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EFFECTS OF BIOLOGICAL CONTROL AGENTS AND EXOTIC PLANT INVASION ON DEER MOUSE POPULATIONS

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Abstract. Exotic insects are commonly introduced as biological control agents to reduce densities of invasive exotic plants. Although current biocontrol programs for weeds take precautions to minimize ecological risks, little attention is paid to the potential nontarget effects of introduced food subsidies on native consumers. Previous research demonstrated that two gall flies (*Urophora affinis* and *U. quadrifasciata*) introduced for biological control of spotted knapweed (*Centaurea maculosa*) dramatically affect the foraging ecology of the deer mouse (*Peromyscus maniculatus*), a native generalist predator with important trophic linkages. In the current study, we found that relative abundance of deer mice was elevated twofold in grassland habitats with high densities of spotted knapweed and gall fly food sources, compared to those dominated by native vegetation, in two of three years. Availability of gall fly larvae during the critical overwinter period appeared to reduce overwinter population declines of mice in knapweed-invaded habitats. These positive effects on populations apparently overshadowed negative effects on breeding productivity associated with knapweed invasion and loss of the gall fly resource during the summer. Our results suggest that insect biocontrol agents can subsidize native consumer populations, setting the stage for various indirect effects on food webs. Comprehensive understandings of the conditions under which introduced biological control agents may exhibit nontarget effects on native food webs are needed to further develop criteria for screening potential biocontrol agents before they are released.

Key words: biological control agents; Centaurea maculosa; *deer mice; exotic plants; food subsidies; spotted knapweed; Lolo National Forest, Montana, USA; nontarget effects;* Peromyscus maniculatus; Urophora *spp.*

INTRODUCTION

Exotic plant invasions present a global threat to the conservation of native systems (Vitousek et al. 1996, Wilcove et al. 1998, Mack et al. 2000). In western North America alone, vast areas have undergone dramatic shifts from native vegetation to domination by exotic plants, resulting in diminished biological diversity and altered ecosystem processes (D'Antonio and Vitousek 1992, Higgins et al. 1999, Sheley and Petroff 1999). A common strategy for combating exotic plant invasions is classical biological control, where exotic insects are introduced to suppress densities of target weeds (McEvoy and Coombs 1999). Although biocontrol agents have successfully controlled several highly invasive species (Huffaker and Kennett 1959, Simmonds and Bennett 1966, McEvoy et al. 1991), biological control practices have proven controversial because of the ecological risks associated with the deliberate introduction of exotic organisms (DeLoach 1991, Simberloff and Stiling 1996*a*, *b*, Follett and Duan 2000, Pemberton 2000, Strong and Pemberton 2000, Louda et al. 2003, Pearson and Callaway 2003). Most of this concern has focused on the potential for introduced insects to have direct, negative effects on nontarget, native plants through host switching (e.g., Louda et al. 1997). To reduce this risk, current weed control programs screen potential biocontrol agents for host specificity prior to release (Rees et al. 1996, McEvoy and Coombs 2000). This emphasis on host specificity as criterion for release implicitly assumes that nontarget effects arise primarily from host switching (Harris 1990, DeLoach 1991, McFadyen 1998).

However, biocontrol agents need not attack nontarget organisms to exhibit nontarget effects (McEvoy 1996, Secord and Kareiva 1996, Simberloff and Stiling 1996*a*, *b*, Callaway et al. 1999, Pearson et al. 2000, Pearson and Callaway 2003). Biocontrol agents that establish, but fail to control the target weed are common (McEvoy and Coombs 1999) and can become superabundant in association with their prolific hosts (e.g., Myers and Harris 1980). These introduced insects are commonly consumed by native predators (Goeden and Louda 1976, Story et al. 1995), and can significantly impact the ecology of nontarget species by serving as an alternate food resource (Pearson et al. 2000). Therefore, superabundant biocontrol agents have great potential to subsidize native consumer populations and could indirectly impact other nontarget species through food web interactions (Pearson and Callaway 2003). Recent papers demonstrate that both natural and an-

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thropogenic food subsidies can elevate consumer populations, touching off a range of indirect effects on community structure and function, sometimes leading to trophic cascades (Ostfeld et al. 1996, Jones et al. 1998, Jefferies 2000). However, the consequences of introduced biocontrol food sources on consumer populations and associated food webs are virtually unstudied. We examined the effects of spotted knapweed (*Centaurea maculosa* Lamarck), an invasive exotic plant, and two of its associated biological control agents on populations of the deer mouse (*Peromyscus maniculatus*), a native generalist predator capable of influencing food webs.

Spotted knapweed is one of the most widely established exotic plants in western North America (Sheley et al. 1998). A perennial forb of Eurasian origin, knapweed invades arid grasslands, prairies, and savannas, displacing diverse native plant communities through a variety of interactions (Tyser 1992, Marler et al. 1999, Ridenour and Callaway 2001, Bais et al. 2002). In an effort to counter spotted knapweed invasion, 13 species of exotic insects have been introduced as biological control agents since the 1970s (Lang et al. 2000). Among the first biological control agents to be released were the gall flies *Urophora affinis* (Frauenfeld) and *U. quadrifasciata* (Meigen). These species oviposit within immature knapweed seedheads in June, and their larvae induce gall formation and overwinter within seedheads from September to May (Story et al. 1992). By current standards, gall flies have performed reasonably well as biological control agents. They quickly dispersed and established throughout the range of spotted knapweed in North America (Story et al. 1992). Moreover, gall flies have remained host specific (Maddox 1982), and their larvae have been shown to reduce knapweed seed production (Story et al. 1992). Nonetheless, densities of spotted knapweed have not been reduced, allowing gall flies to attain seedhead densities 12–18 times greater than those observed in their native range (Myers and Harris 1980). In turn, the superabundance of these insects has provided a new food resource for a variety of predators (Story et al. 1995, Pearson et al. 2000).

Small mammals serve as prominent predators and prey in food webs, influencing plants, arthropods, and larger predators (Holling 1959, Brown and Heske 1990, Korpimaki and Norrdahl 1991, Ostfeld et al. 1996, Maron and Simms 2001, Schnurr et al. 2002). Deer mice are native rodents that numerically dominate small mammal communities in arid grasslands of western Montana (Pearson et al. 2001). These opportunistic feeders have become aggressive gall fly predators, consuming hundreds of larvae per mouse per day in grasslands invaded by spotted knapweed (Pearson et al. 2000). In fact, deer mice in these habitats prey primarily on gall fly larvae during most of the year, patterning their foraging activities after the seasonal availability of the introduced resource (Pearson et al. 2000). Gall fly larvae comprise up to 86% of the deer mouse diet in winter, but become unavailable to mice in summer (June–August) when adult flies emerge from seedheads. During the period of gall fly availability (September–May), deer mice in knapweed-invaded grasslands select microhabitats within dense knapweed stands where larvae are most abundant. In contrast, deer mice avoid dense knapweed in summer when gall flies are unavailable, favoring adjacent microhabitats with the lowest levels of knapweed invasion. This seasonal shift in foraging activities focused around microhabitats with an abundance of gall flies suggests that knapweed-invaded grasslands offer higher quality habitat for deer mice than grasslands dominated by native vegetation due to the availability of the gall fly resource. Because winter is the typical season of resource scarcity for temperate-zone mice, when breeding ceases and population sizes diminish (Sadlier et al. 1973, Fairbairn 1977, Tait 1981), the availability of gall fly larvae during this period could subsidize deer mice by alleviating the winter population bottleneck (Pearson et al. 2000). However, in summer, when gall fly larvae disappear, knapweed-invaded grasslands may provide relatively low quality habitat if native resources have been reduced by knapweed. Because this period represents a substantial portion of the typical breeding season for deer mice in western Montana (Metzgar 1979), breeding productivity could be reduced in knapweed-invaded habitats.

Although animal populations can be controlled from above by predators, food availability serves as an important bottom-up control (e.g., Korpimaki and Krebs 1996, Rose and Polis 1998). Food limitation is a primary factor for *Peromyscus* based on numerous studies correlating increased population size with the periodic abundance of seed crops in forested habitats (Gashwiler 1979, Elkinton et al. 1996, Ostfeld et al. 1996, Morrison and Hall 1998, McCracken et al. 1999, Schnurr et al. 2002) and with supplemental feeding (Fordham 1971, Gilbert and Krebs 1981, Tait 1981, Hall and Morrison 1998). Those studies in which food subsidies spanned the overwinter period linked population increases to higher rates of overwinter residency, suggesting increased survival; higher numbers of unmarked adults, indicating increased immigration; and extended breeding seasons and increased production of juveniles (Gashwiler 1979, Tait 1981, Elkinton et al. 1996, Ostfeld et al. 1996, Morrison and Hall 1998). However, studies of food subsidies conducted in northern continental regions similar to Montana have not reported extended breeding seasons (Gilbert and Krebs 1981, McAdam and Millar 1999).

Previous studies of food limitation in *Peromyscus* predict that deer mouse populations in habitats invaded by spotted knapweed will be positively influenced by the gall fly resource during the overwinter period. However, populations may be negatively influenced by the disappearance of this food source in summer, affecting

the breeding season, particularly if traditional resources have been reduced by knapweed invasion. If overwinter effects on population processes overpower breeding season effects, the availability of gall fly biological control agents may translate into elevated levels of deer mouse populations in knapweed-invaded habitats.

We studied deer mice in grasslands of western Montana that were either invaded by spotted knapweed or dominated by native vegetation to examine population-level effects of altered food resources related to knapweed invasion and the introduction of gall fly biocontrol agents. Such understandings are critical to evaluating the ecological implications of current management strategies aimed at exotic plant invasions. By considering seasonal patterns in deer mouse abundance and population structure, we assessed potential mechanisms of population change in knapweed-invaded vs. native habitats. We predicted that knapweed-invaded habitats would be characterized by (1) elevated levels of deer mice, (2) reduced overwinter population declines, and (3) diminished breeding productivity.

Methods

Study sites

We conducted our studies in bluebunch wheatgrass (*Psuedoroegnaria spicatum*) grassland types (Mueggler and Stewart 1980) occurring on southwest aspects at elevations between 1300 and 1700 m. Common native bunchgrasses also included Idaho fescue (*Festuca idahoensis*), Sandberg's bluegrass (*Poa sandbergii*), and June grass (*Koeleria cristata*). Diverse native forb communities consisted primarily of arrowleaf balsamroot (*Balsamorhiza sagittata*), followed by lupine (*Lupinus* spp.), yarrow (*Achillea millefolium*), and blue-eyed Mary (*Collinsia parviflora*) (Y. K. Ortega, *unpublished data*). Study sites were steep (average slope of 30%) savannas with scatterings of ponderosa pine (*Pinus ponderosa*; 60% of trees) and Douglas-fir (*Pseudotsuga menziesii*; 40% of trees), and were located within a matrix of Douglas-fir-dominated montane coniferous forest on the Lolo National Forest in western Montana. We chose study sites to be as similar as possible while representing either knapweed-invaded or native habitats. The former had dense patches of spotted knapweed with associated gall fly populations intermixed with areas of native vegetation, while the latter were dominated by native vegetation with only trace amounts of knapweed. We located four transects at each of four knapweed and native sites, respectively.

Deer mouse abundance and population status

Mice were trapped on each transect using 20 Sherman live traps (HB Sherman Traps, Tallahassee, Florida, USA) spaced at 10-m intervals. Transects were oriented perpendicular to the slope and 50 m apart. Although transects were located as far from forest edges as possible, all traps fell within 200 m of dense forest because study sites were relatively small openings (mean approximate area = 11.0 ± 1.49 ha, mean ± 1 SE; range 6.0–18.0 ha). Because only 3.6% of mice were captured on >1 transect, we treated each transect as independent. During each sampling period, traps were baited with peanut butter and whole oats, covered with closed-cell foam for protection from heat and cold, and checked two times per morning for 4 days. Mice were tagged with no. 1005-1 monel ear tags (National Band and Tag, Newport, Kentucky, USA); species, sex, mass (to the nearest 0.5 g), pelage characteristics (e.g., Metzgar 1979), and reproductive condition were recorded before release at the trap station. We defined age categories based on mass distributions, using pelage information as a guide, with juveniles ≤13.5 g, subadults 14.0–17.5 g, and adults ≥18 g. Males with enlarged testes and females with enlarged mammae or signs of pregnancy (i.e., swollen abdomen, weighing ≥25.0 g) were considered reproductively active.

From 1999 to 2001, we trapped mice during each of three seasons corresponding to differing periods of *Urophora* availability and mouse population status. Trapping was conducted in spring (May), when gall fly larvae were available within knapweed seedheads and mouse populations were primarily overwintered animals in the early stages of breeding; summer (July), when larvae were unavailable and lactation and weaning were peaking; and fall (September) when larvae were again available and mice were in the final stages of breeding (Metzgar 1979, Story et al. 1992, Pearson et al. 2000). Transects at two knapweed sites and two native sites were not trapped in the fall of 2000 due to severe wildfire threat.

Because captures of mice were well below recommended samples for population estimation models (n = 100 per sample unit; White et al. 1982, Menkins and Anderson 1988), we used the number of unique individuals trapped per transect to index abundance for each trapping period. This measure of relative abundance has been shown to be robust vs. population estimators for comparing study populations at small sample sizes (McKelvey and Pearson 2001). Recaptures of fall-marked animals were low in spring trapping periods (<5%), precluding consideration of overwinter survival (i.e., estimation with open population models) or residency. However, for both of these measures of population turnover, the processes of mortality and emigration are confounded (Lebreton et al. 1993). For these reasons, we used the difference in number of captured individuals per transect between the fall and spring, relative to the initial number of individuals in the fall (included as a covariate; see *Methods: Statistical analyses*), as an overall index of overwinter population change (e.g., Millar and Innes 1983). Assuming juveniles were recently weaned individuals produced on site, we used the total number of juveniles caught across seasons relative to the number of breeding-age

individuals (i.e., nonjuveniles) caught in spring as an index of breeding productivity.

Habitat variables

We visually estimated percent cover of habitat variables within a 5 m radius of each trap station during July of each year after Pearson et al. (2000, 2001). Habitat variables included: spotted knapweed, the primary invasive forb; cheatgrass (*Bromus tectorum*), the primary invasive grass; arrowleaf balsamroot, the dominant native forb; bunchgrasses, native grasses, as described in the *Methods: Study sites;* shrubs, primarily serviceberry (*Amelanchier alnifolia*) and snowberry (*Symphoricarpos albus*); bare ground, including litter and moss; and rocks ≥10 cm. Cover estimates were made by the same pair of observers at all sites within each year, but observers varied among years. In 1999, we also measured diameter at breast height (dbh) of trees within each plot from which we estimated total basal area. Habitat variables were averaged across stations to characterize each transect.

Relationships among gall fly larvae, knapweed, and deer mice

Each year, we collected up to 10 knapweed seedheads from haphazardly selected plants at alternating trap stations on knapweed transects. The number of *Urophora* larvae per seedhead was determined and averaged across stations for each transect. To estimate the average density of gall fly larvae available to mice across years, we multiplied the average number of larvae per seedhead by the approximate density of seedheads per transect. The latter was calculated from the average knapweed cover per transect by applying a regression between knapweed cover and seedhead density (r^2 = 0.78, SE = 15.14, $P < 0.001$) developed from data collected in 2000 at eight additional grassland sites in western Montana (D. E. Pearson, *unpublished data*). For mice captured in knapweed habitats, we used resource selection function analysis of categorical data (Manly et al. 1993) to evaluate microhabitat selection for three levels of knapweed cover by season, following Pearson et al. (2000). This analysis compared stations capturing mice to all available stations in terms of their distribution among knapweed cover classes, yielding selection ratios. Selection ratios >1.0 indicated selection for a knapweed category, while ratios <1.0 indicated avoidance (Manly et al. 1993).

Statistical analyses

To test for differences in relative abundance of mice between knapweed and native transects for each year, we used mixed linear models, treating season as a repeated measure and site as a fixed factor. Because habitat factors unaffected by exotic plant invasion could influence mouse abundance, we also added basal area of trees, shrub cover, and rock cover to models as covariates. However, for all years, shrub cover, rock cover, and basal area of trees had weak influence on relative abundance of mice per transect and did not affect patterns in relative abundance by knapweed invasion or season. We therefore present results for models without covariates.

Comparisons between habitat variables associated with knapweed and native transects were made with general linear models, treating site as a fixed factor and analyzing each year separately. Overwinter population change was analyzed with the same model except that we included the number of individuals captured in the fall as a covariate. We tested assumptions of normality and homogeneity of variance for all dependent variables using Shapiro-Wilk and F_{max} tests (Tabachnick and Fidell 1989). In all cases, variables could not be successfully transformed with standard methods. We therefore used untransformed values under the assumption that ANOVA is robust to violations of normality given adequate sample sizes (error degrees of freedom >20; Tabachnick and Fidell 1989). We also investigated heterogeneity of variance models, but since they did not improve model fit according to AIC scores, we present results for standard variance models. Covariates were tested for homogeneity of regression slopes before addition to models (Tabachnick and Fidell 1989).

To compare the number of mice in each age class between knapweed and native habitats for each season, we used χ^2 goodness-of-fit tests, assuming equal proportions. We used χ^2 homogeneity tests to compare the distribution of individuals by age, sex, and reproductive activity between knapweed and native habitats for each season, and to compare indices of breeding productivity between the two habitat types. For microhabitat analyses, χ^2 homogeneity tests were used to determine whether selection ratios were significantly different from 1.0 (Manly et al. 1993). For all χ^2 analyses, we pooled data across years after inspecting year-specific results because captures of mice per category were low; when patterns appeared to diverge among years, we also present information on year-specific trends. All statistical analyses were conducted with SAS software (SAS Institute 1999).

RESULTS

Trapping efforts from 1999 to 2001 amounted to 21 760 trap nights, producing 913 captures of 583 individual deer mice with low mortality levels (<4%). Also captured were 227 yellow-pine chipmunks (*Tamias amoenos*), 64 Columbian ground squirrels (*Spermophilis columbianus*), 51 golden-mantled ground squirrels (*Spermophilis lateralis*), 12 western jumping mice (*Zapus princeps*), nine red-tailed chipmunks (*Tamias ruficaudus*), six montane voles (*Microtus montanus*), and two long-tailed voles (*Microtus longicaudus*).

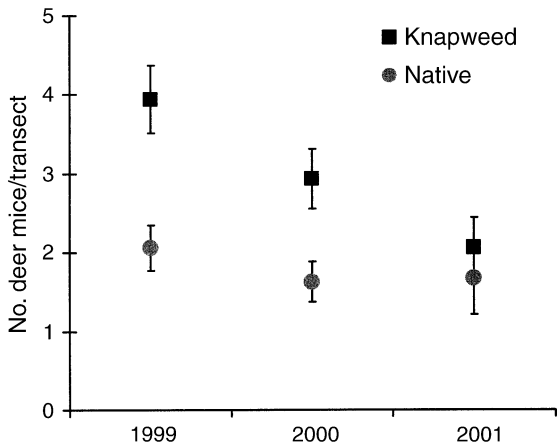

FIG. 1. Comparisons of relative abundance (mean ± 1 SE) of deer mice between knapweed and native transects in grasslands of the Lolo National Forest, Montana, 1999–2001.

Deer mouse abundance and population status

In both 1999 and 2000, relative abundance of mice was significantly higher on knapweed vs. native transects ($F > 13.0$, df = 1, 24, $P = 0.001$; Fig. 1). In these years, mice showed seasonal patterns in relative abundance, peaking in the fall (1999, $F = 5.2$, df = 2, 60, $P = 0.008$; 2000, $F = 10.97$, df = 2, 44, $P < 0.001$; Fig. 2A, B). In 1999, differences between knapweed and native transects appeared to be most pronounced in spring, diminishing in summer and fall, but did not vary significantly with season (knapweed × season interaction: $F = 1.12$, df = 2, 60, $P = 0.33$). In 2000, differences between knapweed and native transects varied significantly with season ($F = 3.25$, df = 2, 44, $P = 0.001$), as spring and fall differences were greater than summer differences (knapweed × season contrast: $t = -2.54$, df = 44, $P = 0.015$). In both years, the proportional difference in mice captured on knapweed vs. native transects was greatest in spring, when we trapped >3.3 times as many mice on knapweed transects compared to a maximum difference of twofold in other seasons. Overwinter decline in abundance from fall 1999 to spring 2000 was significantly less ($F = 7.08$, df = 1, 23, $P = 0.01$) on knapweed transects (least squares mean adjusted for fall relative abundance: 1.8 ± 0.4 mice/transect) relative to native transects (least squares mean adjusted for fall relative abundance: 3.3 ± 0.4 mice/transect).

In 2001, relative abundance of mice did not significantly differ between knapweed and native transects ($F = 2.31$, df = 1, 24, $P = 0.14$; Fig. 1) or by season ($F = 1.0$, df = 2, 60, $P = 0.37$; Fig. 2C), and knapweed and seasonal factors did not interact ($F = 1.36$, df = 2, 60, $P = 0.26$). Overwinter decline in abundance from fall 2000 to spring 2001 did not differ ($F = 0.34$, df = 1, 11, $P = 0.57$) between knapweed (least squares mean adjusted for fall relative abundance: 2.0 ± 0.58 mice/transect) and native transects (least squares mean adjusted for fall relative abundance: 1.4 ± 0.58 mice/transect).

The spring distribution of mice by age class, pooled across years, was skewed toward adults, which comprised >80% of the total sample, and did not differ between knapweed and native habitats ($\chi^2 = 0.41$, df = 1, $P = 0.81$; Table 1). Numbers of both adult and subadult mice trapped in knapweed habitats were more than double those of native habitats ($P < 0.02$). Juveniles showed a similar trend that was not significant ($P = 0.13$), possibly due to small sample sizes. The increased number of spring adults in knapweed vs. native habitats reflected 1999–2000 results, when 83 adults were caught in knapweed habitats vs. 27 in native habitats ($\chi^2 = 28.5$, $P < 0.001$), and not 2001 when captures were comparable between habitat types

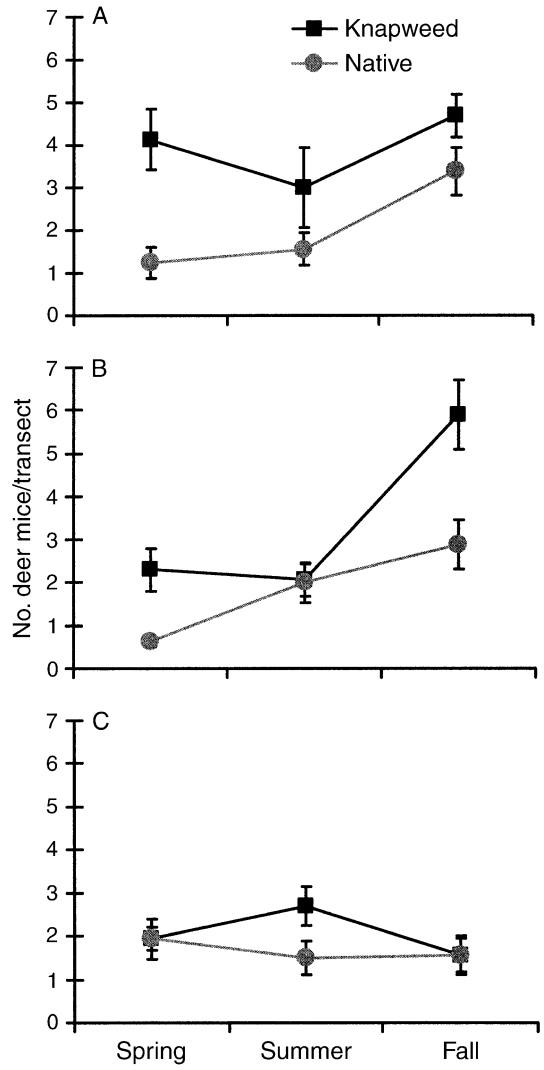

FIG. 2. Seasonal comparisons of relative abundance (mean ± 1 SE) of deer mice between knapweed and native transects in grasslands of the Lolo National Forest for (A) 1999, (B) 2000, and (C) 2001.

TABLE 1. Number of deer mice captured in knapweed vs. native habitats in the Lolo National Forest, Montana, 1999–2001, by age class and season.

Season and age class	Knapweed	Native	Total	χ^2	P
Spring					
Adult	106	51	157	19.27	<0.001
Subadult	19	7	26	5.54	0.02
Juvenile	8	3	11	2.27	0.13
Summer					
Adult	83	45	128	11.28	<0.001
Subadult	26	19	45	1.09	0.3
Juvenile	12	15	27	0.33	0.56
Fall					
Adult	81	44	125	11.28	<0.001
Subadult	40	39	79	1.09	0.3
Juvenile	25	19	44	0.33	0.56

Note: For each season, statistics are given for comparisons of numbers of individuals per age class (χ^2 goodness-of-fit tests, df = 1).

(n = 23 and 24 adults, respectively; $\chi^2 = 0.02$, $P = 0.88$).

In summer, we caught fewer adult mice and more subadults and juveniles relative to spring (Table 1). More adults were trapped in knapweed vs. native habitats ($P < 0.001$), while captures of subadults and juveniles did not differ between knapweed and native habitats ($P > 0.29$). Knapweed vs. native habitats tended to have proportionately fewer juveniles relative to adults, but the distribution of individuals among age classes did not significantly differ between habitat types ($\chi^2 = 4.06$, df = 1, $P = 0.13$).

From summer to fall, captures of juvenile and subadult mice increased with little change in numbers of adults (Table 1). The number of adults trapped in fall was higher in knapweed vs. native habitats ($P < 0.001$), and numbers of subadults and juveniles did not differ between habitat types ($P > 0.3$). Knapweed vs. native habitats tended to have proportionately fewer subadults relative to adults, but the distribution of individuals among age classes did not significantly differ between knapweed and native habitats ($\chi^2 = 4.11$, df = 1, $P = 0.13$).

The proportion of female vs. male mice captured in knapweed and native habitats over all years was comparable in spring (58.0% vs. 55.7% females; $\chi^2 = 0.09$, df = 1, $P = 0.77$), summer (48.3% vs. 57.7% females; $\chi^2 = 1.66$, df = 1, $P = 0.2$), and fall (58.3% vs. 48.0% females; $\chi^2 = 2.55$, df = 1, $P = 0.11$). The proportion of breeding-age females (i.e., nonjuveniles) that were reproductively active did not differ between habitat types in spring (34.7% vs. 30.3%; $\chi^2 = 0.2$, df = 1, $P = 0.66$), summer (48.1% vs. 39.0%; $\chi^2 = 0.76$, df = 1, $P = 0.38$), or fall (33.8% vs. 39.5%; $\chi^2 = 0.56$, df = 1, $P = 0.56$). The proportion of breeding-age males that were reproductively active did not differ between knapweed and native habitats in spring (49.0% vs. 64.0%; $\chi^2 = 1.52$, df = 1, $P = 0.22$) or summer (58.9% vs. 56.5%; $\chi^2 = 0.04$, df = 1, $P = 0.84$), but proportionately more males were reproductively active in knapweed vs. native habitats in the fall (37.7% vs. 17.8%; $\chi^2 = 4.75$, df = 1, $P = 0.03$).

Breeding productivity indexed across years was lower in knapweed vs. native habitats ($\chi^2 = 4.44$, df = 1, $P = 0.04$; Table 1). Patterns were strong in 1999 and 2000 when the total number of juveniles captured relative to spring breeders was 36.7% in knapweed habitats vs. 96.6% in native habitats ($\chi^2 = 8.89$, df = 1, $P = 0.003$). However, in 2001, productivity was 33.3% in knapweed habitats compared to 31.0% in native habitats and did not significantly differ ($\chi^2 = 0.02$, $P = 0.9$).

Habitat variables

Habitat variables related to exotic plant invasion differed significantly between knapweed and native transects in all years (Fig. 3). Knapweed cover on knapweed transects averaged >25% in 1999 and 2000, and 17.6% in 2001, compared to <1% on native transects across years ($F > 17.9$, df = 1, 24, $P < 0.001$). Cheatgrass, the primary exotic grass, occurred at low levels (<7% cover) on both knapweed and native transects, but was more prevalent on knapweed transects ($F > 4.4$, df = 1, 24, $P < 0.05$). Cover of balsamroot, bunchgrass, and bare ground was high relative to other habitat components on native transects and each was reduced on knapweed transects ($F > 5.8$, df = 1, 24, $P < 0.025$).

Habitat variables unrelated to exotic plant invasion also differed between knapweed and native transects (Fig. 3). Knapweed transects had significantly more shrub and less rock ($F > 5.7$, df = 1, 24, $P < 0.025$, except for shrubs in 2000 where $F = 2.15$, $P = 0.16$), but cover was low relative to other habitat components and differences averaged <5%. The density of trees did not differ ($F = 1.41$, df = 1, 24, $P = 0.25$) between knapweed (47.7 ± 8.28 trees/ha) and native (36.0 ± 9.77 trees/ha) transects. However, trees tended to be smaller on knapweed transects such that basal area was significantly lower ($F = 7.38$, df = 1, 24, $P = 0.012$) on knapweed (2.2 ± 0.58 m^2/ha) vs. native transects (5.2 ± 1.05 m^2/ha).

Relationships among gall fly larvae, knapweed, and deer mice

Urophora were the only abundant parasites of knapweed seedheads observed on study sites, occupying 68.4% of 5049 seedheads collected from 1999 to 2001. These larvae occurred on knapweed transects at an average of 1.8 ± 0.14 larvae per seedhead, amounting to >300 larvae/m^2, based on average knapweed cover (22.9%) and its relationship to seedhead density. However, the distribution of the gall fly resource was patchy along knapweed transects, as 45% of trap stations had low knapweed cover (0–15%), 21% had moderate cover (16–30%), and 34% had high cover (>30%).

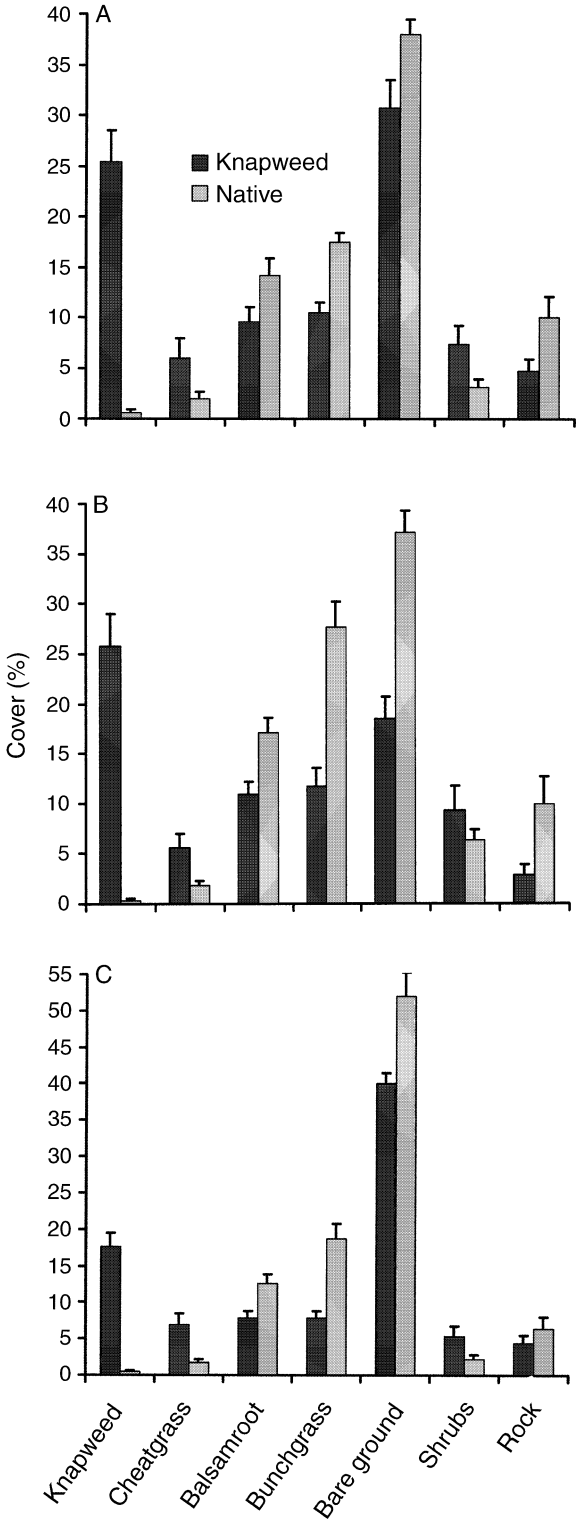

FIG. 3. Comparisons of habitat variables (mean ± 1 SE) between knapweed and native transects in grasslands of the Lolo National Forest for (A) 1999, (B) 2000, and (C) 2001.

Patterns in microhabitat selection by deer mice followed the spatial and seasonal availability of the gall fly resource. In spring, when larvae were available within seedheads, mice selected stations with high knapweed cover ($\chi^2 = 5.72$, df = 1, $P = 0.017$) while avoiding stations with low knapweed cover ($\chi^2 = 17.06$, df = 1, $P < 0.001$; Fig. 4A). Mice did not show selection for any knapweed category ($\chi^2 < 3.44$, df = 1, $P > 0.064$) in summer when larvae were not available (Fig. 4B). In fall, gall fly larvae were again available, and the spring pattern was repeated as mice avoided stations with low knapweed cover ($\chi^2 = 12.03$, df = 1, $P < 0.001$) and selected stations with high knapweed cover ($\chi^2 = 12.27$, df = 1, $P < 0.001$; Fig. 4C). Feeding piles of knapweed seedheads that included the remains of empty *Urophora* galls (see also Story et al. 1995, Pearson 1999) were present in both fall and spring.

DISCUSSION

Although biological control of invasive plants using exotic insects is the only tool that has proven effective at controlling widely established invasive plants (e.g., Huffaker and Kennett 1959, McEvoy et al. 1991), it has been criticized from an ecological standpoint because of the potential for biocontrol agents to impose irreversible nontarget effects on native organisms (Simberloff and Stiling 1996*a*, *b*, Pemberton 2000, Strong and Pemberton 2000, Pearson and Callaway 2003). Documentation of such nontarget effects has been primarily limited to cases of host switching, where introduced herbivores negatively affect native plant species by directly attacking them, with subsequent effects on associated species (Howarth 1983, Louda et al. 1997, Boettner et al. 2000, Louda 2000, Pemberton 2000, Louda et al. 2003, Pearson and Callaway 2003). However, host-specific biocontrols can also exhibit nontarget effects by altering the foraging ecology of native consumers (Pearson et al. 2000), potentially leading to population-level changes that further impact invaded systems (Pearson and Callaway 2003).

Our results are consistent with the hypothesis that introduced gall fly biocontrol agents subsidize native deer mouse populations. Relative abundance of deer mice was substantially higher on knapweed-invaded vs. native transects in 1999 and 2000. Seasonal patterns in relative abundance and population structure of deer mice, coupled with understandings from related studies of *Peromyscus* demonstrating both food limitation (e.g., Gashwiler 1979, Ostfeld et al. 1996) and dietary shifts to *Urophora* (Pearson et al. 2000), suggest that elevated deer mouse populations in knapweed-invaded habitats were driven by the availability of the superabundant gall fly resource. Availability of gall fly larvae during the critical overwinter period appeared to reduce overwinter population declines of mice in knapweed-invaded habitats in 1999–2000. Conversely, disappearance of the gall fly resource in summer during

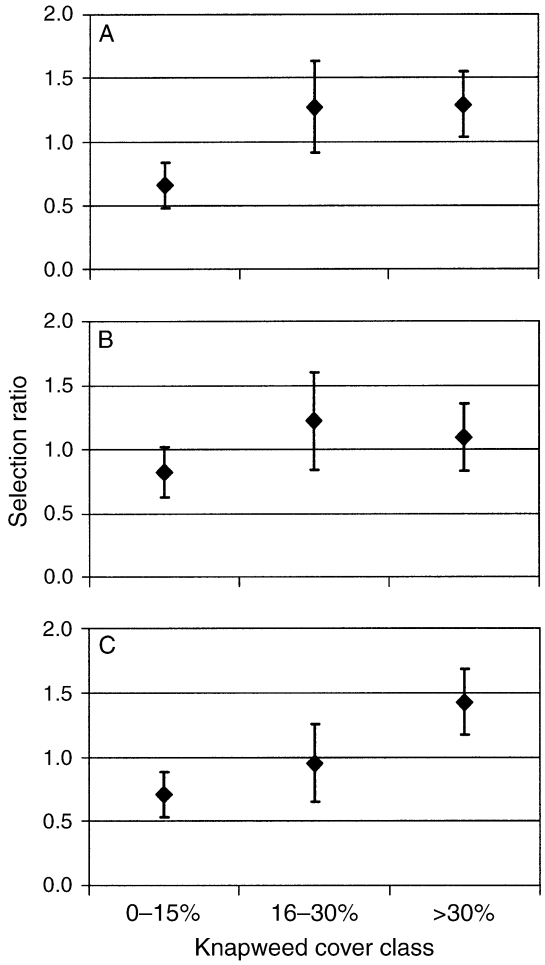

FIG. 4. Selection ratios and Bonferroni-adjusted 95% confidence intervals for deer mouse microhabitat use of three knapweed cover classes in knapweed-invaded grasslands of the Lolo National Forest during (A) spring, (B) summer, and (C) fall.

the peak of the breeding season coincided with diminished indices of breeding productivity in these years (Table 1). Although relative abundance, overwinter declines, and indices of breeding productivity did not differ between knapweed and native habitats in 2001, populations in knapweed-invaded habitats in this year were likely impacted by a drought that reduced knapweed productivity (e.g., Schirman 1981) and consequently, the gall fly resource (D. E. Pearson, *unpublished data*).

Deer mouse foraging patterns and the gall fly resource

High densities of gall fly larvae were available within knapweed seedheads from fall through spring (see also Story and Nowierski 1984, Story et al. 1995), and patterns in deer mouse microhabitat use suggest that deer mice heavily utilized the gall fly resource. During fall and spring, mice targeted patches of high knapweed cover where gall flies were most prevalent, avoiding patches with minimal knapweed cover (Fig. 4A, C); when larvae became unavailable due to emergence of adult gall flies in summer, mice no longer selected for knapweed (Fig. 4B). These results parallel those of Pearson et al. (2000), who linked the seasonal pattern in deer mouse selection for knapweed to a dramatic dietary shift to gall fly larvae, which represented the primary prey item from fall to spring and comprised up to 86% of the diet.

Overwinter effects of gall flies on deer mouse populations

Seasonal patterns in the relative abundance of deer mice suggest that the gall fly resource influenced overwinter population processes in knapweed-invaded habitats, leading to increased populations of mice in knapweed-invaded vs. native habitats in 1999 and 2000. In these years, relative abundance in native habitats was extremely low in spring, following the winter period when high metabolic demands coupled with resource scarcity inhibit breeding and effect population declines (Sadlier et al. 1973, Fairbairn 1977, Tait 1981). In contrast, mice in knapweed-invaded habitats had the advantage of a rich, easily accessible food source available from fall through spring. Pearson et al. (2000) found that gall fly larvae were eaten by deer mice throughout this period, but that consumption was highest during the winter when *Urophora* larvae comprised nearly the entire diet. They suggested that the abundance of gall fly larvae during the critical overwinter period could mitigate the winter population bottleneck in knapweed-invaded habitats. Other studies have stressed the importance of overwinter food supplies on *Peromyscus* populations (Gashwiler 1979, Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998, McCracken et al. 1999). Accordingly, our data indicated that relative abundance of mice in the spring of 1999 and 2000 was over three times higher in knapweed vs. native habitats. Given the earliest possible breeding date (March; Metzgar 1979, Pearson et al. 2000), and the minimum time required from conception to sexual maturity in deer mice (eight weeks; Handley 1999), spring adults (and subadults) represented overwintered animals. Overwintered adults comprised >80% of spring populations and more were captured in knapweed vs. native habitats in 1999 and 2000, indicating that elevated spring populations in knapweed habitats primarily reflected the prevalence of overwintered adults. Moreover, populations in knapweed vs. native habitats lost proportionately fewer mice during the 1999–2000 overwinter period (i.e., between fall 1999 and spring 2000), further suggesting that the availability of gall fly larvae influenced overwinter population processes in knapweed-invaded habitats.

The availability of gall fly larvae coincides with the normal onset of breeding in the spring and termination of breeding in the fall (e.g., Metzgar 1979), potentially

affecting the duration of the breeding season and thereby reducing the winter population bottleneck (Pearson et al. 2000). However, the age distribution of individuals in the springs of 1999 and 2000 did not differ between knapweed and native habitats ($\chi^2 = 1.4$, df = 1, $P = 0.5$ excluding 2001), nor did the proportion of reproductively active mice ($\chi^2 < 0.7$, df = 1, $P > 0.4$ for both males and females, excluding 2001), suggesting that the onset of breeding was comparable between the two habitats in these years. During the fall sampling period, males in knapweed-invaded habitats showed increased evidence of reproductive activity. However, because growth is arrested for deer mice during the nonbreeding season (Tait 1981), extended fall breeding in knapweed vs. native habitats should have resulted in a higher proportion of low-mass (i.e., subadult) individuals in the spring. Pearson et al. (2000) reported that dates of initiation and termination of breeding for deer mice inhabiting knapweed-invaded grasslands in western Montana were comparable to those reported in other studies conducted in the northern continental region (Metzgar 1979, Millar and Gyug 1981). In this region, initiation and termination of breeding is closely associated with temperature (Millar and Gyug 1981), and relevant studies of deer mice have found no effect of increased food on the length of the breeding season (Gilbert and Krebs 1981, McAdam and Millar 1999). In contrast, studies reporting extended breeding seasons in deer mouse populations with increased food were conducted in maritime (Fordham 1971, Gashwiler 1979, Tait 1981) and mediterranean zones (Morrison and Hall 1998), where climatic conditions are less severe (Sadlier et al. 1973). For these reasons, we do not believe that extended breeding caused the observed differences in deer mouse abundance between knapweed and native habitats.

Instead, reduced overwinter declines in abundance and elevated spring populations in knapweed habitats likely resulted from the influence of the gall fly resource on overwinter survival or immigration. Both survival and immigration can increase for deer mouse populations with increased food resources (Fordham 1971, Gashwiler 1979, Gilbert and Krebs 1981, Tait 1981, Hall and Morrison 1998), but measures of the two are confounded (Lebreton et al. 1993). We suggest that the observed pattern of lower overwinter population decline in knapweed-invaded habitats primarily reflects increased survival vs. increased immigration for two reasons. (1) Deer mouse home range size, activity levels, and recruitment of nonresidents are dramatically reduced for most of the overwinter period (i.e., November–March) in Montana (Metzgar 1979). (2) Some immigration from surrounding forest habitats may occur in the fall post-trapping period, but such movements would be limited during winter because snow cover should increase predation risk associated with supranivean travel and subnivean travel should be restricted (Merritt and Merritt 1978). Regardless of mechanism, the observed surplus of mice in knapweed habitats in the spring of 1999 and 2000, and the reduced decline in abundance for the 1999–2000 overwinter period are likely indicative of higher overwinter habitat quality conferred by gall fly larvae in knapweed-invaded vs. native grasslands.

Effects of diminished resources on deer mouse populations in summer

Conversely, habitat quality in summer was probably diminished in knapweed-invaded vs. native grasslands because of the virtual disappearance of the gall fly resource and the effects of knapweed invasion on the native resource base. Mice respond to the disappearance of gall fly larvae by shifting their diets to seeds and other insects (Pearson et al. 2000). However, cover of dominant native plant taxa was reduced on knapweed transects, consistent with other studies describing a decline in native plants in grasslands invaded by spotted knapweed (Tyser 1992, Ridenour and Callaway 2001). Species richness of native forbs and grasses was also diminished on knapweed-invaded vs. native transects ($F = 8.22$, df = 1, 24, $P = 0.009$; Y. K. Ortega, *unpublished data*). Therefore, abundance of seeds, an important food item for deer mice (Vickery et al. 1994), was likely reduced in knapweed-invaded habitats (deer mice consume knapweed seeds only incidentally when foraging for gall fly larvae; Pearson et al. 2000). Bare ground, the interstitial space characteristic of bunchgrass communities (Tyser 1992, Tyser and Worley 1992) and selected by mice in these habitats in summer (Pearson et al. 2001), was also less prevalent on knapweed transects. Arthropods linked to native plants and associated habitat features (e.g., Strong et al. 1984, Fielding and Brusven 1992, Siemann et al. 1998) may have also been impacted by knapweed invasion, and preliminary data from pitfall traps located along transects concurrent with this study demonstrate a substantial reduction in grasshoppers, an important prey item (Belovsky et al. 1990), in knapweed vs. native habitats (D. L. Six, *unpublished data*).

The gall fly resource becomes unavailable to deer mice in knapweed-invaded habitats during the peak period of lactation and weaning of nestlings. During this period, females often require a twofold increase in food consumption to support their young (Millar et al. 1990), and dietary protein obtained from seeds and insects is critical (McAdam and Millar 1999). Accordingly, mice in knapweed-invaded habitats showed evidence of reduced breeding productivity. Despite the greater number of adult mice in knapweed vs. native habitats, numbers of juvenile and subadult recruits were comparable between habitats in summer and fall. Moreover, the ratio of total juveniles produced relative to the number of spring breeders was lower in knapweed vs. native habitats in 1999 and 2000.

Several studies of deer mice have linked resource levels to production of juveniles (Fordham 1971, Gash-

wiler 1979, Gilbert and Krebs 1981, Tait 1981). In our study, the proportion of reproductively active mice did not vary between knapweed and native habitats in summer, suggesting that differences in breeding intensity were not responsible for differential production of juveniles. Other possible mechanisms include effects of resource levels on litter size, nestling survival, and residency (i.e., emigration and mortality) of breeders.

Differences in breeding productivity related to resource levels appeared to influence population dynamics in knapweed vs. native habitats. In 1999 and 2000, relative abundance of mice in native habitats followed the seasonal pattern characteristic of populations in temperate environments (Sadlier et al. 1973, Fairbairn 1977, Tait 1981), building sharply from low to high levels between spring and fall when resources are typically abundant. In contrast, relative abundance in knapweed habitat was less variable from spring to fall, likely reflecting reduced breeding productivity during the period of diminished resources when gall fly larvae are unavailable.

Interpretation of 2001 results

In contrast to results from 1999 and 2000, abundance of mice in 2001 did not differ between knapweed and native habitats. Populations associated with both types of habitats had low indices of productivity in 2001 and failed to build between spring and fall. This breeding season was characterized by two late snowstorms, which may have impacted nestling survival (e.g., Millar and Innes 1983). Population processes in the preceding overwinter period also appeared to differ from other years. Population decline of mice during the 2000–2001 overwinter period did not differ between knapweed and native habitats, and in the spring of 2001, both total abundance and the frequency of adults were comparable in these habitats. Information from regional studies suggests that the drought associated with the 2000 growing season impacted spotted knapweed and consequently the density of gall fly larvae available to deer mice during the 2000–2001 overwinter period. In 2000, precipitation during June, when flowering stems of spotted knapweed develop from basal rosettes (Story and Anderson 1978), was >60% below average (averages 1949–1999 from Missoula Johnson Bell Weather Station), and data from knapweed plants collected at two grasslands sites in western Montana (~45 km from our study sites) demonstrated that stem density was reduced by >60% in 2000 vs. 1999 and 2001 (D. E. Pearson, *unpublished data*). Correlations between the densities of stems and *Urophora* larvae at these sites suggest that this reduction in stem density translated into a comparable decline in the gall fly resource (D. E. Pearson, *unpublished data*). Other studies in the region have reported similar impacts of drought on stem density of spotted knapweed (Schirman 1981, Boggs and Story 1987). Boggs and Story (1987) also reported that in a drought year, young knapweed plants failed to flower and exhibited increased mortality. Our estimates of knapweed cover from July, which included basal rosettes and old as well as new stems, were comparable in 1999 and 2000 (Fig. 3). However, knapweed cover was significantly lower in 2001 ($F = 9.38$, df = 2, 62, $P < 0.001$), suggesting diminished stem production and higher mortality of plants in 2000.

Conclusions

Overall, our results demonstrate that knapweed invasion and the introduction of gall fly biocontrols have contrasting effects on deer mouse populations associated with grassland habitats. Knapweed invasion reduces potential native food resources for mice, leading to decreased indices of breeding productivity for mice in knapweed habitats. However, this resource deficit is more than compensated for by gall fly biocontrol agents, which appear to subsidize deer mouse populations, particularly in winter. These results further support that *Peromyscus* populations are food limited, while underscoring the influence of overwinter processes, over breeding season effects, on population size. In addition, the current study establishes that nontarget effects of gallfly biocontrol agents on deer mouse foraging ecology documented by Pearson et al. (2000) translate into elevated deer mouse populations in knapweed-invaded habitats.

In current biocontrol programs, host switching is recognized as the primary mechanism for nontarget effects, and biocontrol agents that have demonstrated host specificity are typically assumed to be ecologically benign (e.g., DeLoach 1991, Rees et al. 1996, McFadyen 1998; but see McEvoy 1996, Secord and Kareiva 1996, Pearson and Callaway 2003). This ideology has sanctioned the release of multiple control agents per target weed, with the expectation that one or more of these organisms will bring eventual control of the invasion (McEvoy and Coombs 1999, 2000). Biocontrol agents deemed to be host specific are thus numerous, with >90 such species introduced to combat plant invasions in the western continental United States alone (McFadyen 1998). Furthermore, the number of biocontrol species introduced per target plant species continues to increase (McEvoy and Coombs 1999). Most intended control agents have yet to suppress their target species (Julien and Griffiths 1998, McEvoy and Coombs 1999), but many have attained high densities (Myers and Harris 1980, Rees et al. 1996, Powell et al. 2000). Generalist consumers capable of exploiting novel resources, linking the biocontrol agent to the rest of the system, are ubiquitous (e.g., Story et al. 1995, Handley 1999, Pearson et al. 2000) and frequently implicated as factors limiting the efficacy of biological control (Goeden and Louda 1976, McEvoy and Coombs 2000). Given the prevalence of both introduced prey and potential predators in systems invaded by exotic

plants, the risk of nontarget effects spurred by host-specific biocontrol agents alone could be substantial.

Native consumers subsidized by biocontrol agents could have rippling effects on other native taxa (e.g., Ostfeld et al. 1996, Jones et al. 1998, Jefferies 2000), altering community interactions and pushing invaded systems further from the native state. For example, deer mouse populations subsidized by gall flies could have dramatic impacts on arthropod and plant communities (e.g., Holling 1959, Brown and Heske 1990, Maron and Simms 2001, Schnurr et al. 2002), as deer mice prey heavily on these resources in summer when gall fly larvae are unavailable (Pearson et al. 2000). Gall fly subsidies could also impact human health since deer mice are the primary vectors for the Sin Nombre hantavirus, which causes high mortality in humans (Childs et al. 1994). As such, the current practice of biological control could exacerbate rather than resolve the invasive species problem. We suggest further study of nontarget effects to develop ecological understandings of the conditions under which introduction of host-specific biocontrol species may be problematic. Given that it is impossible to recall biocontrol agents once they are introduced, such understandings are critical and should be used to screen exotic organisms prior to release.

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