Predator size and prey size–gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals

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Abstract

Carnivore kill frequency is a fundamental part of predator–prey interactions, which are important shapers of ecosystems. Current field kill frequency data are rare and existing models are insufficiently adapted to carnivore functional groups. We developed a kill frequency model accounting for carnivore mass, prey mass, pack size, partial consumption of prey and carnivore gut capacity. Two main carnivore functional groups, small prey-feeders versus large prey-feeders, were established based on the relationship between stomach capacity (C) and pack corrected prey mass (iMprey). Although the majority of small prey-feeders is below, and of large prey-feeders above a body mass of 10–20 kg, both occur across the whole body size spectrum, indicating that the dichotomy is rather linked to body size-related ecology than physiology. The model predicts a negative relationship between predator size and kill frequency for large prey-feeders. However, for small prey-feeders, this negative relationship was absent. When comparing carnivore prey requirements to estimated stomach capacity, small carnivores may have to eat to their full capacity repeatedly per day, requiring fast digestion and gut clearance. Large carnivores do not necessarily have to eat to full gastric capacity per day, or do not need to eat every day, which in turn reduces kill frequencies or drives other ecological processes such as scavenging, kleptoparasitism, and partial carcass consumption. Where ecological conditions allow, large prey-feeding appears attractive for carnivores, which can thus reduce activities related to hunting. This is particularly so for large carnivores, who can achieve distinct reductions in hunting activity due to their relatively large gut capacity.

Key words: predator–prey size ratio, gut capacity, kill frequency

Introduction

Terrestrial carnivores are important drivers of the top-down control of ecosystems and the shaping of community structure, through both predation and intraguild interactions (Terborgh 1992, McLaren and Peterson 1994, Ritchie and Johnson 2009). Predator-prey relationships are considered fundamental for studying terrestrial and marine ecosystems (Cohen et al. 1993, Heithaus 2001, Carbone et al. 2014). Relating predator size to prey size is a commonly used approach to describe community interactions and feeding relationships at an interspecific level (Rosenzweig 1966, Holling et al. 1976, Paine 1976, Carbone et al. 1999, Tucker et al. 2016, Codron et al. 2018). For example, it is known that carnivore body size drives the choice for a specific prey size (Peters 1983, Carbone et al. 1999, 2014): a switch from small to large prey feeding occurs at a body mass threshold of about 20 kg (Carbone et al. 1999, 2007). Small carnivores (<20kg) tend to specialize on very small prey (vertebrates and a considerable amount of invertebrates) whereas large carnivores (>20kg) tend to opt for large vertebrates equal to or exceeding their own mass (Carbone et al. 2007). Correspondingly, it has been calculated that larger terrestrial carnivores need to hunt and kill less frequently (Peters 1983, Vézina 1985) and can generally be less active (Jeschke 2007, Rizzuto et al. 2018) and have more daily sleep (in contrast to decreasing daily sleep time with body size in herbivores; Siegel 2005). The explanations for the prey size dichotomy and its consequences have focused on the energetics of hunting (Carbone et al. 1999, 2007, Rizzuto et al. 2018) and on detection and encounter rates (Pawar et al. 2012, Carbone et al. 2014). In the present contribution, we use a model for the calculation of kill frequencies to draw attention to another aspect of carnivore physiology, namely a putative discrepancy in the scaling of energy requirements and maximum stomach capacity.

Reports of field kill frequency data are scarce and almost exclusively available for large carnivores, because of the labour intensive field methods and the fact that small prey items are mostly consumed entirely and therefore missed by field methods. Some publications give kill frequencies for small carnivores (e.g. van Aarde 1980; feral cat) but derive the data from caloric requirement estimations rather than on direct observations. Others only consider prey-specific kill frequencies (e.g. the number of moose killed by wolves) and do not consider all prey species killed by the carnivore (e.g. Zimmermann et al. 2015).

Apart from field kill frequency observations, efforts have been made to estimate carnivore kill frequency for a broad carnivore range based on carnivore prey size and energetic requirements (Peters 1983, Vézina

1985). In order to do so, simply stated, data on predator daily food intake (or ingestion rate) are divided by the average prey size of the predator. Typically, these kill frequency estimates predict a decrease in kill frequency with (i) predator body size and (ii) prey size for a range of mammalian and avian carnivores. These models predict that smaller carnivores require higher kill frequencies and thus need to invest a significant portion of their day hunting. Larger carnivores can afford to be 'lazy' since they can produce prey surplus on top of their energetic maintenance requirements (Jeschke 2007).

Several factors have not been accounted for in previous kill frequency modelling. Predators taking large prey can feed selectively, meaning that they can afford to consume highly digestible body parts such as muscles and organs (Hornocker 1967, Bowland and Bowland 1991, Stahler et al. 2006, Gidna et al. 2014, Bosch et al. 2015), whereas predators that kill comparatively small prey will consume their prey entirely (Mills 1996, Bothma and Coertze 2004, Anwar et al. 2011) including less digestible body parts (i.e. fur, skin, bones). Predators might not be able to fully consume large prey, due to the limitation of their own intake capacity; not considering predators separately whose prey does or does not exceed intake capacity may lead, for example, to unrealistic estimates of kill frequencies for a 4 kg cat of 0.8 (Vézina 1985) or 1.6 (Peters 1983) times per day, rather than the 'multiple times' considered realistic for cats (Bradshaw 2006).

Therefore, we wanted to explore the relationship between kill frequency and carnivore body size. In doing so, we develop a kill frequency model based on carnivore mass, the average of most common prey mass per carnivore species, the carnivore specific maintenance energy requirements and metabolisable energy in prey, and an estimate of hunting pack size. Instead of basing the division in carnivore functional groups on carnivore body mass (large vs small predator, with a threshold at which prey size switches), carnivores were appointed to one of two functional groups based on the relation of gut capacity to prey size. The question of how selectively and how much a carnivore will consume will be constrained by the gut capacity, which limits the biomass intake at larger prey sizes (Chakrabarti et al. 2016). Whenever the gut capacity is assumed to exceed prey size, the carnivore is considered a small prey-feeder. Whenever the prey size exceeds the gut capacity, the carnivore is considered a large prey-feeder. The inclusion of gut capacity expands the approaches used in the models of Peters (1983) and Vézina (1985) where energy requirements were derived from caloric food intake data of mainly captive animals (Farlow 1976), which makes it impossible to differentiate gut capacity from energetic requirements. According to the functional

group, prey energetic adjustments are made concerning incomplete and selective use vs complete and non-selective use of prey.

Our working hypothesis was that if the mean prey mass available for the individual predator at a kill scaled lower than, or similar to, energy requirements, then no reduction in kill frequency would occur with increasing predator mass; in contrast, if the prey mass available for the individual predator scaled higher than energy requirements, then a reduction in kill frequency would occur with increasing predator mass. We expected that these results would depend on the difference in the relationship between prey mass and gut capacity.

Material and methods

Data set (Supplementary material Appendices 1 and 2)

A literature review was performed using Web of Knowledge, Pubmed and Google scholar, from January 2014 to December 2015, to identify potentially eligible studies reporting feeding habits of wild carnivores. The literature search was conducted following Leenaars et al. (2012) by using two search terms, one based on the order of the Carnivora (latin name, common name, singular and plural) and the second on feeding habit associated factors (prey size, pack size, kill frequency, gut capacity), including all possible synonyms (e.g. nutrition, feeding habit). Aquatic carnivores or carnivores that depend on aquatic foraging strategies, as well as carnivores whose diet consists mainly ($\geq$ 50 %) of vegetation and/or invertebrates were excluded (based on the quantitative dataset on mammalian diets of Wilman et al. 2014). The latter was done given the difference in foraging strategies between terrestrial vertebrate-prey feeders and omnivorous carnivores, and aquatic carnivores. Clearly, these foraging strategies differ in terms of search and feeding time (e.g. the difference in dispersal of terrestrial vertebrate and invertebrate prey; in the marine environment several small prey can be 'subdued' in the same hunting bout by filter-feeding whereas this is not possible in terrestrial environments; cf. Pawar et al. (2012) and Carbone et al. (2014)).

The following data were extracted from each publication: carnivore species, study location, methods used for diet analysis (scats, kill remains, live views, gastrointestinal content, regurgitation), number of samples, carnivore sex, most frequent prey based on frequency of occurrence (=identified prey items of a certain species/total number of scats or other (%)) or relative frequency of occurrence (= identified prey items of a certain species/total number of prey items (%)), pack size (number of animals) (N_{pack}), kill frequency (1 kill/x days) (the 'real' or actually observed kill frequency) and maximal gut capacity

(kg/carnivore/feeding event) (C). Typically, in herbivores, gut capacity estimates are obtained by measuring the total content of the gastrointestinal tract (Parra 1978, Müller et al. 2013). The carnivore estimates used here stem from the maximal stomach (and not total gut) capacity reported in literature. Nonetheless, these estimates can be considered reliable since the carnivore stomach acts as a 'batch reactor' from which food is dispersed, hence playing a decisive role in the maximal contents that can be sustained in the gastrointestinal tract (Hume 2002). For the lion (*Panthera leo*), the spotted hyena (*Crocuta crocuta*), the tiger (*Panthera tigris*), the leopard (*Panthera pardus*), the cheetah (*Acinonyx jubatus*) and the African wild dog (*Lycaon pictus*), we included the reviews of Hayward and collaborators (Hayward and Kerley 2005, Hayward 2006, Hayward et al. 2006abc, 2012). Therefore, publications used in these reviews were excluded from the dataset to avoid doubling of information. For pack size, maximal gut capacity and kill frequency data, additional literature searches were conducted. For more detailed information on data acquisition, see the Supplementary material Appendix 2.

Actually observed kill frequency data were corrected for the pack size of the carnivore species, obtained from the publication itself (i.e., dividing the reported frequency with pack size). Kill frequencies that apply only to a specific prey species (e.g., the number of moose killed by wolves, irrespective of other prey taken in the same time period) were not taken into account since these estimates did not consider all prey species hunted by the carnivore (Kroshko et al. 2016). Per carnivore species, the average of most common prey mass (M_{prey}), the average N_{Pack} and the average actually observed kill frequency were calculated. We are aware that environmental conditions (such as season or geographical location) (e.g. Zalewski 2005) or the sex within dimorphic species (e.g. Zalewski 2007) can affect the prey size hunted by the carnivore. However, the initial aim was to assess the effect of carnivore body size on kill frequency, and hence generalisations are required. We are also aware that pack size is a general term and can differ depending on the context (population group, foraging group, feeding group, breeding group; Gittleman 1989). However, many reports describe pack size as is, without differentiation of groups. Additionally, one has to generalize in order to study the relationship body size vs kill frequency, hence N_{pack} data obtained in this dataset are of an averaged kind, with the preference, if reported, of the pack size number concerning the feeding group.

Kill frequency modelling

A theoretical kill frequency (KF) model was developed based on M_{pred}, M_{prey}, carnivore specific maintenance energy requirements (Q_{pred}) and metabolisable energy in prey (E_{prey}). For each species, KF is calculated as Q_{pred} / E_{prey}.

Based on the scaling relationships of

$M_{prey} \sim M_{pred}^{p}$

$Q_{pred} \sim M_{pred}^{q}$

and the assumption that the energy content of prey is directly proportional to prey mass, we would expect

$KF \sim M_{pred}^{(q-p)}$

However, given the occurrence of pack hunting, and our considerations about feeding selectivity and gut capacity, several modifications to this simple concept need to be applied. Under the assumption that pack size scales with predator mass

$N_{pack} \sim M_{pred}^{n}$

the amount of prey available for the individual predator (iM_{prey}) scales to

$iM_{prey} \sim M_{pred}^{(p-n)}$

and therefore

$KF \sim M_{pred}^{(q-p+n)}$

Note that a scaling of pack size with body mass may not be expected, but data for individual species must be corrected for pack size nevertheless.

The relationship of $M_{prey} \sim M_{pred}^{p}$ needs to be established for several groups of predators, in relation to their gut capacity C. We divided predators into those where $iM_{prey} < 1\%$ of C (i.e., predators mainly preying on insects), those where 1% of $C < iM_{prey} < C$ (or 'small prey-feeders'), and those where $C < iM_{prey}$ (or 'large prey-feeders' who cannot consume their average prey in one meal). As long as the mass of an individual prey item (M_{prey}) is smaller than C, M_{prey} is the main driver of KF in our dataset. As soon as M_{prey} is larger than C, however, C becomes one factor constraining KF. The E_{prey} for small prey-feeders was estimated at 5348 kJ/kg fresh weight calculated from data given by Plantinga et al. (2011), and prey items < 5 kg were considered to be completely edible whereas prey items of > 5 kg were considered 95% edible (due to inedible portions of skin and skeleton). For large prey-feeders, prey was considered to be consumed as 70% (Mills 1990, Stander 1992, Caro 1994) at a E_{prey} of 8048 kJ/kg fresh weight (the average value given by Bosch et al. 2015, taking into account the selective feeding of wolves *Canis lupus*). Large prey predators were assumed to only consume the equivalent of their gut capacity C per

day. For this group, KF estimates were either based on a single-day feeding on their prey (in a selective mode, i.e. eating the amount of C at 8048 kJ/kg) or a complete consumption of their prey (in a non-selective mode, i.e. with 95% consumption at 5348 kJ/kg, over more than one day), to outline theoretical minimum and maximum kill frequencies.

Following Nagy et al. (1999), we parameterize the relationship of $Q_{pred} = b\ M_{pred}^{q}$ as $Q_{pred} = 791kJ$ $M_{pred}^{0.85}\ d^{-1}$. Hence, maintenance energy requirements are based on field metabolic rates (FMR). The latter is advantageous since data are based on exclusively free ranging animals rather than mainly captive animals (Farlow 1976, Peters 1983, Vézina 1985), and derive physiologically from energy expenditure and not from intake (as in the Farlow dataset used by Peters 1983 and Vézina 1985). One must hereby acknowledge that Q_{pred} is based on the assessment of field metabolic rates (FMR) by scaling it to body mass. Next to body mass, other factors such as taxonomy, diet, habitat and season may determine the FMR of animals.

Evaluations of scaling relationships were performed using linear regressions for log-transformed data in generalized least squares (GLS) in R using the package nlme (Pinheiro et al. 2011). To account for the phylogenetic structure of the dataset, data were linked to a phylogenetic tree (Fritz et al. 2009), and also analysed in phylogenetic generalized least squares (PGLS) with the phylogenetic signal λ estimated by maximum likelihood, using the package caper (Orme et al. 2010). Using GLS regression to analyse the data is important for a comparison with previous work that is also based on linear regression (Peters 1983; Vézina 1985), and with PGLS results, and is also justified because due to the methodological steps involved in deriving an average M_{prey}, the uncertainty in the M_{prey} data is higher than in the M_{pred} data. However, because when scaling allometries are not considered predictive equations where one measure shall be predicted by another, but shall be analysed for the best fit to the data, (standardised) major axis regression is more appropriate (Warton et al. 2006), we also report standardised major axis (SMA) regression results as calculated using the R smatr package (Warton et al. 2012). Extrapolation to other species (for C) was based on GLS scaling, because PGLS scalings are based on phylogenies that do not include the species to which the extrapolation is to be applied. Because we considered the polar bear (*Ursus maritimus*) as an extreme example of a predator that might switch between comparatively small prey (fish) and large prey (seals), we excluded this species from scaling analyses, and used it as an example for the range of kill frequencies available to large carnivores with the option to switch between

two functional carnivore groups. For comparison, the KF models of Peters (1983) and Vézina (1985) were included in the graphs representing our KF.

The original data compilation is available from the Dryad Digital Repository: doi link (De Cuyper et al. 2018).

Results

Carnivore characteristics

A total of 456 studies (listed in Appendix 1), 513 prey size data points, 182 pack size data points, 56 kill frequency data points and 22 stomach capacity data points were incorporated in the database. Seventy-eight carnivore species (listed in Appendix 1) were included in the prey size database. Pack size data could only be obtained for 75 species. Actually observed kill frequency data were obtained for 11 species. Carnivore weight ranged from 0.1375 to 387.5 kg. Data on the maximal stomach capacity (C) were available for 9 species ranging in body mass from 0.19 kg to 150.0 kg; these data were used to determine the allometric function in GLS [with 95% CI] of $C = 0.09\ [0.06;0.14]\ M_{pred}^{1.19\ [1.07;1.30]}$, which was used to extrapolate C for all carnivore species; SMA yielded a similar result of $C = 0.09\ [0.06;0.15]\ M_{pred}^{1.20\ [1.06;1.34]}$.

Of the 75 carnivore species for which pack data were available, 12 species were pack hunters and 63 species were solitary hunters. Pack size scaled nominally to $1\ [1;1]\ M_{pred}^{0.14\ [0.05;0.24]}$ in GLS but to in $1\ [0;1]\ M_{pred}^{0.44\ [0.35;0.54]}$ SMA. Of the 12 pack hunting species, 7 species had a $C < iM_{prey}$, i.e. the pack could not consume the whole prey animal in one day. Five pack hunting species had larger C than iM_{prey}, i.e. were supposedly sharing prey that each individual could have eaten more of - the yellow throated marten (*Martes flavigula*, 2 pack members), the golden/Asian jackal (*Canis aureus*, 2.5 pack members), red wolf (*Canis rufus*, 2.4 pack members), Ethiopian wolf or simien jackal (*Canis simensis*, 5.7 pack members), and bush dog (*Speothos venaticus*, 11 pack members). Of these, only the bush dog had a higher M_{prey} than C (i.e. the pack was killing prey that would have been too large to be consumed by an individual member). Therefore, the bush dog appeared as an outlier in the graph displaying the M_{pred}-M_{prey} relationship (Fig. 1a), but not in the graph linking M_{pred} to iM_{prey} (Fig. 1b).

Actually observed kill frequency data were found for 11 species weighing between 11.2 kg and 175.5 kg. Using species averages, the actually observed kill frequency scaled to $1.11\ [0.20;6.18]\ M_{pred}^{-0.48\ [-0.91;-0.04]}$ in GLS and $4.15\ [0.57;30.53]\ M_{pred}^{-0.81\ [-1.45;-0.46]}$ in SMA, and did not show a phylogenetic signal (λ not significantly different from 0).

Predator-prey mass scaling

Across all carnivore species, prey mass scaled to predator mass with a scaling exponent larger than 1.00, also exceeding linearity in the 95% confidence interval (Table 1). In contrast, when considering carnivore groups individually based on relative prey size, linear scaling was included in the 95% confidence interval of both small and large prey predators in GLS and PGLS (but not in SMA; Table 1). However, there was a large difference in the scaling factor (intercept), which was 0.05 for small prey-feeders and 0.5 for large prey-feeders in GLS (and of similar magnitude in SMA), with no overlap in the 95% confidence intervals (Table 1).

Kill frequency model outcomes

The overall KF scaling in the complete dataset had a very steep scaling with an exponent of -0.66 in PGLS and -1.51 in SMA (Table 2). However, when considering predator groups individually, small prey-feeders did not have a significant scaling of KF with body mass in GLS, PGLS or SMA (Table 2, Fig. 2), and had a mean of 7 ± 12 kills per day. In contrast, large prey-feeders had a significant negative scaling, which was shallower in GLS and steeper in SMA if complete consumption of prey was assumed (Table 2). The range of kill frequencies for large prey predators was between two kills per day and one kill every 29 days (Fig. 2).

A stringent check of the consistency of our approach is that even though there was no significant scaling of pack size with body mass, the scaling exponents should theoretically correspond to $KF \sim M_{pred}^{(q-p+n)}$. In the whole dataset, $q = 0.85$ due to our use of the regression of Nagy et al. (1999), and in GLS $p = 1.56$ (Table 1) and $n = 0.14$. Therefore, we would expect KF to scale, in GLS, to $0.85 - 1.56 + 0.14 = -0.57$, which corresponds closely to the resulting exponent of -0.53 in Table 2. Deviations from the expected exponent are due to the additional data scatter introduced by adjustment factors for carcass use (complete vs. incomplete) and energy content of prey. In SMA, the corresponding values are $p = 2.34$ (Table 1) and $n = 0.44$, leading to a scaling expectation of $0.85 - 2.34 + 0.44 = -1.05$, which deviates substantially from the resulting exponent of -1.51 in Table 2, underlining the fact that SMA cannot be used for deriving predictions based on one main variable (here, body mass).

The polar bear (*Ursus maritimus*) is an example of a species that, depending on its seasonal ecotype (i.e., ice bound, winter prey = seal; land bound, summer prey = mixed, e.g. geese and fish; Russell 1975, Dyck and Romberg 2007, Gormezano and Rockwell 2013), might have a very low kill frequency / be a very selective feeder in winter, and be a non-selective feeder with a higher kill frequency in summer (Fig. 2).

When plotting the amount of prey required to meet energy demands as well as the estimated gut capacity against M_{pred} (Fig. 3), it appears that small predators have to eat more than their gut capacity per day (i.e., must also have a stomach clearance of less than a day), whereas large predators from approximately 4 kg upwards can, in theory, ingest more prey per day than required, and thus might not need to hunt the same number of prey items on a daily basis; from a body mass of approximately 30 kg upwards, large predators could theoretically eat to their full gut capacity (or hunt prey of sufficient size) only once every other day.

Discussion

Although the general output for the whole body mass spectrum is a negative scaling of kill frequency to carnivore bodymass, our results demonstrate that depending on the prey size selected by terrestrial mammalian predators, these predators may vary distinctively in their kill frequencies, and hence their daily activity budgets and hunting behaviours. While for the group of predators that, on average, subdue prey that exceeds their instantaneous gut capacity (large prey-feeders) a decrease in kill frequency with body size is a model output, similar to the general findings of Peters (1983) and Vézina (1985), such a relationship with body size is not evident in predators focussed on prey of a size that is smaller than their instantaneous gut capacity (small prey-feeders). Notably, our dataset showed that whether or not predators focus on prey larger or smaller than their own instantaneous gut capacity is not necessarily a function of body size, because some smaller predators also apparently pursue such a large prey-feeding strategy. However, there was the well-described general pattern that below 10-20 kg of body mass, more predators were 'small prey-feeders' that hunt for prey well below their instantaneous gut capacity, whereas above 10-20 kg, predators mainly go for comparatively larger prey (Carbone et al. 1999). One of the major implications for the ecological impact of predators is that they can be classified into those that only hunt what they will necessarily consume for themselves, and those that potentially (but not necessarily) create a surplus of prey (for themselves, or the wider community of scavengers or kleptoparasites) because they cannot completely consume their prey instantaneously. It is this latter group that must be considered facilitators of additional trophic interactions.

As evident from Fig. 2, our model yields results that differ in relevant ways from those of previous estimates of carnivore kill frequencies. Given the broadness of all of these approaches, we do not claim our model to be superior, but consider its main relevance in emphasizing a dichotomy in potential ecological impact between predator categories. In particular, given the flexibility of predator species in the prey size they use, evident in the different 'preferred' prey species for a given predator species

between original observational studies, we do not suggest that the scaling exponents derived in the present study are biological laws of an exact magnitude. Rather, they describe a pattern that may differ in the exact scaling exponent depending on the original studies considered. When compared to the scaling of actually observed kill frequencies, which were available from the literature exclusively for large prey-feeders, the large confidence interval of its scaling exponent (GLS: $M_{pred}^{-0.48\ [-0.91;-0.04]}$; SMA: $M_{pred}^{-0.81\ [-1.45;-0.46]}$) included the scaling for large prey-feeders in our model (GLS: $M_{pred}^{-0.33\ [-0.34;0.31]}$ for the single meal and $M_{pred}^{-0.22\ [-0.40;-0.04]}$ for the complete consumption strategy; SMA: $M_{pred}^{-0.33\ [-0.35;-0.31]}$ and $M_{pred}^{-0.51\ [-0.74;-0.37]}$, respectively). Differences in the real scaling exponent to model estimates are most likely due to either specific characteristics of the populations under observation, or an under-representation of smaller prey in observational studies (due to unintended bias in behavioural observations towards large prey; Sunquist 1981).

Possibly the most important factor that was implicit to, but not explicitly stated in, the previous models (Peters 1983, Vézina 1985) is gut capacity C. Our model used different estimates for intake capacity (as gut capacity C) and energy requirement that had different scaling exponents (Fig. 3). Conceptually, this approach accounts for the experimental observation that food intake increases asymptotically with larger M_{prey} (Wachter et al. 2012, Chakrabarti et al. 2016). If we assume this difference in scaling to be true for carnivores, this also means that smaller carnivores would have to eat, within the same day, repeatedly to their gut capacity, either from the same large carcass or several small prey items, to meet their energy needs. Correspondingly, assuming intake at C, the model yields two kills - or, in this case, eating events - for a small-bodied large prey-feeder (a mustelid). This can only be achieved if stomach clearance (or digesta passage or retention time) is < 24 hours. At published whole-gut retention times of 1.96 to 11.75 h in mustelids (e.g. Japanese marten *Mustela melampus*; Tsuji et al. 2015), this condition is apparently given.

The situation assumed in our carnivore model, of a discrepancy in the scaling of gut capacity on the one, and requirements on the other hand, resembles a concept in herbivores where gut capacity also scales higher than requirements, thus potentially allowing larger herbivores to subsist on lower quality-diets by just ingesting disproportionately more of them (Clauss et al. 2013, Müller et al. 2013). In carnivores, the discrepancy between gut capacity and requirements does not buffer against a lower quality-diet, but allows larger intervals between hunting (and even eating) events. Evidently, this potential can only be used if these larger carnivores pursue a strategy of large prey feeding. Although larger carnivores could in

theory also meet their energy demands by ingesting many small prey items (such as the Ethiopian wolf *Canis simensis* in our dataset that feeds on small rodents), the combination of their relatively large gut capacity and the ecological availability of large prey allows them to reduce hunting efforts (Carbone et al. 2007, Rizzuto et al. 2018), feed selectively on the large prey they acquire, and become 'full and lazy' (Jeschke 2007).

Alternatively, the production of food surplus could drive other behavioural/ecological processes such as food hoarding, caching and pack defence of the carcass to safeguard excess prey from kleptoparasites (competing predators that try to steal a carcass from other predators) and scavenging, and could lower kill frequencies for large prey-feeders even more since the carnivore could eat from the prey for several subsequent days. For instance, the Eurasian lynx *(Lynx lynx)* and wolverine *(Gulo gulo)* both prey upon reindeer *(Rangifer tarandus)*, with the wolverine (facultative scavenger) being more prone to scavenging lynx (obligate predator) kills. The wolverine kill frequency typically decreases when lynx-wolverine ratio increases from 1 to 2, i.e. the lynx provides more scavenging opportunities (Andrén et al. 2011). Subordinate predators such as cheetah *(Acinonyx jubatus)* or African wild dogs *(Lycaon pictus),* both losing their prey to lions and hyenas (Kruuk 1972, Schaller 1972, Gorman et al. 1998), may choose the time of day or the geographic location of their hunts so that contact with superior predators is minimized (Stander 1990, Mills and Gorman 1997). The leopard *(Panthera pardus)* often moves prey into trees, caves, large burrows or dense vegetation to safeguard its prey surplus, but less so when kleptoparasites are not present (Sunquist and Sunquist 2002, Balme et al. 2017). Food caching has been described in wolves, bears (eg. *Ursus maritimus*), hyenas, felids (eg. bobcats and tigers), and mustelids (Harrington 1981, Sunquist 1981, Vander Wall 1990, Phillips et al. 1990). Thus, some carnivores can feed for several days on the same carcass. Alternatively, if resources and conditions allow, they may choose to not even consume a carcass, but only its most nutritious parts, and rather hunt new prey than consume the less digestible portions (Stirling and McEwan 1975, Gende et al. 2001).

Mid-to-small-sized carnivores show a large variety in kill frequency with our model approach (Fig. 2). Most mid-sized carnivores are not limited by their maximal gastric capacity, but by their choice of small prey. This may also be due to the low availability of large prey in their habitat (cf. Ethiopian wolf) or a lack of sociality in these species that otherwise would help to overcome large prey (Lamprecht 1978). In comparison, larger predators may be limited in their ability to prey on smaller prey species due to the challenge of obtaining a sufficient number of these comparatively small packages. Because small prey

items cannot be filtered out of a terrestrial environment but must be comprehended individually, larger animals are limited in the prey size they can pursue, in contrast to marine predators that can filter small prey items out of their environment (Carbone et al. 2014).

Findings on kill frequencies may have several implications for the feeding of captive (domestic and non-domestic) carnivores. The wildcat *(Felis silvestris)* for example is a solitary hunter that mainly focuses on prey with a lower body mass (e.g. rodents, birds), which makes it necessary to kill several times per day (MacDonald et al. 1984, Bradshaw 2006). Nowadays, domestic cats or wild cats kept in zoos are often offered single meals per day, which may contribute to the increasing problem of obesity in at least in domestic cats (Laflamme 2006, Bissot et al. 2010, Deng et al. 2013). Non-domestic carnivores in captivity such as the lion often suffer from problems related to dietary over-supply (i.e. obesity, inactivity and stereotypy). In a study where lions were gradually adapted from a conventional feeding program to a random gorge feed/fasting day program, it was observed that food digestibility and body weight improved (Altman et al. 2005). In particular, recent speculations suggest that a practice of feeding large-prey feeders, such as lions or tigers, daily - and hence comparatively small - rations, may prevent these animals from ever experiencing the extreme distension of their stomach that occurs after a gorge-feeding event, and that is putatively linked to satiety (Veasey 2017). Hence, these animals might be in a constant condition where their energetic requirements are met but they do not receive an important satiety signal, which could be the reason why these carnivores are particularly susceptible to showing stereotypies (Clubb and Mason 2007). Elucidating feeding strategies in the wild such as the relationships between predator size, prey size and kill frequency is therefore a key part in the management of carnivores *ex situ*. In conclusion, our model outcomes corroborates predictions that at larger predator size, the intake capacity exceeds the energetic requirements, leading to a reduction in kill frequency if the typical prey individual exceeds the predator's gut capacity. Kill frequency outcomes for small prey-feeders were more variable, mostly not limited by gut capacity, and did not result in a kill frequency reduction. Thus, a functional dichotomy seems to exist in carnivores, but ecologic rather than physiologic factors seem to determine whether a carnivore is a 'small prey-feeder' or a 'large prey-feeder'. This functional dichotomy may well occur within species where different individuals are specialized on different prey (Codron et al. 2016), within individuals over ontogeny (Elbroch et al. 2017), or in individuals between hunting events (Lumetsberger et al. 2017). Observations deviating from the general pattern, such as a population of wild cats living on rabbits rather than small rodents (Malo et al. 2004), or a population of wild dogs living

mainly on very small ungulates (Woodroffe et al. 2007), indicate that the underlying cause for the

dichotomy must be sought in ecological circumstances rather than fixed physiological and behavioural

adaptations.

Declarations

Conflicts of interest: The authors declare that they have no conflict of interest.

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Supplementary material

Supplementary material (Appendix 1-2 (OIK-05488) as well as the original data as a file of several Excel spreadsheets at Dryad.

Figure legends

Fig. 1 Relationship between predator mass and (a) average prey mass or (b) average prey mass divided by the number of pack members (iM_{prey}). The dotted line represents y=x (predator mass = prey mass). Predators are grouped according to their iM_{prey} relative to their stomach capacity C. The linked diamonds indicate the two ecotypes of the polar bear (*Ursus maritimus*, see text). Note that due to its comparatively large prey and large pack size, the bushdog (*Speothos venaticus*) is an outlier in (a) but not in (b). For statistics, see Table 1.
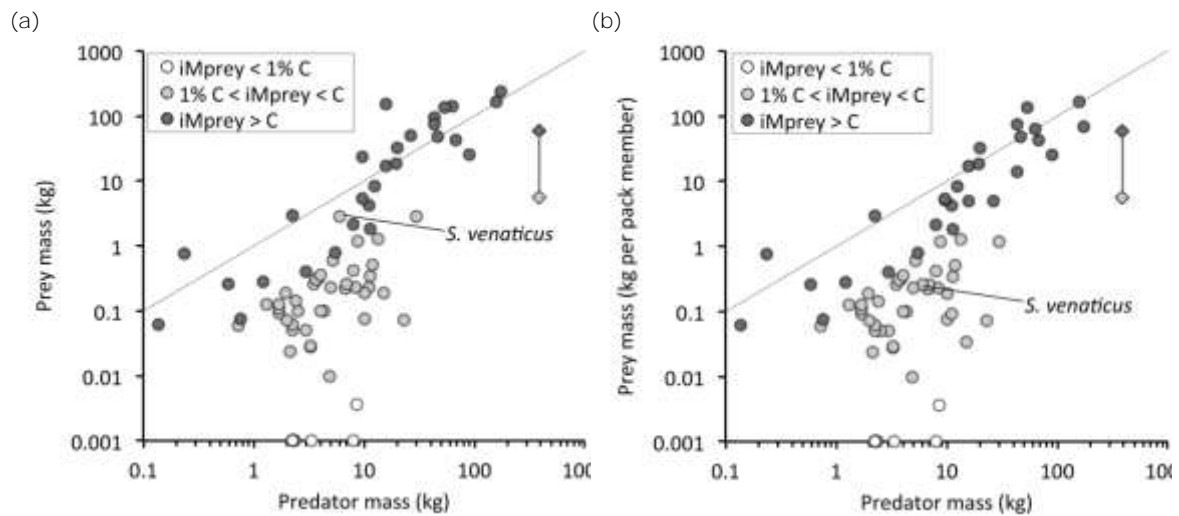
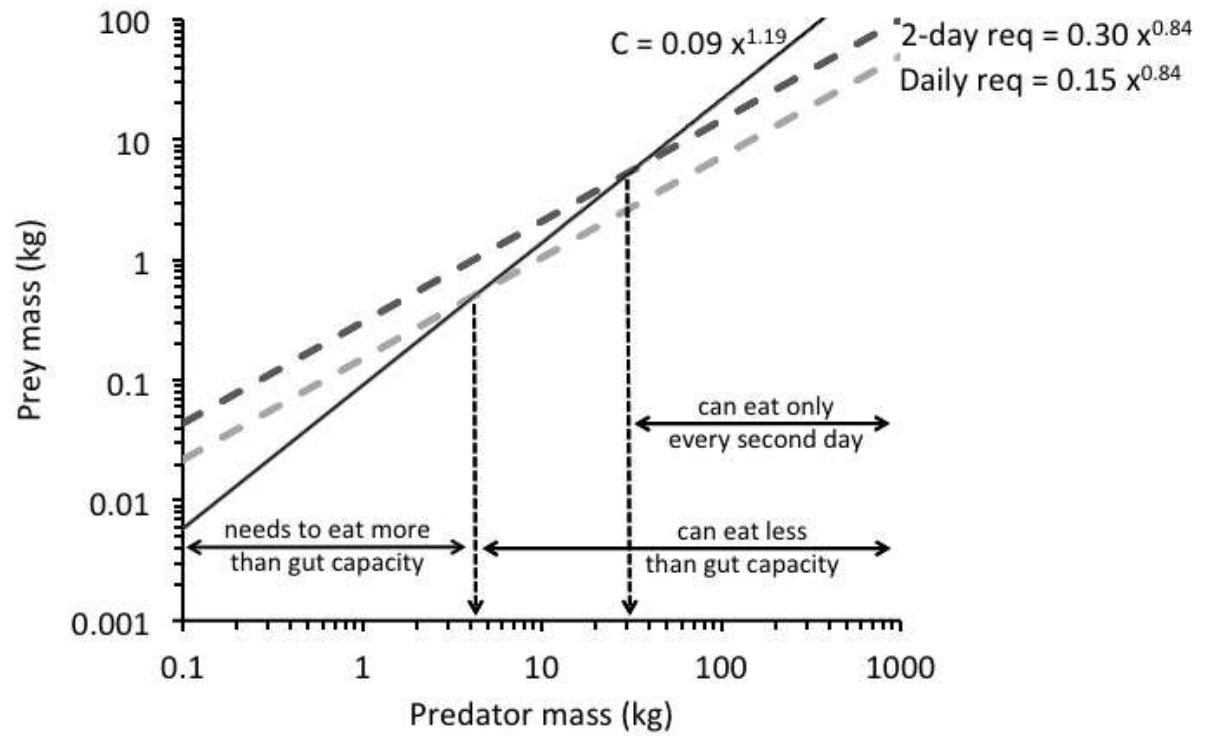**Fig. 2** Relationship between predator mass and the kill frequency (kills per day) necessary to meet energy demands for the species-specific average prey items. Predators are grouped according to their iM_{prey} relative to their stomach capacity C. The linked diamonds indicate the two ecotypes of the polar bear (*Ursus maritimus*, see text). For large prey predators, the two linked data points indicate the kill frequency assuming a single meal from the prey (upper points, constrained by stomach capacity), and the kill frequency assuming that the prey can be consumed completely (i.e., over the course of several days, without scavengers or kleptoparasites), with dark dotted lines indicating the respective GLS regression lines. The bright dotted line indicates the (non-significant) GLS regression line for small prey predators. Actually observed kill frequencies reported in the literature (for sources, see Appendix 1 and the Dryad Digital Repository) are indicated as crosses. The light grey line represents the model by Peters (1983), the dark grey line the model by Vézina (1985). For statistics, see Table 2.
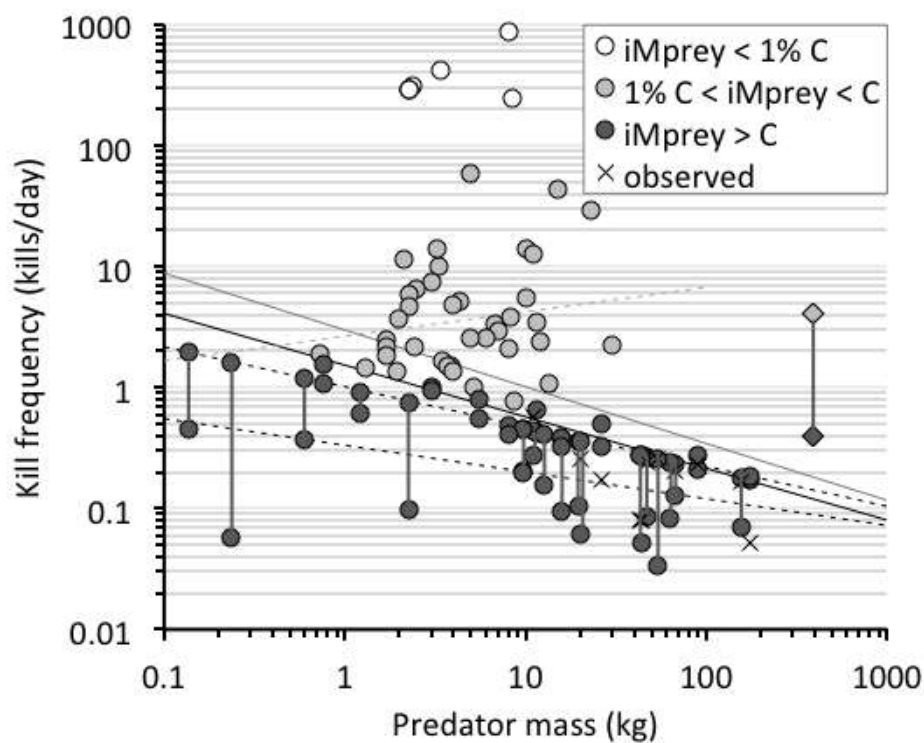
Fig. 3 Comparison of the scaling of stomach capacity C and the daily prey mass requirement with predator mass. Theoretically, below 4 kg, predators have to ingest more than their stomach capacity (i.e., have a shorter stomach passage than one day), whereas above 4 kg, predators can afford to eat less than their stomach capacity per day, and above 30 kg, predators can afford to only hunt/eat every second day.

Table legends

Table 1 Scaling relationships of prey mass (M_{prey}) or prey mass available for the individual predator (iM_{prey}) with predator mass (M_{pred}) according to $a\,M_{pred}{}^{b}$ in different datasets (depending on the relationship between stomach capacity C and iM_{prey}) using standardized major axis regression (SMA), generalized least squares (GLS) or phylogenetic generalized least squares (PGLS)

Dependent variable	Dataset	n	Statistic	λ	*a* (95%CI)	*b* (95%CI)	*p*
M_{prey}	whole	74	SMA	-	0.01 (0.00;0.02)	2.34 (1.97;2.79)	<0.001
			GLS	(0)	0.03 (0.01;0.07)	1.56 (1.17;1.96)	<0.001
			PGLS	0.220*	0.02 (0.00;0.08)	1.74 (1.30;2.18)	<0.001
	$1\%C < iM_{prey} < C$	40	SMA	-	0.02 (0.01;0.04)	1.52 (1.15;2.00)	<0.001
			GLS	(0)	0.05 (0.02;0.10)	0.81 (0.40;1.22)	<0.001
			PGLS	0*	-	-	-
	$iM_{prey} > C$	27	SMA	-	0.39 (0.20;0.78)	1.31 (1.12;1.55)	<0.001
			GLS	(0)	0.52 (0.27;0.98)	1.19 (0.98;1.41)	<0.001
			PGLS	0.189*	0.53 (0.24;1.17)	1.23 (0.99;1.47)	<0.001
iM_{prey}	whole	74	SMA	-	0.01 (0.00;0.02)	2.18 (1.83;2.60)	<0.001
			GLS	(0)	0.03 (0.01;0.06)	1.42 (1.04;1.80)	<0.001
			PGLS	0.321**	0.02 (0.00;0.09)	1.60 (1.18;2.02)	<0.001
	$1\%C < iM_{prey} < C$	40	SMA	-	0.02 (0.01;0.04)	1.41 (1.06;1.88)	0.003
			GLS	(0)	0.06 (0.03;0.11)	0.64 (0.24;1.04)	<0.001
			PGLS	0*	-	-	-
	$iM_{prey} > C$	27	SMA	-	0.36 (0.20;0.64)	1.17 (1.00;1.39)	<0.001
			GLS	(0)	0.45 (0.26;0.78)	1.08 (0.90;1.27)	<0.001
			PGLS	0*	-	-	-

* λ significantly different from 1; ** λ significantly different from 0 and 1

Table 2 Scaling relationships of kill frequency with predator mass (M_{pred}) according to $a\ M_{pred}^{b}$ in different datasets (depending on the relationship between stomach capacity C and prey mass available to the individual predator iM_{prey}) using standardized major axis regression (SMA), generalized least squares (GLS) or phylogenetic generalized least squares (PGLS); for large prey predators, the kill frequency assuming a single meal per prey (i.e., constrained by C) or a complete consumption of the prey (i.e. over several days, assuming an absence of scavenging/kleptoparasitism) are indicated.

Dataset	n	Statistic	λ	a (95%CI)	b (95%CI)	p
whole	74	SMA	-	41.19 (18.24;92.03)	-1.51 (-1.87;-1.21)	0.002
		GLS	(0)	6.95 (3.31;14.56)	-0.53 (-0.86;-0.20)	0.002
		PGLS	0.270**	9.12 (2.71;30.70)	-0.66 (-1.01;-0.30)	0.001
$1\%C < iM_{prey} < C$	40	SMA	-	0.50 (0.23;1.09)	1.29 (0.93;1.77)	0.332
		GLS	(0)	2.64 (1.30;5.36)	0.20 (-0.20;0.61)	0.332
		PGLS	0*	-	-	-
$iM_{prey} > C$	27	SMA	-	1.02 (0.97;1.07)	-0.33 (-0.35;-0.31)	<0.001
(single meal)		GLS	(0)	1.01 (0.96;1.06)	-0.33 (-0.34;-0.31)	<0.001
		PGLS	0	-	-	-
$iM_{prey} > C$	27	SMA	-	0.66 (0.36;1.24)	-0.51 (-0.74;-0.37)	0.024
(complete consumption)		GLS	(0)	0.33 (0.19;0.58)	-0.22 (-0.40;-0.04)	0.024
		PGLS	0*	-	-	-

* λ significantly different from 1; ** λ significantly different from 0 and 1