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Many species of the Carnivora consume grass and other fibrous plant tissues

Alan R. Franck[1,*] **& Arian Farid**[2]

[1] Department of Biological Sciences, Florida International University, Miami, Florida, U.S.A.
[2] Herbarium, Department of Cell, Molecular, and Microbiology,
University of South Florida, Tampa, Florida, U.S.A.

[*] Corresponding author: afranck@fiu.edu

Abstract. Within the Carnivora order, the consumption of fibrous plant tissues (FPT), such as leaves and stems, is only known to serve the nutritional needs of eight species in the Ailuridae and Ursidae. Apart from the Ailuridae and Ursidae, the extent of FPT ingestion in the Carnivora is poorly understood. A literature search was conducted to compile studies containing evidence of FPT consumption in the Carnivora, primarily based on analyses of scats or gastrointestinal tracts. Among 352 studies, there was evidence of FPT consumption in any amount in 124 species, or 41%, of the Carnivora. Grass consumption was documented in 95 species, while ingestion of sedges, marine plants, bryophytes, conifers, and dicots was much less frequent. A few species showed evidence of consuming fungi or soil. Nine studies observed co-occurrences of intestinal parasites with grasses or sedges in the scats of the Carnivora, suggesting these abrasive or hairy plant tissues help to expel intestinal parasites. The relevance of consuming marine plants, bryophytes, conifers, dicots, fungi, or soil has also been underappreciated. Deliberate ingestion of FPT may be more widespread and important than previously realized in the Carnivora.

Keywords. Algivory, carnivore, folivory, fungivory, geophagy, herbivory.

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Introduction

The Carnivora order contains 300 extant species among 129 genera and 16 families (Agnarsson *et al.* 2010; Nyakatura & Bininda-Emonds 2012; Jackson *et al.* 2017; Zhou *et al.* 2017; Burgin *et al.* 2018). Their relatively simplistic gastrointestinal tract (McGrosky *et al.* 2016) is well adapted to carnivory, and approximately 98% of the species are carnivorous, frequently consuming invertebrate or vertebrate animals (see Pineda-Munoz & Alroy 2014). About 58% of the order are considered predominantly carnivorous, feeding primarily on animals, and about 40% are predominantly omnivorous, with significant portions of the diet coming from both animals and plants (Nowak 2005; Kissling *et al.* 2014; Gainsbury *et al.* 2018). Only six species were classified as predominantly herbivorous: *Ailuropoda melanoleuca*, *Ailurus fulgens*, *Ailurus styani*, *Paradoxurus jerdoni*, *Tremarctos ornatus*, and *Ursus thibetanus* (Burgin *et al.* 2018; Gainsbury *et al.* 2018).

Fruits are one of the most important plant dietary items, consumed by nearly all omnivorous and herbivorous Carnivora species (Quadros & Monteiro-Filho 2000; Gainsbury *et al.* 2018), being especially important in the Ursidae and Viverridae (Corlett 2017), with one species, *Paradoxurus jerdoni*, considered predominantly frugivorous (Gainsbury *et al.* 2018). Frugivory is generally absent in the Eupleridae, Felidae, Odobenidae, Otariidae, Phocidae, and Prionodontidae (Gainsbury *et al.* 2018), although there are occasional reports of fruit consumption in the Eupleridae (Durbin *et al.* 2010) and the Felidae (Schaller 1967; Turkowski 1980; Smythe 1986; Romo 1995; Taber *et al.* 1997; Rosalino & Santos-Reis 2009; Corlett 2017).

Consumption of seeds, roots, or nectar is relatively infrequent overall in the Carnivora. Granivory occurs in some species of the Ailuridae, Canidae, Herpestidae, Mephitidae, Mustelidae, Procyonidae, Ursidae, and Viverridae (Amaral 2007; Nadeem *et al.* 2012; Czernik *et al.* 2016; Gainsbury *et al.* 2018). Rhizovory occurs in some species of the Ailuridae, Herpestidae, Mustelidae, and Ursidae (Kalle *et al.* 2012; Gainsbury *et al.* 2018). Nectarivory has been observed in *Galerella pulverulenta* (Herpestidae), *Martes flavigula* and *M. gwatkinsii* (Mustelidae), *Potos flavus* (Procyonidae), and *Genetta tigrina* (Viverridae) (Hutton 1944; Lack 1977; Kays 1999; Parr & Duckworth 2007; Steenhuisen *et al.* 2015).

Herbivory of fibrous plant tissues (FPT; e.g., leaves and stems) is generally considered to serve the nutrional needs of only eight species in two families (Ailuridae and Ursidae) of the Carnivora: *Ailuropoda melanoleuca* (Schaller *et al.* 1989; Sims *et al.* 2007), *Ailurus fulgens*, *A. styani* (Wei *et al.* 2000; Panthi *et al.* 2012; Sharma *et al.* 2014), *Tremarctos ornatus* (Troya *et al.* 2004; García-Rangel 2012), *Ursus americanus* (McLellan 2011), *Ursus arctos* (McLellan 2011), *Ursus maritimus* (Stempniewicz 2017), and *Ursus thibetanus* (Christiansen 2008; Furusaka *et al.* 2017). Apart from these eight species, it is unknown how many other species of the Carnivora ingest FPT and what purpose it serves, although grasses, in particular, may serve to expel intestinal parasites (Huffman & Caton 2001; Hart & Hart 2018).

We hypothesize that FPT consumption is widespread in the Carnivora, especially considering that domesticated species (i.e., cats and dogs) commonly consume FPT such as grass (Hart 2011), suggesting it could be an innate behaviour (Bjone *et al.* 2009). Since herbivory of FPT is already well characterized in eight species (listed above), our main objective was searching for evidence of FPT ingestion in the other 292 extant species of the Carnivora. The types of FPT included were algae, bark, flowers, leaves, stems, and wood. Data for fungi consumption, an organismal group normally overlooked in the Carnivora (Gainsbury *et al.* 2018), were also collated. The peculiar ingestion of soil evidenced in some studies was additionally noted.

Material and methods

The taxonomy here follows Burgin *et al.* (2018), with the exception of the recognition of *Canis familiaris* (Jackson *et al.* 2017). Recently extinct species are not included in the calculations, i.e., *Cryptoprocta spelea*, *Dusicyon australis*, *Dusicyon avus*, *Neomonachus tropicalis*, *Neovison macrodon*, and *Zalophus japonicus*.

Our search strategy was to query each species, genus, family, or order, in combination with the terms “grass”, “leaves”, “plants”, “stems”, “vegetation”, “vegetative”, “fungi”, “soil”, “scat”, or “stomach” in Google Scholar. References cited within studies were also screened. Our focus was on all species of the Carnivora, especially the 292 species not generally known to consume FPT (dietary reviews were provided for the eight species already well known to consume FPT: *Ailuropoda melanoleuca*, *Ailurus* *fulgens*, *A. styans*, *Tremarctos ornatus*, *Ursus americanus*, *U. arctos*, *U. maritimus*, and *U. thibetanus*). Studies were included if they provided evidence of the consumption of algae, bark, flowers, fungi, leaves, soil, stems, or wood. Rarely, studies reported searching for evidence of plant ingestion but found none; these studies were not included here.

For each study, the information compiled included the species of Carnivora, category of plant or fungal tissue ingested, quantitative data on ingestion frequency, and any pertinent notes related to plant, fungi, or soil ingestion. Some studies reported or implied that evidence of FPT herbivory was observed, but explicitly excluded it from the data collection; hence, in these studies quantitative data are not available.

The studies included used a diverse array of terminologies, which were standardized as much as possible to present them as a common category here. The category algae used here includes the terms algae, kelp, and seaweed used in the studies. The category fungi used here includes the terms fungi and mushrooms used in the studies. The category fruit used here includes the terms berries and fruits used in the studies. The category grass here comprises the terms Graminae, graminoids, grass, and Poaceae. Leaves includes the terms leaf or leaves. Moss includes Bryophyta, bryophytes, and moss. Needles includes the terms conifer needles and needles. The category plant includes the terms herbaceous plants, herbs, forbs, plant(s), plant content, plant food, plant fragments, (unidentified) plant material, plant matter, plant remains, plant remnants, and Plantae. The category root includes the terms roots and tubers. Sedge includes the terms Cyperaceae, Cyperales, and sedge. The term Poales in a study was interpreted as including both the grass and sedge categories. Soil includes the terms dirt, sand, and soil. The category stem includes the terms branches, stems, sticks, twigs, and woody material. The category vegetation includes the terms bracts, casuarina needles (presumably actually referring to its stem and whorls of leaves), fibers or fibres, undigested leaves, scales, undigestible plant material, vegetable material, vegetable matter, vegetation, and vegetative. Other categories used here were equivalent to a single term found in the study, such as bark, digested grass, flowers, hair, lichens, miscellaneous, molluscs, plastic, seeds, shells, trap-pan covers, wood, and Zosteraceae. Although categories such as fruit, hair, miscellaneous, plastic, roots, seeds, shells, and trap-pan covers were not the focus of this study, they are included here when they were grouped with other forms of plant eating and not reported individually.

The frequency of occurrence (FO), the most commonly used statistic (KLARE *et al.* 2011a), was the primary quantitative datum compiled from the studies. The FO here is the presence/absence of a plant or fungal category in each sample (usually a scat or stomach) given as a percent of the total number of samples. The FO was sometimes reported as the itemized frequency, being the number of individual food items of one category relative to the total number of food items found.

Sometimes the FO or data to calculate the FO were not provided. In these instances, other data were given such as the mass, relative frequency (RF), relative mass (RM), or relative volume (RV). The mass is the dried mass of a given item. The RF is the FO of one category divided by the sum of all the FOs, which standardizes the FOs so that the sum of all RFs totals 100%. The RM is the mass of one category divided by the sum of all masses, so that the sum of all RMs totals 100%. The RV is the volume of one category divided by the sum of volumes, so that the sum of all RVs totals 100%. Direct observations of animals feeding on FPT were sometimes provided.

Percentages were rounded to the nearest whole number, except anything less than 1% was reported as < 1%. Some studies reported data from different times or locations, but did not summarize the data. In these instances, data were summarized for each species within the particular study.

Personal observations were made of a mixed-breed dog (*Canis familiaris*) in Florida, USA from the ages of 4–10 during leashed walks or when the dog was roaming freely. Additional observations were made of two adult terriers (*C. familiaris*) in their yard in Seattle, Washington, USA (Appendix 1). These dogs were all privately owned and were only observed during their normal daily routines. No experimentation was conducted; no manipulation of any sort was enacted. No permissions or licences were necessary.

Results

The number of published studies included was 357 (Table 1), with some studies including multiple species. Five studies reported only the consumption of fungi but not FPT (Delibes 1978; Grenfell & Fasenfest 1979; Zielinski *et al.* 1999; Helldin 2000; Mattson *et al.* 2002). From 352 studies, there were a total of 124 species and one hybrid from 72 genera and 12 families of Carnivora that showed evidence of consuming FPT (Fig. 1). Eight references were provided as dietary reviews of the eight species already well known to consume FPT, the species in the Ailuridae (*Ailurus fulgens* and *A. styani*) and Ursidae (*Ailuropoda melanoleuca*, *Tremarctos ornatus*, *Ursus americanus*, *U. arctos*, *U. maritimus*, and *U. thibetanus*). The remaining 344 studies documented FPT consumption in 116 species not generally considered to be folivores or algivores for nutritional needs. For seven species among seven genera

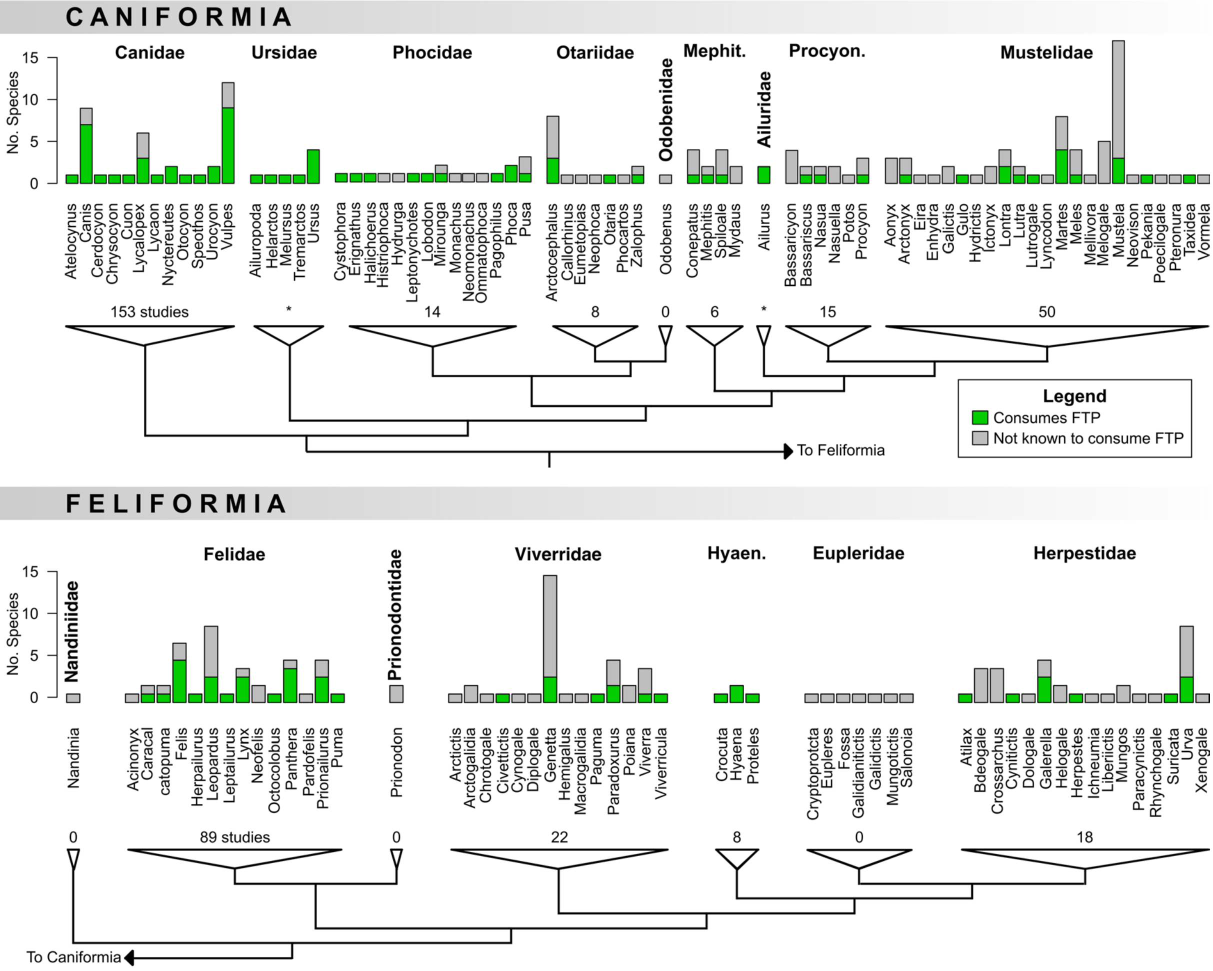

Fig. 1 – Family-level phylogeny of the Carnivora (adapted from Nyakatura & Bininda-Emonds 2012) with the number of species in each genus (Jackson *et al.* 2017; Burgin *et al.* 2018), and the number of species with evidence of fibrous plant tissue (FPT) consumption in green. The number of studies reporting evidence of FPT consumption in each family is given beneath the list of genera. Asterisks denote families well known to consume FPT, for which the number of studies anent FPT is not given.

(excluded from the preceding totals), the only studies identified were too equivocal to conclude if the species had ever eaten any FPT; these species are: *Galictis cuja*, *Herpestes ichneumon*, *Ictonyx striatus*, *Leopardus wiedii*, *Melogale moschata*, *Neovison vison*, and *Procyon cancrivorus*. For *Leopardus* and *Procyon*, other species of these genera were noted to ingest FPT while no other species were included for the other five genera (*Galictis*, *Herpestes*, *Ictonyx*, *Melogale*, and *Neovison*). Thirty-eight studies quantifying data on diet mentioned the occurrence of FPT but excluded it from the data collection. No pertinent studies were found for the Caniformia family Odobenidae, and none were found for the Feliformia families Eupleridae, Nandiniidae, and Prionodontidae.

Evidence for FPT consumption in the Carnivora was primarily derived from studies on scats or gastrointestinal tracts. Species with the most studies included here were *Canis latrans* (28 studies included here), *Canis lupus* (27), *Vulpes vulpes* (22), *Puma concolor* (15), *Leopardus pardalis* (14), *Felis catus* (13), *Canis aureus* (10), *Canis familiaris* (10), and *Chrysocyon brachyurus* (10). Apart from the Ailuridae and Ursidae, direct observations of wild animals feeding on FPT were observed in *Canis familiaris* (Butler & du Toit 2002), *Canis lupus* (Murie 1944), *Canis mesomelas* (Hiscocks & Perrin 1987), *Crocuta crocuta* (Henschel & Skinner 1990), *Cynictis penicillata* (Zumpt 1968), *Leopardus pardalis*, *Panthera onca*, and *Puma concolor* (Montalvo *et al.* 2020).

FPT consumption was found in the following Caniformia families and genera: the Ailuridae (1/1 genera, 2/2 species), including *Ailurus* (2/2 species); the Canidae (12/12 genera, 30/39 species), including *Atelocynus* (1/1 species), *Canis* (7/9 species), *Cerdocyon* (1/1), *Chrysocyon* (1/1), *Cuon* (1/1), *Lycalopex* (3/6), *Lycaon* (1/1), *Nyctereutes* (2/2), *Otocyon* (1/1), *Speothos* (1/1), *Urocyon* (2/2), and *Vulpes* (9/12); the Mephitidae (3/4 genera, 3/12 species) including *Conepatus* (1/4), *Mephitis* (1/2), and *Spilogale* (1/4); the Mustelidae (10/23 genera, 16/63 species), including *Arctonyx* (1/3), *Gulo* (1/1), *Lontra* (2/4), *Lutra* (1/2), *Lutrogale* (1/1), *Martes* (4/8), *Meles* (1/4), *Mustela* (3/17), *Pekania* (1/1), and *Taxidea* (1/1); the Otariidae (3/7 genera, 5/15 species), including *Arctocephalus* (3/8), *Otaria* (1/1), and *Zalophus* (1/2); the Phocidae (9/14 genera, 10/18 species), including *Cystophora* (1/1), *Erignathus* (1/1), *Halichoerus* (1/1), *Leptonychotes* (1/1), *Lobodon* (1/1), *Mirounga* (1/2), *Pagophilus* (1/1), *Phoca* (2/2), and *Pusa* (1/3); the Procyonidae (3/6 genera, 3/14 species), including *Bassariscus* (1/2), *Nasua* (1/2), and *Procyon* (1/3); and the Ursidae (5/5 genera, 8/8 species), including *Ailuropoda* (1/1), *Helarctos* (1/1), *Melursus* (1/1), *Tremarctos* (1/1), and *Ursus* (4/4).

Among the Caniformia, it is well known that the Ailuridae primarily feeds on bamboo grass. Consumption of grass or other FPT was observed in all genera of the Canidae and 75% of its species from 153 studies. Three studies excluded FPT consumption from data collection in *Nyctereutes procyonoides*.

From six studies on the Mephitidae, unidentified plants were relatively frequent for three species: *Conepatus chinga*, *Mephitis mephitis*, and *Spilogale putorius*. In 50 studies, grass and unidentified plants were found for some species of the Mustelidae. Needles of Pinaceae were common in one study on *Pekania pennanti*.

Among the Otariidae, eight studies were identified. Algae and *Phyllospadix* were commonly consumed by three species of *Arctocephalus*; algae consumption was reported less often in *Otaria bryonia* and *Zalophus californianus*. Fourteen studies documented algae consumption in some species of the Phocidae; algae consumption was detected in pups and juveniles of *Pagophilus groenlandicus* and two species of *Phoca*.

Bassariscus astutus (Procyonidae) showed evidence of FPT consumption in seven studies and in one study conifer ingestion was frequent. In two studies on *Procyon lotor*, grass ingestion was apparently quite common. Plant eating is well characterized for most species of the Ursidae, except for the following observations. Consumption of leaves and sticks was documented in *Helarctos malayanus*. Among three studies, FPT consumption was uncommon for *Melursus ursinus*. Data from one study showed *Ursus arctos* ingested several different species of fungi.

FPT consumption was found in the following Feliformia families and genera: the Felidae (11/14 genera, 24/42 species), including *Caracal* (1/2 species), *Catopuma* (1/2), *Felis* (5/7), *Herpailurus* (1/1), *Leopardus* (3/9), *Leptailurus* (1/1), *Lynx* (3/4), *Otocolobus* (1/1), *Panthera* (4/5), *Prionailurus* (3/5), and *Puma* (1/1); the Herpestidae (6/16 genera, 10/36 species), including *Atilax* (1/1), *Cynictis* (1/1), *Galerella* (3/5), *Herpestes* (1/1), *Suricata* (1/1), and *Urva* (3/9); the Hyaenidae (3/3 genera, 4/4 species), including *Crocuta* (1/1), *Hyaena* (2/2), and *Proteles* (1/1); and the Viverridae (6/14 genera, 9/37 species) including *Civetticitis* (1/1), *Genetta* (3/15), *Paguma* (1/1), *Paradoxurus* (2/5), *Viverra* (1/4), and *Viverricula* (1/1).

Among the Feliformia, 89 studies provided evidence of FPT consumption in the Felidae, covering most of the felid genera and about 57% of its species. Several studies excluded grass from data collection for the genera *Herpailurus*, *Leopardus*, *Leptailurus*, *Panthera*, and *Puma*. Consumption of grass and unidentified plants was evidenced in 18 studies on the Herpestidae. From eight studies, FPT consumption was relatively common in all four species of the Hyaenidae. From 22 studies, consumption of grass and other plants was detected in about 24% of the species of the Viverridae.

Grass was the most frequently observed FPT consumed, and usually it was found in relatively small amounts. Kept as pets, several studies on *Canis familiaris* and one study on *Felis catus* found grass ingestion was common. In captivity, *Chrysocyon brachyurus* (Barboza *et al.* 1994) was observed to eat grass. Several other species in captivity were noted to eat grass, but it was unclear if evidence was based on the direct observation of feeding behaviour and/or samples of scat and vomit (Buck *in* Lonsdale 2001).

A high FO (50–100%) of grass consumption was documented in the Canidae for *Canis latrans* (Ellis & Schemnitz 1958; Holle 1973; Best *et al.* 1981), *Canis mesomelas* (Rowe-Rowe 1983), *Cerdocyon thous* (de Araujo 2008), *Chrysocyon brachyurus* (Aragona & Setz 2001), *Nyctereutes viverrinus* (Matsuo & Ochiai 2009), *Panthera tigris* (Sunquist 1981), *Otocyon megalotis* (Klare *et al.* 2011b), *Speothos venaticus* (Lima *et al.* 2009), *Vulpes chama* (Bothma 1966), and *Vulpes vulpes* (Stepkovitch 2017). High FOs were also observed in *Taxidea taxus* (Mustelidae; Sovada *et al.* 1999), *Herpailurus yagouaroundi* (Felidae; Bisbal 1986), *Genetta tigrina* (Viverridae; Roberts *et al.* 2007), and *Paguma larvata* (Viverridae; Matsuo & Ochiai 2009). Several other studies on the Carnivora showed a high FO of FPT (Table 1) but failed to elaborate if grasses were observed, while other studies lumped grasses with other categories such as fruit, preventing an understanding of the frequency of grass ingestion.

In some cases the grass consumed was notably in large amounts, e.g., for *Canis latrans* (Ellis & Schemnitz 1958; Holle 1973; Stoel 1976), *Canis lupus* (Gade-Jørgensen & Stagegaard 2000; Vos 2000; Valdmann *et al.* 2005), *Cerdocyon thous* (de Araujo 2008), *Genetta tigrina* (Roberts *et al.* 2007), *Gulo gulo* (Myhre & Myrberget 1975), *Hyaena brunnea* (Faure *et al*. 2019), *Martes americana* (Marshall 1946; Francis 1958), *Martes martes* (Lockie 1961), *Panthera pardus* (Hoppe-Dominik 1988), *Panthera uncia* (Oli *et al.* 1993), *Puma concolor* (Toweill & Maser 1985), *Vulpes chama* (Bothma 1966), and *Vulpes vulpes* (Hatfield 1939; Scott 1942). In other studies on *Panthera uncia*, large amounts of plants were ingested which may have been grass, but this was not clarified (Wegge *et al.* 2012; Devkota *et al.* 2013).

Consumption of marine plants, bryophytes, conifers, dicots, and fungi was infrequently observed. Algae were consumed by *Lontra canadensis* (Buzzell *et al.* 2014), *Ursus arctos* (Kistchinski 1972), *U. maritimus* (Russell 1975; Stempniewicz 2017), *Vulpes lagopus* (Fay & Stephenson 1989; Kapel

1999; Pagh & Hersteinsson 2008), and several members of the families Otariidae and Phocidae. *Arctocephalus townsendi* consumed the marine plant *Phyllospadix* (Zosteraceae) (Aurioles-Gamboa & Camacho-Ríos 2007). Conifer FPT were consumed by *Bassariscus astutus* (Alexander *et al.*, 1994), *Canis latrans* (Santana 2010; Souther & Wiggers 2012; Santana & Armstrong 2017), *Canis lupus* (Thompson 1952; Śmietana & Klimek 1993; Andersone 1998; Müller 2006), *Lutra lutra* (Bouroş & Murariu 2017), *Lynx rufus* (Rollings 1945), *Martes foina* (Apáthy 1998), *Martes martes* (Pullianinen & Ollinmäki 1996), and *Nyctereutes procyonoides* (Elmeros *et al.* 2018).

Mosses were consumed by *Bassariscus astutus* (Alexander *et al.* 1994), *Canis latrans* (Santana & Armstrong 2017), *Cerdocyon thous* (Pedó *et al.* 2006), *Urocyon cinereoargenteus* (Hatfield 1939), and *Ursus maritimus* (Russell 1975; Gormezano & Rockwell 2013; Stempniewicz 2017).

Dicot species were consumed by the Ursidae. About 25% of the scats of *Cerdocyon thous* contained FPT of the Mimosoideae (Pedó *et al.* 2006). In an unknown FO, *Berchemia* was found in *Civetticitis civetta* scats (Guy 1977). Leaves of *Quercus* were in 14% of scats of *Canis anthus* (Eddine *et al.* 2017). Leaves of *Betula*, *Fraxinus*, and *Quercus* were in 8% of *Canis aureus* scats (Stoyanov 2012). With an unknown FO, leaves of *Fagus* were found in *Canis lupus* scats (Śmietana & Klimek 1993). In 45% of the scats of *Panthera uncia*, FPT of *Myricaria* were detected (Jumabay-Uluulu *et al.* 2014). *Salix* was found in 10% and *Tamarix* was found in 17% of scats of *Genetta genetta* (Sánchez *et al.* 2008). *Euclea* leaves were ingested by *Felis libyca* (Stuart 1976b). About 5% of the feeding observations of *Canis mesomelas* observed the consumption of succulent FPT of *Arthraerua*, *Psilocaulon*, and *Zygophyllum* (Hiscocks & Perrin 1987). *Cynictis penicillata* apparently feeds on the succulent *Chortolirion* (Zumpt 1968). With an unknown FO, *Oxalis* bulbs were ingested by *Otocyon megalotis* (Stuart *et al.* 2003).

Ingestion of fleshy, non-lichenized fungi such as mushrooms or truffles were noted in nine species: *Herpestes ichneumon* (Delibes *et al.* 1984), *Martes foina* (Delibes 1978), *Martes martes* (Pullianinen & Ollinmäki 1996; Helldin 2000), *Meles meles* (Roper & Mickevicius 1995; Hipólito *et al.* 2016), *Mustela erminea* (Belyk 1962), *Pekania pennanti* (Grenfell & Fasenfest 1979; Zielinski *et al.* 1999), *Ursus arctos* (Mattson *et al.* 2002), *Ursus maritimus* (Russell 1975; Gormezan & Rockwell 2013; Stempniewicz 2017), and *Vulpes vulpes* (Bakaloudis *et al.* 2015).

Lichen ingestion was noted in five species of the Carnivora: *Ailurus fulgens* (Panthi *et al.* 2012; Sharma *et al.* 2014), *Bassariscus astutus* (Alexander *et al.* 1994), *Canis mesomelas* (Hiscocks & Perrin 1987), *Martes americana* (Marshall 1946; Bull 2000), and *Vulpes lagopus* (Pagh & Hersteinsson 2008).

Soils or rocks were consumed by *Bassariscus astutus* (Alexander *et al.* 1994), *Canis latrans* (Haight 1937; Bond 1939), *Canis lupus* (Kuyt 1969), *Gulo gulo* (van Dijk *et al.* 2007), *Lynx canadensis* (Hanson & Moen 2008), *Panthera pardus* (Andheria *et al.* 2007), *Panther tigris* (Powell 1957: 211; Schaller 1967: 280; Sunquist 1981; Johnsingh 1983; Khan 2008), *Procyon lotor* (Thompson 1952), and *Vulpes vulpes* (Hamilton, jr. *et al.* 1937; Eadie 1943; Wilson & Dookia 2019).

Discussion

The consumption of leaves or other FPT is widespread in the Carnivora, occurring in at least 124 species (ca. 41% of the Carnivora species). Eight of these species are in the Ailuridae and Ursidae, the only two families generally considered to contain folivores that serve their nutritional needs from FPT consumption. The other 116 species are carnivores and omnivores that are not known to derive nutrition from folivory; their consumption of FPT is here supported by 344 studies. The majority of the studies concerned the Canidae (153 studies), the Felidae (89 studies), and the Mustelidae (50 studies). It is noteworthy that FPT consumption was found not only in omnivores and herbivores of the Carnivora, but also in many predominantly carnivorous species such as those of the Felidae. While the consumption of FPT serves the nutritional needs of the Ailuridae and Ursidae, the purpose of this behaviour in other species of the Carnivora, for the most part, can only be speculated. The consumption of grasses and sedges, marine plants, conifers, bryophytes, dicots, fungi, and soil by species of the Carnivora is most often likely a deliberate behavior. Sometimes these materials were ingested relatively frequently and sometimes in relatively large amounts.

Grasses & Sedges

Grasses (Poaceae) were the most frequently consumed FPT among the Carnivora, being documented in 95 species and one hybrid of the Carnivora (Table 1). Sedges (Cyperaceae) were identified in a few studies but they may have been overlooked in other studies because of their resemblance to grasses. Regardless of the possible confusion between grasses and sedges, grasses are likely ingested more often than sedges in the Carnivora, given that several studies identified the grass genera consumed, but rarely were genera of Cyperaceae indicated (Bothma 1966; Kok & Nel 1992). Presumably the studies included here were reporting observations of the leaves or stems of grasses and sedges, unless their roots or seeds were specifically noted (Table 1).

While grasses are a staple food in some species (of the Ailuridae and Ursidae), in other instances, ingested grass leaves may serve to expel intestinal parasites, which is supported by observations from nine studies on eight species of the Carnivora. The earliest insight into this phenomenom may be that of Murie (1944), who observed that some scats of *Canis lupus* contained both grass and roundworms (presumably Toxocaridae). Murie thought that the grass may act to scour and remove the parasites. One scat of *Panthera tigris* contained both grass and tapeworms (Schaller 1967: 280), and Schaller noted the similarity to Murie's earlier observation. Kuyt (1969) found one fresh scat of *Canis lupus* consisting of a solid mass of grass containing tapeworms (*Taenia*). One scat of *Cuon alpinus* had two different kinds of plants, grass and the leaves of *Lantana*, that were together mixed with three tapeworms (*Taenia*) and mucus (Johnsingh 1983). Toweill & Maser (1985) observed that some scats of *Felis concolor* consisted almost entirely of grass entwined with tapeworms. Gilbert (*in* Huffman 1997) observed in the fall, before hibernation, mature *Carex* spp. being consumed by *Ursus arctos* and subsequently the scats being composed of masses of long tapeworms. Makundi (*in* Huffman & Caton 2001) reportedly observed the expulsion of *Ascaris toxicara* roundworms after dogs (*Canis familiars*) consumed grass. Su *et al.* (2013) found a significant correlation between co-occurrences of grass and *Toxocara paradoxura* in the scats of *Viverricula indica*, also providing photographic evidence (Su *et al.* 2013: fig. 4). Similarly, Laurimaa *et al.* (2016) found a statistically significant positive correlation between infection with helminths (particularly trematodes) in *Nyctereutes procyonoides* and consumption of FPT, mostly grasses.

A few other studies hint at a possible relationship between intestinal parasites and grass consumption in the Carnivora. With about 72% of 50 stomachs of *Lynx rufus* containing intestinal parasites, it was also observed that grass and white cedar leaves occurred in most of their stomachs (Rollings 1945). Urban populations of *Canis latrans* that had higher intestinal parasite species diversity also consumed vegetation more often (probably grasses but this was not clarified), compared to non-urban populations with lower parasite diversity that consumed vegetation less often (Manning 2007). In the scats of *Otocolobus manul*, the rates of parasite frequency and grass frequency were very similar, but it was not indicated if these were correlated (Ross 2009).

The ingestion of grasses and sedges may serve to both 1) irritate and dislodge intestinal parasites and 2) stimulate gastric motility and secretion (Huffman & Caton 2001; McLennan & Huffman 2012). The morphological features of grasses and sedges that help to stimulate the gastrointestinal tract and expel parasites are probably the hardened epidermal serrations and trichomes that are mineralized with silica (Mehra & Sharma 1965; Lanning & Eleuterius 1989; Trembath-Reichert *et al.* 2015). Simpson (1902) stated that cats (*Felis catus*) "always prefer the coarser kind of grass." Robinette *et al.* (1959) observed that *Puma concolor* ingested coarse grasses like *Elymus condensatus* which even livestock avoid in the winter, reinforcing that it is not the nutritional value of the grass that is important to *Puma concolor*. Hoppe-Dominik (1988) noted that of the 30 most frequent grass species in the region, *Panthera pardus* chose to ingest the hairiest two species of grasses. Su *et al.* (2013) described the ingested grasses as all sharp-edged and covered with trichomes. Additionally, *Lantana* (Verbenaceae) leaves can be strongly scabrous, and were found together with grass and tapeworms in the scats of *Cuon alpinus* (Johnsingh 1983). The scats of *Canis anthus* and *Genetta genetta* both reportedly contained long leaf blades of *Ameplodesmos mauritanicus* (Boukheroufa *et al*. 2020), the blades of which are rather tough and strongly serrated (Anderson & Sigaut 2014). Montalvo *et al.* (2020) observed three species of wild Felidae consuming *Oryza latifolia*, which is replete with prickles on the leaf blades (Sánchez *et al.* 2003). Outside of the Carnivora, other animals appear to favor hairy plant tissues to aid parasite expulsion, e.g., in *Ansur caerulescens* (snow goose; Holmes *in* Huffman 1997), *Hylobates lar* (gibbon; Barelli & Huffman 2016), and *Pan troglodytes* (chimpanzee; Wranghman & Nishida 1983; Huffman *et al.* 1996; Fowler *et al.* 2007; McLennan & Huffman 2012). This behaviour is possibly replicated in some marsupials that show evidence of grass ingestion, in three species of *Dasyurus* (Green 1967; Blackhall 1980; Glen & Dickman 2006, 2008; Glen *et al.*, 2009), *Didelphis virginiana* (opossum; Wood 1954; Hopkins & Forbes 1980), and *Sarcophilus harrisii* (Green 1967).

That the morphological features of grasses or sedges may help to expel parasites in the Carnivora is further supported by the observation that their leaves are often swallowed as large fragments instead of being finely chewed, suggesting they are not being consumed for digesting and assimilating nutrients. Among the studies included on the Carnivora (Table 1), ingested grass was described as undigested (Toweill & Maser 1985; Hoppe-Dominik 1988; Loveridge & Macdonald 2003; Bekele *et al.* 2008; Bošković *et al.* 2013), in well-ordered bundles (Gade-Jørgensen & Stagegaard 2000), bundled whole (Su *et al.* 2013), in wads (Murie 1935; Snead & Hendrickson 1942; Thompson 1952), in short lengths (Lindsay & Macdonald 1986), long blades (Haight 1937), or intact (Barboza *et al.* 1994; Chuang & Lee 1997; Chua *et al.* 2016). Other studies noting grass or sedge ingestion (Table 1) generally gave no further description of the plant tissues observed. In the marsupial *Dasyurus viverrinus*, ingested grass blades to 5 cm long were described as common (Blackhall 1980).

Usually, the amount of grass ingested by the Carnivora was noted to be in relatively small amounts and often the FO was not very high (Table 1). Nonetheless, even rare events of grass ingestion may be purposeful in the Carnivora. For example, the earliest known observed association between parasite expulsion and grass ingestion in the Carnivora found the FO of grasses and sedges to be only about 2% for 1,174 scats of *Canis lupus* (Murie 1944). On the contrary, in some studies of scats or gastrointestinal contents, grass ingestion was very frequent, with an FO of 50–100%. Further, in other studies the amount of grass found in a single scat or stomach was notably large, sometimes comprising nearly the entire scat or stomach contents (see Results; Table 1). Possibly, small amounts of grass are ingested occasionally for prevention or control of small-scale infestations of intestinal parasites, while a larger amount or more frequent consumption of grass could be indicative of heavier or more persistent parasite loads.

Grass eating may be an innate behavior in some species of the Carnivora (Bjone *et al.* 2009), as even well-cared for domestic cats (*Felis catus*) and dogs (*Canis familiaris*) that might be free of intestinal parasites often regularly consume grass (Hart 2008; Hart & Hart 2018; Hart *et al*. 2019). A long-held belief is that grasses are consumed by cats or dogs to alleviate nausea or induce vomiting (Huidekoper 1895; Cameron 1927; Powell 1957: 210; Beaver 1981; Bush 1995; Cannon 2013). Culpeper (1666: 89) wrote that "when [dogs] are sick […] they will quickly lead you to [dogs-grass]" which presumably refers to *Elymus repens*, a grass that can be pilose and scabrous (Szczepaniak 2009). Possibly, symptoms of an illness or nausea might sometimes correlate with intestinal parasite infection (Zanzani *et al.* 2014). Other historic references associate grass ingestion by dogs with vomiting (Linnaeus 1758: 39, "*Vomitu a gramine purgatur*"; Morell 1774: "Hound grass" under "*Canaria*"; Booth 1835: 290; Paulini 1834: 29, "*sic canis gramen masticando vomit*, *luppus a fungo purgatur*"). Fenn (1790) wrote that dogs eat grass to vomit, but for cats Fenn stated only that they eat grass as medicine. Recent studies show that when domestic cats or dogs consume grasses or other vegetation, they usually do not vomit nor appear to the owners to be nauseous (Sueda *et al.* 2007; Hart 2008; Bjone *et al.* 2009; McKenzie *et al.* 2010; Hart *et al*. 2019). Dudley (1892: 87) also noticed that dogs frequently ate grass without vomiting, but rather suggested that grass ingestion prevented vomiting.

Detailed quantitative data collected in controlled conditions found that vomiting is quite rare following grass ingestion in domestic dogs (Bjone *et al.* 2007, 2009), while more subjective reports from surveys to pet owners give a sense that vomiting is more frequent (Sueda *et al.* 2007; Hart & Hart 2013; Hart *et al*. 2019). From direct observations of 2,108 total feeding events on grass by 36 dogs (*Canis familiaris*), only 11 times (0.5%) did a vomiting event follow (Bjone *et al.* 2007, 2009). From surveys, pet owners reported that vomiting after grass consumption was relatively common in about 20–30% of domestic cats (Hart & Hart 2013; Hart *et al*. 2019) or dogs (Sueda *et al.* 2007). Possibly a greater amount of variables influences the rates reported in these surveys such as the belief that grass ingestion causes vomiting, a wider variety of breeds, confounding health issues, a wider variety of grass species encountered some of which may be more toxic, and the possibility of toxins like pesticides on grasses causing adverse reactions. In one case, grass ingestion by a poodle always resulted in vomiting, which allegedly was remedied with a high-fiber diet (Kang *et al.* 2007). Murie (1944) reported one incident of *Canis lupus* vomiting after consuming grass. Lockhart (1997) mentioned a dog (*Canis familiaris*) eating a different kind of monocot, chives (*Allium* sp.), and vomiting afterwards, speculating it was to control parasites.

There has also been the suggestion that grass consumption may help to bind cat hair (Still 1908), possibly to regurgitate hair balls (Barrs *et al.* 1999) or pass them in scat (Chame 2003), but strong support for this claim is lacking (Donadelli 2019). Grass was reported as a minor component of hairballs in *Hyaena hyaena* (Alam & Khan 2015). There is some evidence that grass may help to form regurgitated pellets in vultures (Paterson, jr. 1984; Xirouchakis 2005; Houston *et al.* 2007).

Marine Plants

The occasional occurrence of marine plant consumption by some Carnivora species suggests that algae have some value, but whether it serves nutritional or medicinal purposes remains uncertain. Algae were the primary FPT ingested in the marine families Otariidae and Phocidae. Algae such as *Fucus* and *Laminaria* are somewhat commonly consumed by *Ursus arctos* (Kistchinski 1972) and *U. maritimus* (Russell 1975; Stempniewicz 2017). These algal genera are known to contain significant amounts of phenylpropanoids (e.g., phlorotannins) and galactolipids (Tugwell & Branch 1992; Deal *et al.* 2003). Algae also appear to be regularly consumed by *Vulpes lagopus* (Fay & Stephenson 1989; Kapel 1999; Pagh & Hersteinsson 2008). The relative importance of algae for *Lontra canadensis* is difficult to determine since algae were grouped together with other plants (presumably Embryophyta) into one category (Buzzell *et al.* 2014). Perhaps the consumption of *Phyllospadix* (Zosteraceae), noted in 40% of the scats of *Arctocephalus townsendi* (Aurioles-Gamboa & Camacho-Ríos 2007), has nutritive value, as it was also noted in trace amounts in the scats of *Ursus maritimus* (Russell 1975). The phenylpropanoids of *Phyllospadix* might also be relevant to their consumption (Choi *et al.* 2009).

Conifers

Ingestion of the FPT of conifers was noted in eight species of the Carnivora. It is very doubtful that conifer leaves would support the nutritional needs of the Carnivora. The intentional consumption of conifer leaves might be due to their rich terpene content or their phenylpropanoids (Keeling & Bohlmann 2006; Faccoli & Schlyter 2007). The use of turpentine (derived from conifers such as *Pinus* spp.) has been historically utilized as an anthelmintic (Mclanahan 1918; Hall 1919; Le Roux 1930), which might explain the occurrence of conifers in the gastrointestinal tracts of some species recounted below.

Rollings (1945) found that about 72% of bobcats (*Lynx rufus*) had intestinal parasites and that grass and white cedar (*Thuja*) leaves were found in most of their stomachs. In the scats of *Bassariscus astutus*, Alexander *et al.* (1994) noted the conifer leaves were clearly ingested but were mostly undigested. In *Canis latrans*, conifer leaves were considered accidentally ingested or incidentally stuck to the scat samples (Souther & Wiggers 2012) but were recorded as rather frequent in other scat samples (Santana 2010; Santana & Armstrong 2017). In *Canis lupus*, conifer leaves were considered undigestible and unintentionally ingested (Śmietana & Klimek 1993), were relatively frequent in scats (Thompson 1952; Andersone 1998), or were considered non-food items (Müller 2006). Conifer leaves were grouped together with other items into one category in studies on *Lutra lutra* (Bouroş & Murariu 2017), *Martes foina* (Apáthy 1998), *Martes martes* (Pullianinen & Ollinmäki 1996), and *Nyctereutes procyonoides* (Elmeros *et al.* 2018), being considered non-food (Elmeros *et al.* 2018), to be consumed in winter or in mixture with other foods (Apáthy 1998), or to be consumed incidentally with carrion (Golightly *et al.* 2006).

Bryophytes

Reports of moss consumption by the Carnivora are few. Mosses are thought to have low digestibility, even for herbivores (Prins 1982; Ihl & Barboza 2007). Possibly, the secondary metabolites of bryophytes, such as the terpenoids or phenylpropanoids (Peters *et al.* 2018), have medicinal effects in the Carnivora, or the high concentration of essential fatty acids are nutritionally important (Prins 1982). A few investigations have explored the anthelmintic activity of mosses (Gamenara *et al.* 2001; Roldos *et al.* 2008; Kumari 2015), but the pertinence to potential activity in the Carnivora requires further inquiry.

Ursus maritimus occasionally consumes mosses (Russell 1975; Gormezano & Rockwell 2013; Stempniewicz 2017). It was implied that the bryophytes consumed by *Bassariscus astutus* were well masticated and heavily digested (Alexander *et al.*, 1994). Mosses were only consumed in the spring by *Cerdocyon thous* (Pedó *et al.* 2006) and were similarly infrequent in the scats of *Canis latrans* (Santana & Armstrong 2017). Perhaps the most intriguing report was that in two stomachs of *Urocyon cinereoargenteus*, mosses made up the entirety of the contents (Hatfield 1939).

Dicots

Ingestion of the FPT of several dicot species was recorded in the Carnivora, having relatively significant FOs or with direct observations of their consumption, suggesting that it is likely intentional. It is difficult to speculate upon the nutritional or medicinal value of these occurrences. The Ursidae may feed on a variety of dicot leaves (Chhangani 2002; McLellan 2011; Gormezano & Rockwell 2013; Furusaka *et al.* 2017; Stempniewicz 2017; Sethy & Chauhan 2018), probably for nutritional purposes in many instances, but potential medicinal value cannot be summarily dismissed.

Several other FPT of dicots consumed in the Carnivora included *Berchemia* (for *Civetticitis civetta*; Guy 1977), *Euclea* (*Felis libyca*; Stuart 1976b), *Fagus* (*Canis lupus*; Śmietana & Klimek 1993), *Myricaria* (*Panthera uncia*; Jumabay-Ululu *et al.* 2014), *Quercus* (*Canis anthus*; Eddine *et al.* 2017), the Mimosoideae (*Cerdocyon thous*; Pedó *et al.* 2006), *Salix* and *Tamarix* (*Genetta genetta*; Sánchez *et al.* 2008), and *Betula*, *Fraxinus*, and *Quercus* (*Canis aureus*; Stoyanov 2012). The leaves and stems of these plants would probably be considered undigestible to these Carnivora species. The leaves of many of the above plant genera are not particularly hairy but may have significant concentrations of phenylpropanoids (such as lignin and tannins), e.g., in *Berchemia* (Lee *et al.* 1995), *Betula* (Wratten *et al.* 1984), *Euclea* (Maroyi 2017), *Fagus* (Bussotti *et al.* 1998), *Fraxinus* (Schempp *et al.* 2000), *Myricaria* (Chernonosov *et al.* 2017), *Quercus* (García-Villalba *et al.* 2017), *Salix* (Julkunen-Titto 1985), and *Tamarix* (Ksouri *et al.* 2009). Terpenes and alkaloids, such as in *Euclea* (Maroyi 2017), may also be significant. The Mimosoideae notably contain significant amounts of alkaloids (Wink 2013).

Two canids ingested succulent plants in Africa. *Canis mesomelas* consumed FPT of the plant genera *Arthraerua*, *Psilocaulon*, and *Zygophyllum* (Hiscocks & Perrin 1987) and *Cynictis penicillata* consumed *Chortolirion* (Zumpt 1968). Perhaps the water content or the secondary metabolites of these plants are important to these canids.

Unknown woody material was exceptionally frequent in a study of *Vulpes vulpes* (Stepkovitch 2017). *Oxalis* bulbs were ingested by *Otocyon megalotis* (Stuart *et al.* 2003). As previously mentioned, scabrous *Lantana* (Verbenaceae) leaves were found with grass and tapeworms in a scat of *Cuon alpinus* (Johnsingh 1983). It also well known that the Felidae may ingest *Nepeta cataria* (catnip), but their behavior appears to be primarily concerned with the odor and not the ingestion of the plant (Tucker & Tucker 1988).

Fungi

Fungi are occasionally consumed by the Carnivora, probably for nutritional properties but their secondary metabolites cannot be discounted. Fleshy fungi were consumed by nine species of the Carnivora and lichens were ingested by five species (see Results).

Fleshy fungi such as mushrooms are easily masticated and nutritive substances could probably be absorbed (Claridge & Trappe 2005; Urban 2016). Mushrooms were occasionally consumed by some mustelids (Belyk 1962; Delibes 1978; Pullianinen & Ollinmäki 1996; Helldin 2000), and especially *Pekania pennanti* may apparently feed frequently on false truffles (Boletales) (Zielinski *et al.* 1999). False truffles, mushrooms, and puffballs are seasonally useful to *Ursus arctos* (Mattson *et al.* 2002; Vulla *et al.* 2009), which may make some scats liquidy, perhaps indicating a laxative effect and perhaps partly indicative of the high water content of these fleshy fungi. *Vulpes vulpes* was also noted to consume mushrooms (Bakaloudis *et al.* 2015).

Lichens typically have tough thalli and presumably they would not be easily digested by the Carnivora. While lichens might provide some nutrients to carnivores (Dubay *et al.* 2008), the secondary metabolites of lichens may be more relevant (Nybakken *et al.* 2010), though little is known concerning potential medicinal or anthelmintic activity in the Carnivora. *Canis mesomelas* was directly observed once ingesting the crustose lichen *Caloplaca* (Hiscocks & Perrin 1987). Lichens formed the bulk of one scat of *Martes americana* (Marshall 1946). It was implied that the lichens consumed were well masticated and heavily digested in *Bassariscus astutus* (Alexander *et al.* 1994). The amount of lichens consumed by *Vulpes lagopus* was unclear since lichens were lumped into one category with leaves, mosses, and twigs (Pagh & Hersteinsson 2008).

Soils

Ingestion of soils or rocks were occasionally noted in the Carnivora. Geophagy has been speculated to alleviate gastrointestinal problems such as parasites or toxins, or provide minerals (Beyer *et al.* 1994; Wilson 2003; Krishnamani & Mahaney 2009). Like grasses or other scabrous plant tissues, rocks and soils could conceivably mechanically irritate and remove parasites. Schaller (1967: 255) described a scat of *Panthera tigris* consisting of a number of tapeworm segments and a small amount of soil. Soil ingestion appears particularly common in *Panthera tigris* (Johnsingh 1983), sometimes being noted in most of the scats and some scats having fairly large amounts of soil (Powell 1957: 211; Schaller 1967: 280; Sunquist 1981; Khan 2008).

Eadie (1943) noted that occasional scats of *Vulpes vulpes* were almost wholly soil or gravel. The presence of rocks in the scat of *Lynx canadensis* was stated to be "most surprising" (Hanson & Moen 2008). Dirt was in 28% of *Gulo gulo* scats (van Dijk *et al.* 2007) and in 24% of *Panthera pardus* scats (Andheria *et al.* 2007). Earth, gravel, pebbles, and non-grass FPT were encountered with surprising frequency in the scats and stomachs of *Canis latrans* (Bond 1939), and in one scat was a large amount of dirt (Haight 1937). Kuyt (1969) described that several scats of *Canis lupus* were entirely made of an unidentified material resembling dried clay, but then speculated it was undigested material from animal prey. The frequent presence of soil in the scats of *Procyon lotor* was thought to be obtained from the crops and gizzards of bird prey (Thompson 1952). Clearly, some species of the Carnivora consume soil but the reasons for this are unclear.

Is ingestion of FPT accidental?

An overwhelming majority of the 344 studies provided almost no interpretation or discussion concerning the evidence observed of FPT consumption in the Carnivora. About one-sixth of the studies suggested that the consumption of FPT by the Carnivora was accidental or incidental. In contrast, about one-sixth of the studies suggested or concluded that FPT consumption was intentional.

In the studies that favored interpreting the ingestion of FPT as unintentional, the most common explanation given was that the predator incidentally consumed the FPT present in the gastrointestinal tracts of prey. Other reasons given were that the FPT was consumed from herbivore dung, during grooming, or from material near prey. It was occasionally speculated that FPT detritus on the ground had become externally stuck to a scat. One study described "digested grass" to imply it originated from the digesta of the prey, contrasting it with the undigested grass consumed (Loveridge & Macdonald 2003). Nonetheless, in the two Carnivora species studied, the digested grass had a FO of 2%, while undigested grass had a FO of 45–47% (Loveridge & Macdonald 2003).

Behavioral observations indicate carnivores typically avoid the gastrointestinal tracts of prey (Thompson 1952; Schaller 1967; Jobin *et al.* 2000; Buck *in* Lonsdale 2001: appendix B) or eat the tissues of the gastrointestinal tract but avoid the digesta of large herbivorous prey (Johnsingh 1983; Fabregas *et al.* 2016). Peterson & Ciucci (2003: 123) stated that the digesta "is of no interest to" *Canis latrans*, but that they may consume the stomach lining and intestinal wall. However, Wade & Bowns (1985) stated "the milk-filled stomach is a preferred item" for *Canis latrans.* Among several captive species of Carnivora, it was observed that the gastrointestinal tract and its contents are typically avoided, except it was alleged that *Lycaon pictus* may eat a small amount of the digesta (Buck *in* Lonsdale 2001: appendix B). Nonetheless, in captivity, *Lycaon pictus* was also presumably observed to eat grass (Buck *in* Lonsdale 2001: appendix B). Black bears (*Ursus americanus*) were described as "clean […] delicate feeders [whereby] most debris is either spat out or avoided" (Bacon & Burghardt 1976). For the Felidae, it had been stated that their "feeding pattern is relatively neat" (Wade & Bowns 1985). As some smaller prey may be consumed whole (Buck *in* Lonsdale 2001: appendix B), possibly digesta and FPT consumed from small prey could have been detected in carnivore scats or stomachs. The corms of a grass (*Melica*) in the scats of *Canis latrans* were thought to derive from the cheek-pouch contents of rodent prey (Murie 1935). The consumption of seeds from prey intestines, a form of diploendozoochory, has been considered plausible, although proof that seeds have actually been consumed from prey intestines by wild animals is wanting (Hämäläinen *et al.* 2017).

It also been said that the ingestion of FPT or other items was due to the animals being trapped. Gipson (1974) stated that trapped *Canis latrans* "tend to chew and swallow almost anything within reach" as a reason to exclude collecting data on ingestion of FPT. Similarly, in the marsupial *Sarcophilus harrisii*, it was explained that the animals probably chew and ingest grass while trying to escape; on the contrary, the same study implied that the evidence of grass ingestion by *Dasyurus viverrinus* was derived from prey, i.e., the stomach contents of wallabies (Green 1967).

The feeding habits of the Carnivora suggest that accidental ingestion of FPT is a poor explanation for its frequent occurrence in scats or gastrointestinal tracts of the Carnivora, especially when there is a lack of direct evidence that FPT are indeed accidentally consumed. Moreover, there are direct observations of species of Carnivora deliberately eating FPT (e.g., Montalvo *et al.* 2020; see Results). Further, it would be disadvantageous for carnivores to be imprecise in their eating habits (e.g., incidentally consuming prey digesta), which could potentially increase their exposure to infectious diseases or toxins.

Conclusions

Plant eating is widespread in the Carnivora, and includes frugivory, granivory, rhizovory, nectarivory, and folivory. Well over 100 species of the Carnivora deliberately ingest leaves or other FPT, for a variety of purposes. Grasses and sedges are especially useful to the Carnivora, in many cases ostensibly to manage intestinal parasites, as plant leaves with abrasive or hairy structures mineralized with calcium or silicon (Lanning *et al.* 1958; Lanning 1961; Kaufman *et al.* 1981; Dayanandan 1983; Lanning *et al.* 1980; Lanning & Eleuterius 1989; Weigend *et al*. 2018) appear to be most sought after to mitigate intestinal infections. While control of intestinal parasites is a plausible explanation for the ingestion of abrasive or hairy plants (or perhaps soil), additional focused research is desirable to corroborate this. Fresh and old scats might both be useful to observe this potential association (Napoli *et al.* 2016).

The FPT of marine plants, bryophytes, conifers, and dicots are deliberately consumed by some species of the Carnivora, but it is unclear how it may affect their fitness. Many of these plants lack scabrous structures and probably are relative undigestibile, giving cause to consider that their secondary metabolites may have some value, such as anthelmintic properties (e.g., Quinlan *et al.* 2002; Katiki *et al.* 2011; Ndjonka *et al.* 2014; Romero-Benavides *et al.* 2017; Spiegler *et al.* 2017; Liu *et al.* 2020). Several other reasons were provided to explain the ingestion of FPT in the included studies (Table 1), such as the FPT acting as a food, source of minerals or vitamins, toxin elimination, water source, anti-inflammatory, hair elimination, maintenance of the gastrointestinal tract during starvation, or a digestive aid (e.g., for bones, food, hair, or skin). These possibilities also bear consideration. The consumption of fungi or soil also requires further investigation to understand their role and value. The consumption of FPT, fungi, or soil could also be an exploratory behavior that does not always increase fitness. Since diet influences the gut microbiome (Nishida & Ochman 2018), it would be of interest to explore how the consumption of FPT, fungi, or soil could influence the gut microbiome of the Carnivora.

That about 41% (123 species) of the Carnivora may consume FPT is probably an underestimate for several reasons. First, its occurrence has definitely been underappreciated and in many cases probably ignored altogether. Most studies included here were focused on the dietary analysis of carnivory and frugivory, and usually showed negligible interest concerning the consumption of FPT. It is likely that many other studies on the Carnivora found FPT but never reported it. Indeed, 38 studies reported here explicitly excluded FPT evidence from data collection. Some studies stated that the evidence of FPT consumption was only recorded if there was a relatively large amount of FPT detected (e.g., Eadie 1943; Schaller 1967; Andelt *et al.* 1987). Second, potential FPT consumption by other species is unknown because the ecology of many species (e.g., scat analyses) is poorly known; examples include numerous viverrids (Papeş & Gaubert 2007), Bornean felids (Mohamed *et al.* 2009), the canid *Vulpes pallida* (Brito *et al.* 2009), and the mustelid *Bdeogale jacksoni* (De Luca & Rovero 2006) which are all understudied. Lastly, this study undoubtedly failed to include all pertinent studies ever published.

To better understand FPT consumption in the Carnivora, it is requisite that more attention is paid to the species, amounts, and parts of plants ingested (for exceptionally detailed analyses of consumed plant tissues in the Carnivora see Scott 1942; Thompson 1952; Alexander *et al.* 1994; Santana 2010: 24), as well as the health of the animal, such as intestinal parasites. The same is true for investigating the role of fungi (Claridge & May 1994) and soil in the Carnivora. Even the absence of plants, soil, or fungi in scats or stomachs is useful information if it is explicitly stated these items were searched for but not found. If the methodologies are standardized and results are more detailed, then it will be possible to compare across studies and make inferences about conditions that lead to FPT, fungi, or soil consumption. Direct comparisons are not practical nor statistically logical among the 344 studies here (Table 1) because the methodologies and results are excessively heterogeneous. About half of the studies (Table 1) either nebulously defined what kinds of FPT were consumed (e.g., using the vague category "plant material" or "vegetation") or combined multiple discrete items into one category (e.g., grasses and fruits combined). Very rarely (~5%), was plant material treated in detail to identify the genera or species consumed (e.g., Scott 1942; Thompson 1952; Lever 1959; Viljoen & Davis 1973; Bold & Dorzjunduy 1976; Stuart 1976b; Hiscocks & Perrin 1987; Kok & Nel 1992; Śmietana & Klimek 1993; Alexander *et al.* 1994; Chuang & Lee 1997; Melville *et al.* 2004; Álvarez-Castañeda & González-Quintero 2005; Aurioles-Gamboa & Camacho-Ríos 2007; Sánchez *et al.* 2008; Nakwaya 2009; Ramesh *et al.* 2009; Su *et al.* 2013; Habtamu *et al.* 2017; Akrim *et al.* 2019; Boukheroufa *et al.* 2019; Montalvo *et al.* 2020). It is realized that often times the material may be very scant or extremely difficult to identify morphologically without intensive efforts. Availability of DNA sequencing resources will certainly be useful to identify plants or fungi consumed by the Carnivora. Plastid primers were used by Xiong *et al.* (2016) to identify plants in the scats of *Prionailurus bengalensis*, although they were unable to confidently identify plants to the species level.

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TABLE 1

Summary of observations of species of Carnivora ingesting algae, bark, flowers, fungi, leaves, stems, or wood. The suborders (SO) are Caniformia (C) and Feliformia (F). The families (FM) are Ailuridae (Ai), Canidae (Ca), Felidae (Fe), Herpestidae (He), Hyaenidae (Hy), Mephitidae (Me), Mustelidae (Mu), Otariidae (Ot), Phocidae (Ph), Procyonidae (Pr), Ursidae (Ur), and Viverridae (Vi). The categories (Cat.) are algae (A), bark (B), bromeliad (Br), digested grass (dG), flowers (Fl), fruit (Fr), fungi (Fu), grass (G), hair (H), lichen (Li), leaves (Lv), miscellaneous (misc.), mosses (Mo), molluscs (Mu), needles (Nd), plants (P), plastic (plast.), roots (Rt), sedges (S), seeds (Sd), shells (Sh), soil (Sl), stems (St), trap-pan covers (Tpc), vegetation (V), wood (W), and Zosteraceae (Z). Under occurrences (Oc), percentages are rounded to the nearest whole number, unless less than 1%. Studies excluding data on plant consumption (exc) but implying or indicating its occurrence are shown. Occurrence types (OcT) are the frequency of occurrence (FO), mass (M), relative frequency (RF), relative mass (RM), and relative volume (RV). N is the number of samples analyzed. The sample types (SaT) are bears, cats, dogs, items (It), gastrointestinal tracts or intestines (GI), direct feeding observations (Obs), regurgitations (R), scats (Sc), and stomachs (Sm). Categories and notes given here approximate as closely as possible the same terminology used in the cited studies. Within species, observations are ordered chronologically by the reference.

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Ai	*Ailurus fulgens*	Fr, G, Lv	–	–	–	–	Well known that G (bamboo) is primary food source, but Fl, Fr, Li, other Lv, Sd (*Quercus*), and mushrooms are also consumed; see references.	Panthi *et al.* 2012; Sharma *et al.* 2014
		Ailurus styani	Fr, G, Lv	–	–	–	–		
	Ca	*Atelocynus microtis*	P	4%	FO	21	Sc	Estimated from fig. 3.1.5; P excluded Fr.	Leite & Williams 2004
		Canis adustus	G	18%	FO	10894	It	Of 2752 scats; G was 2% of total biomass.	Atkinson *et al.* 2002
			dG	2%	FO	185	Sc		Loveridge & Macdonald 2003
			G	47%					
		Canis anthus	G	9%	FO	246	Sc	Lv was *Quercus*.	Eddine *et al.* 2017
			Lv	14%					
			G	–	–	30	Sc	Long Lv of *Ampelodesma* used frequently, unclear if photo (fig. 2) of G from Sc of *Canis* or *Genetta*.	Boukheroufa *et al.* 2020
		Canis aureus	G	3%	FO	138	Sc	G was grass and grass seeds.	Schaller 1967
			P	6%	RM	814	Sc	Included Fr, Sd, and other plant material.	Lanszki *et al.* 2006
			G	6%	FO	127	Sc		Giannatos *et al.* 2010
			G	13%	FO	16	Sc		Markov & Lanszki 2012
			V	38%	FO	104	Sc	Included G and fruit Sd (e.g., *Zizyphus*).	Mondal *et al.* 2012

C	Ca	*Canus aureus*	G	5%	FO	98	Sc	Excluded wheat but unclear if Lv and/or Sd were included.	Nadeem *et al.* 2012
			G	36%	FO	72	Sm	Lv was ash, birch, hornbeam, and oak.	Stoyanov 2012
			Lv	8%					
			P	45%	FO	238	Sm	Included undigested Fr, G, dried Lv, Sd, St, and vegetables.	Bošković *et al.* 2013
			P	4%	FO	–	It	Included G, Fr, and Sd; no. of It unknown; of 210 stomachs.	Ćirović *et al.* 2014
			G	23%	FO	83	Sc		Khan *et al.* 2017
		Canis familiaris (domestic)	G	–	–	12	dogs	Dogs who eat G; prefer G directly from plants vs. cut/removed Lv; ate G more often before meal; five vomits of 709 G-eating events.	Bjone *et al.* 2007
			G	100%	FO	25	dogs	Veterinary student survey; 40% never vomited eating G.	Sueda *et al.* 2008
			P	79%	FO	47	dogs	Outpatient service of veterinary teaching hospital survey.	
			B, St	6%	FO	1571	dogs	Internet survey for dogs known to eat P; data indicate most frequently eaten plant part; 98% eat G at least sometimes; 68% daily or weekly eat P; 22% frequently vomit after eating P, especially older dogs; estimated from fig. 1.	
			G	79%					
			Lv	3%					
			Rt	1%					
			G	–	–	26	dogs	26 puppies all ate G, with six vomits among 1399 G-eating events.	Bjone *et al.* 2009
			G	–	–	12	dogs	374 grass-eating events were observed among 12 beagles.	McKenzie *et al.* 2010
			G	32%	FO	234	dogs	Based on interviews of dog owners during routine checkups.	Tamimi *et al.* 2013
			G, S	–	–	3	dogs	G included 10+ species; one dog known to eat G (rarely S) weekly; amount consumed generally small.	This study: Appendix 1
		Canis familiaris (feral)	G	80–100%	FO	5	Sc	Also unidentified Lv, wood splinters, and pebbles in some Sc; one Sc mostly contained G.	Scott 1971; Scott & Causey 1973
			P	34%	FO	1085	Sc	Fall Sc principally *Rubus* Sd; no other information given about P.	Lunney *et al.* 1990
			G	<1%	RM	72	dogs	Based on visual observation of feeding behavior.	Butler & du Toit 2002
			V	18%	RF	137	Sc	V frequently was G.	Campos *et al.* 2007
		Canis latrans	G	3%	FO	778	Sc, Sm	Of 714 Sc, 64 Sm; G as a wad of green grass, only broad-leaved species.	Murie 1935
			G	9%	FO	112	Sc	Small amounts of G were in almost every Sc, but 9% of Sc were unusual cases of evidence of G; also noted was a Sc with two large pieces of W and one Sc with a large amount of dirt.	Haight 1937

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Ca	*Canis latrans*	G	2%	FO	311	Sc		Murie 1945
			G	5%	FO	282	Sc, Sm	Of 273 Sc and 9 Sm; St, B, dead Lv, hay, earth, gravel, and pebbles also found with surprising frequency.	Bond 1939
			G	15%	FO	762	Sc	Usually in trace amounts; in four Sc G was more than half of it.	Ellis 1951
			G, S	12%	FO	1096	Sc, Sm	Of 326 Sc and 770 Sm.	Korschgen 1957
			G	50%	FO	16	Sm	Usually found in trace amounts; more than half of contents in one Sm.	Ellis & Schemnitz 1958
			V, misc.	8%	FO	48	Sm	Excluded persimmon and *Opuntia*.	Halloran & Glass 1959
			Lv	15%	FO	671	Sc	Lv excluded grasses.	Holle 1973
			G	65%				G was eaten deliberately (e.g., in large amounts) on only 16 occasions.	
			B, G, Lv, St	exc	–	168	Sm	Was suggested eating P due to being trapped.	Gipson 1974
			G	19%	Sc	1143	Sc	G in small amounts found all year in Sc; a few Sc almost entirely of G.	Stoel 1976
			G	51%	FO	960	Sc	V as miscellaneous vegetation, excluding G.	Short 1979
			V	46%					
			P	15%	FO	55	Sc	P as other plants, mostly G, excluding juniper berries.	Turkowski 1980
			Lv, St	45%	FO	136	Sm		Best *et al.* 1981
			G	82%					
			G	2%	RM	550	Sc	G was referred to as grass macrofragments.	MacCracken & Hansen 1982
			misc.	5%	FO	–	It	Of 6354 scats; possibly included P or G; category only counted if >40% of Sc.	Andelt *et al.* 1987
			G, Sd, Fr	20%	RV	469	Sc	Estimated from fig. 3; Fr was juniper berries.	Kitchen *et al.* 1999
			G	exc	–	59	Sc		Hidalgo-Mihart *et al.* 2001
			P	15%	FO	397	It	Of 239 scats; included *Aristida, Bouteloua, Sesuvium*, *Suaeda*; P probably included Fr and Sd.	Álvarez-Castañeda & González-Quintero 2005

C	Ca	*Canis latrans*	V	54%	FO	120	Sc	More V and higher parasite species diversity in non-urban populations, compared to urban.	Manning 2007
			G	6%	FO	1429	Sc		Morey *et al.* 2007
			V	15%	RF	408	Sc	V included G and berries; RF estimated from fig. 4.	Prugh *et al.* 2008
			P	4%	FO	121	Sm	As plants and berries.	Žunna *et al.* 2009
			G	3%	FO	1460	Sc	G as green grass; V as other vegetation (excluding Fr).	Allen *et al.* 2012
			V	3%					
			P	45%	FO	484	Sc	P was primarily G.	Lukasik & Alexander 2012
			Lv, Nd	exc	FO	72	Sc	Small amounts only counted half of the time.	Souther & Wiggers 2012
			G, Sd	23%					
			B, St	10%	FO	159	Sc	Mo as non-vascular land plants (Bryophyta); Nd was *Pinus;* P was unknown plant matter.	Santana 2010; Santana & Armstrong 2017
			G	43%					
			Mo	3%					
			Nd	9%					
			P	9%					
			G, P, St	–	–	3246	Sc	Pieces of G, small amounts of P, St (twigs), and Sl (dirt) in Sc (of *Canis latrans* and/or *Vulpes macrotis*).	Kelly *et al.* 2019
		Canis lupus	G, S	2%	FO	1174	Sc	G eaten at all seasons; G in Sc sometimes with round worms, seemed to act as a scour; observed a male eat G, leaving a watery Sc and later vomiting some of the G.	Murie 1944
			G	25%	FO	435	Sc	G usually was trace, but about ¼ were a sizable wad; evergreen Nd and twigs were in trace; V(1) was *Abies*, V(2) *Tsuga*, V(3) *Thuja*, V(4) *Chmaedaphne*, V(5) *Picea*, V(6) *Ledum*, V(7) *Pinus*, V(8) *Populus*, and V(9) *Solidago*.	Thompson 1952
			V(1)	11%					
			V(2)	8%					
			V(3)	3%					
			V(4)	3%					
			V(5)	2%					
			V(6)	2%					
			V(7)	1%					
			V(8)	<1%					
			V(9)	<1%					

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Ca	*Canis lupus*	G	exc	–	–	Sm	300 and 350 cubic cm of G found each in two Sm; gravel also mentioned; pine Nd and shredded W not counted.	Stenlund 1955
			G, S	6%	FO	438	Sc		Mech 1966
			G, S	2%	FO	1203	It	Of 595 Sc; P included Nd, Ericaceae Lv, and *Sphagnum*; also 7% of It was sand, clay or ash; one fresh Sc was a solid mass of G containing several tapeworms (*Taenia*); also ⅖ of Sm had a few stalks of S.	Kuyt 1969
			P	3%					
			G, V	1%	FO	203	Sc	Traces of V (such as G and Nd) in nearly all Sc; in two Sc G was larger than trace amount and was a major item in one Sc.	Hill 1979
			G, Lv, Nd	exc	–	221	Sc	Lv included beech; Nd included fir and spruce.	Śmietana & Klimek 1993
			G	14%	FO	28	Sm	G was in minute quantities.	Papageorgiou *et al.* 1994
			G	10%	FO	96	Sc		Andersone 1998
			Nd	15%					
			G	27%	FO	163	Sc	G most often in well-ordered bundles; 50–100% of relative volume in five Sc.	Gade-Jørgensen & Stagegaard 2000
			G, Fr	76%	FO	87	Sc	An important volume of G in some Sc.	Vos 2000
			P, Fr	7%	FO	409	Sc		Andersone & Ozoliņš 2004
			G, S	27%	FO	78	Sc		Rigg & Gorman 2004
			G	exc	–	585	Sc, Sm	Of 67 Sm and 518 Sc; one Sm was filled with G.	Valdmann *et al.* 2005
			P	5%	FO	2063	Sc	P was particularly G, but P presumably also included Nd, Lv, and St.	Müller 2006
			P	74%	FO	530	Sc	P was largely G.	Stahler *et al.* 2006
			P	23%	FO	474	Sc		Nowak *et al.* 2011
			P	13%	FO	10	Sc	P as plant matter or plant material.	Anwar *et al.* 2012
			P	11%	FO	123	It	Of 81 scats; P included G, *Pinus* Nd, and Sd.	Lanszki *et al.* 2012
			G	30%	FO	20	Sc	G as green grass.	Palmer 2012
			P	8%	FO	200	Sc	Excluded Fr; more herb in summer than winter.	Špinkytė-Bačkaitienė & Pėtelis 2012

C	Ca	*Canis lupus*	P	exc	–	47	Sc		Jumabay-Ululu *et al.* 2014
			G, Lv	32%	FO	101	Sc	Lv were of crops.	Atickem *et al.* 2017
			G, Lv	6%	RF	96	Sm	15 Sm were empty and excluded from totals.	Ćirović & Penezić 2019
			V	3%	RF	118	Sc	V as vegetative matter and unidentifiable.	Lyngdoh & Habib 2019
			P	1%	FO	236	Sc	P was Lv, Sd, and others.	Sin *et al.* 2019
		Canis mesomelas	G	36%	FO	425	Sm	1.1% of total volume in Sm.	Bothma 1971
			P	52%	RV	5	Sm	In two Sm, P (39%) included *Eragrostis*; in two other Sm, P (90%), considerable amout was *Grewia* Fr and the rest consisted of G (*Aristida, Cynodon, Eragrostis,* and *Themeda*); in one other Sm, P was trace.	Viljoen & Davis 1973
			G	16%	FO	760	Sc		Stuart 1976a
			Lv	2%	FO	477	Sc	Lv were dicots.	Rowe-Rowe 1983
			G	51%	FO	477	Sc		
			V	5%	FO	102	Obs	V was *Arthraerua, Caloplaca* (Li), and *Psilocaulon.*	Hiscocks & Perrin 1987
			G	6%	FO	47	Sc	St as woody material; *Zygophyllum* in one scat.	
			St	6%					
			dG	2%	FO	397	Sc		Loveridge & Macdonald 2003
			G	45%					
			G, Lv	63%	FO	145	Sc		Klare *et al.* 2011b
			G	12%	FO	154	Sc		Humphries *et al.* 2015
			G, Lv	52%	FO	417	Sc		Drouilly *et al.* 2018
		Cerdocyon thous	G	3%	FO	39	Sc		Juarez & Marinho-Filho 2002
			G	5%	FO	429	It	Of 78 scats.	Bueno & Motta-Junior 2004
			G	<1%	FO	302	It	Of 177 scats.	Jácomo *et al.* 2004
			G, S	33%	FO	80	Sc	Mo as bryophytes; V(1) was Mimosoideae; V(2) was other unidentified plants; plants in Sc only as vegetative parts, except some seeds of G.	Pedó *et al.* 2006
			Mo	3%					
			V(1)	25%					
			V(2)	58%					
			G	6%	FO	226	Sc	Excluded corn.	Amaral 2007
			G	58%	FO	52	Sc	Only five Sc had large amounts of G; the rest had small amounts.	de Araujo 2008
			G, S, Sd	exc	–	4	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Ca	*Chrysocyon brachyurus*	G	exc	–	–	Obs	Captive wolves with access to outdoor G; G found intact in scats.	Barboza *et al.* 1994
			G	12%	RF	105	Sc		Motta-Junior *et al.* 1996
			G	83%	FO	141	Sc		Aragona & Setz 2001
			G	9%	FO	70	Sc		Juarez & Marinho-Filho 2002
			G	46%	FO	397	Sc		Santos *et al.* 2003
			G	13%	FO	1344	It	Of 438 scats.	Bueno & Motta-Junior 2004
			G	3%	FO	4540	It	Of 1673 scats.	Jácomo *et al.* 2004
			G	42%	FO	400	Sc	Insignificant in diet.	Quierolo & Motta-Junior 2007
			G	8%	RF	61	Sc		Müller 2016
			G	11%	FO	93	Sc	FO estimated from bar graph.	Giordano *et al.* 2018
		Cuon alpinus	G	7%	FO	509	Sc	These Sc were almost entirely of fresh G; two Sc had G wrapped around hoof and bone splinters; one Sc had five *Lantana* Lv, *Themeda*, *Cymbopogon*, three tape worms (*Taenia*), and mucous.	Johnsingh 1983
			G	4%	FO	181	Sc	Varying amounts of G and Sl in Sc; Sl in 3% of Sc.	Andheria *et al.* 2007
			G	–	–	1	Sc	Sc contained only G and snake remains.	Krishnakumar *et al.* 2019
		Lycalopex culpaeus	P	11%	FO	116	Sc		Jaksić *et al.* 1983
			P	86%	FO	7	Sm		
			P	16%	FO	202	Sc	Included Fr, Lv, and St.	Iriarte *et al.* 1989
			P	–	–	–	Sc	P was mainly grasses.	Iriarte *et al.* 1991
		Lycalopex griseus	P	77%	FO	104	Sm		Jaksić *et al.* 1983
			P	10%	FO	99	Sc		Simonetti *et al.* 1984
		Lycalopex vetulus	G	3%	FO	37	Sc		Juarez & Marinho-Filho 2002
			G	<1%	FO	596	It	Of 273 scats.	Jácomo *et al.* 2004
		Lycaon pictus	G	–	–	–	Obs	Captive, G often eaten.	Buck in Lonsdale 2001

C	Ca	*Nyctereutes procyonoides*	P	14%	FO	42	Sm	Excluded berries and grain, but unclear if G or Nd were included.	Viro & Mikkola 1981
			G, Lv	exc	–	37	Sm		Sutor *et al.* 2010
			P	exc	–	93	GI	As undigestible P.	Mustonen *et al.* 2012
			P	12%	FO	223	Sm	53% of which were apparently G and decayed plant material, according to Laurimaa *et al.* (2016).	Süld *et al.* 2014
			G, Lv, Nd	exc	–	249	Sm		Elmeros *et al.* 2018
		Nyctereutes viverrinus	G	96%	FO	48	GI	P excluded berries and Sd.	Matsuo & Ochiai 2009
			P	10%					
		Otocyon megalotis	P	15%	RV	1	Sm	Included G (*Aristida* and *Eragrostis*).	Viljoen & Davis 1973
			G	33%	FO	18	Sm	Occurrence of dry G resulted from the intake of termites.	Berry 1981
			G, St	36%	FO	58	Sc		MacDonald & Nel 1986
			P	12%					
			G, S	10%	FO	103	Sc	G was *Chloris, Cyperus, Enneapogon, Eragrostis, Schmidtia*, and *Tragus*; V as unidentified monocotyledons.	Kok & Nel 1992
			V	64%					
			P	25%	FO	450	Sc	Included G, *Oxalis* bulbs, and Sd.	Stuart *et al.* 2003
			G	98%	FO	177	Sc	Most frequent in spring, followed by winter, summer, and autumn.	Klare *et al.* 2011a
		Speothos venaticus	G	–	–	–	Obs	Captive, G often eaten.	Buck in Lonsdale 2001
			G, P	88%	FO	17	Sc	Consisting basically of grass and leaves; volume in Sc was very small.	Lima *et al.* 2009
		Urocyon cinereoargenteus	G	9%	FO	53	Sm	V as miscellaneous vegetation, excluding G; in two Sm Mo made up entire contents.	Hatfield 1939
			V	19%					
			G, V	20%	FO	60	Sc		Wilcomb 1948
			Fr, G	39%	FO	75	GI		
			Fr, G	exc	–	34	GI, Sc	G, *Ilex* Fr, and *Quercus* acorns together were in small quantities; of 16 GI and 18 Sc.	Wood 1954
			P	16%	FO	100	Sc	P as other plants, excluding juniper berries.	Turkowski 1980
			B, Lv, St, Tpc	29%	FO	144	Sm		Hockman & Chapman 1983

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Ca	*Urocyon cinereoargenteus*	G	11%	FO	101	Sc		Arnaud & Acevedo 1990
			P	2.1 g	M	2	Sc		García 1998
		Urocyon littoralis	G, St	exc	–	958	Sc		Phillips *et al.* 2007
		Vulpes bengalensis	G	exc	–	–	Sc	Fragments of G formed part of Sc.	Johnsingh 1978
		Vulpes cana	P	37%	FO	344	Sc	Included Fr, G, and Sd.	Geffen *et al.* 1992
		Vulpes chama	G, S	51%	FO	37	Sm	G usually in small amounts, but 23% of one stomach and 53% of contents of another stomach; included *Brachiaria, Eragrostis, Panicum, Bulbostylis*, and *Scirpus*.	Bothma 1966
			P	trace	RV	1	Sm		Viljoen & Davis 1973
			G, Lv	30%	FO	133	Sc		Klare *et al.* 2011b
		Vulpes lagopus	A	exc	FO	1218	Sm	A was occasional; A as kelp.	Fay & Stephenson 1986
			A	4%	FO	254	GI	A as seaweed.	Kapel 1999
			V	73%	FO	293	Sc	Present only in trace amounts.	Elmhagen *et al.* 2002
			A	22%	FO	41	Sm	Estimated from fig. 2; A as seaweed; P as Li, Lv, Mo, and twigs.	Pagh & Hersteinsson 2008
			P	50%					
		Vulpes macrotis	G, P, St	–	–	1230	Sc	Pieces of G, small amounts of P, St (twigs), and Sl (dirt) in Sc (of *Canis latrans* and/or *Vulpes macrotis*).	Kelly *et al.* 2019
		Vulpes rueppellii	G	32%	FO	100	Sc	Described as traces of short lengths of G.	Lindsay & Macdonald 1986
		Vulpes velox	Fr, G, Sd	2%	RV	659	Sc	FO estimated from fig. 3; Fr was juniper berries.	Kitchen *et al.* 1999
			G	22%	FO	215	Sc	Most often in trace amounts.	Sovada *et al.* 2001
		Vulpes vulpes	S	–	–	–	Sc	One Sc was composed entirely of *Carex*; data obtained from Scott 1942.	Baranovskaia & Kolosov 1935
			G	2%	FO	50	Sm	One Sm had much green grass and one had a mass of dirt.	Errington 1935
			G	<1%	FO	137	Sc	3% had sand and dirt.	Hamilton, Jr. *et al.* 1937
			G	7%	FO	29	Sm	In the two Sm with G, the G formed practically the entire contents.	Hatfield 1939
			V	14%					
			G, S	4%	FO	1454	Sc	Several Sc were nearly entirely G and/or S.	Scott 1942

C	Ca	*Vulpes vulpes*	G	<1%	FO	313	Sc	G was in many Sc, but only one Sc was enough present to indicate it was purposely ingested; Sl and detritus in varying amounts in most Sc; an occasional Sc was almost wholly fine Sl or gravel.	Eadie 1943
			G, etc.	exc	–	537	Sc	Dry G, Lv, Nd, Mo, sand, and small stones found in Sc.	Cook & Hamilton, Jr. 1944
			G, V	20%	FO	160	Sc		Wilcomb 1948
			Fr, G	18%	FO	40	GI		
			G	exc	–	543	Sc, Sm	12 genera of G identified in samples.	Lever 1959
			B, Lv, St	52%	FO	205	Sm		Hockman & Chapman 1983
			P	2%	FO	288	Sm	Same study noted no vegetable matter in cat Sm studied.	Catling 1988
			P	43%	FO	613	Sc	Autumn Sc principally *Rubus* Sd; no other information given.	Lunney *et al.* 1990
			P	11%	FO	389	Sc	Included G and Sd.	Jędrzejewski & Jędrzejewska 1992
			V	75%	FO	177	Sc	Present only in trace amounts.	Elmhagen *et al.* 2002
			P	20%	FO	163	Sc	Excluded Fr.	Goldyn *et al.* 2003
			G	1%	FO	206	Sc		Padial *et al.* 2002
			P	18%	RM	894	Sc	Included Fr, Sd, and other plant material.	Lanszki *et al.* 2006
			P	11%	FO	?	It	Of 2242 scats; total number of food items not given; P included G, excluded Fr.	Hartová-Nentvichová *et al.* 2010
			G	28%	FO	224	Sm		Kidawa & Kowalczyk 2011
			Fu	3%	FO	219	Sm	Fu as mushroom; P as plant remains (excluding Fr).	Bakaloudis *et al.* 2015
			P	85%					
			Fl	4%	FO	108	Sm	Lv as other leaves; St as woody material; V(1) as *Casuarina* needles; V(2) as other vegetative matter.	Stepkovitch 2017
			G	80%					
			Lv	25%					
			St	54%					
			V(1)	3%					
			V(2)	4%					
			G, etc.	–	–	1230	Sc	G, pebbles, and debris found substantially in all Sc and were the major category in ca. 25% of Sc (Fig. 1).	Wilson & Dookia 2019
		Vulpes zerda	V	25%	RF	21	Sc	V included G and Rt.	Incorvaia 2005
			P	55%	FO	105	Sc	Included Fr (dates), G, and Rt.	Brahmi *et al.* 2012

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Me	*Conepatus chinga*	P	7%	FO	217	Sc	Excluded Fr.	Zapata *et al.* 2001
		Mephitis mephitis	G, Rt	28%	FO	353	Sm		Dixon 1925
			V	50%	FO	149	Sc	0.9% of total Sc volume.	Selko 1937
			V	22%	RV	–	–	In winter season; V as vegetable matter; data given as from a Davis ms.	Wood 1954
			Lv	0.5 g	M	1	Sc		García 1998
		Spilogale putorius	V	22%	FO	59	Sc	0.6% of total Sc volume.	Selko 1937
			G	4%	FO	844	Sc	Apparently sometimes in large amounts.	Crabb 1941
	Mu	*Arctonyx collaris*	G, Lv, Rt, St	88%	FO	735	Sc		Zhou *et al.* 2015
		Galictis cuja	G, S, Sd	exc	–	1	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
		Gulo gulo	V	25%	FO	121	Sm	Constituted a significant amount in six Sm; two Sm had mass of wood splinters and one Sm large amount of oakum.	Myrhe & Myrberget 1975
			P	37%	FO	159	Sc	Sl as dirt in 28% of Sc.	van Dijk *et al.* 2007
		Ictonyx striatus	P	1%	RV	1	Sm		Viljoen & Davis 1973
		Lontra canadensis	A, P	22%	FO	219	Sc		Buzzell *et al.* 2014
		Lontra longicaudis	P	9%	RF	205	Sc		Gori *et al.* 2003
			V	4%	RF	61	Sc		Mayor-Victoria & Botero-Botero 2010
			G, S, Sd	exc	–	14	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			V	<1%	FO	335	Sc	V included G.	Quintela *et al.* 2012
		Lutra lutra	P	<1%	RM	1547	Sc	Of no dietary significance.	Wise *et al.* 1981
			P	5%	FO	37	Sc		Gourvelou *et al.* 2000
			P	2%	RF	1151	Sc	Included G and S in negligible proportions.	Lanszki & Molnár 2003
			P	exc	–	1460	Sc	Included G, piece of rush, and Sd; occasionally in very small quantities.	Lanszki *et al.* 2009b
			P	exc	–	2269	Sc	Mainly G, found sporadically.	Krawczyk *et al.* 2011
			P	10%	FO	174	Sc	P included G and conifer Nd.	Bouroş & Murariu 2017

C	Mu	*Lutrogale perspicillata*	G, Rt	2%	FO	553	Sc	Rt was grass roots.	Hussain 2013
		Martes americana	G	7%	FO	46	Sc	G was appreciable in three Sc and Li was bulk of one Sc.	Marshall 1946
			Li	2%					
			G	<1%	FO	250	Sc		Quick 1955
			V	3%	FO	192	It	V as duff debris (G, Lv, Nd, W, etc.), only recorded if composing at least half of Sc; almost all Sc had debris and some were composed entirely of it; two Sc had only fresh green G.	Francis 1958
			V	11–17%	FO	32	GI	V was 11% of 18 Sm and 17% of intestines; actual amounts of V were negligible.	Gordon 1986
			V	5%	FO	1014	Sc	V as G, Li, and wood fibers.	Bull 2000
		Martes foina	Fu	<1%	FO	157	Sc, Sm	Of 14 Sm and 148 Sc; Fu as mushroom.	Delibes 1978
			P	exc	–	87	Sc	Little percent of G, pine Nd, and Thuja Lv; FO of dry parts of plants (excluding Fr and Sd) was 44% of subset of 25 Sc.	Apáthy 1998
			P	6%	FO	103	Sc	Mainly Fr.	Romanowski & Lesiński 1991
			G	<1%	FO	650	Sc		Padial *et al.* 2002
			P	10%	FO	1227	Sc	Excluded Fr and Sd.	Lanszki *et al.* 2009a
			P	35%	FO	827	Sc	Included G, corn, and W.	Czernik *et al.* 2016
			G	<1%	FO	–	It	Of 310 scats; unknown number of food items; overall FO here estimated from data provided; V as monocots (excluding G).	Hisano *et al.* 2016
			V	3%	FO				
		Martes martes	G	<1%	RM	337	Sc	Some Sc contained only G; other Sc had G in small quantities.	Lockie 1960
			Fu	<1%	RV	5677	Sc	Estimated from fig. 3; Fu as mushrooms; misc. included Nd, decayed W, cardboard, plast., frogs, and insects.	Pullianinen & Ollinmäki 1996
			misc.	4%					
			G	2%	FO	1373	Sc		Clevenger 1993
			G	<1%	FO	728	Sc		Clevenger 1995
			V	exc	–	398	Sc	Included Lv and St; also 483 GI tracts were examined.	Helldin 1999
			Fu	<1%	FO	450	GI, Sc	Fu as mushroom.	Helldin 2000
			P	<1%	FO	1222	Sc	Excluded berries and apples.	Sidorovich *et al.* 2005

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Mu	*Martes melampus*	P	10%	FO	1236	Sc	Most of which were leaves of G.	Tatara & Doi 1994
			P	39%	FO	425	Sc	Included Lv, Rt, and St.	Tsuji *et al.* 2014
			Lv	–	–	286	Sc		Okawara *et al.* 2020
		Meles meles	V	93%	FO	686	Sm	V as plant litter, consisting mainly of G, Lv, Rt, and W.	Cleary *et al.* 2009
			F	35%	FO	318	Sc	Fu as mushroom.	Hipólito *et al.* 2016
			P	15%	FO	159	Sm	P as other plants, including G.	Gomes *et al.* 2020
		Melogale moschata	P	8%	FO	67	Sc	No further information provided, but G noted in Sc of *Viverricula* from same study.	Chuang & Lee 1997
		Mustela erminea	Fu	3%	FO	482	–	Fu as mushrooms; P as other plants (probably excluding Fr); data obtained from Dubinin 2012 (unknown if Sc or Sm).	Belyk 1962
			P	5%					
		Mustela putorius	P	exc	–	–	GI, Sc	Of 120 Sm, 83 intestines, and 354 Sc; G, hay, straw, and tree Lv were excluded, but salad Lv were recorded twice as significant food items.	Weber 1989
		Mustela sibirica	P	2%	FO	218	Sc	Most of which were leaves of G.	Tatara & Doi 1994
		Neovison vison	P	<1%	RM	513	Sc	Of no dietary significance.	Wise *et al.* 1981
		Pekania pennanti	Fu	50%	FO	8	Sm	Fu were hypogeous fungi; data obtained from Zielinski *et al.* 1999.	Grenfell & Fasenfest 1979
			Fu	92%	FO	24	Sc	Fu were hypogeous fungi.	Zielinski *et al.* 1999
			G	6%	FO	388	Sc	Lv as Cupressaceae; Nd as Pinaceae.	Golightly *et al.* 2006
			Lv	6%					
			Nd	76%					
		Taxidea taxus	G	<8%	RV	37	Sc	G, other V, feathers, egg shells, dirt, etc. together comprised 8% RV.	Errington 1937
			P	10%	FO	188	Sc	Also said that plant remains in trace amounts were in more than half of Sc; in three Sc, small wads of grass stems and leaves.	Snead & Hendrickson 1942
			G	54%	FO	52	GI	P as unknown plant material; St as woody material.	Sovada *et al.* 1999
			P	46%					
			St	2%					

C	Ot	*Arctocephalus gazella*	A	13%	FO	105	Sc		Daneri & Coria 1992
			A	17%	FO	133	Sc		Daneri *et al.* 2008
			A	2%	FO	1195	Sc		Casaux *et al.* 2016
		Arctocephalus tropicalis	A	16%	FO	56	Sm	A as seaweed.	Condy 1981
		Arctocephalus townsendi	Z	40%	FO	218	Sc		Aurioles-Gamboa & Camacho-Ríos 2007
			P	–	FO	114	Sc	P as sea grass or plant material; in 83% of summer Sc; winter frequency not given.	Pablo-Rodríguez *et al.* 2016
		Otaria bryonia	A	–	–	–	–	References given that A is an occasional food item.	George-Nascimento *et al.* 1985
		Zalophus californianus	A	6%	FO	1085	Sc		Lowry *et al.* 1991
	Ph	*Cystophora cristata*	A, H, etc.	15%	FO	335	GI	Study on only pups and juveniles.	Haug *et al.* 2000
		Erignathus barbatus	A	5%	FO	39	GI		Hjelset *et al.* 1999
		Halichoerus grypus	A	50%	FO	2	GI	Bulk of A very small.	Duncan 1956
		Leptonychotes weddelli	A	38%	FO	8	Sm	A as kelp.	Clarke & MacLeod 1982
			A	17%	FO	845	Sc	Estimated from Appendix 1.	Green & Burton 1987
			A	29%	FO	41	Sc		Casaux *et al.* 1997
		Lobodon carcinophaga	A	50%	FO	2	Sm	The one Sm had 15 g of A (*Dictyota* and *Plocamium*).	Ross *et al.* 1978
		Mirounga leonina	A	50%	FO	3	Sc	A as seaweed.	Dykyy 2009
		Pagophilus groenlandicus	A	10%	FO	110	Sm		Nilssen *et al.* 1998
			A, H, etc.	3%	FO	237	GI	Study on only pups and juveniles.	Haug *et al.* 2000
			A, H, Mu	14%	FO	272	GI	Study on only pups and juveniles.	Nilssen *et al.* 2001
		Phoca largha	A	>39%	FO	141	Sm	Only given that >50% of 110 Sm from Russian gulfs had A; A most common in pups.	Bukhtiyarov *et al.* 1984
		Phoca vitulina	A	4%	FO	100	Sm	A and hydroids together were about 8% of contents of 4 Sm.	Scheffer & Sperry 1931
		Pusa hispida	A	6%	FO	267	GI	A was considered secondary prey.	Labansen *et al.* 2007

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
C	Pr	*Bassariscus astutus*	G	<1%	RF	256	GI	Mentioned only in summer samples.	Taylor 1954
			G	trace	RV	29	GI, Sc	Of 10 GI and 19 Sc.	Wood 1954
			G	4%	FO	–	Sc	V as miscellaneous vegetable matter; obtained from Alexander *et al.* 1994	Trapp 1978
			V	17%					
			G	5%	FO	55	Sc	Lv(1) as undigested leaves, scales, and bracts of *Abies*; Lv(2) as undigested leaves, scales, and bracts of *Pseudotsuga*; Lv(3) as *Calocedrus*; Lv(4) as *Taxus*; P as unidentified plant material; St as wood; V as *Porella*.	Alexander *et al.* 1994
			Li	14%					
			Lv(1)	42%					
			Lv(2)	36%					
			Lv(3)	25%					
			Lv(4)	2%					
			Mo	16%					
			P	50%					
			St	11%					
			V	4%					
			Lv	4.5 g	M	3	Sc		García 1998
			Fl	21%	FO	98	Sc		Nava-Vargas *et al.* 1999
			Lv	35%					
			V	46%	FO	67	Sc	Excluded Sd.	Ackerson & Harveson 2006
		Nasua nasua	V	85%	FO	226	Sc	Included Lv and St.	Alves-Costa *et al.* 2004
			G, S, Sd	exc	–	38	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			G	4%	FO	23	Sm	Lv (including G and other species) were in 20% of stomachs.	Aguiar *et al.* 2011
			V	39%	FO	56	Sc		Ferreira *et al.* 2013
		Procyon cancrivorus	G, S, Sd	exc	–	1	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
		Procyon lotor	V	70%	FO	223	Sc	V as miscellaneous vegetation; Sl also frequent.	Yeager & Elder 1945
			G	<1%	FO	135	Sc		Schoonover & Marshall 1951

C	Pr	*Procyon lotor*	Fr, G	<4%	RV	217	GI, Sc	Included G and less frequently eaten Fr; of 53 GI and 164 Sc.	Wood 1954
			G	10%	FO	10	Sc		Turkowski 1980
			G	97%	FO	96	GI	P excluded berries and Sd.	Matsuo & Ochiai 2009
			P	3%					
			G, Sh, Sl, W	69%	RM	96	Sm	Sl was sand.	Parsons *et al.* 2013
	Ur	*Ailuropoda melanoleuca*	G	–	–	–	–	Well known that G (bamboo) is primary food source; see reference.	Schaller *et al.* 1989
		Helarctos malayanus	Lv, Sd, St	54%	RF			Estimated from fig. 5; 10 plant species consumed; unclear which genera were found as Lv or St.	Sethy & Chauhan 2018
		Melursus ursinus	Fl	trace	FO	139	Sc	Fl as *Bombax ceiba*; G as grass fibres; one occasion appeared to graze *Cynodon*.	Laurie & Sedensticker 1977
			G	1%					
			B, Fl, Fr, Lv, Rt, St	–	–	–	bears	40 species of plants consumed by unknown number of bears observed from 1994-2002.	Chhangani 2002
			G	3%	FO	93	Sc	G was *Heteropogon* and *Setaria*.	Ramesh *et al.* 2009
		Tremarctos ornatus	Br	–	–	–	–	Well known that bromeliad Lv and St are primary food source; see reference.	García-Rangel 2012
		Ursus americanaus	P	–	–	–	–	Well known to eat vegetation, such as G and Lv; see reference.	McLellan 2011
		Ursus arctos	P	–	–	–	–	Well known to eat vegetation, such as G, Lv, and Rt; see reference.	McLellan 2011
			Fu	1%	FO	7459	Sc	Fu included *Calvatia, Lactarius, Rhizopogon, Russula, Suillus,* and *Tricholoma*.	Mattson *et al.* 2002
		Ursus maritimus	P	–	–	–	–	Well known to eat vegetation, especially A, Fu, G, Lv (e.g., *Cochlearia*), and Mo; see reference.	Gormezano & Rockwell 2013; Stempniewicz 2017
		Ursus thibetanus	P	–	–	–	–	Well known to eat vegetation, such as Fl, G, and Lv; see reference.	Furusaka *et al.* 2017
F	Fe	*Caracal caracal*	P	8%	RV	2	Sm		Viljoen & Davis 1973
			V	17%	FO	100	Sc	Included G and St, which were 6% of scats.	Palmer & Fairall 1988
			G	–	–	–	Obs	Captive, G occasionally eaten.	Buck in Lonsdale 2001

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
F	Fe	*Caracal caracal*	P	47%	FO	391	Sc		Avenant & Nel 2002
			G	39%	FO	116	Sc	All occurrences of G attributed to *Schmidtia as Lv or Sd*; P as unidentifiable plant material.	Melville *et al.* 2004
			P	2%					
			G, Lv	52%	FO	182	Sc		Drouilly *et al.* 2018
		Catopuma temminckii	G	–	–	1	Sc	Photo (fig. 197) of one Sc composed of undigested G.	McShea *et al.* 2018
		Felis catus (domestic)	P	–	cats	1021	cats	Internet survey; G most frequently eaten plant; 27% vomit after eating P.	Hart & Hart 2013; Hart *et al.* 2019
		Felis catus (feral)	P	37%	FO	116	Sm		van Aarde 1980
			G	31%	FO	78	Sm	Identified all as *Lepturus* except one sample as *Cenchrus*, all in trace volume.	Kirkpatrick & Rauzon 1986
			Plast., Sd, V	89%	FO	41	Sc	V was mainly G.	Arnaud *et al.* 1994
			G	41%	FO	93	GI	In small quantities.	Tidemann *et al.* 1994
			G	23%	FO	290	Sc		Clevenger 1995
			V	26%	FO	499	Sc	Included sweet briar Fr, *Rosa*, and G.	Molsher *et al.* 1999
			P	6%	FO	560	It	Included G, *Pyrus*, vegetables, and *Vitis*; from 264 GI samples.	Biró *et al.* 2005
			V	16%	RF	97	Sc	G said to be frequent.	Campos *et al.* 2007
			G, St	exc	–	602	Sc		Phillips *et al.* 2007
			V	3%	RV	152	Sm	Especially B, G, and dicot Lv.	Yip *et al.* 2015
			G	12%	FO	33	Sc		Mesa-Cruz *et al.* 2016
			G	9%	FO	67	Sc		Ortiz-Alcaraz *et al.* 2017
		Felis catus × *F. silvestris*	P	11%	FO	64	It	Especially G but grape occurred once; from 30 GI samples.	Biró *et al.* 2005
		Felis chaus	G	4%	FO	67	Sc		Johnsingh 1983
		Felis libycus	P	14%	FO	199	Sc	Included *Euclea* Lv, Fr (e.g., *Euclea*), G, and Sd.	Stuart 1976b
		Felis margarita	G	–	–	–	Obs	Captive, G occasionally eaten.	Buck in Lonsdale 2001
		Felis silvestris	P	21%	FO	220	Sc	Essentially G.	Sarmento 1996
			P	4%	FO	57	It	Essentially G; from 22 GI samples.	Biró *et al.* 2005

F	Fe	*Herpailurus yagouaroundi*	Lv	60%	FO	10	Sc	Particularly G.	Bisbal 1986
			G	12%	FO	26	R, Sc	From 24 scats and two regurgitations.	Tófoli *et al.* 2009
			G, S, Sd	exc	–	14	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			G	exc	–	35	Sc	Sporadically ingested, in small amounts; G was leaves.	Silva-Pereira *et al.* 2011
		Leopardus colocolo	G	exc	–	43	Sc	G was grass leaves.	Fajardo *et al.* 2014
		Leopardus pardalis	Lv	40%	FO	10	Sc	Particularly G.	Bisbal 1986
			G	11%	FO	62	Sc		Emmons 1987
			G	4%	FO	23	Sc	G as zacate.	Chinchilla 1997
			P	60%	FO	10	Sc	As plant, monocot, and dicot.	Farrell *et al.* 2000
			G	–	–	–	Obs	Captive, together with *Prionailurus viverrinus*, said to regularly eat G, sometimes daily, based on feces and “grass vomit”.	Buck in Lonsdale 2001
			G	8%	FO	51	Sc		de Villa Meza *et al.* 2002
			S	5%	FO	239	Sc	Possibly included G.	Moreno *et al.* 2006
			P	33%	FO	60	Sc		Bianchi & Mendes 2007
			P	exc	–	42	Sc		Abreu *et al.* 2008
			G, S, Sd	exc	–	9	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			P	exc	–	–	Sc	Mentioned as part of Sc of captive animals, but no other information provided.	Pires *et al.* 2011
			G	exc	–	15	Sc	G was leaves; sporadically ingested, in small amounts.	Silva-Pereira *et al.* 2011
			G	5%	FO	38	Sc	FO estimated from bar graph.	Giordano *et al.* 2018
			G	–	–	1	Obs	G was photograph of live consumption of Lv of *Oryza*.	Montalvo *et al.* 2020
		Leopardus tigrinus	G, S, Sd	exc	–	102	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			G	exc	–	30	Sc	G was leaves; sporadically ingested, in small amounts.	Silva-Pereira *et al.* 2011
		Leopardus wiedii	G, S, Sd	exc	–	5	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
		Leptailurus serval	G	exc	–	90	Sc	In small quantities in nearly all Sc; 0.7% of total scat mass.	Bowland & Perrin 1993

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
F	Fe	*Lynx canadensis*	V	54%	FO	87	Sc	Majority from conifers, followed by G, wood, deciduous Lv, and B; presence of rocks in Sc was most surprising.	Hanson & Moen 2008
		Lynx lynx	G	–	–	–	Obs	Captive, G often eaten.	Buck in Lonsdale 2001
			P	11%	FO	49	Sc	P found in small quantities.	Krofel *et al.* 2011
			P	57%	FO	37	Sm		
		Lynx rufus	V, Sl	20%	RF	186	Sm		Dixon 1925
			G	2%	FO	140	Sm	G was found in sufficient quantity; many Sm had small green twigs and bark; more than half of the Sm had heavy infestations of roundworms (*Physaloptera*).	Hamilton, Jr., & Hunter 1939
			G, V	exc	–	50	Sm	G and white cedar Lv in high percent of Sm; 72% of 50 GI had one or more intestinal parasites.	Rollings 1945
			G	20%	FO	10	Sm	Buffalo grass seed was in one stomach and was the greater part of the G remains.	Ellis & Schemnitz 1958
			V	8%	FO	177	Sc		Nussbaum & Maser 1975
			V	exc	–	150	Sm	As B, G, Lv, and St.	Fritts & Sealander 1978
			P	10%	FO	67	Sc	P as other plants, excluding juniper berries.	Turkowski 1980
			P	14%	FO	413	Sm	P as plant material (G or other herbaceous monocots).	Maehr & Brady 1986
			G	0.8 g	M	14	Sc		García 1998
			Lv	1.3 g	M	14	Sc		
			Lv	7.8 g	M	4	Sc		
			Lv	30.5 g	M	1	Sc		
			V	0.3 g	M	7	Sc		
		Otocolobus manul	V	24%	FO	146	Sc	Parasite eggs had 24% and parasite worms had 7% FO.	Ross 2009
		Panthera onca	G	48%	FO	25	Sc		Emmons 1987
			G	18%	FO	22	Sc	G as zacate.	Chinchilla 1997
			P	21%	FO	106	Sc	Included Fr and Lv in small amounts.	Taber *et al.* 1997
			P	100%	FO	3	Sc	P as plant and dicotyledon.	Farrell *et al.* 2000
			P	30%	FO	101	Sc	G in 2 of 5 sequential Sc.	Garla *et al.* 2001
			G	22%	FO	9	Sc		Mesa-Cruz *et al.* 2016
			G	–	–	1	Obs	G was photograph of live consumption of Lv of *Oryza*.	Montalvo *et al.* 2020

F	Fe	*Panthera pardus*	P	2%	RV	1	Sm	Unidentifiable except for the grass *Heteropogon*.	Viljoen & Davis 1973
			G	10%	FO	215	Sc	Almost all G was *Isachne* or *Streptogyna*, both very hairy; unchewed, undigested; leopards may identify grass by licking surface; G probably for GI during starvation.	Hoppe-Dominik 1988
			G	4%	FO	334	Sc		Johnson *et al.* 1993
			V	14%	FO	125	Sc	Mainly G.	Sankar & Johnsingh 2002
			G	16%	FO	111	Sc	Varying amounts of G and Sl in Sc; Sl in 24% of Sc.	Andheria *et al.* 2007
			G	37%	FO	46	Sc		Ott *et al.* 2007
		Panthera tigris	G, P	–	–	–	–	Small amount added to diet in summer at zoo; P was clover.	Cline 1966
			G	2%	FO	335	Sc	G and Sl only counted if 50% or more of Sc; some G, bamboo Lv, and other V were in the majority of Sc, but a few were almost entirely G blades; one scat had G and tapeworm; Sl in 4% of Sc.	Schaller 1967
			G, Sl	exc	–	55	Sc	G and Sl in almost every Sc; two Sc almost entirely of Sl.	Sunquist 1981
			G	6%	FO	36	Sc	These Sc had large quantities of G mixed with animal remains; three Sc had soil and animal remains.	Johnsingh 1983
			V	19%	FO	146	Sc	Mainly G.	Sankar & Johnsingh 2002
			G	15%	FO	381	Sc	Varying amounts of G and Sl in Sc; Sl in 8% of Sc.	Andheria *et al.* 2007
			G	exc	–	145	Sc	G (*Imperata*) and rarely Lv found in a number of Sc, but only one Sc had G being more than 50% of the Sc volume; 51% of Sc had large quantities of soil, being more than 50% of the volume, and 80% of these found in winter.	Khan 2008
			G, Lv	exc	–	77	Sc		Kapfer *et al.* 2011
		Panthera uncia	G	18%	FO	50	Sc	G was *Stipa*; data obtained from Mallon *et al.* 2016.	Bold & Dorzjunduy 1976
			P	19%	FO	213	Sc	Included G and Lv of various spp.; most occurrences in small amounts but six Sc consisted mainly of plant materials.	Oli *et al.* 1993
			G, St	17%	RF	29	Sc	St was forb stems.	Schaller *et al.* 1994
			V	0.7–11%	FO	?	Sc	Data obtained Mallon *et al.* 2016.	Zhiryakov & Baidavletov 2002
			P	31%	FO	49	Sc		Anwar *et al.* 2011
			P	62%	?	41	Sc	Unclear what 62% represents; often dominating the Sc content.	Wegge *et al.* 2012
			P	3%	RF	40	Sc	Included G, Lv, and St; one Sc consisted only of plant materials.	Devkota *et al.* 2013
			P	exc	–	39	Sc	Omitted from analysis, but later stated remains of *Myricaria* in 45% of Sc.	Jumabay-Uulu *et al.* 2014

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
F	Fe	*Prionailurus bengalensis*	P	79%	FO	350	Sc	Most of which were leaves of G.	Tatara & Doi 1994
			G	6%	FO	53	Sc		Grassman *et al.* 2005
			G	11%	FO	72	Sc		Rajaratnam *et al.* 2007
			P	9%	FO	56	It	From 11 Sm.	Lee *et al.* 2013
			G	33%	FO	51	Sc		Lorica & Heaney 2013
			P	29%	FO	280	Sc	Two samples identified as *Arundinella* and *Panicum*, the rest unidentified.	Lee *et al.* 2014
			G	57%	FO	65	Sc	Found intact in Sc.	Chua *et al.* 2016
			G	5%	FO	42	Sc	Closest DNA match was *Lolium/Festuca/Agrostis*.	Xiong *et al.* 2016
			G	–	–	1	Sc	Photo (fig. 204) of one Sc containing grass fibers.	McShea *et al.* 2018
			G, S	3%	FO	121	Sc	S was *Carex*.	Seryodkin & Burkovskiy 2019
		Prionailurus rubiginosus	G	–	–	–	Obs	Captive, said to regularly eat G, sometimes daily, based on feces and “grass vomit”.	Buck in Lonsdale 2001
		Prionailurus viverrinus	G	–	–	–	Obs	Captive, together with *Leopardus pardalis*, said to regularly eat G, sometimes daily, based on feces and “grass vomit”.	Buck in Lonsdale 2001
		Puma concolor	G	7%	FO	43	Sm		Dixon 1925
			G	6%	FO	275	Sm	G was *Elymus* (avoided by livestock even in winter) and other coarse G.	Robinette *et al.* 1959
			G	8%	FO	277	GI, Sc	GI was intestines.	
			G	10%	FO	61	Sm	G was masticated, often in large amounts; also 23.0% (61) colons; recently passed Sc consisting almost entirely of masticated G with entwined tapeworms.	Toweill & Maser 1985
			P	6%	FO	405	Sc		Iriarte *et al.* 1991
			G, Lv	37%	FO	159	Sc	Probably consumed with other foods.	Cashman *et al.* 1992
			P	14%	FO	95	Sc	Included Fr and Lv in small amounts.	Taber *et al.* 1997
			P	80%	FO	4	Sc	As plant and dicot.	Farrell *et al.* 2000
			G	13%	FO	89	It	Of 65 Sc.	Wolff 2001
			S	5%	FO	88	Sc	Possibly included G; no further information given.	Moreno *et al.* 2006

F	Fe	*Puma concolor*	P	exc	–	38	Sc		de la Torre & de la Riva 2009
			G	48%	FO	104	Sc		Monroy-Vilchis *et al.* 2009
			G, S, Sd	exc	–	10	Sc	Unclear if present in this species and/or the other nine species studied; Sd was of G.	Rocha-Mendes *et al.* 2010
			G	7%	FO	183	Sc		Gómez-Ortiz *et al.* 2011
			V	60%	FO	25	Sc	Trace amounts, usually oak or juniper Lv, rarely G or other plant materials.	Stiner *et al.* 2012
			G	–	–	1	Obs	G was photograph of live consumption of Lv of *Oryza*.	Montalvo *et al.* 2020
	He	*Atilax paludinosus*	G	39%	FO	57	Sc		Stuart & Stuart 1998
			G	28%	FO	40	Sc		Stuart & Stuart 2003
		Cynictis penicillata	P	11%	FO	95	Sm	Obs of *Chortolirion*, apparently feed on this plant; P resembled dung of cattle.	Zumpt 1968
			P	trace	RV	1	Sm		Viljoen & Davis 1973
			G, St	4%	FO	50	Sc	P as other plant material.	MacDonald & Nel 1986
			P	2%					
			P	32%	FO	418	Sc	Contributed only a small percentage of total volume.	Avenant & Nel 1992
			P	49%	FO	2600	Sc	P was G fragments, although 12 Sc had Fr and Sd of *Solanum*.	Cronk & Pillay 2019
		Galerella nigrata	Lv, St	6%	FO	149	Sc	Included G (*Eragrostis*) and Lv of *Acacia*.	Nakwaya 2009
		Galerella pulverulenta	P	6%	FO	16	Sc	Possibly consisted only of *Oxygonum* Fr, but was unclarified.	MacDonald & Nel 1986
			P	2%	RF	234	Sc	Included G and Sd; always occurred in small quantities.	Cavallini & Nel 1990
			G	7%	FO	103	Sc		Stuart & Stuart 1998
		Galerella sanguinea	G	36%	FO	2000	Sc	G as fragments.	Cronk & Pillay 2019
		Herpestes ichneumon	P	3%	FO	188	Sc, Sm	Most of P was Fu, but also *Rubus* Sd; from 105 Sc, 83 Sm.	Delibes *et al.* 1984
		Suricata suricatta	P, Sd	14%	FO	21	Sm	Included young plants, Sd, and other vegetable matter.	Zumpt 1968
			P	11%	RV	2	Sm		Viljoen & Davis 1973
		Urva edwardsii	V	6%	FO	708	Sc	V as vegetative matter, included Lv of G and herbs.	Kalle *et al.* 2012
			G	5%	RF	57	Sc	G was *Cynodon* and *Themeda*.	Akrim *et al.* 2019

SO	FM	Species	Cat.	Oc	OcT	N	SaT	Notes	Reference
F	He	*Urva javanica*	P	92%	FO	4404	Sc	Usually Sd (of G, *Carica*, and *Psidium*) and represent a small intake.	Gorman 1975
			V	9%	FO	126	Sc		Cavallini & Serafini 1995
			P	57%	FO	30	Sc	Included Lv and St.	Mahmood *et al.* 2011
			G	6%	RF	69	Sc	G was *Cynodon* and *Themeda*.	Akrim *et al.* 2019
		Urva urva	P	8%	FO	202	Sc	No further information provided, but G noted in Sc of *Viverricula* from same study.	Chuang & Lee 1997
			G	7%	FO	112	Sc		Wang & Fuller 2003
	Hy	*Crocuta crocuta*	G	exc	–	525	Sc	G found in scats, but frequency not reported; one Obs of *Blepharis*.	Henschel & Skinner 1990
		Hyaena brunnea	P	35%	RV	1	Sm	P included G (*Setaria, Panicum*?, and *Aristida*).	Viljoen & Davis 1973
			G	exc	–	383	Sc	Photo G from Sc depicted in fig. 1, but G apparently excluded from analysis.	Mills & Mills 1978
			G	2%	FO	128	Sc	Three Sc were almost exclusively G, 2 of which the G was finely broken up possibly from prey digesta; undefined "plant material" was in 18% of Sc.	Faure *et al.* 2019
		Hyaena hyaena	V	13%	FO	86	Sc	Included G and Sd (e.g., *Zizyphus*).	Mondal *et al.* 2012
			G	17%	FO	82	Sc	G reportedly present in 10% of 12 hairballs.	Alam & Khan 2015
		Proteles cristata	V	20%	FO	79	Sc	V as vegetable fibres.	Kruuk & Sands 1972
			P	5%	?	81	Sc	Ambiguous if percent represents relative volume, mass, or frequency.	Cooper & Skiner 1979
			G, P, Sl	100%	FO	89	Sc	Sl was sand.	Matsebula *et al.* 2009
	Vi	*Civetticitis civetta*	V	81%	FO	97	Sc	Included Fr, inflorescences, Lv, and Sd of both monocotyledons and dicotyledons; and consisted mainly of Fr Sd.	Guy 1977
			V	8%	FO	591	It	V as grass, leaves, and fibres.	Bekele *et al.* 2008
			Lv, V	3%	FO	578	Sc	V included fibres and shoots.	Mullu & Balakrishnan 2014
			G	3%	RM	382	Sc	G included six spp., and two spp. (*Urochloa* and *Berchemia*) constituted 75.5% of grass biomass (however, *Berchemia* is not a grass).	Habtamu *et al.* 2017

F	Vi	*Genetta genetta*	P	1%	RV	1	Sm		Viljoen & Davis 1973
			P	9%	FO	125	Sc	Included Lv and Sd of *Euclea* and Sd of *Salvadora*.	Stuart 1976b
			G	18%	FO	1513	Sc		Clevenger 1995
			G	–	FO	52	Sc	FO unclear from data; G present in Sc of May, August, and December.	Stuart & Stuart 1998
			G	27%	FO	60	Sc	Lv(1) as *Salix*; Lv(2) as *Tamarix*.	Sánchez *et al.* 2008
			Lv(1)	10%					
			Lv(2)	17%					
			G	–	–	30	Sc	Long Lv of *Ampelodesma* used frequently, unclear if photo (fig. 2) of G from Sc of *Canis* or *Genetta*.	Boukheroufa *et al.* 2020
		Genetta maculata	G	14%	FO	515	Sc	G was leaves.	Engel 1998
			G	39%	FO	18	Sc		Stuart & Stuart 2003
		Genetta tigrina	G	69%	FO	372	Sc	G was highest volume food; Lv as leaf litter; St as wood.	Roberts *et al.* 2007
			Lv	68%					
			St	15%					
		Paguma larvata	G	8%	FO	37	Sc		Wang & Fuller 2003
			G	97%	FO	77	GI	P as other plants (excluding berries and Sd).	Matsuo & Ochiai 2009
			P	1%					
			P	85%	FO	52	Sm	Included G, St, and plant galls.	Iwama *et al.* 2017
		Paradoxurus hermaphroditus	G	4%	RF	112	Sc		Khan *et al.* 2019
		Paradoxurus jerdoni	G	1%	FO	1013	Sc	G was grass plugs and were usually along with vertebrate remains; one Sc had beeswax.	Mudappa *et al.* 2010
		Viverra tangalunga	Lv	21%	FO	58	Sc		Colon & Sugau 2012
		Viverricula indica	P	56%	FO	154	Sc	Included Lv, Sd, and stems of *Miscanthus* and *Setaria*; G fragments often not chewed and passed almost intact.	Chuang & Lee 1997
			Lv	21%	FO	44	Sc		Wang & Fuller 2003
			G	43%	FO	7	Sm	G as grass pieces, excreted as a wad entangled with mucus.	Balakrishnan & Sreedevi 2007
			G	14%	FO	307	Sc	G was folded/bundled whole, not chewed (included *Axonopus, Miscanthus, Setaria*, and unknown, all sharp-edged and hairy); positively correlated with *Toxocara paradoxura* occurrences.	Su *et al.* 2013

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Appendix 1

Hundreds of hours of observations of Kait and Alan's dog (*Canis familiaris*) living in Florida, USA over the course of six years reveal that the dog frequently consumes a few pieces of unmowed grass blades (typically several times per week). This dog has consumed several different genera of Poaceae, including *Cortaderia*, *Dactyloctenium*, *Eleusine*, *Neyraudia*, *Sorghum*, and *Urochloa*. One species of Cyperaceae (*Cyperus croceus*) was also consumed. During a visit to a friend in Seattle, Washington, USA, his two dogs were observed eating unmowed patches of *Festuca rubra* adjacent to the mowed lawn, said to be a frequent behavior by the owner. In all instances with the above three dogs, it was noticed that the dog preferred to consume long, uncut grass blades that were near head height, and the dogs avoided cut, mown short grass. Vomiting or nausea was not observed in any of these instances. Vouchers of the actual plants consumed are deposited in the University of South Florida herbarium (collection nos 4039, 4063, 4064, 4077, 4082, 4083, 4795, and s.n. [Aug. 2016]).