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PERSPECTIVE

Middle-out ecology: small carnivores as sentinels of global change

Courtney J. MARNEWECK* *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: courtney.marneweck@gmail.com*
Benjamin L. ALLEN *Institute for Life Sciences and the Environment, University of Southern Queensland, Toowoomba, QLD 4350, Australia and Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth 6034, South Africa. Email: benjamin.allen@usq.edu.au*
Andrew R. BUTLER *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: abutle5@clemson.edu*
Emmanuel DO LINH SAN *Department of Zoology and Entomology, University of Fort Hare, Alice 5700, South Africa. Email: emmanuel.dolinhsan@gmail.com*
Stephen N. HARRIS *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: sh2@clemson.edu*
Alex J. JENSEN *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: ajense2@clemson.edu*
Elizabeth A. SALDO *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: ereghis@clemson.edu*
Michael J. SOMERS *Mammal Research Institute, Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa. Email: michael.somers@up.ac.za*
Keifer TITUS *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: ktitus@clemson.edu*
Michael MUTHERSBAUGH *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA. Email: mmuther@clemson.edu*
Abi VANAK *Ashoka Trust for Research in Ecology and the Environment, Bengaluru 560064, India and School of Life Sciences, University of KwaZulu-Natal, 3629, South Africa. Email: avanak@atree.org*
David S. JACHOWSKI *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA and School of Life Sciences, University of KwaZulu-Natal, 3629, South Africa. Email: djachow@clemson.edu*

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*Correspondence

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ABSTRACT

Species that respond to ecosystem change in a timely, measurable, and interpretable way can be used as sentinels of global change. Contrary to a pervasive view, we suggest that, among Carnivora, small carnivores are more appropriate sentinels than large carnivores. This reasoning is built around six key points: that, compared to large carnivores, small carnivores 1) are more species-rich and diverse, providing more potential sentinels in many systems; 2) occupy a wider range of ecological niches, exhibiting a greater variety of sensitivities to change; 3) hold an intermediate trophic position that is more directly affected by changes at the producer, primary consumer, and tertiary consumer levels; 4) have shorter life spans and higher reproductive rates, exhibiting more rapid responses to change; 5) have smaller home ranges and are more abundant, making it easier to investigate fine-scale management interventions; 6) are easier to monitor, manage, and manipulate. Therefore, we advocate for incorporating a middle-out approach, in addition to the established top-down and bottom-up approaches, to assessing the responses of ecosystems to global change.

Mots-clés
Carnivore, changement, global, indicateur, mésocarnivore, petit carnivore, sentinelle

RÉSUMÉ EN FRANÇAIS

Les espèces qui réagissent au changement de l'écosystème de manière opportune, mesurable et interprétable peuvent être utilisées comme sentinelles du changement global. Contrairement à une opinion répandue, nous suggérons que, parmi l'ordre des Carnivora, les petits carnivores sont des sentinelles plus appropriées que les grands carnivores. Ce raisonnement est construit autour de six points-clés: que, comparés aux grands carnivores, les petits carnivores 1) sont plus riches en espèces et plus diversifiés, fournissant plus d'espèces sentinelles potentielles dans de nombreux systèmes; 2) occupent un plus large éventail de niches écologiques, présentant une plus grande variété de sensibilités au changement; 3) occupent une position trophique intermédiaire plus directement affectée par les changements au niveau du producteur, du consommateur primaire et du consommateur tertiaire; 4) ont des durées de vie plus courtes et des taux de reproduction plus élevés, présentant des réponses plus rapides au changement; 5) ont des domaines vitaux plus petits et sont plus abondants, ce qui facilite l'étude des interventions de gestion à petite échelle; 6) sont plus faciles à surveiller, gérer et manipuler. Par conséquent, nous préconisons l'intégration d'une approche intermédiaire, en plus des approches descendantes et ascendantes établies, pour évaluer les réponses des écosystèmes au changement global.

INTRODUCTION

Global change due to anthropogenic disturbance is taking place at an unprecedented rate. Biologists, habitat managers, and policy-makers struggle to find ways to monitor structural and functional responses to this change at the individual, population, community, and ecosystem levels (Dirzo et al. 2014, Johnson et al. 2017). Monitoring at each level is difficult, creating a need to identify species that can serve as reliable indicators of environmental change. The use of indicator species has existed for several decades and has become widespread (Landres et al. 1988, Caro 2010, Lindenmayer et al. 2015). However, the criteria used for selecting species to serve as indicators within ecosystems vary considerably and include functional importance, sensitivity to change, rarity, ease of monitoring, and charisma or public appeal (Dalerum et al. 2008, Heink & Kowarik 2010). These varying rationales for determining appropriate indicator species have led some to argue that indicator species are selected without justification and without testing their capacity to improve management decision making (Siddig et al. 2016, Bal et al. 2018). However, given appropriate selection, indicator species can be important for improving conservation management over time (Carignan & Villard 2002, Bal et al. 2018). There is thus increased interest in identifying indicator species to monitor the functional response of ecosystems in the face of rapid climate and environmental change (Siddig et al. 2016, Hazen et al. 2019).

Sentinel species are a specific form of indicator species that respond to ecosystem variability in a timely, measurable, and interpretable manner, such that they provide insight into the condition of ecosystem-level processes (Hazen et al. 2019). In the top-down approach, large mammalian carnivores (Carnivora) positioned at the apex of food webs are identified as sentinel species because changes in these species' behaviours and/or demographics are often indicative of changes at lower trophic levels (Ray 2005, Morrison et al. 2007, Sergio et al. 2008, Hazen et al. 2019). However, while large carnivores respond directly to changes in the availability of medium-sized to large prey, they only respond to changes at lower trophic levels indirectly, which means that responses to changes at the lowest trophic levels are weaker and more difficult to observe. Evaluating these bottom-up effects is important when assessing the suitability of a species as a sentinel for environmental change, so there is a need to reassess the utility of large carnivores as the standard sentinels. Moreover, because large carnivore populations have relatively slow rates of change, responses to ecosystem variability may not present in a timely manner. A more appropriate group of target species would include those that have fast rates of population change and are directly impacted by both bottom-up and top-down processes, allowing one to take a 'middle-out' approach.

Though less popularised, small carnivores can serve as global sentinels of ecosystem structure, function, and change. In several ecosystems, small carnivores are already successfully used as sentinels. Examples include black-footed ferrets *Mustela nigripes* as sentinels of prairie biodiversity (Jachowski 2014), meerkats *Suricata suricatta* as sentinels of climate change (van de Ven et al. 2020), ocelots *Leopardus pardalis* as sentinels of landscape connectivity (Perez 2019), Eurasian otters *Lutra lutra* as sentinels of bioaccumulation (Brand et al. 2020), and several canid species as sentinels of human health via disease prevalence (Aguirre 2009).

We build on these sentinel examples by providing six reasons why small carnivores are more efficient and appropriate than large carnivores as sentinels of ecosystem change. We define small carnivores as species in the order Carnivora weighing <21.5 kg. Below this body weight, most species meet their energy requirements from small prey (invertebrates weighing <10 g and small vertebrates <2 kg); above it, most take larger prey (large vertebrates typically weighing >10 kg; Carbone et al. 1999, Carbone et al. 2007, Do Linh San et al. 2022). We thus define large carnivores as Carnivora species weighing >21.5 kg. We compare data on small carnivores defined in this way (n = 231 species; Appendix S1) with data on large carnivores (n = 25 species). We included only fully and semi-terrestrial Carnivora; however, we believe that our rationale could equally be applied to other carnivorous species, e.g. the order Dasyuromorphia.

SIX WAYS IN WHICH SMALL CARNIVORES OUTPERFORM LARGE CARNIVORES AS SENTINELS OF GLOBAL CHANGE

Higher taxonomic diversity

The utility of indicator species is increased when monitoring programs include several species representing various taxa and life histories (Carignan & Villard 2002). Small carnivores are more taxonomically diverse than large carnivores, making it possible for multiple species to act as sentinels for different processes within ecosystems. Our criteria included 231 species of small carnivores in 12 families (Appendix S1), compared to only 25 species of large carnivores in five families. Unlike large carnivores, which are absent and unlikely to recover in many systems,

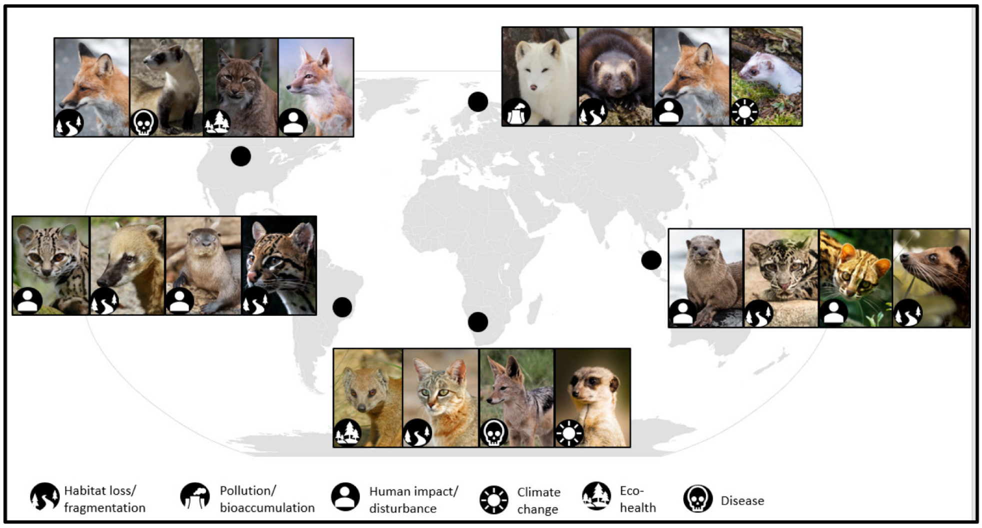

Fig. 1. The diversity of small carnivore (Carnivora) species that have been used as sentinels of environmental change in five different biomes globally. Temperate grassland in North America: red foxes *Vulpes vulpes* and human development (Kellner et al. 2020), black-footed ferrets *Mustela nigripes* and disease (Matchett et al. 2010), bobcats *Lynx rufus* and riparian health (Mosby et al. 2012), swift foxes *Vulpes velox* and land-use change (Butler et al. 2021). Tropical forest in South America: margays *Leopardus wiedii* and anthropogenic disturbance (Horn et al. 2020), South American coatis *Nasua nasua* and habitat fragmentation (Massara et al. 2016), Neotropical otters *Lontra longicaudis* and human impact (Andrade et al. 2019), ocelots *Leopardus pardalis* and forest loss (Cruz et al. 2019). Arid savanna in southern Africa: yellow mongooses *Cynictis penicillata* and bush encroachment (Blaum et al. 2007), black-backed jackals *Canis mesomelas* and disease (Bellan et al. 2012), African wild cats *Felis silvestris* and habitat fragmentation (Le Roux et al. 2015), meerkats *Suricata suricatta* and climate change (van de Ven et al. 2020). Tundra in northern Europe: Arctic foxes *Vulpes lagopus* and bioaccumulation (Fuglei et al. 2007), wolverines *Gulo gulo* and habitat fragmentation (May et al. 2006), red foxes and human impact (Elmhagen et al. 2017), least weasels *Mustela nivalis* and climate change (Mills et al. 2018). Tropical forest in Southeast Asia: smooth-coated otters *Lutrogale perspicillata* and land-use change (Kamjing et al. 2017), Sunda leopard cats *Prionailurus javanensis* and biodiversity (Chiaverini et al. 2022), leopard cats *Prionailurus bengalensis* and human impact (Chen et al. 2016), Hose's civets *Diplogale hosei* and habitat fragmentation (Jennings et al. 2013).

small carnivores are widely distributed and persist in most ecosystems (Fig. 1; Do Linh San et al. 2022).

Wider range of ecological niches and sensitivities

Small carnivores occupy a wider range of ecological niches than large carnivores and exhibit a wider variety of sensitivities to change (Flores-Morales et al. 2019, Do Linh San et al. 2022), providing flexibility in determining which small carnivore species is appropriate for a given context. Small carnivores also provide important ecosystem services. European badgers *Meles meles* increase habitat heterogeneity through digging behaviour (Kurek et al. 2014); golden jackals *Canis aureus* remove animal waste (Ćirović et al. 2016); several species are important seed dispersers (Nakashima & Do Linh San 2022); others control agricultural pests (Williams et al. 2018), where rodent predation can also reduce tick-borne disease transmission (Hofmeester et al. 2017); and some can even act as apex or dominant predators where large carnivores do not exist or have been extirpated (Roemer et al. 2009). As a result of these diverse ecological pathways, small carnivores can provide multiple measures of, or responses to, environmental change in a range of systems globally (Fig. 1).

Intermediate trophic position

Large carnivores that are apex predators respond directly to changes in the availability of medium-sized to large prey. Large carnivores can also respond to changes at lower trophic levels, though indirectly, and thus impacts are weaker and more difficult to observe. In contrast, small carnivores tend to be more centrally located within food webs, so that a change in small carnivore behaviour and/or abundance may more readily signal change resulting from changes in a number of trophic levels or processes. Small carnivores also fall on a generalist–specialist diet continuum and display a wide variety of diets. These traits make small carnivores more useful sentinels than large carnivores because they are directly affected by many pathways (Fig. 2).

At one end of the diet continuum, generalists such as coyotes *Canis latrans*, Indian foxes *Vulpes bengalensis*, and black-backed jackals *Canis mesomelas* exploit a wide range of food resources (Vanak & Gompper 2010, Fourie et al. 2015, Jensen et al. 2022). Generalist small carnivores can shift their dietary intake and are thus buffered from changes in the availability of certain foods, providing biodiversity monitoring in an effective, non-invasive, and economically viable way (e.g. via faecal DNA metabarcoding; Shao et al. 2021). At the other end of the continuum, there are several diverse specialists; aardwolves *Proteles cristatus* eat almost exclusively termites of the genus *Trinervitermes* (de Vries et al. 2011), black-footed ferrets specialise on prairie dogs *Cynomys* spp. (Jachowski 2014), and jungle cats *Felis chaus* specialise on rodents (Mukherjee et al. 2004). Specialists can make good sentinel species because they are more sensitive than generalists to changes that impact their prey availability (i.e. they cannot shift diet composition and are thus more directly impacted). For example, the population recovery of black-footed ferrets is dependent on the sufficient availability of prairie dogs (Jachowski et al. 2011).

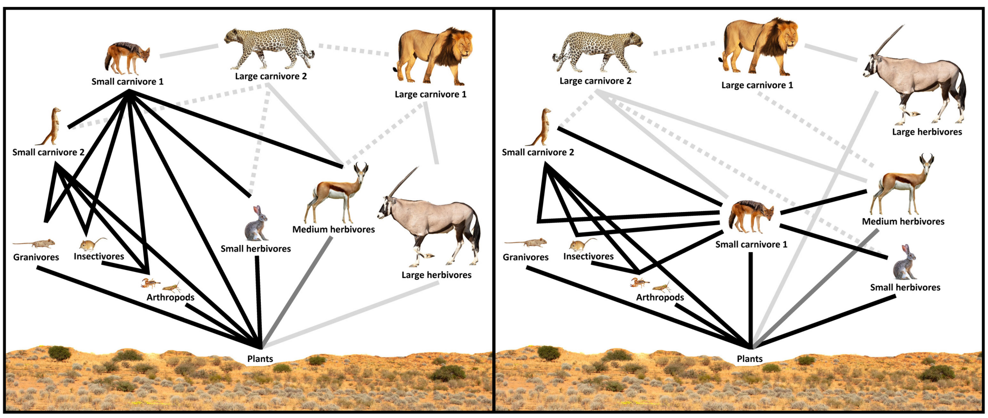

Fig. 2. The direct and indirect pathways impacting small and large carnivores (Carnivora) within a food web (Kalahari, sub-Saharan Africa). The left panel represents the established top-down food web, and the right panel represents our proposed middle-out perspective of the same food web. Pathways for large carnivores are indicated in light grey, and those for small carnivores are in black. A pathway that is included for both large and small carnivores is in dark grey (i.e. plants to medium herbivores). The dashed lines represent additional pathways for large carnivores that do not occur as frequently as solid lines or do not represent a significant proportion of biomass. This conceptual diagram is a simplified food web. However, it represents the notion that, proportionally, the networks are much more complex for small carnivores, with a wider range of prey taxa included in their diet and, ultimately, more nodes/food levels than for large carnivores.

The ecological diversity and intermediate trophic position of small carnivores mean they can be sentinels for changes at the producer, primary consumer, and tertiary consumer levels, thus allowing researchers to employ a 'middle-out' approach (Fig. 2).

Shorter lifespans and higher reproductive rates

Small carnivores are typically shorter-lived than large carnivores and have higher reproductive rates, making their populations more responsive to seasonal or annual fluctuations in environmental conditions (Holliday 2005). The mean maximum longevity of the 231 small carnivore species included in our database is 186 months (compared to 327 months for the 25 large carnivore species; Jones et al. 2009). On average, small carnivores have two litters per year with three offspring in each (compared to one litter per year with two offspring in each for large carnivores; Jones et al. 2009; Fig. 3). Shorter life cycles, higher reproductive rates, and larger litters make it easier to detect demographic and physiological responses to short-term and long-term fluctuations in environmental conditions. Examples include the demographic response of Canada lynx *Lynx canadensis* to the snowshoe hare *Lepus americanus* cycle (Krebs et al. 2001), and the rapid population increase of golden jackals following wolf *Canis lupus* extirpation in Europe (Krofel et al. 2017).

Smaller home ranges and higher abundance

Small carnivores typically have smaller home ranges than large carnivores, making it easier to assess how fine-scale changes or management interventions influence individuals or populations. The median home range size of the small carnivores in our database is 2 km^2, compared to 56 km^2 for large carnivores (Jones et al. 2009). From an experimental standpoint, the smaller home ranges of small carnivores also mean that populations can be manipulated and monitored more easily (also see below, 'Easier to monitor and manage'). While small and large carnivores are similarly threatened with extinction (Marneweck et al. 2021), small carnivores are often easier to monitor where they persist because they typically occur at higher densities than large carnivores (Chapman & Reiss 1999), ultimately providing larger sample sizes to assess species' responses to environmental change. For example, a density of 14 honey badgers *Mellivora capensis* per 100 km^2 was estimated for Tadoba-Andhari Tiger Reserve, India (Chatterjee et al. 2020), compared to three tigers *Panthera tigris* per 100 km^2 in the same reserve (Karanth et al. 2004). This research efficiency presents benefits in meeting management goals where funding is finite and other resources often limited.

Easier to monitor and manage

While some small carnivores are cryptic, they are generally easier to monitor and manage than large carnivores. For

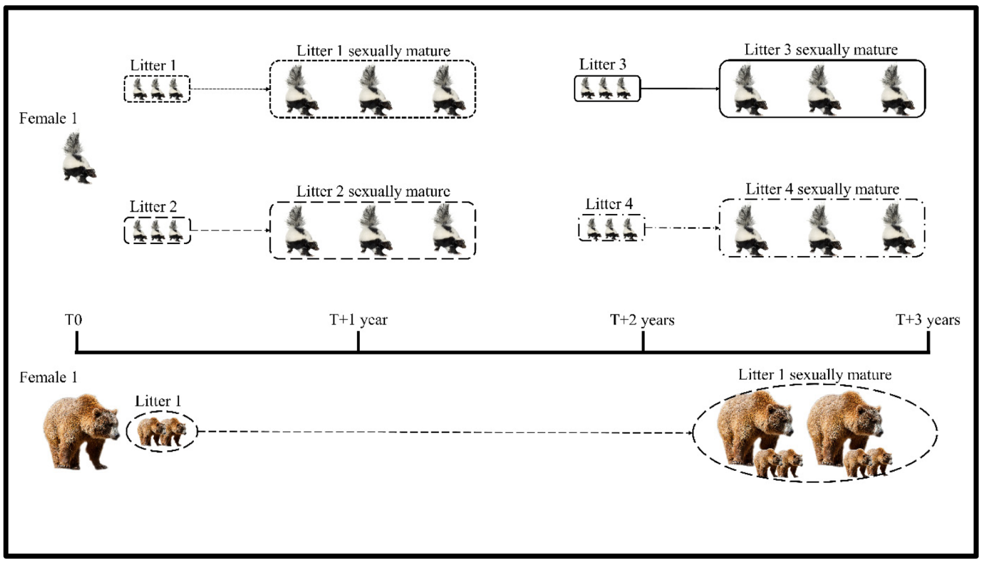

Fig. 3. Conceptual figure comparing the average reproductive rates over time for a large and a small carnivore (Carnivora). In this example, over approximately three years, one female brown bear *Ursus arctos* is able to produce one litter to sexual maturity, with on average one litter of two per year, the offspring of which reach sexual maturity at three years. In comparison, over the same time period, one female striped skunk *Mephitis mephitis* is able to produce four litters to sexual maturity, with on average two litters of three, twice per year, the offspring of which reach sexual maturity at one year (Jones et al. 2009).

example, free-ranging meerkats have been habituated to climbing on scales for regular weighing without sedation (Russell et al. 2002), and free-ranging bat-eared foxes *Otocyon megalotis* have been habituated to take part in sensory experiments (Renda & le Roux 2017). Moreover, manipulative experiments, such as where Haswell et al. (2018) used scent to study the foraging behaviour of red foxes *Vulpes vulpes*, would be very difficult to conduct with a large carnivore that ranges farther and occurs at lower densities than the red fox. Population management of small carnivores also tends to be less contentious and less polarising than it is with large carnivores. Small carnivores often occur in urban areas or in areas where large carnivores are absent, and handling them presents less dangerous working conditions in the field. These are important considerations for study implementation or monitoring, especially in community science projects.

CONCLUSIONS

Human-driven global change can have both negative and positive impacts on small carnivores. Increasing temperature negatively affects offspring survival (e.g. meerkats; van de Ven et al. 2020) and imposes a trade-off between foraging and thermoregulation (e.g. least weasels *Mustela nivalis*; Zub et al. 2013), which could have knock-on effects for food-web dynamics. Droughts, which will become more frequent (IPCC 2014), reduce the space and food available to species dependent on water (e.g. Eurasian otters; Ruiz-Olmo et al. 2007). Changing climate can also increase intra- and inter-specific competition pressure because of the reduced space and/or time available for coexisting (Lancaster et al. 2017). Although anthropogenic pressure causes habitat fragmentation, urban and transformed environments can provide important habitat for small carnivores (e.g. African golden cats *Profelis aurata*, Bahaa-el-din et al. 2016; jungle cats, Katna et al. 2022; water mongooses *Atilax paludinosus*, Streicher et al. 2021), and may facilitate dispersal (e.g. banded mongooses *Mungos mungo*; Verble et al. 2021). Moreover, anthropogenically provided food supports many species, which may relax intra- and interspecific competition for generalists (Newsome et al. 2013, Lancaster et al. 2017). Because there are multiple directions of impact, changes in the physiology, behaviour, distribution, and/or abundance of small carnivores can indicate environmental change, and their life-history traits make these changes observable in a timely manner. These characteristics highlight their utility as sentinels.

We do not dispute that large carnivores are sensitive to change due to their low densities, limited dispersal ability, and lower reproductive potential (Henle et al. 2004, Sergio et al. 2008). However, their longevity, slow reproductive rates, large area requirements, and the difficulty and cost of monitoring them result in slow data collection. At the same time, the ability of conservation managers to respond timeously in an era of rapid global change is critical to the conservation and maintenance of functional, biodiverse ecosystems in the Anthropocene. Therefore, identifying effective and efficient sentinel species is crucial. Accordingly, we advocate for embracing middle-out ecology (Fig. 2, right panel) and making much greater use of small carnivores as sentinels of global change.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. All Carnivora species considered small by our review criteria (i.e. order Carnivora, <21.5 kg, fully and semi-terrestrial; weight as per Jones et al. 2009, or estimated from similar sized species if unavailable, denoted by ~).