

Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird

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Abstract Although exotic plant invasions threaten natural systems worldwide, we know little about the specific ecological impacts of invaders, including the magnitude of effects and underlying mechanisms. Exotic plants are likely to impact higher trophic levels when they overrun native plant communities, affecting habitat quality for breeding songbirds by altering food availability and/or nest predation levels. We studied chipping sparrows (*Spizella passerina*) breeding in savannas that were either dominated by native vegetation or invaded by spotted knapweed (*Centaurea maculosa*), an exotic forb that substantially reduces diversity and abundance of native herbaceous plant species. Chipping sparrows primarily nest in trees but forage on the ground, consuming seeds and arthropods. We found that predation rates did not differ between nests at knapweed and native sites. However, initiation of first nests was delayed at knapweed versus native sites, an effect frequently associated with low food availability. Our seasonal fecundity model indicated that breeding delays could translate to diminished fecundity, including dramatic declines in the incidence of double brooding. Site fidelity of breeding adults was also

substantially reduced in knapweed compared to native habitats, as measured by return rates and shifts in territory locations between years. Declines in reproductive success and site fidelity were greater for yearling versus older birds, and knapweed invasion appeared to exacerbate differences between age classes. In addition, grasshoppers, which represent an important prey resource, were substantially reduced in knapweed versus native habitats. Our results strongly suggest that knapweed invasion can impact chipping sparrow populations by reducing food availability. Food chain effects may be an important mechanism by which strong plant invaders impact songbirds and other consumers.

Keywords *Centaurea maculosa* · Food availability · Grasshoppers · *Spizella passerina* · Timing of breeding

Introduction

Exotic plant invasions have emerged as a major threat to natural systems (Wilcove et al. 1998; Levine et al. 2003), yet our knowledge of their specific ecological impacts is limited. Although it is widely recognized that exotic plant invaders can reduce diversity of native plant communities, few studies of natural systems have addressed the nature of diversity loss and the associated consequences for higher trophic levels, including the magnitude of effects and underlying mechanisms (Ostfeld and LoGiudice 2003). Such knowledge is critical to formulating effective management strategies, as impacts of exotic species are likely to be complex and require careful consideration before weed control strategies are implemented (Pearson and Callaway 2003; Ortega and Pearson 2005).

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Studies addressing impacts of plant invasions on higher trophic levels have primarily documented negative effects of specific invaders on abundance or diversity of arthropods, with limited treatment of mechanism (Levine et al. 2003). The extent to which such impacts may ripple through systems to affect higher trophic levels such as songbirds remains largely unexplored. Relatively few studies have examined impacts of exotic plant invasions on birds, and they have generally reported neutral or negative effects on abundance of species breeding in invaded habitats (Wilson and Belcher 1989; Ramos 1996; Feare et al. 1997; Whitt et al. 1999; Scheiman et al. 2003). However, bird abundance can be a poor indicator of habitat quality, failing to elucidate underlying ecological interactions when considered alone (Van Horne 1983). Only by documenting how exotic plant invasions affect higher trophic levels can we identify specific pathways of impact that may be applicable beyond the taxa under study.

Strong plant invaders, i.e., exotic species that overrun plant communities (Ortega and Pearson 2005), may impact habitat quality for breeding songbirds in two major ways. First, these invaders may affect food availability by displacing important native plant taxa and thereby altering abundance of plant (e.g., seed, fruit) and arthropod food resources and/or access to these resources. Food availability often limits reproductive success of birds, typically by delaying nest initiation when low (Martin 1987; Boutin 1990; Tye 1992; Kelly and Van Horne 1997; Marshall et al. 2002; see also Nagy and Holmes 2005). Additionally, shifts in plant communities induced by strong plant invaders may affect nest predation levels, impacting habitat quality by altering the quality of available nest sites (e.g., degree of concealment or predator access) and/or nest predator activity (e.g., density or behavior). Nest predation has a major influence on reproductive success, and is considered the primary source of nest mortality for open-nesting songbirds (Martin 1992). Food and nest predation typically affect different components of reproductive success, interacting to influence fecundity (e.g., Rodenhouse and Holmes 1992; Marshall et al. 2002). Therefore, to thoroughly assess impacts of exotic plant invasions on songbirds, including underlying mechanisms, comprehensive measures of reproductive success which account for nest predation and factors sensitive to food availability must be evaluated.

Changes in reproductive success induced by strong plant invaders may translate into significant population-level impacts for songbirds. In migratory species, fecundity in one year can drive recruitment of yearling

breeders in the subsequent season (Sillett et al. 2000). Reproductive success also influences breeding site fidelity, an important determinant of demography and genetic variability (Hoover 2003). In fact, site fidelity in some species appears to be driven by decision rules, where an adult's tendency to return to a breeding location versus disperse to a new one is based on the degree of reproductive success attained by itself and its neighbors in the previous breeding season (Payne and Payne 1993; Haas 1998; Hoover 2003). Therefore, low-quality habitats characterized by reduced reproductive success may also show reduced site fidelity. However, for migratory songbirds, such low-quality habitats can be replenished by annual recruitment of yearlings produced elsewhere due to the high degree of dispersal from natal to breeding sites (Greenwood and Harvey 1982). This site fidelity-recruitment pattern in low-quality habitats may be reinforced by age effects because, compared to older birds, yearling birds often exhibit: (1) reduced reproductive success, arriving later on breeding grounds and competing less effectively for high-quality territories and mates (Holmes et al. 1996; Hunt 1996; Lozano and Lemon 1999); and (2) reduced site fidelity (Bollinger and Gavin 1989; Payne and Payne 1993; Hoover 2003). Impacts of exotic plant invasions on habitat quality may therefore include significant changes in reproductive success and site fidelity not reflected in measures of abundance.

To date, few studies examining impacts of exotic plant invasions on birds have considered reproductive success, and none have considered site fidelity. Research, in some cases, has shown differing nest predation levels for birds using exotic versus native nest substrates, attributing effects primarily to changes in nest site quality (Schmidt and Whelan 1999a; Schieman et al. 2003; Borgmann and Rodewald 2004). However, potential impacts of exotic plant invasion on reproductive success extend beyond changes in nest site quality, and studies examining invader impacts have not considered components of fecundity that may be sensitive to changes in food availability, such as the timing of nest initiation. Thorough assessment of reproductive success may be especially critical for multi-brooded species, whose fecundity can be strongly linked to the number of broods produced, as influenced by factors including food availability (Rodenhouse and Holmes 1992; Holmes et al. 1996; Marshall et al. 2002; Nagy and Holmes 2005).

We examined breeding populations of a multi-brooded migratory songbird, the chipping sparrow (*Spizella passerina*), to evaluate how shifts in plant communities induced by a strong plant invader may impact higher trophic levels. Study sites were savannas

either dominated by native vegetation or invaded by the perennial forb spotted knapweed (*Centaurea maculosa*), an aggressive exotic species that has overrun vast areas of western North America (Sheley et al. 1998, 2000). Knapweed invasion leads to significant declines in diversity and abundance of native perennial forbs and bunchgrasses, dramatically shifting composition and structure of herbaceous plant communities (Ortega and Pearson 2005). We chose chipping sparrows to examine associated impacts on higher trophic levels because they: (1) forage primarily on the ground within vegetation impacted by knapweed; (2) consume both arthropods and seeds during the breeding season (Middleton 1998), making them sensitive to potential impacts of knapweed invasion on food availability; (3) nest aboveground, mainly in trees, minimizing the possibility that nest site quality is affected by knapweed invasion to allow focus on alternate mechanisms of impact; and (4) are of conservation concern in western North America due to habitat declines (Hejl 1994).

To provide a comprehensive assessment of impacts of knapweed invasion on habitat quality for breeding chipping sparrows and distinguish between food and nest predation-related effects, we studied birds breeding at knapweed-invaded and native sites, evaluating: (1) abundance; (2) critical components of reproductive success, including the timing of nest initiation and nest predation rates, which we used to model seasonal fecundity; and (3) site fidelity. To further assess the possibility that food availability may decline due to knapweed invasion, we also measured relative abundance of grasshoppers (Orthoptera: Acrididae), a major prey item for chipping sparrows and other ground-foraging songbirds (Belovsky et al. 1990; Middleton 1998).

Materials and methods

Study sites

We studied chipping sparrows in Ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) savannas located at elevations of 1,300–1,700 m on the Lolo National Forest in western Montana. Study sites were chosen to be as similar as possible (Ortega and Pearson 2005) while representing either knapweed-invaded ($n=3$) or native habitats ($n=3$). Each site was surrounded by montane coniferous forest and represented a discrete habitat patch [mean approximate area = 9.2 ± 1.14 ha ($\pm$ SE)] for chipping sparrows given their affinity for open forest types and associated edges (Middleton 1998). Availability of nest sites, as measured by density and basal area of trees (Ortega et al.

2004), was comparable between knapweed and native sites ($t_4 < 1.4$, $P > 0.2$). Slopes were steep with south to west aspects, and shrubs occurred at low densities. Native ground cover consisted primarily of diverse forbs and bunchgrasses. Knapweed-invaded sites included dense patches of spotted knapweed intermixed with native vegetation, while native sites had only trace levels of knapweed (Ortega and Pearson 2005). At each site, we established a 6.0-ha rectangular plot oriented perpendicular to the slope and marked with four 250-m transects flagged at 10-m intervals and spaced 50 m apart. All study plots fell within 25 m of dense forest and were separated by >2 km.

Marking and counting birds

Intensive mist-netting efforts were used to mark chipping sparrows at each study site from 2000 to 2002. We captured adults using a target banding approach, luring them into nets with tape playbacks of songs and calls or placing nets near known nests. Each bird was banded with a unique combination of four bands, including one USFWS aluminum band and three color celluloid bands. Using plumage criteria from Pyle et al. (1987), we assigned adults to age classes (i.e., yearling versus older). Because age determination is difficult in chipping sparrows and data from a later study showed that yearlings tend to be under-classified using the more obvious plumage criteria (Y. K. Ortega, B. Ogle, T. Rodriguez, unpublished data), we do not report age ratios in the current study. However, we considered age effects in analyses where sample sizes permitted and note that reported differences between age classes are likely conservative since the older age class included misclassified yearlings.

From 1999 to 2001, we delineated territories of chipping sparrows using standard spot mapping methods (IBCC 1970). To minimize bias, observers were rotated among sites. During each of seven systematic surveys between mid-May and mid-July each year, observers recorded locations of all birds seen or heard on grid maps depicting transect lines, prominent vegetation, and topographic features. Spot mapping was conducted independently of banding efforts to avoid effects of playback on territorial behavior. We used clusters of locations from differing visits supplemented with nest and color-band information to identify territories and derive territory density per study site and year.

Measuring components of reproductive success

Observers searched for and monitored nests during bi-weekly visits to sites until nesting activity ceased,

1999–2001, using standard protocols (Martin and Geupel 1993; Martin et al. 1997). Nests were primarily located <3 m high and in trees (60% and 88% of nests, respectively; Y. K. Ortega, unpublished data). Only initiated nests (i.e., those known to have eggs) were considered in analyses. We defined the breeding season as the period when nests could be initiated, and marked the onset by examining dates of initiation of first nests per pair. The earliest initiation date across years (23 May) represented day 1 of the season. For each pair, the first nest found was assumed to be its first if initiated in the first 3 weeks of the season since 96% (54 of 56) of known renests were initiated after this period. As a measure of the duration of breeding, we examined the tendency of birds to renest (after either success or failure of a previous nest) over the course of the season; if we did not find a new nest after termination of a prior known nest attempt, we assumed pairs renested if they remained on territory and showed signs of renewed breeding (i.e., singing male, copulation, and/or nest building). The maximum extent of the breeding season was determined from the median date for the latest recorded nest initiation across years. To determine clutch size, we checked nest contents with the aid of mirrors mounted on poles. We assessed nest predation levels by calculating daily mortality rates according to Mayfield (1975), adjusting for the number of days each nest was observed, and fate was determined as described by Tewksbury et al. (1998). Although chipping sparrow nest site quality could not be impacted by knapweed, nest predation levels could still be sensitive to invasion given potential changes in nest predator activity (e.g., Ortega et al. 2004). Brood parasitism of chipping sparrow nests by brown-headed cowbirds (*Molothrus ater*) was not observed in the study area.

Site fidelity

To evaluate fidelity of adults to breeding sites, observers conducted systematic searches for banded birds on study plots and within a 50-m-wide area surrounding each plot, with equal effort at knapweed and native sites in each breeding season, 2000–2002. Banded adults were classified as residents of a site in a given year if they were observed within plot boundaries during at least two different visits and/or were associated with a nest located on the plot. To measure site fidelity, we assessed return rates of residents from year t by distinguishing those that were observed within plots or surrounding 50-m zones in year $t+1$ from those that were not. Because chipping sparrow territories are typically circular and <1 ha in area (i.e., <50 m in radius;

Middleton 1998), our search protocol was sufficient to account for local dispersal of resident birds between seasons, i.e., when territories shifted within a study site. Given our intensive census of birds, we assumed that resighting probabilities were high and that birds not observed within the search area had dispersed from sites or died (Martin et al. 1995). For birds returning to sites, we evaluated the degree of local dispersal between seasons by measuring territory movements, defined as the distance (to the nearest 10 m) between the new territory center (defined by mapped movements from a minimum of two visits) and the prior year's.

Grasshopper relative abundance

We used pitfall traps (Cooper and Whitmore 1990) to measure relative abundance of grasshoppers on the study sites in 1999 and 2000. We focused efforts on grasshoppers not only because they are an important prey item, but also because they are considered the dominant aboveground invertebrates in grassland habitats in terms of biomass (Scott et al. 1979). On each of the four transects per site, 13 traps were placed at 20-m intervals. Sampling periods were 2 weeks in length and generally corresponded to early (late May) and late (late July) in the breeding season. Pitfall traps were made from 2-l clear plastic soda bottles with the upper portion cut off and inverted into the lower to act as a funnel. Traps were placed level with the soil surface, and a 1% formalin solution was added to retard sample decomposition. Counts of grasshopper adults plus nymphs represented relative abundance per trap and sampling period.

Statistical analyses

We conducted statistical analyses with SAS software (SAS Institute 1999), primarily using mixed linear models to test for differences by knapweed class (i.e., knapweed versus native habitat) while including site and year as fixed factors. The interaction of knapweed class and year was initially included in all statistical models but eliminated in final versions given lack of significance ($P > 0.2$). For assessment of territory density, we treated year as a repeated measure and included site-level measures of tree density and basal area from a related study as covariates (Ortega et al. 2004) since trees are an important habitat variable for this species. After testing initiation dates of first nests with the basic model, we added age and knapweed $\times$ age effects. For this test, we included cases where age class had been determined for only one bird

in a pair (59% of 64 pairs with age information). Remaining cases where age class was known for both birds in a pair indicated that age classes tended to match within pairs (65% of 26 pairs); where age class differed between birds (nine pairs), pairs were assigned to the yearling class, but results were comparable if mixed-age pairs were instead assigned to the older age class. Using the basic model structure, we used logistic regression to see whether the probability of renesting differed for pairs at knapweed versus native sites; fate of previous nest attempt did not affect the probability of renesting at either type of site ($P > 0.58$) and was not included in the final model. Because clutch size and probability of renesting can decline over the course of the season (e.g., Martin 1987), we accounted for seasonal effects on these variables by including week of the breeding season and its interaction with knapweed class as fixed factors in associated analyses. Seasonal differences were most pronounced for weeks 1–5 of the season compared to later, so we re-ran models to generate estimates for each of these periods. Maximum-likelihood estimators of variance were calculated for daily nest mortality rates to test for knapweed and seasonal effects (Johnson 1979; Hensler and Nichols 1981). We assessed whether the probability of birds returning to sites differed by knapweed class using a mixed model version of logistic regression (Littell et al. 1996), which included sex as an additional fixed factor and individual as a repeated measure; age and knapweed $\times$ age were also considered in a separate model. We compared territory movements with a mixed model incorporating these same factors. To assess relative abundance of grasshoppers per trap, we tested each sampling period separately and treated year as a repeated measure.

We screened for violations of assumptions of normality and homoscedasticity for all dependent variables analyzed with mixed models by inspecting scatterplots of residuals. For comparison between groups (e.g., by knapweed class), we used least squares means instead of raw means to adjust for background factors included in models.

Seasonal fecundity model

We conducted simple simulations to consider how measured differences in components of reproductive success for birds breeding at knapweed versus native sites could affect seasonal fecundity. Models are often used to assess fecundity because complete nesting histories, required for direct measurement of fecundity, are difficult to obtain for a sufficient sample of birds (e.g., Marshall et al. 2002). Our modeling approach was

similar to previous efforts (Pease and Grzybowski 1995; Schmidt and Whelan 1999b), and incorporated breeding season length, seasonal variation in components of reproductive success, and multiple brooding. Each model run tracked the number of young and number of broods fledged by a pair within a season given a fixed set of input values for reproductive parameters representing conditions at either knapweed or native sites. We based input values on field data described previously, assuming parameters were identical at knapweed and native sites unless statistical analyses indicated that differences were significant. We also incorporated seasonal effects into the model using these same criteria. Means were used as input values for first nest initiation date (rounded to the nearest day) and clutch size (rounded to the nearest egg). In each model run, daily nest mortality rate was used in conjunction with a random number generator to determine the outcome of each nest attempt. After termination of an attempt, nesting ceased if the maximum extent of the breeding season had been exceeded; otherwise, the probability of renesting was applied as for the daily nest mortality rate to determine whether a new nest was initiated. Number of young fledged per successful simulated nest was calculated from clutch size and the clutch survival rate, defined as the slope estimate ($\beta = 0.9$, $SE = 0.32$, $P = 0.009$) from a regression of observed number fledged per nest (from counts of nestlings conducted during the latter half of the nestling period) against clutch size. Other model constants included a 25-day nesting cycle for a four-egg clutch (median length from initiation to fledging) and a 6-day time delay (mean = 5.9 ± 0.51 days) between nest termination and initiation of a reneest. We ran simulations 100,000 times to obtain a distribution of expected number of broods and young fledged per pair at knapweed and native sites, respectively.

To evaluate whether differences in model output for knapweed versus native sites were influenced by variation in input values for reproductive parameters, we re-ran our model incorporating a Monte Carlo sensitivity analysis (Klepper et al. 1994). Observed differences in reproductive parameters at knapweed versus native sites were again represented by fixed input values derived from statistical analyses, but background parameters (i.e., those showing no statistical differences and model constants) were allowed to vary across 10,000 model runs. In each of these model runs, an input value for each background parameter was randomly and independently drawn from a bounded range of values corresponding to the range of values in field data or to 95% confidence intervals derived from SEs of estimates (see Results). Each run was repeated

10,000 times to obtain expected number of broods and young fledged per pair at knapweed versus native sites for a given set of input values. To assess sensitivity, we regressed the difference in expected fecundity at knapweed versus native sites against the input values for background parameters.

Results

Mean density of chipping sparrow territories across years was lower at knapweed (10.8 ± 0.75 territories/10 ha) versus native (13.9 ± 0.75 territories/10 ha) sites when tree density and basal area were accounted for, but not significantly so ($F_{1,3} = 4.98$, $P = 0.11$). Initiation of first nests was delayed at knapweed sites, peaking in the third week of the breeding season compared to the first week at native sites (Fig. 1). Overall, mean initiation dates of first nests at knapweed (day 12.3 ± 1.04) compared to native (day 8.7 ± 0.92) sites differed by >3 days ($F_{1,69} = 6.59$, $P = 0.012$). Separate analysis indicated that yearling pairs initiated first nests later compared to older pairs ($F_{1,37} = 6.6$, $P = 0.014$). However, even when age class was accounted for, the onset of breeding was still delayed at knapweed versus native sites ($F_{1,37} = 4.5$, $P = 0.04$). Moreover, the delay in breeding at knapweed versus native sites varied in magnitude by age class (knapweed $\times$ age interaction: $F_{1,37} = 3.98$, $P = 0.05$), with a difference in mean initiation date of 8 days for yearlings compared to 1 day for older birds (Fig. 2a).

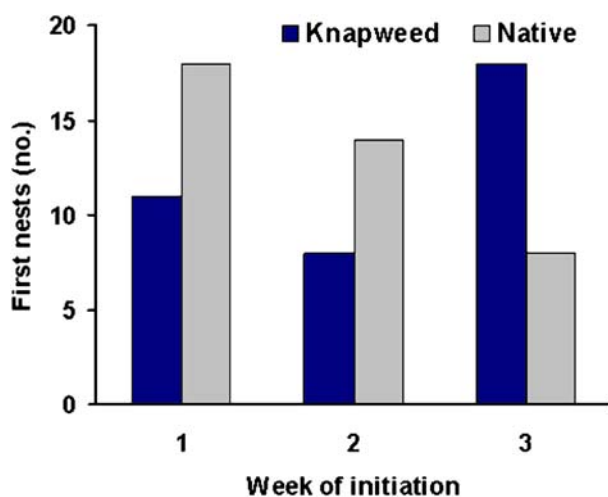


Fig. 1 Distribution of first nests according to timing of initiation for chipping sparrows (*Spizella passerina*) at knapweed (*Centaurea maculosa*) versus native sites in western Montana, 1999–2001. Sample size per year was consistent between knapweed and native sites ($n = 77$, $\chi^2_2 = 0.69$, $P = 0.71$)

The maximum extent of the breeding season in terms of latest recorded nest initiation date varied by only ± 2 days across years and yielded a total season of 49 days. Probability of renesting did not differ by knapweed class ($\chi^2_1 = 0.004$, $P = 0.95$), but declined over the course of the breeding season ($\chi^2_1 = 21.85$, $P < 0.001$) at both types of sites (i.e., no knapweed $\times$ week interaction: $\chi^2_1 = 0.04$, $P = 0.85$): pairs renested following 98.8% of nest attempts terminating in the first 5 weeks of the season ($n = 84$) compared to 51.9% of those terminating in the final 2 weeks of the season ($n = 54$). Similarly, clutch size did not differ between knapweed and native sites ($F_{1,59} = 0.16$, $P = 0.69$), but declined over the course of the breeding season ($F_{6,59} = 4.05$, $P = 0.0018$) at both types of sites (i.e., no knapweed $\times$ week interaction: $F_{1,59} = 0.48$, $P = 0.82$), averaging 3.9 ± 0.07 eggs in the first

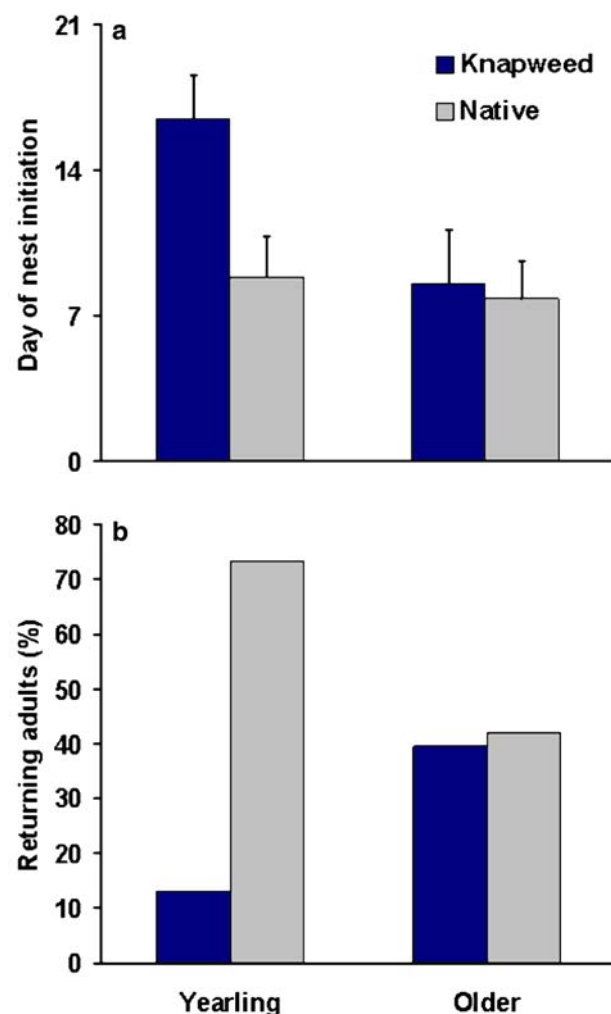


Fig. 2 Comparison of **a** initiation dates (mean $\pm$ SE) of first nests ($n = 47$), 1999–2001, and **b** percentage of resident adults ($n = 82$) that returned between breeding seasons, 2000–2002, for chipping sparrows by age class (yearling or older) at knapweed versus native sites in western Montana

5 weeks of the season versus 3.1 ± 0.19 eggs in the final 2 weeks.

The daily mortality rate due to predation did not differ ($P > 0.78$) for nests at knapweed ($n=62$; $1.7 \pm 0.41\%$) versus native ($n=73$; $1.9 \pm 0.44\%$) sites, and translated to an overall predation rate of 36.3%. Including other natural causes of nest failure (primarily weather), daily mortality was $2.5 \pm 3.49\%$, giving an overall mortality rate of 52.8% for the nesting cycle. Seasonal effects on daily mortality rates were not apparent; e.g., rates were comparable for nests initiated in weeks 1–5 versus later ($P > 0.87$).

Incorporating observed values for reproductive factors, including the breeding season of limited length, seasonal declines in probability of reneating and clutch size, and moderate nest mortality rates, our seasonal fecundity model indicated that delays in the onset of breeding could result in reduced fecundity at knapweed versus native sites. Based simply on the difference in mean initiation dates (i.e., assuming all other factors were equal), simulations showed a marked reduction in the frequency of double brooding at knapweed versus native sites, with only 19.5% of pairs at knapweed sites expected to fledge two broods versus 36.6% of pairs at native sites (Fig. 3a). Accordingly, birds at knapweed versus native sites were expected to fledge fewer young per season (Fig. 3b), averaging 3.52 versus 4.07 young/pair. Sensitivity analysis indicated that even when background reproductive parameters were allowed to vary (Table 1), the observed difference in initiation dates resulted in fewer young produced at knapweed versus native sites in 98% of model runs.

When initiation dates were adjusted to reflect observed age-related differences in the onset of breeding, our fecundity model indicated that knapweed effects could be much greater for yearling versus older pairs. Delays in breeding for yearling pairs at knapweed compared to native sites lead to an expected frequency of double brooding of 17.2 versus 36.6%, with an average of 3.29 young/year fledged versus 4.07 young/year. In contrast, the relatively short delay for older pairs amounted to minimal declines in measures of expected fecundity, with frequencies of double brooding of 36.6 and 37.4% for knapweed and native sites, respectively, and an average of 4.07 young/year fledged compared to 4.11 young/year.

Following trends in reproductive success, birds breeding at knapweed versus native sites showed reduced site fidelity. The overall return rate for resident birds ($n=60$ male and 27 female) between years was 33.8% at knapweed sites compared to 56.6% at native sites ($F_{1,84}=4.19$, $P=0.044$). This sharp decline in return rates as a function of knapweed invasion held when age class was

statistically accounted for ($F_{1,81}=6.32$, $P=0.014$). Although return rates did not differ between age classes overall ($F_{1,79}=0.02$, $P=0.9$), knapweed effects were much stronger for yearling versus older birds (knapweed $\times$ age interaction: $F_{1,80}=6.14$, $P=0.015$): yearlings rarely returned to knapweed sites but readily returned to native sites while older birds had moderate return rates at both types of sites (Fig. 2b). In addition, birds returning to knapweed sites appeared to show a higher degree of local dispersal compared to those returning to native sites, as 58.3 versus 25.0% of territories moved >50 m (Fig. 4). Overall, territories shifted 1.5 times farther ($F_{1,38}=5.08$, $P=0.03$) at knapweed compared to native sites (mean= 88.3 ± 10.61 and 58.3 ± 9.88 m, respectively).

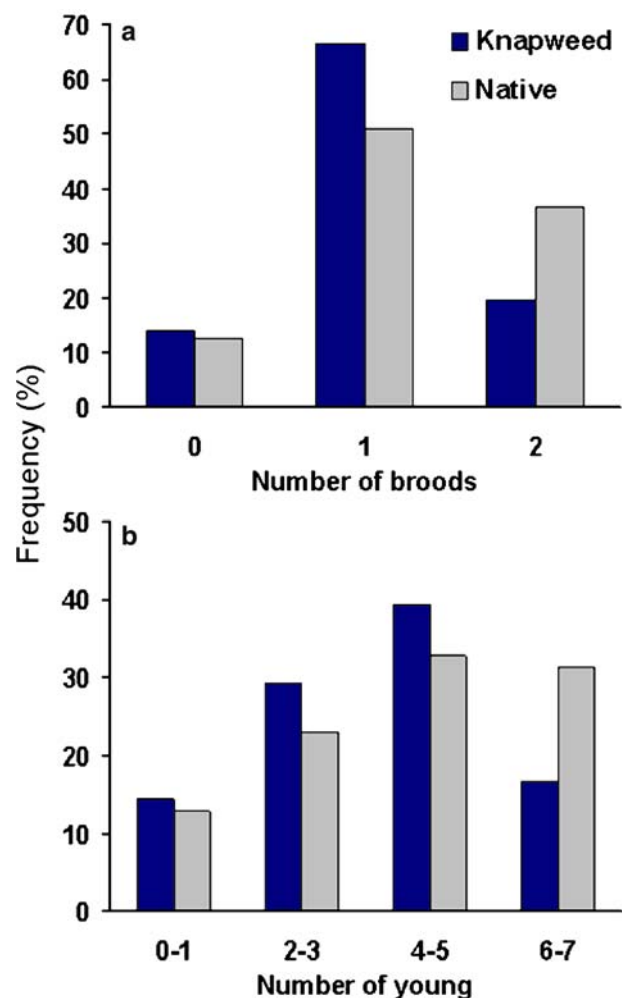


Fig. 3 Distribution of output from a seasonal fecundity model showing expected number of **a** broods fledged and **b** young produced per pair for chipping sparrows at knapweed versus native sites, based on reproductive parameters measured in western Montana, 1999–2001

In line with results for chipping sparrows, grasshoppers showed diminished relative abundance in pitfall traps at knapweed versus native sites (Fig. 5), as measured both early ($F_{1,306}=18.6$, $P<0.001$) and late ($F_{1,306}=34.05$, $P<0.001$) in the breeding season.

Discussion

Despite the widely recognized threat of exotic plant invasions, we still lack understanding of the magnitude of the impacts and the underlying mechanisms. It is largely unknown how shifts in plant communities induced by strong invaders affect higher trophic levels. Songbirds may be impacted if exotic plant invasions alter food availability or levels of nest predation. Most work to date has examined effects on nest predation, focusing on changes in nest site quality related to displacement of native plants by invaders. Although strong plant invaders may also significantly impact seeds and arthropods that serve as important food resources for songbirds, we know of no study that has evaluated this mechanism. In our study system, direct effects of spotted knapweed on nest site quality were unlikely given that chipping sparrows nest primarily in trees, but effects on food availability were possible since this species feeds primarily on the ground. We found that nest predation levels did not differ in habitats invaded by knapweed compared to those dominated by native vegetation, despite potential differences in nest predator communities associated with knapweed invasion (e.g., Ortega et al. 2004). Nonetheless, habitat quality for chipping sparrows was

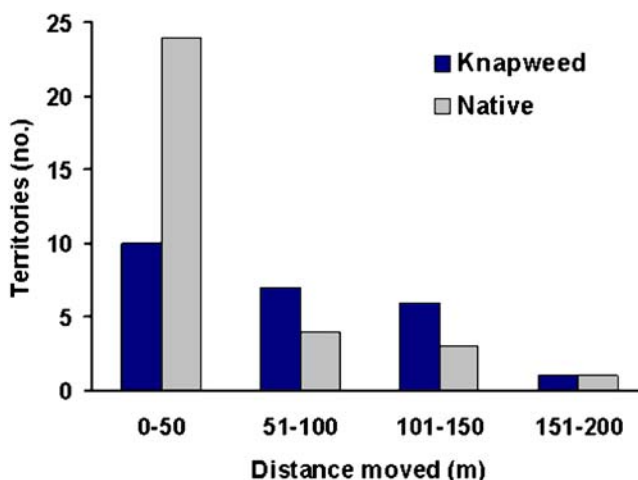


Fig. 4 Distribution of distance moved between breeding seasons for mapped territories of individual chipping sparrows ($n=45$) at knapweed versus native sites in western Montana, 2000–2002

Table 1 Results of a Monte Carlo sensitivity analysis for a seasonal fecundity model comparing knapweed and native sites by incorporating the difference in first nest initiation dates measured in western Montana, 1999–2001. Input values for background reproductive parameters were allowed to vary across 10,000 runs within the specified range. For each run, model outcome was assessed as the difference in expected fecundity (frequency of double brooding and mean number of young fledged, respectively) at knapweed versus native sites. Sensitivity is given as the squared semi-partial correlation between model outcome and input parameter values

Parameter	Range	Sensitivity	
		Double brood	Young fledged
Season length (days) ^a	47–51	<0.001	<0.001
Nesting cycle (days) ^{a,c}	21–29	0.05	0.012
Delay between nests (days) ^a	3–11	<0.001	0.013
Renesting probability, week 1–5 ^b	91.5–100	0.005	0.005
Renesting probability, week >5 ^b	1.8–98.4	0.1	0.074
Clutch size, week 1–5 ^a	3–5	0.011	0.039
Clutch size, week >5 ^a	2–4	<0.001	0.006
Daily nest mortality ^b	1.8–3.1	0.025	0.014
Clutch survival rate ^b	0.3–1.0	<0.001	0.11

^a Range derived from field data

^b Range derived from 95% confidence intervals

^c For a four-egg clutch

clearly reduced by knapweed invasion. Birds in knapweed versus native habitats showed delayed nest initiation, which, according to our simulations, could translate to diminished fecundity. Site fidelity of breeding adults was also greatly reduced in knapweed compared to native habitats. Following declines in native plants (Ortega and Pearson 2005), abundance of grasshoppers, an important arthropod group, was also reduced in knapweed versus native habitats. These results strongly suggest that food-related effects may underlie impacts of knapweed invasion on chipping sparrows.

Reduced food availability as mechanism

We identified significant delays in the onset of nest initiation at knapweed-invaded versus native sites that likely signal reduced food availability in these habitats. Numerous experimental and observational studies of birds have linked delays in breeding to reduced food availability, and food is considered the primary proximate factor influencing the timing of nest initiation (Martin 1987; Boutin 1990; Kelly and Van Horne 1997; Marshall et al. 2002). According to this body of studies,

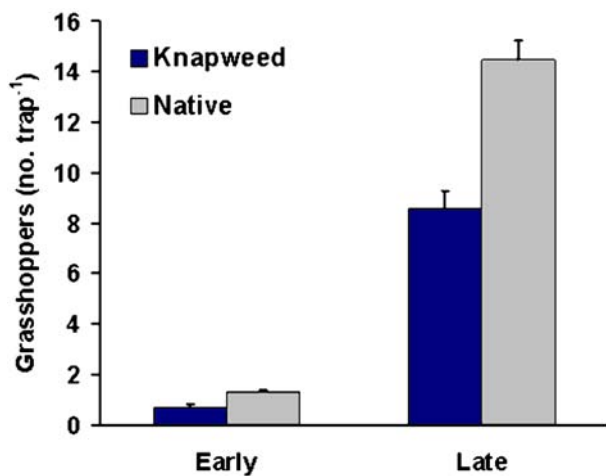


Fig. 5 Number of grasshoppers (mean $\pm$ SE) sampled per pitfall trap ($n=312$) early and late in the chipping sparrow breeding season at knapweed versus native sites in western Montana, 1999–2000

although food availability can affect several components of reproduction for songbirds, including the duration of breeding and clutch size, it most often appears to affect the onset of breeding. Additional factors influencing the onset of breeding include age, arrival dates on breeding grounds, and access to territories and mates, all of which are inter-correlated and linked to habitat quality (Holmes et al. 1996; Hunt 1996; Kelly and Van Horne 1997; Lozano and Lemon 1999). We not only found that yearling pairs initiated nests later than older pairs, but that this difference was much greater at knapweed versus native sites, signaling a fundamental shift in conditions.

Food availability is a major component of habitat quality for songbirds (Tye 1992; Holmes et al. 1996; Sillett et al. 2000; Nagy and Holmes 2005), and background data further suggest that this factor may be impacted by knapweed invasion. Previous work conducted on our study sites indicates that knapweed invasion causes steep declines in diversity and abundance of native perennial forbs and bunchgrasses (Ortega and Pearson 2005). This shift in the plant community should amount to a substantial reduction in potential food sources for ground-foraging songbirds like chipping sparrows for several reasons. First, production of native seeds diminishes with declines in major plant groups (Y. K. Ortega, unpublished data). Second, arthropods should also decline with native plants because of tight linkages between trophic levels (e.g., Kemp et al. 1990; Knops et al. 1999). Supporting this, we found reduced abundance of grasshoppers, important prey items for chipping sparrows and other consumers, in knapweed-invaded versus native habitats. Third, replacement food sources provided by knapweed should be limited because its seeds do not mature

until late summer (Sheley et al. 1998), after the breeding season, and because exotic plants should generally support fewer arthropods than native plants since their specialist consumers are lost with invasion (Crawley 1997). Access to food by ground-foraging songbirds could also be altered since knapweed invasion alters habitat structure (Ortega et al. 2004).

Impacts on reproductive success

Delayed breeding can confer several disadvantages on birds that reduce fecundity (Martin 1987; Holmes et al. 1992; Tye 1992; Kelly and Van Horne 1997; Lozano and Lemon 1999; Marshall et al. 2002). First, delays effectively shorten the available breeding season if the end of the season is constrained, as found in our study and others (e.g., Marshall et al. 2002). Fecundity of double-brooding species may be especially sensitive to changes in breeding season length (Tye 1992; Marshall et al. 2002). Breeding delays also push nest attempts later into the season, when environmental and physiological conditions may be less favorable (Martin 1987). Accordingly, we found that both clutch size and the tendency of birds to reneest declined in the latter portion of the breeding season. Incorporating seasonal declines in reproductive parameters into a fecundity model, we found that delays in the onset of breeding observed in knapweed versus native habitats could reduce the incidence of double brooding by nearly 50%, with average fecundity declining 14% overall, and 19% for yearling pairs compared to <1% for older pairs. Simulations were based on differences in mean initiation dates alone, and model conclusions were robust to variation in other reproductive parameters.

Impacts on site fidelity

Site fidelity in songbirds appears to be strongly influenced by reproductive success and is therefore a powerful measure of habitat quality (Bollinger and Gavin 1989; Holmes et al. 1996; Hoover 2003). According to experimental work on songbirds manipulating reproductive success while controlling for individual quality, birds producing fewer broods tend to have lower return rates because they disperse to new breeding locations between years and not because they suffer higher mortality (Haas 1998; Hoover 2003). In our study, return rates were reduced by nearly 50% for chipping sparrows at knapweed-invaded compared to native sites, matching the overall decline in the expected incidence of double brooding. That reduced return rates for birds nesting at knapweed versus native sites resulted from increased dispersal was

supported by comparison of between-season territory movements. In addition, 25% of 24 birds resident to sites in 2000 but failing to return in 2001 were detected on sites in 2002, further indicating that disappearance of birds from sites between years was influenced by dispersal. Although mortality inevitably contributed to return rates, levels were unlikely to differ markedly due to knapweed invasion, especially when age class was accounted for, given that survival in migratory birds is largely determined off the breeding grounds where most of the year is spent (e.g., Sillett et al. 2000).

Age may be an important factor influencing site fidelity in songbirds because: (1) reproductive success and associated factors including access to high-quality habitat are correlated with age, and (2) decision rules for dispersal may vary with age (Payne and Payne 1993; Holmes et al. 1996; Hoover 2003). We found that chipping sparrow age classes responded differently to knapweed invasion: yearlings had greatly reduced return rates at knapweed versus native sites, while older birds had comparable rates. This site fidelity pattern also matched observed differences in reproductive success, where yearling versus older pairs had much longer knapweed-related breeding delays, which could produce greater declines in fecundity. Other studies of songbirds have reported similar interactions of habitat quality with age, where yearlings appear to be more sensitive to habitat differences than older birds (Holmes et al. 1996; Hunt 1996).

Conclusions

Previous studies have evaluated effects of exotic plant invasions on abundance of songbirds, but in large part, have not comprehensively addressed the extent of impacts on populations. In our study, effects of spotted knapweed invasion on abundance of chipping sparrows appeared weak. However, declines in reproductive success related to the timing of breeding at knapweed versus native sites were substantial. Furthermore, consideration of site fidelity indicated that knapweed versus native sites had much higher turnover of adults likely due to breeding dispersal. Both reproductive success and site fidelity are critical indicators of habitat quality and determinants of population dynamics (e.g., Donovan et al. 1995; Holmes et al. 1996; Hoover 2003). Therefore, our results strongly suggest that knapweed invasion produces population-level impacts on chipping sparrows. Implications of knapweed invasion may be heightened since impacts appear to fall primarily on yearlings, thereby compounding differences between age classes. Because population status also depends on juvenile and adult rates of survival and dispersal, measures which are typically confounded

and difficult to obtain for migratory songbirds (Pulliam et al. 1992; Lebreton et al. 1993), comparison of seasonal fecundity and site fidelity may provide the best assessment of severity of strong invader impacts.

Mechanistic understanding of strong invader impacts is also critical to advancing invasion ecology and developing effective strategies to manage invasions (Levine et al. 2003). Studies of breeding songbirds suggest that exotic plant invasions may impact nest predation levels by altering nest site quality (e.g., Schmidt and Whelan 1999a), but other potential impacts, including those on food availability, have received little attention. In our study, several lines of evidence suggest that food availability was the critical resource driving observed differences in habitat quality between knapweed-invaded and native sites. By informing the likely mechanism for knapweed's impacts, our results can be used to develop general understandings of strong invader impacts on higher trophic levels. Based on our study, we hypothesize that exotic plant species overrunning herbaceous native plant communities and reducing abundance and diversity of dominant taxa may readily impact breeding populations of ground-foraging songbirds dependent on seeds and arthropods. This pathway of impact may broadly apply to other consumers relying on similar food resources. For example, summer breeding productivity of deer mice (*Peromyscus maniculatus*) also declines in knapweed-invaded versus native habitats, likely due to diminished native seed and arthropod resources (Pearson et al. 2000; Ortega et al. 2004). Alternatively, strong invader impacts may be idiosyncratic and depend on specific interactions among taxa. To determine the generality of food-related effects of strong invaders on consumers, more attention must be paid to mechanism in studies of invader impacts.

As strong invaders such as spotted knapweed continue to spread, impacts on higher trophic levels are likely to become increasingly severe. At the same time, measures used to control exotic plant invasions come with unintended non-target effects (e.g., Tyser et al. 1998), which may exacerbate problems induced by strong invaders (Pearson and Callaway 2003; Ortega and Pearson 2005). The ecological efficacy of weed management efforts depends on knowledge of the non-target effects of control measures and the specific impacts of strong invaders. Although more work is needed to thoroughly evaluate knapweed's impacts on arthropod prey resources, our results suggest that exotic plant invasions can generate effects that ripple through food chains from native plants to songbirds. Food chain effects may be an important mechanism by which strong invaders impact higher trophic levels.

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