

Prospects & Overviews

Do wild carnivores forage for prey or for nutrients?

Evidence for nutrient-specific foraging in vertebrate predators

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A widespread perception is that carnivores are limited by the amount of prey that can be captured rather than their nutritional quality, and thus have no need to regulate macronutrient balance. Contrary to this view, recent laboratory studies show macronutrient-specific food selection by both invertebrate and vertebrate predators, and in some cases also associated performance benefits. The question thus arises of whether wild predators might likewise feed selectively according to the macronutrient content of prey. Here we review laboratory studies demonstrating the regulation of macronutrient intake by invertebrate and vertebrate predators, and address the question of whether this is likely to also occur in the wild. We conclude that it is highly likely that wild predators select prey or selectively feed on body parts according to their macronutrient composition, a possibility that could have significant implications for ecological and foraging theory, as well as applied wildlife conservation and management.

Keywords:

carnivores; diet choice; predator–prey interactions; prey quality; prey selection

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Introduction

Vertebrate predators play important roles in maintaining ecosystem diversity, often through top-down processes that regulate prey populations and alter ecosystem structure [1, 2]. Many of these predators are also among the large, charismatic animals that draw public interest to conservation efforts [3]. Unfortunately, most vertebrate predators are experiencing population declines and threats of extinction [2]. Prey selection may be a key factor driving these declines [4], often through human–wildlife conflict [5]. Thus, to effectively address conservation of vertebrate predators, it is critical to understand their nutritional ecology.

It has long been realized that herbivores and omnivores face nutritionally variable landscapes and adjust diet selection to optimize nutrient intake [6, 7]. However, a persistent assumption surrounding carnivores is that nutrient balancing is unnecessary, because prey nutrient content is thought to be relatively invariant compared to foods consumed by omnivores and herbivores, and nutritionally balanced relative to their requirements [8–11]. Instead, predators are often assumed to select prey to maximize energy intake, and are therefore limited by prey availability rather than prey nutrient content [8, 12–14].

The nutrient composition of prey, however, varies seasonally, regionally, with ontogeny, and among body tissues both within and among species [15–18]. Furthermore, wild carnivores may not be as energy limited as traditionally believed, because prey is often available in surplus relative to requirements [19, 20]. This suggests the possibility that vertebrate carnivores might often have the context to balance their nutrient intake through selective predation or feeding. Additionally, the evidence that nutrient balance substantially influences animal fitness [21] suggests that vertebrate carnivores might also have an incentive to forage selectively for a balanced diet. Finally, recent lab-based studies show that several predatory species including invertebrates [22–25], fish [26–28], and mammals [29–33] forage selectively to balance their nutrient intake in laboratory conditions.

Together this evidence casts doubt on traditional suppositions regarding food choice in wild predators, suggesting an important aspect of predator biology has been neglected.

Here, we review and critically evaluate existing behavioral, physiological, and ecological evidence for nutrient-specific selective foraging in vertebrate predators. Throughout the review we will use the terms “predator” and “carnivore” interchangeably in reference to animals that obligately derive the majority of their energy from consuming other animals. Our aim is not to provide a comprehensive review of foraging in predators, but specifically to highlight information relevant to the question of whether the foraging choices of wild predators might be influenced to a greater extent than currently believed by the blend of macronutrients comprising the energy content of prey. Our broader goal is to draw attention and attract research effort towards a possibility that we consider both highly likely and, if substantiated, would have important implications for several research fields in ecology.

Measuring nutrient-specific foraging

Traditional approaches to nutritional ecology tend to focus on the independent effects of nutrients, usually either energy or protein [34]. Similarly, animal nutrition science has largely progressed using the “one-variable-at-a-time” approach, in which experimental manipulations involve varying the levels of single nutrients in foods [35]. Research into human nutrition has similarly emphasized the effects of single nutrients [36]. Although useful for some purposes, single-nutrient manipulations are ineffective for detecting nutrient-specific foraging, especially where the foraging goal is to gain a balanced intake of multiple nutrients [21]. For that, an approach is needed in which the animal’s responses to bi- or multi-dimensional variation in food composition are measured, either using natural variation in wild foods [37] or systematic experimental manipulations [38]. A state-space framework, called the Geometric Framework for nutrition, was developed for this purpose [39, 40].

A primary aim of the Geometric Framework is to measure the responses of animals to variation in the nutritional composition of foods to detect cases in which its food choices and feeding decisions homeostatically prioritize specific nutritional states. In this way, an “intake target” state can be identified, and the consequences in terms of fitness-relevant measures (e.g. growth, reproduction) of achieving this state versus being constrained from achieving it (e.g. due to nutritional imbalance in available foods) compared. Additionally, comparisons of the target nutrient intake with intakes when the animal is constrained from reaching the target provide powerful information about the nutritional drivers of foraging. Specifically, when the animal is restricted to a diet that contains two nutrients in a different ratio than the target ratio, it is forced into a trade-off between over-ingesting one to achieve the target intake of the other, under-ingesting the other to achieve the target intake of the first, or reaching the target for neither nutrient. This response, termed a “rule of compromise,” provides a direct measure of the relative priorities assigned by the regulatory systems to the

two nutrients. It also provides a definitive test of whether an animal prioritizes energy intake per se or a specific blend of macronutrients [41].

Nutritional geometry has been applied both in laboratory studies to demonstrate nutrient-specific foraging in a range of herbivores, omnivores and carnivores (see below), and herbivores and omnivores in the wild [37, 42, 43].

All calories are not equal: Macronutrients and predators

Although the nutritional requirements of animals are complex, involving a range of inorganic, micro- and macronutrients [43, 44], much of the focus to date on nutrient-specific foraging has concerned the energetic macronutrients: proteins, lipids, and carbohydrates. As studies have consistently demonstrated a role for macronutrient balance in foraging, we will likewise focus our survey on these nutrients, although micronutrient balance might also play a role [43, 44]. In this section, we provide a broad overview of physiological evidence indicating that predators, like other feeding groups, have specific requirements for different macronutrients.

Proteins, carbohydrates, and lipids

Protein, which is composed of essential and non-essential amino acids, is often consumed by carnivores in high proportions relative to other macronutrients, particularly carbohydrates, reflecting the composition of their prey [16–18, 45]. Carnivores show several adaptations to a high-protein diet, including specialized gut microbiota [46] and the ability to up-regulate nitrogen excretion to avoid accumulation of toxic levels in the body [47, 48]. However, many predators are unable to down-regulate rates of protein catabolism when feeding on low protein diets [49, 50] or when fasting [51, 52]. High activities of protein catabolizing enzymes may result in the degradation of endogenous protein stores and thus negative nitrogen balance [49]. These physiological limitations may compromise a carnivore’s ability to utilize low protein food sources [16] and may be particularly disadvantageous during periods of low prey abundance.

In contrast to protein, the prey of carnivores typically contains little carbohydrate [16–18], and as a result predators seem to have lost the ability to effectively regulate glucose homeostasis, as demonstrated in several taxa [53–57]. Therefore, carnivores must create glucose from other substrates, usually amino acids, to fuel activity and some tissues, such as the brain [16]. To compensate for low dietary carbohydrates, some carnivores maintain constitutively high levels of gluconeogenic enzymes [56, 58], though rainbow trout (*Oncorhynchus mykiss*) are able to modulate these enzymes [50].

Lipids are the most energy dense macronutrient, which may help explain the traditional assumption that carnivores forage to maximize energy intake [22]. In addition to serving as an energy source, lipids play important roles in cellular processes and membrane fluidity [59]. Due to a normally lipid-rich diet, some carnivores have lost the ability to convert fatty

acids, making some of them essential nutrients that carnivores must consume [60, 61].

Macronutrient balance

Studies using nutritional geometry have linked the ratios of macronutrients consumed by animals to several aspects of fitness, including longevity and aging [38, 62, 63], immunity [64], fecundity [38], predation risk [65], sexual display [66], and body size and rate of mass gain [41, 67, 68].

Laboratory research has shown that a diverse range of both herbivorous and omnivorous animals self-select specific ratios of macronutrients from nutritionally complementary foods [44, 67–70]. Macronutrient balance has also been shown to be a driving force behind the food selection of wild primates [37, 42].

In some ecosystems, the grizzly bear (*Ursus arctos*), an omnivorous carnivore, moves between habitats to form a mixed-diet of salmon and fruit, despite the higher energy content of a salmon-only diet [71]. Subsequent research found that captive grizzly bears preferentially selected among complementary foods to compose a diet of 17% protein: 83% non-protein energy, and that this ratio maximized mass gain (a fitness proxy; [67]), thereby shedding light on observed wild behavior.

Despite the evidence for adaptive nutrient-specific foraging in other trophic groups, traditional assumptions maintain that such regulation is not necessary for strict carnivores. There is, however, a growing body of evidence from laboratory studies that carnivores do, in fact, just that.

Macronutrient regulation in laboratory studies of carnivores

Predatory invertebrates

The majority of evidence for macronutrient regulation in predators comes from studies of invertebrates. In a seminal study, invertebrate predators were shown to regulate their intake of protein and lipid to correct existing nutritional imbalances in those nutrients [23]. Nutrient selection occurred at different stages of prey handling depending upon the species and predation strategy: highly mobile ground beetles (*Agonum dorsale*) selected among foods differing in nutrient balance; ambush-predator wolf spiders (*Pardosa prativaga*) adjusted their proportional consumption of a single prey type depending on its nutrient composition; and web-building desert spiders (*Stegodyphus lineatus*) selectively extracted nutrients from single prey items [23]. These regulatory responses were likely adapted to diurnal variation in prey composition, because they were in response to short bouts of pre-feeding on imbalanced foods (24–48 hours). Wolf spiders were further shown to exhibit differential prey capture rates and extraction of protein and lipid in response to prey mass and nutrient composition [25].

Food selection in predatory beetles (*A. dorsale*) was shown to be dynamic dependent upon the nutritional state of the predator and prey composition [24]. Beetles prioritized lipid

intake for 2 days following diapause, and thereafter progressively increased the ratio of protein in their diet. Beetles confined to imbalanced diets showed a strong prioritization of lipid intake, consuming excess protein to gain limiting lipid; in contrast, they tended not to consume excess lipid to gain more protein when limiting. Similar behavior was found in the wolf spider [25], and another predatory beetle (*Anchomenus dorsalis*) [22]. The greater capacity to over-ingest protein exhibited by these predators compared to most terrestrial herbivores or omnivores that have been studied in this way is likely an adaptation to a high protein diet that may be lipid-limited. For example, Wilder et al. (2013) demonstrated that lipid, not protein, becomes increasingly limiting as arthropod trophic level increases [72].

Importantly, one study has linked macronutrient balance in an invertebrate predator to fitness. Jensen et al. (2012) used nutritional geometry to demonstrate that *A. dorsalis* selectively feeds among foods varying in protein to lipid ratio, composing a diet that maximized egg production [22]. The selected macronutrient ratio was higher in protein than expected if feeding was random, showing that this diet was actively selected and not merely an outcome of indiscriminately feeding on the available foods. When beetles were confined to one of a range of single imbalanced diets, egg production decreased, suggesting a fitness cost; however, in each case the beetles consumed an amount of food that maximized egg production relative to what was possible on their respective diets, irrespective of energy intake. This study demonstrated unequivocally that rather than energy per se, the macronutrient ratios of foods drove the foraging behavior of the beetles, and that such behavior maximized relative fecundity.

Carnivorous fish

Several predatory fish have demonstrated the ability to self-select specific ratios of macronutrients from complementary diet formulations in the laboratory, including European seabass (*Dicentrarchus labrax*), Senegalese sole (*Solea senegalensis*), and rainbow trout [26–28]. Protein was the dominant macronutrient selected, with overall dietary ratios (% protein:lipid:carbohydrate) of 55P:22L:23C for seabass, 68P:16L:16C for sole, and ~58P:15L:29C trout [26–28].

The macronutrient preferences of seabass – which have been the focus of several studies – are highly dynamic, responding to both internal and external cues. For example, sea bass have the ability to regulate macronutrient intake through post-ingestive signaling mechanisms [26], and change macronutrient preference in response to environmental conditions such as salinity [73]. Seabass also show complex endogenous seasonal preferences for macronutrients: fish held under constant laboratory conditions selected diets highest in protein during April, and highest in lipid during July [74]. Such annual changes in seabass macronutrient preference and body composition may be synchronized to environmental changes and their reproductive cycle, rather than strictly an adaptive response to prey availability as traditionally assumed [74].

In Geometric Framework studies, both whitefish (*Coregonus lavaretus*) and rainbow trout showed a strong defense of protein intake over lipid when fed imbalanced diets [35, 75]. For example, whitefish fed low protein diets ate to gain sufficient amounts of protein at the cost of overeating non-protein energy, while fish on high protein diets over consumed protein to gain non-protein energy to a much lesser extent [35]. The macronutrient balance of diets affected the body composition of whitefish, such that fish on low protein diets had high body fat due to over-consuming non-protein energy, while fish on high protein diets had low body fat levels due to not substantially over-consuming high-protein diets. This phenomenon, in which non-protein energy is over-consumed in a compensatory response for dietary protein dilution, is known as *protein leveraging*, and has been demonstrated in some omnivorous mammals, including mice and humans [62, 76].

Mammalian carnivores

A few species of mammalian carnivores have demonstrated the ability to self-select diets composed of specific ratios of macronutrients when offered complementary foods in the laboratory, including the domestic cat (*Felis catus*; [30, 33]), domestic dog (*Canis lupus familiaris*; [29]), and mink (*Neovison vison*; [31, 32]). Of these, domestic cats selected the highest ratio of protein energy (52P:36L:12C; [30]), while mink selected the second highest at 35P:50L with carbohydrate held constant at 15% energy [32]. The domestic dog selected a diet lowest in protein but highest in lipid (~30P:63L:7C on an energy basis), and was very similar among several breeds examined [29].

A further study on mink demonstrated that they balanced their intake of protein to non-protein energy when confined to imbalanced diets: mink showed a strong preference for lipid as a source of energy and avoided high protein intakes, suggesting that there were costs associated with consuming greater than required amounts of protein [31]. Furthermore, mink demonstrated compensatory feeding for specific macronutrients to redress imbalances accrued while confined to imbalanced diets likely to negatively affect fitness—e.g. mink growth parameters and liver function are impaired when fed a low protein diet (~15% of metabolizable energy; [86]).

The influence of domestication on laboratory studies of mammalian carnivores

A critical question is to what extent results observed in laboratory studies are due to domestication versus the ancestral environment. Interestingly, one study showed that the diets of feral domesticated cats had the same level of protein, although a somewhat lower carbohydrate content (52P:46F:2C; [77]), than selected by domestic cats in laboratory experiments [30]. The similarity in the protein:non-protein energy ratio (52P:48NP) is striking, suggesting that the macronutrient priorities demonstrated in captivity while feeding on manufactured foods are representative of diet selection in the wild. Interestingly, studies have shown that

the ratio of protein:non-protein energy is the primary regulatory target of grizzly bears [67] and domesticated dogs [29]: while high-fat was preferred, both species used carbohydrate to maintain the protein energy ratio if fat was limiting. Cats are less flexible in the ability to use carbohydrate as a source of energy, having an absolute ceiling on the amounts they can consume [30]. It remains to be determined whether the difference in the fat:carbohydrate ratio in experimental and feral cats is biologically significant, perhaps reflecting developmentally induced preferences by domesticated cats raised on high-carbohydrate proprietary foods compared with natural prey. Alternatively, it might reflect ecological constraint in which the low availability of carbohydrates in natural prey [16] prevented feral cats from achieving the same proportional carbohydrate intake. Domestic dogs and mink in the wild would also be ecologically constrained in achieving the relatively high proportions of carbohydrate measured in laboratory studies.

The evolution of nutritional preferences in domestic dogs may be due to several factors. For one, wolves (from which domestic dogs are derived) are pack hunters able to capture and consume larger prey than small mammals, which is significant because the lipid content of prey tends to increase with body size [78]. This may explain the higher lipid preference in dogs over domestic cats and mink, the ancestors of which were solitary hunters. However, the estimated diet composition of wolves (54P:45L:1C; % energy; [45]) is different from that selected by domestic dogs, and very similar to that selected by the feral cat. The relatively lower preference for protein and higher preference for lipid may be due to exposure to a wider range of anthropogenic foods during domestication [29], but see [45].

Evidence for nutrient-specific foraging in wild carnivores

Laboratory studies strongly suggest that carnivores across taxa have evolved mechanisms for balancing nutrient intake, and that such mechanisms optimize fitness—e.g. the similarity between the rules of compromise in mink and predatory beetles is striking. It seems unlikely that such behavior would be confined to the laboratory, giving rise to the question of whether wild vertebrate predators might similarly select prey and prey combinations to meet specific macronutrient targets. However, no study has been done directly testing this in wild carnivores. Here we review indirect evidence that pertains to this question.

Linking laboratory studies of mammalian carnivores to the wild

Consistent with the prediction that the intake target of animals will evolve to reflect the composition of available foods, as well as food choice adapting to meet nutrient needs [34], the self-selected protein intake of both domestic and feral cats is similar to midpoint body composition estimates of small vertebrate prey (50.5%, range 33–68%; [16]). Similarly, estimated diet composition of wolves is similar to that

of an average moose (*Alces alces*) carcass (53P:47L, % energy; [17]), which is a primary prey species [45]. On the other hand, nutritional estimates for white-tailed deer are much lower in protein (30P:70L % metabolizable energy; [17]), being very similar to the diet selected by the domestic dog. The high-lipid preference of domestic dogs is therefore not outside the range of the natural prey of wolves. Similar to domestic cats, small mammals are also among the natural prey of mink; however, they are higher in protein content than the selected ratio. This might suggest that mink may be limited by non-protein energy in the wild, especially lipid [31], which also occurs seasonally for wild grizzly bears [17]. Alternatively, the macronutrient preferences of farmed mink may reflect developmental exposure to carbohydrates or evolution under domestication.

Selective predation in the wild

It has long been known that wild carnivores often selectively predate species at different frequencies than they appear in the environment [79]. Tigers (*Panthera tigris*), for example, show preference and avoidance of specific prey species (and age classes), in addition to some prey that are consumed proportional to availability [80]. As suggested by the laboratory studies reviewed above – in particular the feral cat that select the same macronutrient ratios from proprietary foods as in wild prey [77] – such selective predation is expected if wild predator foraging behavior is aimed at optimizing macronutrient intake. An example may come from the European badger (*Meles meles*; an omnivorous carnivore) which showed no intraspecific variation in protein intake despite living in different habitats across Europe and consuming different foods [81]; however, lipid and carbohydrate intake was more variable, suggesting protein:non-protein regulatory behavior similar to the aforementioned grizzly bear [67] and domestic dog [29]. Whether such a relationship may be found among conspecific obligate carnivores in different habitats warrants investigation.

As considerable variability exists in the nutrient balance of prey both within and among species [15, 17, 18, 78] it is highly likely that predators face a nutritionally variable landscape from which to select prey, especially given that energy is likely not limiting for carnivores [19, 20]. For example, scarcity of wild ungulates is associated with increased depredation of domestic livestock by wolves. The presence of several prey species, however, seems to be more effective in lowering depredation rates than the presence of a single abundant species [82]. These findings suggest that a diet of mixed prey, and therefore a variety of prey nutrient compositions, might be a driving force behind wolf foraging behavior.

In the face of a nutritionally variable landscape, we could make predictions about a predator's prey selection given knowledge of the animal's current nutritional state. For example, if a predator were lipid limited relative to its optimal state, we would expect, *ceteris paribus*, that given a choice the predator would preferentially prey upon the species with higher lipid content. This might explain why two insectivorous marsupials not only selected among prey types and sizes,

but also fed selectively on body parts with high-lipid density, suggesting that consuming lipid was a priority [83].

There are many situations in which wild predators are likely to have depleted lipid stores. White sharks (*Carcharodon carcharias*), for example, undertake long-distance annual migrations between foraging sites and reproductive areas, relying on lipid reserves to power their migratory transit [84]. The principle prey species of sharks for building up stores pre-migration, or replacing stores post-migration, remains to be determined [84]. Seals are a principle prey species of white sharks during specific seasons (e.g. May–August at Seal Island, South Africa; [85]). Additionally, white sharks selectively scavenge on high-blubber sections of dead whales, with feeding activity decreasing as blubber-rich tissues are depleted [85]. Whether such feeding behavior is influenced by white shark macronutrient preferences and the composition of prey remains an important point to resolve. White sharks may also shift macronutrient preferences with ontogenic changes in diet, as previously demonstrated for predatory beetles [24]. Consistent with this is the observation that these marine predators consume more lipid-rich foods (e.g. mammals) as they increase in size [85].

Selective consumption of body parts

There are numerous examples of carnivores selectively consuming specific body parts of prey, which is not surprising given considerable differences in the nutrient composition of prey body tissues and organs [18]. Oftentimes selective feeding occurs during periods of high resource availability. Harbour seals (*Phoca vitulina*), for example, selectively consumed bellies of pre-spawning female salmon (*Oncorhynchus nerka*) containing high-lipid roe, but consumed most male salmon (which lacked especially lipid rich parts) in their entirety [86]. Omnivorous bears also target the lipid-rich brain tissue and roe of salmon when abundant [87]. During feast times, wolves first feed on the internal organs of large ungulates [45]. There are also casual observations of predators selecting specific body parts from prey, such as cape fur seals selectively feeding on the stomach contents and livers of blue sharks (*Prionace glauca*; [88])—the livers of sharks are particularly fat-rich [84].

Prey choice and the fitness of predators in the wild

If, as demonstrated in the laboratory, macronutrient preferences of wild animals have evolved to optimize fitness, we would expect evidence of such in the wild. Studies in marine systems clearly show how differential prey selection can influence the fitness and reproductive success of predators, suggesting that declines of marine mammal and bird communities are due to dietary switches to prey items low in lipids and energy [4]. Many studies such as this, however, are not nutritionally explicit [34] and often use energy density or digestibility as a measure of nutritional “quality”. For example, experiments on bobcats (*Lynx rufus*; [89]), Stellar

sea lions (*Eumetopias jubatus*; [90]), and various birds of prey [91] illustrate how digestive efficiency varies when feeding on different prey species. Interestingly, harbor seals exhibit higher digestive efficiency when feeding on a mixed-fish diet compared to a diet of a single fish type [92]. It is likely that differences in digestibility are driven by differences in macronutrient concentration [93].

A study of herring gulls (*Larus argentatus*) demonstrated that energy density per se is not the only currency that determines fitness in the wild [94]. Gulls that specialized on mussels had higher reproductive success than gulls specializing on other prey items, despite mussels having the lowest energy density of available prey [94]. Thus, the nutritional composition of food items was more important in determining reproductive success of herring gulls than their energy content [94], though it remains unclear whether total food consumption differed across groups of gulls. Similarly, nutritional stress in black-legged kittiwakes (*Rissa tridactyla*) was stronger in birds on low-lipid versus high-lipid isocaloric diets [95]. Low-lipid diets during development reduced performance in red-legged kittiwakes (*Rissa brevirostris*) and may explain population declines during climatic events that decrease abundance of high-fat fish [96].

The reproductive success of kestrels (*Falco tinnunculus*) correlates positively with the fraction of the diet composed of voles, suggesting that alternative prey do not satisfy nutritional requirements for reproduction [97]. Studies of stoat (*Mustela ermine*) and long-eared owl (*Asio otus*) have also related reproductive output to relative amounts of prey species in the diet [98, 99]. However, such studies are often confounded by the fact that the diet switches may be driven by variation in prey density, and do not control for ecological factors influencing prey choice, such as search or handling time. Yet despite the challenges, determining the role of nutritionally-explicit foraging behavior in wild predator performance is an important priority, and is likely to lead to innovative and informative research [100].

The influence of nutrient-specific foraging is far reaching

Nutrient-specific foraging of predators may go beyond influencing performance by also affecting community structure and ecosystem processes. For example, perceived predation risk impacts the physiology of prey by increasing stress levels [101], which alters prey macronutrient preferences [65]. Subsequent nutrient specific changes in prey foraging behavior may thus change the nutrient flow of an entire ecosystem [101].

Trophic cascades are another powerful representation of how the prey selection of carnivores can influence ecosystems [2, 100, 102]. Additionally, predation can impact ecosystem processes, such as rates of plant-litter decomposition [103]. Such research may be further informed by incorporating a nutrient specific approach, which considers the nutrient requirements of the predator and the nutrient composition of available and preferred prey. Such information

may also allow us to predict ecosystem outcomes after the loss of prey species, where predators may be forced to consume sub-optimal prey.

Given the far-reaching effects of nutrient-specific foraging, knowledge of such behavior would also improve our insight into the nature of human-wildlife conflict and inform conservation and management strategies. For example, a nutrient specific approach has been applied to solve conservation problems in non-carnivorous species [104, 105]. Understanding the nutrient preferences of carnivores offers a more refined understanding of human-wildlife conflict than simple food- and energy-based approaches. For example, if wolves prefer high-fat diets similar to their domestic cousins, this may help explain why depredation of livestock – which are often higher in fat than wild game [17] – can remain high despite ample wild prey abundance [82].

Micronutrients and other food components

Nutrient-specific research could be extended beyond macronutrients, given that amino and fatty acids, vitamins, and micronutrients are likely to influence the foraging behavior in wild predators. For example, preferential foraging by wolves on the liver of large ungulates may be due to both macronutrient composition and high vitamin A content [45]. As well, wolves are known to consume small amounts fruit and other vegetation [45], which may serve as sources essential fatty acids (e.g. omega-3; [106]) and other nutrients not found in animal-based foods. Diets imbalanced in micronutrients and amino or fatty acids can have deleterious effects [107–109] likely to impact predator fitness. Furthermore, other lesser-examined aspects of carnivore nutrition, such the importance of animal fiber (e.g. bones, tendons, hair, or feathers; [93, 110]), chitin [111], and toxins [112] on foraging behavior could lead to further insights.

Conclusion and outlook

Our review demonstrates the sophisticated ability of invertebrate and vertebrate predators to regulate their macronutrient intake and balance, provides examples of where such situations likely occur in the wild, and draws attention to some lesser-considered aspects of predator nutritional ecology that might be interpreted in this light. Overall, this provides significant evidence that macronutrient-specific food selection is relevant to wild vertebrate carnivores, and might help to explain their foraging behavior. However, the bulk of direct studies on vertebrate predators have been undertaken on domesticated animals. This raises the questions of how widespread similar responses are among non-domesticated vertebrate predators, under what ecological circumstances they are expressed, and how they influence individual performance. Answers to such questions will have significant implications for managing predator populations and the ecological communities of which they are a part [34, 72, 100].

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