



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



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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 data set 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, naturally long chase distances during hunts now also predicted more severe route tracing. Previous research had also identified naturally long travel distances and large home ranges as risk factors for CIM. 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 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 when their homeostatic needs are met, and also suggests new strategies for environmentally enriching their enclosures more effectively.

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Billions of wild and semiwild 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, 2010; Mason et al., 2013). 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 coevolution (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

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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, Bacher, 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 that are 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 wellbeing. Such research can even raise new fundamental research questions (e.g. Mason et al., 2013; Sih, 2013).

Here we applied 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 cat, *Felis nigripes*) and infant mortality (e.g. black-footed ferrets, *Mustela nigripes*; giant pandas, *Ailuropoda melanoleuca*: reviewed by Curry, Safayi, Meyerson, & Roth, 2015; Diez-Leon et al., 2013; Diez-Leon & Mason, 2016). These responses are all affected by stress (reviewed by e.g. Clubb et al., 2009; Mason & Veasey, 2010), suggesting species differences in typical welfare (where welfare means wellbeing 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 in e.g. giant pandas and kinkajous, *Potos flavus*, through to relying on live prey in 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 data set on 33 species that was finalized 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 principal reasons to now replicate and expand upon this research are described below.

First, several recent developments allowed the 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](http://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). Second, some hypotheses previously rejected by

the original study nevertheless seemed supported by growing experimental evidence, making it worth retesting them with a more powerful data set. In particular, stereotypic route tracing (e.g. pacing) had long been hypothesized 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 prefeeding 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 and Mason (2003). One was that species at risk to anthropogenic changes in the wild are more vulnerable in captivity (Mason, 2010; 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 focused on the potential mechanisms by which species-typical wild behaviours, such as 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 increase 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 hypothesized mechanism makes an alternative 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). In this paper we therefore re-examine 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 and 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's (2003, 2007) 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

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