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The Provision of Browse and Its Impacts on the Health and Welfare of Animals at the Zoo: A Review

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ABSTRACT

Browsers are animals that consume significant proportions of leaves, twigs, and bark from woody plants. These species have evolved morphological, physiological, and behavioral adaptations to subsist on a specialized diet. In zoos and other managed care facilities, the provision of browse in appropriate amounts helps promote positive animal welfare. Feeding on browse fulfills behavioral needs and reduces stereotypies, promotes satiety, and provides opportunities for dietary choice and control. However, there are several obstacles that can prevent institutions from providing browse, including physical and chemical hazards, palatability issues, and the difficulty in quantifying the nutritional value of browse. In addition, providing large enough quantities of browse can be challenging, and fresh browse may be especially difficult to provide for zoos in temperate climates. We describe the methods currently utilized to preserve browse and discuss their strengths and weaknesses. We recommend areas of future research for browse provision in zoos.

1 | Introduction

Browsers (also termed folivores in certain taxa such as primates) can be found across many taxonomic groups and feed primarily on dicotyledonous plants, including the leaves, twigs, and barks of woody plants; grazers subsist mainly on monocot grasses (Duncan and Poppi 2008). Many common species in zoos are browsers (Table 1). Unlike grazing species, browsers cannot be adequately maintained on diets extrapolated from domestic species consisting only of hay/grass and commercial concentrate feeds (Clauss and Dierenfeld 2008). Grasses (including bamboo) have different nutrient contents, higher silica contents, and impact digestive morphology differently than browse; browsers' consumption of grasses can lead to nutritional deficiencies, improper tooth wear, and digestive issues in zoos (Clauss and Dierenfeld 2008). Therefore, they should not be the primary forage source for browsers. In addition, the categorization of browsers as "concentrate selectors" historically led to an overestimation of the amount of easily digestible carbohydrates (concentrate feeds) necessary for browsers (Van Soest 1996). Zoo herbivores (especially ungulates) were historically fed diets adapted from domestic diets including grass and grass hay (Dierenfeld 1997). Browsing species have been found to have shorter life expectancies in managed care compared to grazers, suggesting that these diets did not fully meet the needs of browsers (Müller et al. 2011). In modern facilities, research has focused on alleviating health issues through the reformulation of diets; the addition of browse and other appropriate sources of roughage and the reduction of easily digestible carbohydrates are recommended as best practice guidelines for optimal browser health and welfare in managed care (Clauss and Dierenfeld 2008). Modern zoos recognize the provision of browse as essential to maintaining animal welfare for browsers and ensure that browse programs are created with the animal's best interests at heart, supported by research and expert knowledge to ensure that browse is safe and that plants are cultivated and selected to promote optimal health (Fidgett 2023). The goal of this review is to highlight in further detail the behavioral and welfare benefits of browse when added to typical zoo diets, discuss the

Summary

- Feeding on browse fulfills behavioral needs, reduces stereotypies, promotes satiety, and allows for dietary choice and control.
- Browse programs should mitigate any hazards before feeding.
- Preserved browse provides a food source year-round.

limitations and challenges of providing browse to animals in managed care, particularly for those in temperate climates, and review the literature exploring potential alternatives for fresh browse when it is not available. We recommend areas of future research to improve the health and welfare of browsing species in managed care.

2 | Behavioral and Welfare Benefits of Browse

2.1 | Fulfills Behavioral Needs and Reduces Stereotypies

Browsing species have evolved behavioral adaptations to effectively forage for and consume browse. In natural environments, browse grows in spatially complex habitats and is unevenly distributed throughout an area. Grass, on the other hand, is found in open habitats in a more uniform distribution (Jarman 1974; Shipley 1999). In addition, grasses tend to grow closer to the ground while browse grows throughout three-dimensional space. Browsers utilize specialized body parts to forage effectively (e.g., lip shape, muscular tongues), and these adaptations allow them to be generally more selective and consume higher quality plant parts in smaller bites (Venter, Vermeulen, and Brooke 2019). Consequently, diets in managed environments should reflect these properties of browse to provide opportunities to express natural feeding behaviors.

Foraging and feeding behaviors constitute behavioral needs, specific behavior patterns that animals are highly motivated to perform. When given the opportunity to fulfill their behavioral needs in managed care, animals experience positive affective states and improved welfare (Boissy et al. 2007). If prevented from completing those behavior patterns, the animal can experience compromised welfare (Dawkins 1983, 1990). Chronic inability to express behavioral needs may lead to the development of stereotypic behaviors; for example, ruminants tend to perform stereotypic behaviors derived from foraging behaviors (e.g., repetitive licking, gnawing, tongue movement; Bergeron et al. 2006). The addition of browse to managed diets is a promising method to reduce stereotypies and provide browsers with the opportunity to express species-specific, highly motivated foraging behaviors to improve animal welfare (Table 2).

2.2 | Promotes Satiety

The provision of higher proportions of browse as a source of roughage may also improve browser welfare by promoting satiety. Historical concentrate-heavy diets often led to insufficient gut fill in addition to digestive diseases such as rumen acidosis; while the animal consumed enough calories and nutrients for the day, they would still be motivated to feed due to feelings of hunger (Bergeron et al. 2006). Browse has been shown to increase food intake (Boyd, Collins, and Urness 1996; Clauss et al. 2013; Hatt et al. 2005). Modern diets aim to provide sufficient gut fill and promote satiety to support positive welfare. Increasing the amount of browse in zoo diets increases the dietary fiber concentration, which can lead to improved satiety in zoo browsers. While it is difficult to measure hunger, and there is some debate over the effectiveness of high roughage diets to promote satiety (D'Eath et al. 2009), evidence suggests that increasing the browse portion of the diet may promote satiety in browsers. For example, gorillas (*Gorilla gorilla gorilla*) tested on four diets (baseline diet, including browse; experimental diet with high fiber pellet, browse, tamarind, and fiber supplement; experimental diet without browse; baseline diet without browse) rested more and displayed fewer foraging behaviors when they had access to browse, which the authors interpreted as increased satiety (B. K. Smith, Remis, and Dierenfeld 2020). In addition, increased satiety through increased fiber intake was one rationale given for providing honey locust seed pods to two small browsing species in one study (Dunham et al. 2023). While more research is needed to investigate the relationship between dietary components and satiety in managed care, as a high-fiber item that takes longer for an animal to consume, browse has the potential to promote appropriate gut fill without providing excessive calories.

2.3 | Provides Opportunities for Dietary Choice and Control

Browse provides opportunities to exercise more choice in animal diets. They can choose to consume different parts of the branch offered, including the stems, leaves, and bark. In ruminants, providing opportunities to exercise dietary choice has also been suggested to improve physical health by allowing individuals to maintain optimal rumen conditions (Cooper, Kyriazakis, and Oldham 1996). Research from intensive livestock feeding systems using a single complete feed have shown that feeding a single type of ration may become aversive over time due to sensory-specific satiety and leads to a restriction of intake and compromised welfare (Villalba, Provenza, and Manteca 2010). By providing browse as a form of roughage that allows browsers to express natural foraging behaviors, individual animals can control what parts to feed on at different times according to their preferences and improve overall welfare.

3 | Obstacles to Developing a Browse Program

For many species in managed care, the amount of browse offered has remained relatively low since browse is typically considered enrichment rather than a staple diet item (Hatt et al. 2005; Wright et al. 2011). However, browse should serve as a dietary staple, making up a significant proportion of the diet. In fact, recommendations for many browser species indicate that they should receive as much browse as possible or even ad libitum (e.g., moose, *Alces alces*, Clauss, Kienzle, and

TABLE 1 | Examples of common species that consume browse in temperate zoos.

Classification	Genus/species	Common name
Mammalia		
Diprotodontia (Marsupial)		
Macropodidae	*Dendrolagus* spp.	Tree kangaroos
	Macropus fuliginosus	Western gray kangaroo
Phascolarctidae	*Phascolarctos cinereus*	Koala
Primates		
Atelidae	*Alouatta* spp.	Howler monkeys
Colobinae	*Colobus* spp.	Colobus monkeys
	Trachypithecus spp.	Langurs and leaf monkeys
Hominidae	*Gorilla gorilla*	Western lowland gorilla
	Pongo spp.	Orangutans
Hylobatidae	*Hylobates* spp.	Gibbons
Indriidae	*Propithecus* spp.	Sifaka lemurs
Proboscidea		
Elephantidae	*Elephas maximus*	Asian elephant
	Loxodonta africana	African elephant
Rodentia		
Castoridae	*Castor canadensis*	American beaver
Ungulata		
Bovidae	*Bubalus depressicornis*	Lowland anoa
	Cephalophus spp.	Duikers
	Capra spp.	Goats, both wild and domestic
	Madoqua spp.	Dik-diks
	Oreotragus oreotragus	Klipspringer
	Tragelaphus spp.	Browsing antelopes for example, nyala, bongo
Camelidae	*Camelus bactrianus*	Bactrian camel
Cervidae	*Alces alces*	Moose
	Capreolus capreolus	Roe deer
	Dama dama	Fallow deer
	Elaphurus davidianus	Pere David's deer
	Muntiacus reevesi	Reeves' muntjac
	Pudu spp.	Pudus
	Rangifer tarandus	Reindeer/caribou
Giraffidae	*Giraffa camelopardalis*	Giraffe
	Okapia johnstoni	Okapi
Hippopotamidae	*Choeropsis liberiensis*	Pygmy hippo
Rhinocerotidae	*Diceros bicornis*	Black rhino
Tapiridae	*Tapirus indicus*	Malayan tapir
	Tapirus terrestris	South American tapir
Xenarthra		
Folivora	*Bradypus* spp.	Three-toed sloth
	Choloepus spp.	Two-toed sloth
Reptilia		
Squamata		
Iguanidae	*Iguana* spp.	Green iguana
	Cyclura spp.	Rock iguana

TABLE 2 | Studies investigating the effects of browse provision on zoo animal behavior and welfare.

Feeding type	Species	Diet change	Effect on abnormal behaviors	Other behavioral effects	Citation
Browser	Giraffe (*Giraffa camelopardalis*)	Provision of fresh browse as enrichment overnight	Browse provision significantly reduced pacing behavior. Tongue play decreased, but not significantly.	Increased overall feeding behavior at night when browse was added.	Duggan, Burn, and Clauss (2016)
		Provision of fresh browse as enrichment overnight	Increased browsing time was correlated with decreased oral stereotypies.	NA	Ellersgaard et al. (2022)
		Evergreen browse consumption measured in relation to the seasons and stereotypies	No significant correlations were found between the weight of browse consumed and oral stereotypies.	N/A	Okabe et al. (2019)
		Provision of fresh browse	Stereotypic licking was negatively correlated with the amount of browse enrichment consumed.	N/A	Okabe et al. (2022)
		Provision of chopped fresh browse	Chopped browse provision did not significantly affect the occurrence of oral stereotypies.	N/A	Schaub et al. (2004)
Browser	Giraffe and Okapi (*Okapia johnstoni*)	Survey of husbandry factors in relation to stereotypic behaviors	Animals that received browse were significantly less likely to perform stereotypic licking.	N/A	Bashaw et al. (2001)
	Gorilla (*Gorilla gorilla*)	Increased frequency of forage (browse or alfalfa) provision	The presence of forage significantly reduced the frequency of R&R.	Presence of forage significantly increased time feeding and decreased noncontact aggression.	Fuller et al. (2018)
		Provision of fresh browse	Browse provision significantly decreased the frequency of R&R compared to diets without browse.	Browse provision doubled the amount of time spent feeding.	Gould and Bres (1986)
		4 diet trials: (1) Normal zoo diet with browse, (2) Diet with high fiber pellet, browse, tamarind, and	Diets with browse led to a significant reduction in R&R.	Gorillas rested significantly more on diets with higher fiber and foraged significantly more on diets lower in fiber.	B. K. Smith, Remis, and Dierenfeld 2020

(Continues)

TABLE 2 | (Continued)

Feeding type	Species	Diet change	Effect on abnormal behaviors	Other behavioral effects	Citation
		Metamucil (3) Diet 2 without browse, (4) Diet 1 without browse			
		Diet change eliminating biscuits and increasing fibrous vegetables, browse, and alfalfa hay	Diet change significantly reduced R&R and eliminated the behavior entirely for some individuals.	Overall activity decreased and time spent feeding increased significantly.	Less et al. (2014)
Browser	Gorilla (*Gorilla gorilla*)	Provision of fresh browse	Browse provision did not significantly reduce R&R.	Sedentary behaviors decreased significantly.	Rooney and Sleeman (1998)
	Orangutan (*Pongo* sp.)	Provision of fresh browse	N/A	Browse provision led to significant decrease in inactivity and increase of foraging behavior.	Birke (2002)
		Provision of fresh browse	Presence of browse decreased frequency of R&R by 50%, but was not statistically significant.	Feeding time significantly increased.	Cassella, Mills, and Lukas (2012)
		Diet change eliminating biscuits and increasing fibrous vegetables and browse	R&R occurred significantly less often after the diet change.	There was no significant change in inactivity after the diet change.	Hamilla (2018)
Intermediate feeder	African elephant (*Loxodonta africana*)	Changed diet from high energy pellet to high fiber pellet and increased browse 7× the original amount offered	Increased browse did not significantly reduce repetitive behaviors.	Browse provision provided opportunities for increased foraging in the afternoon and significantly increased foraging frequency.	Lasky et al. (2021)
Intermediate feeder	African elephant (*Loxodonta africana*)	Provision of fresh browse	Browse provision significantly reduced stereotypic behavior.	Browse provision significantly increased feeding frequency.	B. Smith 2022
		New diet where browse composed 11% of diet, compared with old diet with no browse	No significant differences in abnormal behaviors, though they were reduced.	Browse provision significantly decreased inactivity and increased feeding time.	Stoinski, Daniel, and Maple (2000)
Omnivore	Chimpanzee (*Pan troglodytes*)	Provision of fresh browse	Provision of browse significantly reduced R&R in this case study.	Time spent foraging and feeding increased.	Struck et al. (2007)

Wiesner 2003; Matschie's tree kangaroo, *Dendrolagus matschiei*, Dunham et al. 2022; black rhinoceros, *Diceros bicornis*, K. E. Sullivan et al. 2020). However, selecting safe and palatable browse species with appropriate nutritional profiles in adequate amounts can be challenging; these concerns must be addressed whenever developing a browse program for animals in managed care.

3.1 | Physical and Chemical Hazards

All plants have evolved methods to protect themselves from herbivory to various degrees, and these defense mechanisms can be either structural or chemical (Skarpe and Hester 2008). In the wild, animals cope with these hazards through several strategies, including avoidance, dilution, gastrointestinal degradation, or detoxification (Fowler 1981). Animals in managed care are not always able to use these strategies and are thus at higher risk of illness from toxic plants than their wild counterparts. This occurs for several reasons. First, animals in managed care only have access to the food provided by animal care staff. As a result, zoo browsers often do not have the opportunity to learn from experience or from conspecifics which novel, potentially toxic plants are safe to consume and in which quantities. When given the opportunity, however, it seems that zoo primates can self-regulate their consumption of potentially toxic plant species and may even utilize some for their medicinal qualities (Cousins 2006), although all parts of a browse species should be evaluated for safety before feeding. Second, many physiological adaptations to plant toxins rely on exposure to the specific toxin to function properly, whether due to an upregulation of enzymes in saliva or presence of beneficial microbiota in the gut to degrade or detoxify (Moore et al. 2005). Third, historically, it has been suggested that animals with less dietary variety and limited environmental enrichment would become bored and manipulate/consume plants that otherwise would not have been palatable to them (Fowler 1981).

Published reports of poisonings and deaths in browsers from toxic and dangerous plants are rare in peer-reviewed literature, although such cases may be underreported. Instead, most cases are reported between veterinary professionals or in gray literature sources. Of the published cases, very few resulted from browse purposefully fed out to browsing species, instead mostly occurring from accidental feedings on ornamental plants located inside or near an enclosure (Table 3). To avoid accidental poisonings, many institutions developed databases of safe and palatable browse species through experience and word of mouth (Irlbeck, Moore, and Dierenfeld 2006; Jelinger and Toddes 2021; Lehr et al. 1997; Plowman and Turner 2001). For example, ZSL, in partnership with BIAZA, EAZA, and ZooLex, has developed an expert-edited database so zoo professionals can reference information about toxicity and add their own records of past feeding successes (Beer et al. 2015). In addition, many institutions utilize local resources and region-specific guidebooks to identify plant species toxic to domestic animal species in their area (J. Watts, personal communication, January 16, 2024). While technology is still improving in terms of accuracy, mobile apps such as Leafsnap are useful tools to assist identification efforts (Kumar et al. 2012). These resources are valuable for ensuring animal care staff are properly trained to ensure that dangerous species are not misidentified and fed to browsers.

To reduce the risk of feeding dangerous browse species, animal care staff should take multiple precautions. First, all relevant staff (e.g., groundskeepers, zookeepers, veterinarians, and nutritionists) should be trained in the identification of safe and dangerous browse species. Browse and other forage should be inspected before feeding to confirm positive identification and to ensure that it is not contaminated by toxic species (Fowler 1981). In addition, staff should conduct regular surveys of animal habitats and the adjacent areas to prevent accidental poisoning. This is especially important when moving animals to a novel habitat or during seasonal changes, but should be done regularly regardless of how long the animal has lived there. For example, one instance of poisoning in Grevy's zebra *(Equus grevyi*) occurred even though the maple trees had been in the habitat without issues for over 15 years before the incident, which the authors attributed to the unseasonably warm winter and a change in husbandry procedures which prompted the zebra to forage on the wilted leaves when they otherwise would not be motivated to do so (Weber and Miller 1997). Finally, browsers should be fed a variety of browse species whenever possible, as a mixed diet allows the animal to better cope with smaller concentrations of multiple toxins instead of ingesting too much of one toxin (Moore et al. 2005). A varied diet not only allows for the animal to choose which foods to eat, it allows them to regulate their intake of plant secondary metabolites (PSMs) and prevent them from building to toxic levels in the body.

3.2 | Palatability of Browse

While there is no single agreed upon definition, one review defines palatability as “a complex phenomenon that integrates odor, taste, and texture with the post-ingestive effects of nutrients and toxins in food” (Provenza et al. 2007, 394). Herbivores tend to select for foods with the highest digestibility (e.g., lowest fiber) and lowest PSM concentrations to maximize their nutrient intake (McArthur et al. 1993; Ndlovu and Mundy 2009). In managed care, however, diets are nutritionally complete and thus animals may focus more strongly on additional characteristics when determining whether a plant is palatable. It is not known for certain which characteristics of browse help an animal make dietary choices, and an animal's perception of the palatability of a food source can be influenced by genetics, the animal's current internal state, environmental conditions, and social interactions (Favreau-Peigné, Baumont, and Ginane 2013). Browsers in managed care are usually only exposed to a few species in their lifetime and thus do not have the opportunity to learn from experience which additional browse species are palatable (Moore et al. 2005). Therefore, browsers in managed care should be exposed to a variety of different browse species from a young age to provide choice and facilitate acceptance of a variety of browse species later in their lives, for a review of how palatability and other factors influence diet selection in zoo animal diets, see Moore et al. (2005).

It is difficult to predict which browse species will be palatable, especially since they are rarely the same species encountered in an animal's wild range and may vary in their physical and

TABLE 3 | Published cases of injuries and death from the consumption of hazardous browse by browsers in managed care.

Animal species	Plant species	Toxin/physical hazard	Clinical signs and/or diagnosis	Circumstances of feeding	References
Two-toed sloth (*Choloepus hoffmanni*)	Oleander (*Nerium oleander*)	Glycosides	Glycoside poisoning (gastroenteritis and cardiac symptoms), death	Leaves eaten from shrub outside of enclosure	Fowler (1981)
Two langur species (*Semnopithecus entellus* and *Pygathrix nemaeus*)	Acacia *saligna* and *A. longifolia*	GIT obstruction and peritonitis	Anorexia and discomfort, peritonitis with phytobezoar, death	Fed as browse	Ensley et al. (1982)
Colobus (*Colobus guereza*)	*Viburnum* x *rhytidophylloides* "Alleghany" shrub	Small "spicule like structures" on plant, GIT obstruction	Pain, lethargy, ulcers, death	Animal group consumed an ornamental bush in a novel habitat in its entirety	Irlbeck et al. (2001)
François langur (*Trachypithecus francoisi*)	Hybrid yew shrub (*Taxus baccata* x *T. cuspidata*)	Alkaloids	Sudden death	Leaves pulled from shrub within reach just outside of novel enclosure and eaten	Lacasse et al. (2007)
Pere david's deer (*Elaphurus davidianus*)	Sycamore (*Acer pseudoplatanus*)	Hypoglycin A	Atypical myopathy, death	Samaras (seeds) and seedlings of the plant eaten from tree in habitat	Bunert et al. (2018)
Bactrian camel (*Camelus bactrianus*)	Sycamore (*Acer pseudoplatanus*)	Hypoglycin A	Atypical myopathy, death	Samaras (seeds) and seedlings of the plant eaten from tree in habitat	Hirz et al. (2021)

chemical profiles. Anecdotal evidence of which species and/or individual animals consume different browse are useful and can be a helpful starting point; for example, the ZooPlants.net online database allows zoo professionals to record which animals consumed each browse species in the designated webpage (Beer et al. 2015). However, formal preference tests should provide valuable resources for assessing browse preferences, and can help contribute to the general body of knowledge for the factors that may impact palatability. Preference tests conducted on several species including colobus monkey (*Colobus* spp.; Kirschner et al. 1999; Lisi, Edwards, and Hoang 2001; Tovar, Moore, and Dierenfeld 2005), mule and black-tailed deer (*Odocoileus hemionus;* McArthur et al. 1993), black rhinoceros (Ndlovu and Mundy 2009), koala (*Phascolarctos cinereus*; Galindo et al. 2011), and bonobo (*Pan paniscus*; Depauw et al. 2019) have shown that animals in managed care have preferences for different browse species when given the choice. Preference tests also have potential for evaluating the relative palatability of preserved browse (Przybyło et al. 2020). Ideally, future research should evaluate the relative palatability of the browse species on hand for each animal in a zoo's collection to determine which browse species are generally most palatable for different taxa. This knowledge can assist animal care staff to provide varied, nutritionally complete, and highly palatable diets attuned to individual animals' preferences.

3.3 | Difficult to Quantify Nutritional Value

Unlike other diet components, measuring the nutritional composition of browse is not straightforward. Different species vary in their energy, nutrient, and PSM composition. Additionally, browse of the same species can differ depending on the season it was harvested and the location it was grown (Lehr et al. 1997). Within an individual branch, each part of the plant has differing nutrient compositions (Nijboer and Dierenfeld 1996). While nutritional values can vary, several studies have analyzed the nutritional composition of different browse species fed to their zoo animals, and these values can serve as useful guidelines for zoo nutritionists. Table 4 highlights some relevant species utilized by zoos in Europe and North America for reference.

While these guidelines are useful when planning a complete diet, it is difficult to measure how much plant matter is actually consumed by the animal and which parts of the plant will be consumed preferentially by each individual. For example, some species prefer to eat primarily leaves (e.g., howler monkeys, *Alouatta* spp., Pastor-Nieto 2015), while others readily consume bark (e.g., Caucasian tur *Capra cylindricornis*; Martin 2019). Therefore, the total edible components of browse offered must be estimated depending on which components the target animal consumes. While a researcher can pluck the constituent parts from the plant and weigh them before feeding, offering browse parts separately prevents natural foraging behaviors. As a result, practical feeding recommendations for browse are often given in number of branches offered or by total weight (Clauss and Dierenfeld 2008). A few studies have explored developing allometric equations for calculating the amount of edible material on a branch of browse, with a significant correlation found between the total weight of a branch and the weight of its leaves with the diameter of the branch at the point

TABLE 4 | Nutritional values of representative temperate browse species commonly fed in zoos.

					%DM										
Family/species	**Month**	**Loc-ation**[a]	**Plant part**[b]	**DM**	**CP**	**NDF**	**ADF**	**ADL**	**CF**	**Ash**	**Lignin**	**Total soluble sugars**	**Total tannins**	**Silica**	**References**
Aceraceae *Acer negundo* Boxelder	July	NA	L & T	33.1	12.4	46.8	35.5			6.7	12.1				Nijboer and Dierenfeld (1996)
Acer negundo Boxelder	September	NA	L & T	42.6	9.5	67.4	55.3			8.9	17.5				Nijboer and Dierenfeld (1996)
Acer saccharinum Silver maple	July	NA	L & T	49.9	10.7	38.7	28.5			5.9	8.8				Nijboer and Dierenfeld (1996)
Acer saccharinum Silver maple	September	NA	L & T	26.1	11.1	66.4	52.1			6.9	16.5				Nijboer and Dierenfeld (1996)
Acer saccharum Sugar maple	July	NA	L & T	48.7	8.5	45.9	36.8			7.6	14.9				Nijboer and Dierenfeld (1996)
Acer saccharum Sugar maple	September	NA	L & T	56.2	9.4	57.8	43.3			3.6	11.9				Nijboer and Dierenfeld (1996)
Betulaceae *Betula pendula* European white birch	June	EUR	L & T	40.5	10.1	36.3	29.5	10.8	6.3	3.6		8.0	1.8	0.8	Beer et al. (2015)
Betula pendula European white birch	August	EUR	L & T	43.3	11.7	38.1	26.2	10.2	8.4	5.4		2.3	1.6	0.6	Beer et al. (2015)
Betula pendula European white birch	October	EUR	L & T	47.4	5.4	36.1	26.7	11.0	10.6	4.6		1.8	1.3	1.5	Beer et al. (2015)
Betula spp. Birch	October	NA	L	39.1	15.6	36.9	21.3		7.7	7.6	9.5				Dierenfeld, Bezjian, and Dabek (2020)
Corylus avellana Common Hazel	June	EUR	L & T	34.5	15.0	26.1	27.0	8.9	2.9	7.9		13.7	1.9	0.4	Beer et al. (2015)
Corylus avellana Common Hazel	August	EUR	L & T	29.6	13.7	28.6	29.1	10.6	3.9	10.0		12.3	1.5	0.3	Beer et al. (2015)

(Continues)

TABLE 4 | (Continued)

Family/species	Month	Location[a]	Plant part[b]	DM	%DM CP	NDF	ADF	ADL	CF	Ash	Lignin	Total soluble sugars	Total tannins	Silica	References
Corylus avellana Common Hazel	October	EUR	L & T	35.7	13.9	24.1	25.8	11.1	4.7	9.8		13.8	1.2	0.1	Beer et al. (2015)
Elaeagnaceae Elaeagnus angustifolia Russian olive	June	EUR	L & T	29.7	18.7	43.6	29.7	5.4	3.4	6.9		9.4	1.9	0.6	Beer et al. (2015)
Elaeagnus angustifolia Russian olive	July	NA	L	29.3	28.3	62.1	48.3			7.9	27.3				Tovar, Moore, and Dierenfeld (2005)[c]
Elaeagnus angustifolia Russian olive	August	EUR	L & T	34.0	19.5	43.8	29.9	6.2	4.2	6.9		7.8	1.9	0.2	Beer et al. 2015
Elaeagnus angustifolia Russian olive	October	EUR	L & T	40.2	22.7	41.0	26.6	5.9	5.9	7.9		7.6	1.5	0.3	Beer et al. 2015
Elaeagnus pungens Thorny olive	March to May	NA	L & T	55.9	11.7	70.9	58.2		1.7	3.3	21.6				Wood et al. (2020)
Elaeganus pungens Thorny olive	September to November	NA	L & T	45.0	14.6	66.6	50.4		3.0	3.9	19.2				Wood et al. (2020)
Elaeganus pungens Thorny olive	Unknown	NA	L		18.5	60.3	45.8		2.1	5.9	18.0				Dierenfeld, Bezjian, and Dabek (2020)
	Unknown	NA	B		14.1	63.6	52.1		1.0	4.7	24.1				
Fabaceae *Acacia longifolia* Golden/coast wattle	September	NA	L	81.3	12.1	35.1	26.9		3.0	10.7	15.1				Dierenfeld, Bezjian, and Dabek (2020)
	September	NA	T	80.3	5.2	70.6	52.4		1.7	4.2	12.8				
Fagaceae *Fagus grandifolia* Beech	Unknown	NA	L	50.0	17.0	46.4	24.8		2.9	5.1	8.9				Dierenfeld, Bezjian, and Dabek (2020)
	Unknown	NA	T	62.5	5.9	68.0	49.3		2.1	2.9	19.2				
Fagus sp. Beech	July	NA	L & T	41.9	8.2	75.1	61.0			4.3	19.6				Nijboer and Dierenfeld (1996)
Fagus sp. Beech	September	NA	L & T	62.2	8.6	78.9	57.0			3.6	20.2				Nijboer and Dierenfeld (1996)

(Continues)

TABLE 4 | (Continued)

					%DM										
Family/species	**Month**	**Location[a]**	**Plant part[b]**	**DM**	**CP**	**NDF**	**ADF**	**ADL**	**CF**	**Ash**	**Lignin**	**Total soluble sugars**	**Total tannins**	**Silica**	**References**
Fagus sylvatica European beech	June	EUR	L & T	43.2	13.0	38.5	31.6	10.1	4.1	4.5		11.2	1.5	0.5	Beer et al. (2015)
Fagus sylvatica European beech	August	EUR	L & T	51.8	12.5	42.4	32.8	8.4	4.3	5.2		6.3	1.7	1.4	Beer et al. (2015)
Fagus sylvatica European beech	October	EUR	L & T	53.2	7.3	37.4	33.7	12.6	5.4	5.9		11.9	1.6	0.9	Beer et al. (2015)
Quercus cerris Turkey oak	June	EUR	L & T	42.5	11.9	33.4	32.9	11.2	5.9	8.0		15.0	1.6	0.4	Beer et al. (2015)
Quercus cerris Turkey oak	August	EUR	L & T	43.5	10.8	32.4	34.3	13.0	5.6	6.6		15.8	1.2	0.2	Beer et al. (2015)
Quercus cerris Turkey oak	October	EUR	L & T	46.8	12.0	33.8	34.3	12.9	5.8	6.7		16.5	1.4	0.1	Beer et al. (2015)
Quercus robur Pedunculate oak	June	EUR	L & T	43.8	12.2	29.9	27.5	10.8	4.2	4.0		19.8	1.7	0.8	Beer et al. (2015)
Quercus robur Pedunculate oak	August	EUR	L & T	40.5	13.3	32.0	28.3	10.5	5.4	5.2		15.9	1.5	0.5	Beer et al. (2015)
Quercus robur Pedunculate oak	October	EUR	L & T	44.8	8.0	33.6	29.9	12.0	6.2	5.6		14.7	1.4	1.2	Beer et al. (2015)
Hamamelidaceae *Liquidambar* sp. Sweet-gum	July	NA	L & T	40.0	7.9	51.1	42.7			3.8	19.9				Nijboer and Dierenfeld (1996)
Liquidambar sp. Sweet-gum	September	NA	L & T	43.4	4.8	61.1	51.5			7.2	19.9				Nijboer and Dierenfeld (1996)
Liquidambar styraciflua Sweet-gum	March to May	NA	L & T	45.5	5.1	55.9	45.9		1.8	5.2	14.9				Wood et al. (2020)
Liquidambar styraciflua Sweet-gum	June to August	NA	L & T	35.1	6.6	49.1	39.7		2.3	4.8	11.2				Wood et al. (2020)
Liquidambar styraciflua Sweet-gum	September to November	NA	L & T	44.1	6.4	51.1	36.8		1.9	5.8	10.5				Wood et al. (2020)

(Continues)

TABLE 4 | (Continued)

Family/species	Month	Loc-ation[a]	Plant part[b]	DM	%DM									Silica	References
					CP	NDF	ADF	ADL	CF	Ash	Lignin	Total soluble sugars	Total tannins		
Magnoliaceae *Liriodendron tulipifera* Tulip poplar	March to May	NA	L & T	42.5	5.3	58.2	43.0		5.8	5.1	10.0				Wood et al. (2020)
Liriodendron tulipifera Tulip poplar	June to August	NA	L & T	37.1	6.1	52.2	39.8		5.4	4.7	13.6				Wood et al. (2020)
Liriodendron tulipifera Tulip poplar	September to November	NA	L & T	42.5	7.5	61.4	40.6		4.4	5.2	10.8				Wood et al. (2020)
Moraceae *Ficus benjamin* Ficus	Unknown	NA	L	59.5	8.0	43.3	42.2			17.3					Dierenfeld, Wildman, and Romo (2000)
	Unknown	NA	T	50.8	3.5	66.2	55.0			8.7					
Ficus benjamina Ficus	Unknown	NA	L	45.4	9.6	42.3	36.8			9.1					Dierenfeld, Wildman, and Romo (2000)
	Unknown	NA	T	43.3	5.8	63.2	54.4			6.8					
Ficus microcarpa nitida Jewel leaf ficus	Unknown	NA	L	40.1	9.4	44.3	38.4			15.4					Dierenfeld, Wildman, and Romo (2000)
	Unknown	NA	T	42.1	5.6	66.1	57.3			8.7					
Ficus microcarpa nitida Jewel leaf ficus	Unknown	NA	L	33.8	10.8	42.0	35.5			13.0					Dierenfeld, Wildman, and Romo (2000)
	Unknown	NA	T	36.7	5.0	60.1	56.7			8.5					
Grewia occidentalis Crossberry	September	NA	L	72.0	19.3	45.3	19.1		5.0	11.5	4.9				Dierenfeld, Bezjian, and Dabek (2020)
	September	NA	T	63.0	9.5	76.3	47.4		0.9	7.3	9.0				
Morus alba Mulberry	July	NA	L	29.1	23.0	35.9	24.6			15.9	12.4				Tovar, Moore, and Dierenfeld (2005)[c]
Morus nigra Black mulberry	June	EUR	L & T	19.1	21.9	28.3	21.0	2.9	3.0	8.9		15.6	1.8	0.7	Beer et al. (2015)
Morus nigra Black mulberry	August	EUR	L & T	26.6	15.3	29.4	23.1	5.5	3.1	10.7		14.3	1.7	1.3	Beer et al. (2015)
Morus nigra Black mulberry	October	EUR	L & T	25.3	15.3	29.1	23.0	5.3	3.5	12.8		15.1	1.5	1.1	Beer et al. (2015)

(Continues)

TABLE 4 | (Continued)

Family/species	Month	Location[a]	Plant part[b]	DM	%DM CP	NDF	ADF	ADL	CF	Ash	Lignin	Total soluble sugars	Total tannins	Silica	References
Morus nigra Black mulberry	July	NA	L & T	40.0	11.3	44.0	34.3			10.4	12.3				Nijboer and Dierenfeld (1996)
Morus nigra Black mulberry	September	NA	L & T	49.6	10.9	57.2	43.9			11.9	11.8				Nijboer and Dierenfeld (1996)
Morus spp. Mulberry	October	NA	L	33.6	22.3	23.1	14.2		4.1	19.8	3.3				Dierenfeld, Bezjian, and Dabek (2020)
	October	NA	T	52.7	7.6	65.7	50.5		2.2	7.3	14.7				
	October	NA	B	51.0	7.7	50.3	41.5		4.4	9.5	10.3				
Myricaceae *Morella cerifera* Wax myrtle	March to May	NA	L & T	54.2	8.5	56.8	42.6		2.9	3.1	14.9				Wood et al. (2020)
Oleaceae *Fraxinus excelsior* European ash	June	EUR	L & T	30.1	15.7	33.9	29.4	6.3	3.1	5.0		11.6	1.6	0.9	Beer et al. (2015)
Fraxinus excelsior European ash	August	EUR	L & T	39.5	17.0	27.6	23.8	4.7	3.7	8.9		12.1	1.6	0.5	Beer et al. (2015)
Fraxinus excelsior European ash	October	EUR	L & T	35.8	12.5	32.1	26.8	5.9	4.5	10.7		11.3	1.5	1.4	Beer et al. (2015)
Rosaceae *Cotoneaster frigidus* Tree cotoneaster	June	EUR	L & T	39.5	6.6	22.8	28.2	10.9	4.3	4.4		17.2	1.6	0.2	Beer et al. (2015)
Cotoneaster frigidus Tree cotoneaster	August	EUR	L & T	43.8	4.8	22.2	27.8	11.5	5.0	4.3		17.2	1.6	0.5	Beer et al. (2015)
Cotoneaster frigidus Tree cotoneaster	October	EUR	L & T	44.7	6.9	26.4	29.2	11.3	5.4	8.0		13.6	2.1	0.8	Beer et al. (2015)
Cotoneaster sp. Cotoneaster	Unknown	NA	L		13.9	39.7	28.1		3.8	7.0	8.7				Dierenfeld, Bezjian, and Dabek (2020)
	Unknown	NA	T		6.0	63.4	48.2		1.8	3.5	8.1				
	Unknown	NA	B		5.3	52.8	42.1		2.1	4.3	12.7				
Malus spp. Apple	May to October	NA	L	39.0	10.0	34.0	23.0		2.0	7.0					Gourlie (2016)
	May to October	NA	B	47.0	4.0	40.0	31.0		2.0	6.0					

(Continues)

TABLE 4 | (Continued)

Family/species	Month	Location[a]	Plant part[b]	DM	%DM CP	NDF	ADF	ADL	CF	Ash	Lignin	Total soluble sugars	Total tannins	Silica	References
	May to October	NA	T	50.0	4.0	62.0	45.0		1.0	4.0					
Malus spp. Apple	June to September	NA	L, T, & B	44.5	7.4	46.7	36.8		1.3	4.7	12.6				Lachance (2012)
Salicaceae *Populus alba* White poplar	June	EUR	L & T	35.5	11.5	41.3	34.2	8.8	4.1	9.8		8.8	1.5	1.0	Beer et al. (2015)
Populus alba White poplar	July	NA	L & T	33.4	12.9	48.9	38.9			11.0	16.5				Nijboer and Dierenfeld (1996)
Populus alba White poplar	August	EUR	L & T	40.5	7.5	34.1	31.2	10.2	4.8	7.6		10.7	1.4	1.1	Beer et al. (2015)
Populus alba White poplar	September	NA	L & T	50.1	9.7	61.6	44.8			9.8	19.7				Nijboer and Dierenfeld (1996)
Populus alba White poplar	October	EUR	L & T	44.8	3.7	36.7	33.2	11.3	5.6	8.0		11.3	1.4	1.7	Beer et al. (2015)
Populus tremula European aspen	June	EUR	L & T	34.5	14.9	40.5	27.9	6.8	5.6	8.0		8.2	1.5	1.2	Beer et al. (2015)
Populus tremula European aspen	August	EUR	L & T	42.0	11.2	38.3	30.0	11.0	5.9	7.9		11.8	1.7	0.7	Beer et al. (2015)
Populus tremula European aspen	October	EUR	L & T	43.2	8.5	42.0	29.8	8.9	6.7	7.0		5.9	1.2	1.9	Beer et al. (2015)
Salix babylonica Weeping willow	July	NA	L	28.8	22.1	44.6	33.3			10.6	19.0				Tovar, Moore, and Dierenfeld (2005)
Salix babylonica Weeping willow	July	NA	L & T	41.4	12.5	44.1	37.6			9.6	16.7				Nijboer and Dierenfeld (1996)
Salix babylonica Weeping willow	September	NA	L & T	38.3	11.6	55.9	47.0			6.3	14.9				Nijboer and Dierenfeld (1996)

(Continues)

TABLE 4 | (Continued)

Family/species	Month	Location[a]	Plant part[b]	DM	%DM CP	NDF	ADF	ADL	CF	Ash	Lignin	Total soluble sugars	Total tannins	Silica	References
Salix caprea Goat willow	June	EUR	L & T	35.4	8.5	36.7	31.1	11.1	6.7	4.8		11.0	1.6	1.0	Beer et al. (2015)
Salix caprea Goat willow	August	EUR	L & T	30.5	6.7	42.4	33.1	8.4	6.6	7.3		1.4	1.7		Beer et al. (2015)
Salix caprea Goat willow	October	EUR	L & T	43.6	4.0	32.9	30.1	11.3	7.2	6.9		12.3	1.5	1.7	Beer et al. (2015)
Salix nigra Black willow	July	NA	L & T	40.9	13.9	47.3	35.9			7.7	16.0				Nijboer and Dierenfeld (1996)
Salix nigra Black willow	September	NA	L & T	54.2	10.5	71.8	47.5			8.7	17.7				Nijboer and Dierenfeld (1996)
Salix spp. Willow	June to July	NA	L	39.5	14.5	35.4	25.1								Martin (2019)
	June to July	NA	B	50.0	5.2	42.3	34.7								
	June to July	NA	T	56.8	4.6	67.6	54.3								
Salix spp. Willow	August to September	NA	L	43.7	14.5	35.3	25.0								Martin (2019)
	August to September	NA	B	55.1	5.5	43.0	35.1								
	August to September	NA	T	54.2	3.9	69.1	55.3								
Salix spp. Willow	Unknown	NA	L, T, & B	47.1	8.5		52.2				20.2				Valdes and Schlegel (2012)
Scrophulariaceae *Buddleja davidii* Butterfly bush	June	EUR	L & T	34.3	13.6	32.7	27.0	5.8	3.3	5.9		0.6	1.6	Trace	Beer et al. (2015)
Buddleja davidii Butterfly bush	August	EUR	L & T		10.6	38.1	26.7	11.1	3.7	5.2		1.5	1.8		Beer et al. (2015)
Buddleja davidii Butterfly bush	October	EUR	L & T	35.2	11.2	34.4	27.4	6.5	4.0	4.2		5.8	1.0	1.0	Beer et al. (2015)

(Continues)

TABLE 4 | (Continued)

					%DM										
Family/species	**Month**	**Location[a]**	**Plant part[b]**	**DM**	**CP**	**NDF**	**ADF**	**ADL**	**CF**	**Ash**	**Lignin**	**Total soluble sugars**	**Total tannins**	**Silica**	**References**
Buddleja spp. Butterfly bush	Unknown	NA	L		15.7	23.7	16.1		4.0	8.3	5.8				Dierenfeld, Bezjian, and Dabek (2020)
	Unknown	NA	B		6.9	57.6	46.6		2.5	4.9	22.3				
Ulmaceae Celtis occidentalis Hackberry	July	NA	L & T	47.6	11.0	53.8	35.4			8.0	11.8				Nijboer and Dierenfeld (1996)
Celtis occidentalis Hackberry	September	NA	L & T	62.9	6.6	71.8	47.5			8.7	17.7				Nijboer and Dierenfeld (1996)
Celtis occidentalis Hackberry	November	NA	L		12.7	31.9	16.1		6.9	23.9	3.6				Dierenfeld, Bezjian, and Dabek (2020)
Ulmus parvifolia Chinese elm	October	NA	L	47.1	18.7	42.1	19.7		4.6	20.9	5.6				Dierenfeld, Bezjian, and Dabek (2020)
	October	NA	T	54.4	10.1	55.0	40.4		2.2	8.6	14.1				
	October	NA	B	51.4	9.1	65.4	38.7		2.3	9.2	13.4				
Vitaceae vitis sp. Grapevine	July	NA	L & T	19.6	9.9	45.1	35.0			8.4	11.1				Nijboer and Dierenfeld (1996)
Vitis sp. Grapevine	September	NA	L & T	25.3	15.1	52.9	39.1			12.7	19.1				Nijboer and Dierenfeld (1996)

Note: Column abbreviations are as follows: ADF = acid detergent fiber, CF = crude fat, CP = crude protein, DM = dry matter, NDF = neutral detergent fiber.
[a]Location in which plant was grown (NA = North America, EUR = Europe).
[b]Part of plant analyzed (L = leaves, T = twigs, B = bark).
[c]These values are averages calculated from two consecutive years of data.

of cutting (Clauss, Kienzle, and Wiesner 2003; Gourlie 2016; Martin 2019). These equations may be helpful to determine how much browse to harvest to maximize the amount of edible material offered and thus make more specific dietary recommendations.

3.4 | Difficult to Provide Enough Browse

Even with some nutrient values available in the literature and allometric equations to aid in estimating diet formulations, one question that remains unanswered is how much browse is considered sufficient, and whether that amount differs by individual animal needs. While more browse is generally better, and many best practice guides advocate for browse to be provided "on a regular basis" (Clauss and Hatt 2006, 205), ideal amounts of browse may be too large for animal care staff to harvest on a day-to-day basis. For example, Clauss, Kienzle, and Wiesner (2003) found if the recommendations for moose were followed at 25 kg of fresh browse daily, each individual would need 26 branches cut at a diameter of 30 mm to obtain a sufficient amount of edible material, meaning the total weight of the browse offered would instead be between 60 and 67 kg. When harvesting browse from a biomass plantation over the course of a year, one study estimated that one hectare's harvest can provide browse for five moose or three giraffes (Höllerl et al. 2006). As a result, zoos must have access to large amounts of browse to adequately feed all their browsing animals.

Although it can be difficult, it is possible to develop a browse program large enough to sustain browsing species in managed care. For example, Disney's Animal Kingdom makes it a goal to provide browsers with enough browse to comprise 30% of their diet, and uses browse collected from their 100-acre farm to fulfill that goal (Livingston et al. 2013). For some institutions, however, harvesting such large quantities is currently not feasible. In many cases, browse can be collected on site, but the institution simply does not have enough plants to utilize without over-harvesting. San Diego Zoo has invested in browse production since the 1970s but based on one survey was still only capable of providing around 42% of the browse required for all of their animals based on current diet formulations, and that over 50,000 feet of browse in total was needed per week (D'Amato-Anderson et al. 2019).

To combat the need for more browse, several zoos have developed creative methods to acquire more browse. Many institutions request donations of pesticide-free trimmings from the public on their website, such as the Santa Barbara Zoo (Santa Barbara Zoo n.d.). In one study, some surveyed zoos collaborated with municipal parks and recreation departments (B. K. Smith, Remis, and Dierenfeld 2014). The Toronto Zoo formed a contract with the owners of a disused apple orchard to provide browse and silage (Gourlie 2016; Lachance 2012; Martin 2019). Others work with corporate partners. For example, the browse program at Brookfield Zoo Chicago coordinates with a local electrical utility company, receiving almost 40 cubic meters of donated trimmings per week removed from power lines (J. Watts, personal communication, June 1, 2023). Another potential solution is to establish a plantation of suitable browse species on land outside of the zoo grounds. The Toronto Zoo, for example, purchased land for plantations and began planting various species to ensure a continuous, permanent source of browse (Martin 2019; Wensvoort et al. 2017).

Regardless of where the browse is grown, the main limiting factor for collecting enough browse is the cost, either through the cost of labor or the cost of obtaining browse from other sources. To have a successful browse program, zoos need to invest in staff specifically dedicated to browse provision. Reflecting this need, the Association of Zoos and Aquariums' accreditation standards require at least one qualified staff member to supervise the acquisition of browse (AZA 2024). Ideally, there should be staff members dedicated to coordinating logistics and maintaining safety protocols, as well as staff for planting, harvesting, and delivering browse to animal care staff. Because browse is essential to positive animal health and welfare, zoos must both find creative solutions to expand their access and invest in the monetary and labor costs needed to maintain an effective browse program.

4 | Alternatives to Fresh Browse

While institutions can increase their supply using the methods above, fresh browse is not always available; in temperate areas where deciduous species lose their leaves in the winter or in tropical dry seasons, fresh browse is hard to come by (Mbatha and Bakare 2018). Therefore, alternatives to fresh browse must be used to ensure that browsers have access to appropriate nutrition year-round and to provide similar health and welfare benefits as fresh browse (Hatt and Clauss 2006; Nijboer, Clauss, and Nobel 2006). Several alternatives have been utilized in managed care, each with its own strengths and weaknesses. Like fresh browse, preserved browse can be costly, either due to the labor needed to preserve it or the expenses in procuring it from commercial sources.

4.1 | Dried Browse

One of the simplest forms of preserving browse is by drying, which involves placing cut branches in a warm, dry room or a low-temperature oven until moisture has evaporated. The dried leaves are then fed out. One study placed bundles of 3–10 branches in a 55°C oven for 2 days, which were then stored in a dark, dry place until leaves were picked for feeding (Przybyło et al. 2020). This method of drying browse is effective but takes up a lot of storage space. If a zoo does not have the space to dry its own browse, it can be bought from commercial sources (Nijboer, Clauss, and Nobel 2006). Generally, dried browse is less palatable than fresh browse (Nijboer, Clauss, and Nobel 2006). However, in one preference test nyala (*Tragelaphus angasii)* overall preferred dried over ensiled leaves, but preferences varied between different browse species (Przybyło et al. 2020). Overall, drying browse is an effective method of preservation.

4.2 | Frozen Browse

Freezing is another common method of preservation; browse is packed into plastic bags and vacuum-sealed flat into 3 × 4 ft sized bags to prevent oxidation and frozen to −20°C (Watts 2017). Larger containers should not be packed airtight to prevent spoilage from occurring in the center. Alternatively, Rotterdam Zoo has successfully stored browse by simply freezing large bundles of willow branches up to 12 kg without packing in plastic bags (J. Nijboer, personal communication, October 2024). Brookfield Zoo Chicago has used their method to store browse successfully and reported a high palatability overall as all species offered the browse consumed it readily, even after 8 months of storage (Watts 2017). However, other sources have reported that thawed browse is less palatable for some species (Nijboer, Clauss, and Nobel 2006; van Herk et al. 2019). While not cheap, if animal care staff have access to the needed equipment and the institution can afford the cost of maintenance and storage, freezing browse is an excellent method of preserving fresh browse and has been used with great success.

4.3 | Browse Silage

Silage is the process in which plant material with a high moisture content is preserved by fermentation in anaerobic conditions (McDonald, Henderson, and Heron 1991), and aims to preserve animal feed while maintaining its nutritional value throughout the fermentation and storage process (Muck, Moser, and Pitt 2003). Commonly used in agricultural applications to preserve feeds such as grass and grain, browse can be preserved just as effectively using the same methods (Nijboer, Clauss, and Nobel 2006). Most commonly browse is packed into large plastic drums (Depauw et al. 2020; Hatt and Clauss 2006; Livingston et al. 2013; Nijboer, Clauss, and Nobel 2006), wrapped in bales (Depauw et al. 2020; Nijboer, Clauss, and Nobel 2006), or in bunker silos (K. Sullivan et al. 2011), and compressed to remove as much air as possible before sealing the container to promote anaerobic fermentation. Because each species of browse can have different fermentation characteristics, additives such as molasses or fermenting bacteria can be helpful to ensure maximum nutrient preservation and minimum spoilage. For example, alfalfa added to ensiled willow helped achieve better fermentation and eliminated the growth of yeast and mold (Depauw et al. 2020) Importantly, the ensiling process must be implemented using the correct methods to ensure that harmful microorganisms such as *Bacillus* and *Clostridium* sp. do not overtake the beneficial ones (Nijboer, Clauss, and Nobel 2006). While some yeast growth is acceptable and can simply be removed before feeding out, the silage should be carefully inspected for signs of spoilage such as mold growth and an unpleasant smell arising from excess butyric acid (Hatt and Clauss 2006). Animal care staff responsible for feeding out silage should be trained to recognize signs of spoilage to prevent illness or death from occurring due to spoiled feed.

Browse silage methods can vary depending on what part of the plant is preserved, with most research focusing on either the leaves alone or on mulched/chaffed browse (Hatt and Clauss 2006). Even fewer have focused on silage for the preservation of whole branches, which promotes opportunities for species-specific feeding behaviors (Lachance 2012). Preserving whole branches is more difficult, however, due to the increased risk of air pockets preventing complete fermentation. To overcome this issue, the Toronto Zoo uses a custom built a hydraulic press to fill barrels with whole browse while packing it as tightly as possible (Lachance 2012; Wensvoort et al. 2017). Like other methods of preservation, the limiting factors for silage production are the costs of time, labor, and materials. Silage may also be less palatable than fresh browse, but overall seems well accepted by many species (Depauw et al. 2020, 2021; Hatt and Clauss 2006). Preserved browse should provide similar nutritional and behavioral benefits to browsers as well as being as cost and labor efficient as possible.

4.4 | Ensuring Behavioral Needs Are Met by Preserved Browse

As summarized above, browse provides zoo browsers with the opportunity to satisfy the behavioral need to forage on spatially and physically complex food items using specific behaviors for acquisition and processing. While fresh browse in its intact form does fulfill these requirements, preserved browse, on the other hand, often does not fully satisfy these requirements. While browse can be preserved in an unprocessed state, it is often cheaper and easier to preserve browse as sticks, leaves, or mulch/chaffed feed.

Consequently, browser diets should focus on not only providing enough browse but also presenting preserved browse and other dietary components in a biologically relevant manner. For example, efforts to provide diet components in enrichment devices that stimulate more biologically relevant foraging behaviors, such as a wire mesh hay feeder with bolt "acacia thorns" or hanging feeders for a preserved browse or other diet items, can act as a suitable substitution for fresh browse, increasing foraging and locomotion while reducing the incidence of oral stereotypies (e.g., Fernandez et al. 2008; Troxell-Smith et al. 2017). Two recent studies of giraffes suggest that providing the entirety of the non-fresh browse daily diet in feeders that require the use of species-specific foraging behaviors (e.g., lips/tongue manipulation, reaching for raised feeders) instead of using traditional trough/crib feeders significantly reduced stereotypic behaviors and improved overall giraffe welfare (Depauw et al. 2023; Walldén 2023). From simple attachments for browse branches to built-in enrichment devices, managers should incorporate feeding enrichment into habitat design to ensure that diets are presented in a biologically relevant manner while minimizing the impact on staff workloads (Brando and Coe 2022). Instead of offering enrichment only, these feeding devices should ideally be used for preserved browse and other diet components (minus rations for training and management) to better simulate wild browser diets and promote positive welfare.

5 | Conclusions

The provision of browse is clearly beneficial for zoo browsers, and institutions should be making efforts to invest in the infrastructure and staffing needed to provide fresh browse in significant amounts when available and to provide suitable alternatives to fresh browse in a biologically relevant manner when unavailable. However, much more research is needed on a variety of fronts to ensure the safety and nutritional value of different types of both fresh and preserved browse. In addition, palatability research can help tailor diets for individual animals to provide dietary choices and improve welfare (Kirschner et al. 1999).

Future research should also focus on additional alternatives to browse. For example, more easily obtainable plant sources with similar chemical profiles to browse may be suitable for smaller browser species, such as honey locust seed pods or tamarind seeds (Dunham et al. 2023; B. K. Smith, Remis, and Dierenfeld 2020). Additionally, like much zoo research, studies focusing on the benefits of browse are heavily biased toward mammals and even more strongly biased toward so-called "charismatic megafauna" such as elephants, giraffes, and great apes (see Table 1, for example). More research should be focused on understudied taxa, especially those with specialized diets that require as much browse as possible. All browsing species should have access to fresh or preserved browse to enhance their long-term health and welfare in managed care.

While the primary goal of browse provision is optimal animal health and welfare, it can also help zoos fulfill another major goal through education. By giving animals the opportunity to express species-specific feeding and foraging behaviors, visitors can develop connections with animals and improve their educational experience (Luebke et al. 2016; Miller, Luebke, and Matiasek 2018). While the performance of stereotypic behavior can negatively affect visitor perception of animal behavior (Miller 2012) and may hinder the development of an empathic link (Hill 2018), viewing species-specific behaviors in the correct context can improve visitor empathy and learning. In one multi-institutional study, viewing active animals correlated with positive affect in visitors, as well as an increase in meaning-making (Luebke et al. 2016). Positive affective and educational outcomes may lead to increased conservation action and engagement at home (Godinez and Fernandez 2019), which helps further the health and welfare of animals around the globe, not just those in managed care. Providing fresh browse when available and suitable alternatives when unavailable is not an easy task; however, the benefits of doing so far outweigh the difficulties by promoting positive health and welfare for zoo browsers.

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Ethics Statement

This review did not generate new data and did not require the use of animals. Therefore, ethical approval was not required for this study.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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