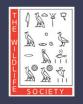Invasive Plants and Wildlife Habitat

Conservation Planning in an Era of Change

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Invasive Plants and Wildlife Habitat

Non-Native Plants and Wildlife in the Intermountain West

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ABSTRACT Non-native plant invasions can change communities and ecosystems by altering the structure and composition of native vegetation. Changes in native plant communities caused by non-native plants can influence native wildlife species in diverse ways, but the outcomes and underlying mechanisms are poorly understood. Here, we review and synthesize current information for the Intermountain West of the United States, to develop a general mechanistic understanding of how invasions by non-native plants affect wildlife, and we identify important information gaps. In this region, most species of recognized conservation and management concern are non-native forbs (e.g., leafy spurge [*Euphorbia esula*], spotted knapweed [*Centaurea stoebe*]), although non-native grasses (e.g., cheatgrass [*Bromus tectorum*], medusahead [*Taeniatherum caput-medusae*]) also have greatly altered vegetation communities. These invasions by non-native plants affect native fauna through both trophic and non-trophic (habitat) pathways and via both direct and indirect effects. The degree to which these invasions affect wildlife depends largely on the degree to which non-native plants alter form and function of native vegetation communities. Reciprocally, native animals can influence distribution and abundance of non-native plants by facilitating or inhibiting invasions through herbivory, seed predation, seed dispersal, soil disturbance, and pollination. Current understanding of interactions between non-native plants and wildlife is limited because few invasions have been studied in sufficient detail to quantify population-level effects on wildlife reliably or to identify underlying mechanisms causing the observed effects. Although management of non-native plants has increased in this region, we understand even less about whether control measures can mitigate the adverse effects of non-native plants on organisms that occupy higher trophic levels. © 2013 The Wildlife Society.

KEY WORDS arthropods, birds, exotic plants, habitat, herpetofauna, Intermountain West, invasive plants, mammals, non-native plants, trophic interactions.

Non-native plant invasions can alter native communities and ecosystems dramatically (D'Antonio and Vitousek 1992, Mack et al. 2000). Many studies have examined how invasions by non-native plant species affect composition and structure of native plant communities (e.g., Mack 1981, Sheley et al. 1998, Weaver et al. 2001, Ortega and Pearson 2005, Lehnhoff et al. 2012) and, to a lesser extent, ecosystem processes (e.g., D'Antonio and Vitousek 1992). However, much less is known about how changes in native vegetation brought about by non-native plants affect native fauna. Here, we review current studies of the effects of non-native plant invasions on terrestrial native wildlife ranging from invertebrates to herpetofauna, birds, and mammals for the Intermountain West region of western United States. Our intent is to synthesize current information to develop a general mechanistic understanding of how invasions by non-native plants affect wildlife and identify important information gaps.

The Intermountain West generally is defined as the region bounded by the Cascade and Sierra-Nevada Mountain Ranges to the west and the Rocky Mountains to the east (Fig. 1; Mack 1981, Parks et al. 2005). The southern boundary is more nebulous, extending through the Great Basin (Mack 1981) or into Arizona. For this review, we focus mainly on the northern part of this region, from the southern end of the Great Basin north, because effects of non-native plants on wildlife in arid grasslands of the southwestern United States are assessed by Steidl et al. (2013). The Intermountain West is a large and diverse area in terms of climate, elevation, topography, vegetation communities, and soils (Mack 1981, Parks et al. 2005), and many species of non-native plants have invaded this region (Rice 2012). The proportion of non-native plants in the mountainous northwest is lower relative to other areas in the United States (Withers et al. 1999), which may be attributed in part to reduced dissemination of weed propagules and lower disturbance resulting from limited human settlement and the abundance of public and protected lands (e.g., national and state forests, national grasslands, national and state parks, wilderness areas). However, the proportion of invaders relative to native species does not necessarily indicate the
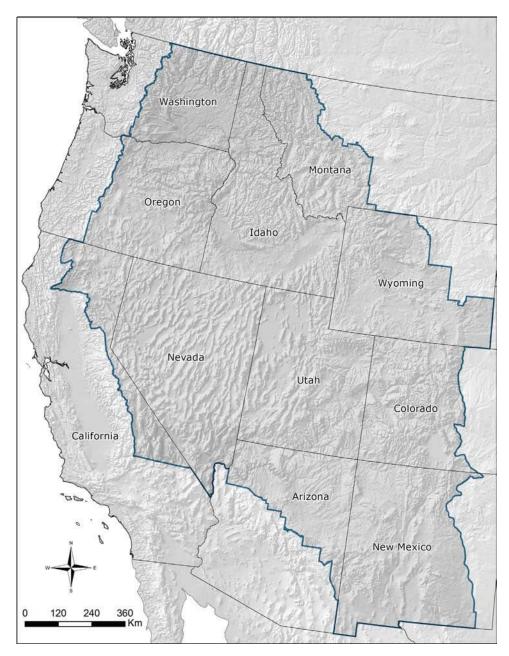
Figure 1. Approximate distribution of the Intermountain West in the United States.

degree of impact; most invaders have low impacts on recipient communities, whereas a few invaders do extensive damage (Williamson 1996, Ortega and Pearson 2005). Arid and semi-arid grasslands within the Intermountain West are particularly hard-hit by approximately a dozen aggressive invaders (Sheley et al. 1998, DiTomaso 2000). Pyke (1999) identified 46 species of non-native plants that occur in sagebrush ecosystems in the Intermountain West and Ortega and Pearson (2005) found that non-native plants comprised 21% of the 113 plant species identified in Intermountain bunchgrass grasslands in west-central Montana. In contrast, high-elevation ecosystems within this region have fewer species and lower densities of non-native plants relative to lowland ecosystems such as grasslands, sagebrush steppe, and low-elevation forests and riparian areas (Weaver et al. 2001,

Parks et al. 2005, Mac Nally et al. 2008). The pattern of fewer non-native plant species at higher elevations could reflect lower rates of anthropogenic disturbance and propagule pressure (Pauchard et al. 2009), but may also reflect reduced establishment success of non-native plants due to more severe environmental conditions.

NON-NATIVE HERBACEOUS PLANTS

In the Intermountain West, most species of recognized conservation and management concern are non-native forbs (Sheley et al. 1998, DiTomaso 2000, Davies and Johnson 2008), such as Dalmatian toadflax (*Linaria dalmatica*), yellow toadflax (*Linaria vulgaris*), leafy spurge (*Euphorbia esula*), St. Johnswort (*Hypericum perforatum*), Canada thistle (*Cirsium arvense*), spotted knapweed (*Cen-*

taurea stoebe), diffuse knapweed (*Centaurea diffusa*), and yellow starthistle (*Centaurea solstitialis*). These forbs are recognized as noxious species on numerous state weed lists (Rice 2012). In contrast, non-native grasses rarely are declared noxious or recognized as problem species on state weed lists (Rice 2012), in part because they provide forage for livestock to varying degrees. However, a few annual grasses do cause severe impacts in this region. Cheatgrass (*Bromus tectorum*) is perhaps the single most widely invasive and problematic weed across the Intermountain West in terms of overall distribution and local density (Mack 1981). For example, this species was the most common and locally abundant weed in grasslands sampled across 400 km^2 of west-central Montana (D. E. Pearson and Y. K. Ortega, Rocky Mountain Research Station, unpublished data). Cheatgrass is particularly problematic because it can alter the disturbance regime by dramatically shortening fire-return intervals (Whisenant 1990). Medusahead (*Taeniatherum caput-medusae*), an annual grass that is ecologically similar to cheatgrass, represents a similar and rapidly growing problem within the region (Davies and Johnson 2008). Although perennial grasses such as crested wheatgrass (*Agropyron cristatum*) and smooth brome (*Bromus inermis*) are often planted intentionally and are not commonly recognized as noxious or problematic, these plants also can have strong impacts on native wildlife (e.g., Larrison and Johnson 1973, Groves and Keller 1983, McAdoo et al. 1989).

Although many species of non-native plants are invading native systems, relatively few non-native plants have strong interactions with the native flora and fauna. To understand and predict the effects of non-native plants on wildlife, we need to understand how invaders differ from the native plants they displace. As non-native plants become dominant in an area, composition of the vegetation community clearly changes, but the degree to which changes in vegetation composition and structure affect wildlife will depend on the degree to which invasions by non-native plants alter form and function of vegetation communities (Crooks 2002, Pearson 2010). Several species of non-native plants invading the Intermountain West differ in biomass, height, phenology, or growth form relative to the native vegetation (Pyke 1999, Pearson et al. 2012*a*). Pearson et al. (2012*a*) compared morphological and phenological traits of several non-native and native forbs that are dominant in grasslands of western Montana and found that non-native forbs had taller and wider flowering stems, shorter and narrower vegetation growth, bolted and flowered later, and had higher survival and flowering after wildfire. Such changes in vegetation morphology can have extensive ramifications for native fauna. For example, these shifts in plant architecture resulting from invasion by non-native forbs dramatically increased the native spider populations, as well as their predation rates on native invertebrate prey (Pearson 2009, 2010).

In more extreme cases, non-native plants can alter nutrient cycling, hydrology, litter decomposition rates, disturbance, and other ecosystem processes by differing in nutrient content, resource requirements or water or nutrient uptake (D'Antonio and Vitousek 1992, Hook et al. 2004, Rimer and Evans 2006, Thorpe et al. 2006, Thorpe and Callaway 2011). In the Intermountain West, cheatgrass creates contiguous fine fuels in areas where vegetation was historically sparse, thereby dramatically increasing fire frequency, which perpetuates cheatgrass but eliminates native plants not adapted to fire (West 1983, Whisenant 1990, D'Antonio and Vitousek 1992, Brooks et al. 2004). Furthermore, increases in annual grasses, with shallower root systems relative to perennial grasses, results in reduced water infiltration, increased runoff and erosion, and alterations in nutrient cycling, further favoring the non-native annual grasses (Cox 1999). Hence, a shift in community dominance from perennial grasses to annual grasses or perennial forbs or the conversion of sagebrush-steppe to annual grasslands dominated by cheatgrass and medusahead (e.g., Weaver et al. 2001, Wisdom et al. 2005) represent large changes in ecosystem structure and function, with large concomitant ramifications for native fauna. To understand how invasions by non-native plants affect native wildlife, we also need to understand how these changes in vegetation form and function relate to the needs of native wildlife species.

EFFECTS OF NON-NATIVE PLANTS ON WILDLIFE

Although many studies have examined how non-native plant species affect native plant communities (e.g., Mack 1981, Knapp 1996, Sheley et al. 1998, Weaver et al. 2001, Ortega and Pearson 2005), studies of the effects of non-native plants on wildlife are lacking for many taxa. Invasions by non-native plants are generally perceived to decrease richness or abundance of native fauna by reducing richness and biomass of native plants. However, non-native plant invasions can have negative, positive, or neutral effects on wildlife (Crooks 2002, Rodriguez 2006, White et al. 2006, Litt and Steidl 2011). Cheatgrass and medusahead invasions have been associated with reduced occurrence or abundance of rodents such as Great Basin pocket mouse (*Perognathus parvus*), deer mouse (*Peromyscus maniculatus*), kangaroo rats (*Dipodomys* spp.), Townsend's ground squirrel (*Spermophilus townsendii*), and least chipmunk (*Tamias minimus*; Larrison and Johnson 1973, Longland 1994, Cox 1999, Ostoja and Schupp 2009). In contrast, densities of harvest mice (*Reithrodontomys megalotis*) increased with invasion by Russian thistle (*Salsola kali*; Larrison and Johnson 1973), abundance of deer mice increased with medusahead invasion (Longland 1994), abundance of ants (Hymenoptera: Formicidae) increased with cheatgrass invasion (Ostoja et al. 2009), and activity of elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) increased with invasion by spotted knapweed (Wright and Kelsey 1997); activity of mule deer (*O. hemionus*) seemed unaffected by spotted knapweed invasion (Wright and Kelsey 1997). The nature of such outcomes likely depends on the specific requirements of different faunal groups relative to the structure and services provided by native versus non-native plants. For example, Larrison and Johnson (1973) showed that the generalist Ord's kangaroo rat (*Dipodomys ordii*) was

more abundant in sites invaded by Russian thistle compared with uninvaded sites, whereas abundance of the more specialized, chisel-toothed kangaroo rat (*D. microps*) was reduced. When sagebrush communities are invaded by cheatgrass or crested wheatgrass, richness and densities of breeding birds decrease; these declines likely are due to decreased abundance of sagebrush and grassland specialists such as sage grouse (*Centrocercus urophasianus*), sage thrasher (*Oreoscoptes montanus*), horned lark (*Eremophila alpestris*), Brewer's sparrow (*Spizella breweri*), grasshopper sparrow (*Ammodramus savannarum*), and sage sparrow (*Amphispiza belli*; McAdoo et al. 1989, Cox 1999, Earnst and Holmes 2012). In contrast, when sagebrush shrubs are eliminated with cheatgrass invasion, densities of burrowing owls (*Athene cunicularia*) and long-billed curlews (*Numenius americanus*) increase (Cox 1999, Earnst and Holmes 2012).

Non-native plants may increase or decrease food resources or remove or create unique habitat characteristics as they replace native vegetation. Hence, effects of non-native plants on native animals can occur via changes in trophic (i.e., food) or non-trophic pathways (i.e., habitat); effects may occur simultaneously via both pathways and the distinctions between effects transmitted through the 2 pathways are not always clear. Moreover, direct effects by either pathway may produce indirect effects. Changes in vegetation composition can affect food quality or availability for some native animals directly and others indirectly via cascading effects on trophic interactions; whereas, changes in vegetation structure may influence nesting substrates, resting sites, thermal cover, escape cover, or hiding cover, which can affect abundance of some species directly and indirectly affect other species by altering predator–prey interactions and competition.

Trophic Pathways

Increased dominance by non-native plants clearly can affect presence, abundance, and quality of food resources for herbivores, which will create potential ramifications for higher trophic levels. Although consumption or avoidance of non-native food resources is sometimes documented, the implications of such outcomes for fitness and population-level changes of native wildlife often remain unknown. Thompson (1996) documented increased foraging activity of elk in winter on sites where spotted knapweed had been removed via application of broadleaf herbicides, suggesting that spotted knapweed invasion decreased forage quality. However, Wright and Kelsey (1997) documented larger aggregations of elk and white-tailed deer in areas dominated by spotted knapweed relative to areas dominated by native plants, and they quantified high frequencies of consumption of both rosettes and seed heads of the non-native plant. Nutrient content of these parts of spotted knapweed approached that of native vegetation (Wright and Kelsey 1997). Seedheads of spotted knapweed may provide an important food source for these wild ungulates in winter, because these plant parts are commonly available above snow cover (Wright and Kelsey 1997). Crested wheatgrass and cheatgrass can comprise a large proportion of mule deer diets

when these grasses are accessible during winter, as well as during periods of new plant growth before forbs are abundant (Austin and Urness 1983, Austin et al. 1994). Other plants, such as leafy spurge, contain toxic compounds (Messersmith and Lym 1983) that may be avoided by native animals, contributing to decreases in abundance or use of invaded areas (e.g., bison [*Bison bison*] in North Dakota; Trammell and Butler 1995). Grizzly bears (*Ursus arctos horribilis*) consume large quantities of non-native dandelion (*Taraxacum officinale*) and clover (*Trifolium* spp.), but these plants provide less energy relative to other native food sources, so the net energetic value for the bears overall is unclear (Reinhart et al. 2001). However, lower quality food resources still can offer greater energetic returns if they are easy to obtain in large quantities. Because invasions often result in increased densities of non-native plants over larger areas, the balance between quantity and quality is an important factor to consider when evaluating the relative value of non-native versus native food resources.

Many species of insects, small mammals, and birds forage extensively on seeds (Janzen 1971). Diversity and abundance of seeds are likely to change with increased dominance of non-native plants, with concomitant effects on these native animals. Non-native plant seeds have been found in cheek pouches or stomachs of some species of rodents (e.g., kangaroo rats [*Dipodomys* spp.; LaTourrette et al. 1971, Henderson 1990]). Deer mice readily consume seeds of many non-native plants, particularly favoring larger seeded species, but they avoid spotted knapweed seeds, despite their large size, possibly due to chemical defenses in knapweed (Pearson et al. 2011). Ostoja et al. (2009) documented a 10-fold increase in abundance of ants in areas dominated by cheatgrass relative to native sagebrush areas, and they hypothesized that the change was due to an increase in seeds of 1–2 orders of magnitude in cheatgrass-invaded areas (Anderson and MacMahon 2001) or decreased seed predation by rodents.

Arthropod species that are herbivores may have species- or taxa-specific preferences for plant foods (Ehrlich and Raven 1964). In the absence of their native host plants, diversity and abundance of some native arthropods may decline (Knops et al. 1999). Hansen et al. (2009) documented a shift in the composition of the carabid beetle community in areas dominated by spotted knapweed, finding fewer generalist predators and more omnivores and specialist predators. The authors hypothesized that this shift was a function of changes in food availability, namely increases in Lepidoptera and spotted knapweed, which presumably were consumed by specialized and omnivorous beetles, respectively.

Changes in arthropod populations and communities following invasions can have subsequent effects on other native wildlife, including reptiles, small mammals, and birds that rely on arthropods as primary food sources. For example, areas dominated by spotted knapweed have fewer grasshoppers (Orthoptera: Acrididae), which is a major food source for many insectivorous songbirds (Ortega et al. 2006). Reductions in abundance of grasshoppers associated with

spotted knapweed invasion were correlated with delayed nest initiation in chipping sparrows (*Spizella passerina*), as well as reductions in territory density, site fidelity, and rates of double-brooding (Ortega et al. 2006). These cascading effects are not limited to changes in arthropod populations, because changes in abundance of any animal species resulting from non-native plants can have implications at higher trophic levels. For example, conversion of shrub-steppe to cheatgrass was associated with reduced abundance of small mammals and leporids, increased abundance of coyotes (*Canis latrans*), and declines in kit fox (*Vulpes macrotis*) densities (Arjo et al. 2007).

Non-Trophic Pathways

Because habitat for many species is a function of certain characteristics of vegetation structure and composition (Rotenberry 1985), shifts in vegetation characteristics resulting from invasions by non-native plants can dictate which native animals can occur in invaded areas. Increased dominance by individual species of non-native plants can result in monocultures that decrease heterogeneity of vegetation structure and diversity of native fauna because fewer species can find habitat (Crooks 2002, Martin and Murray 2011). Ostoja and Schupp (2009) observed that the majority of the Ord's kangaroo rats captured in areas dominated by cheatgrass were within 0.5 m of a Western harvester ant (*Pogonomyrmex occidentalis*) mound, where very little vegetation was present, presumably because this rodent species prefers more open sites. Invasion by cheatgrass and other non-native grasses can homogenize vegetation over large areas, greatly reducing the amount of open space. Native shrub cover can provide refugia from predators, nest sites, and clustered food resources for some native animals (Nelson and Chew 1977). The loss of native shrub species following invasion by non-native grasses may result in a shift in composition of the community of breeding birds (Wiens and Rotenberry 1985, McAdoo et al. 1989), as well as reduced presence and abundance of native rodents.

Non-native plants also can affect mobility of native animals. When non-native plants, such as cheatgrass, create dense stands and reduce open space between plants, movement of some terrestrial species may be inhibited, making predator avoidance and foraging more difficult, with implications for survival, growth, and reproduction (Newbold 2005, Rieder et al. 2010). Desert horned lizards (*Phrynosoma platyrhinos*), leopard lizards (*Gambelia wislizenii*), side-blotched lizards (*Uta stansburiana*), western whiptails (*Aspidoscelis tigris*), Great Basin pocket mice, Ord's kangaroo rats, and deer mice all move more slowly through, and often are less abundant in, areas dominated by cheatgrass (Newbold 2005, Rieder et al. 2010). Species that are larger or wider in size or use saltatory movements may be especially affected by reductions in the open space between plants (Rieder et al. 2010) as non-native plants become dominant.

Changes in vegetation structure created by a non-native plant also may be beneficial and could facilitate increased abundance, particularly if the non-native plant creates structural characteristics that are preferred by the native animal but are currently limited in the environment. For example, spotted knapweed and other non-native forbs provide taller and wider flowering stalks relative to native forb species (Pearson et al. 2011), and such flowering stalks are readily used by native spiders (Pearson 2009). Invasion by these non-native forbs into native grasslands has dramatically increased substrate availability and released native web-building spiders from substrate limitations, resulting in 20- to 85-fold increases in densities of native spiders (Pearson 2009). Additionally, the more expansive architecture of the non-native forb species allows spiders to construct larger webs that double capture rates of prey. Hence, these invasions have not only affected native spider densities, they also have altered interactions between native spiders and their prey (Pearson 2010). Although such interactions are not commonly documented in such detail, they likely are common and mechanistically predictable. For instance, raptors use perches and construction of artificial perches can increase raptor use in areas with limited perch sites (Hall et al. 1981); increased raptor use of an area where perches have been added can reduce abundance of small mammal populations (Kay et al. 1994). Hence, any non-native plant providing novel architecture such as perches, nesting sites, hiding cover, or roosting areas can influence densities of certain wildlife species, with the potential for concomitant indirect effects that result from altering interactions among predators and prey, herbivores and plants, or competitors (e.g., Pearson 2010).

EFFECTS OF WILDLIFE ON NON-NATIVE PLANTS

Although increases in distribution and abundance of non-native plants have clear implications for wildlife species, wildlife also can influence the distribution and abundance of non-native plants through pollination, herbivory, seed dispersal, seed predation, and soil disturbance (LaTourrette et al. 1971, Vander Wall 1993, Huntly and Reichman 1994, Richardson et al. 2000, Maron et al. 2012). Granivorous species, particularly ants, some birds, and small mammals, can influence plant distribution, survival, and abundance via selective seed consumption, dispersal, or caching behaviors (Vander Wall 1994, Maron and Kauffman 2006, Zwolak et al. 2010, Pearson et al. 2011). Many non-native plants, including some species in the Intermountain West such as leafy spurge and spotted knapweed (Pemberton and Irving 1990), have seeds with elaiosomes (fatty bodies that promote seed dispersal by ants; Brew et al. 1989). Jensen and Six (2006) documented native ants selecting and removing seeds of spotted knapweed, while leaving native seeds. The authors proposed that seeds of the non-native plant were being dispersed preferentially presumably due to presence of elaiosomes, which native species lacked (Jensen and Six 2006). However, seed fates were not determined in this study, so it is not known whether seeds were ultimately dispersed or consumed. Rodents typically select large-seeded species and have been shown to suppress recruitment of a number of large-seeded, non-native plants in Intermountain

grasslands through seed predation (Pearson et al. 2011, Maron et al. 2012). Although seed size is an important trait determining the effect of seed predators on non-native plants, other factors also may be important. Laboratory and field studies of predation by deer mice on spotted knapweed seeds suggest that this non-native species is avoided by deer mice despite its large seed size, which may be due to chemical defenses (Pearson et al. 2011). Herbivory by rodents also may be important in suppressing some non-native plants. Long-term studies have shown that the combined effects of flower herbivory by Columbian ground squirrels (*Spermophilus columbianus*) and seed predation by deer mice decrease abundance of the non-native biennial, *Tragopogon dubius*, ≥5-fold (Pearson et al., 2012b). Rodent herbivory also seems to reduce recruitment of cheatgrass (Pierson and Mack 1990) and a variety of non-native forbs (MacDougall and Wilson 2007). In contrast, long-term studies of ungulate exclosures in this region have provided no indication that large herbivores favor or suppress non-native plants (Detling 1998, Stohlgren et al. 1999).

The overall influence of native consumers on non-native plant invasions will depend on the relative selectivity and resulting effect of consumers on non-native versus native species. Based on seed addition experiments in the field, large-seeded natives were affected more by rodent seed predation than were large-seeded non-natives, possibly due to defense mechanisms occurring more commonly in the non-native species (Maron et al. 2012); however, seeds of non-native plants were more common in pouches of *Dipodomys* spp. than were seeds of native plants (LaTourrette et al. 1971). Animals also may facilitate invasions by non-native plants through soil disturbance. Recent studies show that non-native plants had higher recruitment under disturbed conditions than did native plants in Intermountain grasslands (Maron et al. 2012), suggesting that non-native plants may benefit more when animals disturb the soil. Native consumers may seek refuge in the increased vegetation cover provided by non-native plants, which in turn may result in increased predation pressure on the native seeds and facilitate further invasion (i.e., apparent competition; Orrock et al. 2008, 2010).

Wildlife may also facilitate invasions by dispersing non-native plant seeds. Seed consumption may result in seed dispersal, intentionally or unintentionally, as long as passed seeds remain viable (Pearson and Ortega 2001, Wald et al. 2005). Seeds of non-native plants, including leafy spurge and spotted knapweed, have been found in feces of white-tailed and mule deer (Wright and Kelsey 1997, Wald et al. 2005), elk (Wright and Kelsey 1997), sharp-tailed grouse (*Tympanuchus phasianellus*; Wald et al. 2005), and even great-horned owls (*Bubo virginianus* [likely via consumed deer mice; Pearson and Ortega 2001]), but rates of germination of passed seeds were relatively low. Although mourning doves (*Zenaida macroura*) readily consume seeds of leafy spurge, very few seeds remain intact after digestion; nestlings may not be able to digest seeds fully, so intact seeds may remain in nesting material and could germinate if nests fall to the ground (Blockstein et al. 1987). Seeds of some

non-native plants may be dispersed on fur and feet of animals (e.g., bison; Wald et al. 2005), especially when seeds have structures that promote adherence, such as barbed awns of medusahead (Davies and Johnson 2008).

INTENTIONAL INTRODUCTIONS OF NON-NATIVE SPECIES

Land managers, including wildlife managers, have a long history of intentionally introducing non-native plants to provide both food and habitat for wildlife species. Plantings of non-native species for habitat improvement have occurred in the Intermountain West, including several species of non-native grasses and woody plants (e.g., crested wheatgrass, Russian olive [*Elaeagnus angustifolia*], Siberian peashrub [*Caragana arborescens*]; Borell 1951, McAdoo et al. 1989, Katz and Shafroth 2003, Parks et al. 2005, Fischer et al. 2012). Crested wheatgrass was planted widely in the Great Basin for livestock and wildlife forage, and as a barrier to cheatgrass invasion (Clements and Young 1997). Data from studies examining the value of crested wheatgrass plantings for mule deer suggest this plant can provide valuable forage if it does not displace critical browse (reviewed in Clements and Young 1997). Although intentional planting of some species has slowed or stopped altogether, these plants continue to spread, along with seed contaminants (e.g., Canada thistle and musk thistle [*Carduus nutans*]; Parks et al. 2005). The practice of introducing non-native plants for wildlife habitat is questionable where information is insufficient to fully understand the broader ramifications for animal species and other organisms.

Weed management sometimes involves the intentional introduction of non-native organisms, which can affect wildlife populations. Classical biological control is the intentional introduction of non-native insects to control non-native plants—an approach that is widely practiced across the Intermountain West (Coombs et al. 2004). This method can effectively reduce the abundance and distribution of some non-native plant populations (e.g., McFadyen 1998), which likely will mitigate weed impacts on wildlife, although this rarely is quantified. However, in some cases, the use of introduced insects to control the non-native plant has resulted in complex changes to populations and communities of native animals and reduced the efficacy of the control measures (Pearson 1999, Ortega et al. 2004, Stanley 2005, Pearson and Fletcher 2008, Crider 2011). The cinnabar moth (*Tyria jacobaeae*) and gall flies (*Urophora* spp.) that were released to control tansy ragwort (*Senecio jacobaea*) and spotted knapweed, respectively, were utilized as food resources by native ants, small mammals, and birds; this reduced populations of the biological control species and, in some cases, increased abundance of native animal populations (Ortega et al. 2004, Stanley 2005, Pearson and Fletcher 2008, Crider 2011). The larvae of gall flies that now infest seed heads of spotted knapweed provide an abundant and important food subsidy for deer mice in winter when food is less abundant, resulting in increased survival and population size of deer mice, shifts in mouse use of the landscape, and increased prevalence of hantavirus in mouse

populations (Pearson et al. 2000, Pearson and Callaway 2006, Pearson and Fletcher 2008). Exploitation of these same larvae by native birds illustrates how the plasticity of native wildlife may influence their ability to capitalize on non-native species as novel resources. Although black-capped chickadees (*Poecile atricapillus*) co-occur with mountain chickadees (*P. gambeli*) in mixed winter flocks and have similar diets and foraging behaviors, black-capped chickadees are able to exploit gall fly larvae many times more effectively than are mountain chickadees, resulting in potentially important ramifications for interspecific competition and the ecology of black-capped chickadees (Greenwood 2011).

FUTURE DIRECTIONS, MANAGEMENT IMPLICATIONS, AND RESEARCH NEEDS

New invaders continue to enter native ecosystems and current invaders continue to spread. Additionally, distributions of many species of non-native plants are predicted to change with altered climate patterns; some plant species are likely to increase in distribution and abundance in the region, others may decrease, and the distribution of other species may shift (Chornesky et al. 2005, Bradley et al. 2009). Although non-native species have been somewhat less problematic in high-elevation ecosystems, changes in climatic conditions that include longer growing seasons and reduced snow pack (Mote et al. 2005), and increased human access may result in increased presence and abundance of non-native plants in higher elevation environments (Pauchard et al. 2009). Further, changes in disturbances such as fire frequency and intensity, grazing, road construction, and vehicular traffic, which leads to increased seed distribution at all elevations can also contribute to increases in distribution and abundance of non-native plants (Mack 1981, Pyke 1999, Keeley 2006, Pauchard et al. 2009).

Management of non-native plants in the Intermountain Region has increased greatly in the past 2 decades. Broadleaf herbicides are used widely to control invasive forbs, with applications over large areas, usually by helicopter, often applied repeatedly to maintain control over time. Additionally, many species of non-native insects have been introduced for weed control in the context of classical biological control (Coombs et al. 2004). Herbicides are quite effective at suppressing some broadleaf forbs, such as spotted knapweed (Rice et al. 1997; Pearson and Fletcher 2008; Ortega and Pearson 2010, 2011), and in some cases, biocontrol agents may suppress major weed species (Story et al. 2006, Seastedt et al. 2007, Myers et al. 2009, Butler and Wacker 2010). However, researchers only recently are beginning to take a more comprehensive approach to examine how whole-plant communities respond to weed management (Rinella et al. 2009, Butler and Wacker 2010, Ortega and Pearson 2010, 2011). Such studies have found complex outcomes of management actions for weed control, which include secondary invasion by other weeds, suppression of native forbs, and intricate effects on food webs (Pearson and Callaway 2003, Pearson and Ortega 2009, Rinella et al. 2009, Ortega and Pearson 2010). Thus, weed management of natural areas is in its infancy and very little work has been done to examine whether weed control measures can mitigate the effects of non-native plants on higher trophic levels (e.g., Pearson and Fletcher 2008). There is an urgent need for studies examining efficacy of weed management on plants at the community level, as well as the effects on wildlife that may be affected by invasions or impacted by treatments (see Table 1 in Chambers and Wisdom 2009). This need is particularly acute given that wildlife sometimes experience side effects of weed management actions directly (e.g., Pearson and Callaway 2003, Greenwood 2011).

Although effects of some non-native plants on some species of wildlife in this region have been well-studied (such as spotted knapweed in MT), sizeable information gaps remain regarding effects of most non-native plants on most native fauna in the Intermountain West. In particular, although various interactions have been documented, we have poor understanding of how non-native plants actually influence populations of most wildlife species. In other words, many studies document habitat use or quantify how non-native plants may affect wildlife food, but effects of non-native plants are rarely quantified in terms of fitness or demographic parameters (e.g., survival, reproduction, age, and sex ratios) that may be masked when assessing presence or abundance alone (e.g., Ortega et al. 2006). Beyond this, the mechanisms for documented changes are rarely examined, with few exceptions (e.g., Newbold 2005, Ortega et al. 2006, Pearson and Fletcher 2008, Pearson 2009). From an approach standpoint, combining observational studies with large or small-scale experiments is necessary to isolate these causal mechanisms. Further, much of the existing research draws comparisons between areas dominated by native plants and invaded areas, perhaps at low and high densities of the non-native plant. Research projects that seek to quantify changes along a gradient of dominance by the non-native plant would provide important information to identify thresholds where responses of wildlife species may change in direction and magnitude. Although a good deal more work should be done to fully understand how non-native plants affect populations, communities, and ecosystem function, our review suggests that general understandings of the habitat and dietary requirements of wildlife species and the structure and function of non-native plants relative to the native plants they replace can help to build a predictive framework regarding the effects of plant invasions on higher trophic levels.

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