FEEDING STRATEGIES IN WILD CARNIVORES: PROGRESS REPORT OF A MODEL APPROACH

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Abstract
Feeding strategies among wild carnivores are still partly unexplained. Carnivore mass is a determining factor in the choice for a specific range in prey size (Carbone et al., 1999). According to Carbone et al. (2007), two dietary groups can be distinguished: small carnivores hunting on small prey (< 20 kg) and large carnivores hunting on large prey (> 20 kg). Prey size in his turn might influence feeding habit-associated factors such as meal size, feeding frequency and kill frequency but this has, hitherto, been left unexplained. A literature search was performed and yielded 690 potentially eligible studies of which already 194 (57 species) were extracted with data on feeding habit-associated factors. Moreover, a theoretical kill frequency model was developed based on carnivore weight, typical prey weight, maintenance energy requirements of mammals and metabolizable energy in small prey (Plantinga et al., 2007). So far, carnivore mass was positively related to absolute prey mass ($P < 0.001$). The kill frequency model showed that carnivore mass was negatively related to the theoretical kill frequency ($P < 0.001$), meaning that large carnivores will kill less frequently than smaller carnivores. This model approach might, once fully elaborated, give more insights into feeding strategies in wild carnivores with possible further applications for carnivores in captivity and domestic carnivores.

Introduction
In general, wild carnivores spend a high amount of energy hunting their prey. It is hypothesized that hunting energy expenditure becomes a determining factor for prey size in relation to carnivore size: smaller prey is easier to catch, but at a certain point, the energy cost per prey exceeds the energy gain in terms of nutritional value. In the literature, it has been suggested that wild carnivores switch from small- to large-prey-feeding at a body mass threshold of about 20 kg (Carbone et al., 1999; 2007). A relatively large prey size would logically imply a large relative meal size unless the larger prey has to be shared among so many individuals that meal size drops to levels of solitary predators of relatively small prey (Hornocker, 1967; Owen-Smith and Mills, 2008). Increasing meal size implies decreasing feeding frequency (i.e. increasing the time between meals), consequently decreasing hunting behavior (i.e. kill frequency) which is triggered by hunger (Hall and Bradshaw, 1998). This suggests that the choice for a specific range in prey size by carnivore species may have co-evolved with adaptations in meal size and kill frequency. Efforts have been made for different individual carnivore species to document their feeding habits but no broad literature survey is available, and the existing information is fairly scattered. Gathering this information could help to improve our understanding in the digestive physiology and satiety mechanisms not only in wild carnivores but also in carnivores in captivity and even domestic carnivores.

Materials and Methods

A literature review was performed from January to August 2014 using Web of Knowledge, PubMed and Google Scholar to identify potentially eligible studies reporting feeding habits of wild carnivores. The literature search yielded 690 potentially eligible studies of which already 194 (57 species) were confirmed eligible and extracted with data. Per carnivore species, data on prey species, prey mass (kg), most frequent prey (%), meal size (kg/day/carnivore), kill frequency (1 kill/x days) and pack size were extracted. Data were log transformed and linear curve fitting was performed on the relationship carnivore mass vs. mean prey mass of most common prey and a provisional regression equation was derived. Additionally, a theoretical kill frequency model was developed based on carnivore weight, typical prey weight, maintenance energy requirements of mammals and metabolizable energy in small prey (Plantinga et al., 2007).

$$\text{Total amount of prey (kg/carnivore/day)} = \frac{\text{MER (kJ/kg}^{0.75}\text{/day) x kg}^{0.75}\text{ carnivore}}{\text{ME prey (kJ/kg fresh weight)}}$$

$$\text{Theoretical kill frequency (kills/day)} = \frac{\text{Total amount of prey (kg/carnivore/day)}}{\text{Average prey weight (kg)}}$$

Data were log transformed and linear curve fitting was performed on the relationship carnivore mass vs. theoretical kill frequency and a provisional regression equation was derived. So far, pack size was not modeled in for both relationships. Meal size data turned out not usable for analysis and were therefore omitted from the database.

Results

Carnivores ranging in mass from 0.620 kg to 188 kg were included in the dataset. Carnivore mass was positively related to absolute prey mass ($P < 0.001$). Smaller carnivores (< 20 kg) typically hunt prey smaller then themselves, large carnivores (> 20 kg) hunt prey that are similar in weight or larger than themselves. Insectivorous carnivores (both large and small carnivores) showed prey masses of less than one gram. The kill frequency model showed that carnivore mass was negatively related to the theoretical kill frequency ($P < 0.001$), meaning that large carnivores will kill less frequently than smaller carnivores.

Discussion

Carnivore mass was positively related to prey mass as also shown by Carbone et al. (1999). The theoretical kill frequency decreased as predator mass increased which could be expected since a relative large prey implies a relative large meal, rendering long term satiation, which in turn leads to a low kill frequency (Hall and Bradshaw, 1998; Hornocker, 1967; Owen-Smith and Mills, 2008). However, caution is warranted when interpreting the results. Insectivorous carnivores show kill frequencies up to one kill/100 days indicating that the theoretical model does not apply to insectivorous carnivores. Therefore, insectivorous carnivores will be omitted, putting the focus on vertebrate prey feeders. The previous relationships might be influenced by the pack size of carnivores (i.e. solitary hunters vs group hunters). Therefore, inclusion of a pack size factor in both relationships is crucial. Moreover, the kill frequency model needs to be personalized per carnivore species in terms of MER values and energy contents of typical prey, taking feeding selectivity into account. Finally, data on kill frequency from literature are necessary to confirm the theoretical kill frequency model. Analyzing feeding strategies of wild carnivores will show how the choice for a specific range in prey size by carnivore species co-evolved with adaptations in meal size, kill frequency and even satiation mechanisms, rendering two possible strategy groups: the large carnivores showing a typical feast and famine style whereas smaller carnivores are typical frequent feeders. Unraveling these strategies in the wild might render possible applications for carnivores in captivity and even domestic carnivores.

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