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Non-target effects of an introduced biological control agent on deer mouse ecology

Received: 04 May 1999 / Accepted: 14 August 1999

Abstract Release of exotic insects as biological control agents is a common approach to controlling exotic plants. Though controversy has ensued regarding the deleterious direct effects of biological control agents to non-target species, few have examined the indirect effects of a “well-behaved” biological control agent on native fauna. We studied a grassland in west-central Montana infested with spotted knapweed (*Centaurea maculosa*) to examine the effects of knapweed invasion and two gall fly biological control agents (*Urophora affinis* and *U. quadrifasciata*) on the native deer mouse (*Peromyscus maniculatus*). Stomach-content analysis revealed that *Urophora* were the primary food item in *Peromyscus* diets for most of the year and made up 84–86% of the winter diet. Stomach contents indicated that wild-caught mice consumed on average up to 247 *Urophora* larvae mouse⁻¹ day⁻¹, while feeding trials revealed that deer mice could depredate nearly 5 times as many larvae under laboratory conditions. In feeding trials, deer mice selected knapweed seedheads with greater numbers of galls while avoiding uninfested seedheads. When *Urophora* larvae were present in knapweed seedheads, deer mice selected microhabitats with moderately high (31–45% cover) and high knapweed infestation ($\geq 46\%$ cover). After *Urophora* emerged and larvae were unavailable to *Peromyscus*, mice reversed habitat selection to favor sites dominated by native-prairie with low knapweed infestation (0–15%). Establishment of the biological control agent, *Urophora* spp., has altered deer mouse diets and habitat selection by effecting changes in foraging strategies. Deer mice and other predators may reduce *Urophora* populations below a threshold necessary to effectively control spotted knapweed.

Key words Biological control · *Centaurea maculosa* · *Peromyscus maniculatus* · Exotic plants · *Urophora*

Introduction

Exotic plants have invaded vast areas of grasslands, prairies, and savannas in western North America, greatly reducing the extent and, in some cases, threatening the viability of these systems (Harris and Myers 1984; Baker 1986; Mack 1986; Harris 1988; Tyser and Key 1988; Lacey 1989; DeLoach 1991; Tyser 1992; Tyser and Worley 1992). In spite of the dramatic vegetation changes that follow noxious weed invasion in native grasslands (Myers and Berube 1983; Tyser and Key 1988; Rice et al. 1997), little is known about how these shifts in plant community composition affect ecological interactions at higher trophic levels. Moreover, many systems invaded by exotic plants have been further complicated by the introduction of exotic insects intended as biological control agents. In some cases, introduced insects fail to significantly affect the target weed while rapidly achieving high biomass in response to the elevated densities of its host plant (e.g., Myers and Harris 1980). Under such circumstances, the insect introduced for biological control may begin to interact with native organisms to effect its own influence as an exotic agent. Effects of biological control agents on non-target species can be detrimental (Howarth 1983, 1991; Simberloff 1991, 1992; Simberloff and Stiling 1996a, 1996b).

Spotted knapweed (*Centaurea maculosa*) is among the most aggressively invasive and extensively established of the exotic plants in western North America (Maddox 1979; Harris and Myers 1984; Lacey 1989; Sheley et al. 1998). As of 1988, spotted knapweed occupied nearly 3 million ha in the northwestern United States and western Canada, resulting in the loss and degradation of large expanses of native prairies, grasslands, and savannas (Lacey 1989).

As many as 12 species of exotic insects have been released in the West to control spotted knapweed (Sheley

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et al. 1998). Two species of gall fly (*Urophora affinis* and *U. quadrifasciata*) introduced in the early 1970s, were among the first insects released to control spotted knapweed in western North America (Harris 1980a; Story and Nowierski 1984). *Urophora* lay eggs in immature knapweed seedheads from mid-June to September (Story et al. 1992). The larvae induce the plant to form a gall within which the larvae overwinter in the knapweed seedheads until pupating in May and emerging in mid June (Zwolfer 1970; Story et al. 1992). This behavior reduces seed production by creating a metabolic sink at the critical period of seed development (Harris 1980b) and physically displaces seeds due to competition for space (Story 1977).

Urophora spp. are currently established in most areas where spotted knapweed occurs (Harris 1980b; Maddox 1982; Story and Nowierski 1984; Story et al. 1987; Story et al. 1992) and reach high biomass where knapweed attains high densities. For example, populations of *Urophora* spp. in British Columbia have attained densities 12–18 times greater than those observed in their native habitats in Europe (Myers and Harris 1980). In addition to their elevated biomass, which may serve to attract predators, *Urophora* are vulnerable to predation throughout the year because the larvae overwinter in galls within knapweed seedheads. Additionally, adults are susceptible to predation while mating on and ovipositing within knapweed flowerheads. As a result, *Urophora* spp. have acquired several native predators that attack both larval and adult stages. Story et al. (1995) determined that deer mice (*Peromyscus maniculatus*), white-tailed deer (*Odocoileus virginianus*), and black capped chickadees (*Parus atricapillus*) were the primary predators of *Urophora* larvae, and that the native spider, *Dytina major*, preyed heavily on adult flies. Pearson (1999) suggested that *Peromyscus maniculatus* were the dominant predator of larval stages of *Urophora* spp. He showed that in February mice consumed an average of 212 *Urophora* larvae mouse⁻¹ day⁻¹ and that *Urophora* made up an average of 90% of the stomach contents of *P. maniculatus* during a period of food shortage that coincided with the onset of breeding. He speculated that the presence of an abundant, readily accessible resource such as *Urophora* larvae during the historical population bottleneck for *P. maniculatus* (Sadleir 1965; Fairbairn 1977) could have a profound impact on their populations, altering the affected small-mammal communities and the predators that depend on them. Such indirect effects (see Strauss 1991) of exotic weeds and biological control agents have wide-ranging implications for natural systems, but have seldom been documented, particularly in North America, and are poorly understood (for reviews see Harris 1988; Howarth 1991; Simberloff and Stiling 1996a, 1996b).

We studied a grassland infested with spotted knapweed on Mount Sentinel near Missoula, Montana, United States, to better understand the direct and indirect effects of spotted knapweed invasion and establishment of the biological control agents *U. affinis* and *U. quad-*

rifasciata on the food habits and habitat use of the native deer mouse.

Materials and methods

We conducted research in rough fescue (*Festuca scabrella*) and bluebunch wheatgrass (*Agropyron spicatum*) grassland types (Mueggler and Stewart 1980) that were heavily invaded by spotted knapweed. Knapweed cover ranged from 0 to 95%, resulting in a mosaic of knapweed and native-vegetation patches. Most of the native portions of the study area were dominated by rough fescue followed by Idaho fescue (*F. idahoensis*) and a mix of native forbs (see Mueggler and Stewart 1980 for descriptions and species lists for vegetation types) with bluebunch wheat grass making up a lesser component. Bluebunch wheatgrass dominated other sites followed by rough fescue, Idaho fescue, and native forbs. The study area ranged from 1100 to 1700 m elevation on the west aspect of Mount Sentinel, due east of Missoula, Montana. Average annual precipitation is 34 cm year⁻¹ with about one-third of this occurring as rain in May and June. Average monthly temperatures range from -6°C in January to 19°C in July (averages 1949–1994 from Missoula Johnson Bell National Weather Station).

We snap-trapped the study area monthly from March 1997 to February 1998. Twenty mousetraps were placed at 10-m intervals along each of three transects. Transects were chosen over grids to maximize captures and more effectively assess the community sampled (D.E. Pearson and L.F. Ruggiero, unpublished work). Transects were located ≥200 m apart, parallel to each other and perpendicular to the slope. We set out traps for 3–7 days (usually 5 days), generally during the first week of each month, and checked them once each day. Trapping effort varied between transects to equalize sample size among months for stomach content analysis. We baited traps with approximately 1.0 g of peanut butter within the enclosed metal loop of the trap treadle using a 30-ml syringe. Transect, trap station, and date were recorded for each animal upon capture and animals were frozen within approximately 1 h of collection.

We separated our data into two seasons to test the hypothesis that habitat selection by *P. maniculatus* differed between the period when *Urophora* larvae were present in knapweed seedheads (September–May) and the post-emergence period when *Urophora* larvae were unavailable to *P. maniculatus* (June–August). Because snap-trapping generated insufficient captures from June to August 1997 for habitat analysis (24 animals), we intensively live-trapped an additional area of Mount Sentinel in August 1998. We set out seven transects of 25 Sherman live traps placed at 10-m intervals to encompass patches of near-pristine native grasslands and sites exhibiting a range of knapweed infestation. Traps were baited with peanut butter and whole oats and checked once each morning for 4 days. We marked animals with #1005–1 monel ear tags (National Band and Tag Co., Newport, Ky., USA) and identified to species, weighed, sexed, aged, and determined reproductive status of each individual prior to release. The live-trapping area was located on the same aspect of the mountain and approximately 200 m higher in elevation than the snap trapping transects. The new site was chosen to maximize the contrast between native prairie and high-density knapweed-infested sites.

Percentage cover of spotted knapweed was estimated to the nearest 5% based on ocular estimates for a 5-m-radius circle centered on each trap station. Cover estimates were assigned to four categories that approximated natural breaks in the data distribution: 1–15%, 16–30%, 31–45%, >45%, for analysis of habitat selection.

All snap-trapped animals were weighed, sexed, aged, and reproductive status was determined in the laboratory prior to stomach content analysis. Animals were submerged in viricide before necropsy as a precaution against hantavirus infection (Mills et al. 1995). Sex and reproductive status were confirmed during necropsy and number of placental scars and embryos were tallied. Stomach contents were analyzed macroscopically as described in Pear-

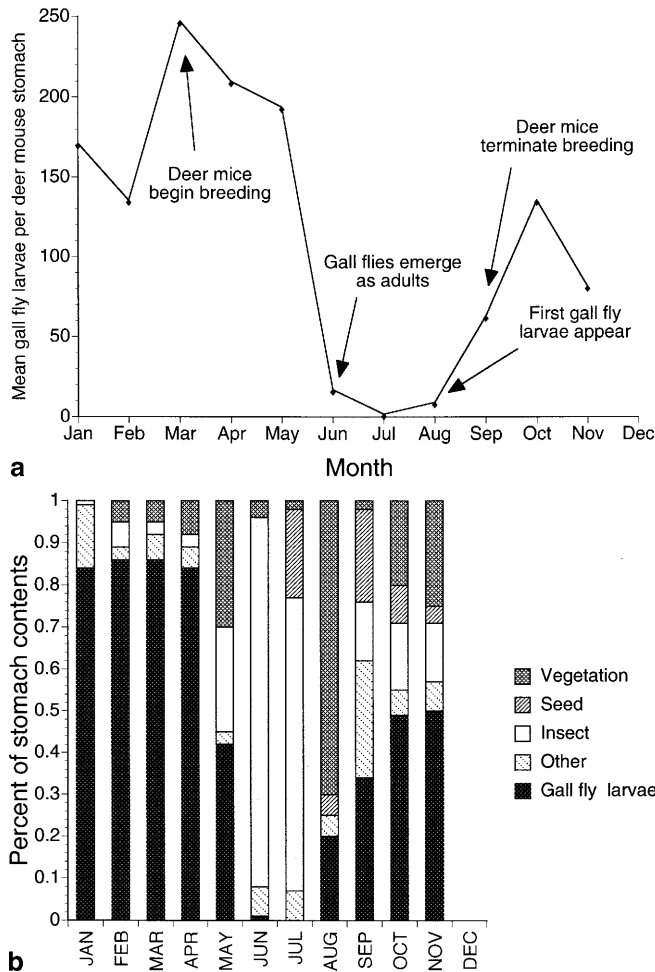


Fig. 1a,b Results from stomach content analysis of 127 deer mice snap trapped on Mount Sentinel from March 1997 through February 1998. **a** Average number of *Urophora* larvae per mouse by month. **b** Percentage occurrence of stomach contents for each of 5 categories. No animals were captured in December

son (1999). All *Urophora* larvae were counted in each stomach and cecum, and stomach contents were assigned to one of six categories (*Urophora* larvae, other insects, vegetation, seeds, trap bait, other) based on an estimate of the percentage occurrence of each item in the stomach. We did not break down the category of insect below the level of Class. Only animals with stomachs containing $\leq 50\%$ trap bait ($n=127$; 71% of captures) were included when examining mean number of *Urophora* larvae consumed per month and proportional consumption of *Urophora* larvae relative to other diet categories.

We conducted feeding trials on ten adult *P. maniculatus* (5 males, 5 females) captured from 24 to 26 March 1998 near the Mount Sentinel snap-trapping transects. Animals were captured with Sherman live-traps baited with approximately 5 g of peanut butter and oats. Baiting was minimized to limit potential effects of trap bait on the feeding trials. Traps were covered with 0.64-cm-thick insulation to protect animals from sub-freezing temperatures. We checked traps each morning.

Captured mice were placed in individual cages with bedding material and water in an unheated building with ambient light. Feeding trials began at 2200 hours on 26 March and ended at 2200 hours on 29 March. We offered each individual 1000 knapweed seedheads (collected from the Mount Sentinel study area in March 1998) for 24 h. At the end of each feeding trial, residual material was removed

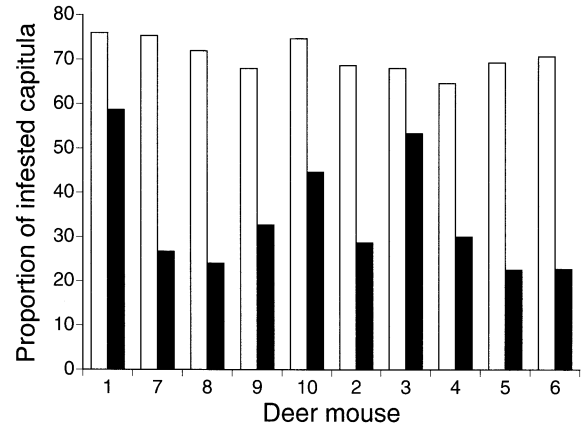


Fig. 2 Average proportion of knapweed seedheads that contained ≥ 1 *Urophora* larvae in offered and residual samples presented to 10 deer mice. Each mouse received 3 offerings of 1000 knapweed seedheads for 24 h periods. The 5 mice on the left are females the 5 on the right are males. (open bars offered samples, closed bars residual samples)

from the cage, bagged, labeled, and frozen for later examination. Feeding trials were repeated three times for each mouse.

Prior to feeding trials, 50 seedheads were randomly sampled from each offering (1050 seedheads had been counted into each sample to allow for removal of 50 seedheads). These samples were dissected to estimate the average number of *Urophora* larvae per seedhead and the proportion of infested seedheads that were offered to each mouse on each feeding trial. Residual material from feeding trials was examined to determine the number of seedheads depredated. A seedhead was considered depredated if the flower bracts had been removed so that inner flower parts were visible. From each residual sample 50 seedheads were taken and dissected to estimate the number of *Urophora* per seedhead and the proportion of seedheads infested for comparison with offered samples.

We used resource selection function analysis of categorical data (Manly et al. 1993) to determine *P. maniculatus* selection for the four categories of knapweed-infestation when *Urophora* larvae were present (September–May) and when they were absent (June–August). Selection ratios equal to 1.0 indicate no selection whereas ratios >1.0 indicate selection and those <1.0 indicate avoidance. Selection ratios are considered significantly different from 1 if the 95% Bonferroni-adjusted confidence intervals exclude 1.0 and significantly different from each other if confidence intervals do not overlap. Comparison of the proportion of seedheads occupied by *Urophora* larvae between offered and residual feeding samples was made via repeated measures analysis of variance using SPSS software version 6.1.1 for the Macintosh. Comparison of the distributions for numbers of larvae per seedhead between offered and residual samples was made using a chi-square homogeneity of variance test (Jelinski 1991).

Results

We snap-trapped 180 *P. maniculatus* from March 1997 through February 1998 (total trap nights=3340). Of these, 156 were captured from September through May, and 24 were captured from June through August. No mice were captured in December during a period of unusually low temperatures. Nine individuals of two other species were snap trapped: eight montane voles (*Microtus montanus*) and one vagrant shrew (*Sorex vagrans*).

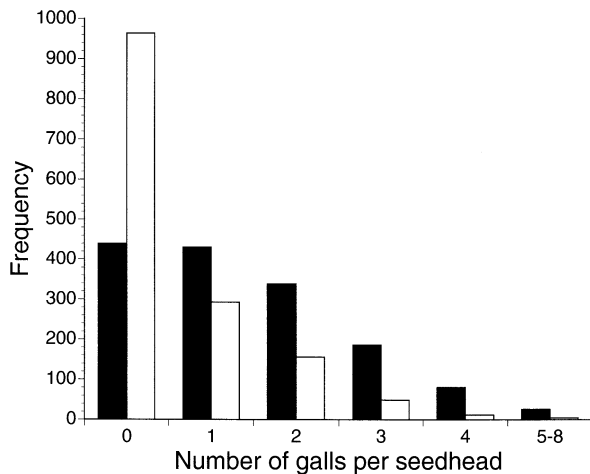


Fig. 3 Distributions depicting the number of seedheads with 0, 1, 2, 3, 4, and ≥ 5 *Urophora* larvae per seedhead in offered and residual samples for 10 deer mice that were each presented with 3 offerings of 1000 knapweed seedheads for 24 h periods. Only offered samples contained seedheads with >5 larvae. (closed bars offered samples, open bars residual samples)

August live-trapping in 1999 produced 142 individual *P. maniculatus*, 4 *M. montanus*, and 1 unidentified shrew (*Sorex* sp.) (total trap nights=700).

Peromyscus males were in breeding condition (testes scrotal) from February through September. Females were observed with embryos from early April through September, indicating that they were estrous in March. The breeding season, therefore, ran from March through September.

The average number of *Urophora* larvae per stomach and cecum combined for snap-trapped mice varied by month from 1.6 in July to a peak of 247.3 in March (Fig. 1a). The overall pattern of larval consumption was essentially one of increasing predation from late summer (August) to early spring (March). This period was followed by a slight decline in larval predation in spring and little feeding in summer (June–August). Numbers of *Urophora* larvae consumed per individual *P. maniculatus* per day ranged from 0 in June and July to 690 for a large adult male captured in May.

Estimates of stomach contents indicated that *Urophora* larvae were the primary food item of *P. maniculatus* for most of the year in knapweed-infested grasslands on Mount Sentinel (Fig. 1b). *Urophora* larvae began to become an important resource in August. Larvae increased in importance from 20% of stomach contents in August to 84% in January where they stabilized at 84–86% until April. In May, larvae declined to 42% of the diet and other insects and vegetation increased in importance. Other species of insects dominated June and July stomach contents, whereas, August *P. maniculatus* ate mostly vegetative material. Seeds made up 4–22% of *P. maniculatus* diets from July through November when seeds disappeared from *P. maniculatus* stomachs. Of the 180 stomachs examined, 17 (9%) contained knapweed seeds. All stomachs with knapweed

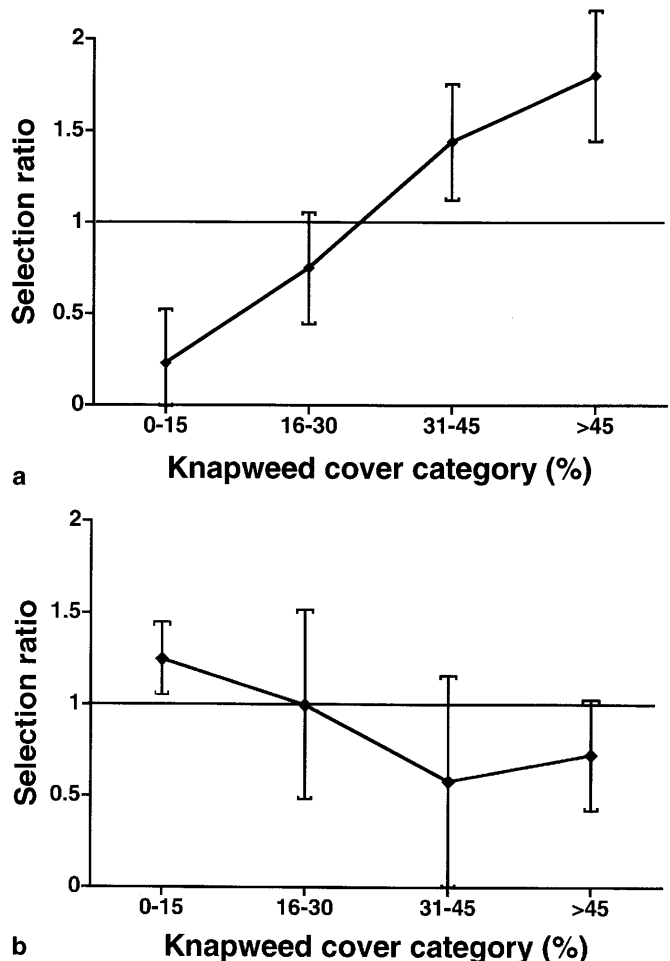


Fig. 4 Selection ratios and Bonferroni-adjusted 95% confidence intervals for deer mouse habitat use in 4 spotted knapweed cover categories in knapweed-infested grasslands on Mount Sentinel during **a** the period when *Urophora* larvae were present in knapweed seedheads (September to May) and **b** the period when they were absent from knapweed seedheads (August)

seeds came from animals trapped in September (6%), October (53%), or November (41%), during the seed dispersal phase for spotted knapweed (Story et al. 1992).

Stomach contents were also examined for nine *M. montanus*, eight captured animals and one individual found dead near a trap station. No *Urophora* larvae were found in any *M. montanus* stomachs. *Microtus* stomachs contained 99.7% vegetative material on average with the remaining material from the categories of “other insects” or “other”.

The average number of seedheads depredated per individual in 24 h under laboratory conditions was $837.3 \pm \text{SD}=76.9$ ($n=10$ mice; 3 trials each; Fig. 2). At an average of 1.4 ± 0.3 *Urophora* larvae per seedhead estimated from the 30 samples of seedheads offered in feeding trials, this translates to $\bar{x}=1172.2$ *Urophora* larvae consumed per mouse per 24 h. Males ($\bar{x}=843.7$) and females ($\bar{x}=830.8$) did not differ in the number of seed-

heads depredated ($F=0.06$, $df=1, 8$; $P=0.808$). Time effects in the repeated-measures ANOVA, which might indicate either insufficient offerings or saturation, were not significant ($F=3.48$, $df=2, 7$; $P=0.089$). Proportions of knapweed seedheads infested with *Urophora* larvae were significantly lower in residual samples ($\bar{x}=34.4\%$) than in samples offered to *P. maniculatus* ($\bar{x}=70.7\%$; $F=74.45$, $df=1, 8$; $P<0.001$), but did not differ between male and female mice ($F=1.43$, $df=1, 8$; $P=0.266$) (Fig. 2). Distributions for numbers of larvae per seedhead also differed significantly between offered and residual samples ($\chi^2=433.67$, $df=5$, $P<0.001$; Fig. 3).

From September through May, mice selected sites with high (45–70%; $\chi^2=26.67$, $df=1$, $P<0.001$) and moderately high (31–45%; $\chi^2=10.14$, $df=1$, $P=0.001$) knapweed density while avoiding areas of low (0–15%; $\chi^2=35.53$, $df=1$, $P<0.001$) knapweed density (Fig. 4). Summer (June to August) patterns of selection reversed with *P. maniculatus* selecting for native-prairie-dominated sites with low knapweed infestations ($\chi^2=8.41$, $df=1$, $P=0.004$) over areas of high knapweed infestation (Fig. 4b).

Discussion

Deer mice are aggressive predators of gall flies released for biological control of spotted knapweed. Snap trapping data indicated that deer mice consumed an average of 247 larvae mouse⁻¹ day⁻¹ during peak predation (Fig. 1a). These data are consistent with estimates of 213 larvae mouse⁻¹ day⁻¹ reported by Pearson (1999) for February of the previous year. However, snap trapping undoubtedly under-estimates true predation rates, as deer mice are often captured before foraging is complete, and mice likely forage more than once per night. Laboratory feeding trials indicated adult deer mice could consume nearly 1200 larvae mouse⁻¹ day⁻¹. Although feeding trials may overestimate gall fly predation by deer mice due to reduced handling time afforded by unlimited access to pre-harvested seedheads, these data support the conclusion that snap-trapping may greatly underestimate deer mouse foraging on gall fly larvae in the wild.

Urophora larvae offer a rich but volatile food resource for deer mice. Overwintering larvae can attain high densities in knapweed infested grasslands from September through May (Myers and Harris 1980; Story et al. 1992), but rapid emergence of larvae in June (Story et al. 1992) results in the virtual disappearance of this resource for nearly 3 months (June–August). Mount Sentinel deer mice exploited the *Urophora* resource by prey switching (Murdoch 1969). Deer mice began to consume *Urophora* larvae immediately after the first larvae became available in August (although most larvae overwinter from September to May, bivoltinism results in a small percentage of larvae maturing during August; Story et al. 1992), and predation on larvae increased until it peaked in March (Fig. 1) at the onset of the deer mouse breeding season. Larval presence in deer mouse

diets then declined to approximately 42% in May and nearly zero in June when *Urophora* emergence caused deer mice to switch back to other insects as their primary food source.

Because *Urophora* spp. are restricted to knapweed flowerheads (Zwolfer 1970), deer mice had to “habitat switch” into knapweed habitats in order to exploit the *Urophora* resource through prey switching. Prey switching and therefore habitat switching was necessitated by the fact that *Urophora* emergence occurred during the deer mouse breeding season (March–September during this study). Deer mice therefore selected sites with heavy knapweed cover during those periods when larvae were available and reversed selection to favor native prairie sites after *Urophora* larvae emerged (Fig. 2).

Although we present data from only 1 year on Mount Sentinel, *Peromyscus* predation on *Urophora* larvae was also intense on Mount Sentinel during the previous winter (Pearson 1999) and was documented for 6 sites in westcentral Montana from 1979 to 1981 (Story and Nowierski 1984) and from 19 sites throughout westcentral Montana from 1987 to 1989 (Story et al. 1995). These data suggest that this phenomenon occurs annually throughout westcentral Montana and may well occur over much of the northwestern US and western Canada where knapweed, *Urophora*, and *P. maniculatus* are sympatric.

Peromyscus exhibited functional and numerical responses (Holling 1959) in preying on *Urophora* larvae. Laboratory work indicated *P. maniculatus* successfully discriminated between infested and uninfested seedheads without processing the seedheads (Fig. 2), thereby greatly reducing handling time (Holling 1965). We believe *P. maniculatus* assess seedheads for the presence of larvae when they climb the flower stalk to harvest them, as Story et al. (1995) observed that spring-sampled seedheads remaining on knapweed stalks after winter depredation had significantly lower infestation rates and fewer larvae on average per seedhead than did fall-sampled seedheads collected prior to *P. maniculatus* foraging. Although we did not attempt to isolate the proximal mechanisms allowing *P. maniculatus* to make this discrimination, Holling (1958) established that *P. maniculatus* use olfaction to locate pine sawfly cocoons in forest-floor litter. Deer mice may similarly use olfaction to detect *Urophora* larvae in knapweed seedheads.

Deer mice exhibited a numerical response to *Urophora* larvae as evidenced by the higher capture rates at high density knapweed sites when *Urophora* larvae became available. Increased *P. maniculatus* captures at high density knapweed sites likely resulted from habitat switching in response to the increased resource abundance. Such movements have been documented for *Peromyscus* in response to natural resource fluctuations such as acorn mast (McShea and Gilles 1992) and pinon nut mast (Morrison and Hall 1998) as well as supplemental feeding (Hall and Morrison 1998; Gilbert and Krebs 1981). Where the knapweed-native-bunchgrass mosaic is fine-grained relative to *P. maniculatus* home-

range size, habitat shifting may represent a within-home-range or microhabitat shift to exploit changing resources. In extensive knapweed monocultures, the resource bottleneck brought about by *Urophora* emergence during the breeding season may force *P. maniculatus* into a macrohabitat shift comparable to a short-distance migration between habitats or result in a positive edge effect wherein *P. maniculatus* are most abundant along knapweed edges adjacent to alternative habitats. In Europe, wood mice (*Apodemus sylvaticus*) which exploit resources within forests and agricultural lands (Montgomery and Gurnell 1985) attain higher numbers at forest edges than within forests or adjacent agricultural lands (Garcia et al. 1998). At the landscape scale this translates to higher densities of mice in more highly fragmented landscapes (Geuse et al. 1985; Telleria et al. 1991). Habitat switching by *P. maniculatus* between knapweed and adjacent habitats could similarly result in higher mouse population densities at knapweed edges such as herbicide treatment boundaries and agricultural landscapes or at knapweed invasion fronts where high-density knapweed mixes with native habitats in a fine-grained matrix.

Urophora larvae offer a valuable resource at a time of resource scarcity for *P. maniculatus* (Sadleir 1965; Fairbairn 1977; Taitt 1981). If food limits *P. maniculatus* populations during winter (Sadleir et al. 1973; Sadleir 1974; Krebs and Myers 1974; Fairbairn 1977; Taitt 1981), then the abundance of *Urophora* larvae in knapweed-infested habitats could be expected to negate or reduce the effect of the winter population bottleneck by increasing over-winter survival or reducing or eliminating the non-breeding season. For example, Morrison and Hall (1998) documented over-winter breeding in *P. maniculatus* in eastern California in response to pinyon pine (*Pinus monophylla*) masting and Gashwiler (1979) observed winter breeding and higher over-winter survival in Oregon *Peromyscus maniculatus* during Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) mast years. Supplemental feeding can also initiate winter breeding in deer mice (Taitt 1981).

Deer mice in our study did not breed through the winter, nor did initiation of breeding in our population (March) appear to differ from that reported for *Peromyscus maniculatus* in western Montana (Metzgar 1979), Oregon (Gashwiler 1979), or Manitoba (Millar and Gyug 1981). In fact, breeding appears to have terminated earlier in our study area (September) than it did at a nearby western Montana location (October) in 1971 (Metzgar 1979) even though *Urophora* larvae reach their highest densities for the year in September (Story et al. 1995). Factors other than food appeared to control *P. maniculatus* breeding on Mount Sentinel during this study. We could not examine over-winter survival since our study involved removal trapping.

The fact that *Urophora* occupied only 71% of the knapweed seedheads on Mount Sentinel suggests that they occur below carrying capacity (peak infestations reported for Montana were 99% in 1981: Story and

Nowierski 1984). Given that *P. maniculatus* and other predators can depredate 54–64% of the knapweed seedheads produced in a year (Story et al. 1995) as well as reduce the mean proportion of infested seedheads and mean number of *Urophora* larvae within the remaining seedheads, the most parsimonious explanation for *Urophora* populations occurring below carrying capacity is predation. Harris and Cranston (1979) and Maddox (1982) determined that *U. affinis* impacts on spotted and diffuse knapweed were insufficient to control these species independent of additional biological control agents, and Story and Nowierski (1984) implicated *P. maniculatus* in inhibiting the establishment of *Urophora affinis* at one release site in west-central Montana. *P. maniculatus* predation may be an important factor in reducing *Urophora* densities below a level necessary to effectively control spotted knapweed.

Simberloff and Stiling (1996a, 1996b) have questioned the efficacy of biological control programs from an ecological standpoint. Louda et al. (1997) offer further examples of how native species are deleteriously affected when biological control agents are not host-specific. We suggest that even host-specific biological control agents can have direct and indirect effects on many native organisms. *Urophora* species are “well-behaved” biological control agents given the current standards for biological control releases (Harris 1991; U.S. Congress 1995; Williamson 1996). They are aggressive seed predators that have proven to be host-specific (Maddox 1982). However, because they have not achieved control over the target species (Maddox 1982), they have become extremely abundant. In so doing, they now also function as exotic agents that currently affect numerous species of animals that were not previously directly impacted by spotted knapweed. These species comprise a wide range of taxa that have been documented to date including: spiders, white-tailed and mule deer (*Odocoileus hemionus*), black-capped chickadees, and deer mice (Harris 1990; Story et al. 1995; Wright and Kelsey 1997; Pearson 1999). We have also observed yellow-pine chipmunks (*Tamias amoenus*), house finches (*Carpodacus mexicanus*), and pine siskins (*Carduelis pinus*) foraging on *Urophora* larvae. Although *Urophora* have remained host-specific, they have nonetheless affected a wide range of taxa in ways not clearly understood.

Because it is difficult if not impossible to recall an insect once released for biological control, the effects of the *Urophora* introduction are likely to remain until its host is eradicated or controlled. To date there is little indication that this will occur. However, if spotted knapweed is successfully controlled, removal of *Urophora* species could also be problematic. *Urophora* may now exist as an exotic keystone species (Simberloff 1991; but see Power et al. 1996; Mills et al. 1993) in the West. Given its current importance, its elimination would have a ripple effect on numerous species including those identified above and others not yet known to be affected by *Urophora* spp.

Acknowledgements Ray Callaway, Kerry Foresman, and Yvette Ortega offered valuable reviews of draft manuscripts. Rudy King provided helpful advice on data analyses. We thank Dan Cariveau, Lance Krigbaum, Amy Lindsley, and Todd Musci for help in the field and laboratory. Kerry Foresman loaned us cages for feeding trials.

References

- Baker HG (1986) Patterns of plant invasion in North America. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, Berlin Heidelberg New York, pp 44–57
- DeLoach CJ (1991) Past success and current prospects in the biological control of weeds in the United States and Canada. *Nat Areas J* 11:129–42
- Fairbairn DJ (1977) Why breed early? a study of reproductive tactics in *Peromyscus*. *Can J Zool* 55:862–871
- Garcia FJ, Diaz M, Alba JM de, Alonso CL, Carbonell R, Carrion ML de, Monedero C, Santos T (1998) Edge effects of winter abundance of wood mice *Apodemus sylvaticus* in Spanish fragmented forests. *Acta Theriol* 43:255–262
- Gashwiler JS (1979) Deer mouse reproduction and its relationship to the tree seed crop. *Am Mid Nat* 102:95–112
- Geuse P, Bauchau V, Le Boulenger E (1985) Distribution and population dynamics of bank voles and wood mice in a patchy woodland in central Belgium. *Acta Zool Fenn* 173:65–68
- Gilbert BS, Krebs CJ (1981) Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia* 51:326–331
- Hall LS, Morrison ML (1998) Responses of mice to fluctuating habitat quality II. a supplementation experiment. *Southw Nat* 43:137–146
- Harris P (1980a) Establishment of *Urophora affinis* (Fröhl.) and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) in Canada for the biological control of diffuse and spotted knapweed. *Z Angew Entomol* 90:190–201
- Harris P (1980b) Effects of *Urophora affinis* (Fröhl.) and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Compositae). *Z Angew Entomol* 90:190–210
- Harris P (1988) Environmental impact of weed-control insects. *BioScience* 38:542–548
- Harris P (1990) Environmental impact of introduced biological control agents. In: Mackauer M, Ehler LE, Roland J (eds) Critical issues in biological control. Intercept, Andover, pp 289–299
- Harris P (1991) Invitation paper (C. P. Alexander Fund): classical biological control of weeds: its definition, selection of effective agents, and administrative-political problems. *Can Entomol* 123:827–849
- Harris P, Cranston R (1979) An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Can J Plant Sci* 59:375–382
- Harris P, Myers JH (1984) *Centaurea diffusa* Lam. and *C. maculosa* Lam. s. lat., diffuse and spotted knapweed (Compositae). In: Kelleher JS, Hume MA (eds) Biological control programs against insects and weeds in Canada 1969–1980. Commonwealth Agricultural Bureau, Farnham Royal, pp 127–137
- Holling CS (1958) Sensory stimuli involved in the location and selection of sawfly cocoons by small mammals. *Can J Zool* 36:633–653
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can Entomol* 91:293–320
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem Entomol Soc Can* 45:5–60
- Howarth FG (1983) Classical biological control: panacea or Pandora's box? *Proc Hawaii Entomol Soc* 24:239–244
- Howarth FG (1991) Environmental impacts of classical biological control. *Annu Rev Entomol* 36:485–509
- Jelinski DE (1991) On the use of chi-square analysis in studies of resource utilization. *Can J For Res* 21:58–65
- Krebs CJ, Myers JH (1974) Population cycles in small mammals. *Adv Ecol Res* 8:267–399
- Lacey C (1989) Knapweed management a decade of change. In: Fay PK, Lacey RJ (eds) Knapweed symposium proceedings EB45. Plant and Soil Department and Extension Service, Montana State University, Bozeman, pp 1–7
- Louda SM, Kendall D, Connor J, Simberloff D (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science* 277:1088–1090
- Mack RN (1986) Alien plant invasion into the Intermountain West: a case history. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, Berlin Heidelberg New York, pp 191–213
- Maddox DM (1979) The knapweeds: their economics and biological control in the western states, USA *Rangelands* 1:139–141
- Maddox DM (1982) Biological control of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Sci* 30:76–82
- Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman Hall, London, pp 1–177
- McShea WJ, Gilles AB (1992) A comparison of traps and fluorescent powder to describe foraging for mast by *Peromyscus leucopus*. *J Mammal* 73:218–222
- Metzgar LH (1979) Dispersion patterns in a *Peromyscus* population. *J Mammal* 60:129–145
- Millar JS, Gyug LW (1981) Initiation of breeding by northern *Peromyscus* in relation to temperature. *Can J Zool* 59:1094–1098
- Mills JN, Yates TL, Childs JE, Parmenter RR, Ksiazek TG, Rollin PE, Peters CJ (1995) Guidelines for working with rodents potentially infected with *Hantavirus*. *J Mammal* 76:716–722
- Montgomery WI, Gurnell J (1985) The behaviour of *Apodemus*. *Symp Zool Soc Lond* 55:89–115
- Morrison ML, Hall LS (1998) Responses of mice to fluctuating habitat quality I. patterns from a long-term observational study. *Southw Nat* 43:123–136
- Mueggler WF, Stewart WL (1980) Grassland and shrubland habitat types of western Montana (General Technical Report INT-66). USDA Forest Service, Washington
- Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol Monogr* 39:335–354
- Myers JH, Erube DE (1983) Diffuse knapweed invasion into rangelands of the dry interior of British Columbia. *Can J Plant Sci* 63:981–987
- Myers JH, Harris P (1980) Distribution of *Urophora* galls in flower heads of diffuse and spotted knapweed in British Columbia. *J Appl Ecol* 17:359–367
- Pearson DE (1999) Deer mouse predation on the biological control agent, *Urophora* spp., introduced to control spotted knapweed. *Northw Nat* 80:26–29
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46:609–620
- Rice PM, Toney JC, Bedunah DJ, Carlson CE (1997) Plant community diversity and growth form responses to herbicide applications for the control of *Centaurea maculosa*. *J Appl Ecol* 34:1397–1412
- Sadleir RMFS (1965) The relationship between agonistic behavior and population changes in the deer mouse. *J Anim Ecol* 34:311–252
- Sadleir RMFS (1974) The ecology of the deer mouse (*Peromyscus maniculatus*) in a coastal coniferous forest. II. Reproduction. *Can J Zool* 52:119–131
- Sadleir RMFS, Casperson KD, Harling J (1973) Intake and requirements of energy and protein for the breeding of wild deer mice, *Peromyscus maniculatus*. *J Repr Fert Suppl* 19:237–252
- Sheley RL, Jacobs SJ, Carpinelli MF (1998) Distribution, biology and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Tech* 12:353–362

- Simberloff D (1991) Keystone species and community effects of biological introductions. In: Ginzburg L (ed) Assessing ecological risks of biotechnology. Butterworth-Heinemann, Boston, pp 1–19
- Simberloff D (1992) Conservation of pristine habitats and unintended effects of biological control. In: Kauffman WC, Nechols JE (eds) Selection criteria and ecological consequences of importing natural enemies. Entomological Society of America, Lanham, pp 103–117
- Simberloff D, Stiling P (1996a) Risks of species introduced for biological control. *Biol Conserv* 78:185–192
- Simberloff D, Stiling P (1996b) How risky is biological control. *Ecology* 7:1965–1974
- Story JM (1977) Effect of *Urophora affinis* on spotted knapweed seed production in Montana. In: Proceedings of the knapweed symposium. Kamloops, British Columbia, p 208
- Story JM, Nowierski RM (1984) Increase and dispersal of *Urophora affinis* (Diptera: Tephritidae) on spotted knapweed in western Montana. *Environ Entomol* 13:1151–1156
- Story JM, Nowierski RM, Boggs KW (1987) Distribution of *Urophora affinis* and *U. quadrifasciata*, two flies introduced for biological control of spotted knapweed (*Centaurea maculosa*) in Montana. *Weed Sci* 35:145–148
- Story JM, Boggs KW, Good WR (1992) Voltinism and phenological synchrony of *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae), two seed head flies introduced against spotted knapweed in Montana. *Environ Entomol* 21:1052–1059
- Story JM, Boggs KW, Good WR, White LJ, Nowierski RM (1995) Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed seedheads. *Environ Entomol* 24:1467–1472
- Strauss SY (1991) Indirect effects in community ecology: their definition, study and importance. *Trends Ecol Evol* 6:206–210
- Taitt MJ (1981) The effect of extra food on small rodent populations. I. Deermice (*Peromyscus maniculatus*). *J Anim Ecol* 50:111–124
- Telleria JL, Santos T, Alcantara M (1991) Abundance and food-searching intensity of wood mice (*Apodemus sylvaticus*) in fragmented forests. *J Mammal* 72:183–187
- Tyser RW (1992) Vegetation associated with two alien plant species in a fescue grassland in Glacier National Park, Montana. *Great Basin Nat* 52:189–193
- Tyser RW, Key KW (1988) Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northw Sci* 62:151–160
- Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to roads and trail corridors in Glacier National Park, Montana (U.S.A.). *Conserv Biol* 6:253–262
- U.S. Congress (1995) Biologically based technologies for pest control (Office of Technology Assessment OTA-ENV-636). U.S. Government Printing Office, Washington DC
- Williamson M (1996) Biological invasions. Chapman Hall, New York
- Wright AL, Kelsey RG (1997) Effects of spotted knapweed on a cervid winter-spring range in Idaho. *J Range Manage* 50:487–496
- Zwölfer H (1970) Investigations on the host-specificity of *Urophora affinis* Frfld. (Diptera: Trypetidae) (Progress report 25). Commonwealth Institute of Biological Control, London