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Native Consumers and Seed Limitation Constrain the Restoration of a Native Perennial Grass in Exotic Habitats

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Abstract

Native consumers and seed limitation may be particularly important in the restoration of native plants where they have been displaced by exotic plants. We used experimental exclosures and seed additions to examine the role of native mammalian consumers and seeding density (500 or 1,000 seeds/m^2) in affecting the establishment of a native perennial grass, Purple needlegrass (*Nassella pulchra*), in the grasslands of California. To focus solely on consumers and propagule density, experimental areas were tilled and weeded. Consumers were important determinants of restoration success: averaged across propagule density, consumers reduced *N. pulchra* seedling recruitment by nearly 30%, reduced seedling height by 44%, reduced plant establishment by 52%, and reduced reproductive tiller length by 43%. Small rodents affected seedling establishment, especially where seeding density was high but did not affect seedling height. Plots accessible by squirrels and rabbits exhibited significantly decreased seedling height and plant establishment, whereas there was no additional impact of allowing large consumers (i.e., deer) access. Despite strong, spatially variable effects of consumers, doubling seed density led to nearly doubled *N. pulchra* establishment on average. Consumer effects were persistent, shaping *N. pulchra* abundance in the subsequent growing season and remaining evident over 18 months after the experiment was initiated. Our work suggests that, despite strong consumer effects, seed addition may be a viable strategy for restoration of *N. pulchra* in invaded areas where it has been displaced by exotic plants, especially when combined with restoration strategies that reduce competition with exotic plants.

Key words: exotic plants, herbivory, granivory, grassland.

Introduction

Consumers are capable of affecting plant populations (e.g., Crawley 2000; Goheen et al. 2004), changing the structure and composition of plant communities (e.g., Bartholomew 1970; Hulme 1996; Howe & Lane 2004; Howe et al. 2006), and influencing the success of invasive plants (Mitchell et al. 2006). The effect of consumers may vary depending upon consumer foraging mode (Reichman 1979; Goheen et al. 2004), their preference for particular plants (Batzli & Pitelka 1970; Borchert & Jain 1978; Howe & Lane 2004; Howe et al. 2006), and particular plant life stages (Howe & Brown 1999). Given these varied consumer impacts, understanding how different consumers affect native plants is of paramount importance because consumers play a key role in the success of conservation (e.g., McGraw & Furedi 2005) and restoration efforts (Hatch et al. 1999; Howe & Brown 1999; Dyer 2003; Martin & Wilsey 2006).

The effect of consumers on plant populations may also depend upon the density of propagules available (Crawley 2000; Turnbull et al. 2000; Clark et al. 2007). When seed density is high, it may overwhelm the ability of consumers to limit plant populations (Crawley 2000). However, high seed density may also attract mobile consumers (Holt & Kotler 1987) or lead to increases in the size of consumer populations (Holt 1977), thus increasing consumer pressure on plants. Interactions among consumers and seed density are also possible, e.g., avian granivores may be attracted to high seed densities, whereas rodent consumers may be more effective at altering community structure at low seed densities (Howe & Brown 1999). Interactions among consumers and seed density are of particular interest in the context of restoration efforts in areas with invasive plants because native plants in invaded habitats may be seed limited (Hamilton et al. 1999; Seabloom et al. 2003) and seed limitation may be driven by consumers (e.g., Orrock et al. 2006). Moreover, native consumers may target native plants (Mitchell et al. 2006). As such, when levels of natural seed production are reduced due to competition with exotic plants (e.g., Dyer & Rice 1999), consumers may constrain restoration of native plants.

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Although grasslands in Mediterranean ecosystems are increasingly targeted for restoration (Valladares & Gianoli 2007), the potentially interactive role of consumers and seed density in affecting local plant establishment is poorly known. We coupled experimental consumer exclosures and seed additions to determine the role of consumers and seed density in affecting the restoration of a native perennial grass in the grasslands of California. California grasslands are characterized by a Mediterranean climate, where seeds lie dormant over long, dry summers and experience a large pulse of germination following autumn rains. California grasslands represent one of the most invaded systems in North America, with 7–9.2 million hectares of grassland currently dominated by exotic annual plants (Jackson 1985).

Portions of the California grasslands, particularly in coastal areas (Corbin et al. in press), may once have been dominated by the perennial bunchgrass, *Nassella pulchra* (Stromberg & Griffin 1996). As a result, *N. pulchra* has been the focus of intensive study, with researchers examining the role of cattle grazing (Stromberg & Griffin 1996; Dyer 2002, 2003; Marty et al. 2005), fire regime (Dyer 2002, 2003; Marty et al. 2005; Moyes et al. 2005), land use (Stromberg & Griffin 1996), competitive interactions (Dyer & Rice 1997, 1999; Hamilton et al. 1999; Seabloom et al. 2003; Corbin & D'Antonio 2004; Morghan & Rice 2005; Corbin et al. 2007), and pathogens (Malmstrom et al. 2005; Borer et al. 2007). Despite this work, the successful reestablishment of *N. pulchra* in large portions of California grasslands remains elusive (Stromberg & Griffin 1996).

Native consumers may be one reason why restoration of *N. pulchra* has been hindered in contemporary California grasslands. Although native mammalian consumers are ubiquitous (Lidicker 1989; Schiffman in press) and have potentially large impacts (Batzli & Pitelka 1970; Borchert & Jain 1978; Rice 1987; Lidicker 1989; Reichman & Seabloom 2002; Schiffman in press), there is no comprehensive experimental study of the role of native consumers in affecting the restoration of *N. pulchra.* Furthermore, although evidence points to seed limitation as a key component of *N. pulchra* establishment (Hamilton et al. 1999; Seabloom et al. 2003), it is unknown whether the effect of seed limitation is due to the limiting effects of consumers or whether the effect of consumers depends upon seed density.

We used experimental exclosures and two seed density treatments to specifically determine (1) which mammalian consumers have the greatest effect on *N. pulchra* recruitment and reproduction and (2) if the effect of consumers on *N. pulchra* recruitment is a function of the number of seeds available. Our approach explicitly examined recruitment, seedling herbivory, adult establishment, and reproduction to provide a comprehensive examination of the interplay between consumers, seed density, and *N. pulchra* dynamics. We focused solely on the role of consumers and propagule density by removing all competitive interactions among native and exotic plants. This approach has the benefit of mimicking site-preparation techniques (e.g., tilling, soil disturbance to reduce competition) that may be used in contemporary restoration of old fields or abandoned agricultural fields (e.g., Stromberg & Kephart 1996; Potthoff et al. 2005) as well as ecological experiments (Seabloom et al. 2003).

Methods

The study was conducted in Cheeseboro Canyon, part of the Santa Monica Mountains National Recreation Area near Agoura Hills, California. Once likely dominated by perennial bunchgrasses like *N. pulchra,* the study area is presently dominated by a mix of exotic annual grasses and forbs, including *Bromus diandris*, *B. hordeaceous*, *Brassica nigra, Erodium cicutarium, Melilotus officianalis*, and *Medicago polymorpha* (Moyes et al. 2005). Although stands of remnant *Nassella pulchra* exist in Cheeseboro Canyon, none were within the study area.

Experimental Exclosures and Site Preparation

Within the study area, we installed a set of experimental exclosures at each of eight sites (Fig. 1). Each set of exclosures was a rectangular area divided into four smaller areas. Each of these four areas received one of four different exclosure treatments (Fig. 1): (1) "No Consumer" treatments excluded all nonvolant vertebrate consumers; (2) "Small" treatments permitted small-mammal consumers (i.e., voles and mice) to access plots but prohibited access by squirrels, rabbits, and deer; (3) "Small and Medium" treatments allowed rodents, squirrels, and rabbits to enter but prohibited access by deer; (4) "All" treatments were an unfenced treatment that allowed all consumers to access plots. To control for the disturbance created by fence installation, each exclosure area was trenched prior to exclosure installation and filled after exclosure installation, even if plots were not designated for fencing. Exclosures for No Consumer treatments consisted of 1.22-m-tall hardware cloth (0.8 × 0.8–cm mesh size) projected 20 cm into the soil. Although deer are capable of jumping over fencing of this height, the small area of our exclosures presented very little area within the exclosure for landing, providing a substantial deterrent to deer entry (no deer tracks were seen within exclosures during the course of the experiment). The top of the fencing was surrounded with a 15-cm band of aluminum flashing to discourage rodents from climbing over the fence. Small treatments were open to rodent consumers and constructed of poultry wire with 2.5 × 2.5–cm holes and a band of aluminum flashing at the top. Small and Medium treatments were identical to Small treatments but had 20 × 20–cm holes cut into the fence at uniform intervals. Consumers that were not likely to be excluded by exclosure treatments include pocket gophers, arthropods (e.g., ants, beetles, grasshoppers), and birds.

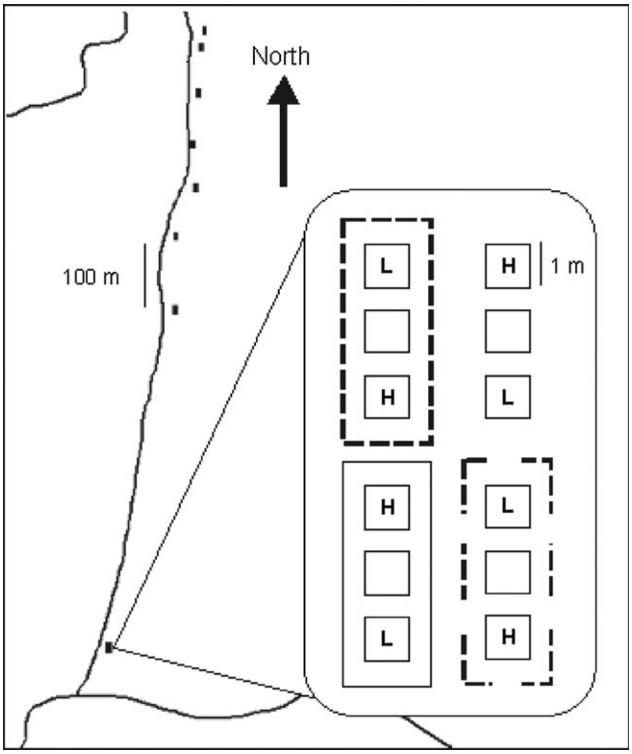

Figure 1. Overview of the study area within the Santa Monica Mountains National Recreation Area. Contoured lines represent a single-lane trail for visitor access. Within the study area, eight sites were established. At each site, a series of four experimental exclosures was created. Each exclosure treatment (see inset) was a 5 × 2–m area that allowed access by a specific mammalian consumer guilds. No Consumer treatments (solid lines) excluded all mammalian consumers. Small treatments (small dashed lines) allowed small consumers (e.g., mice and voles) access to plots. Small and Medium treatments (dashed lines with large openings) allow mice, voles, rabbits, and squirrels to access plots. All treatments (no lines) allowed all mammalian consumers to access plots. Within each exclosure treatment, there were three 1-m^2 experimental plots. North and south plots were randomly assigned a seed density treatment, receiving either low-density seeding (500 seeds/m^2) or high-density seeding (1,000 seeds/m^2) indicated by L or H, respectively. The middle plot was not used in this experiment.

Importantly, these consumers have equal access to all our experimental exclosure treatments, reducing opportunities for confounding.

Sites were tilled on 18–20 January 2005 and exclosures were installed on 27–28 January 2005. Within each exclosure type, two of the three 1 × 1–m plots were used for the seed addition study (Fig. 1), with a 0.5-m buffer between each plot and the exclosure fence. The third plot in each exclosure was used for a study where seedlings of *N. pulchra* were directly planted with varying mycorrhizal treatments and forms the basis of another experiment to be reported elsewhere. Our experimental exclosure treatments are not confounded by soil or latent seed bank effects because (1) the design is a complete block, with all treatments randomly assigned within each block; (2) there is very little carryover of grass seeds from one year to the next in California grasslands (Young et al. 1981); and (3) *Nassella pulchra* was not present in any of our plots prior to the experiment.

On 1 February 2005, plots were seeded by broadcasting locally collected *N. pulchra* seeds onto the surface of the tilled soil. Within each exclosure, seeds were sown at two densities, 500 seeds/m^2 and 1,000 seeds/m^2 (Fig. 1). Restoration studies often use 500 seeds/m^2 (Seabloom et al. 2003; Moyes et al. 2005), which also approximates the number of seeds produced by a single mature *N. pulchra* (Hamilton et al. 1999). Because of limited supplies of local seeds, the high-density seed treatment was only replicated at five of our eight sites. The timing of seed addition was chosen to make our work relevant to restoration efforts, which generally add seeds during the growing season to promote establishment (*N. pulchra* typically shed their seeds in May and June, with seeds lying dormant until winter rains). As a result, there was less time for granivores to find and consume seeds before seeds escaped granivory via germination. Thus, although this approach generates an estimate of consumer impacts more relevant to restoration, it also generates a conservative estimate of the impact of granivores in natural stands. All plots were weeded monthly to remove seedlings of plants other than *N. pulchra.*

Data Collection and Analyses

To quantify the effect of consumers on *N. pulchra* dynamics, we measured seedling recruitment, seedling herbivory, and adult establishment. To determine how consumers may shape future *N. pulchra* recruitment, we also measured the length of the longest flowering tiller; tiller length is strongly related to the number of tillers produced by plants (unpublished data, $r^2 = 0.73$, $F_{[1,51]} = 137.80$, $p < 0.01$) as well as the number of seeds produced per tiller (unpublished data, $r^2 = 0.82$, $F_{[1,51]} = 230.21$, $p < 0.01$).

Seedling recruitment was quantified by counting the number of seedlings in four 500-cm^2 areas within each plot from 28 to 30 March 2005. On 21–28 April 2005, herbivory was quantified by measuring the height of 10 randomly selected seedlings in each plot. The number of mature plants in each plot was counted on 16 June–6 July 2005. During this time, 10 plants were randomly selected within the plot, and the length of the longest reproductive tiller was measured. To assess the longer-term effect of consumers on *N. pulchra* survival, the number of mature plants alive in each plot was measured again on 12–25 October 2005.

We used a mixed-model analysis of variance (ANOVA) to examine how consumers affect recruitment, seedling herbivory, establishment, and tiller length of *N. pulchra.* Our model treats each exclosure site as a random effect, each exclosure treatment as a fixed effect, and seed density as a fixed effect. Our design represents a split-plot design with exclosures as the main plot and seed addition plots as the small plots within the main exclosure plots (Quinn & Keough 2002). Because we are specifically interested in the role of propagule density in affecting recruitment, herbivory, establishment, and reproduction, we dissect the interaction between exclosure and seed addition into linear contrasts that examine whether predator effects in each exclosure type were contingent upon seed densities.

Small-Mammal Sampling Methods

To determine if exclosures were successfully manipulating access of small- and medium-sized consumers, we sampled the small-mammal community at each site using 16 Sherman live traps and 4 Tomahawk live traps from 17 to 19 August 2005. These two different trap types were used to capture both small and medium-sized consumers; half of the Sherman traps at each site were placed within exclosures, and all Tomahawk traps were placed within the exclosures. Upon capture, animals were marked using ear tags and immediately released at the site of capture.

Results

Seedling Recruitment and Herbivory

Consumers significantly affected the recruitment of *Nassella pulchra,* and the strength of this effect depended upon the portion of the consumer community that was excluded as well as the density of seeds (Fig. 2A; Table 1). Compared to exclosures with no consumer access, allowing rodent consumers access to seeds did not significantly reduce seedling recruitment, regardless of seed density (Fig. 2A). However, by reducing seedling recruitment in high-density treatments, rodents did eliminate the effect of seed addition: Adding twice as many seeds led to 1.57 times more recruitment in plots without consumer access, whereas doubling seed density had no effect on recruitment where rodents had access (Table 1; Fig. 2A). Compared to No Consumer treatments, allowing small rodents, rabbits, and squirrels access (Small and Medium treatments) led to a significant reduction in *N. pulchra* recruitment when seeds were at high density (No Consumer vs. Small and Medium treatments, linear contrast $F_{[1,16]} = 6.33$, $p = 0.02$) as well as when seeds were at low density (linear contrast $F_{1,16} = 8.24$, $p = 0.01$). Plots accessible to squirrels and rabbits exhibited differences due to seeding density, with high-density plots producing twice as many seedlings as low-density plots (Table 1). Allowing all consumers access to *N. pulchra* (All treatments) did not significantly alter recruitment compared to exclosures allowing small- and medium-sized consumer access (Fig. 2A). However, seedling recruitment increased in low-density plots when all consumers had access, such that

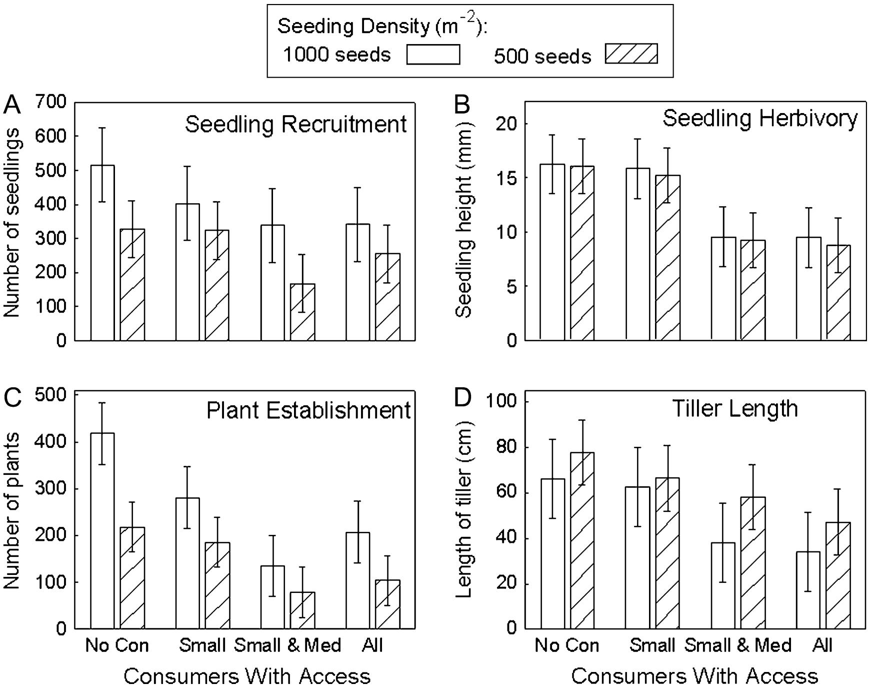

Figure 2. The effect of mammalian consumers and seeding density on *Nassella pulchra* (A) mean seedling recruitment; (B) mean seedling height; (C) mean plant establishment; and (D) mean length of the longest tiller. Exclosure treatments refer to the relative size of the mammalian consumer with access to experimental plots. No Consumer (No Con) treatments allowed no mammalian consumers to access plots; Small treatments allowed mice and voles to access plots; Small and Medium treatments allowed mice, voles, rabbits, and squirrels to enter plots; and All treatments allowed access by all mammalian consumers (including deer). Error bars indicate 95% confidence limits.

Table 1. Summary of mixed-model ANOVA analyses of the effect of excluding mammalian consumers (Exclosure) and different seeding density on the recruitment of *Nassella pulchra* seedlings (i.e., the number of seedlings alive) and mean seedling height.

	Seedling Recruitment			*Seedling Height*		
Effect	*F*	*df*	*p*	*F*	*df*	*p*
Exclosure treatment	5.4	3,21	<0.01	8.24	3,21	<0.001
Seeding density	15.8	1,16	0.001	1.23	1,16	0.28
Seeding density × exclosure treatment						
Low and high density equal in No Consumer treatments	8.41	1,16	0.01	0.05	1,16	0.83
Low and high density equal in Small treatments	1.5	1,16	0.24	0.56	1,16	0.46
Low and high density equal in Small and Medium treatments	6.92	1,16	0.02	0.18	1,16	0.68
Low and high density equal in All treatments	1.78	1,16	0.20	0.71	1,16	0.41

Tests for interaction terms presented in text. Interaction terms are dissected into linear contrasts to focus on the effect of seeding density at particular consumer exclusion treatments. No mammalian consumers have access to No Consumer treatments; rodents have access to Small treatments; rodents, rabbits, and squirrels have access to Small and Medium treatments; and All treatments are open to all mammalian consumers.

there was no difference in seedling recruitment between high- and low-density plots when all consumers had access (Table 1).

In addition to affecting recruitment, exclosure treatments had significant effects on herbivory of seedlings after recruitment, as measured by seedling height (Exclosure main effect; Table 1). Seedlings protected from rabbits, squirrels, and other large consumers were nearly twice as tall as seedlings closed to all consumers and seedlings open only to rodent consumers (Fig. 2B; linear contrast, $F_{[1,21]} = 24.58$; $p < 0.001$). There was no difference in height among seedlings protected from all consumers and seedlings open to small consumers (linear contrast, $F_{[1,21]} = 12$; $p < 0.74$) and no difference in height among seedlings open to all consumers and seedlings open to small and medium consumers (linear contrast, $F_{[1,21]} = 0.02$; $p < 0.90$) There was no effect of seeding density on seedling height (Table 1) and no interaction between exclosure and density treatments ($F_{[3,16]} = 0.08, p = 0.97$).

Plant Establishment and Tiller Length

The effect of consumers on seedling recruitment and height led to differences in mature plant establishment at the end of the growing season. These patterns largely mirrored patterns of seed recruitment, as there was a strong relationship between the number of seedlings counted in March and the number of plants in July ($r^2 = 0.56$, $F_{[1,50]} = 63.81$, $p < 0.001$). An analysis of seedling mortality, measured as the difference between the number of seedlings and the number of adult plants, indicates that there was no difference in seedling loss due to exclosure treatment ($F_{[3,21]} = 0.23$, $p = 0.88$), seed density ($F_{[1,16]} = 0.34$, $p = 0.57$), or the interaction between exclosure treatment and seed density ($F_{[3,16]} = 1.19$, $p = 0.34$), supporting the hypothesis that the majority of differences in adult plant recruitment are due to impacts of granivores and herbivores early in the life cycle of *N. pulchra.* In No Consumer treatments, doubling seed density nearly doubled plant establishment (Fig. 2). Small rodent consumers reduced the establishment of *N. pulchra* on high-density plots to 67% of establishment in No Consumer treatments, whereas allowing rodents access to low-density plots led to no reduction in establishment (Fig. 2C). Despite the greater impact of rodents on high-density plots, there were still significant differences in establishment between high- and low-density plots in Small treatments (Table 2), with 1.5 times more established plants in high-density plots (Fig. 2C). Compared to Small treatments, establishment was significantly lower in Small and Medium treatments for both low- and high-density plots, with 58 and 52% less establishment, respectively. Consumer pressure in Small and Medium treatments also eliminated the effect of seeding density (Table 2), although there was still a trend ($p = 0.09$; Table 2) of greater establishment in high-density plots. Relative to Small and Medium treatments, establishment was slightly higher in All treatments open to all consumers, although this difference was not statistically significant (Fig. 2C). Increases in the establishment of *N. pulchra* in high-density treatments contributed to a significant difference between seeding density treatments in exclosures open to all consumers, with nearly twice as many *N. pulchra* becoming established (1.99 times more plants) in high-density seeding plots.

Although there was a significant difference in tiller length among exclosure treatments (a significant exclosure main effect; Table 2), this was largely driven by reduced tiller length in exclosures where medium-sized and larger consumers had access (Fig. 2). Although there was no difference among exclosures closed to all consumers and exclosures open to only small consumers (linear contrast, $F_{[1,21]} = 0.55$; $p = 0.47$), and no difference among exclosures open to all consumers and exclosures open to small- and medium-sized consumers (linear

Table 2. Summary of mixed-model ANOVA analyses of the effect of excluding mammalian consumers (Exclosure) and different seeding density on the number of established *Nassella pulchra* plants and the length of the longest flowering tiller at the end of the growing season.

	Plant Establishment			*Tiller Length*		
Effect	*F*	*df*	*p*	*F*	*df*	*p*
Exclosure treatment	13.24	3,21	<0.001	4.26	3,21	0.016
Seeding density	50.21	1,16	<0.001	8.61	1,16	<0.01
Seeding density × exclosure treatment						
Low and high density equal in No Consumer treatments	40.42	1,16	<0.001	2.06	1,16	0.17
Low and high density equal in Small treatments	9.26	1,16	<0.01	0.23	1,16	0.64
Low and high density equal in Small and Medium treatments	3.19	1,16	0.09	6.16	1,16	0.025
Low and high density equal in All treatments	10.66	1,16	<0.01	2.58	1,16	0.13

Tests for interaction terms presented in text. Interaction terms are dissected into linear contrasts to focus on the effect of seeding density at particular consumer exclusion treatments. No mammalian consumers have access to No Consumer treatments; rodents have access to Small treatments; rodents, rabbits, and squirrels have access to Small and Medium treatments; and All treatments are open to all mammalian consumers.

contrast, $F_{[1,21]} = 0.57$; $p = 0.46$), there was a significant difference between exclosures that allowed medium-sized mammals access and those that did not allow them access (linear contrast, $F_{[1,21]} = 11.65$; $p < 0.01$). Tiller length was also greater in low-density seeding treatments (Table 2). There was no overall interaction between seeding density and exclosure on tiller length ($F_{[3,16]} = 0.68$, $p = 0.58$). However, planned contrasts show that tiller length in Small and Medium exclosure treatments was significantly reduced in high-density seeding plots compared to low-density seeding plots (Table 2; Fig. 2); average tiller length was 34% lower in high-density seeding plots located within Small and Medium treatments.

Subsequent surveys of the experimental plots provide strong evidence that the influence of consumers had lasting effects on the number of *N. pulchra*. Despite a fire on 29 September 2005 that passed through the study area, the effect of consumers persisted through the summer, with the number of plants still alive in October 2005 strongly related to the number of plants alive in July 2005 (Fig. 3; $r^2 = 0.85$, $F_{[1,50]} = 233.00$, $p < 0.001$). The effect of consumers on *N. pulchra* restoration continued to be evident over a year later, with the percent cover of *N. pulchra* in August 2006 significantly related to the number of plants alive in July 2005 ($r^2 = 0.31$, $F_{[1,50]} = 22.46$, $p < 0.001$).

Consumers and Efficacy of Exclosures

Small-mammal sampling within and around each exclosure yielded 40 total captures of three species: Pocket mice (*Chaetodipus californicus,* 10 captures), Harvest mice (*Reithrodontomys megalotis,* 14 captures), and Deer mice (*Peromyscus maniculatus*, 16 captures). During sampling, a single *P. maniculatus* was captured within one No Consumer exclosure. As expected, there was a significant difference between the total captures of small-sized consumers between No Consumer exclosure treatments and all other trapping locations (ANOVA, $F_{[1,31]} = 4.40$; $p = 0.04$). On average, captures outside of No Consumer treatments (Small, Small and Medium, Large, and areas outside the exclosures) were over five times greater than captures within No Consumer treatments. Although we captured no medium-sized or large consumers during our sampling session, these animals were present, as squirrels and rabbits were captured nearby as part of another project in the same study area and squirrel burrows, rabbit feces, and deer tracks were frequently seen around the experimental plots (unpublished data). However, signs of

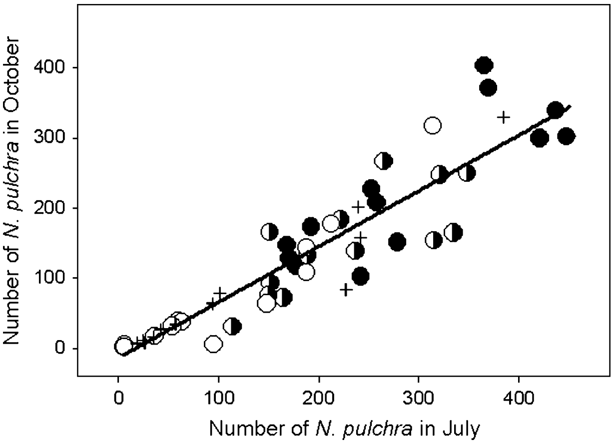

Figure 3. The relationship between the number of *Nassella pulchra* plants established at the end of the growing season (July 2005) and the number of *N. pulchra* alive at the beginning of the next growing season (October 2005). Different symbols represent different consumer treatments: No Consumer (No Con) treatments excluded mammalian consumers; Small treatments excluded all mammalian consumers except mice and voles; Small and Medium treatments allowed mice, voles, rabbits, and squirrels to enter plots; and All treatments allowed access by all mammalian consumers (including deer).

these consumers were never observed in plots where they were meant to be excluded.

Discussion

Consumers are an important component of restoration in grasslands throughout the world (e.g., Hobbs & Huenneke 1992; Muller et al. 1998; Howe & Lane 2004; Schiffman 2007). Our work demonstrates that small- and medium-sized mammalian consumers, which are often not the focus of restoration efforts, can also have important bearing on the success of restoration. Consumers had significant impacts on the restoration of *Nassella pulchra:* Averaged across seeding density, consumers reduced seedling recruitment by nearly 30% and reduced plant establishment by 52%. These strong consumer effects suggest that consumers may underlie the seed limitation often found in natural populations of *N. pulchra* (Hamilton et al. 1999; Seabloom et al. 2003; Corbin et al. 2007), providing an ecological mechanism for the frequent ineffectiveness of restoration efforts. Our results provide guidance for future restoration by lending support to the idea that seed addition may be a viable method of restoration for *N. pulchra,* at least in situations where soil cultivation and reduction of competitors are also employed. Because the dynamics of many plant species are constrained by seed limitation (Turnbull et al. 2000; Clark et al. 2007), and consumers may generate this limitation (Orrock et al. 2006), our work also suggests that seed addition may be a useful restoration approach in a variety of systems.

In the context of Mediterranean ecosystems, restoration often hinges upon characterization of how environmental heterogeneity affects plant performance (Valladares & Gianoli 2007). Our work demonstrates that consumers constitute a biotic component of this environmental heterogeneity and further show that the degree of heterogeneity in consumer impact can be large. This variation in consumer impact may contribute to the variable success of using “nurse plants” during restoration, providing insight into why this approach, although it has been highlighted for its potential importance in Mediterranean systems, has also yielded mixed results (Padilla & Pugnaire 2006; Valladares & Gianoli 2007). Importantly, despite the considerable variation in consumer pressure we observed, increasing the number of seeds added to experimental plots led to an increase in plant establishment, even when all consumers were allowed to access plants.

Stage-Specific Consumer Effects and the Role of Seed Density

Each consumer guild had stage-specific effects on *N. pulchra.* Small mammals appeared to have greatest effects via granivory, as they did not reduce seedling height or tiller length. Small mammal impacts on establishment became more evident as time passed, such that rodent effects on the number of mature *N. pulchra* in high-density plots were significant by the end of the growing season. Previous studies have shown that the effect of small mammals on grassland communities can be considerable, reducing the abundance of annual grasses (Borchert & Jain 1978) and leading to changes in community composition (Batzli & Pitelka 1970; Borchert & Jain 1978; Lidicker 1989). Our study shows that the impact of granivory was most evident in high-density seed plots, where small mammals reduced recruitment to low-density seeding levels. The reduction of high-density seedings we detected has also been found in studies using exotic grass seedings (Borchert & Jain 1978), suggesting that small mammals generally responded to high-density patches of seed resources and may be particularly important in grassland restoration efforts where high-density seedings are used.

Rabbits and squirrels compounded the effects of small mammals: although rabbits and squirrels did not alter seedling recruitment relative to small mammals alone, they did create significant increases in seedling herbivory. This cumulative effect of small rodent granivores and medium-sized herbivores led to a significant reduction in the establishment of *N. pulchra* within Small and Medium treatments relative to the Small treatments. These results confirm other studies which suggest that ground squirrels and rabbits can have important impacts on grassland vegetation (Fitch & Bentley 1949; Bartholomew 1970; Lidicker 1989). Interestingly, there was a trend where the effect of small- and medium-sized consumers on *N. pulchra* plants was qualitatively greater than the effect of all consumers. This suggests that, when large consumers are not allowed access, small- and medium-sized consumers are more effective at removing *N. pulchra* biomass. Although this could signal competitive interactions between large- and medium-sized consumers, an alternative explanation may be equally plausible. For medium-sized consumers, proximity to refuge can greatly increase foraging rates, such that plant biomass away from the refuge can be 15 times greater (Bartholomew 1970). In our study, rabbits and squirrels may have foraged more intensively within Small and Medium treatments because they offer shelter from predators relative to All exclosure treatments, which had no fencing and were thus much more exposed.

Medium-sized consumers (e.g., rabbits and squirrels) also reduced reproductive output in high-density *N. pulchra* plots by reducing tiller length. These effects were not evident in Small treatments, and were also not evident in low-density seed additions, suggesting that medium-sized herbivores may have targeted high-density patches of established *N. pulchra*. We also found that high-density seeding reduced tiller size, suggesting that intraspecific competition may constrain *N. pulchra* reproduction at high densities. These results are in agreement with the work of Dyer and Rice (1999) who found that the number of reproductive tillers produced was affected by *N. pulchra* density. At high densities, this reduction in reproductive output can become equivalent to the reduction in output caused by interspecific competition with exotic annual plants (Dyer & Rice 1999).

Our results suggest that the effect of large consumers (e.g., deer) is not greater than the combined effect of small and medium consumers, as allowing large consumers access to plots did not result in any additional deleterious effect on *N. pulchra*. Although large consumers alone did not lead to large changes in tiller length relative to Small- and Medium-sized consumers, the cumulative effect of multiple consumer guilds on tiller length became apparent in All treatments. Tiller length in high-density seeding treatments remained low, and tiller length in low-density seeding treatments in All exclosures were significantly less than in No Consumer treatments ($t = 2.93$, df 16 $p < 0.01$). Given the strong relationship between tiller length, the number of tillers produced, and the number of seeds per tiller (see Data Collection and Analyses section), our findings suggest that consumers may continue to affect rates of *N. pulchra* establishment via reducing local seed density.

Although they were free to access all our experimental plots, our work did not explicitly focus on avian or arthropod consumers. The effect of these consumers is most evident in the No Consumer treatments, where only birds and arthropods could access seeds. Importantly, the striking differences among exclosures suggest that mammalian consumers have large effects that are significant even when arthropod and avian consumer effects are fully included.

Consumers and Restoration of *N. Pulchra*

We show that mammalian consumers have important effects on *N. pulchra* restoration and these effects are evident in the next growing season as well as over a year later. As such, our work suggests that consumers may play an important role in promoting the seed limitation that can hinder restoration of *N. pulchra* (Hamilton et al. 1999; Seabloom et al. 2003). Our work also highlights the high level of variability in consumer impact: consumer impact was not homogeneous, leading to a substantial reduction in *N. pulchra* recruitment in some areas but little reduction in others. In areas where consumer pressure is very high, consumer control measures may be warranted. Because of its lower price and the substantial impact of squirrels and rabbits, fencing restoration areas with poultry wire (used for the construction of our Small exclosures) rather than hardware cloth (No Consumer exclosures) is likely to yield the greatest amount of consumer control at the most economical price. Although consumer control might also be achieved by poisoning programs, these methods present substantial dangers to nontarget wildlife (Brakes & Smith 2005) that may limit their usefulness.

Even in plots where all consumers had access, doubling the number of added seeds nearly doubled the number of *N. pulchra* plants that established on average. As such, our work demonstrates that when coupled with site preparation (e.g., tilling) and weeding to reduce competition with exotic species, seed addition may be sufficient to reestablish *N. pulchra* in areas where it has been eliminated. However, because the competitive ability of *N. pulchra* may depend upon the geographic region, annual and seasonal precipitation regimes, and a suite of other factors (reviewed in Corbin et al. 2007), seed addition is likely to be most effective when the timing and location of addition maximizes the competitive ability of *N. pulchra* relative to exotic grasses. Given evidence that *N. pulchra* can successfully compete with exotic plants in some habitats (Seabloom et al. 2003; Corbin & D'Antonio 2004; Corbin et al. 2007), future work that examines how consumers alter the efficacy of seed additions when tilling and weeding are not employed would be a profitable next step.

Although our work suggests that seed additions may be promising for grassland restoration, in light of recent reviews that find seed limitation in a diverse array of plant communities (Turnbull et al. 2000; Clark et al. 2007), more work is needed to determine whether seed addition can override consumer pressure and promote restoration in other grassland systems. Another interesting possibility suggested by our work is that the efficacy of restoration techniques implemented in grassland systems throughout the world, such as fire and grazing (Hobbs & Huenneke 1992; Muller et al. 1998; Dyer 2003; Moyes et al. 2005), may be due to the way these techniques affect consumer pressure, in addition to the way they reduce interspecific competition. For example, fire reduces the density of small-mammal consumers by direct mortality as well as by altering habitat and removing protective litter cover (Cook 1959), and grazing is likely to differentially affect members of the native mammalian consumer community (Lidicker 1989). Future studies that combine these restoration techniques with consumer exclosures would be useful for determining how much of their beneficial effect is due to consumer alteration as opposed to alteration of the competitive environment.

Implications for Practice

- In sites where tilling and weeding are used to reduce competition with other plants, protecting seeded plots from rodents, squirrels, and rabbits can greatly increase seedling establishment, adult establishment, and reproductive tiller length of Purple needlegrass (*Nassella pulchra*).
- For sites where consumer pressure is high, fencing may be a practical method of increasing *N. pulchra* establishment by 50–100%.
- Even in the absence of any consumer control, doubling the amount of seed added nearly doubled the number of established *N. pulchra* plants.

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