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Diet Overlap of Mammalian Herbivores and Native Bees: Implications for Managing Co-occurring Grazers and Pollinators

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ABSTRACT: Many federal, state, and tribal agencies, as well as nonprofit organizations, have recently increased efforts to understand how natural areas can be managed to enhance native pollinators and the ecosystem services they provide. However, managing this important group must be balanced with other services that natural areas provide including hunting, timber production, and livestock grazing. Significant knowledge gaps exist about how to effectively manage habitats used by large ungulates (e.g., cattle (*Bos taurus*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*)) in ways that also enhance pollinators. One key gap is understanding the degree to which diets of mammalian herbivores overlap with floral resources used by bees, and how this overlap varies spatially and temporally. Invertebrate pollinators, including bees, rely on flowering forbs and shrubs for nectar and pollen. Ungulates also feed on flowering plants, although preferences vary by ungulate species, vegetation community, and season. Here we review existing literature on ungulate diets relative to flowering plants and compare this information with flower preferences of bees, drawing on studies of bee abundance and diversity at the Starkey Experimental Forest and Range in northeastern Oregon. Our review can inform managers about the potential dietary overlap between ungulates and native bees and aid planning efforts aimed at biodiversity conservation of pollinators. We discuss management implications relative to seasonal habitat use and dietary preferences of ungulates and variation in bee phenology, and conclude with guidance about timing and intensity of ungulate grazing when managing for multiple conservation objectives, especially in sensitive habitats like riparian areas.

Index terms: dietary overlap, livestock, native bees, Starkey Experimental Forest and Range, wild ungulates

INTRODUCTION

Humans enjoy a variety of benefits, or services, from the structure and functions associated with ecosystems (MEA 2005). Historically, natural resource management of public lands in the United States focused primarily on producing food and fiber, so-called provisioning ecosystem services (Bengston 1994; MEA 2005; Chapin et al. 2010). Sustained production of timber and livestock in US forests and rangelands was an overarching priority from the late 1800s until the 1930s, when "multiple use forestry" emerged in response to public interest in, and demand for, additional types of ecosystem services (Bengston 1994). These included cultural services such as hunting, fishing, and other recreational activities, and supporting services such as clean water and soil retention (Bengston 1994; MEA 2005). In the last 30 years, the types of services considered in natural resource decisions have become even more diverse in response to paradigm shifts (e.g., the "forest ecosystem management" approach), and to the emergence of ecosystem services management frameworks (Bengston 1994; Chapin et al. 2010; Deal et al. 2012). As a result, managers now consider a wider variety of ecosystem services, many of which are supporting and regulating services that are less directly connected to end products that humans value (MEA 2005; Deal et al. 2012; Ringold et al. 2013). With growing emphasis on diverse services, as well as concerns over their vulnerability to various human activities, land managers are increasingly seeking ways to manage multiple ecosystem services, often in the absence of adequate data (Kremen and Ostfeld 2005; Mooney et al. 2009).

Pollination exemplifies a supporting ecosystem service of increasing concern to managers, both because of the decline of some pollinator species (Potts et al. 2010; Dumroese et al. this issue pps. 499-511); Hanula et al. this issue pps. 427-439) and the significant role pollinators play in food production and supporting flowering plant diversity in natural areas (Ollerton et al. 2011). Thus, a new challenge for resource managers is to continue providing traditional services (e.g., timber, livestock production, hunting, and fishing), but in ways that also conserve or benefit pollinators. Research aimed at understanding how to effectively manage diverse ecosystem services in ways that maximize benefits and minimize negative tradeoffs is scarce but growing (Bennett et al. 2009; Wainger et al. 2010).

In this paper, we examine one potential area of interaction between two key ecosystem service providers: vertebrate grazers and invertebrate pollinators. For vertebrate grazers, we focus on three ungulates: cattle (*Bos taurus* Linnaeus), elk (*Cervus elaphus*

Linnaeus), and mule deer (*Odocoileus hemionus* Rafinesque). Cattle production is an important provisioning service supported by public lands, with cattle making up the largest proportion of livestock produced in the United States. Deer and elk, the most significant game animals in the United States, provide important cultural and provisioning services, such as hunting, wildlife viewing and serving as traditional foods for many Tribal nations (Bolon 1994, McCabe 2002). For pollinators, we focus on native bees, the most diverse and abundant pollinators in natural areas, with approximately 4000 species in North America (NRC 2007).

Several studies have examined effects of ungulate herbivory on pollinators, including native bees (see Black et al. 2011; Hanula et al. this issue pps. 427-439; for reviews). Results of these studies vary depending on several factors, including plant and bee community composition, intensity of grazing, type of grazer, timing and duration of grazing, and land use. Several studies of livestock grazing and native bees have found significant effects, some negative (Kruess and Tscharntke 2002; Hatfield and LeBuhn 2007; Sjödin 2007; Xie et al. 2008; Kearns and Oliveras 2009) and some positive (Carvell 2002; Vulliamy et al. 2006; Yoshihara et al. 2008). Most studies have been observational, but a large scale manipulation in the Pacific Northwest showed cattle grazing altered native bee abundance, richness, diversity, and community composition, with taxa varying in their sensitivity to grazing (Kimoto et al. 2012b). However, the mechanisms driving observed responses in most of these studies are seldom directly examined.

Ungulate herbivory can impact native bees through various mechanisms, including effects on plant growth, architecture, diversity, and quality, as well as soil characteristics and microhabitat conditions (Kruess and Tscharntke 2002; DeBano 2006a, b; Black et al. 2011; Schmalz et al. 2013). These changes can impact nesting resources and/or food that native bees depend on (Vázquez and Simberloff 2004; Black et al. 2011). For example, plant material is often necessary for nest construction, and the physical structure of plants plays a role for some pollinators that build above-ground nests. Soil characteristics, such as compaction, bare ground, and stability, can affect ground nesting bees (Cane 1991; Potts and Willmer 1997, 1998). However, here we focus on potential effects of ungulate grazing on floral resources used by native bees for food by examining the potential for dietary overlap amongst these groups. While some studies have examined ungulate grazing effects on floral resource availability (Carvell 2002; Hatfield and LeBuhn 2007; Sjödin 2007; Sjödin et al. 2008; Xie et al. 2008; Kimoto et al. 2012b), none that we are aware of have explored how dietary preferences of different ungulates, in combination with temporal and spatial patterns of use, may affect their dietary overlap with native bees.

Ungulate diets have been an active area of research in range science and wildlife biology for decades, with numerous studies across the western United States (Table 1), often in the context of understanding dietary or niche overlap between wild and domestic ungulates. While deer, elk, and cattle diets do overlap as they all feed on graminoids, forbs, and browse (including flowering shrubs), the relative proportions consumed by each can vary in time and space. Although elk and cattle generally prefer graminoids over other forage, their diets may consist of up to 51 and 20% forbs, respectively (Cook 2002; Stewart et al. 2003; Findholt et al. 2005; Christianson and Creel 2010). When preferred forages are less abundant, browse is also consumed by elk and cattle, and can comprise 18 to nearly 100% and 4–18% of diets, respectively (Kufeld 1973; Cook 2002; Findholt et al. 2005; Christianson and Creel 2010). Mule deer diets are typically more variable, with forbs composing 14–56% of the diet and browse composing 16–48% (Hansen and Reid 1975; Stewart et al. 2003; Findholt et al. 2005).

Ungulate diets vary in time and space in response to a variety of factors including changing plant diversity and phenology, general patterns of habitat use, and intra and interspecific competition for forage. For example, late summer and early fall can be a period of intense competition for forage, especially in drought-prone areas, as the availability of nutritious resources decrease (Findholt et al. 2005). As vegetation senesces in late summer, cattle move closer to water and may consume relatively more forbs and browse if grass is less available in those areas (Findholt et al. 2005; Roever et al. 2015). However, cattle consumption of forbs may actually decline as summer progresses and forbs senesce and become less palatable (Holechek et al. 1982a).

Unlike mammalian herbivores, bees rely almost entirely on forbs and flowering shrubs for pollen and nectar, with forbs being particularly important because this species-rich group is most likely to provide floral resources to the range of bees active throughout the growing season (Dumroese et al. this issue pps. 499-511). Although certain forb species may be particularly attractive to large numbers of pollinators (Dumroese et al. this issue pps. 499-511)), bee species, like mammalian herbivores, may vary strongly with respect to diet. Most specialization occurs relative to pollen, with bees typically ranging from being broad generalists (polylectic) to relative specialists that focus on related or morphologically similar plant taxa (oligolectic) (Westerkamp 1996; Michener 2007). Specialization is often associated with morphological differences that presumably allow bees to more easily access certain flowers (e.g., long proboscises, specialized pollen collecting hairs, facial modifications) (Thorp 1979). Although much is still unknown about floral specialization and preferences of many bee species, numerous studies have examined specific bee-flower relationships. This work has been supplemented with inferences based on matching morphological features and phenologies between bees and flowers, and assumptions of similarities among taxa. The result is that geographically-targeted technical guides that identify the genus and species of flowering plants preferred by pollinators are becoming more common (Pendergrass et al. 2008; Ogle et al. 2011a, b; Pollinator Partnership n.d. a, b; Tilley et al. 2013; Vaughan et al. 2015).

Although much is known about diets of ungulates and native bees, information from these disparate fields has not been

Table 1. Blooming plant species present during four sampling bouts at the USFS Starkey Experimental Forest and Range. "N" indicates native status, "I" indicates introduced, and "N/I" indicates that status depends on subspecies. Columns for elk, mule deer, and cattle diets indicate whether the genus or species has been detected in diets of those ungulates in the literature examined. Bee plants indicate taxa identified in the literature as important to native bees. Bold-faced font indicates species-level matches and normal font indicates genus-level matches. Plant nomenclature follows NRCS (2015).

	Native status	May-14	Jun/Jul 2014	Jul/Aug 2014	Sep-14	Elk diet	Mule Deer diet	Cattle diet	Bee plant
Family Apiaceae									
Angelica canbyi J.M. Coult. & Rose	N	x				K			
Heracleum maximum W. Bartram	N		x			K, **BR, YR**			
Lomatium ambiguum (Nutt.) J.M. Coult. & Rose	N	x				CO[a]			P, Oa, PPB, Ob, T
Perideridia gairdneri (Hook. & Arn.) Mathias	N			x		**PR**			
Family Asteraceae									
Achillea millefolium L. var. *occidentalis* DC.	N		x	x		**K, D**	**D**	**Ha, Hb, Hc, D, W**	**P, Oa, PPA, Ob, T**
Agoseris glauca (Pursh) Raf.	N	x	x			**K,** D			**P**
Arnica chamissonis Less./ *Arnica sororia* Greene	N		x	x		**K,** D, **CO**	D, DE	Hb, D, **W**	
Cirsium arvense (L.) Scop.	I			x		K, D, **SI,** CL, GO, GRa, GRd, PE, SC, KN, CO	D	D, V	
Erigeron corymbosus Nutt.	N			x	x	MS, K, D, ST, CO	HR, D, DE	D	P, Oa, T
Erigeron speciosus (Lindl.) DC.	N			x		MS, K, D, ST, CO	HR, D, **DE**	D	**P, Oa, T**
Grindelia nana Nutt.	N			x					P
Madia glomerata Hook.	N			x				V	P
Senecio serra Hook.	N		x	x		K, D, BL, GA, N, ROa, SI, YR, PI, CO	BA		P
Solidago missouriensis Nutt.	N			x	x	K, GA, BO, **CO**	DE		P, **Oa,** T
Stenotus lanuginosus (A. Gray) Greene	N		x						
Symphyotrichum spathulatum (Lindl.) G.L. Nesom	N		x	x		K, MS, D, E, KN, CO	MS, D	D	**P, Oa,** PPA, Ob, T
Taraxacum officinale F.H. Wigg.	N/I	x	x			**K, D, BL, BO, BR, KN, PR, SI, SK,** E, KR, SE, **CO**	**D, DE**	**D**	
Tragopogon dubius Scop.	I		x	x		**K, GO, MC, SC,** D, GRa	D	D	
Family Boraginaceae									
Myosotis stricta Link ex Roem. & Schult.	I	x				K, ROa			
Family Brassicaceae									

(Continued)

Table 1. (*Continued*)

	Native status	May-14	Jun/Jul 2014	Jul/Aug 2014	Sep-14	Elk diet	Mule Deer diet	Cattle diet	Bee plant
Barbarea orthoceras Ledeb.	N	x							
Descurainia sp		x					HR		
Thlaspi arvense L.	I	x							
Table									
Family Caryophyllaceae									
Dianthus armeria L.	I			x		CO			
Family Clusiaceae									
Hypericum perforatum L.	I			x			**D**		
Hypericum scouleri Hook.	N		x	x			D		
Family Crassulaceae									
Sedum stenopetalum Pursh	N		x			**Wi**	**D**		P
Family Fabaceae									
Astragalus reventus A. Gray	N	x				K	HR,MS, **D,** DE	**D,** W, T	P, Oa, PPB, Ob, T
Lotus unifoliolatus (Hook.) Benth.	N			x					**P,** Ob, T
Medicago lupulina L.	I			x		HR, K, A, MA	HR	V	Oa, Ob, T
Thermopsis montana Nutt.	N	x	x			**K, D, ROa,** BC,	**D**	**D**	**T**
Trifolium pratense L.	I			x		K, D, SE, BR, CA, E, HS, KN, ROb, CO	D, DE	Ha, D, V	P, Oa, Ob, T
Trifolium pratense/repens	I		x			K, D, SE, BR, CA, E, HS, KN, ROb, CO	D, DE	Ha, D, V	P, Oa, Ob, **T**
Trifolium repens L.	I	x				**K, D, SE,** BR, CA, E, HS, KN, ROb, CO	**D,** DE	Ha, **D,** V	P, Oa, Ob, **T**
Trifolium wormskioldii Lehm.	N	x		x		K, D, SE, BR, CA, E, HS, KN, ROb, CO	D, DE	Ha, D, V	**P,** Oa, Ob, T
Vicia cracca L.	I	x	x			K, BL, KO, MC		V	P, Ob, T
Family Gentianaceae									
Gentianopsis simplex (A. Gray) Iltis	N			x		**D**			
Family Grossulariaceae									
Ribes cereum Douglas	N	x				**K, ST, BY,** GA, SK, YR, PI, **CO**		**Hb. Ha**	**P, Oa,** PPA, PPB, Ob, T
Ribes hudsonianum Richardson	N	x				**YR,** K, GA, SK, BY, PI, CO		Hb, Ha	P, Oa, PPA, PPB, Ob, T
Family Iridaceae									
Iris missouriensis Nutt.	N	x				**K, D, Wi, BC**	**Wi**	V	**P, T,** PPB
Olsynium douglasii (A. Dietr.) E.P. Bicknell	N		x						
Family Lamiaceae									
Agastache urticifolia (Benth.) Kuntze	N			x		**K, CO**			**P, T**

(Continued)

Table 1. (*Continued*)

	Native status	May-14	Jun/Jul 2014	Jul/Aug 2014	Sep-14	Elk diet	Mule Deer diet	Cattle diet	Bee plant
Monardella odoratissima Benth.	N			x					**P, PPA**
Prunella vulgaris L.	N		x	x		**D, CO**	**D**		**P**
Family Liliaceae									
Allium acuminatum Hook.	N		x			K		V	
Allium madidum S. Watson	N		x			K,		V	
Camassia quamash (Pursh) Greene	N	x				**Wi, CO**			**P, PPA**
Triteleia grandiflora Lindl.	N	x	x						
Veratrum californicum Durand	N		x			K, YR, HS, **CO**		V	
Family Malvaceae									
Sidalcea oregana (Nutt. ex Torr. & A. Gray) A. Gray	N		x	x		**CO**	**D**		**P**
Family Onagraceae									
Epilobium brachycarpum C. Presl	N			x		K, **D,** CO	MS, **D**	**D**	
Epilobium ciliatum Raf.	N			x		K, D, CO	MS, D	D	
Family Polemoniaceae									
Microsteris gracilis (Hook.) Greene	N	x							
Polemonium occidentale Greene	N		x			K, YR			PPA
Family Polygonaceae									
Eriogonum heracleoides Nutt.	N		x	x		HBE,**K, KF, PI,** MS, GA, GRc, MC, **CO**, SE	BA	**Hb, Hc, P**	**P, Oa,** PPB, **Ob, T**
Polygonum bistortoides Pursh	N		x			K, PI, YR			
Family Ranunculaceae									
Ranunculus orthorhynchus Hook.	N	x				K, KN, BR			
Ranunculus uncinatus D. Don ex G. Don	N	x				K, KN, BR			
Family Rosaceae									
Crataegus douglasii Lindl.	N	x				**CO**			**Oa, PPA, Ob, T**
Fragaria virginiana Duchesne	N	x				**K, D, Wi, PR, SE,** BO, GA, GRd, KN, YR, **CO**	**D,** DE	**D**	**P**
Potentilla glandulosa Lindl.	N	x	x	x		HBE,**K, PI, SI, YR,** D, Wi, BO, CA, E, GRd, KR, KN, ROa, SE, PR, **CO**	D, Wi	D, W	T
Potentilla gracilis Douglas ex Hook.	N	x	x	x		HBE, **K, D, KR,** BO, CA, E, GRd, KN, ROa, SE, PR, PI, SI, YR, **CO**	**D, Wi**	**D,** W	T
Rosa nutkana C. Presl	N		x			HBE, K, Wi, GA, HS, SC, YR, BL, PT, KW, **CO**	Wi	Ha	**P, Oa, PPA,** Ob, T
Sanguisorba canadensis L.	N		x			**K,** PI, CO			Oa, Ob, T

(Continued)

Table 1. (*Continued*)

	Native status	May-14	Jun/Jul 2014	Jul/Aug 2014	Sep-14	Elk diet	Mule Deer diet	Cattle diet	Bee plant
Family Rubiaceae									
Galium aparine L.	N			x		K, D, KF, SC, **CO**	D	V	
Galium boreale L.	N		x	x		**K, D, SC**, KF, **CO**	D	V	
Family Saxifragaceae									
Lithophragma parviflorum (Hook.) Nutt. ex Torr. & A. Gray	N	x	x						
Saxifraga nidifica Greene	N	x							
Saxifraga oregana Howell	N		x						
Family Scrophulariaceae									
Castilleja cusickii Greenm.	N	x				K, D, CO			PPB
Penstemon sp.		x				K, D, BO, CL, GA, SK, YR, PI, CO	D		P, Oa, PPA, PPB, Ob, T
Verbascum thapsus L.	I			x		S	S	V	
Family Valerianaceae									
Valeriana dioica L.	N	x				K			
Family Violaceae									
Viola adunca Sm.	N	x		x		K, BR			PPB
Viola nuttallii Pursh	N	x				**K, BR**			**PPB**

[a]Plant species for this reference are those eaten equal to or in excess of their availability. These data are based on grazing trials of tame female elk collected April - October, 2004-2006 in the Sled Springs Game Management Unit in the Blue Mountains Ecoregion of Northeast Oregon.

Legend:

Elk, Deer, and Cattle Literature Cited:

A = Anderson et al. (1956)*; BA = Bartmann (1983); BL = Blood (1966)*; BO = Bohne (1974)*; BR = Brazda (1953)*; BC = Burt and Cates (1959)*; BY = Boyd (1970)*; CA = Capp (1967)*; CL = Claar (1973)*; CO = Cook et al. (2014); D = Damiran (2006); DE = Deschamp et al. (1979); E =Eustace (1967)*; GA = Gaffney (1941)*; GO = Gordon (1968)*; GRa = Greer (1959)*; GRc = Greer (1960)*; GRd = Greer et al. (1970)*; HR= Hansen and Reid (1975)*; HBE = Hobbs et al. (1981); Ha = Holecheck et al. (1982a); Hb = Holechek et al. (1982b); Hc = Holechek et al. (1982c); HS = Hash (1973)*; K = Kufeld (1973)*; KF = Korfhage (1974)*; KN = Knight (1970)*; KO = Komberec (1976)*; KR = Kirsch (1963)*; KW = Knowles (1975)*; MA = Martinka (1969)*; MC = Mackie (1970)*; MS = Mower and Smith (1989)*; N = Nichols (1957)*; PE = Peek (1963)*; PI = Pickford and Reid (1943)*; PR = Probasco (1968)*; PT = Picton (1960)*; R = Rosiere (1975); ROa = Rouse (1957)*; ROb = Rouse (1958)*; S = Sandoval et al. (2005); SC = Schallenberger (1965)*; SI = Singer (1975)*; SK = Stark (1973)*; SE = Stevens (1966)*; ST = Stewart et al. (2011); T = Thetford et al. (1971); V = Van Dyne and Heady (1965); Wi = Wickstrom et al. (1984); W = Wyffels (2009); YR = Young and Robinette (1939)*

* = As reported in Cook (2002)

Native Bee Literature Cited:

P = Pendergrass et al. (2008); Oa = Ogle et al.(2011a); Ob = Ogle et al. (2011b); PPA = Pollinator Partnership (n.d.a); PPB = Pollinator Partnership (n.d.b); T = Tilley et al. (2013).

synthesized, making it difficult for managers to evaluate the magnitude of potential dietary overlap between these groups and to mitigate negative effects resulting from overlap. Ultimately, the degree of realized dietary overlap is determined by three factors: spatial separation, temporal asynchronicity, and dietary differences (Stewart et al. 2011). Understanding the first two factors requires quantifying the spatial and temporal variability of native bees and blooming forbs and shrubs, which, in temperate zones, often show strong seasonal patterns related to phenology (Williams et al. 2001; Kimoto et al. 2012a). These data can then be combined with results in published studies of diets and habitat use of ungulates and bees to identify when and where the most significant overlap may occur, and to inform management of sensitive areas. We illustrate this approach with a case study of riparian areas along Meadow Creek at the US Forest Service (USFS) Starkey Experimental Forest and Range (Starkey) in eastern Oregon. Riparian areas are of special concern, given their key role in supporting high levels of biodiversity and ecological services, their history of frequent disturbance and subsequent restoration, and their sensitivity to ungulate grazing (Case and Kauffman 1997; Clary and Kruse 2003; DeBano et al. 2003; DeBano and Wooster 2003; Hanula and Horn 2011; Williams 2011). The objectives of this paper are to (1) describe the spatial and temporal variability of native bees and blooming forbs and shrubs in riparian areas along Meadow Creek at Starkey, (2) conduct a literature review of flowering plant composition of ungulate diets, (3) survey technical guides for lists of plants preferred by native bees, and (4) combine information from the literature reviews and technical guides with bee and plant data from Meadow Creek to determine the potential degree of dietary overlap between mammalian herbivores and native bees at Starkey. Our experiences at Starkey will illustrate one approach to identifying and addressing factors posing the greatest management challenges to enhancing native pollinators given their dietary overlap with ungulates, and highlight management implications relative to seasonal habitat use by ungulates and their dietary preferences. This approach can aid managers in using current knowledge of dietary overlap to inform the timing and intensity of ungulate grazing, especially in sensitive habitats like riparian areas, with the goal of supporting multiple, compatible uses.

THE STARKEY EXPERIMENTAL FOREST AND RANGE AS A CASE STUDY

Study Area

Starkey is located in the Blue Mountains of northeastern Oregon (Rowland et al. 1997; Wisdom et al. 2005) (Figure 1). Elevations range from 1130 m to 1500 m and annual precipitation is approximately 50 cm, with the majority falling as snow (Skovlin 1991). The forest and rangeland habitats at Starkey were formally designated as a research site by the USFS in 1940 to evaluate how management actions and natural disturbance affect multiple resources in this ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson)/mixed conifer/native bunchgrass setting (Skovlin 1991). Beginning with the arrival of settlers on the Oregon Trail, much of Starkey and the surrounding landscape have been heavily degraded from grazing and logging (Skovlin 1991). In the 1980s, approximately 10,000 ha at Starkey were enclosed with game-proof fencing so that closed populations of wild elk and deer could be manipulated, and effects of management evaluated, in an experimental setting. Research at Starkey since that time has focused on increased understanding of ungulate population dynamics, interactions and grazing effects of wild and domestic ungulates, how common management activities affect ungulates and other resources, and effects of natural disturbance regimes on vegetation and wildlife (Rowland et al. 1997; Wisdom et al. 2005). These efforts have included numerous studies of deer, elk, and cattle diets (Holechek et al. 1982a, b, c; Stewart et al. 2003, 2011).

Our study was conducted at 12 riparian sites located along a 13-km reach of Meadow Creek, a major tributary of the upper Grande Ronde River that flows through Starkey (Figure 1). Discharge in Meadow Creek varies within and across years, with severe scouring by ice and high flows often occurring in spring (Filip et al. 1989). Dominant riparian shrubs include willow (*Salix* spp. L.), black hawthorn (*Crataegus douglasii* Lindl.), thinleaf alder (*Alnus incana* (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung), black cottonwood (*Populus balsamifera* L. subsp. *trichocarpa* (Torr. & A. Gray ex Hook.) Brayshaw), and common snowberry (*Symphoricarpos albus* (L.) S.F. Blake). Scattered ponderosa pine, Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western larch (*Larix occidentalis* Nutt.) are also found in the riparian corridor. Herbaceous vegetation includes a variety of forbs (described below) as well as sedges (*Carex* spp. L.), rushes (*Juncus* spp. L.), common spikerush (*Eleocharis palustris* (L.) Roem. & Schult.), creeping bentgrass *(Agrostis stolonifera* L.), and fowl mannagrass (*Glyceria striata* (Lam.) Hitch.). Upland habitat consists of mixed coniferous forest with Douglas-fir and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), along with lodgepole (*P. contorta* Douglas ex Loudon) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson).

Because of legacies associated with past land uses (e.g., logging, livestock grazing, planting exotic forage) in the riparian corridor (Skovlin 1991; USFS 2012), the USFS began actively restoring approximately 11 km of Meadow Creek in 2013, primarily to improve habitat for salmonids (USFS 2012). Restoration efforts included planting approximately 40,000 native shrubs and conifers along the stream, placing boulders and large woody debris throughout the reach, and developing upland water sources and fencing to support a deferred rotation grazing system for cattle (USFS 2012). In addition, research exclosures were built in three pastures along Meadow Creek to evaluate effects of ungulate herbivory on restoration plantings, fish habitat, and other variables within the riparian system. To better understand effects of riparian restoration on multiple ecosystem services, and to partition effects of wild vs. domestic ungulate grazing on floral resources, we conducted a study documenting spatial and temporal variation in native bees and flowering plants of Meadow Creek. These data not only provide a baseline to inform planned future studies, but also to better understand potential overlap between diets

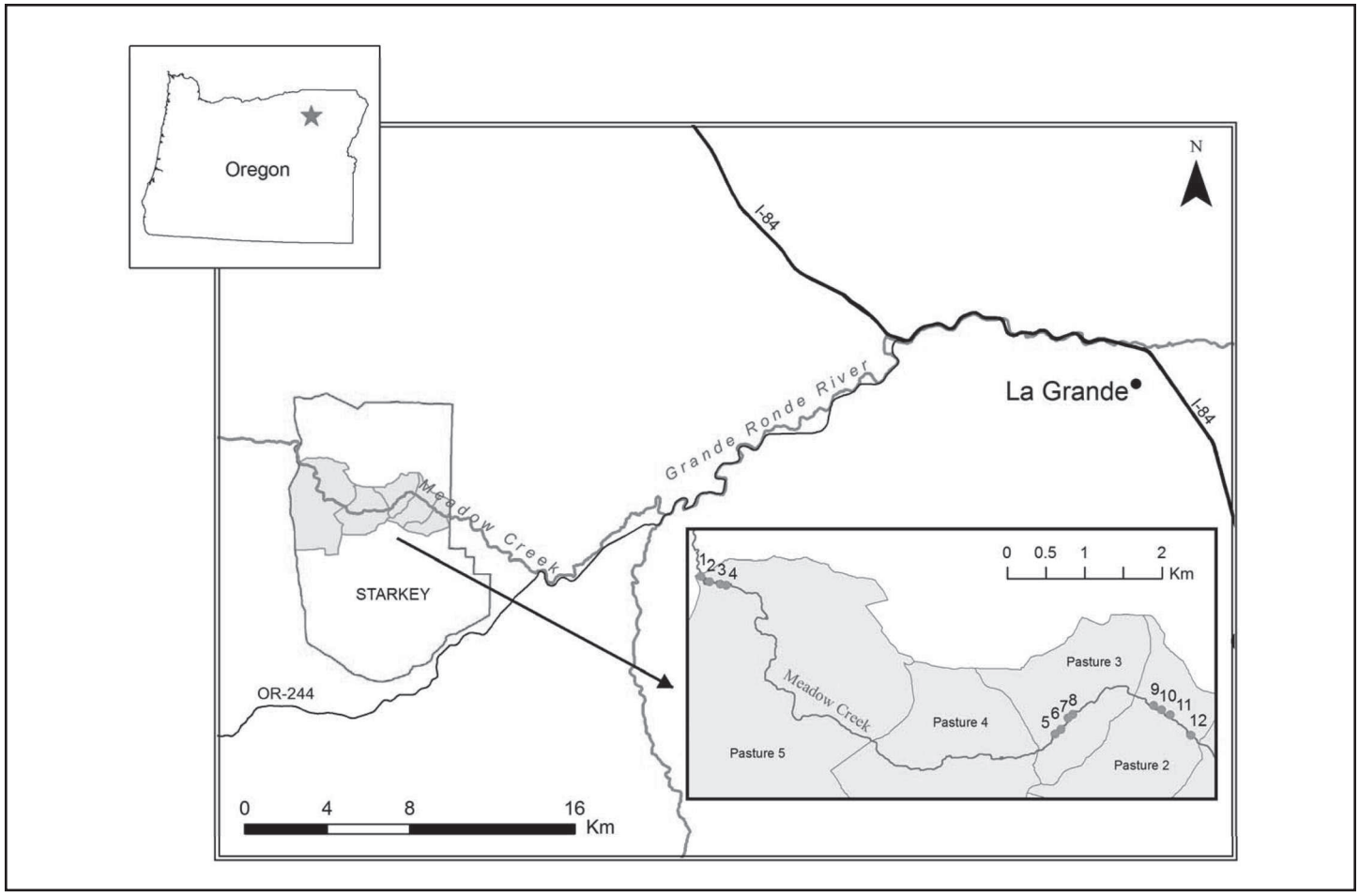

Figure 1. Location of the USFS Starkey Experimental Forest and Range in Oregon and the 12 study sites for sampling native bee and floral resources along Meadow Creek. Site 1 is the furthest upstream and Site 12 is the furthest downstream.

of vertebrate grazers and native bees, and the implications of that overlap.

Use of Starkey by Deer, Elk, and Cattle

Mule deer, elk, and cattle have been dominant herbivores in the Blue Mountains ecoregion for well over a century. Traditionally deer were summer residents at Starkey, whereas elk were spring and fall migrants (Skovlin et al. 1968). Since the initiation of the Starkey Project in 1989 and concomitant erection of the game-proof fence, deer and elk no longer migrate out of Starkey but are fed on a winter feedground (Rowland et al. 1997). Current pre-parturition estimates of deer and elk are 150 and 350, respectively, for the Main Study Area of 7760 ha, which includes Meadow Creek. Cattle have grazed the Starkey landscape since the 1860s. Currently, approximately 400 cow-calf pairs graze at Starkey in a deferred rotation grazing system, including portions of Meadow Creek. Cattle grazing in the new Meadow Creek pastures will begin in summer 2016, with approximately 120 cow-calf pairs in addition to the cattle that graze the remainder of Starkey.

Long-term research on deer, elk, and cattle at Starkey has demonstrated strong separation among these species in space and time, including habitat use in relation to riparian areas and other water sources. Research prior to the erection of the fence around Starkey revealed that elk and mule deer use was greater in pastures not grazed by cattle and that the effect of cattle was greater on elk than deer (Skovlin et al. 1968). Johnson et al. (2000) explored distributions of mule deer and elk in spring and found strong separation between the species. Similarly, Stewart et al. (2002) found that niche overlap between mule deer, elk, and cattle varied by season and factor. For example, cattle used more gentle slopes and lower elevations than did mule deer and elk in spring and summer, whereas distributions in relation to xeric grasslands and the percentage of logged forest were similar among the species in summer.

Water is a consistent driver of ungulate distributions in Starkey and elsewhere, although the magnitude of this effect differs across species and time. Cattle distribution is often influenced by distance to water (Ganskopp 2001) and, in general, they prefer areas with gentle slopes in close proximity to water (Roever et al. 2015). In evaluating patterns of use by mule deer and elk at Starkey, Ager et al. (2003) found that the average distance from water was 300 m for elk and approximately 280 m for deer. Stewart et al. (2002) examined

distributional overlap of deer, elk, and cattle at Starkey and found that distance to water was a strong predictor of resource use; all species preferred areas closer to water.

Native Bees and Floral Resources in Riparian Areas at Starkey

Dietary competition not only depends on the overlap in preferred plants of focal species, but also on the degree of spatial and temporal overlap of foraging activities. Thus, managing potential overlap will be impacted by variability in both plant availability and animal activity. Although habitat use patterns of deer, elk, and cattle are relatively well studied, little work has examined temporal and spatial variability of native bees and their floral resources in riparian areas. The objective of our field study was to describe the spatial and temporal patterns in native bee communities and floral resources at the 12 Meadow Creek sites. These data will help address several questions that have significant implications for ungulate management. For example, are there "hotspots" of bee and/or floral abundance and diversity in riparian areas, either in time or space? Are bee and floral resource availability generally correlated through time and space? Does the composition of the bee and flowering plant communities vary seasonally?

Field Study Methods

To address these questions, we sampled native bees and floral resources at the 12 Meadow Creek sites four times in 2014 (Table 1; Figure 1). Native bees were sampled using three methods: vane traps, pan traps, and hand-netting. Vane traps consist of a UV-reflective yellow plastic container (15 cm diameter × 15 cm high) with a UV-reflective blue polypropylene screw funnel with two 24 × 13-cm cross vanes measuring 3-mm in thickness (SpringStar, Woodinville, WA, USA) (Stephen and Rao 2005). One vane trap was placed at each of the 12 sites, suspended approximately 1.2 m from the ground with a wire hanger inserted into an aluminum pipe. No liquids or other killing agents were used in traps. Vane traps have been found to be effective in sampling native bees in other studies in the region (e.g., Kimoto et al. 2012a, b; Gonzalez et al. 2013; Tubbesing et al. 2014). Vane traps were open for approximately 2 days ($\bar{X}$ = 29.9 ± 0.6 daylight hours). We conducted vane trapping at all sites during all sampling bouts. We also used pan traps and hand netting, two methods commonly used to sample native bees (Westphal et al. 2008), during some of the sampling bouts (Table 2). Pan traps were 6 oz cups in fluorescent blue, florescent yellow, or white. We placed pan traps filled with a solution of water and dishwashing soap at each of the 12 sites along five parallel 20-m transects. The transects were positioned perpendicular to the stream and each separated by 15 m. The array of transects was centered on the blue vane trap located in each study site. Three pan traps (one of each color) were placed in the center of each transect and left open for approximately 1.5 days ($\bar{X}$ = 23.5 ± 0.7 daylight hours). Pan trapping was not conducted in May. Eight sites were sampled with the method in June, and all sites in July and September. Hand-netting was also conducted at each site for 15–20 minutes for a total of 740 minutes in 2014 (eight sites in May and June, 11 sites in July, and all sites in September). Bees collected with all methods were frozen, pinned, labeled, and identified to genus. Because only vane trapping was conducted at all sites during all bouts, we used these data for all direct comparisons between bouts and locations.

We collected data on the presence and abundance of blooming plant species at each site during the same periods when bees were sampled (Table 2) on 0.3-m wide belts along the same five parallel transects described above. The species and number of stems of each blooming plant within the belt transect were recorded and all plants were identified to species with the following exceptions: *Trifolium repens* L. and *T. pratense* L. were combined into a single category, as were *Arnica sororia* Greene and *A. chamissonis* Less. Two taxa were identified to genus level only (*Descurainia* and *Penstemon*).

To standardize effort across sites and times when making spatial and temporal comparisons of bee abundance, we calculated a catch per vane trap per hour rate, accounting for the number of daylight hours each trap was open. We report plant richness as number of species and bee richness as number of genera. SYSTAT Version 12.0 (2007) was used for all Pearson's correlations and means are reported ± one standard error.

Bee and plant community composition were characterized with non-metric multidimensional scaling (NMS) ordination using the abundance of taxa and a relative Sorenson's distance measure. All counts were transformed (log(X+1)) before analyses. For ordination analyses, rare taxa (<20 individuals of a species for plants

Table 2. Dates of four bouts of native bee sampling and blooming flower surveys at 12 study sites in riparian areas of Meadow Creek, USFS Starkey Experimental Forest and Range, Oregon in 2014.

Bout	Vane Traps	Pan Traps	Hand-Netting	Blooming Flower Surveys
I	24 − 26 May	N/A	25 − 26 May	25 − 26 May
II	29 June – July 1	30 June – 1 July	30 − June	1 − July
III	29 July – 1 August	29 July – 1 August	31 July – 1 August	31 July – 1 August
IV	19 – 22 September	19 – 22 September	20 – 22 September	20 − 21 September

and <2 individuals of a genus for bees) were eliminated because rare taxa often mask general patterns in community composition in multivariate analyses (McCune and Grace 2002); 34 plant species and 14 bee genera were included in ordination analyses. The best solution was determined through 250 runs of randomized data and dimensionality was determined by evaluating the relationship between final stress and the number of dimensions. We used Pearson's correlation coefficients to quantify relationships between bee and blooming plant species abundance and ordination axis scores (McCune and Mefford 2006).

We used multi-response permutation procedures (MRPP) to determine whether nonanemophilous plant and bee community composition varied significantly through time. MRPP is a multivariate, nonparametric procedure for testing the hypothesis of no difference between two or more groups. MRPP calculates the mean within group distance and generates an expected distance through permutation (McCune and Mefford 2006). The *P* value generated by the test is the probability of observing a within group distance smaller than the observed distance due to chance alone. MRPP tests also provide a measure of the effect size (A), which is one minus the ratio of the observed mean within group distance to the expected within group distance. An effect size of 1 indicates that all items within each group are identical (i.e., the within group distances are zero), a value of 0 indicates that the heterogeneity within group is no different from that expected by chance, and a negative effect size indicates there is more heterogeneity within groups than expected by chance (McCune and Grace 2002). We used a relative Sorensen's distance measure in all MRPP analyses.

Literature Review Methods

To determine the potential degree of overlap between ungulate diets and floral resources used by bees, we compared blooming plant data collected on riparian transects at Meadow Creek during four sampling bouts in 2014 with published literature on flowering forbs and shrubs in deer, elk, and cattle diets. We also used several technical reports to identify which plants found on our transects were likely to be important as floral resources to bees. We focused our review on literature from the western US, particularly studies from the Northwest. There were several limitations to our approach: (1) our review was not exhaustive, (2) more studies are available on certain taxa than others (e.g., elk diets are more studied than deer), (3) we generally did not account for preferences in ungulate diets since those data were seldom available, (4) technical bulletins that identify plant species important to bees may underrepresent nonnative species because these publications are meant to encourage best management practices, which typically exclude planting nonnative species, (5) we did not review the primary literature for bee-plant association data given the magnitude of that effort, and (6) we focused on the 74 flowering species found on our transects during our 2014 sampling bouts. Although additional species occur in our study area, the most common flowering forbs and shrubs should be represented in our review (with the exception of some mass blooming shrubs like willows, which bloomed before our first sampling bout).

RESULTS

Field Studies of Native Bee and Plant Communities in Starkey Riparian Areas

During four sampling bouts in 2014, we collected 2259 bees in 29 genera using vane traps (760 individuals), pan traps (1245 individuals), and hand-netting (254 individuals). The nine most common genera comprised over 94% of all bees sampled, with *Bombus*, *Lasioglossum*, and *Halictus* the most common (Figure 2a). We observed and collected one species of concern, the western bumble bee (*Bombus occidentalis* Greene). *Bombus occidentalis* is listed as imperiled on the Xerces Society's Red List of bees (http://www.xerces.org/pollinator-redlist), although populations have been detected in nearby regions of eastern Oregon (Rao et al. 2011). During the same four sampling bouts, we counted 7644 blooming stems of 74 species on belt transects (Table 1). The ten most common species accounted for more than 70% of all stems counted, with *Achillea millefolium* L., *Potentilla gracilis* Douglas ex Hook., and *Myosotis stricta* Link ex Roem. & Schult. being the most common species on riparian transects (Figure 2b).

Spatial variation in bee abundance and flowering plants was high; the mean number of bees and number of genera collected per site in vane traps varied considerably (Figure 3a, b), as did the mean blooming plant stem count and plant species richness (Figure 3c, d). The high variability associated with mean abundance and richness per site of bees and blooming plants was, in large part, due to marked seasonal fluctuations in abundance and richness (Figure 4). The number of bees collected per site was lowest in May and highest in the July/Aug sampling bout (Figure 4a). Genus richness showed similar trends as bee abundance, except that richness was high in both the June/July and July/August bouts (Figure 4b). In contrast, blooming plant abundance and richness was lowest in September, and relatively high for all other sampling bouts (Figure 4c, d).

While sites were quite variable through time and space, sites that, on average, had greater abundance in floral resources throughout the season also had, on average, more bees throughout the season. Mean bee abundance per site was highly correlated with mean number of blooming stems per site ($r = 0.69$, $P = 0.01$, $n = 12$). However, this pattern was not observed in the relationship between mean richness in bee genera and blooming plant richness per site ($r = -0.09$, $P = 0.78$, $n = 12$), suggesting that sites that had more species of blooming plants through the season did not necessarily have more bee genera, on average. In addition, there was little correspondence in site quality with regard to bee or blooming forb and shrub abundance and richness from one sampling bout to another. Sites with high abundance and richness of bees or blooming plants did not necessarily have high abundance and richness during the next sampling bout (Table 3). The only exception was for blooming plant richness between the second and third bouts. This suggests that one cannot generalize the relative value of

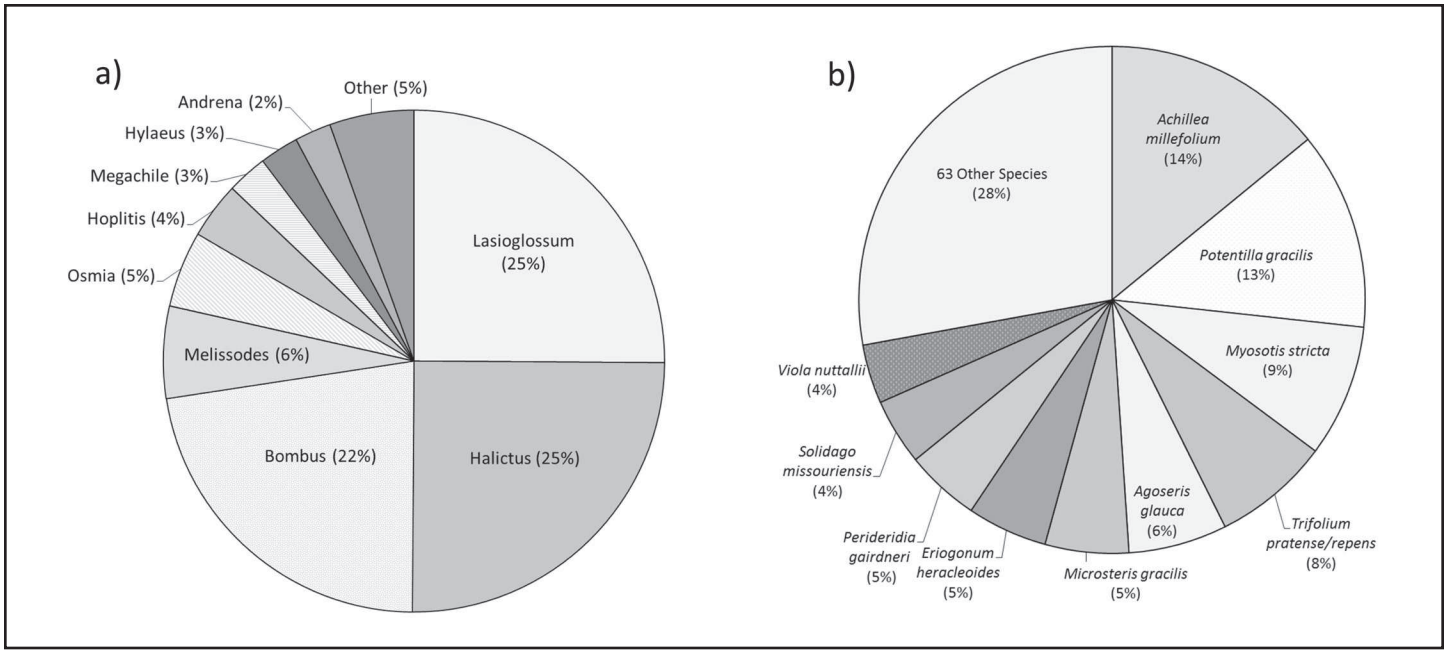

Figure 2. Relative abundance of (a) genera of 2269 bees collected using vane traps, pan traps, and hand-netting, and (b) blooming forb species identified in four bouts of sampling in 2014 at 12 riparian study sites on Meadow Creek at the USFS Starkey Experimental Forest and Range in Oregon.

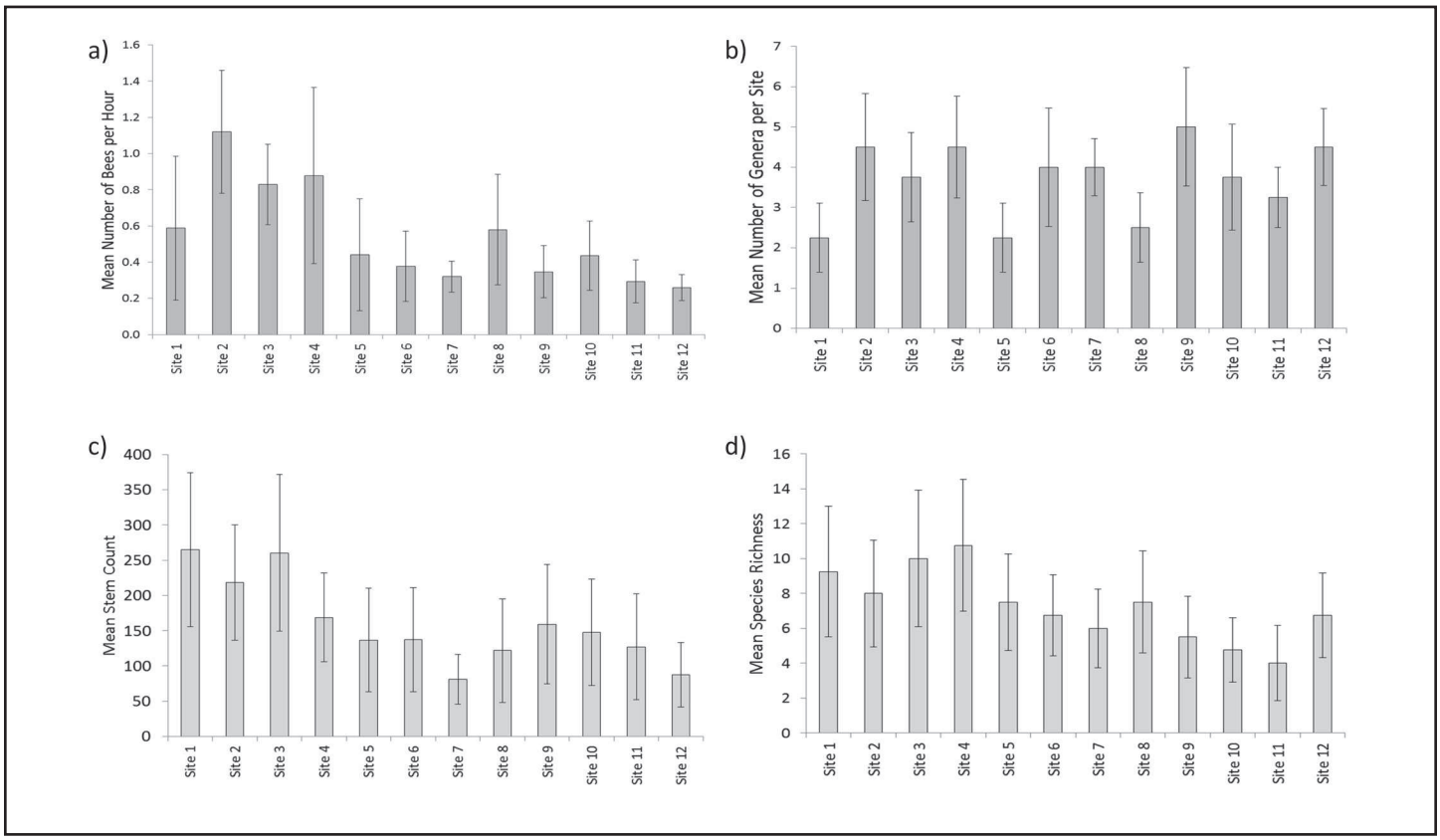

Figure 3. Mean (± one SE) (a) bee abundance, (b) bee genus richness, (c) floral resource abundance, and (d) floral resource species richness at each riparian site on Meadow Creek at the USFS Starkey Experimental Forest and Range in Oregon, averaged over all four sampling bouts in 2014. Sites are arranged from upstream (Site 1) to downstream (Site12).

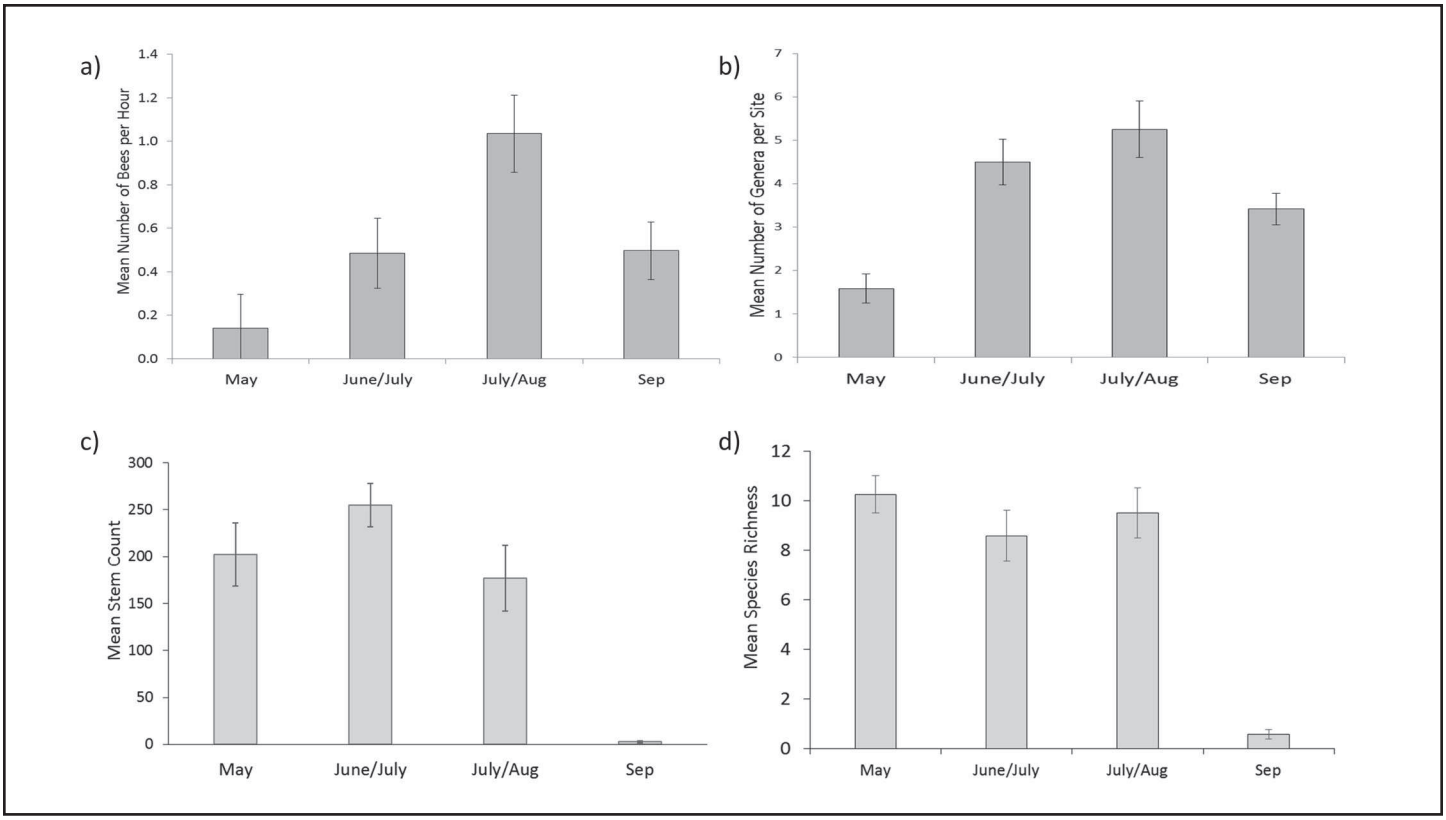

Figure 4. Mean (± one SE) (a) bee abundance, (b) bee genus richness, (c) floral resource abundance, and (d) floral resource species richness for each sampling bout, averaged over all 12 riparian sites on Meadow Creek at the USFS Starkey Experimental Forest and Range in Oregon in 2014.

a site at one point in time with regard to its ability to support bees or floral resources to future times.

Not only did bee and blooming plant communities show strong seasonal changes in abundance and richness, but the composition of communities also changed across the season. Ordination results revealed that bee composition of sites varied seasonally (Figure 5a). A three dimensional solution explained 84% of the variation in bee community composition at the genus level, with the first two axes explaining most of that variation (Table 4). Three genera (*Bombus*, *Melissodes*, and *Anthophora*) were significantly positively correlated with Axis 1 (and, thus, more common in mid-season sampling bouts 2 and 3) (Table 4). One genus (*Lasioglossum*) was negatively correlated with Axis 1 (and, thus, more common early and late in the season, during sampling bouts 1 and 4) (Table 4). The three genera positively associated with Axis 2 (*Andrena*, *Lasioglossum*, and *Osmia*) were more abundant early in the season (during bout 1); the three genera negatively associated with Axis 2 (*Megachile*, *Halictus*, and *Anthidium*) were more common late in the season. MRPP analysis showed that the differences in generic composition through the season was statistically significant (A = 0.22, $P < 0.001$).

Trends in the species composition of blooming forb and shrub communities likewise showed strong seasonal changes. Ordination results revealed that blooming species composition of sites varied seasonally (Figure 5b), and a one dimensional solution explained 75% of the variation in

Table 3. Seasonal correlations across 12 sites for blooming plant and native bee richness and abundance in riparian areas of Meadow Creek, USFS Starkey Experimental Forest and Range, Oregon in 2014. Correlation coefficients are Pearson's and statistical significance at $P = 0.01$ is indicated with "".**

	Bout I vs. II	Bout II vs. III	Bout III vs. IV
Mean Bee Abundance	-0.11	-0.01	-0.014
Mean Bee Genus Richness	0.06	-0.01	0.25
Blooming Plant Abundance	0.34	0.24	-0.13
Blooming Plant Richness	0.34	0.78**	0.17

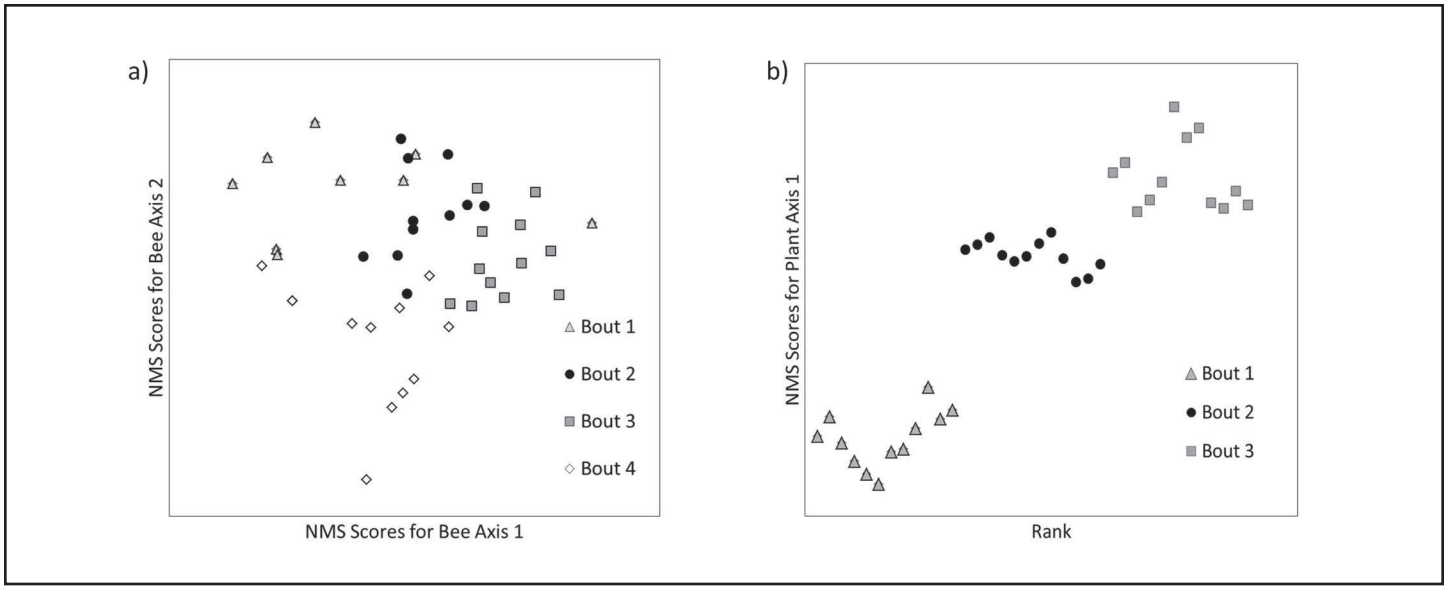

Figure 5. Non-metric multidimensional scaling ordination results for all sites from bouts in 2014 for (a) Axes 1 and 2 for the 14 most common bee genera and (b) Axis 1 for the 34 most common blooming plant species on Meadow Creek at the USFS Starkey Experimental Forest and Range in Oregon. Only three of the four sampling bouts were included in the ordination for plants because, in September, most sites had no blooming flowers on transects and so could not be used in community composition analyses. See Table 4 for genus/species correlations and percent variation explained for each axis.

community composition. Six plant species were positively associated with Axis 1 (and, thus, were species that bloomed relatively late in the season) and 14 species were negatively correlated with Axis 1 (and, thus, bloomed earlier in the season) (Figure 5b; Table 4). MRPP analysis showed that the differences in blooming species composition through the season was statistically significant (A = 0.32, $P < 0.001$).

Literature Review of Ungulate and Bee Diets

We examined 43 diet studies of elk, seven studies of deer, and eight studies of cattle and compiled data on flowering plants preferred by native bees from six technical guides (Table 1). Although elk had the highest number of diet records in the literature that matched plant species found on riparian transects at Starkey, the relative percentage of species in ungulate diets that were also identified as species important to bees was approximately the same across the three ungulates (ranging from 60–64% generic overlap and 50–57% species overlap) (Table 5). We identified 17 species that occurred in both a genus identified in the diets of all three focal ungulates and in a genus of plants identified as important to bees. A subset of three of those species matched at the species level (*Achillea millefolium*, *Thermopsis montana* Nutt., and *Fragaria virginiana* Duchesne) (Table 1). However, many riparian plant species were recorded in diets, or as preferred plants by only one or two of the focal groups (i.e., deer, elk, cattle, and bees) and approximately 12% of plant species belonged to genera not identified as food for any ungulate species (Table 1).

DISCUSSION AND CONCLUSIONS

We were able to take advantage of a well-studied system at Starkey with much known about the population dynamics, behavior, diet, and habitat use of its key ungulate species (Skovlin 1991; Holechek et al. 1982a, b, c; Rowland et al. 1997; Wisdom et al. 2005; Stewart et al. 2003, 2011). Mule deer, elk, and cattle are all key players, with elk being the most abundant wild ungulate grazer in the system and the largest consumer of biomass per individual due to their large body mass and presence from spring to fall in the study area. Habitat use by the three species is generally spatially separated, with elk and deer avoiding areas grazed by cattle, and deer more common in areas where elk are less abundant (Skovlin et al. 1968; Johnson et al. 2000). Key periods in which the three species may spatially and temporally overlap in riparian areas are late summer and early fall, when water and the presence of green forage in riparian areas attract ungulates, while forage quality and quantity decrease in the uplands. During these times, high ungulate densities and broadly overlapping niches can potentially have large effects on forbs in riparian areas (Stewart et al. 2011) with cascading effects on native bees.

The degree of dietary overlap among ungulates at Starkey with regard to forbs that occur in riparian areas was less clear. General diet preferences of each species have been described, with elk and cattle typically eating more graminoids and deer consuming more browse. However, all three are known to strongly select for particular forbs in certain circumstances, yet data on this potential diet overlap had not been synthesized. In addition, there was no existing data on native bee communities and flowering shrubs and forbs in riparian areas at Starkey. Thus, there were obvious gaps in our knowledge about the Starkey system that we addressed with our empirical study and review.

Our work quantifying spatial and temporal patterns of bee and flowering plant communities in riparian areas at Starkey revealed

Table 4. Pearson correlation coefficients of bee genera and plant species that were significantly correlated with non-metric multidimensional scaling ordination axes during sampling bouts at 12 riparian sites of Meadow Creek, USFS Starkey Experimental Forest and Range, Oregon in 2014. Correlations statistically significant at *P* = 0.05 are indicated with "*" and those significant at *P* = 0.01 are indicated with "". Bee axis 3, not shown, explained only 12% of variation in generic composition of bee communities.**

Axis	Bee Axis 1	Bee Axis 2	Plant Axis 1
Variation Explained:	40%	32%	75%
Taxa and r	Positive:	Positive:	Positive:
	Bombus 0.74**	*Andrena* 0.41**	*Achillea millefolium* 0.71**
	Melissodes 0.36*	*Lasioglossum* 0.34*	*Perideridia gairdneri* 0.65**
	Anthophora 0.35*	*Osmia* 0.33*	*Solidago missouriensis* 0.56**
			Symphyotrichum spathulatum 0.53**
	Negative:	Negative:	*Monardella odoratissima* 0.46**
	Lasioglossum -0.68**	*Megachile* -0.62**	*Hypericum perforatum* 0.43*
		Halictus -0.53**	
		Anthidium -0.40**	Negative:
			Myosotis stricta -0.81**
			Microsteris gracilis -0.70**
			Agoseris glauca -0.60**
			Penstemon sp. -0.64**
			Camassia quamash -0.60**
			Taraxacum officinale -0.64**
			Ranunculus uncinatus -0.48**
			Fragaria virginiana -0.42*
			Lomatium ambiguum -0.40*
			Thlaspi arvense -0.40*
			Thermopsis montana -0.38*
			Viola adunca -0.37*
			Viola nuttallii -0.37*

several important points. First, as noted by Dumroese et al. (this issue pps. 499-511), forbs are indeed the most common and diverse flowering plants in riparian areas at Starkey. Second, bee and blooming plant abundance and richness in riparian areas at Starkey varied spatially and temporally, with strong interactions between time and space. For example, spatial patterns in bee and flowering forb and shrub abundance and richness were generally not temporally stable. This means that sites with relatively high diversity and abundance at one-time period may have relatively low diversity and abundance at other times. This lack of a "hot spot" effect makes management based on "snapshots" of bee or floral resources ineffective. Instead, our results suggest that average floral resource abundance throughout the season is the best predictor for average native bee abundance, although the same relationship did not hold for floral and bee taxa richness.

Our data also suggests that bee and floral resources in riparian areas at Starkey are temporally decoupled. Like Williams et al. (2001) and Kimoto et al. (2012a), we found that native bee communities showed strong seasonal fluctuations that did not correspond with cooccurring changes in floral resource abundance and richness. For example, the lowest bee abundance and richness occurred in May, when blooming flower abundance and richness were relatively high. Conversely, bee abundance and richness were still relatively high in September, when almost no blooming plants were found on transects. This asynchronicity may partially be driven by differential responses of plants and bees to weather conditions. May is often cold and wet, and bees will delay emergence and/or decrease activity in inclement weather, regardless of how many floral resources are available (Michener 2007). Forb senescence in late summer and fall is also a common phenomenon, yet many bee species are active in late summer and fall, mating and preparing for overwintering.

Our data also showed that the community composition of bees and plants varied substantially through the season. For example,

Table 5. Summary of number of plant genera and species on riparian transects sampled in 2014 at the Starkey Experimental Forest and Range, northeastern Oregon, that were identified in ungulate diets and as significant floral resources for bees (see Table 1), and their potential overlap.

Focal Group	# of Studies[a]	# of Generic Matches with Riparian Transects (%)[b]	# of Species Matches with Riparian Transects (%)[c]	Generic Bee Plant Overlap (%)[d]	Species Bee Plant Overlap (%)[e]
Elk	43	58 (78%)	32 (43%)	35 (60%)	17 (50%)
Deer	7	35 (47%)	14 (19%)	22 (63%)	8 (57%)
Cattle	8	33 (45%)	12 (16%)	21 (64%)	6 (50%)
Bees	6	40 (50%)	22 (30%)	--	--

[a] Number of studies reviewed; bee studies were technical reviews.

[b] Number (and percentage) of flowering forb and shrub species found on riparian transects that matched the genus identified in the diets of the focal group from literature review (Table 1).

[c] Number (and percentage) of flowering forb and shrub species found on riparian transects that matched species identified in the diets of the focal group from literature review.

[d] Number of species of flowering forbs and shrubs found on riparian transects corresponding to a genus recorded in the diet of the focal ungulate and also identified as an important bee plant. Percentages reflect the percent of all plant species documented in the ungulate's diet that occur in genera identified as important bee plants in the literature.

[e] Number of species of flowering forbs and shrubs found on riparian transects that were both recorded in the diets of the focal ungulate and identified as an important bee plant. Percentages reflect the percent of all plants documented in the ungulate's diet that were identified as important bee plants in the literature.

Andrena, *Osmia*, and some *Lasioglossum* were dominant early in the season; *Bombus*, *Melissodes*, and *Anthophora* were dominant midseason; and *Megachile*, *Halictus*, and *Anthidium* were dominant late in the season. These patterns have significant implications for managing dietary overlap as members of each genus have their own degree of specialization (e.g., *Bombus* and *Osmia* are frequent visitors of *Astragalus* and *Penstemon*, Ogle et al. 2011a). In fact, seasonal variation in community composition of native bee communities is expected, not only because of variation among taxa in their ability to tolerate inclement weather (Goulson 2010), but also because of variation in the degree of specialization and the phenology of plants upon which specialists depend (Michener 2007). Indeed, our study suggests that floral resources also show strong seasonal changes in composition, which may be a strong driver of bee responses.

Finally, our literature review allowed us to delve more deeply into specific areas of dietary overlap with regard to forbs and flowering shrubs among the four focal groups. Our review showed that forbs are frequently found in the diets of all three species of ungulates with elk reported to eat the greatest variety. The relative breadth of elk diets may be an artifact of the fact that our sample size of elk diet studies was much larger than of deer or cattle studies. Regardless, elk diets do include many forbs, with a relatively high overlap with plants thought to be preferred by native bees. However, dietary intake of forbs important to native bees varied among ungulate species, and so must be considered in combination with the temporal habitat use by ungulates, and the phenologies of bees and flowers. Our review allows managers to quickly assess flowering species and genera that may be of particular concern with regard to the diet overlap of particular ungulates and native bees. For Starkey, September may be the time of greatest overlap among the four focal groups. In fall, few floral resources are available, the abundance and nutritive value of forbs are low, ungulates are more likely to concentrate near water, potentially resulting in high ungulate densities in riparian areas, and bee abundance is still relatively high.

While our approach identified potential overlap and generated more specific hypotheses to test, it has several limitations. First, as discussed above, relatively few studies have examined deer and cattle diets relative to elk; therefore, concluding that elk have the greatest diet breadth relative to forbs is uncertain. Second, our sampling period did not coincide with several mass blooming events of shrubs even though these species are common in the area, including willow (*Salix* spp.) and common snowberry (*Symphoricarpos albus)*. Both are valuable forage for cattle (Holechek et al. 1982a, b), deer (Peek and Krausman 1996), and elk (Cook 2002), as well as bees. Bee taxa that specialize on these resources may be more influenced by deer herbivory given their preference for grazing on browse. In addition, our review does not reflect the relative preferences of ungulates for particular species in most cases, it only indicates whether the species or genus has been recorded in a diet. For example, one species reported as consumed by all three ungulates that is also a preferred bee plant is *Thermopsis montana* or mountain goldenbanner. However, *T. montana* is highly toxic to elk and other livestock (Burrows and Tyrl 2001) and, therefore, is proba-

bly seldom consumed. Likewise, species listed as bee friendly plants in technical guides, such as *Achillea millefolium* or common yarrow, may only be useful to a fairly small subset of bees (Dumroese et al. this issue pps. 499-511). Finally, the role of nonnative species in supporting native bees is still unclear (Hanula et al. this issue pps. 427-439), yet these species are almost certainly underrepresented in the technical guides reviewed. However, some nonnative species in the region have been found to be used by a large number of native bees (McIver et al. 2009; McIver and Erickson 2012).

Management Implications

Our work at Starkey suggests the following steps for managers investigating the degree of ungulate and bee diet overlap in their own systems:

1. Assess the current situation. This process includes considering the type and abundance of grazers and their spatial and temporal use of habitat in the area of interest in addition to understanding the basic characteristics and phenology of the native bee and the floral communities. While identifying the key players in the bee community should be a top priority, identifying any sensitive species will also be important.
2. Identify key areas of potential overlap based on ungulate movement patterns and phenology of flowering plants that support native bees.
3. Consider management options. Changes in cattle management may be the most readily implemented solution, including avoiding grazing in areas during sensitive periods or when high degrees of overlap with bees are indicated. However, managers should also consider wild ungulate management when feasible. Fencing could also be used to protect particularly valuable bee habitat, although the costs of building big game fences would not be cost effective for any but the smallest scales. Restoration plantings represent another opportunity to decrease overlap by providing bees with preferred forage plants (Dumroese et al. this issue pps. 499-511). However, planting flowering shrubs, as is common in many riparian restoration projects, may decrease the overall suitability of the habitat for native bees if precautions are not taken (Hanula et al. this issue pps. 427-439), as well as increase the probability of use by deer and elk attracted to the plantings.

Future Research Directions

The work presented here is the first published attempt to synthesize results from a diverse set of sources concerning potential overlap of native bee floral preferences and ungulate diets. We used the Starkey Experimental Forest and Range as a case study to illustrate an approach that combined empirical data on temporal and spatial variability in bee communities and their floral resources in a riparian area with a literature review aimed at identifying the relative importance of riparian plants found at Starkey as food for ungulates and bees. This approach can be adapted to other systems and will allow managers to begin to systematically evaluate the magnitude of potential dietary overlap between these groups and design management plans that mitigate negative effects resulting from overlap. Realized dietary overlap at Starkey was estimated by considering the degree of separation of the focal groups in space, time, and dietary preferences.

This case study illustrates how existing information can be used to guide ungulate management and restoration to enhance multiple ecosystem services, including biodiversity conservation of pollinators. However, there are several areas of research that can enhance our knowledge of ungulate herbivory impacts on native bees, both through diet overlap and nonconsumptive effects. First, the refinement of current, coarse-scale relationships between ungulate diets and floral preferences of bees is greatly needed. Significant gaps remain in our understanding of floral preferences of specific bee species as well as of deer, elk, and cattle. Additional details about ungulate landscape movement through the season are also needed, especially as climate change potentially magnifies conditions that affect spatial and dietary overlap, such as drought stress (Roever et al. 2015). Second, experimental manipulations of native ungulates and cattle will allow us to directly test hypotheses about dietary overlap, including the relative importance of particular herbivores. Studies that address these uncertainties are currently underway at Starkey and should lead to significant advances in our current understanding of the interaction of ungulate grazers and native bees in the future.

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