{c,d}$	$t_{1,17}=1.54, P=0.143^{c,d}$	$Tt_{1,44}=0.51, P=0.611^d$
Naturally high activity levels	Time spent active in the wild (% 24 h)	$t_{1,13}=0.08, P=0.470^a$	$t_{1,12}=0.58, P=0.288^a$	$t_{1,19}=-1.31, P=0.103^{a,c}$
Natural ranging behaviour	Home-range size (km ²)	$t_{1,14}=1.66, P=0.060 (+)$ ^a	$t_{1,13}=3.42, P=0.002 (+)$ ^a	$t_{1,26}=-1.64, P=0.056 (-)^{a,b,c}$
	Daily distance travelled in the wild (km)	$t_{1,11}=0.35, P=0.367$	$t_{1,10}=2.00, P=0.037 (+)$	$t_{1,16}=1.15, P=0.133^c$
Territorial patrolling	Territoriality	<i>Only data for route-tracing</i>	$t_{1,5}=-0.29, P=0.390^c$	$t_{1,10}=1.16, P=0.136$
Vulnerability in the wild	IUCN status	$t_{1,19}=-0.25, P=0.405^a$	$t_{1,19}=-0.48, P=0.317^a$	$t_{1,41}=0.06, P=0.478^a$
Intelligence	Relative cranial volume (brain size)	$t_{1,16}=1.45, P=0.167^{a,d}$	$t_{1,14}=-1.43, P=0.174^{a,d}$	$t_{1,36}=0.18, P=0.860^{a,d}$

Analyses looking at the relationship between species-level potential risk factors and stereotypic behaviour have a maximum of 23 species included; those for captive infant mortality tests contain data on up to 49 species. Tests that reached significance are shown in bold. All p-values are one-tailed unless otherwise indicated.

^a Body mass controlled for; ^b Trend in opposite direction of prediction; ^c Outlier removed; ^d Two-tailed tests performed on this variable as there was no directional prediction.

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Table 2. Relationships between species-level potential risk factors and stereotypic behaviour (total, and route-tracing only), re-calculated controlling for confounding aspects of species-typical husbandry

Species-level potential risk factor	Species-typical husbandry/rearing variable needing to be statistically controlled for	Results of analyses controlling for this confound, for total SB	Results of analyses controlling for this confound, for route-tracing SB
Diet breadth	Foraging enrichment	$t_{1,15}=0.02, P=0.984^b$	$t_{1,13}=-1.98, P=0.069^b$
Time spent foraging in the wild	Foraging enrichment	$t_{1,4}=-0.04, P=0.484$	$t_{1,4}=-1.50, P=0.104$
Home-range size	Cover	$t_{1,7}=1.97, P=0.044 (+)^a$	$t_{1,7}=2.86, P=0.012 (+)^a$
Trophic level	Foraging enrichment	$t_{1,15}=-1.23, P=0.118$	$t_{1,13}=-0.80, P=0.220$
Territoriality	Meal frequency	Insufficient data	Insufficient data

All *P*-values are one-tailed unless otherwise indicated

^a Body mass controlled for
^b Two-tailed tests performed on this variable

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870 **Figure 1:** (a) Relationship between the median time stereotypers
871 spend route-tracing and median natural home-range size (km²), controlling
872 for body mass; (b) relationship between the median time stereotypers
873 spend route-tracing and median daily distance travelled in the wild; (c)
874 relationship between the median time stereotypers spend route-tracing
875 and median chase distances made while hunting (m). Each datapoint
876 represents an independent contrast between two species or ancestral
877 nodes (for test statistics see Table 1).

879 Table A1. Species medians for stereotypic behaviour (SB): total, plus route-tracing only

Species	In original Clubb & Mason database? Y = yes; N = no, thus new species	Median total SB (affected animals only): % observations	No. of affected animals	Median route-tracing SB (affected animals only): % observations	No. of affected animals
<i>Acinonyx jubatus</i>	Y	24.60	8	24.60	8
<i>Ailuropoda melanoleuca</i>	Y	4.50	4	5.25	3
<i>Canis latrans</i>	N	N/A		N/A	
<i>Canis lupus</i>	N	N/A		N/A	
<i>Caracal caracal</i>	Y	14.74	10	14.74	10
<i>Catopuma temminckii</i>	N	23.56	5	23.56	5
<i>Eumetopias jubatus</i>	N	N/A		N/A	
<i>Felis chaus</i>	Y	12.45	3	12.45	3
<i>Felis manul</i>	N	N/A		N/A	
<i>Felis margarita</i>	Y	12.68	9	12.68	9
<i>Felis nigripes</i>	N	N/A		N/A	
<i>Felis silvestris</i>	Y	1.50	2	1.50	2
<i>Genetta tigrina</i>	Y	8.30	1	8.30	1
<i>Halichoerus grypus</i>	N	54.64	11	54.64	11
<i>Helarctos malayanus</i>	N	25.59	18	24.65	4
<i>Hyaena brunnea</i>	Y	24.70	1	24.70	1
<i>Leopardus colocolo</i>	N	24.50	2	24.50	2
<i>Leopardus geoffroyi</i>	Y	11.50	9	11.50	9
<i>Leopardus pardalis</i>	Y	6.46	18	6.46	18
<i>Leopardus wiedii</i>	Y	12.49	4	12.49	4
<i>Leptailurus serval</i>	Y	8.74	6	8.74	6
<i>Lontra canadensis</i>	Y	4.34	2	4.07	2
<i>Lontra longicaudis</i>	N	26.00	2	26.00	2
	N	6.25	2	6.25	2
<i>Lynx canadensis</i>					
<i>Lynx lynx</i>	Y	10.83	10	10.83	10
<i>Martes foina</i>	N	N/A		N/A	
<i>Melursus ursinus</i>	Y	16.76	5	15.49	5
<i>Nasua nasua</i>	N	22.74	2	43.48	1
<i>Neophoca cinerea</i>	N	23.29	2	23.29	2
<i>Neovison vison</i>	Y	N/A		N/A	
<i>Odobenus rosmarus</i>	N	51.27	4	51.27	4
<i>Panthera leo</i>	Y	9.50	10	9.50	10

<i>Panthera onca</i>	Y	18.69	18	18.69	18
<i>Panthera pardus</i>	Y	10.42	27	10.42	27
<i>Panthera tigris</i>	Y	12.96	28	12.96	28
<i>Phoca vitulina</i>	N	51.15	10	51.15	10
<i>Potos flavus</i>	Y	57.20	1	57.20	1
<i>Prionailurus bengalensis</i>	Y	11.00	4	11.00	4
<i>Prionailurus viverrinus</i>	Y	9.17	3	9.17	3
<i>Puma concolor</i>	Y	33.88	2	33.88	2
<i>Puma yagouaroundi</i>	Y	7.42	3	6.04	1
<i>Suricata suricatta</i>	Y	10.00	5	10.00	5
<i>Tremarctos ornatus</i>	Y	36.00	1	36.00	2
<i>Uncia uncia</i>	Y	6.20	20	N/A	
<i>Ursus americanus</i>	Y	15.06	1	15.06	1
<i>Ursus arctos</i>	Y	19.90	8	19.90	8
<i>Ursus maritimus</i>	Y	21.87	79	29.78	26
<i>Ursus thibetanus</i>	Y	7.13	50	3.81	14
<i>Vulpes lagopus</i>	N	0.55	42	0.55	42
<i>Vulpes vulpes</i>	Y	0.16	11	0.16	11
<i>Vulpes zerda</i>	N	9.68	4	9.68	4
Total # species with N ≥ 5		23		21	

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891 Table A2: Species summary statistics for husbandry and housing variables (please see text for details)

Species	Median study date	Median enclosure size (m ²)	Median cover (ranked)	Median vertical complexity (ranked)	Social grouping (% 'yes')	Median meal frequency (per day)	Typical meal timing (% AM/AM+PM)	Median diet diversity (sum)	Starve day (% 'no')	Processed food? (% 'yes')	Foraging enrichment (% 'no/unknown')
Acinonyx jubatus	1996	1150	3	3	0.64	1	0.29		1	0.33	0.92
<i>Ailuropoda melanoleuca</i>	1990	241.7	3	3	1			3		1	1
<i>Canis latrans</i>	2009	1000	3	2	1	1	1		1		1
<i>Canis lupus</i>	2001										
Caracal caracal	1991		2	3.5							1
Catopuma temminckii	2002.5										1
<i>Eumetopias jubatus</i>	1998				1	3	1		1		1
<i>Felis chaus</i>	1997.5										
<i>Felis manul</i>	1998										
Felis margarita	1990.5		4	2							1
<i>Felis nigripes</i>	1998										
<i>Felis silvestris</i>	1998										
<i>Genetta tigrina</i>	1990										
Halichoerus grypus	2000	162			1	2	1		1		1
Helarctos malayanus	2001	20	2	3		1	0.31	3	1	0.31	0.78
<i>Hyaena brunnea</i>	1980										
<i>Leopardus colocolo</i>	1998										
Leopardus geoffroyi	1993		1.5	3			0		1	0	1
Leopardus pardalis	1997.5	41.8	4	4		1	0.91	1	1	0.15	1
<i>Leopardus wiedii</i>	1999.5	11	3	4							1
Leptailurus serval	1998		4								1
<i>Lontra canadensis</i>	2008										
<i>Lontra longicaudis</i>	2001										
<i>Lynx canadensis</i>	1998										

Lynx lynx	1997										1
<i>Martes foina</i>	1993	2.97	2	3		1	0	1	1	1	1
Melursus ursinus	1992										1
<i>Nasua nasua</i>	1996										
<i>Neophoca cinerea</i>	2010										
<i>Neovison vison</i>	1994		2	1	1	1	0.95	1	1	1	1
<i>Odobenus rosmarus</i>	1989										
Panthera leo	1998	164	3	2	0.82	1	0.14	1	0.47	0.16	0.84
Panthera onca	1997	70	3	4	0.30				0.09	0.05	0.92
Panthera pardus	1997	106.26	2	3.5	0.35	1	0.48	1	0.19	0	0.85
Panthera tigris	1997	1080	3	3	0.14	1	0.09	1	0.37	0.33	0.94
<i>Phoca vitulina</i>	2001.5				1						1
<i>Potos flavus</i>	1990										
<i>Prionailurus bengalensis</i>	1993	5.85		3		1		2.5	1	1	1
<i>Prionailurus viverrinus</i>	1995.5										1
<i>Puma concolor</i>	2007										1
<i>Puma yagouaroundi</i>	2001		3								1
Suricata suricatta	1989		2	3	1	1	0	2	1		1
<i>Tremarctos ornatus</i>	2000.5										
Uncia uncia	1997	152		4	0.13				0	0	0.87
<i>Ursus americanus</i>	1991										
Ursus arctos	1997	890	2	2		2	0.9	2.5	1	0.25	0.8
Ursus maritimus	1995	700	1	2	0.14	2	0.75	5		1	0.86
Ursus thibetanus	2003	10000	4	4		2	0.78	3	1	0.78	0.23
Vulpes lagopus	1999.5										
Vulpes vulpes	2001										
<i>Vulpes zerda</i>	1989										1
Total # species		17	21	21	14	16	16	13	18	16	32

Table A3: Species median values for captive infant mortality (CIM)

Species	Median CIM (% infants dying within 30 days)	No. of births
<i>Acinonyx jubatus</i>	25.00	844
<i>Canis latrans</i>	44.44	30
<i>Canis lupus</i>	20.00	2061
<i>Caracal caracal</i>	27.27	406
<i>Catopuma temminckii</i>	16.67	30
<i>Eumetopias jubatus</i>	46.43	26
<i>Felis chaus</i>	40.00	395
<i>Felis manul</i>	90.91	45
<i>Felis margarita</i>	20.00	121
<i>Felis nigripes</i>	1.32	113
<i>Felis silvestris</i>	28.57	886
<i>Genetta tigrina</i>	21.05	36
<i>Halichoerus grypus</i>	33.33	125
<i>Helarctos malayanus</i>	40.00	60
<i>Leopardus colocolo</i>	56.25	16
<i>Leopardus geoffroyi</i>	33.33	147

<i>Leopardus pardalis</i>	28.57	328
<i>Leopardus wiedii</i>	25.00	51
<i>Leptailurus serval</i>	40.91	773
<i>Lontra canadensis</i>	0.00	89
<i>Lontra longicaudis</i>	63.64	14
<i>Lynx canadensis</i>	19.09	137
<i>Lynx lynx</i>	24.04	904
<i>Martes foina</i>	0.00	25
<i>Melursus ursinus</i>	33.33	71
<i>Nasua nasua</i>	29.15	1523
<i>Neophoca cinerea</i>	8.33	7
<i>Neovison vison</i>	3.71	269
<i>Odobenus rosmarus</i>	33.33	6
<i>Panthera leo</i>	42.16	2552
<i>Panthera onca</i>	20.00	494
<i>Panthera pardus</i>	25.00	580
<i>Panthera tigris</i>	33.33	2292
<i>Phoca vitulina</i>	19.05	390
<i>Potos flavus</i>	0.00	114
<i>Prionailurus bengalensis</i>	33.33	892
<i>Prionailurus viverrinus</i>	28.57	209

<i>Puma concolor</i>	25.00	586
<i>Puma yagouaroundi</i>	16.67	133
<i>Suricata suricatta</i>	36.84	1983
<i>Tremarctos ornatus</i>	31.67	148
<i>Uncia uncia</i>	14.29	546
<i>Ursus americanus</i>	11.11	281
<i>Ursus arctos</i>	0.00	1005
<i>Ursus maritimus</i>	64.71	263
<i>Ursus thibetanus</i>	12.50	250
<i>Vulpes lagopus</i>	17.20	575
<i>Vulpes vulpes</i>	22.22	599
<i>Vulpes zerda</i>	55.00	316

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