OPEN ACCESS

University of BRISTOL

Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlager, A., & Mason, G. (2016). Stereotypic route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles. Animal Behaviour, 117, 197-209. DOI: 10.1016/j.anbehav.2016.05.010

Peer reviewed version

Link to publication record in Explore Bristol Research

PDF-document

University of Bristol - Explore Bristol Research

General rights

1   **Stereotypic route-tracing in captive Carnivora is predicted by species-typical**

2   **home range sizes and hunting styles**

3

4   **Abstract**

5   In captive conditions (e.g. zoos), some Carnivora species typically show negligible

6   stereotypic behaviour (SB) and reproduce successfully, while others tend to

7   reproduce poorly and be very stereotypic. We used comparative methods to identify

8   species-level risk factors for SB and captive infant mortality (CIM). Candidate

9   predictor variables were natural ranging behaviour, territoriality, aspects of natural

10   foraging, wild activity levels, cranial volume, and IUCN Red List status. Previous

11   research had identified naturally long daily travel distances, and being large-bodied

12   and wide-ranging, as SB risk factors. We nearly doubled the size of this original SB

13   database, and then imposed stricter quality controls (e.g. on minimum sample sizes

14   for inclusion). Analysing the resulting 23-species dataset confirmed naturally large

15   ranges and travel distances as risk factors. It also showed that the range size effect:

16   is independent of body mass (although body mass and range size together predicted

17   SB most strongly); is stronger for stereotypic route-tracing (e.g. pacing) than for all

18   SB forms combined; and explains the apparent daily travel distance effect (which

19   vanished when range size was controlled for). Furthermore, a new finding emerged:

20   that naturally long chase distances during hunts also predicted more severe route-

21   tracing. Turning to CIM, previous research had also identified naturally long travel

22   distances and large home ranges as risk factors. We failed to replicate this, or to

23   confidently identify any species-level risk factor (despite CIM significantly varying

24   between related species, at least for Canidae and Ursidae). Understanding what

25   underlies high species-typical CIM thus requires more current data, and further

26   research. Overall, naturally wide-ranging Carnivora with long chase distances are

27   thus most prone to extensive stereotypic route-tracing in captivity. This suggests that

28   captive carnivores cannot relinquish aspects of ranging and pursuit hunting, even

1

29   when their homeostatic needs are met; and also suggests new strategies for

30   environmentally enriching their enclosures more effectively.

31

32

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).

65   Here we apply comparative methods to investigate why Carnivora differ so

66   greatly in their responses to captivity. For example, they vary in susceptibility to

67   abnormal behaviours such as stereotypic pacing. Within the Ursidae for instance,

68   pacing is rare in brown bears (*Ursus arctos*), yet prevalent and often time-consuming

69   in polar bears (*Ursus maritimus*) (Clubb & Mason, 2007). Furthermore, while some

70   captive Carnivora reproduce readily (e.g. American mink, *Mustela vison*; brown bears

71   [Joergensen, 1985; Malmkvist, Gade, & Damm, 2007]), others are prone to breeding

72   problems including high rates of acyclicity (e.g. black-footed cats, *Felis nigripes*) and

73   infant mortality (e.g. black-footed ferrets, *Mustela nigripes*; giant pandas, *Ailuropoda*

74   *melanoleuca*) (reviewed Diez-Leon et al., 2013, Diez-Leon & Mason 2016; Curry,

75   Safayi, Meyerson, & Roth, 2015). These responses are all affected by stress

76   (reviewed e.g. Clubb et al., 2009, Mason & Veasey 2010), suggesting species

77   differences in typical welfare (where welfare means well-being or affective state;

78   Dawkins, 1990; Mason & Mendl, 1993). The Carnivora is an ideal group to apply

79   comparative methods to because all of its 286 species (Nyakatura & Bininda-

80   Emonds, 2012) are held in zoos (Conde, Flesness, Colchero, Jones, & Scheuerlein,

81   2011); this is important because species are the units of replication in such analyses.

82   Furthermore, they are well studied in the wild, where they exhibit great diversity in

83   natural ecology and life history (Gittleman, 1986a, 1986b) (including varying in diet,

84   from herbivory [e.g. giant pandas; kinkajous, *Potos flavus*]) through to relying on live

85   prey [e.g. tigers, *Panthera tigris*]): variation that facilitates testing hypotheses about

86   risk factors.

87   Our research updates work conducted over a decade ago. Clubb and Mason

88   (2003) used a dataset on 33 species that was finalised in 1999, to identify species-

89   typical risk factors predicting levels of stereotypic behaviour (SB) and infant mortality

90   in captive Carnivora. They found that the extent to which species ranged in the wild

91   predicted their captive welfare: naturally long daily travel distances, and the

4

92 combination of being large-bodied and wide-ranging, were risk factors for SB; while

93 naturally long daily travel distances, large home ranges and also being territorial

94 were risk factors for elevated infant mortality. No aspect of natural foraging

95 behaviour, in contrast, appeared to predict welfare. The three principle reasons to

96 now replicate and expand upon this research are described below.

97   First, several recent developments allowed inclusion of more species,

98 potentially giving new analyses greater power. For example, a previous culture of

99 excluding Pinnipeds had become outdated (Bininda-Emonds & Gittleman, 2000;

100 Bininda-Emonds, Gittleman, & Kelly, 2001), allowing these to be included. Many

101 additional publications on captive carnivores had also accumulated since 1999, while

102 an expanded International Species Information System (www.isis.com) run by the

103 zoo community potentially enabled greater access to quality zoo data on

104 reproductive issues. Furthermore, a comprehensive source of data on natural

105 ecology and behaviour variables now existed: the 'PanTHERIA' database (Jones et

106 al., 2009). Secondly, some hypotheses previously rejected by the original study

107 nevertheless seemed supported by growing experimental evidence, making it worth

108 re-testing them with a more powerful dataset. In particular, stereotypic route-tracing

109 (e.g. pacing) had long been hypothesised to derive from frustrated hunting (Clubb &

110 Vickery, 2006; Hoenig & Gusset, 2010; Jenny & Schmid, 2002; Mason & Mendl,

111 1997), an idea persistently supported by its timing (a marked pre-feeding peak) and

112 successful reduction with foraging-based enrichment (e.g. Clubb & Vickery, 2006;

113 Hoenig & Gusset, 2010).

114   Finally, the third reason to update the original work was that three new,

115 testable hypotheses had been advanced since Clubb & Mason (2003). One was that

116 species at risk to anthropogenic changes in the wild are more vulnerable in captivity

117 (Mason, 2010b; Mason et al., 2013; Martin, Lurbiecki, Joy, & Mooers, 2014).

118 Consistent with this, as well as being prone to welfare issues in captivity, wide-

5

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

146 We updated the three databases compiled by Clubb & Mason (2003): a Captive

147 Carnivore Stereotypic Behaviour Database, and, for the species listed within this, a

148 Captive Infant Mortality and 'Potential Risk Factors' Database.

149

150 *Updating the Captive Carnivore Stereotypic Behaviour Database*

151 Data from 2000-2010 inclusive were added from Zoo Biology and International Zoo

152 Yearbooks, following Clubb and Mason (2003; 2007)'s methods. Additionally, all

153 issues, from the first to 2010 inclusive, of the publication Shape of Enrichment, and

154 all International Conference on Environmental Enrichment abstracts were

155 systematically searched, as were abstracts in three further journals: Animal Welfare,

156 Applied Animal Behaviour Science, and Journal of Applied Animal Welfare Science

157 (which publish many relevant studies; Shyne, 2006; Walker, Diez-Leon, & Mason,

158 2014). As previously, studies were included only if meeting certain criteria: the

159 observation period was at least one day; subjects were adults, and not food

160 restricted or – to avoid transient novelty effects – affected by recent changes in group

161 structure or husbandry. Studies were also excluded if deemed poor quality (e.g.

162 using inconsistent data recording), or – a new criterion not used by Clubb and Mason

163 – if individuals had been selectively bred for high or low stereotypic behaviour

164 (relevant for American mink, *Neovison vison*). About 60 additional new studies met

165 all these criteria. In addition, individual information such as each animal's ISIS

166 'accession number' (an identity code), name, birthdate and sex, was used to identify

167 recurring observations of the same subjects (common for zoos where repeated

168 studies were conducted by undergraduates). Such duplicates affected ~24% of

169 studies; when found, a mean value for stereotypic behaviour was calculated for

170 relevant individuals, to ensure the final database had only one entry per subject.

171   This first update yielded 18 new species (Table A1). This resulting set of 51

172   species became the focus of the two subsequent databases. However, like Clubb

173   and Mason, for this first database we focussed on stereotypic individuals only,

174   because study biases towards stereotypers would inflate population-level estimates

175   of prevalence or average time budgets, rendering them unreliable. Subsequent

176   analyses thus investigate average time budgets for stereotypic individuals only, since

177   these values could be well-estimated. Data on this measure, henceforth called the

178   'severity' of stereotypic behaviour (defined as the average % observation time spent

179   in SB), were available for 42 species (Table A1). Of these, species were only

180   included in final analyses if data were available for at least five stereotypic

181   individuals: a stricter criterion than that used by Clubb and Mason. This new cut-off

182   criterion follows precedents set by Thorpe, Black, & Malhotra (1996), Clubb and

183   Mason for their infant mortality studies, and a recent comparative analysis of parrot

184   welfare (McDonald Kinkaid, 2015); and was applied to enhance the accuracy of

185   species estimates, while also allowing retention of a fair number of species (23). For

186   each of these 23 species, median values of stereotypic behaviour (SB) were

187   calculated (study means being calculated from individual means, and these used to

188   calculate species medians). Wherever possible, SB was also categorized as to

189   whether it involved route-tracing (e.g. circling, linear pacing, or the following of any

190   fixed, repeated path); or instead was 'stationary' (i.e. performed in one spot, for

191   example: digging, rocking, head-rolling) or 'oral' (i.e. involving jaws, tongue and/or

192   lips, e.g. sucking, fur chewing, regurgitation). The aim was to calculate median

193   values for each sub-type, but in practice, forms other than route-tracing were so rare

194   that a median was only calculated for this one sub-type (Table A1).

195   Where possible, each subject's birth origin (wild-caught versus captive-bred)

196   was recorded, to investigate how such effects interacted with birth origin, for testing

197   hypotheses about underlying mechanism. This was published for fewer than 15% of

8

198 individuals, and so the authors of each study and institutions housing the individuals

199 were contacted. Eighty-eight percent of zoos and 67% of authors contacted supplied

200 information on rearing history. However, birth origin was again only known for a small

201 fraction of these subjects (~15%): only twelve species contained five or more

202 stereotypic subjects of known birth origin. We also requested information as to

203 whether individuals were mother- or hand-reared (which could act as a confound;

204 Mason 1994, Latham & Mason, 2008), and the age at which wild-caught individuals

205 entered captivity (since subjects caught from the wild in infancy can resemble

206 captive-bred animals in adulthood, becoming highly stereotypic: Jones, Mason, &

207 Pillay, 2011). However, this was known for only ~40% of the fraction for whom birth

208 origin was known: a lack of information that greatly compromised data quality.

209 Consequently, the aim of investigating how birth origin interacted with species-level

210 risk potential factors was abandoned, due to concerns about low power and poor

211 data quality.

212   Finally, data on aspects of husbandry were also extracted from all studies, to

213 check for relationships between husbandry and wild behaviour (see below).

214 *Housing and husbandry data*

215 Some aspects of housing and husbandry conditions could both affect SB *and* vary

216 systematically across species, potentially being confounds (c.f. Mason, 2010a;

217 Pomerantz et al., 2013). We therefore gleaned data from the publications used to

218 compile the SB database on all variables that could potentially affect SB (Clubb &

219 Vickery, 2006; Morgan & Tromborg, 2007; Shyne, 2006; Swaisgood & Shepherdson,

220 2005), using these to calculate species medians for: enclosure size (controlling for

221 body mass), daily meal frequency (excluding starve days), and diet diversity (sum of

222 different food types in the diet). The remaining variables were either categorical or

223 ranked. For categorical variables, each species was given a summary value

224   reflecting the proportion of animals in one of the two categories (Table A2). These

225   variables were social grouping (similar to or different from the wild); meal timing

226   (morning [or morning and afternoon] or afternoon only); presence of weekly starve

227   day (yes/no); meal processing level (entirely processed or with non-processed

228   components like carcasses); and presence of foraging enrichment, as defined by the

229   authors (yes/no or unknown). Ordinal variables were ranked from 1 to 4 (1 being

230   poorest, 4 being best) and were: availability of cover (allowing escape from the view

231   of visitors); and vertical complexity of enclosure (provision of elevated platforms,

232   trees and/or rocks to climb) (Table A2). Species-level summary statistics for each

233   husbandry/housing variable were then analysed for correlations with the potential risk

234   factors using phylogenetic independent contrasts (see Methods). For those found to

235   correlate, the relevant SB analyses were rerun including it as a covariate (see

236   Methods).

237

238   *Updating the Captive Infant Mortality Database*

239   The original database contained data from the International Zoo Yearbook (1988-

240   2000 editions,1988 being the lower cut-off because 95% of the SB data came from

241   1988 or later), and from fur farms, for Clubb and Mason's 33 species. Two little-

242   breeding species (giant pandas; brown hyaenas, *Parahyaena brunnea*) were

243   excluded to leave 31. The International Zoo Yearbook stopped publishing captive

244   infant mortality data in 2000, so could not be used to update values for these 31

245   species. However, data from the same sources were used to generate values for our

246   18 new species. Using Clubb and Mason's methods, births and deaths by 30 days of

247   age were recorded. The ratio of deaths over total births for each was calculated for

248   each site (except for leopards and lions, *Panthera pardus* and *P. leo*, for which data

249   were not reported by site due to their large populations). These were used to

250   calculate species medians (Table A3). Again, species were only included in final

251   analyses if data were available for at least five subjects (here five births, individual

252   mothers or litters being unidentifiable). We also applied to ISIS to obtain fuller, more

253   up-to-date infant mortality data for each species, along with information regarding

254   each mother's birth origin in hope of investigating how birth origin interacted with

255   potential species-typical predispositions (like range size) to influence infant mortality.

256   However we were unsuccessful.

257

258   *Updating the 'Potential Risk Factors' Database*

259   This originally contained information from a literature search of 18 journals for 1960-

260   1999 inclusive, for the 33 focal species. The aims were to test the ranging, hunting

261   and territoriality hypotheses already mentioned, as well as two further hypotheses:

262   that omnivory could either predict successful adjustment to captivity, or instead put

263   species at risk of 'boredom' (see competing ideas from Boorer, 1972; Morris, 1964;

264   and Ormrod, 1987); and that naturally more active species may be particularly

265   susceptible to SB (Hediger, 1950; McDougall, Reale, Sol, & Reader, 2006; Meyer-

266   Holzapfel, 1968; Morris, 1964; Ormrod, 1987). To retest these hypotheses, wherever

267   possible (in practice for home-range size, trophic level and diet breadth), revised

268   species medians for natural behaviour in the wild were obtained from PanTHERIA

269   (Jones et al. 2009). Territoriality data for our additional 18 species came from Grant

270   (1992). For other variables (kill frequency per 24hrs; hunt frequency per 24hrs; chase

271   distance; distance between kills; daily activity levels; daily foraging time budgets;

272   daily travel distance; minimum hone range size), Clubb and Mason's database was

273   updated with new data were obtained by searching all articles in each of the 18

274   journals used previously, for the past/present scientific names and all common

275   names of our 51 target species. We did this for 1960-2010 for the 18 new species,

276 and for recent literature only (2000-2010, inclusive) for the 33 original ones. For

277 inclusion, each study had to be at least 10 months long, span multiple seasons, and

278 focus on non-provisioned adults. For estimates of hunting and kill rate a new

279 criterion was added: studies were excluded if estimates did not include observed kills

280 or hunts for *all* prey species (for example, some studies looked at reindeer kills only,

281 omitting other prey). One final modification from the previous Clubb and Mason study

282 was excluding "% vertebrate flesh" as an index of hunting, since distinguishing

283 carrion from live-caught prey in stomach contents was judged too difficult.

284   To test the new hypotheses about intelligence, we used brain volume as a

285 proxy (Deaner, Isler, Burkart, & van Schaik, 2007; Lefebvre, 2011; Reader, Hager, &

286 Laland, 2011; Schuck-Paim, Alonso, & Ottoni, 2008), obtaining cranial volumes from

287 Finarelli and Flynn (2009) and Swanson, Holekamp, Lundrigan, Arsznov, and Sakai

288 (2012). To test the new hypothesis about vulnerability in the wild as a risk factor,

289 information was obtained from the IUCN Red List (www.iucnredlist.org; Nov 2013).

290 Each IUCN Red List category was given a rank for analysis (1, least concern; 2, near

291 threatened; 3, vulnerable; 4, endangered; 5, critically endangered).

292   Table A4 lists all variables recorded and the species medians for each, along

293 with the number of species that had data for each variable (Kroshko 2015 gives more

294 details as to how each was calculated). Note that because data for many variables

295 were not available for certain species, final sample sizes were greatly reduced in

296 many analyses.

297

298 *Statistical Analyses used in Hypothesis-testing*

299 Phylogenetically independent contrasts (Felsenstein, 1985) were calculated using

300 the PDAP module in Mesquite version 2.75 (Maddison & Madison, 2006), using a

301 recent Carnivora super-tree (Nyakatura & Bininda-Emonds, 2012) that is so well

302   resolved that no adjustments for polytomies (Garland & Diaz-Uriarte, 1999) were

303   required. Least squares regressions were then run to investigate relationships

304   between each wild variable and SB (total, plus route-tracing only) and captive infant

305   mortality. To do this, contrasts were exported into JMP 10.0, with all regressions

306   forced through the origin (necessary because the signs of each x and y value for

307   contrasts are arbitrary; the regression line must therefore go through the origin

308   because the absolute distance of each contrast from the origin is important [Garland,

309   Harvey, & Ives, 1992]).

310   Appropriate transformations were used to normalise residuals. Results were

311   also graphed and visually inspected for potential outliers, while for models with

312   multiple independent variables, residuals were examined to identify potential outliers.

313   Potential outliers were then confirmed/rejected using Grubbs' test

314   (http://graphpad.com) with alpha set at 0.05 (two-tailed). If confirmed, outliers were

315   removed and data reanalyzed. Results are given as T or F-values depending on

316   JMP's output. Tests were one-tailed in almost all cases, due to clearly directional

317   predictions (see Introduction; Levine & Banas, 2002; Rice & Gaines, 1994).

318   Consequently, trends are typically not reported.

319   Analyses were typically simple univariate regressions (missing values

320   precluding more complex model-building). The three main exceptions were as

321   follows. First, because many aspects of natural behaviour and biology covary with

322   body mass (Gittleman, 1985), body mass was an important potential confound.

323   Before hypothesis-testing analyses were run, relationships between all potential risk

324   factors and body mass (obtained from PanTHERIA) were therefore determined, three

325   variables being found to correlate positively with body mass: home-range size, daily

326   activity levels, cranial volume and IUCN Red List status. In analyses using these,

327   body mass was therefore included as a covariate in each General Linear Model

328   (GLM), using a sequential sums of squares procedure with the term of interest – the

13

329   potential risk factor – placed last, and body mass first (c.f. Doncaster & Davey,

330   2007). The second set of analyses to use GLMs rather than simple univariate

331   regressions occurred when more than one wild variable proved predictive, and there

332   were biological reasons to believe that these variables might inter-relate. In practice

333   these involved hunting and ranging because the two may inter-relate: compared to

334   herbivorous Carnivora, carnivorous species typically have larger home-ranges

335   (Hendriks, Willers, Lenders, & Leuven, 2009; Kelt & Van Vuren, 2001) and greater

336   daily travel distances (Carbone, Teacher, & Rowcliffe, 2005). Where we wanted to

337   disentangle their relative effects, we therefore ran GLMs with both variables included,

338   to assess which was the main driver of observed effects. Twice, however, these

339   tests would not run as planned due to small sample sizes. To overcome this, these

340   analyses were rerun using *all* species, even those for which data came from four or

341   fewer individuals. These two analyses are clearly indicated in the text (see Results).

342   A third set of GLMs was run when species-typical husbandry covaried with a

343   potential risk factor. Diet breadth, time spent foraging, home-range size, trophic level

344   and territoriality all significantly correlated with at least one value for species-typical

345   husbandry (Table A4). Here, relevant SB analyses were therefore rerun with this

346   husbandry variable included as a covariate (again using sequential sums of squares

347   with the variable of interest as the last term).

348

349   **Results**

350

351   *Descriptive findings for captive SB and infant mortality*

352   Our literature search increased the number of individuals observed from around 800

353   (Clubb & Mason, 2007) to over 1,300, and the number of stereotypers from about

354   270 (Clubb & Mason, 2007) to 450. These spanned all families of the Carnivora,

14

355   though data from Felidae predominated (Table A1), with a median study date of

356   1997. Most SB involved route-tracing: this sub-type occurred in 45 of the 50

357   stereotypic species, and 78% of the stereotypic individuals performed it. In contrast,

358   only 22% of individuals and 10 species exhibited the other sub-types (stationary or

359   oral SB). In the 23 species with data on five or more stereotypers (representing 417

360   individual animals), median daily time budgets devoted to SB (of all sub-types)

361   showed great variation, ranging from under 1% to c.55%. In the 21 species with data

362   on five or more individual route-tracers, median daily time budgets devoted to route-

363   tracing were similar, reflecting its status as the main sub-type of SB in Carnivora. The

364   number of births included in the updated Captive Infant Mortality (CIM) Database

365   increased from c. 18,000 (Clubb & Mason, 2007) to over 25,000 through the

366   inclusion of additional species, with more than 8,900 of these infants dying before 30

367   days (Table A3). For the 49 species with data on five or more births, median CIM

368   values also showed great variation, ranging from 0% (e.g. North American river otter,

369   *Lontra canadensis*) to more than 90% (e.g. Pallas's cat, *Felis manul*).

370

371   *Predictors of Stereotypic Behaviour*

372   Relationships between each potential risk factor and the severity of total stereotypic

373   behaviour, route-tracing, and captive infant mortality are presented in Table 1.

374   Initially there seemed to be no significant correlations between total stereotypic

375   behaviour and any potential risk factor (Table 1), but once relevant husbandry

376   variables were statistically controlled for (the availability of cover), median home-

377   range size emerged as a predictor (Table 2). The severity of the route-tracing sub-

378   type of SB was, however, far more clearly related to natural behaviour than total SB

379   was: route-tracing was significantly predicted by median home-range size (Figure

15

380   1a), daily distance travelled (Figure 1b), and chase distance (Figure 1c) in both initial

381   analyses and those controlling for husbandry variables (Table 2).

382

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

384   Were these correlations between stereotypic route-tracing and chase

385   distance, home-range size and daily distance travelled in the wild, three independent

386   effects or an inter-related cluster? To tease apart their relative influence, each

387   variable was regressed against route-tracing while controlling for one of the others

388   (and body mass where appropriate), with the following results. Home-range size

389   remained a predictor of route-tracing when daily travel distance was controlled for

390   ($t_{1,7}$ = 2.20, P = 0.032). However, daily distance travelled no longer predicted route-

391   tracing when home-range size was controlled for ($t_{1,7}$ = -1.71, P = 0.065 -- the

392   apparent trend being in the opposite direction to predicted). Planned tests for

393   relationships between route-tracing and chase distance controlling for home-range

394   size, or home-range size controlling for chase distance, could not be run due to lack

395   of data. The same held for models investigating the relative importance of chase

396   distance and daily distance travelled. Therefore data from stereotypic individuals of

397   *all* species, regardless of the number of individuals contributing to the species

398   median, were now included and these three sets of analyses rerun. Sample sizes

399   were still very small, and so here we do present trends. Chase distance remained a

400   predictor of route-tracing after controlling for home-range size ($t_{1,4}$ = 2.18, P = 0.048),

401   and home-range size still tended to predict route-tracing after controlling for chase

402   distance ($t_{1,4}$ = 1.90, P = 0.065). Chase distance also tended to still predict route-

403   tracing when daily travel distance was controlled for ($t_{1,3}$ = 1.73, P = 0.091). However,

404   daily travel distance stopped predicting route-tracing when chase distance was

405   controlled for ($t_{1,3}$ = -0.11, P=0.460). Finally, following Clubb and Mason (2003;

16

406 2007), we investigated the relationship between route-tracing and home-range size

407 and body mass together, to determine if being heavy with a large home-range size is

408 a greater risk factor than just being wide-ranging. This combination was highly

409 significant ($F_{2,13}$ = 19.13, P <0.0001): far more so than effects of home-range

410 partialling out body mass (Tables 1 and 2), and despite body mass alone (i.e.

411 independent of its effects on range size) not predicting route-tracing ($F_{2,13}$ = 0.427, p

412 >0.1).

413

414 *Predictors of Captive Infant Mortality*

415 There were no significant correlations between the potential risk factors and CIM

416 (Table 1). To replicate Clubb and Mason, and mirror the analyses conducted for SB,

417 we assessed whether home-range size and body mass together predict infant

418 mortality. This model was significant ($F_{2,26}$ = 3.633, P = 0.021), with large, wide-

419 ranging carnivores having higher CIM. However, unlike the case for SB, within this

420 model the relationship between infant mortality and body mass was highly significant

421 ($t_{1,26}$ = 2.70, P = 0.006, one-tailed) and appeared to be the sole variable driving this

422 relationship. Minimum home-range sizes gleaned from the literature were also

423 assessed as predictors (Table A4), since these had a particularly strong relationship

424 with CIM in the previous research (Clubb & Mason 2003). However this was still not

425 significant ($t_{1,20}$ = -1.10, P = 0.143). Various measures of infant development (e.g.

426 altriciality) at birth were investigated as potential confounds, but still no effects were

427 observed (see Kroshko 2015 for details).

428   To then investigate whether related species actually varied in CIM (an

429 underlying assumption of our approach), data were split by family, and species

430 effects on CIM (site being used as the unit of replication; *P. leo* and *P. pardus* were

431 therefore excluded) were analysed with Kruskall Wallis tests (since data could not be

432 normalized). There were no significant effects within Phocidae or Mustelidae, but

433 species differed in CIM within Ursidae ($\chi^2_{1,7}$ = 24.54, P = 0.0009) and Canidae ($\chi^2_{1,4}$

434 = 12.09, P = 0.0167) (with a weak potential tendency within Felidae: $\chi^2_{1,21}$ = 30.03, P

435 = 0.091).

436

437 **Discussion**

438 Before discussing our significant findings, we review the non-significant ones, and

439 consider some limitations in our analyses. Mirroring the previous study (Clubb &

440 Mason, 2003; Clubb & Mason 2007), territoriality and being highly active in the wild

441 did not seem to predict SB, and the same held for many aspects of foraging (chase

442 distance being the one new exception). Furthermore, two new hypotheses, that IUCN

443 Red List status would predict welfare problems, as would being of high or low

444 intelligence (estimated from cranial volume), also appeared to have no predictive

445 value. In some instances, these non-significant results could just reflect low statistical

446 power (e.g. for distance between kills, we had data for just five stereotypic species).

447 Data quality issues could also have obscured effects. For example, although we

448 eliminated species whose data came from four or fewer subjects, this criterion far

449 from guarantees accurate values for species-typical SB. Furthermore, despite

450 controlling for husbandry as best we could in SB analyses, we were often hampered

451 by insufficient details in published papers. So, before confidently rejecting the various

452 unsupported hypotheses, it might be wise to retest them once more data have

453 accumulated in the literature. The ideal future dataset would contain fuller information

454 on husbandry, SB data for far more species, and larger sample sizes per species.

455 Future research could also refine the predictor variables when re-testing some

456 hypothesised risk factors. For example, the idea that IUCN Red List status predicts

457 captive welfare arose from suggestions that high timidity and low behavioural

458 plasticity predict both poor abilities to cope with anthropogenic threat in the wild and

459 poor abilities to adapt to captivity (Mason et al., 2013). Gleaning data on habitat

460 breadth and other proxies of behavioural plasticity, as well as flight distance (cf.

461 Møller, 2008) or other measures of timidity, might therefore be more fruitful (since

462 measures of overall threat status will reflect both intrinsic risk factors -- the interest

463 here -- *and* extrinsic ones that are less likely to be relevant to captive animals).

464   Re-thinking which aspects of natural biology may act as risk factors is even

465 more important for understanding captive infant mortality. Home-range size, daily

466 distance travelled and territoriality, previously shown to predict captive infant

467 mortality, now did not. Unfortunately we cannot tell whether the original published

468 effects were Type I errors, or the new non-significant findings are Type II errors.

469 Furthermore, no other variable tested predicted CIM, save, unexpectedly, body

470 mass. Whether this unexpected relationship between species-typical body mass and

471 CIM is robust, or merely an artifact of these infants being easier to count and

472 monitor, will need more research. Pending this future work, being unable to

473 confidently identify predictors of CIM has two frustrating implications. The first is that

474 we cannot shed light on the fundamental causes of species differences in captive

475 infant mortality, despite great variation, at least within Ursidae and Canidae. This is

476 problematic: infant mortality levels were high (at least up to 2000), and likely greater

477 than one would expect in the wild or captive breeding centres (Clubb & Mason 2007,

478 Curry et al. 2015, Diez-Leon & Mason 2016). We therefore suggest this as an urgent

479 topic for future work, one best addressed using both a broader range of species-

480 typical potential risk factors, and ISIS data on infant mortality (more current and

481 comprehensive than International Zoo Yearbook values). The second implication is

482 that this makes it difficult to interpret our significant SB results -- the predictive effects

483 of ranging and hunting behaviour, as discussed below -- in terms of overall welfare.

484 Ample evidence shows that SB reflects poor lifetime well-being (e.g. Gottlieb,

485 Captanio, & McCown, 2013; Mason & Rushen, 2006), but SB can be insensitive as a

486 welfare indicator because not all individuals or species develop it when stressed,

487 some displaying inactivity instead (e.g. Cabib, 2006; Fureix & Meagher, 2015; Mellor,

488 Hunt, & Gusset, 2015; Fureix et al. 2016). Thus while the presence of SB indicates

489 poor welfare (here, as we show, linked to certain life-history traits of species in the

490 wild), the absence of SB does not guarantee good welfare. To therefore assess

491 whether species with small ranges and negligible chase distances have better overall

492 captive welfare, not just lower SB, analyses that regress these species-level risk

493 factors against other potential welfare indicators are needed, ideally run by

494 researchers with access to ISIS data. Such indicators might include infant mortality

495 again, but repeated using better quality data; fertility (cf. Janczak, Pedersen,

496 Rydhmer, & Bakken, 2003; Wingfield & Sapolsky, 2003); and/or measures reflecting

497 how likely zoo Carnivora are to survive into old age (cf. Clubb et al., 2008; Mueller et

498 al., 2011).

499   Turning to our significant results, we successfully replicated previous findings

500 that species like polar bears, grizzly bears, caracals and others with naturally long

501 daily travel distances and large home ranges (combined with body mass) are at risk

502 of SB. These variables predicted how severely affected stereotypic individuals were

503 (a measure that, in primates, co-varies with true population-level average SB time-

504 budgets: Pomerantz et al., 2013). Our results also now revealed that this effect is

505 independent of body mass, and stronger for stereotypic route-tracing than for all SBs

506 combined. Furthermore, the daily travel distance effect proved to be just a side-effect

507 of the home range effect (vanishing when range size was statistically controlled for) –

508 suggesting that relevant aspects of wide-ranging lifestyles that predict SB do not

509 include active travelling: a topic revisited below. Our findings join some new, broadly

510 concordant results from other taxa. In several species where males have larger

511 home ranges than females, males also show more route-tracing in captivity (Bennett,

512 et al. 2015); and in comparative analyses of zoo primates, how far a species typically

513 travels each day in the wild tended to predict the time budgets they spent route-

514 tracing, though, in this taxon, irrespective of range size (Pomerantz et al., 2013).

515   In addition, we newly found that species with long average chase distances in

516 the wild (e.g. cheetahs, and canids like the coyote) are also vulnerable to more

517 severe route-tracing: the first comparative evidence implicating hunting behaviour in

518 pacing and similar SBs. As far as we could ascertain, the chase distance and home

519 range effects on route-tracing were independent. These results do need treating with

520 caution, being based on few species and thence few contrasts. However, the

521 importance of aspects of hunting is further indicated by strong circumstantial

522 evidence from our analyses: the significance of the overall model combining body

523 mass and home range size was very high (far higher than for range size alone, or

524 any other risk factor). This is relevant because, as a rule, carnivore body mass

525 predicts hunting strategy (independently of its relationship with home-range size;

526 Hendriks, Willers, Lenders, & Leuven, 2009; Nilsen & Linnell, 2006), with larger,

527 heavier species feeding on larger prey, and expending more energy on the hunting of

528 each (Carbone et al., 2007). Thus, although further research is needed here,

529 together this does suggest that attributes of natural foraging niche relating to hunting

530 help determine the severity of route-tracing. If hunting style does indeed complement

531 ranging by being a second risk factor, then one possibility is that these two risk

532 factors predict two distinct types of SB within the route-tracing category. Detailed

533 data on the precise morphologies, locations and timings of SB (e.g. Cless, 2015;

534 Dixon, Duncan, & Mason, 2008) would be needed to test this idea. Instead, another

535 possibility is that chase distance and home-range size have additive effects on a

536 common behavioural outcome, both predicting the same types of route-tracing. The

537 explanations for such additive effects could be motivational, with both aspects of

538 natural behaviour combining to elevate motivations to escape the enclosure (cf.

539 Clubb & Vickery 2006); or instead neurological, with both forms of deprivation

540 combining to cause impaired brain function. Seeing how species-typical risk factors

541 interact with birth origin (as presented earlier) could be one way to investigate this in

542 the future.

543   Overall however, regardless of such mechanistic details, these two species-

544 typical predictors of stereotypic route-tracing do suggest that within Carnivora,

545 aspects of being naturally wide-ranging and a pursuit predator cannot readily be

546 relinquished, even when humans address an animal's homeostatic needs. These

547 may therefore be 'behavioural needs': "activities that animals have instinctive,

548 intrinsic propensities to perform … even when the physiological needs that the

549 behaviour serves are fulfilled, and even when these behaviours are not [now]

550 necessary for fitness" (Mason & Burn, 2011). More precisely identifying the nature of

551 these needs is fundamentally interesting; important for animal welfare; and useful for

552 any zoo wanting to reduce SB by replacing it with more naturalistic activities (e.g.

553 Mellor et al. 2015). The best approach for both identifying what these specific

554 behavioural needs are, and creating effective 'environmental enrichments' (sources

555 of stimulation and outlets for highly motivated behaviour that improve captive welfare

556 and reduce SB) will be to now combine further comparative studies with experimental

557 work in zoos. For example, our data suggest that the relationship between home-

558 range size and SB is mediated by aspects of a wide-ranging lifestyle other than

559 active locomotion. These might include, for example, needs for novelty (since wide-

560 ranging animals are often semi-nomadic, covering only a tiny fraction of their annual

561 ranges each day); for control (since wide-ranging carnivores often facultatively shift

562 location in response to resource availability); or for multiple different denning sites

563 (Clubb & Mason, 2003; Clubb & Mason, 2007). The further use of comparative

564 methods could thus help assess whether these aspects of ranging confer risk, by

565 exploring the predictive power of species' ratios of day range to annual range, the

566   annual numbers of denning sites used, how often animals completely shift location

567   per year, and measures of the habitat diversity experienced by individuals. In

568   parallel, experimental, enrichment-oriented studies in zoos could investigate whether

569   captive carnivores with naturally large home ranges particularly benefit from having

570   multiple denning sites; being able to explore; gaining access to novel environments;

571   viewing novel/variable vistas; or being able to control/modify their own enclosures.

572   Turning to chase distance, to better understand *this* predictive trait and use it to

573   design better ways to enrich enclosures, future comparative studies should

574   investigate the predictive roles of the gaits that different species typically use when

575   hunting; the peak speeds they attain during chases; and the killing methods typically

576   used in the wild. Complementary experimental, enrichment-oriented research in zoos

577   could likewise explore whether carnivores with long chase times are particularly

578   motivated to express sustained appetitive pre-feeding behaviour (e.g. via

579   opportunities to chase moving objects; Quirke, O'Riordan, & Davenport, 2013)*,* or to

580   perform particular forms of consummatory behaviour (perhaps as allowed by feeding

581   large whole carcasses). Thus, inspired by our comparative findings, we hope such

582   ideas for experiments could ultimately result in feasible, imaginative, evidence-based

583   enrichments that tackle route-tracing effectively.

584

585   *Conclusions*

586   Our comparative evidence supports the hypotheses that aspects of wild hunting

587   behaviour (long prey chase distances) and ranging behaviour (large home range

588   sizes) are independent risk factors for stereotypic route-tracing in captive Carnivora.

589   Further research should now pinpoint the specific components of hunting or ranging

590   that are the key, partly to reveal which have evolved to be 'behavioural needs', and

591   partly for practical reasons, to help create the best captive environments and most

592   effective enrichments for these animals. Further research is also needed to explain

593   why captive Carnivora vary so greatly in their infant mortality levels.

594

595   **References**

596   Bennett, C., Torgensen-White, L., Fripp, D., Watters, J. & Petric, A. (2015). A multi-

597   institutional assessment of factors influencing locomotion and pacing in

598   captive okapis (*Okapia johnstoni*). *Journal of Applied Animal Welfare*

599   *Science, 18*, S43-S61.

600   Bininda-Emonds, O. R. P., & Gittleman, J. L. (2000). Are pinnipeds functionally

601   different from fissiped carnivores? The importance of phylogenetic

602   comparative analyses. *Evolution*, *54*, 1011-1023.

603   Bininda-Emonds, O. R. P., Gittleman, J. L. & Kelly, C. K. (2001). Flippers versus feet:

604   comparative trends in aquatic and non-aquatic carnivores. *Journal of Animal*

605   *Ecology, 70*, 386-400.

606   Boorer, M. K. (1972). Some aspects of stereotyped patterns of behaviour exhibited

607   by zoo animals. *International Zoo Yearbook, 12*, 164-168.

608   Burns, J. G., Saravanan, A. & Rodd, F. H. (2009). Rearing environment affects the

609   brain size of guppies: lab-reared guppies have smaller brains than wild-

610   caught guppies. *Ethology, 115*, 122-133.

611   Cabib, S. (2006). *The Neurobiology of Stereotypy II: the Role of Stress.* In G. Mason,

612   & J. Rushen (Eds.), *Stereotypic Animal Behaviour: Fundamentals and*

613   *Applications to Welfare* (pp.227- 255) (2nd ed.). Wallingford, U.K.: CABI.

614   Carbone, C., Cowlishaw G., Isaac, N. J. B., & Rowcliffe, J. M. (2005). How far do

615   animals go? Determinants of day range in mammals. *American Naturalist,*

616   *165*, 290-297.

617   Carbone, C., Teacher, A., & Rowcliffe, J. M. (2007). The costs of carnivory. *PLoS*

618   *Biology*, *5*, 363-368.

619   Cassey, P., Blackburn, T. M., Russell, G. J., Jones, K. E., & Lockwood, J. L. (2004).

620   Influences on the transport and establishment of exotic bird species: an

621   analysis of the parrots (Psittaciformes) of the world. *Global Change Biology,*

622   *10*, 417-426.

623   Cless, I. T. (2015). *A dissection of pacing in zoo-housed polar bears: how details of*

624   *the behavior can suggest motivational and causal factors* (Masters

625   dissertation). Cleveland, Ohio: Case Western Reserve University.

626   Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature,*

627   *425*, 473-474.

628   Clubb, R., & Mason, G. (2004). Pacing polar bears and stoical sheep: testing

629   ecological and evolutionary hypotheses about animal welfare. *Animal*

630   *Welfare, 13*, S33-S40.

631   Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in

632   carnivore welfare: how analysing species differences could help zoos improve

633   enclosures. *Applied Animal Behaviour Science, 102,* 303-328.

634   Clubb, R., Rowcliffe, M., Lee, P., Mar, K. U., Moss, C. & Mason, G. J. (2008).

635   Compromised survivorship in zoo elephants, *Science, 322*, 1649.

636   Clubb, R., Rowcliffe, M., Lee, P., Mar, K. U., Moss, C., & Mason, G. J. (2009).

637   Fecundity and population viability in female zoo elephants: problems and

638   possible solutions. *Animal Welfare, 18,* 237-247.

639   Clubb, R., & Vickery, S. (2006). Locomotory stereotypies in carnivores: does pacing

640   stem from hunting, ranging or frustrated escape? In G. Mason, & J. Rushen

641   (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to*

642   *Welfare* (pp.58 - 85) (2nd ed.). Wallingford, U.K.: CABI.

643   Conde, D. A., Flesness, N., Colchero, F., Jones, O. R., & Scheuerlein, A. (2011). An

644   emerging role of zoos to conserve biodiversity. *Science, 331*, 1390-1391.

645 Curry, E., Safayi, S., Meyerson, R. & Roth, T. L. (2015). Reproductive trends of

646   captive polar bears in North American zoos: a historical analyses. *Journal of*

647   *Zoo and Aquarium Research, 3*, 99-105.

648 Davies, A. C., Nicol, C. J., & Radford, A. N. (2015). Effect of reward downshift on the

649   behaviour and physiology of chickens. *Animal Behaviour, 105*, 21-28.

650 Dawkins, M. S. (1990). From an animals point of view: motivation, fitness, and animal

651   welfare. *Behavioral and Brain Sciences, 13*, 1-9.

652 Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007) Overall brain size, and

653   not encephalization quotient, best predicts cognitive ability across non-human

654   primates. *Brain Behavior and Evolution, 70*, 115-124.

655 Diez-Leon, M., Bowman, J., Bursian, S., Filion, H., Galicia, D., Kanefsky, J.,

656   Napolitano, A., Palme, R., Schulte-Hostedde, A., Scribner, K., & Mason, G.

657   (2013). Environmentally enriched male mink gain more copulations than

658   stereotypic, barren-reared competitors. *PLoS One, 8,* e80494.

659 Diez-Leon, M. & Mason, G. (2016). Effects of environmental enrichment and

660   stereotypic behavior on maternal behavior and infant viability in a model

661   carnivore, the American mink (*Neovison vison*). *Zoo Biology, 35*, 19-28.

662 Dixon, L. M., Duncan, I. J. H., & Mason, G. (2008). What's in a peck? Using fixed

663   action pattern morphology to identify the motivational basis of abnormal

664   feather-pecking behaviour. *Animal Behaviour, 76*, 1035-1042.

665 Doncaster, C., & Davey, A. (2007). *Analysis of Variance and Covariance: How to*

666   *Choose and Construct Models for the Life Sciences*. Cambridge, U.K.:

667   Cambridge University Press.

668 Felsenstein, J. (1985). Phylogenies and the comparative method. *American*

669   *Naturalist, 125*, 1-15.

670 Finarelli, J. A., & Flynn, J. J. (2009). Brain-size evolution and sociality in Carnivora.

671   *Proceedings of the National Academy of Sciences of the United States of*

672   *America, 106*, 9345-9349.

673   Fisher, D. O., & Owens, I. P. F. (2004). The comparative method in conservation

674   biology. *Trends in Ecology & Evolution, 19*, 391-398.

675   Forthman Quick, D. L. (1984). An integrative approach to environmental engineering

676   in zoos. *Zoo Biology, 3*, 65-77.

677   Fureix, C., & Meagher, R. K. (2015). What can inactivity (in its various forms) reveal

678   about affective states in non-human animals? A review. *Applied Animal*

679   *Behaviour Science, 171*, 8-24.

680   Fureix, C., Walker, M., Reynolds, K., Harper, L., Saldivia-Woo, A., & Mason, G. J.

681   (2016). Being inactive but awake is a depression-like alternative to

682   stereotypic behaviour in C57BL/6 mice. Behavioural Brain Research.

683   Garland, T., & Diaz-Uriarte, R. (1999). Polytomies and phylogenetically independent

684   contrasts: Examination of the bounded degrees of freedom approach.

685   *Systematic Biology, 48*, 547-558.

686   Garland, T., Harvey, P. H., & Ives, A. R. (1992). Procedures for the analysis of

687   comparative data using phylogentically independent contrasts. *Systematic*

688   *Biology, 41*, 18-32.

689   Garner, J. P. (2006). Perseveration and stereotypy: systems-level insights from

690   clinical psychology. In G. Mason, & J. Rushen (Eds.), *Stereotypic Animal*

691   *Behaviour: Fundamentals and Applications to Welfare* (pp.121 - 152) (2nd

692   ed.). Wallingford, U.K.: CABI.

693   Ginsberg, J. R., & Macdonald, D. W. (1990). *Foxes, wolves, jackals and dogs: an*

694   *action plan for the conservation of canids*. Switzerland: IUCN.

695   Gittleman, J. L. (1985). Carnivore body size: ecological and taxonomic correlates.

696   *Oecologia, 67*, 540-554.

697   Gittleman, J. L. (1986a). Carnivore brain size, behavioural ecology, and phylogeny.

698   *Journal of Mammalogy, 67*, 23-36.

699   Gittleman, J. L. (1986b). Carnivore life-history patterns: allometric, phylogenetic, and

700   ecological associations. *American Naturalist, 127*, 744-771.

701   Gottlieb, D. H., Capitanio, J. P., & McCowan, B. (2013). Risk factors for stereotypic

702   behavior and self-biting in rhesus macaques (*Macaca mulatta*): Animal's

703   history, current environment, and personality. *American Journal of*

704   *Primatology, 75*, 995-1008.

705   Grant, J. W. A., Chapman, C. A., & Richardson, K. S. (1992). Defended versus

706   undefended home range size of carnivores, ungulates and primates.

707   *Behavioural Ecology and Sociobiology, 31*, 149-161.

708   Healy, K., McNally, L., Ruxton, G. D., Cooper, N., & Jackson, A. L. (2013). Metabolic

709   rate and body size are linked with perception of temporal information. *Animal*

710   *Behaviour, 86*, 685-696.

711   Hediger, H. (1950). *Wild Animals in Captivity.* London, U.K.: Butterworth.

712   Hendriks, A. J., Willers, B. J. C., Lenders, H. J. R., & Leuven, R. S. E. W. (2009).

713   Towards a coherent allometric framework for individual home ranges, key

714   population patches and geographic ranges. *Ecography, 32*, 929-942.

715   Hoenig, D., & Gusset, M. (2010). A test of multiple hypotheses on the occurrence of

716   stereotypic behaviour in big cats at Leipzig Zoo. *Zoologische Garten, 79*, 38-

717   52.

718   Janczak, A. M., Pedersen, L. J., Rydhmer, L., & Bakken, M. (2003). Relation

719   between early fear- and anxiety-related behaviour and maternal ability in

720   sows. *Applied Animal Behaviour Science, 82*, 121-135.

721   Jenny, S., & Schmid, H. (2002). Effect of feeding boxes on the behavior of

722   stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich,

723   Switzerland. *Zoo Biology, 21*: 573-584.

724   Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success

725   in Europe and North America. *Global Change Biology, 12*: 1608-1619.

726   Joergensen, G. (1985). *Mink production*. Hilleroed, Denmark: Scientifur.

727   Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, D. L., Safi, K.,

728   Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster,

729   J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A, Rist, J.,

730   Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M., &

731   Purvis, A. (2009). PanTHERIA: a species-level database of life history,

732   ecology, and geography of extant and recently extinct mammals. *Ecology, 90*,

733   2648.

734 Jones, M. A., Mason, G., & Pillay, N. (2011). Early environmental enrichment

735   protects captive-born striped mice against the later development of

736   stereotypic behaviour. *Applied Animal Behaviour Science, 135*, 138-145.

737 Kelt, D. A., & Van Vuren, D. H. (2001). The ecology and macroecology of

738   mammalian home range area. *American Naturalist, 157*, 637-645.

739 Kroshko, J. (2015). *Population-level risk factors for stereotypic behaviour and infant*

740   *mortality in captive carnivores* (Masters dissertation). Guelph, Canada:

741   University of Guelph.

742 Latham, N. R. & Mason, G. J. (2008). Maternal deprivation and the development of

743   stereotypic behaviour. *Applied Animal Behaviour Science, 110*, 84-108.

744 Lefebvre, L. (2011). Taxonomic counts of cognition in the wild. *Biology Letters, 7,*

745   631-633.

746 Levine, T. R. & Banas, J. (2002). One-tailed F-tests in communication research.

747   *Communication Monographs, 69*, 132-143.

748 Lewis, M. H., Presti, M. F., Lewis, J. B., & Turner, C. A. (2006). The neurobiology of

749   stereotypy I: environmental complexity. In G. Mason, & J. Rushen (Eds.),

750   *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*

751   (pp.190 - 226) (2nd ed.). Wallingford, U.K.: CABI.

752 Maddison, W. P., & Madison, D. R. (2006). *Mesquite: A modular system for*

753   *evolutionary analysis.* Version 2.75.

754 Malmkvist, J., Gade, M., & Damm, B. I. (2007). Parturient behaviour in farmed mink

755   (*Mustela vison*) in relation to early kit mortality. *Applied Animal Behaviour*

756   *Science, 107*, 120-132.

757 Martin, T. E., Lurbiecki, H., Joy, J. B., & Mooers, A. O. (2014). Mammal and bird

758   species held in zoos are less endemic and less threatened than their close

759   relatives not held in zoos. *Animal Conservation, 17*, 89-96.

760 Mason, G. J. (1994). Tail-biting in mink (*Mustela vison*) is influenced by age at

761   removal from the mother. *Animal Welfare 3*, 305-311.

762 Mason, G. J. (2010). Species differences in responses to captivity: stress, welfare

763   and the comparative method. *Trends in Ecology & Evolution, 25*, 713-721.

764 Mason, G., & C. Burn (2011). Behavioural deprivation. In M. Appleby, J. A. Mench, A.

765   Olsson, & B. O. Hughes (Eds.), *Animal Welfare* (pp.98 - 119). Wallingford,

766   U.K.: CABI.

767 Mason, G., Burn, C. C., Dallaire, J. A., Kroshko, J., Kinkaid, H. M., & Jeschke, J. M.

768   (2013). Plastic animals in cages: behavioural flexibility and responses to

769   captivity. *Animal Behaviour, 85*, 1113-1126.

770 Mason, G., & Mendl, M. (1993). Why is there no simple way of measuring animal

771   welfare. *Animal Welfare, 2*, 301-319.

772 Mason, G., & Mendl, M. (1997). Do the stereotypies of pigs, chickens and mink

773   reflect adaptive species differences in the control of foraging? *Applied Animal*

774   *Behaviour Science, 53*, 45-58.

775 Mason, G., & Rushen, J. (2006). *Stereotypic Animal Behaviour: Fundamentals and*

776   *Applications to Welfare*. Wallingford, U.K.: CABI.

777 Mason, G. J., & Veasey, J. S. (2010). How should the psychological well-being of

778   zoo elephants be objectively investigated?. *Zoo Biology*, *29*, 237-255.

779 McDonald Kinkaid, H. Y. (2015). *Species-Level Determinants of Stereotypic*

780   *Behaviour, Reproductive Success, and Lifespan in Captive Parrots*

781   *(Psittaciformes)* (Doctoral dissertation). Guelph, Canada: University of

782   Guelph.

783 McDougall, P. T., Reale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation

784   and animal temperament: causes and consequences of evolutionary change

785   for captive, reintroduced, and wild populations. *Animal Conservation, 9*, 39-

786   48.

787 Mellen, J. D. (1991). Factors influencing reproductive success in small captive exotic

788   felids (*Felis* Spp): a multiple-regression analysis. *Zoo Biology, 10*, 95-110.

789 Mellor, D. J., Hunt, S. & Gusset, M. (Eds.) (2015) *Caring for Wildlife: The World Zoo*

790   *and Aquarium Animal Welfare Strategy*. Gland, Switzerland: WAZA Executive

791   Office.

792 Meyer-Holzapfel, M. (1968). Abnormal behaviour in zoo animals. In M. W. Fox (Ed.),

793   *Abnormal Behaviour in Animals* (pp.476 - 503). London, U.K.: Saunders.

794 Montgomery, S. H. (2014). The relationship between play, brain growth and

795   behavioural flexibility in primates. *Animal Behaviour, 90*, 281-286.

796 Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied*

797   *Animal Behaviour Science, 102*, 262-302.

798 Morimura, N., & Mori, Y. (2010). Effects of early rearing conditions on problem-

799   solving skill in captive male chimpanzees (*Pan troglodytes*). *American Journal*

800   *of Primatology, 72*, 626-633.

801 Morris, D. (1964). The response of animals to restricted environments. *Symposia of*

802   *the Zoological Society of London, 13*, 99-118.

803 Mueller, D. W. H., Lackey, L. B., Streich, W. J., Fickel, J., Hatt, J.-M., & Clauss, M.

804   (2011). Mating system, feeding type and ex situ conservation effort determine

805   life expectancy in captive ruminants. *Proceedings of the Royal Society B-*

806   *Biological Sciences, 278*, 2076-2080.

807 Mueller, D. W. H., Lackey, L. B., Streich, W. J., Hatt, J. M., & Clauss, M. (2010).

808   Relevance of management and feeding regimens on life expectancy in

809   captive deer. *American Journal of Veterinary Research, 71*, 275-280.

810 Møller, A. P. (2008). Flight distance and population trends in European breeding

811   birds. *Behavioral Ecology, 19*, 1095-1102.

812   Nilsen, E. B., & Linnell, J. D. C. (2006). Intra-specific variation and taxa-sampling
813   affects the home range body mass relationship. *Acta Theriologica, 51*, 225-
814   232.
815   Nyakatura, K., & Bininda-Emonds, O. R. P. (2012). Updating the evolutionary history
816   of Carnivora (Mammalia): a new species-level supertree complete with
817   divergence time estimates. *BMC Biology, 10*, 31.
818   Ormrod, S. A. (1987). Standards for modern captive animal management.
819   *Proceedings of the Animal Welfare Foundation's Fourth Symposium: 'The
820   Welfare of Animals in Captivity',* pp. 22 - 27.
821   Pomerantz, O., Meiri, S., & Terkel, J. (2013). Socio-ecological factors correlate with
822   levels of stereotypic behavior in zoo-housed primates. *Behavioural
823   Processes, 98*, 85-91.
824   Quirke, T., O'Riordan, R., & Davenport, J. (2013). A comparative study of the speeds
825   attained by captive cheetahs during the enrichment practice of the "cheetah
826   run". *Zoo Biology, 32*, 490-496.
827   Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general
828   and cultural intelligence. *Philosophical Transactions of the Royal Society B-
829   Biological Sciences, 366*, 1017-1027.
830   Rice, W. R., & Gaines, S. D. (1994). Heads I win, tails you lose - testing directional
831   hypotheses in ecological and evolutionary research. *Trends in Ecology &
832   Evolution, 9*, 235-237.
833   Schuck-Paim, C., Alonso, W. J., & Ottoni, E. B. (2008). Cognition in an ever-
834   changing world: Climatic variability is associated with brain size in neotropical
835   parrots. *Brain Behavior and Evolution, 71*, 200-215.
836   Shyne, A. (2006). Meta-analytic review of the effects of enrichment on stereotypic
837   behavior in zoo mammals. *Zoo Biology, 25*, 317-337.

838 Sih, A. (2013). Understanding variation in behavioural responses to human-induced

839   rapid environmental change: a conceptual overview. *Animal Behaviour, 85*,

840   1077-1088.

841 Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the

842   success of mammal species introduced into novel environments. *American*

843   *Naturalist, 172*, S63-S71.

844 Swaisgood, R. R., & Shepherdson, D. J. (2005). Scientific approaches to enrichment

845   and stereotypies in zoo animals: what's been done and where should we go

846   next? *Zoo Biology, 24*, 499-518.

847 Swanson, E. M., Holekamp, K. E., Lundrigan, B. L., Arsznov, B. M., & Sakai, S. T.

848   (2012). Multiple Determinants of Whole and Regional Brain Volume among

849   Terrestrial Carnivorans. *PLoS One, 7*, e38447.

850 Thorpe, R. S., Black, H., & Malhotra, A. (1996). Matrix correspondence tests on the

851   DNA phylogeny of the Tenerife lacertid elucidate both historical causes and

852   morphological adaptation. *Systematic Biology, 45*, 335-343.

853 Walker, M., Diez-Leon, M. & Mason, G. (2014). Animal welfare science: recent

854   publication trends and future research priorities. *International Journal of*

855   *Comparative Psychology*, 27, 80-100.

856 Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress:

857   When and how. *Journal of Neuroendocrinology, 15*, 711-724.

858 Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of

859   populations inside protected areas. *Science, 280,* 2126-2128.

860 Zeaman, D. (1949). Response latency as a function of the amount of reinforcement.

861   *Journal of Experimental Psychology, 39*, 466-483.

862

863

Table 1. Relationships between species-level potential risk factors and stereotypic 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)	*Only data for route-tracing*	**$t_{1,3}$=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)	*Only data for route-tracing*	$t_{1,4}$=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	*Only data for route-tracing*	$t_{1,5}$=-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.

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

869
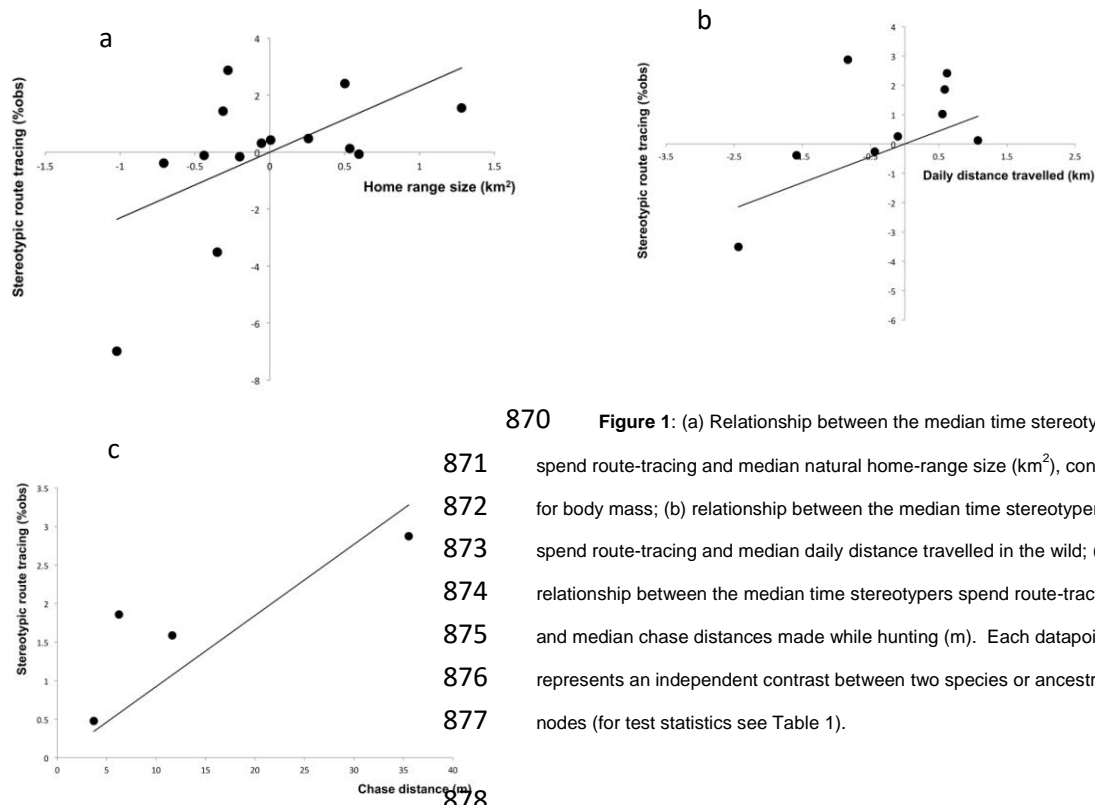
870 **Figure 1**: (a) Relationship between the median time stereotypers
871 spend route-tracing and median natural home-range size (km^2), controlling
872 for body mass; (b) relationship between the median time stereotypers
873 spend route-tracing and median daily distance travelled in the wild; (c)
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).

878

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
Acinonyx jubatus	Y	**24.60**	8	**24.60**	8
Ailuropoda melanoleuca	Y	4.50	4	5.25	3
Canis latrans	N	**N/A**		**N/A**	
Canis lupus	N	**N/A**		**N/A**	
Caracal caracal	Y	**14.74**	10	**14.74**	10
Catopuma temminckii	N	**23.56**	5	**23.56**	5
Eumetopias jubatus	N	**N/A**		**N/A**	
Felis chaus	Y	12.45	3	12.45	3
Felis manul	N	**N/A**		**N/A**	
Felis margarita	Y	**12.68**	9	**12.68**	9
Felis nigripes	N	**N/A**		**N/A**	
Felis silvestris	Y	1.50	2	1.50	2
Genetta tigrina	Y	8.30	1	8.30	1
Halichoerus grypus	N	**54.64**	11	**54.64**	11
Helarctos malayanus	N	**25.59**	18	24.65	4
Hyaena brunnea	Y	24.70	1	24.70	1
Leopardus colocolo	N	24.50	2	24.50	2
Leopardus geoffroyi	Y	**11.50**	9	**11.50**	9
Leopardus pardalis	Y	**6.46**	18	**6.46**	18
Leopardus wiedii	Y	12.49	4	12.49	4
Leptailurus serval	Y	**8.74**	6	**8.74**	6
Lontra canadensis	Y	4.34	2	4.07	2
Lontra longicaudis	N	26.00	2	26.00	2
Lynx canadensis	N	6.25	2	6.25	2
Lynx lynx	Y	**10.83**	10	**10.83**	10
Martes foina	N	**N/A**		**N/A**	
Melursus ursinus	Y	**16.76**	5	**15.49**	5
Nasua nasua	N	22.74	2	43.48	1
Neophoca cinerea	N	23.29	2	23.29	2
Neovison vison	Y	**N/A**		**N/A**	
Odobenus rosmarus	N	51.27	4	51.27	4
Panthera leo	Y	**9.50**	10	**9.50**	10

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

880

881

882

883

884

885

886

887

888

889

890

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

Species	Median study date	Median enclosure size (m²)	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
Ailuropoda melanoleuca	1990	241.7	3	3	1			3		1	1
Canis latrans	2009	1000	3	2	1	1	1		1		1
Canis lupus	2001										
Caracal caracal	1991		2	3.5							1
Catopuma temminckii	2002.5										1
Eumetopias jubatus	1998				1	3	1		1		1
Felis chaus	1997.5										
Felis manul	1998										
Felis margarita	1990.5		4	2							1
Felis nigripes	1998										
Felis silvestris	1998										
Genetta tigrina	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
Hyaena brunnea	1980										
Leopardus colocolo	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
Leopardus wiedii	1999.5	11	3	4							1
Leptailurus serval	1998		4								1
Lontra canadensis	2008										
Lontra longicaudis	2001										
Lynx canadensis	1998										

38

Species	Year										
Lynx lynx	1997										1
Martes foina	1993	2.97	2	3		1	0	1	1	1	1
Melursus ursinus	1992										1
Nasua nasua	1996										
Neophoca cinerea	2010										
Neovison vison	1994		2	1	1	1	0.95	1	1	1	1
Odobenus rosmarus	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
Phoca vitulina	2001.5				1						1
Potos flavus	1990										
Prionailurus bengalensis	1993	5.85		3		1		2.5	1	1	1
Prionailurus viverrinus	1995.5										1
Puma concolor	2007										1
Puma yagouaroundi	2001		3								1
Suricata suricatta	1989		2	3	1	1	0	2	1		1
Tremarctos ornatus	2000.5										
Uncia uncia	1997	152		4	0.13				0	0	0.87
Ursus americanus	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										
Vulpes zerda	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
Acinonyx jubatus	25.00	844
Canis latrans	44.44	30
Canis lupus	20.00	2061
Caracal caracal	27.27	406
Catopuma temminckii	16.67	30
Eumetopias jubatus	46.43	26
Felis chaus	40.00	395
Felis manul	90.91	45
Felis margarita	20.00	121
Felis nigripes	1.32	113
Felis silvestris	28.57	886
Genetta tigrina	21.05	36
Halichoerus grypus	33.33	125
Helarctos malayanus	40.00	60
Leopardus colocolo	56.25	16
Leopardus geoffroyi	33.33	147

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

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

892

893

894