# EXOTIC HERBIVORES FACILITATE THE EXOTIC GRASSES THEY GRAZE: MECHANISMS FOR AN UNEXPECTED "INVASIONAL MELTDOWN"

by

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### ABSTRACT

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Native communities increasingly host exotic species at multiple trophic levels, but most current hypotheses about community invasibility consider only a single invader. In addition to the simultaneous effects of native herbivores and native plant competitors on community invasibility, we must also consider the possibility of positive or negative feedback cycles between exotic species at multiple trophic levels. Though examples of mutually-beneficial interactions between exotic species have been described, and the possibility of subsequent "invasional meltdown" scenarios raised, few studies have been quantitative or mechanistic. I studied the co-invasion of an endangered island ecosystem by exotic Canada geese (Branta canadensis) and eight exotic annual grasses to estimate the synergistic effects of novel inter- and intra-trophic interactions on the invasion success of the grasses. Geese fed selectively on the exotic grasses, causing them to produce a higher number of short stems. This appeared to be an efficient reproductive and competitive strategy, allowing the grasses to form dense lawns with reduced occurrence of native forbs not adapted to compete under grazing or with grass. The demographic success of the exotic grasses was thus a product of both novel inter-trophic interactions with geese and novel intratrophic interactions with the native plant community. In combination, these interactions produced an unexpected outcome. Current theory suggests the grasses should be limited by a selective enemy, but my work shows that co-evolved grazer and grass strategies benefited exotic species at both trophic levels. Selective herbivory by geese also facilitated their dispersal of exotic grass seed between heavily invaded feeding areas and small islands used for nesting. In sum, selective herbivory by geese resulted in the spread and proliferation of their preferred food source. This unexpected case of positive feedback between invaders

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suggests two avenues for strengthening current theoretical frameworks. Robust hypotheses for predicting invasion success must account for multiple novel interactions, and for the degree of shared evolutionary context between multiple invaders.

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#### **INTRODUCTION**

While most research on biotic resistance has considered a single type of interaction between native and exotic species, community invasibility depends on multiple interactions, both within and across trophic levels. Assessing only the effects of competition or only the effects of herbivory is insufficient; predicting invasion success requires a multi-factor approach (Mitchell et al. 2006). In addition, with rising rates of species introductions (Levine and D'Antonio 2003), the success of one exotic species will increasingly depend on intra- and inter-trophic interactions with other exotic species. Simberloff and Von Holle (1999) suggested that positive feedbacks between exotics species might lead to "invasional meltdown." They reviewed qualitative reports of exotic animals pollinating or dispersing the seeds of exotic plants, and of one exotic plant or animal benefiting from habitat modification by another. So far, however, there have been few quantitative studies of the impact these feedbacks might have on invasion success or native persistence (Simberloff and Von Holle 1999). I studied the ongoing co-invasion of an endangered island ecosystem by an exotic herbivore (Canada geese, Branta canadensis (Linnaeus)) and eight exotic grass species to determine the synergistic impacts of novel intra- and inter-trophic interactions on the demographic success of the grasses. In this thesis, I briefly review separate predictions about the impact of herbivory and competition on invasion success, then use observational and experimental evidence to show that in combination, multiple novel interactions can yield opposite results.

Herbivores can exert inter-trophic control both by opening spaces in the native vegetation for exotic plant species to germinate and spread (Hobbs and Huenneke 1992), and

by failing to attack the exotic species themselves. The latter mechanism underlies the enemy release hypothesis, which predicts that exotic plants should benefit from the absence of their co-evolved enemies (Williamson 1996, Keane and Crawley 2002). In some circumstances, however, the opposite can be true. Exotic grasses benefit from the presence of their co-evolved grazers when those grazers do greater damage to grazing-intolerant native grasses (DiTomaso 2000, Hobbs 2001). To explain this observation, Colautti *et al.* (2004) formulated the "enemy of my enemy" hypothesis, which predicts that exotic plants may benefit from their exotic generalist enemies if they are more tolerant of these enemies than the native species are. Using the same logic, Mitchell *et al.* (2006) point out the opposite; plant invasions should be limited by specialist herbivores that consume only the invading species.

In my study system, the selectivity of goose herbivory is therefore important. Generalist herbivory could benefit the exotic grasses by removing native plant species, whereas selective consumption of the grasses should limit their invasion success. Elsewhere in North America, Brant (*B. bernicla*) and Canada geese have modified competitive interactions between plant species through selective herbivory (Conover 1991, Mulder *et al.* 1996). The effects of goose herbivory on island plant communities may be particularly strong because the islands lack native vertebrate herbivores. Nesting in the islands since the 1980s, the geese originate from the Giant and Great Basin subspecies, which were introduced to the Lower Fraser Valley of southwestern British Columbia from Minnesota, Ontario, Saskatchewan, Alberta, and south-central British Columbia in the 1960s (Hanson 1997, Smith 2000, Banks *et al.* 2004). Because the geese fly between their island nesting sites and cultivated feeding grounds, the selectivity of their herbivory may also impact seed dispersal.

In the case of intra-trophic interactions between native and exotic species, theory has focused on species similarity in function (Fox's assembly rule, 1987) or phylogeny (Daehler 2001), predicting that similarity in resource partitioning should decrease invasion success when species from the same functional or taxonomic group are already present. Empirical support for this theory is mixed. Recently reviewed by Mitchell et al. (2006), some authors have shown lower invader biomass or abundance in the presence of functionally similar natives, while others have not. Mitchell et al. (2006) also point out that this prediction should hold at the local scale, while abiotic constraints at the landscape scale may limit native and exotic species with the same life history strategies to the same locations (Stohlgren et al. 2005). At the plot scale, the invasion success of the exotic grasses in this system should therefore depend not only on the foraging selectivity of geese, but also on the differences between native and exotic plant species pools, which leaves space for the exotic grasses to benefit from novel strategies for capturing resources. The native plant community is forbdominated, with low litter accumulation, while the exotic annual grasses produce substantial litter without grazing, or dense, short lawns under grazing.

I tested the impact of novel inter- and intra-trophic interactions on the invasion success of the grasses using open and exclosed plots along a gradient of grazing intensity. Combining pattern (vegetation change observed along the grazing gradient) with process (direct experimental evidence from exclosures) allowed me to identify short term mechanisms consistent with longer term change. I assessed foraging selectivity by geese and the impact of grazing on grasses and forbs, then identified underlying demographic mechanisms by testing the effect of grazing on grass flowering and stem production. I tested the hypothesis that the functional difference between native forbs and exotic grasses benefits

the grasses by assessing grass stem production in the presence of litter, which only the grasses produce. Finally, I tested the hypothesis that selective herbivory by geese may result in their dispersal of exotic propagules by collecting goose feces in the field and germinating viable seeds in a growth chamber. I provide quantitative evidence that the combination of novel interactions produced an overall demographic benefit to the exotic grasses even though they were selectively grazed by geese. Geese should also benefit from the proliferation of their selected food source. In sum, I show that novel inter- and intra-trophic interactions can combine to produce "invasional meltdown" scenarios even in circumstances where our current theories of biotic resistance would predict the opposite.

#### **METHODS**

### **Study Area**

I conducted this study in the southern Gulf Islands of British Columbia, which includes over 100 smaller islands between the south-west corner of mainland Canada and the southern end of Vancouver Island (approximately 48°41' N, 123°23' W) . The endangered Garry oak ecosystem, which stretches south along the Pacific coast to southern California (Fuchs 2001), covers the margins or the entirety of these islands. On the smallest islands, ranging in size from 0.04 to 600 ha (Van Vliet *et al.* 1991), 10 % to 55 % of the herbaceous plant biomass is exotic, compared to 80 % to 90 % on the larger islands in the Gulf Islands archipelago (E.K. Gonzales, unpublished data). These small islands have shallow sandy to sandy loam soils that have accumulated in depressions and crevices sheltered from the wind (Ward *et al.* 1998), and the climate is Mediterranean, with mild winters and dry summers (Roemer 1972). Germination begins in October or November and continues until April or May, and flowering begins as early as January but is concentrated between March and May. Geese establish territories and maintain nests between March and June.

#### **Experimental design**

I selected 19 sites where fellow researchers had previously observed geese during their nesting season. Sites were spread over eight islands, with island size ranging from 0.4 ha to 3.6 ha (Van Vliet *et al.* 1991). At each site, I established two to four pairs of 30 cm by 60 cm plots in mid-February 2005. Plots were dominated by herbaceous vegetation, had < 10 % rock, and were on slopes <  $20^{\circ}$ . For each pair, I identified two areas having similar

vegetation composition and soil depth, and randomly assigned one to be open, and one to be enclosed by a 75 cm high fence of 2.5 cm square wire mesh.

For the centre 20 cm x 50 cm of each plot, I recorded abundance as the number of stems of each species. This is an appropriate measure because the stem is the unit of reproduction, and the grasses in this system are able to flower at a range of heights. I also recorded grazed and flowering stems by species, average plant height by species, total percent cover of litter, and three soil depth measurements. Soil depth ranged from 1 to 18 cm. In 2005, I surveyed all plots between March 23 and April 17, and between May 11 and May 24. There was sufficient overlap in phenologies that I surveyed only once in 2006, between April 14 and May 2.

### Analysis

#### **Grazing selectivity**

To assess goose foraging selectivity, I calculated a use to availability ratio for each group of plants: native perennial grasses, exotic perennial grasses, exotic annual grasses, native perennial forbs, native annual forbs, exotic perennial forbs, and exotic annual forbs. I used the forage index ( $\hat{w}_i$ ), which is a group's proportion of the grazed stems ( $o_i$ ) divided by its proportion of the total stems ( $\hat{\pi}_i$ ), as in Eqn. 1 (Manly *et al.* 2002). I calculated a value for each group in all open plots where at least one stem was grazed.

$$\hat{w}_i = o_i / \hat{\pi}_i \tag{Eqn. 1}$$

Given the limited distributions of some groups, I tested for selection or avoidance of each group using the non-parametric Sign test. A value of  $\hat{w}_i$  significantly higher than 1 indicates selective grazing, while a value less than 1 indicates avoidance. I present the 2006 data

because the single survey for that year captured the middle of the goose grazing season, but results were comparable when the analysis was based on the 2005 surveys.

#### Abundance and diversity models

To determine the impacts of herbivory on plant community composition, I tested the similarity of open and exclosed plots along the gradient of grazing intensity. If goose herbivory impacts community dynamics, I would expect a large divergence between the exclosed and open plots when the open plot is heavily grazed, and no divergence where there is no grazing. The principal approach for all analyses was therefore to test for interactions between the exclosure treatment (open or exclosed), and the intensity of grazing. Grazing intensity was measured as the proportion of all stems in the open plot that were grazed. The same value of this co-variate was recorded for the exclosed member of the pair, as recording a zero value would confound the lack of grazing due to experimental manipulation and that due to goose site selection. I also tested for interactions with survey year. For all analyses, I used linear mixed models to incorporate spatial clustering and repeated measures. Mixed models can accurately represent random spatial and temporal autocorrelations in ecological data (Schabenberger and Pierce 2002, Buckley et al. 2003). I used the MIXED procedure in SAS (SAS Institute 2003) with the REML estimation method and the Satterthwaite method for estimating denominator degrees of freedom in models with multiple error terms (Littell et al. 1996).

To test responses of total stem abundance, richness, and  $E_{var}$  evenness (Smith and Wilson 1996), and the proportional representation and richness of grasses and forbs, I used a single model for each response variable to incorporate observations from all three sampling periods over two years. The hypothesized time correlation structure for these models was

two-banded unstructured (*i.e.*, different covariance within and between years). Candidate fixed effects were Julian date of survey, soil depth, grazing intensity, year, exclosure treatment, a year by exclosure interaction, and the year by grazing intensity, exclosure by grazing intensity, and year by exclosure by grazing intensity interactions to test for equivalence of slopes. For the forb proportional abundance and richness models, I coded forb type, based on species origin and life history, as an additional fixed effect. I also included all possible interactions with forb type. Candidate random effects were plot (when there were multiple forb measurements from a single plot), plot pair, and island.

For each model, I checked assumptions for the conditional residuals using residual vs. predicted plots and normal probability plots. I used likelihood ratio tests to test the covariance structure against a completely unstructured model and to eliminate non-significant random factors. I eliminated non-significant fixed-effects based on Type 3 hypothesis tests with  $\alpha = 0.05$ . For all models, response variable transformations and statistical results are reported in Table 1. I show results for the grazing intensity, exclosure, and year fixed effects, and give parameter estimates for those that are significant. The final models included the two-banded unstructured temporal correlation structure, plus spatial correlation at the level of the plot pair. Island was not significant as a random factor; nor was the interaction between island and grazing.

#### Exotic annual grass demography

To identify mechanisms for the impacts of grazing on particular demographic processes in the exotic annual grasses, I again used mixed models. I first tested the impact of grazing intensity and exclosure on the proportion of exotic annual grass stems flowering in 2005. I used a second model to test the different impacts of grazing and litter accumulation

on the production of one year's stems from the previous year's inflorescences. Here the response variable was the number of 2006 stems produced per 2005 flowering stem. I used a third model to assess the overall impact of grazing on the number of 2006 grass stems. For the 2006 models I removed an outlying site, where five of the six plots had less than 3 % total cover in 2006. Although this site was included in the full models outlined above, it was eliminated to obtain better fit in these single time period models.

## **Propagule dispersal**

To assess the potential for seed dispersal by geese, I collected a total of 10 samples of fresh feces from seven islands between April 25 and June 20, 2005, a period coincident with local seed production and the movement of geese between the islands and cultivated habitats near Sidney, BC. Feces were collected from multiple territories on each island, within a few hours of deposition and from rock surfaces. All feces were carefully inspected to ensure they were free of windblown seed (Myers *et al.* 2004). I collected a total of 314 g dry weight, with individual sample weights ranging from 9 g to 43 g. Feces were air dried, weighed, cold-dry-stratified for two months at 4°C, then spread over 4 cm of Redi-Earth sterile medium (Sun Gro Horticulture Canada Ltd) and watered as needed. Growth chamber conditions simulated April to June temperatures in the islands, with 12 hours of light (initially 17 °C, increasing to 19 °C after one month and 22 °C after two months; dark temperature 2 °C lower). Feces were initially left whole to simulate field conditions for germination. After 3 months any feces without emerging plants were separated manually, but no further germination occurred. All seedlings were grown to flowering for identification.

Response	Effect	df	F	р	Estimate <sup>*</sup>	SE <sup>*</sup>	Estimate <sup>*</sup>	SE*
Overall abundance and diversity								
√(# stems)	Graze intensity	1, 174	25.23	< 0.0001	b <sub>graze</sub> : 5.0	0.99		
	Exclosure	1,63.6	2.33	0.13	Entre			
	Year	1, 141	2.98	0.086				
$\sqrt{(\text{richness} + 0.5)}$	Graze intensity	1,216	7.87	0.0055	b <sub>graze</sub> : -0.28	0.098		
· · · ·	Exclosure	1,62.9	0.23	0.63	Fine			
	Year	1, 123	15.38	0.0001	$b_{0(05)}$ : 3.45	0.085	$b_{o(06)}$ : 3.20	0.10
Asin√(E <sub>var</sub> )	Graze intensity	1, 169	4.37	0.038	b <sub>graze</sub> : -0.076	0.037	•()	
	Exclosure	1,61.5	0.33	0.57	0			
	Year	1, 141	1.04	0.31				· · ·
Exotic annual grass prop	portional abundance and diversity	•		• ,				
Asin√(prop. stems)	Graze intensity*Year*Exclosure	1, 81	3.96	0.049	b <sub>graze(05 O)</sub> : 0.27	0.053	$b_{graze(06 \text{ O})}: 0.29$	0.20
	-				$b_{graze(05 F)}: 0.20$	0.053	b <sub>eraze(06 E)</sub> : -0.31	0.20
	Exclosure	1,64.6	0.05	0.83	2.022(00 0)		E.1120(00 2)	
	Year	1, 136	0.04	0.84				
$\sqrt{(\text{richness} + 0.5)}$	Graze intensity	1,221	2.99	0.085				
	Exclosure	1,87.1	0.31	0.58			·	
	Year	1, 130	3.42	0.067	•			
Exotic annual grass dem	ographic processes							
Asin√(05 prop. flow.)	Graze intensity*Exclosure	1, 52	21.80	< 0.0001	b <sub>graze(O)</sub> : -0.88	0.16	bgraze(E): -0.042	0.16
· · ·	Exclosure	1,51	4.28	0.044	b <sub>o(O)</sub> : 1.17	0.080	b <sub>o(E)</sub> : 1.04	0.080
Ln(06 stem/05 inflor.)	Graze intensity*Exclosure	1, 49.2	14.26	0.0004	$b_{\text{graze}(O)}$ : 0.86	0.51	$b_{graze(E)}: -1.2$	0.52
	Exclosure	1, 57.3	4.24	0.044	$b_{o(O)}$ : 1.24	0.15	b <sub>o(E)</sub> : 1.52	0.18
	Percent cover litter	1, 88.3	14.42	0.0003	b <sub>litter</sub> : -0.018	0.0048	- \ - )	
√(06 stems)	Graze intensity*Exclosure	1, 53	20.72	< 0.0001	$b_{graze(O)}$ : 19.2	5.3	b <sub>graze(E)</sub> : -0.36	5.3
	Exclosure	1, 52	0.15	0.70	<i>cc</i> ,			

 Table 1: Significance of grazing intensity gradient, exclosure treatment, and year effects

Response	Effect	df	F	р	Estimate	SE <sup>*</sup>	Estimate <sup>*</sup>	SE <sup>*</sup>
Forb proportional abur	ndance and diversity							
Asin√(prop. stems)	Graze intensity*Forb type*Year	2, 350	10.65	< 0.0001	b <sub>graze(05 na)</sub> : -0.21	0.037	b <sub>graze(06 na)</sub> : -0.25	0.13
					b <sub>graze(05 np)</sub> : -0.07	0.037	b <sub>graze(06 np)</sub> : -0.75	0.13
					b <sub>graze(05 ea)</sub> : -0.03	0.037	$b_{graze(06 ea)}: 0.13$	0.13
	Forb type*Year	2, 438	- 31.55	< 0.0001	b <sub>o(05 na)</sub> : 0.62	0.045	b <sub>o(06 na)</sub> : 0.45	0.048
					b <sub>o(05 np)</sub> : 0.27	0.045	b <sub>o(06 np)</sub> : 0.49	0.048
					b <sub>o(05 ea)</sub> : 0.29	0.045	b <sub>o(06 ea)</sub> : 0.20	0.048
	Exclosure	1, 577	0.43	0.51				
$\sqrt{(\text{richness} + 0.5)}$	Graze intensity*Forb type	2, 794	3.71	0.025	bgraze(na): -0.18	0.082	b <sub>graze(ea)</sub> : 0.052	0.082
					bgraze(np): -0.23	0.082	-	
•	Forb type*Year	2,480	31.46	< 0.0001	b <sub>o(05 na)</sub> : 1.98	0.056	b <sub>o(06 na)</sub> : 1.59	0.055
					b <sub>o(05 np)</sub> : 1.75	0.056	b <sub>o(06 пр)</sub> : 1.89	0.055
					b <sub>o(05 ea)</sub> : 1.64	0.056	b <sub>o(06 ea)</sub> : 1.41	0.055
	Exclosure	1, 580	1.74	0.19				

\* Parameter estimates and standard errors (SE) are in transformed units.

,

# **RESULTS**

# **Grazing selectivity**

Forage ratios for the plant groups present in this system show that geese fed selectively on the exotic annual grasses. Of the seven groups tested, only these grasses had a forage ratio significantly above 1 (Fig. 1). These grasses were grazed in 36 of the 39 plots where they occurred, and had a mean forage ratio of 1.47. Exotic perennial grasses occurred in only seven plots, but were grazed in six (mean ratio 2.46, not significant). All other plant groups were not selected; the native forbs and exotic annual forbs showed significant avoidance (Fig. 1). **Figure 1:** Mean forage ratio by plant type. Plant types are abbreviated as: E = exotic, N = native; A = annual, P = perennial; and G = grass, F = forb. Sample size, n, is the number of plots where the plant type occurred and where there was grazing on at least one stem of any species. Error bars are 95% confidence intervals, but significant deviations from  $H_0$ :  $\hat{w}_i = 1$  were identified using the Sign test. I used  $\alpha = 0.05/7 = 0.007$  to account for multiple groups. Values of  $\hat{w}_i$  significantly different from 1 indicate selection or avoidance, and are identified with \*.



# Overall abundance and diversity under grazing

In both 2005 and 2006, the total number of stems per plot increased with grazing intensity. There were no significant interactions, no difference between open and exclosed plots or between years, and no effect of soil depth. In contrast, total species richness and total evenness ( $E_{var}$ ) declined with increasing grazing intensity. In addition, species richness over all plots was reduced in 2006. Calculated from back-transformed intercepts and end points,

the estimated drop in species richness over the observed grazing gradient was 1.7 in 2005 and 1.6 in 2006. In the two years of this study, there was no effect of exclosure on species richness or evenness.

### Grasses under grazing

I examined the impact of grazing on the proportional abundance and species richness of the exotic annual grasses in this system, which occurred in 98 % of the study plots and included eight species: *Aira caryophyllea* L., *Aira praecox* L., *Bromus diandrus* Roth, *Bromus hordeaceus* L., *Hordeum murinum* L., *Poa annua* L., *Vulpia bromoides* (L.) S.F. Gray, and *Vulpia myuros* (L.) K.C. Gmel. Only one of the 59 species I observed in the plots was a native perennial grass (*Festuca idahoensis* Elmer ssp. *roemeri* (Pavl.) S. Aiken, in 14 % of plots), and only three were exotic perennial grasses (collectively in 13 % of plots). Because of their limited distribution these were not included in any analyses. Native annual grasses were absent from all plots (Table 2), and were not observed elsewhere in the study area over the course of my surveys.

Duration	For	rbs	Gr	Total	
- And Barrowski and	Native	Exotic	Native	Exotic	
Annual	15	10	0	8	33
Perennial	16	6	1	3	26
Sub-Total	31	16	1	11	
Total	4	7	•.	12	59

 Table 2: Origin and life history of species observed in study plots

In both 2005 and 2006, the proportional abundance of exotic annual grasses in the open plots increased with grazing intensity (Fig. 2). In exclosed plots, the proportion increased along the grazing intensity gradient only in 2005, the year plots were established. In 2006, the grasses' proportional abundance in the exclosed plots decreased along the same gradient (Fig. 2). The significant year by exclosure by grazing interaction showed the slopes to be significantly different. As expected, there was no significant difference in intercept, where the grazing intensity, and therefore the magnitude of the treatment difference between open and exclosed plots, is zero. Given a single intercept and significantly different slopes, I conclude grass abundance was significantly higher in open plots at high grazing intensities. I have presented these results based on proportional abundance by stem number, but similar results were obtained using percent cover values.

**Figure 2:** Proportional abundance of the exotic annual grasses (EAG) along the grazing intensity gradient. Grazing intensity is the total proportion of stems grazed, and is measured in the open plots. Symbols are: --- = 2005 open plots; --- = 2005 exclosed; --- = 2006 open (slope same as 2005 open); --- = 2006 exclosed. Overall, slopes are significantly different; parameter estimates are given in Table 1. Data are displayed adjusted to the beginning of the survey period, to average soil depth, and to average levels of the random factors. EAG proportional abundance is arcsine square root transformed.



#### **Demographic mechanisms**

Grazing appeared to affect two important demographic processes in the exotic annual grass populations. First, grazing decreased the proportion of grass stems that were flowering. In open plots, I observed a negative relationship between grazing intensity and the proportion flowering (Fig. 3a). Second, in contrast, grazing appeared to increase the conversion of one year's inflorescences into the next year's stems. The relationship between grazing intensity

**Figure 3:** Impacts of grazing on demographic processes in the exotic annual grasses. Grazing intensity is the total proportion of stems grazed, and is measured in the open plots. Symbols are:  $\circ$ --- = open,  $\bullet$  --- = exclosed. In a, b, and c, slopes are significantly different. Panels b and d both show significant relationships from a single model which included litter and grazing intensity as predictor variables. Response variables are transformed as indicated in Table 1.



and the production of 2006 stems per 2005 inflorescence was positive in the open plots but negative in the exclosed plots (Fig. 3b). Obviously there is a trade-off between these two demographic processes, and this trade-off ultimately favored grasses being grazed. Overall, grazing increased the number of grass stems along the grazing intensity gradient, while protection from grazing removed this relationship (Fig. 3c). Furthermore, the greater accumulation of litter in the exclosed plots explains some of this divergence. I observed a significant negative relationship between litter cover and the conversion of one year's inflorescences into the next year's stems (Fig. 3d). The prevention of litter accumulation therefore appears to be an important factor underlying the increased production of grass stems under grazing. Grazing and the absence of litter also significantly reduced overall vegetation height. In the open plots, average vegetation height declined with increasing grazing intensity ( $F_{1, 102} = 9.49$ , p = 0.003,  $b_{graze} = -0.62$  for ln-transformed height).

### **Forbs under grazing**

Native perennial forbs, native annual forbs, and exotic annual forbs each occurred in over 80% of plots, while exotic perennial forbs occurred in only 24 % of plots and were therefore omitted from analyses. Native perennial and annual forbs in this system exhibited a pattern opposite to that of the exotic annual grasses. First, from the full model over all time periods, it is clear that the relationship between grazing intensity and proportional representation differs between exotic annuals, native annuals, and native perennials. The grazing intensity by year by forb type interaction was significant, as was the year by forb group interaction, testing for difference in intercept. In 2005, native annual forbs showed a steeper decline with grazing intensity than the exotic annuals or the native perennials. In

**Figure 4:** Proportional abundance of forbs along the grazing intensity gradient. Grazing intensity is the total proportion of stems grazed, and is measured in the open plots. Symbols are:  $\blacktriangle --- =$  native annual forbs,  $\square --- =$  native perennial forbs,  $\square --- =$  exotic annual forbs. Slopes are significantly different; response variable transformations and parameter estimates are given in Table 1. Data are displayed adjusted to the beginning of the survey period, to average soil depth, and to average levels of the random factors.



2006, both native annual and native perennial forbs declined with grazing intensity, while the exotic annuals increased slightly (Fig. 4). There were no significant differences in forb abundance between open and exclosed plots, but there was a significant interaction between soil depth and forb group, with native perennials increasing with soil depth, native annuals decreasing, and exotic annuals showing no pattern. This was consistent over both years.

Species richness of native forbs also declined with grazing intensity. The grazing intensity by forb type interaction was significant, with native forb richness declining and exotic annual forb richness remaining relatively constant across the grazing gradient. Slopes

were not different between years, and the exclosures did not produce significant differences in species richness over the two years of the study.

# **Propagule dispersal**

I observed 25 germinants from 314 g of dried feces, 80 % of which were exotic annual grasses (72 % *Poa annua* L.; 8 % *Aira praecox* L.). The remainder were one exotic annual forb (12% *Silene gallica* L.), one native annual forb (4 % *Myosurus minimus* L.), and one native perennial forb (4 % *Epilobium ciliatum* Raf.). *Poa annua* was by far the most common species overall, at an estimated density of one viable seed per 18.7 g of dry feces. Only the smallest sample failed to produce any germinants.

### DISCUSSION

My results show a pattern of increasing proportional abundance of exotic annual grasses along the gradient of increasing grazing intensity (Fig. 2). Along the same gradient, the proportional abundance and species richness of native forbs declined (Fig. 4). Because geese selectively consumed the grasses, these patterns are contrary to the predictions of current theory. The "enemy of my enemy" hypothesis states that novel herbivores that consume native plant species may indirectly benefit grazing-tolerant grasses, whereas herbivores that selectively feed on the grasses should limit their abundance. To understand how exotic grasses in this system benefited from selective grazing, I must consider the germination trials and the experimental evidence of mechanisms that incorporate both interand intra-trophic interactions. The germination trials suggest that geese may have contributed to the colonization phase of grass invasion in this system. The differences between open and exclosed plots provide evidence that goose grazing modified competitive interactions between exotic grasses and native forbs to favor the establishment of their selected food source. In sum, my results show that geese transported and facilitated the grasses, and that the grasses provided the majority of their diet. This is a positive feedback loop, with the proliferating grasses likely to attract more grazing pressure.

### **Propagule dispersal**

Canada geese are capable of increasing propagule supply for the exotic annual grasses by dispersing their seeds from cultivated lawns, golf courses, and fields on Vancouver Island and the larger Gulf Islands. Of the individuals germinating from viable seeds in goose feces, 80 % were exotic annual grasses, either *Poa annua* or *Aira praecox*. In

addition, many of the other annual grass species proliferating in the islands (*e.g., Bromus diandrus, Hordeum murinum, Vulpia* spp.) have long, rough awns, an adaptation which can facilitate external transport by animals (Sorensen 1986, Romermann *et al.* 2005). Both internal and external dispersal by animals has been an important factor in the spread of exotic plant species in other systems (Malo and Suarez 1997, Simberloff and Von Holle 1999). Furthermore, grass seed production in this system is seasonally coincident with the interisland movement of geese flying between their nesting sites and additional feeding grounds on the larger islands. Since seasonal timing and short flight distances are important determinants of viable seed dispersal by birds (Clausen *et al.* 2002), this increases the likelihood that geese are contributing to the supply of exotic grass propagules on the small islands where they nest.

# Species interactions: Grasses under grazing

My experimental results show that grass abundance was significantly higher in plots exposed to grazing (Fig. 2). Furthermore, there are clear mechanisms for this divergence. Grazing removes inflorescences or prevents their production on severely grazed stems, so that a lower proportion of stems flowered in open plots than exclosed plots (Fig. 3a). In the open plots, however, reproductive output was translated into the next generation of stems at a higher rate (Fig. 3b). Shading from litter appears to play an important role in determining this rate of stem production, as the number of stems produced per previous season's inflorescence showed a significant negative relationship with litter cover (Fig. 3d). Once the exclosures had been up for a full year, litter from ungrazed grasses was substantially higher in the exclosed plots, as evidenced by the distribution of the closed circles further to the right in Fig. 3d.

While the removal of biomass and prevention of litter accumulation should elevate germination rates to benefit all annual species, the increased proportional abundance of the grasses suggests they receive an additional benefit relative to the annual forbs. This may be because annual grasses can produce more stems per individual under grazing. This has been documented with other grazers and annual grasses (NoyMeir and Briske 1996, Gutman et al. 2002), and under mowing (Lush 1988), and may be a direct response to leaf injury or an indirect response to light availability. Van der Graaf et al. (2005) also showed increased production of branches in the perennial grass *Festuca rubra* under grazing by Barnacle geese (Branta leucopsis). It is important to note that I do not interpret my results as evidence of compensatory biomass production under grazing, as has been demonstrated in other systems with goose herbivory (Cargill and Jefferies 1984, Van der Graaf et al. 2005), because I have not measured total production of biomass in the presence and absence of grazing. Rather than increasing total primary production in the grasses, grazing appears to facilitate their demographic success by switching the allocation of biomass to stem number, rather than stem height. I found that stem height is significantly reduced under heavy grazing, while stem number is increased.

# **Species interactions: Grazed grasses and ungrazed forbs**

Although native forb species declined along the grazing gradient, I did not observe significant differences in forb abundance or richness between the open and exclosed plots. Upon further inspection of the data, it appears that the decreased proportional abundance of the annual grasses in the exclosures was partly countered by an increased abundance of a few patchily distributed exotic perennial forbs and grasses. These groups were excluded from the

analyses because they were not sufficiently common to fit models, and any part of the increased proportional abundance left to the well-distributed forbs was too small to detect (Table 1, forb models, exclosure effect not significant). This suggests that, given multiple exotic plant species now in the species pool, simply removing grazing will not return the system to one dominated by native forbs.

Given the direct evidence that the exotic annual grasses increase under grazing, along with the decline in the native forbs along the grazing gradient, I conclude that grazing assists the grasses in out-competing these forbs. Because grazing is almost entirely on the exotic annual grasses (Fig. 1), any impact of grazing on forbs occurs through a modification of the intra-trophic interactions between plant species. For grasses to replace forbs, the grasses' increased stem production must either enable higher reproductive output or enhance competitive abilities. Increased production of stems increases potential for the production of inflorescences, but many of these additional stems may be grazed before producing seeds. It is therefore also important to consider the effects that altered growth habit under grazing may have on the competitive interactions between the grasses and other species in the community.

In systems where grazing prevents litter build-up and shading, the production of many short stems may evolve as an efficient strategy for space occupation and reproduction. Under grazing, the annual grasses tend to form a short, highly branched mat which occupies a large percentage of available space. *Poa annua*, for example, is a common golf course weed known for its ability to move into disturbed patches and create an impenetrable cover that prevents invasion by other species (Hutchinson and Seymour 1982, Lush 1988, Bergelson 1990). Falster and Westoby (2003), in their review of theoretical work on plant height strategies, point out that the production and maintenance of tall stems is an inefficient

use of resources resulting from the "evolutionary arms race" of light competition. Larger size requires diversion of resources to the maintenance of structural and transport tissues, away from reproductive output and away from the production of additional lateral shoots to occupy additional space. Again using *Poa annua* as an example, this grass is a successful weed in putting greens because of its ability to flower even at very low mowing height (Johnson and White 1998). Reviewing 10 studies of grazing systems in Scotland, Pakeman (2004) showed that plant traits increasing under grazing included low minimum height and an annual life history strategy. The short stem strategy has also been demonstrated in systems where biomass is frequently removed by fire, creating a niche space for short, efficient reproducers to thrive immediately following disturbance (Falster and Westoby 2005).

In this study system, the absence of the annual grass functional group in the native species pool seems to play an important role in determining the success of the exotic grasses. Both the grazer and the species adapted to thrive under grazing are introduced. The benefits of grazing for the efficient production of stems therefore accrue only to the exotic members of the species pool. In addition, because the forbs do not produce litter, they cannot have the same suppressive effect on the exotic annual grasses that other grasses might produce. Evidence from other systems also suggests that native perennial grasses can limit the demographic success of exotic annual grasses under grazing. Quigley and Ford (2002) reported that the abundance of *Vulpia myuros* and *Poa annua* was more strongly associated with sheep grazing in the absence of perennial grasses (Quigley and Ford 2002). Similarly, Whitson and Koch (1998) found that native perennial grasses reduced *Bromus tectorum* establishment through the suppressive effects of litter. The only native perennial grass found

in my plots, however, is *Festuca idahoensis* ssp. *roemeri*, which is limited to clumps in rock crevices.

# Implications for biotic resistance theory

The most surprising aspect of the joint success of geese and grasses in this system is that it occurs despite the grazers' selection of the grasses and avoidance of the forbs. In this case current theory would predict that goose herbivory should limit, rather than facilitate, the invasion success of the grasses (Mitchell et al. 2006). Instead of doing better in the absence of their enemies, however, the grasses appear to benefit from the herbivory. This is different from the previous findings that generalist herbivores can facilitate exotic grasses by grazing on intolerant native species (DiTomaso 2000, Hobbs 2001), because the native forbs decline without being grazed. It also suggests that high herbivore attack rates are not necessarily indicators that exotic plant species are being limited by enemies, whether native or exotic (e.g., Agrawal and Kotanen 2003). This also reaffirms the importance of quantitative studies of demographic impacts in our documentation of interactions between exotic species. Qualitatively, the relationship between geese and grasses would likely have been interpreted as a (+/-) relationship in Simberloff and Von Holle's 1999 inventory simply because grasses are consumed by geese. I required an experimental approach to uncover what I interpret to be a mutually beneficial relationship (i.e., +/+).

Much theory about community invasibility has considered the escape from evolutionary constraints to be a distinct advantage for invading species. The enemy release (Williamson 1996, Keane and Crawley 2002), evolution of increased competitive ability (Blossey and Notzold 1995), and novel weapons (Callaway and Aschehoug 2000) hypotheses

are all based on this premise. In this system, it is likely that the introduced European grasses evolved with grazing pressure, and certain that the large bodied forms of Canada geese, which are native to the central prairies of North America (Hanson 1997), evolved with grasslands. The native forb community, however, has evolved without grazers and with few grasses. The success of the exotic annual grasses therefore appears to be due to the combination of a known enemy and novel, dissimilar competitors. Instead of the grasses bringing novel abilities to a new game, they do better playing their old game against a community of inexperienced opponents. My results suggest that shared evolutionary context can be a benefit as well as a constraint.

With co-occurrence of multiple exotic species increasing globally, it is possible that invasion success may depend as much on common evolutionary history between invaders as on a single invader's escape from competitors or enemies. In fact, I have shown that multiple exotic species from similar systems can create mutual benefits by making an invaded system more, rather than less, like home. Testing if a common evolutionary context also underlies facilitation between other pairs of exotic species would be an interesting avenue for further research. For example, facilitation between exotic frugivorous birds and exotic fruit bearing plants, wherein the bird is fed and the plant dispersed, is particularly common (Simberloff and Von Holle 1999). Studies of the red-whiskered bulbul (*Pycnonotus jocosus*), a frugivorous bird native to India, have shown clear mutualisms with exotic fruiting plants in Hawaii and Florida. The rapid expansion of bulbuls in both of these invaded ranges has been tied to the similarity between the exotic fruits introduced to Hawaiian and Floridian gardens and agricultural systems, and those native to India (Carleton and Owre 1975, Williams and Giddings 1984). This suggests that overlap of the native ranges of interacting exotic species pairs may help predict their invasion success. Additionally, the benefit to the plant species in the co-invaded range should be strongest if suitable native dispersers are not already present. Testing for relationships between the quantitative strength of such facilitative interactions and the similarity of vegetation composition in the plant's native range, the bird's native range, and their co-invaded range, would therefore be a useful next step. Ecologists have recently recognized the importance of biogeographical comparisons of invaders' native and exotic ranges (Hierro *et al.* 2005); I suggest this will need to be expanded to consider the home ranges of multiple co-occurring invaders.

#### Further research on co-invasion in the Gulf Islands

Because the islands where I conducted this research are important remnants of an endangered ecosystem, and are as such protected in a National Park, there is considerable interest in conserving and restoring their native plant communities. My research suggests that removing geese from these islands might decrease the spread of established exotic annual grasses into new areas, but that it may not result in recovery of native forb species in areas already dominated by these grasses. There are thus three directions for future research that could make important contributions to building a conservation strategy for this system.

First, continued observation of the open and exclosed plots I established will enable stronger predictions about the long term impact of goose removal on island plant communities. In my relatively short term study I found that excluding grazing geese and allowing grass litter to accumulate had no significant effect on the abundance of native forbs. A decline in the proportional abundance of grasses appeared to be balanced by an increase in

a few exotic forbs. Keeping my field plots in place for an additional three to five years will allow me to determine if this response persists, or if native forbs are able to recover.

Second, it would be useful to test the possibility for native forb recovery in the absence of both geese and grasses by establishing at each existing pair of field plots a third plot which was both exclosed and cleared of extant grasses. With both components of the positive feedback loop removed, the possible mechanisms preventing native forb recovery would be competition from exotic forbs or re-colonization by exotic grasses from nearby seed sources or the seed bank. It should be possible to evaluate the relative importance of these two mechanisms by observing which of these groups of exotic species tended to dominate plots where grasses were removed. Characterization of the seed bank in these island soils would also contribute to our understanding of the constraints on community restoration. Removing exotic forbs as well as exotic grasses would allow further separation of these two mechanisms, but may require an additional treatment plot. Plots are likely too small to be subdivided, and variation between sites is high enough that all treatments should be replicated at every site. Though the obvious completion of a fully factorial set of geese and grass treatments would be an open plot with grasses removed, the known deposition of grass seed in goose feces renders this treatment unlikely to promote native species recovery.

Third, if geese are to be removed from the islands, with or without simultaneous control of grasses, managers will need to understand where the geese nesting in these islands are coming from. The first possibility is that geese successfully reproduce in the islands, and that high natal site fidelity (Allen *et al.* 1995) results in mature offspring returning there to nest. In this case, destruction of eggs or nests on the islands may help reduce the number of birds nesting there in the future. The second possibility, however, is that geese nesting on the

islands are simply overflow from increasing populations on Vancouver Island and the rest of British Columbia (Figure 5). In this case, a landscape level strategy to reduce the large goose populations supported by agricultural and cultivated areas may be necessary.

Figure 5: Population trend for *Branta canadensis* in British Columbia. Data are from the Breeding Bird Survey (Sauer *et al.* 2005). An exponential function provided the best fit:  $R^2 = 0.87$ ,  $I^2 = 0.82$ .



# **CONCLUSIONS**

"Invasional meltdown," or positive feedback between mutually facilitating exotic species, severely complicates restoration of the original community assembly and stability processes that might favor native species. Understanding how and when this occurs is critical for the conservation of global biodiversity. By identifying a positive feedback cycle between exotic geese and the grasses they graze selectively, I have demonstrated that current biotic resistance theory is inadequate for predicting the occurrence of such cycles. By identifying the mechanisms underlying the demographic success of these grasses, I have found that the relative similarity of evolutionary context in the home and co-invaded ranges may determine the strength of facilitation between exotic species. Testing this hypothesis for other pairs of exotic species should help us to better assess the likelihood of "invasional meltdown" scenarios in the future.

In the Gulf Islands system, the restoration of native plant species may only depend on halting the positive feedback cycle between geese and grasses, or it may additionally require control of established exotic grasses and forbs. Continuing the field experiment I began for my thesis research, possibly with additional components and collaborators, will help to identify the management strategies required to ensure native persistence in this system of multiple invaders.

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