Aspects of foraging ecology of carnivores that impact digestive physiology and metabolism

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Introduction

The order Carnivora contains 270 extant species, living in all major habitat types around the globe and varying considerably in life history traits (Agnarsson *et al.*, 2010, Brooke *et al.*, 2014). Besides a carnivorous feeding ecology, the order also contains species that are omnivorous (e.g. maned wolf, *Chrysocyon brachyurus*), herbivorous (e.g. giant panda, *Ailuropoda melanoleuca*), and frugivorous (e.g. African palm-civet, *Nandinia binotata*). The carnivorous species show a large variation in body mass, varying from the least weasel (*Mustela nivalis*) weighing approximately 80 g to the polar bear (*Ursus maritimus*) weighing up to 365 kg (Gittleman, 1985). The body mass of the terrestrial carnivores relates to the size of their prey. Species weighing less than about 20 kg thrive on invertebrate and small vertebrate prey whereas species of more than 20 kg feed on vertebrate prey near their own mass (Carbone *et al.*, 1999, Gittleman, 1985). Compared to the behaviour and morphology of these species, relatively few comparative studies have been performed on the digestive physiology and metabolism as affected by the feeding ecology. Energy expenditure and requirements in carnivores have been linked to feeding strategies and to body size (Carbone *et al.*, 1999, Carbone *et al.*, 2007, McNab, 2000). Regarding digestive physiology, Clauss et al. (2010) reviewed literature data on the digestive efficiency in groups of carnivores (canids, felids, hyenids, mustelids, ursids, pinnipeds) and showed that the variation in efficiency of protein and fat digestion among studied carnivores is low. For domestic cats (*Felis catus*), however, it was highlighted that fat digestion is less efficient than that in dogs (*Canis familiaris*) (Clauss *et al.*, 2010).

The digestive physiological and metabolic traits of dogs and cats have been studied in detail and a range of similarities but also differences between these species have been revealed. Cats show various "metabolic idiosyncrasies", such as a reduced capacity to down-regulate amino acid catabolism and a low synthesis capacity for niacin, taurine and arginine, which were suggested to reflect the carnivorous nature of cats (Morris, 2002). As these idiosyncrasies are not or to a lesser extent shown by dogs, dogs have been labelled in authoritative scientific reference books as omnivorous in nature (Hand *et al.*, 2010, NRC, 2006). However, the 'omnivorous' physiological and metabolic traits do not match with the carnivorous foraging ecology of the dog's ancestor, i.e. the grey wolf (*C. lupus*). We have recently postulated that the differences in foraging ecology between the wild relatives of domestic dogs and cats might underlie the differences in specific traits (Bosch *et al.*, 2014).

Wildcats (*F. silvestris*) and feral/stray domestic cats are predominantly solitary and hunt individually catching a variety of mainly rodents (e.g. mice, voles) but also lagomorphs, birds reptiles and insects can be part of their diet (Malo *et al.*, 2004, Pearre and Maass, 1998, Plantinga *et al.*, 2011). Larger prey and opportunistic feeding have been reported like for feral cats on Macquarie Island (Australia) where cats preyed on rabbits over 1300 g and scavenged on dead elephant seals (*Mirounga leonina*) and penguins particularly during Winter time (Jones, 1977). It is difficult to actually measure kill rates of and biomass consumed by cats in the field, but estimates can be made. With an average prey mass of cats of 41.2 g (1.16% of their body mass) (Pearre and Maass, 1998) and an average energy content of 221 kJ (Kremen *et al.*, 2013), an adult cat of 4 kg with a daily energy requirement of 334.7 kJ/kg (Van Aarde, 1980) has to consume six prey. When preying on mice or voles (respectively 73.4 and 180.5 kJ, Kremen et al. 2013) the cat would require about 18 mice or 8 voles every day. Small prey species such as those from the genus Microtus or Peromyscus reach high population densities and remain fairly common (Gittleman, 1985) and can support small carnivores like cats.

In contrast to the assumed 'omnivorous' nature of dogs, modern-day wolves are carnivores with a varied but essentially animal-based diet and vegetal matter (nutritionally) being a minor to negligible component. Wolves predominantly live and hunt in packs on large ungulates but also opportunistically feed on smaller mammals (e.g. beavers, lagomorphs, rodents), birds, reptiles, fish, and insects (Bosch *et al.*, 2014). The amount of vegetal matter is low and composed out of grasses and various species of berries and nuts with a contribution to the total biomass consumed varying from 0.1% to 3%. Wolves can ingest large amounts of animal tissues, with feast meal weights of up to 22% of their body weight (Stahler *et al.*, 2006). Wolves do not consume the rumen contents but consume the rumen and intestinal walls. Estimates of daily biomass consumed in 19 studies ranged from 0.5 to 24.8 kg per wolf (Mech and Boitani, 2003). Based on energetic requirements (5 × basal metabolic rate; $70 \times BM^{0.75}$) and energy content of prey (7.7 kJ/g), a 35 kg wild wolf would require about 3.25 kg prey (Mech and Boitani, 2003). Based on our own estimates, a prey like an adult moose (*Alces alces*) would provide 8.2 kJ/g edible biomass and the wolf would require 3.05 kg every day. The number of prey to supply the biomass depends on the size of prey but also on the size of the pack and biomass lost to scavengers. With an average pack size of 8 hunting on a moose (Mech and Boitani, 2003) of 350 kg and edible biomass of 70%, the pack needs to kill a moose approximately once every 10 days. Obviously, these are rough estimations and prey interval will vary considerably given the variation in prey type and size and in energy expenditure and pack size (2 to 42 individuals, Mech and Boitani, 2003). Other large carnivores like cougars (*Puma concolor*) kill on average one ungulate every 9 days but also prey on smaller nonungulates (Knopff *et al.*, 2010), Amur tigers (*Panthera tigris altaica*) kill every 3.7 to 10.1 days (Miller *et al.*, 2013), and lions (*Pathera leo*) have a prey every 2.5 days in the plains and 3 to 3.5 days in the woodlands (Schaller, 1972).

It is important to point out that prey and carrion availability as well as prey vulnerability fluctuates around the year, for example due to cold and deep snow in Winter in the northern temperate and droughts and disease outbreaks during the dry season on the African savannah (Pereira *et al.*, 2014). This can result in seasonal food shortages that carnivores have to cope with. A pack of wolves may go days consuming only smaller prey and left-overs of old prey (Mech, 1970) and wolves have been observed to scavenge on bone and hide for even up to 10 weeks (Stahler *et al.*, 2006). Also cougars have been observed to go without an ungulate kill for 75 days, but survived by consuming smaller meals consisting of other carnivores, small mammals, birds,

or carrion (Knopff *et al.*, 2010). To have such a feast-or-famine lifestyle and withstand periods of food shortages like wolves and other carnivores experience, animals may respond in different ways. Predictable seasonal declines in food availability may result in torpor and hibernation, strategies to reduce metabolic rates (Millar and Hickling, 1990). Alternatively, energy may be stored in the form of endogenous lipid reserves or exogenous food caches. Wolves tend to increase lipid stores during Fall and Winter and caching of prey parts is also performed by wolves (Mech and Boitani, 2003). Wolves can also quickly recover from weight loss after fasting. Captive wolves lost 7-8% of their body mass after 10 days of fasting, which was replenished after 2 days of consuming white-tailed deer meat with daily amounts between 15 and 19% of their body mass (Kreeger *et al.*, 1997). Resistance to prolonged periods of famine is also shown by dogs. The longest fast of a dog on record is 117 days with the dog weighing only 37% of its initial body weight when the fast was stopped (Howe *et al.*, 1912). Ability to efficient use energy stores, decrease metabolic losses and to endogenously synthesise essential nutrients for on-going metabolic processes would be vital for survival prolonged periods of food shortage. During prolonged fasting where glycogen stores may become exhausted, the available lipid stores need to be effectively used for energy purposes and body proteins preserved (phase II of fasting). Ability of body tissues like the brain and heart to use ketone bodies from fatty acid catabolism decreases the demand for glucose from amino acids via gluconeogenesis pathways (McCue, 2010). Dogs efficiently switch to peripheral use of ketone bodies during fasting (de Bruijne and van den Brom, 1986) making them less dependent on amino acid catabolism for glucose. Conservation of body proteins is a common and vital coping strategy in animals adapted to seasonal fasting. Cats, however, are less capable of conserving protein as they maintain high activities of amino acid catabolizing enzymes for gluconeogenesis (Morris, 2002). This low ability to down-regulating enzymes involved in amino acid catabolism also becomes apparent when fed a diet without protein; adult cats produce twice as much urinary urea as dogs (243 vs. 116 mg kg$^{-0.75}$ d^{-1}) (Hendriks *et al.*, 1997). American mink (*Mustela vison*), a small opportunistic carnivore like the cat, has relatively poor adaptations to food deprivation (Mustonen *et al.*, 2005). During fasting, body protein catabolism of mink continues with reductions of 54-67% in liver proteins and 23-31% in muscle proteins after 5-7 days of fasting. After 7 days of fasting, proteolysis is increased (phase III). Several bear species like brown bears (*Ursus arctos*) and polar bears (*Ursus maritimus*) have even the capacity to reduce N losses 0 by recycling urea N back to protein and go for months without any food (Nelson, 1987, Stenvinkel *et al.*, 2013).

At times of feast, when large ungulates are killed, wolves in general rapidly open the body cavity and the internal organs such as the liver and heart are consumed (Stahler *et al.*, 2006), a consumption behaviour also observed in cougars (Beier *et al.*, 1995) and in lions (Schaller, 1972). The liver of an ungulate would provide stored vitamin A and potentially glycogen. Like most carnivores, dogs transport vitamin A mainly as retinyl esters bound to lipoproteins in the blood (Schweigert *et al.*, 1990). Dogs are also able excrete vitamin A and retinyl esters via the urine, which makes them more resistant to hypervitaminosis A (Raila *et al.*, 2000) and can be considered as functional for wolves and other carnivores consuming large quantities of vitamin A.

The array of physiological and metabolic traits showed by dogs are hypothesised to be shaped by the carnivorous feast-or-famine lifestyle rather than an omnivorous foraging ecology of their ancestor, the wolf (Bosch *et al.*, 2014). At present, these traits are not well studied in other large carnivorous species. It may be expected that similar capacities are also found in, for example,

cougars, tigers and bears, that share a feast-or-famine lifestyle and enabling them to survive prolonged periods of food shortage as observed in nature.

Acknowledgements

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