

Revisiting the dietary niche: When is a mammalian herbivore a specialist?

Lisa A. Shipley,^{1,*} Jennifer S. Forbey[†] and Ben D. Moore[‡]

^{*}Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410, USA; [†]Department of Biological Sciences, Boise State University, Boise, ID 83725-1515, USA; [‡]Ecology Group, Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

Synopsis Understanding dietary specialization in herbivores has theoretical and practical implications in ecology, yet defining niche breadth consistently has been problematic. To increase clarity and communication among ecologists and among disciplines (i.e., chemists, pharmacologists), we propose a specialization key for mammalian herbivores that assigns “obligatory” and “facultative” modifiers to the terms “specialist” and “generalist”. These modifiers are assigned based on (1) relative breadth of the animal’s realized niche and diet (what it eats), (2) relative breadth of the fundamental niche and available diet (what it could eat), (3) the extent of chemical or physical characteristics, termed “difficulty”, that make food items either low in value or unpalatable to most herbivores, and (4) relevant temporal and spatial scales at which diets and niche breadth were measured. Obligatory specialists always have a narrow realized niche consisting of difficult food items, and morphological adaptations and/or the loss of redundant behavioral flexibility that effectively limit their fundamental niches, precluding them from expanding their diet under changed environmental conditions. Facultative specialists have a consistently narrow realized niche for difficult foods during at least one spatial or temporal scale, but have a broad enough fundamental niche to allow them to expand their diet to include less difficult foods when environmental conditions allow. Facultative generalists have the broadest fundamental niche, allowing them to consume a wide variety of foods. However, they may occasionally demonstrate a narrow realized niche, focused on less difficult plants than is the case with specialists. Finally, the obligatory generalists always have a wide realized niche because of a relatively narrow fundamental niche, precluding them from eating much of any difficult plant. We summarize hypothesized characteristics of mammalian herbivores in each of the four categories of specialization. We demonstrate the need for further work on defining the realized and fundamental niches, comparing among herbivores across categories conducted under similar conditions, and understanding the nature of trade-offs required for specialization and generalization for both community and phylogenetically based analyses.

Introduction

The question of what governs the dietary niche of an animal has been a central focus of community ecology for decades (Hutchinson 1957; Levins 1962). Because species are faced with evolutionary trade-offs between performing a few activities well, or many poorly (Kawecki 1994), the concept of specialization is at the heart of theories on the evolution of the niche (Julliard et al. 2006). Ordering species along a generalist–specialist gradient and separating those with smaller niches from those with broader niches is both practical and theoretical (Julliard et al. 2006). Theoretical concepts founded in the mid-twentieth century are being newly explored and enhanced (Futuyma and Moreno 1988; Sherry 1990; Simpson and Raubenheimer 1999; Irschick

et al. 2005), especially in light of the new capability to understand genetic control and consequences of specialization (Kawecki 1994; Wilson and Yoshimura 1994; Kassen 2002).

In contrast to phytophagous insects in which most feed on only one plant family or genus, dietary specialization is considered the exception rather than the rule in vertebrate herbivores (Freeland and Janzen 1974; Crawley 1983; Bernays and Chapman 1994; Dearing et al. 2000). A number of recent studies have focused on dietary specialization in mammals, primarily the costs and unique anatomical and physiological capabilities of a few key mammalian herbivores (e.g., woodrats, arboreal marsupial folivores) for coping with plant secondary metabolites (PSMs) (e.g., Lawler et al. 1998;

From the symposium “PharmEcology: A Pharmacological Approach to Understanding Plant-Herbivore Interactions” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2009, at Boston, Massachusetts.

¹E-mail: Shipley@wsu.edu

Integrative and Comparative Biology, volume 49, number 3, pp. 274–290

doi:10.1093/icb/icp051

Advanced Access publication June 23, 2009

© The Author 2009. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology. All rights reserved.

For permissions please email: journals.permissions@oxfordjournals.org.

Boyle et al. 1999; Marsh et al. 2003; Sorensen and Dearing 2003; Shipley et al. 2006). This research has enhanced our understanding of the causes and consequences of breadth in diet, and thus of selective pressures on diet and on habitat selection, herbivory, and coevolution (Iason and Villalba 2006).

Although the ecological niche has been part of the ecologist's vocabulary for almost a century, criteria for defining specialists has remained ambiguous and inconsistent (Begon et al. 1990; Sherry 1990; Bernays and Chapman 1994; Robinson and Wilson 1998), especially in reference to mammalian herbivores. Diverse and vague definitions raise conceptual and methodological problems, and inhibit clear communication among scientists within and among disciplines. A clear, consistent definition of feeding specialization is required to refine hypotheses and test predictions about generalists and specialists and their roles in communities (Fox and Morrow 1981). In this review, we describe the problems inherent in existing definitions of dietary specialization, and propose a general "specialization key" that will help researchers place their subjects along a specialist-generalist continuum. We also present hypotheses that emerge from the literature that can be explored using this specialization key. Our goal is to untangle the complexity of existing terms and definitions to provide researchers with common language that will facilitate comparisons among studies and a framework to better understand the ecological and evolutionary constraints and consequences of dietary specialization across taxa, populations and individuals.

Problems with defining and measuring dietary specialization in mammalian herbivores

Traditionally, ecologists have classified herbivores as specialists only if they consume one or a small number of different food items in their native habitat (i.e., a limited realized diet) (Crawley 1983; Bernays and Chapman 1994). Recently, many ecologists have defined a specialist herbivore as one that displays unique behavioral, physiological, or morphological adaptations to consume what Robinson and Wilson (1998) referred to as an intrinsically "difficult" diet. A difficult diet is one that is not commonly used by other herbivores because of chemical or physical characteristics that make it generally unpalatable or of nutritional low value (McArthur et al. 1991, Dearing et al. 2000). However, defining dietary specialization solely by either what an animal eats,

or is able to eat, can be problematic, if not sometimes contradictory (Sherry 1990).

First, studies that rely strictly on animals' diets as measured in the field may provide an incomplete understanding of dietary specialization. Plants selected at any particular time and place by a herbivore represent a subset of those which it can potentially digest and metabolize (Freeland and Janzen 1974). Diets selected by herbivores vary with environmental conditions that influence the availability and quality of plants, and the ability of animals to forage for them. For example, in the winter the white-throated woodrat (*Neotoma albigula*) consumes a higher proportion (~34%) of one-seeded juniper (*Juniperus monosperma*), a plant with low-digestible nitrogen and energy and high levels of secondary metabolites, than it does in the summer (~17%) (Dial 1988). The seasonal change in the proportion of juniper in the diet has been attributed to both the lack of availability of plants of higher quality in the winter (Dial 1988) and the effects of temperature on tolerance to juniper PSMs (McLister et al. 2004; Dearing et al. 2008). Interspecific competition among sympatric herbivores also may reduce dietary breadth, as evidenced by populations of hyraxes (*Heterohyrax brucei* and *Procavia johnstoni*, Hoeck 1989), and folivorous lemurs (*Lepilemur mustelinus* and *Avahi occidentalis*, Ganzhorn 1993). Likewise, barriers to movement or the lack of other requisites for survival in the habitat may restrict the number and type of plants selected by free-ranging herbivores at any one foraging period. For example, dugongs (*Dugong dugon*) may consume diets primarily of a few species of sea grasses (Erftemeier et al. 1993) because it is the only type of food they can eat, or because sea grass is the most abundant plant available to a large herbivore in the warm, shallow, marine environment in which they reside. Finally, niche breadth may depend, in part, on learning and experience. For example, naïve lambs ate fewer foods with PSMs than did experienced lambs (Villalba et al. 2004).

Second, identifying specialist herbivores may depend on which level of taxonomic or ecological hierarchy an ecologist finds relevant or practical (Fox and Morrow 1981). When based on the number of food items eaten, a herbivore could potentially be defined as a specialist in some areas or seasons but a generalist in others. For example, the desert woodrat (*Neotoma lepida*) is referred to as a specialist by Dial (1988) and a generalist by Skopec et al. (2008). Differences in how a species is classified may be caused by variability in diets among local populations or even among individual herbivores

(Bolnick et al. 2003). For example, dusky-footed woodrats (*Neotoma fuscipes*) inhabiting juniper woodlands consumed primarily western juniper (*Juniperus occidentalis*), whereas populations or individuals <1 km away in mixed coniferous forest preferred incense cedar (*Calo cedrus decurrens*) (Atsatt and Ingram 1983; McEachern et al. 2006).

Likewise, plant species may not always be the most appropriate taxonomic level for measuring dietary specialization. Even specialist insects rarely consume only one species of plant (i.e., are monophagous, Crawley 1983; Bernays and Chapman 1994), and arguably one of the most specialized mammalian herbivores, the koala (*Phascolarctos cinereus*), consumes 120 plant species in the genus *Eucalyptus* and 30 noneucalypts (Moore and Foley 2000). In our survey of literature in which a mammalian herbivore was described as a “specialist”, a single type of food ranged from 25% to 100% of the natural diet (Table 1). Therefore, many ecologists have relaxed the definition of specialist for mammalian herbivores, classifying mammalian species as specialists if ~60% of their diet consists of a single, distinctive genus (Dearing et al. 2000), or family of plants (Fox and Morrow 1981).

Plant taxonomy poses further problems for defining niche breadth. Herbivores specializing on well-represented plant groups such as the genus *Eucalyptus* will appear more polyphagous or “generalist” than those that specialize on monospecific genera of uncommon plants (Crawley 1983), simply because more plant species are included in the former diets. Dietary specialization defined in this way is also vulnerable to the labile nature of plant taxonomy, which is often based upon characteristics of limited (if any) significance to herbivores. In addition, estimates of niche breadth expand with the number of studies investigating them (Poore et al. 2007). As a consequence, rare and poorly studied species appear to have a less species-rich diet than do common and well-studied species. This issue can be partly remedied by the use of indices of evenness, diversity, or selection (e.g., Crawley 1983; Sprent and McArthur 2002). Furthermore, available techniques for measuring dietary composition, such as microhistological analyses of plant fragments or plant cuticle markers (*n*-alkanes) in feces, stomach analyses, and visual observations are limited in accuracy and reproducibility, or may be invasive to animals (Kronfeld and Dayan 1998; Bugalho et al. 2002; Shrestha and Wegge 2006). However, new technologies such as molecular analyses of feces (Valentini et al. 2009) may improve our ability to measure realized diets.

When selection of diet is considered at a still finer scale, we find that genetics and environmental conditions cause differences in chemistry, nutrients, and architecture among and within individual plants. Because plants are chemically variable even within species, some herbivores specialize on individual plants or tissues of plants (e.g., arboreal marsupial folivores) (Lawler et al. 1998; Marsh et al. 2003; Moore and Foley 2005). For example, although Abert’s squirrels (*Scuirus aberti*) feed almost exclusively on ponderosa pine (*Pinus ponderosa*), they choose individual trees with lower levels of oleoresins and higher levels of carbohydrates (Snyder 1992). Similarly, three species of bamboo lemurs (*Hapalemur* and *Prolemur* spp.) specialize on different parts of bamboo (*Cephalotachyum* spp.), such as shoots, culm pith, or young leaf bases, regardless of the bamboo species (Glander et al. 1989; Tan 1999). Generally, we should expect a stronger association between specialization and the chemical or physical attributes of plants that may occur across taxa, than with taxonomy itself (Freeland 1991; Moore and Foley 2000, 2005). For example, moose (*Alces alces*, Hagerman and Robbins 1993) and common ringtail possums (*Pseudocheirus peregrines*, Marsh et al. 2003) consume plants with high levels of phenolics regardless of taxa, especially hydrolyzable and condensed tannins. They have mechanisms such as salivary proteins that bind to tannins (Hagerman and Robbins 1993) and cecal separation and cecatrophy (McArthur et al. 1995) that allow them to consume a variety of plants with similar chemical profiles (e.g., linear condensed tannins, Shimada 2006). Because phenolics occur so widely throughout the plant kingdom, these adaptations allow the inclusion of a broad suite of plant species in the animals’ diets.

Measuring an animal’s fundamental niche can also be difficult. Accurately measuring an animal’s tolerances or requirements for a range of PSMs or nutrients normally requires research under artificial laboratory conditions, which can be expensive and logistically difficult. Animals may have difficulty acclimating behaviorally to food offered in unfamiliar ways, such as in mash or pellets, decoupled from natural feeding cues (Boyle and McLean 2004; Sorensen et al. 2005a; Shipley et al. 2006). For example, koalas refuse to eat artificial diets unless they look like, smell like, or taste like *Eucalyptus* (Pahl and Hume 1991). An animal’s ability to consume particular foods may take time to adjust to laboratory conditions. For example, animals do not maintain complete sets of microsomal enzymes and maintain many at low activities; thus, new enzymes

Table 1 Species and location of mammalian herbivores referred to as “specialists” in the ecological literature and their primary food

Taxa	Animal species	Primary food plant	Location	Amount in diet	References
Lagomorpha					
Leporidae	Pygmy rabbit ^a (<i>Brachylagus idahoensis</i>)	Big sagebrush (<i>Artemisia tridentata</i>)	Northwestern USA	≤99% in winter ≤50% in summer	Thines et al. (2004) Shiple et al. (2006)
Rodentia					
Sciuidae	Abert's squirrel (<i>Sciurus aberti</i>)	Ponderosa pine (<i>Pinus ponderosa</i>)	Northcentral Arizona	80–100% annually	Murphy and Linhart (1999) Keith (1965)
Sciuridae	Woolly flying squirrel ^a (<i>Eupetaurus cinereus</i>)	Blue pine (<i>P. wallichiana</i>) Edible-seed pine (<i>P. gerardiana</i>)	Western Himalayas, Pakistan	92–100% annually	Zahler and Kahn (1993)
Cricetidae	Arizona woodrat (<i>Neotoma devia</i>)	Ephedra (<i>E. viridis</i> and <i>E. torreyana</i>)	Great Basin desert, Arizona	57% annually	Dial (1988)
Cricetidae	Stephens woodrat (<i>Neotoma stephensi</i>)	One-seeded juniper (<i>Juniperus monosperma</i>)	Great Basin desert, Arizona	75–90% annually	Dial (1988) Vaughan (1982)
Cricetidae	Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	Western juniper (<i>J. occidentalis</i>) Incense cedar (<i>Calo cedrus decurrens</i>)	California	38% 53%	McEachern et al. (2006)
Cricetidae	Desert woodrat (<i>Neotoma lepida</i>)	Creosote bush (<i>Larrea tridentata</i>) One-seeded juniper (<i>J. monosperma</i>) Cholla cactus (<i>Opuntia bigelovii</i>) Prickly pear cactus (<i>O. occidentalis</i>)	Mojave desert, California Great Basin, Utah Southern and coastal California Inland California	22–75% Almost entirely 13%—primarily	Sorensen et al. (2005b) Cameron and Rainey (1972) Dial (1988) Stones and Hayward (1968) Mangione et al. (2000) MacMillen (1964) Brown et al. (1972)
Cricetidae	Big-eared woodrat (<i>Neotoma macrotis</i>)	Coast live oak (<i>Quercus agrifolia</i>)	Coastal California	85%	Skopec et al. (2008) Linsdale and Tevis (1951) Atsatt and Ingram (1983)
Cricetidae	Red tree vole ^a (<i>Arborimus longicaudus</i>)	Douglas fir (<i>Pseudotsuga menzeseii</i>)	Coastal Oregon	Almost exclusively	Carey (1999) Hayes (1996) Hamilton (1962)
Muridae	Black-tailed tree rat (<i>Thallomys nigricauda</i>)	Acacia spp., (esp. <i>A. erioloba</i> and <i>A. reficiens</i>)	Arid southern Africa	43–90%	Downs et al. (2003) Eccard et al. (2004)
Marsupialia					
Phascolarctidae	Koala (<i>Phascolarctos cinereus</i>)	<i>Eucalyptus</i> spp.	Eastern Australia	>93% annually	Moore and Foley (2000)
Pseudocheiridae	Greater glider (<i>Petauroides volans</i>)	<i>Eucalyptus</i> spp.	Eastern Australia	Exclusively	Kavanagh and Lambert (1990) Moore et al. (2004a)
Pseudocheiridae	Common ringtail possum (<i>Pseudocheirus peregrinus</i>)	<i>Eucalyptus</i> spp.	Eastern Australia	61–98%	Pahl (1987) Marsh et al. (2003)
Pseudocheiridae	Green ringtail possum (<i>Pseudocheirus archeri</i>)	<i>Ficus</i> spp. <i>Aleuritis rockinghamensis</i>	Rainforest and coastal Queensland	21–51% annually	Jones et al. (2006)
Primates					
Lemuridae	Golden bamboo lemur ^a (<i>Haplemur aureus</i>)	Giant bamboo (<i>Cephalotachyum vigueri</i>)	Madagascar	70–90% monthly	Glander et al. (1989) Tan (1999)
Lemuridae	Gentle bamboo lemur ^a (<i>Haplemur griseus</i>)	Giant bamboo (<i>C. viguieri</i>)	Madagascar	72% monthly	Glander et al. (1989) Tan (1999)

(continued)

Table 1 Continued

Taxa	Animal species	Primary food plant	Location	Amount in diet	References
Lemuridae	Greater bamboo lemur ^a (<i>Prolemur simus</i>)	Giant and viny bamboo (<i>C. viguieri</i> and <i>C. perrieri</i>)	Madagascar	95% monthly	Glander et al. (1989) Tan (1999)
Carnivora					
Ursidae	Giant panda ^a (<i>Ailuropoda melanoleuca</i>)	Bamboo (esp. <i>Fargesia</i> and <i>Gelidocalamus</i> spp.)	Wolong Nature Reserve, China	>99% annually	Johnson et al. (1988) Gittleman (1994)
Ailuridae	Red panda ^a (<i>Ailurus fulgens</i>)	Bamboo (esp. <i>Fargesia</i> and <i>Gelidocalamus</i> spp.) <i>Arundinaria maling</i> & <i>A. aristata</i>)	Wolong Nature Reserve, China Eastern Himalayas, India	>95% annually	Roberts and Gittleman (1984) Johnson et al. (1988) Pradhan et al. (2001)

^aAnimals classified as vulnerable to endangered by the International Union for Conservation of Nature and Natural Resources (IUCN, <http://www.iucnredlist.org>) or by the United States Fish and Wildlife Service (Federal Register 2003)

must be synthesized to reach full efficiency (Sipes and Gandolfi 1986). Likewise, it can take from one to several weeks to acclimate the flora of the gut to new diets (Hungate 1966). Furthermore, tolerances and requirements must be measured relative to fitness (Raubenheimer et al. 2005), which can be difficult to ascertain in the field or laboratory. Therefore, the width of the fundamental dietary niche measured in the laboratory may not fully describe an animal's capacity for consumption of food in their natural habitat.

Establishing a common language

Dietary specialization is a complex process shaped by genes, physiology, and behavior. We offer a set of definitions that reflect the limitations imposed by these factors on animals and their interactions with food. To improve clarity, we draw a distinction between the dietary niche, and the diet itself. The dietary niche is a theoretical construct that describes the physicochemical properties of a diet. The niche was envisaged by Hutchinson (1957) as an n-dimensional hypervolume, which in the case of a dietary niche, is bounded by maxima and minima on an indeterminate number of nutritional and nonnutritional axes. An animal's diet consists of a list of food items (e.g., plant parts, individual plants, species, genera) and their proportional contributions to the diet, thus can be described on a continuum from restricted to diverse. The distinction between niche and diet is important because very different diets, selected from different plant assemblages, might nonetheless conform to identical niches.

To define dietary specialization, we must consider what food is available to an animal, what food the animal is capable of eating in the absence of extrinsic

factors such as competition, and what food it actually eats in its natural habitat. Those elements of a plant assemblage that are accessible, but not necessarily acceptable, to herbivores we call the "available diet". The "fundamental niche" describes an animal's upper and lower tolerances for concentrations of nutrients and toxins (i.e., what the animal is able to eat), and the subset of the available diet that falls within this niche we call the "acceptable diet". The diet actually selected from the acceptable diet and eaten by a herbivore we call the "realized diet" (what the animal eats) and the niche enclosing this diet is the "realized niche". Others have referred to the fundamental niche as "functional", "evolutionary", or "strategic" and to the realized niche as "ecological" or "tactical" (Fox and Morrow 1981; Sherry 1990; Irschick et al. 2005). Our terms better describe testable attributes of dietary selection because their inter-relationships are clear. The acceptable diet results from the intersection of the available diet with the fundamental niche, but the realized diet may include only part of the acceptable diet. A small realized niche can arise because (1) the fundamental niche is narrow; (2) the available diet is not diverse; (3) the overlap between the fundamental niche and the available diet is small; or because (4) factors such as interspecific competition, specialized foraging strategies, or learned behaviors may cause animals to use only part of the acceptable diet.

Because the acceptable and realized diets are subsets of the available diet, which varies in space and time, temporal and spatial locations, and scales must be clearly specified in any discussion of dietary specialization. For a given animal species, the fundamental niche varies less with scale, but nutritional requirements and tolerance of PSMs can vary among seasons (McLister et al. 2004) and locations

(Twigg and King 1991). The concept of the fundamental niche depicts animals' requirements for nutrients and tolerances of nonnutritional components that make plants difficult to exploit. Unfortunately, dietary breadth is often difficult or impossible to quantify empirically, partly for the practical reasons discussed earlier and partly because we know little about how animals balance deficiencies and surpluses in nutrients and chemicals. In an effort to address this gap, Simpson and Raubenheimer (1999, 2001, and this issue) have developed the geometric framework to directly test how animals incorporate the target intake of both nutritional and nonnutritional components, such as PSMs, when selecting diets. Such an approach will aid researchers in determining the acceptable and realized diets of herbivores under static and dynamic conditions.

Consider some simple examples of how using our concepts of niche and diet allows a better understanding of dietary specialization and facilitates comparisons among species (Fig. 1). For illustrative purposes, our niche is defined by only two axes: concentrations of digestible nutrients and of PSMs, which have opposite effects on the "difficulty" of plant foods. In niche space, dietary difficulty increases from the "easy" top left-hand corner

(LHC) towards the "difficult" lower right-hand corner (RHC; shaded area A in Fig. 1). Shaded area B in Fig. 1 represents an animal that lives in a benign nutritional environment (the available niche is found towards the top LHC of the niche space) and has a restricted fundamental niche that includes only the "easier" foods from this environment. Competition for these foods will be intense and so this animal makes full use of its acceptable diet, foraging as generally as possible within the confines of its fundamental niche. Shaded area C in Fig. 1 represents a herbivore in a much more challenging plant assemblage, in which the available diet is less nutritious and more chemically defended. This animal has a generous fundamental niche that yields a rather broad acceptable diet. Because competition in this environment is relatively low, this herbivore can specialize on a restricted realized diet. Note that the top and left-hand boundaries of the fundamental niche in Shaded area C in Fig. 1 are dashed to indicate "soft" boundaries to the fundamental niche, which may arise when an animal relies on particular plant cues to prompt feeding. In this situation, the fundamental niche cannot generally extend beyond the nutritional and chemical distribution of one type of plant. Shaded area D and E in Fig. 1 illustrates the herbivore population, which

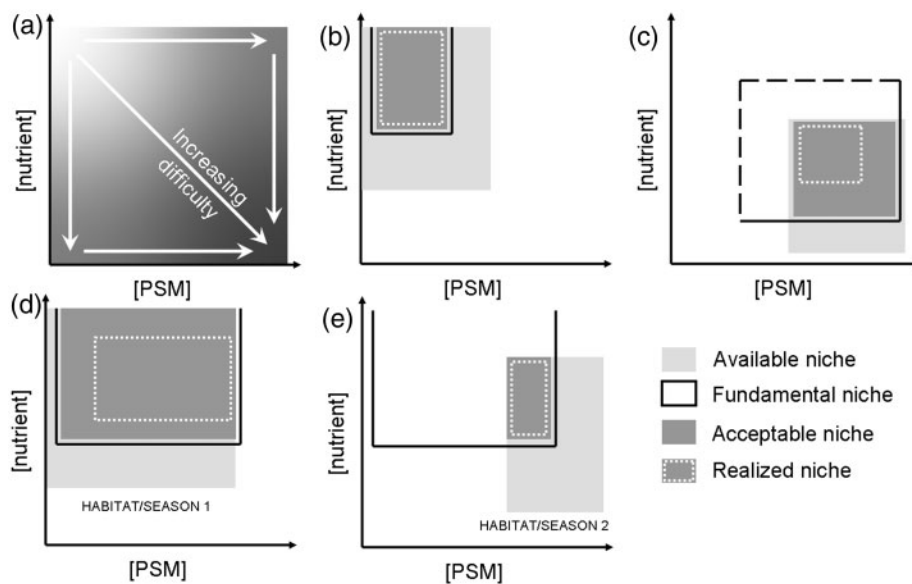


Fig. 1 Example of how available, fundamental, acceptable, and realized niches can be compared graphically amongst several idealized herbivores. Shading in (A) demonstrates how the "difficulty" of foods increases throughout niche space as PSM concentrations increase and nutrient concentrations decrease. Shading in (B) represents an obligate generalist, which must select a moderately diverse diet from throughout its small fundamental niche. The fundamental niche of the obligate specialist in (C) includes very difficult foods and excludes very easy foods because, through evolution, it has lost the behavioral and anatomical flexibility seen in generalists. Shading in (D) and (E) represent the same facultative specialist, but in two different available niches. In a broad, easy available niche, its broad fundamental niche permits a diverse, relatively easy diet, but in a narrow, difficult available niche (faced in a different habitat or season), only a restricted, difficult diet is possible. See text for a more detailed commentary.

might be of the same or of different species. Regardless, the two populations possess identical, broad, fundamental niches, which are imposed on quite different available diets. In shaded area D in Fig. 1, the herbivore has a broad acceptable diet, and adopts a rather broad realized niche, avoiding only the easiest food, for which it is outcompeted, and the most difficult food, for which there may be some cost to consume. Thus, it behaves as a generalist. In shaded area E in Fig. 1, the same fundamental niche imposed on a much more difficult plant assemblage produces only a very small acceptable diet and the herbivore expands its realized niche to take full advantage of it. The small realized niche forces this herbivore to behave as a specialist. The contrast between shaded areas D and E in Fig. 1 could be explained by different plant assemblages growing in different climates or under different abiotic conditions, or by seasonal changes in availability and quality of plants.

In theory, we can imagine a perfect specialist (a monophage) and a perfect generalist that are genuinely indiscriminate in their feeding. However, the complexity of interactions between the environment, plants, and herbivores that drives dietary selection reveals that most herbivores cannot be lumped into broad “specialist” and “generalist” categories (Fig. 1). Rather, specialization is specific to a time and place and is often best illustrated by comparison to other herbivore species. To further ensure consistency in communication and improve comparisons across herbivores and studies, we propose a “specialization key” that helps define a herbivore’s location along the specialist–generalist continuum by considering the fundamental niche, available, acceptable and realized diets, and the intrinsic “difficulty” of plants consumed (Table 2).

Classifying herbivores using the specialization key

Researchers must first establish whether their species of interest is a specialist as determined by three connected and measurable parameters: difficulty of diet, adaptations that overcome diet difficulty, and proportion of food in diet relative to availability. First, the food must have characteristics that make it difficult, such as low nutrients, high PSMs or physical defences. Second, the suspected specialist must have mechanisms such as enhanced detoxification, digestive, or morphological capacity that help overcome the difficult features of the diet. Finally, these features must result in most herbivores consuming this difficult food at a lower proportion than its availability, and the suspected specialist must consume the diet in higher proportions than do most other herbivores with similar access, or in higher proportions than its availability. If all three parameters are met, then a herbivore would be considered a specialist. However, because dietary specialization is clearly part of a continuum rather than a discrete category (Fox and Morrow 1981; Bernays and Chapman 1994; Julliard et al. 2006), we suggest that the modifiers “obligatory” and “facultative” should be used based on knowledge of niche breadth. We believe that the terms “obligatory” and “facultative” convey a more precise meaning in defining specialization in herbivorous mammals than do the terms “stereotyped” (Sherry 1990), “extreme” (Fox and Morrow 1981), “phenotypic” (Robinson and Wilson 1988) or “opportunistic” (Sherry 1990) used in previous works. Using these modifiers according to the proposed specialization key (Table 2) will increase the clarity and usefulness of comparing methods, results, and definitions from studies investigating

Table 2 Specialization key for ordering mammals along the specialist–generalist continuum based on the relative breadth of the realized and fundamental niches, relevant spatial/temporal scale, and difficulty of food consumed

Herbivore type	Fundamental niche	Available diet	Realized niche	Realized diet
Obligate specialist	Very broad along some axes but narrow ^a along most	Difficult; often restricted	Very narrow; difficult	Restricted; difficult
Facultative specialist ^b	Very broad along some axes, broad along others	Difficult; restricted or Moderately difficult; diverse	Narrow; difficult or Very broad; moderately difficult	Restricted; difficult or Diverse; difficult to moderately easy
Facultative generalist ^b	Broad along most axes	Moderately easy; diverse or An easy component is abundant	Broad; moderately easy or Narrow; easy	Diverse; moderately difficult or Easy plants restricted; easy
Obligate generalist	Moderately narrow along most axes	Easy; diverse	Moderately narrow; easy	Moderately diverse; easy

Difficult food items are those that are avoided by most herbivores because of chemical or physical characteristics that lower the quality of the food per unit time invested to obtain the food (Robinson and Wilson 1998).

^aSome boundaries on the “easy” side of the niche may be maintained by behavioral mechanisms which may sometimes be overcome.

^bRealized diet is dependent upon available diet and may shift between seasons or habitats.

the foraging strategies of multiple herbivores from a variety of experiments. The key accommodates cases in which the degree of dietary specialization is influenced by the available diet, which can differ seasonally or among habitats. It does not accommodate cases in which animals' fundamental niche changes, for example, between developmental stages. We offer a subset of the existing examples of each specialization category and summarize from the literature predicted characteristics of each category that help separate categories.

Obligatory specialist

Herbivores that always have a narrow realized niche are classified as obligatory specialists (Table 2). Obligatory specialists are defined by three main characteristics. First, although they may have a broader fundamental niche than do other herbivores along a few axes (e.g., tolerance for a specific PSM), their fundamental niche is narrow along most axes, particularly for PSMs that do not feature in their natural diet, thus preventing their realized niche from expanding in the laboratory and also limiting their realized diet (shaded area C in Fig. 1). Second, the food on which they specialize is "difficult", possessing chemical or physical characteristics that make it generally unpalatable or of low value to most consumers (Robinson and Wilson 1998). Third, they possess unique physiological, behavioral, or anatomical characteristics that allow them to consume large amounts of one food type, but prevent them from consuming difficult foods of other types (Fig. 2).

Many ecologists have made predictions and gathered supportive evidence for the ecological and physiological conditions that favor herbivores closer to the obligatory specialist side of the continuum (Table 3). First, obligatory specialists are expected to be favored in stable environments when abundant, often monospecific patches of chemically defended or physically defended forage are available that also provide conspicuous cues (e.g., smell of terpenes; Table 3) (Freeland and Janzen 1974; Westoby 1978; Crawley 1983; Lawler et al. 1998; Dearing et al. 2000; Moore et al. 2004a). Furthermore, these herbivores would likely be small or immobile relative to the size of food patches (Westoby 1978; Freeland 1991). Smaller herbivores, or herbivores with lower absolute metabolic rates, would be more likely to meet their energy requirements from a single difficult plant species or plant part that is available in the habitat. Because obligatory specialists feed primarily on one type of food, their foraging behavior can be highly

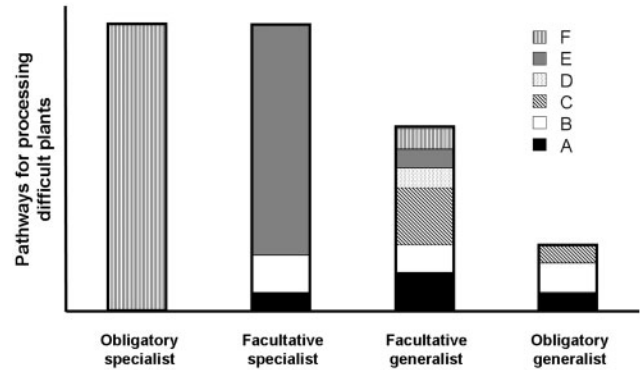


Fig. 2 Hypothesized differences between the ability of four types of herbivores classified according to our specialization key (Table 2) to process plants with intrinsically "difficult" chemical or physical attributes (A–F). The obligatory specialist can process one type of difficult plant very well (e.g., one plant secondary metabolite, PSM) due to specialized pathways, but may not have pathways to process other plants. The facultative specialist can process one type of plant well, but can also process a few other types of difficult plants to a lesser degree. The facultative generalist can process a variety of difficult plants, but not in the quantity that the specialists can process any one plant. The obligatory generalist can only process a few types of difficult plants to a minimum degree. Pathways may relate to any biochemical, morphological, physiological, or behavioral adaptations that allow the animal to process a difficult plant.

ritualized, making behavioral plasticity largely superfluous. Therefore, they may require low neural sophistication and thus spend less energy maintaining a metabolically expensive brain (Smith 1979; Bernays and Funk 1999; Martin and Handasyde 1999). They are, instead, sensitive to specific, conspicuous sensory cues from their preferred forage, maintained by conditioned aversions and postingestive feedback (Provenza and Balph 1987; Lawler et al. 1998; Simpson and Raubenheimer 1999). This results in faster, more accurate decisions when selecting forage within the habitat or quality parts of their host plant, but yields aversion to unfamiliar stimuli as well as a limited behavioral repertory (Futuyma and Moreno 1988; Bernays and Funk 1999). Obligatory specialists should also have specialized feeding anatomy (e.g., specialized molars that grind plants) and physiology (e.g., detoxification enzymes, microorganisms) (Crawley 1983; Sorensen et al. 2005a) that help exploit a nutritionally, chemically or physically difficult diet. For example, obligatory specialists may possess enhanced mechanisms that prevent the absorption of PSMs (Shimada 2006; Sorensen and Dearing 2006; da Costa et al. 2008), enhance detoxification and elimination of potentially toxic PSMs (Freeland and

Table 3 Predicted characteristics that differentiate specialist and generalist herbivores

	Specialist	Generalist
Food	Found in large, predictable, monospecific patches Chemically or physically defended Conspicuous stimuli	Dispersed or unpredictable in time/space, searching expensive or risky Relatively nutritious
Forager	Small or immobile relative to food patches ^a Relatively low metabolic rate Low neural sophistication ^a Specialized feeding anatomy, physiology, or behavior Advanced detoxification systems for narrow range of plant chemicals	Large or mobile relative to food patches High level of information processing Generalized feeding adaptations that proceed along multiple pathways Detoxification proceeds along multiple pathways ^b
Competition and Plasticity	Avoids competition by consuming chemically or physically defended food Reduced capacity to consume novel foods Responds poorly to changing ^a environment Difficult to feed in captivity ^a More likely to be rare or endangered ^a	Good competitor on abundant/nutritious food, poor competitor on chemically or physically-defended foods Improved ability to consume novel foods ^b Adaptable ^b Consumes generalized herbivore diets in captivity More likely to be common

^aCharacteristics that might be relaxed for facultative specialists.

^bCharacteristics tightened for obligatory generalists.

Janzen 1974; Futuyma and Moreno 1988; Glander et al. 1989; Dearing et al. 2000) or result in the excretion of less expensive metabolites (Boyle et al. 1999; Sorensen et al. 2005b). Herbivores may also rely on symbiotic microorganisms that facilitate specialization (Ganzhorn 1989).

As a consequence, obligatory specialists may efficiently use “difficult” foods that are unpalatable to other herbivores, thus avoiding interspecific competition (Table 3, Fig. 2, Dial 1988). However, the mechanisms that allow obligatory specialists to exploit a difficult plant often come with the trade-off of limited capacity to consume novel foods (Futuyma and Moreno 1988; Berenbaum and Zangerl 1994). For example, the Stephen’s woodrat (*Neotoma stephensi*) has behavioral and physiological mechanisms that process the secondary metabolites in one-seeded juniper (Sorensen et al. 2005b), but cannot tolerate secondary metabolites in a novel plant (Sorensen et al. 2005a). Specialization may also limit a population’s ability to respond to environmental changes on either a short- or long-term basis (Crawley 1983), which may threaten their populations. Likewise, specialists are predicted to be difficult to feed in captivity. For all of these reasons, obligatory specialists are likely to be the rarest type of mammalian herbivore and also to have a restricted ecological range.

Koalas are the most well-known obligatory specialist and exemplify many of the predicted conditions

that facilitate specialization. Not only do they normally eat *Eucalyptus* leaves virtually exclusively year round (Moore and Foley 2005), but they are sedentary, have a relatively low metabolic rate (McNab 1978), and use chemical cues to recognize abundant and seasonally predictable *Eucalyptus* across their range in Australia (Moore et al. 2004b). Koalas also have one of the smallest, most primitive brains relative to their size, which limits their behavioral repertory (Martin and Handasyde 1999). Although the capacity of koalas for detoxification is not known, they do use less costly detoxification pathways than do their generalist counterparts (Boyle et al. 1999). Koalas seem to have a restricted capacity to consume foods other than *Eucalyptus*. In captivity, koalas must be fed *Eucalyptus* leaves and never consume >40% of their diet in artificial leaf diet (Pahl and Hume 1991). However, koalas are not absolutely restricted to *Eucalyptus*—individual koalas can occasionally learn to feed on other plant genera to a significant extent (e.g., *Pinus radiata*) (Moore and Foley 2000). Thus, some facultative niche boundaries for obligate specialists are maintained largely by behavioral mechanisms, and to the extent that behavior is more malleable than physiology, they can be breached.

The endangered woolly flying squirrel (*Eupetaurus cinerus*) of northern Pakistan is a lesser-known and lesser-studied example of an obligatory specialist,

but also exemplifies many expected traits (Table 3). This rodent has unique hypsodont molars useful in consuming the thick, waxy cuticle of needles from two abundant species of pine (*Pinus wallichiana* and *P. gerardiana*) year round (Zahler and Khan 2003; Shafique et al. 2006). Pine needles contain high levels of terpenes, so the woolly flying squirrel likely has adaptations for detoxification, although this has not been investigated. The animals tend to be slow moving and thus also likely have a slow metabolic rate (Zahler and Khan 2003). In captivity, woolly flying squirrels refuse all other foods but pine needles (Zahler and Khan 2003).

Although large amounts of plant fiber present a difficulty to herbivores, many species of grasses, shrubs, and other plants contain high fiber. Therefore, behavioral, anatomical, and physiological adaptations needed to cope with high fiber tend to be rather generalized, and herbivores would be unlikely to specialize on one genus or species of plant solely because of its fiber content. In contrast, specialized biochemical adaptations to deal with PSMs have evolved as the result of a much tighter coevolutionary interaction. However, the giant (*Ailuropoda melanoleuca*) and red (*Ailurus fulgens*) pandas are examples of obligatory specialists that consume bamboo almost exclusively (Roberts and Gittleman 1984; Johnson et al. 1988; Gittleman 1994; Pradhan et al. 2001), when the main “difficulty” of bamboo is that it is fibrous and avoided by most herbivores (except bamboo lemurs, bamboo rats of *Rhizomys* spp., and some primates). Pandas have developed unique morphological adaptations, such as dense, massive skulls, and zygomatic arches and heavily cusped teeth (Zhang et al. 2007). Their forepaws have an elongated radial sesamoid used in grasping and harvesting bamboo (Roberts and Gittleman 1984; Wei et al. 1999). Although they may consume several genera of bamboo across their range, they are sedentary, have low metabolic rates and are endangered (Wei et al. 1999; Pradhan et al. 2001).

Facultative specialist

Like the obligatory specialist, the facultative specialist has a special ability to detoxify a specific chemical or harvest a difficult plant that most herbivores avoid; thus it always has a restricted realized diet (e.g., consumes the same plant or plant parts) and hence a narrow restricted niche over some level of temporal (e.g., season) or spatial (e.g., specific habitat) scales (Table 2, Fig. 2). However, what sets that facultative specialist apart from the obligatory

specialist is that the fundamental niche is broad enough along some axes to allow the animal to consume plants with few chemicals or simple architecture, when available, as ecological pressure lessens (e.g., shaded areas D and E in Fig. 1; Robinson and Wilson 1988). Although it may seem contradictory that both obligatory and facultative specialists have broader fundamental niches along some axes than do generalists, we propose that evolving adaptations that cope with the extremes of “difficult” axes does not necessarily mean that specialists lose their ability to tolerate the easy ends of difficult axes (e.g., PSMs).

Although little is known about the fundamental niche of many herbivores, most mammalian herbivores defined in the literature as “specialists” likely fall into this category. Some of the characteristics expected of a “specialist” are relaxed in the facultative specialist (Table 3). The benefits of this strategy are similar to those reaped by obligatory specialists, but unlike obligatory specialists, facultative specialists do not sacrifice the option of consuming many plants by specializing on one plant. Therefore, these animals have the advantage of flexibility, allowing them to respond to changes in abundance and quality of food, and thus they can better cope with variable environments (Irschick et al. 2005). They would also avoid competition with generalists when resources are scarce, because they can exploit resources that are rarely used by other herbivores (Robinson and Wilson 1998). They may, however, sacrifice some efficiency for extracting nutrients from a novel plant with difficult characteristics that differ from those required to exploit the specialized diet (e.g., specific chemical or physical defences, Fig. 2).

The unique characteristic of the facultative specialist that distinguishes it from the obligatory specialist is that the breadth of the facultative specialist’s available diet, and consequently of its realized niche, varies at different times and locations. For example, in summer, when a variety of nutritious plants are available, pygmy rabbits (*Brachylagus idahoensis*) eat a mixed diet with <50% sagebrush. However, in winter when other plants are scarce, the pygmy rabbit’s uniquely high tolerance for terpenes and other PSMs in sagebrush allows it to eat big sagebrush (*Artemisia tridentata*) exclusively, a food avoided by other herbivores (Thines et al. 2004). Similarly, in the Mojave Desert, desert woodrats consistently specialize on creosote (*Larrea tridentata*), which contains high levels of phenolic resins (up to 25% of leaves’ dry mass), some of which are toxic to most mammals (Mangione et al. 2000; Lambert et al. 2002). However, in the Great Basin of

Utah, desert woodrats primarily feed on western juniper, which contains high levels of PSM's, especially α -pinene (Mangione et al. 2000). Moreover, the ability to consume each of these difficult plant species, avoided by other herbivores, is thought to be associated, in part, with differential detoxification pathways active in the different populations (Haley et al. 2008). Therefore, researchers investigating herbivores in a single habitat or season may erroneously link the restricted diet and associated physiological adaptations with obligatory specialization, whereas the flexibility of the species, not the population, suggests that they are instead facultative specialists (e.g., desert woodrat). Likewise, researchers may erroneously link a diverse diet observed during a specific season or habitat to a generalist foraging strategy, whereas the consistent intake of a difficult plant over a short time suggests that this species is a facultative specialist (e.g., pygmy rabbits).

Facultative generalist

The key characteristics of generalists that distinguish them from specialists is that difficult plants make up a lower proportion of their realized diet than is true of the available diet, or of the realized diet of their specialist counterparts. Facultative generalists do share one characteristic with facultative specialists in that they are occasionally able to survive on a restricted diet over short periods or when the available diet is locally restricted (Table 2). However, when compared with plants consistently consumed by facultative specialists the plants consistently eaten at these smaller scales typically would (1) be less difficult as characterized by lower levels of PSMs and physical defences; (2) be consumed by many other herbivores and in similar proportion to the available diet; (3) represent larger taxonomic groups (i.e., family or plant form versus genus or species); and (4) vary with time and location. The mechanisms used by facultative generalists to detoxify PSMs are expected to proceed along generalized or multiple pathways (Table 3, Fig. 2; Dearing et al. 2000) and are advantageous in most situations and at larger spatial and temporal scales. Thus, they broaden the facultative generalist's fundamental niche on many axes, and although the breadth may not be large on any one axis, the outcome is that the animal can expand its realized diet (shaded area D in Fig. 1 and Fig. 2). The adaptability of facultative generalists allows them to occur commonly and across wide distributions and may allow them to be more successful than are specialists in environments where food is scarce, heterogeneous,

unpredictable, or contains a wide range of PSMs, or when searching for food is difficult or risky (Table 3; Crawley 1983; Kassen 2002). These animals tend to be larger, more mobile and require higher levels of information processing for selecting diverse diets (Table 3, Freeland 1991; Bernays and Funk 1999).

The marsupial brushtail possum (*Trichosurus vulpecula*) has many of the characteristics of a facultative generalist. In most areas across its range, brushtail possums consume a wide mixture of fruits and leaves (McIlwee 2001; Boyle et al. 2003). In laboratory studies, brushtail possums have commonly been used as a typical "generalist" for comparison with their "specialist" arboreal folivore counterparts, such as greater gliders (*Petauroides volans*), ringtail possums, and koalas (Marsh et al. 2003), and have reduced abilities to cope with many PSMs. However, in some parts of Australia, their diets contain >60% *Eucalyptus* spp., which includes high levels of terpenes, phenolics and formylated phloroglucinol compounds (Freeland and Winter 1975; DeGabriel et al. 2009). Similarly, white-throated woodrats typically have a broad diet, but in Arizona their diet can consist of up to 27% yucca, which is a difficult food avoided by other herbivores (Dial 1988). Like the brushtail possum, white-throated woodrats have been used as a generalist with which to compare with more specialized woodrat species, and have demonstrated a lesser ability to detoxify particular PSMs than can specialists, but an enhanced ability to cope with novel PSMs (Sorensen et al. 2005b).

Even some large herbivores may be facultative generalists. For example, willow (*Salix* spp.) constitutes over 70% of the summer and winter diet of moose in many parts of North America (Risenhoover 1989; Dungan and Wright 2005), but in other seasons or places moose eat a broad diet of leaves, stems, and forbs. For example, in winter moose in Sweden consumed only 14% willow in favor of the more abundant Scot's pine (*Pinus sylvestris*) (Shipley et al. 1998). Although willow contains moderate levels of condensed tannins (Hanley et al. 1992), and moose are adept at quickly stripping willow leaves and stems to meet their high-energy requirements, willow is commonly used by many herbivores, thus would not be considered a particularly "difficult" food.

Obligatory generalist

Obligatory generalists differ from facultative generalists in that they must always have a broad realized

niche because their fundamental niche is sufficiently narrow along some axes and restricts them from eating large quantities of one food type, especially foods with PSM's (Table 2). Their narrow tolerances for diverse "difficulties" in plants forces these herbivores to consume small amounts of a wide range of plants, thereby obtaining the proper mixture of nutrients and avoiding large amounts of one type of PSM (shaded area B in Fig. 1 and Fig. 2, e.g., detoxification limitation hypothesis Freeland and Janzen 1974; nutrient constraint hypotheses Westoby 1978).

These animals consume foods that are intrinsically easy to use and preferred by most consumers, and avoid those that are difficult to harvest or digest or that require specialized morphology, behavior, or physiology (Robinson and Wilson 1998). Obligatory generalists are expected to be relatively rare, but compete well with other herbivores under conditions in which less difficult food is relatively abundant, but they are poor competitors when plant availability is restricted to difficult foods by weather or by degradation of habitat (Table 3).

To our knowledge, no research has compared the fundamental niches of facultative and obligatory generalists under similar conditions. However, insects like grasshoppers (*Chorthippus parallelus*) that have higher survival and fecundity when they consume a larger mixture of relatively nutritious grasses, legumes, and forbs (Unsicker et al. 2008), exemplify obligatory generalist herbivores. In mammalian herbivores, some animals such as roan antelope (*Hippotragus equines*) that fall toward the intermediate or grazer end of the browser-grazer continuum, might be considered obligatory generalists because they eat less difficult plants without substantial PSMs or complex architecture (McArthur et al. 1991). For example, roan antelope seem to select primarily the most nutritious grasses, and occasionally shrubs, available in their habitats, and declining populations may be caused by degradation of appropriate foraging patches and competition with other herbivores for these foods (Wilson and Hirst 1977; Kröger and Rogers 2005). Likewise, herbivores with simpler digestive tracts, or those that tend toward omnivory, granivory, or frugivory, would likely be considered obligatory generalists. In contrast, large grazers that can consume high levels of plant fiber that is difficult to digest and a single taxon of plants (e.g., domestic horses eating a monospecific diet of timothy hay (*Phleum pratense*)) would be better classified as a facultative generalist.

Future directions for research and application of the specialization key

When using the specialization key as a guide for comparing strategies of herbivores or placing them more accurately along the generalist-specialist continuum, researchers will undoubtedly find that in many cases only a hazy line separates the four categories of herbivores, and many herbivores do not conform completely to hypothesized characteristics of specialists and generalists (Table 3). The level of clarity depends, in part, on the type of data available to describe and quantify the realized and fundamental niches. Unfortunately, for most species, data on realized diets are scarce, or are limited to one season or geographic area. Data on the fundamental niche, which must be conducted under controlled laboratory conditions, are perhaps even more difficult to obtain.

Despite these difficulties, recent advances in pharmacology (e.g., McLean and Duncan 2006; Sorensen et al. 2006), molecular biology (e.g., Magnanou et al. in press), chemistry (Rochfort 2005; DeGabriel et al. 2009), and modeling (Raubenheimer and Simpson 2005) offer opportunities to fill in gaps in our knowledge related to factors that limit or expand dietary niches. First, chemical assays have revealed novel chemicals that drive selection of diet. For example, Pass et al. (1998) used bioassay-guided fractionation and subsequent preference experiments and pharmacological experiments to detect formylated phloroglucinol compounds, a group of previously unknown PSM, which when de-coupled from common and co-occurring PSMs in *Eucalyptus* (i.e., terpenes, tannins, and other phenolics), explained feeding preferences and habitat use by folivorous marsupials. Likewise, microarray technology is being used to identify specific enzymatic differences that may explain tolerance to a difficult plant in specialist and generalist herbivores (Skopec et al. 2008). Although ecologists will never be able to describe and quantify all relevant axes of a herbivore's dietary niche, new geometric modeling approaches promise to simplify exploration of the realized and fundamental niches of herbivores by synthesizing and reducing many relevant axes (Simpson and Raubenheimer 2001).

Comparative studies will further facilitate exploring specific axes of niches in detail, especially when coupled with studies that examine characteristics of plants and physiological capabilities and responses of herbivores. Such comparisons will enable ecologists to test long-standing hypotheses about specialists

and generalists (Table 3) and to understand the mechanisms that limit or expand dietary breadth. For example, generalists are expected to have more diverse enzymes and detoxification pathways than are specialists (Fig. 2). An enhanced ability to detoxify PSMs may allow a herbivore to exploit a greater number of plant species with similar PSMs, thus broadening the realized niche. On the other hand, detoxification enzymes that effectively metabolize the PSMs in one plant may not metabolize PSMs in another plant, thus narrowing the realized niche. The proposed specialization key and common language is designed to assist researchers with understanding both the components that make a plant difficult and the mechanisms that limit or expand tolerance to those difficult components within an overall framework of niche breadth.

Further work should also explore dietary specialization of herbivores in context of the community, including its effects on competitiveness, plasticity, and need for conservation (Robinson and Wilson 1998; Julliard *et al.* 2006). For example, some evidence suggests that specialists, including herbivores such as marsupials (Fisher *et al.* 2003), lagomorphs (Smith 2008), and primates (Harcourt *et al.* 2002) have been declining disproportionately to generalists throughout the world. Likewise, exploration of niche breadth should be directly related to fitness of animals (Levins 1962; Wilson and Yoshimura 1994; Raubenheimer *et al.* 2005), such as testing the hypothesis that mean fitness of a specialist on its own host plant is higher than the mean fitness of a generalist on that host plant (Kawecki 1994; Unsicker *et al.* 2008), or comparing costs and benefits of the two different specialists and between the two generalist strategies (*i.e.*, facultative versus obligatory). Finally, employing phylogenetically based analyses will allow ecologists to search for patterns and explain contradictions across all animal taxa (Irschick *et al.* 2005), such as why herbivory in general, and specialization in particular, tends to be rare in most vertebrate taxa (Crawley 1983; Dearing *et al.* 2000; López-Calleja and Bozinovic 2000; O'Grady *et al.* 2005; Taylor and Steinberg 2005; da Silva and de Britto-Pereira 2006; Mountfort *et al.* 2006).

Such questions could help resolve not only patterns of foraging behavior among herbivores, but may also help ecologists understand the mechanisms that limit or expand dietary breadth. Although there are many adaptations that can facilitate functional specialization (Sorensen *et al.* 2004), little is known about how adaptations that give rise to functional specialization influence the acceptable

diet and the realized and fundamental niches. For example, Kinnear *et al.* (1979) suggested that symbiotic gut microbes have enabled pregastric fermenters to expand their realized niche to include more fibrous food and reduce competition with nonpregastric fermenters. Likewise, an enhanced ability to detoxify PSMs may allow a herbivore to exploit a greater number of plant species with similar PSMs, thus broadening their realized niche. On the other hand, detoxification enzymes that effectively metabolize the PSMs in one plant may not do so in another plant, thus narrowing the realized niche.

Conclusion

In summary, our specialization key is based on the breadth of realized and fundamental niches, the difficulty and availability of dietary items, and the relative use of the diet compared to that of other herbivore species. Moreover, we assign modifiers “obligatory” and “facultative” to the terms “specialist” and “generalist” herbivore to help researchers better describe herbivores. The language set forth allows for consistency and clarity among investigations at multiple scales of time and place, under varying environmental and ecological conditions, between and within taxa, and captures the dynamic aspects of dietary selection in animals. We suggest that ecologists distinguish a specialist herbivore from a generalist herbivore by defining the scale, ecological conditions, and level of ecological or taxonomic hierarchy (Fox and Morrow 1981). Furthermore, like Futuyma and Moreno (1988) and Crawley (1983), we argue that an animal's degree of specialization can really only truly be measured by direct comparison with other animals under the same conditions. Much progress has been made in our understanding of causes and consequences of niche breadth through recent studies that have compared performance of specialist and generalist herbivores in controlled laboratory settings (Lawler *et al.* 1998; Boyle *et al.* 1999; Marsh *et al.* 2003; Sorensen and Dearing 2003; Sorensen *et al.* 2004, 2005b). Future research examining the causes and consequences of dietary specialization of herbivores across taxa in both the field and laboratory will generate new theory and practical solutions for herbivores and the plants they consume.

Funding

The opportunity to present and synthesize ideas relative to this work was supported by National Science Foundation (grant number 0827239 to J. S. Forbey),

Society for Integrative and Comparative Biology, and Agilent Technologies, Santa Clara, CA.

Acknowledgments

We thank W. J. Foley, M. D. Dearing, and the Pharm-Ecology Symposium participants for ideas, insights, and review of earlier drafts of this manuscript.

References

- Atsatt PR, Ingram T. 1983. Adaptation to oak and other fibrous, phenolic-rich foliage by a small mammal, *Neotoma fuscipes*. *Oecologia* 60:135–42.
- Begon M, Harper JL, Townsend CR. 1990. *Ecology*. 2nd Edition. Boston: Blackwell Scientific Publications.
- Berenbaum MR, Zangerl AR. 1994. Facing the future of plant-insect interaction research: Le Retour à la “Raison d’Être”. *Plant Physiol* 146:804–11.
- Bernays EA, Chapman RG. 1994. Host-plant selection by phytophagous insects. New York: Chapman & Hall.
- Bernays EA, Funk DJ. 1999. Specialists make faster decisions than generalists: experiments with aphids. *Proc R Soc Lond B* 266:151–6.
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28.
- Boyle B, McArthur C, McLean S, Wiggins NL. 2003. Effects of two plant secondary metabolites, cineole and gallic acid, on nightly feeding patterns of the common brushtail possum. *J Chem Ecol* 29:1447–64.
- Boyle RR, McLean S. 2004. Constraint of feeding by chronic ingestion of 1,8-cineole in the brushtail possum (*Trichosurus vulpecula*). *J Chem Ecol* 30:757–75.
- Boyle RT, McLean S, Davies N, Foley W, Moore B. 1999. Folivorous specialization: adaptations in the detoxification of the dietary terpene, p-cymene, in Australian marsupial folivores. *Am Zool* 39:120A.
- Brown JH, Lieberman GA, Dengler WF. 1972. Woodrats and cholla: dependence of a small mammal population on the density of cacti. *Ecology* 53:310–3.
- Bugalho M, Mayes RW, Milne JA. 2002. The effects of feeding selectivity on the estimation of diet composition using the *n*-alkane technique. *Grass For Sci* 57:224–31.
- Cameron GN, Rainey DG. 1972. Habitat utilization by *Neotoma lepida* in the Mohave Desert. *J Mamm* 53:251–66.
- Carey AB. 1999. Red tree vole/*Arborimus longicaudus*. In: Wilson D, Ruff S, editors. *The Smithsonian book of North American mammals*. Washington, DC: Smithsonian Institution Press. p. 620–2.
- Crawley MJ. 1983. *Herbivory: the dynamics of animal-plant interactions*. Studies in ecology, Vol. 10. Oxford: Blackwell Scientific Publications.
- da Costa G, Lamy E, Silva FCE, Andersen J, Baptista ES, Coelho AV. 2008. Salivary amylase induction by tannin-enriched diets as a possible countermeasure against tannins. *J Chem Ecol* 34:376–87.
- da Silva HR, de Britto-Pereira MC. 2006. How much fruit do fruit-eating frogs eat? An investigation on the diet of *Xenohyla truncata* (Lissamphibia:Anura:Hylidae). *J Zool* 270:692–8.
- Dearing MD, Mangione AM, Karasov WH. 2000. Diet breadth of mammalian herbivores: nutrient vs. detoxification constraints. *Oecologia* 123:397–405.
- DeGabriel JL, Moore BD, Foley WJ, Johnson CN. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* 90:711–9.
- Dial KP. 1988. Three sympatric species of *Neotoma* – Dietary specialization and coexistence. *Oecologia* 76:531–7.
- Downs CT, McDonald PM, Brown K, Ward D. 2003. Effects of *Acacia* condensed tannins on urinary parameters, body mass, and diet choice of an *Acacia* specialist rodent, *Thallomys nigricauda*. *J Chem Ecol* 29:845–58.
- Dungan JD, Wright RG. 2005. Summer diet composition of moose in Rocky Mountain National Park, Colorado. *Alces* 41:139–46.
- Eccard JA, Meyer J, Sundell J. 2004. Space use, circadian activity pattern, and mating system of the nocturnal tree rat *Thallomys nigricauda*. *J Mamm* 85:440–5.
- Erfteemeier PL, Djunarin A, Moka W. 1993. Stomach content analysis of a dugong (*Dugong dugong*) from Sulawesi, Indonesia. *Aust J Mar Freshwater Res* 44:229–33.
- Federal Register, November 10, 2003. Endangered and threatened wildlife and plants; final rule to list the Columbia Basin Distinct Population Segment of Pygmy Rabbits (*Brachylagus idahoensis*) as endangered 68:10388–409.
- Fisher DO, Blombert SP, Owens IPE. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc R Soc Lond B* 270:1801–8.
- Fox LR, Morrow PA. 1981. Specialization: species property or local phenomenon. *Science* 211:887–93.
- Freeland WJ. 1991. Plant secondary metabolites: biochemical coevolution with herbivores. In: Palo RT, Robbins CT, editors. *Plant defenses against mammalian herbivory*. Boca Raton, Florida: CRC Press. p. 61–81.
- Freeland WJ, Janzen DH. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *Am Nat* 108:269–89.
- Freeland WJ, Winter JW. 1975. Evolutionary consequences of eating: *Trichosurus vulpecula* (Marsupialia) and the genus *Eucalyptus*. *J Chem Ecol* 1:439–55.
- Futuyma DL, Moreno G. 1988. The evolution of ecological specialization. *Ann Rev Ecol Syst* 19:207–33.
- Ganzhorn JU. 1989. Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia* 79:279–86.
- Ganzhorn JU. 1993. Flexibility and constraints of *Lepilemur* ecology. In: Kappeler PM, Ganzhorn JU, editors. *Lemur*

- social systems and their ecological basis. New York: Plenum Press. p. 153–65.
- Gittleman JL. 1994. Are pandas successful specialists or evolutionary failures? *Bioscience* 44:456–64.
- Glander KE, Wright PC, Seigler DS, Randrianasolo V, Randrianasolo B. 1989. Consumption of cyanogenic bamboo by a newly discovered bamboo lemur. *Am J Primatol* 19:119–24.
- Hagerman A, Robbins CT. 1993. Specificity of tannin-binding proteins relative to diet selection by mammals. *Can J Zool* 71:628.
- Haley SL, Lamb JG, Franklin MR, Constance JE, Dearing MD. 2008. “Pharm-Ecology” of diet shifting: Biotransformation of plant secondary compounds in creosote (*Larrea tridentata*) by a woodrat herbivore, *Neotoma lepida*. *Phys Biochem Zool* 81:584–93.
- Hamilton WJ III. 1962. Reproductive behaviour of the red tree mouse. *J Mamm* 43:486–504.
- Hanley TA, Robbins CT, Hagerman AE, McArthur C. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. *Ecology* 73:532–41.
- Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization and extinction in primates. *J Biogeogr* 29:445–56.
- Hayes JP. 1996. *Arborimus longicaudis*. *Mamm Spec* 532:1–5.
- Hoek HN. 1989. Demography and competition in hyrax. A 17 years study. *Oecologia* 79:353–60.
- Hungate RE. 1966. The Rumen and its microbes. New York: Academic Press.
- Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symp Quant Biol* 22:415–27.
- Iason GR, Villalba JJ. 2006. Behavioral strategies of mammalian herbivores against plant secondary metabolites: The avoidance – tolerance continuum. *J Chem Ecol* 32:1115–32.
- Irschick D, Dyer L, Sherry DW. 2005. Phylogenetic methodologies for studying specialization. *Oikos* 110:404–8.
- Johnson KF, Schaller CB, Jinchu H. 1988. Behavior of red and giant pandas in the Wolong Reserve, China. *J Mamm* 69:552–64.
- Jones KM, Maclagan SJ, Krockenberger AK. 2006. Diet selection in green ringtail possum (*Pseudochirops archeri*): a specialist folivore in a diverse forest. *Aust Ecol* 31:799–807.
- Julliard R, Clavel J, Devictor V, Jiguet F, Couvet D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecol Lett* 9:1237–44.
- Kassen R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J Evol Biol* 15:173–90.
- Kavanagh RD, Lambert MJ. 1990. Food selection by the greater glider *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? *Aust Wildl Res* 17:285–99.
- Kawecki TJ. 1994. Accumulation of deleterious mutations and the evolutionary cost of being a generalist. *Am Nat* 144:833–8.
- Keith JO. 1965. The Abert squirrel and its dependence on ponderosa pine. *Ecology* 46:150–63.
- Kinnear JE, Cockson A, Christensen P, Main AR. 1979. The nutritional biology of the ruminants and ruminant-like mammals – a new approach. *Comp Biochem Phys* 64A:357–65.
- Kröger R, Rogers KH. 2005. Roan (*Hippotragus equinus*) population decline in Kruger National Park, South Africa: influence of a wetland boundary. *Eur J Wildl Res* 51:25–30.
- Kronfeld N, Dayan T. 1998. A new method of determining diets of rodents. *J Mamm* 79:1198–202.
- Lambert JD, Zhao D, Meyers RO, Kuester RK, Timmermann BN, Dorr RT. 2002. Nordihydroguaiaretic acid: hepatotoxicity and detoxification in the mouse. *Toxicol* 40:1701–8.
- Lawler IR, Foley WJ, Eschler BM, Pass DM, Handasyde K. 1998. Interspecific variation in *Eucalyptus* secondary metabolites determines food intake by folivorous marsupials. *Oecologia* 116:160–9.
- Levins R. 1962. Theory of fitness in a heterogeneous environment. 1. The fitness set and adaptive function. *Am Nat* 96:361–73.
- Linsdale JM, Tevis IP. 1951. The dusky-footed woodrat. Berkeley: University of California Press.
- López-Calleja MV, Bozinovic FF. 2000. Energetics and nutritional ecology of small herbivorous birds. *Rev Chilena Hist Nat* 73:411–20.
- MacMillen RE. 1964. Population ecology, water relations, and social behavior of a southern California desert rodent fauna. *Univ Calif Publ Zool* 71:1–66.
- Magnanou E, Malenke J, Dearing MD. Expression of biotransformation genes in woodrat (*Neotoma*) herbivores on novel and ancestral diets: identification of candidate genes responsible for dietary shifts. *Molecular Ecol* (in press).
- Mangione AM, Dearing MD, Karasov WH. 2000. Interpopulation differences in tolerance to creosote bush resin in desert woodrats (*Neotoma lepida*). *Ecology* 81:2067–76.
- Marsh KJ, Wallis IJ, Foley WJ. 2003. The effect of inactivating tannins on the intake of *Eucalyptus* foliage by a specialist *Eucalyptus* folivore *Pseudocheirus peregrinus* and a generalist herbivore *Trichosurus vulpecula*. *Aust J Zool* 51:31–42.
- Martin R, Handasyde K. 1999. The koala: Natural history, conservation and management. Australian Natural History Series. 2nd Edition. Sydney: UNSW Press.
- McArthur C, Hagerman AE, Robbins CT. 1991. Physiological strategies of mammalian herbivores against plant defenses. In: Palo RT, Robbins CT, editors. Plant defenses against mammalian herbivory. Boca Raton, Florida: CRC Press. p. 103–114.
- McArthur C, Sanson GD, Deal AM. 1995. Salivary proline-rich proteins in mammals—roles in oral homeostasis and counteracting dietary tannin. *J Chem Ecol* 21:663–91.
- McEachern MB, Eagles-Smith LA, Efferson CM, Van Vuren DH. 2006. Evidence for local specialization in a

- generalist mammalian herbivore, *Neotoma fuscipes*. *Oikos* 113:440–5.
- McIlwee AP. 2001. The distribution and abundance of arboreal folivores in response to variation in soil fertility, climate and the nutritional quality of eucalypt foliage. PhD Dissertation. Queensland: James Cook University.
- McLean S, Duncan AJ. 2006. Pharmacological perspectives on the detoxification of plant secondary metabolites: implications for ingestive behavior of herbivores. *J Chem Ecol* 32:1213–28.
- McLister JD, Sorensen JS, Dearing MD. 2004. Effects of consumption of juniper (*Juniperus monosperma*) on cost of thermoregulation in the wood rats *Neotoma albigula* and *Neotoma stephensi* at different acclimation temperatures. *Phys Biochem Zool* 77:305–12.
- McNab BK. 1978. The comparative energetics of neotropical marsupials. *J Comp Phys B* 125:115–28.
- Moore BD, Foley WJ. 2000. A review of feeding and diet selection in koalas (*Phascolarctos cinereus*). *Aust J Zool* 48:317–33.
- Moore BD, Foley WJ. 2005. Tree use by koalas in a chemically complex landscape. *Nature* 435:488–90.
- Moore BD, Wallis IR, Marsh KJ, Foley WJ. 2004a. The role of nutrition in the conservation of the marsupial folivores of eucalypt forests. In: Lunney D, editor. *The Conservation of Australia's Forest Fauna*. 2nd Edition. Mosman, NSW: Royal Zoological Society of New South Wales. p. 549–75.
- Moore BD, Wallis IR, Palá-Paúl J, Brophy JJ, Willis RH, Foley WJ. 2004b. Antitherbivore chemistry of *Eucalyptus*—cues and deterrents for marsupial herbivores. *J Chem Ecol* 30:1743–69.
- Mountfort DO, Campbell J, Clements KD. 2002. Hindgut fermentation in three species of marine herbivorous fish. *Appl Environ Microbiol* 68:1374–80.
- Murphy SM, Linhart YB. 1999. Comparative feeding morphology of the gastrointestinal tract in the feeding specialist, *Sciurus aberti* and several generalist congeners. *J Mamm* 80:1325–30.
- O'Grady SP, Morando M, Avila L, Dearing MD. 2005. Correlating diet and digestive tract specialization: examples from the lizard family Liolaemidae. *J Zool* 108:201–10.
- Pahl LI. 1987. Feeding behaviour and diet of the common ringtail possum, *Pseudocheirus peregrinus*, in *Eucalyptus* woodlands and *Leptospermum* thickets in Southern Victoria. *Aust J Zool* 35:487–506.
- Pahl LI, Hume I. 1991. Preferences for *Eucalyptus* species of the New England Tablelands and initial development of an artificial diet for koalas. In: Lee AK, Handasyde KA, Sanson GD, editors. *Biology of the koala*. Sydney: Surrey Beatty & Sons and the World Koala Research Corporation. p. 123–8.
- Pass DM, Foley WJ, Bowden B. 1998. Vertebrate herbivory on *Eucalyptus*—identification of specific feeding deterrents for common ringtail possums *Pseudocheirus peregrinus* by bioassay-guided fractionation of *Eucalyptus ovata*. *J Chem Ecol* 24:1513–27.
- Poore AGB, Hill NA, Sotka EE. 2008. Phylogenetic and geographic variation in host breadth and composition by herbivorous amphipods in the family ampithoidae. *Evolution* 62:21–38.
- Pradhan S, Saha GK, Akhan J. 2001. Ecology of the red panda *Ailurus fulgens* in the Singhalila National Park, Darjeeling, India. *Biol Cons* 98:11–18.
- Provenza FD, Balph DF. 1987. Diet learning by domestic ruminants – theory, evidence, and practical implications. *Appl Anim Behav Sci* 18:211–32.
- Raubenheimer D, Lee KP, Simpson SJ. 2005. Does Bertrand's rule apply to macronutrients? *Proc R Soc Lond B* 272:2429–34.
- Risenhoover KL. 1989. Composition and quality of moose winter diets in interior Alaska. *J Wildl Manage* 53:568–77.
- Roberts MS, Gittleman JL. 1984. *Ailurus fulgens*. *Mamm Spec* 222:1–8.
- Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liem's Paradox. *Am Nat* 151:223–35.
- Rochfort S. 2005. Metabolomics reviewed: a new “omics” platform technology for systems biology and implications for natural product research. *J Nat Prod* 68:1813–20.
- Shafique CM, Barkati S, Oshida T, Ando M. 2006. Comparison of diets between two sympatric flying squirrel species in northern Pakistan. *J Mammal* 87:784–9.
- Sherry TW. 1990. When are birds dietarily specialized? Distinguishing ecological from evolutionary approaches. *Stud Avian Biol* 13:337–52.
- Shimada T. 2006. Salivary proteins as a defense against dietary tannins. *J Chem Ecol* 32:1149–63.
- Shipley LA, Blomquist S, Danell K. 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry and morphology. *Can J Zool* 76:1722–33.
- Shipley LA, Davila TB, Thines NJ, Elias BA. 2006. Nutritional requirements and diet choices of the pygmy rabbit (*Brachylagus idahoensis*): a sagebrush specialist. *J Chem Ecol* 32:2455–74.
- Shrestha R, Wegge P. 2006. Determining the composition of herbivore diets in trans-Himalayan rangelands: a comparison of field methods. *Range Ecol Manage* 59:512–18.
- Simpson SJ, Raubenheimer D. 1999. Assuaging nutritional complexity: a geometrical approach. *Proc Nutr Soc* 58:770–89.
- Simpson SJ, Raubenheimer D. 2001. The geometric analysis of nutrient-allelochemical interactions: a case study using locusts. *Ecology* 82:422–39.
- Sipes IG, Gandolfi AJ. 1986. Biotransformation of toxicants. In: Klaassen CD, Amdur MO, Doull J, editors. *Casarett and Doull's toxicology: the basic science of poisons*. 3rd Edition. New York: McMillan. p. 64–98.
- Skopec MM, Haley S, Torregossa A-M, Dearing MD. 2008. An oak (*Quercus agrifolia*) specialist (*Neotoma macrotis*) and a sympatric generalist (*Neotoma lepida*) show similar

- intakes and digestibility of oak. *Phys Biochem Zool* 81:426–33.
- Smith M. 1979. Behaviour of the koala, *Phascolarctos cinereus* Goldfuss, in captivity I. Non-social behaviour. *Aus Wildl Res* 6:117–29.
- Smith AT. 2008. Conservation of endangered lagomorphs. In: Alves PC, Ferrand N, Hackländer K, editors. *Lagomorph biology: evolution, ecology and conservation*. Berlin: Springer-Verlag. p. 297–315.
- Snyder MA. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. *Ecology* 73:1730–40.
- Sorensen JS, Dearing MD. 2003. Elimination of plant toxins by herbivorous woodrats: revisiting an explanation for dietary specialization in mammalian herbivores. *Oecologia* 134:188–94.
- Sorensen JS, Dearing MD. 2006. Efflux transporters as a novel herbivore countermechanism to plant chemical defenses. *J Chem Ecol* 32:1181–96.
- Sorensen JS, McLister JD, Dearing MD. 2005a. Novel plant secondary metabolites impact dietary specialists more than generalists (*Neotoma* spp.). *Ecology* 86:140–54.
- Sorensen JS, McLister JD, Dearing MD. 2005b. Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecology* 86:125–39.
- Sorensen JS, Skopec MM, Dearing MD. 2006. Application of pharmacological approaches to plant-mammal interactions. *J Chem Ecol* 32:1229–46.
- Sorensen JS, Turnbull CA, Dearing MD. 2004. A specialist herbivore (*Neotoma stephensi*) absorbs fewer plant toxins than does a specialist (*Neotoma albigula*). *Phys Biochem Zool* 77:139–48.
- Sprent JA, McArthur C. 2002. Diet and diet selection of two species in the macropodid browser-grazer continuum: do they eat what they 'should'? *Aust J Zool* 50:183–92.
- Stones RC, Hayward CL. 1968. Natural history of the desert woodrat, *Neotoma lepida*. *Am Midl Nat* 80:458–76.
- Tan CL. 1999. Group composition, home range size and diet of three sympatric bamboo lemur species (Genus *Haplemur*) in Ranomafana National Park, Madagascar. *Int J Primatol* 20:547–66.
- Taylor RB, Steinberg PD. 2005. Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. *Ecology* 86:2955–67.
- Thines NJ, Shipley LA, Saylor RD. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). *Biol Cons* 119:525–34.
- Twigg LE, King DR. 1991. The impact of fluoroacetate-bearing vegetation on native-Australian fauna—a review. *Oikos* 61:412–30.
- Unsicker SB, Oswald A, Köhler G, Weisser WW. 2008. Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia* 156:313–24.
- Valentini A, et al. 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the tmL approach. *Mol Ecol Res* 9:51–60.
- Vaughan TA. 1982. Stephen's woodrat: a dietary specialist. *J Mamm* 63:53–62.
- Villalba JJ, Provenza FD, Han G-D. 2004. Experience influences diet mixing by herbivores: implications for biochemical diversity. *Oikos* 107:100–9.
- Westoby M. 1978. What are the biological bases of varied diets? *Am Nat* 112:627–31.
- Wilson DE, Hirst SM. 1977. Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildl Monogr* 54:3–11.
- Wilson DS, Yoshimura J. 1994. On the coexistence of specialists and generalists. *Am Nat* 144:692–707.
- Zahler P, Khan M. 2003. Evidence for dietary specialization on pine needles by the woolly flying squirrel (*Eupetaurus cinereus*). *J Mamm* 84:480–6.
- Zhang S, Pan J, Oxnard C, Wei F. 2007. Mandible of the giant panda (*Ailuropoda melanoleuca*) compared with other Chinese carnivores: functional adaptation. *Biol J Linnean Soc* 92:449–56.