Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago

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ABSTRACT

Declines in forest and woodland birds have largely been attributed to habitat loss and fragmentation. In the past decade, however, the potential for herbivores to influence bird species abundance and community composition via their direct impact on vegetation structure has also been recognised. We tested the hypothesis that deer influence vegetation structure and bird assemblages in a large island archipelago in western North America using surveys of 18 islands with deer densities ranging from 0 to over 1 deer/ha. Amongst these islands, reduced predation and hunting pressure has allowed deer populations to increase above those likely to have existed in pre-European times. Our results support a growing body of evidence that deer regulate both the cover and architecture of understory vegetation which in turn profoundly affects island bird assemblages. Deer-free islands supported the most abundant and diverse bird fauna. Iconic songbirds such as the rufous hummingbird, song and fox sparrow were abundant on islands with no deer but substantially reduced on islands with high deer densities. Only one bird species, the dark-eyed junco, preferred moderate and high density deer islands. Our observations suggest that current cohorts of palatable shrubs on islands with high deer densities are relatively old and potentially represent an impending extinction debt, where the full effects of high deer density on island biota may take decades to fully unfold. Our results suggest that deer densities below a threshold of 0.1 deer/ha should allow native vegetation to recover and a rich and diverse bird species assemblage to persist. We suggest that adaptive management be used to test the validity of this threshold, and that without active management of deer abundance, local extinctions of native flora and fauna appear likely to accelerate.

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1. Introduction

In less than a century, deer management has moved from a focus on recovering overexploited populations to managing deer over-abundance (Côté et al., 2004). As deer populations have recovered, their effects on ecosystems have also become evident (Côté et al., 2004; Crête, 1999; Gaston et al., 2008; Vila et al., 2003b; Waller and Alverson, 1997). Deer drive forest dynamics in many parts of North America and Europe (Stockton et al., 2005; Tremblay, 2004; Veblen et al., 1989) by affecting plant structure and community composition (Alverson et al., 1988; Crête, 1999; Russell et al., 2001; Vila et al., 2003b; Waller and Alverson, 1997), invertebrate assemblages (Allombert et al., 2005b; Wardle et al., 2001), and food and nesting resources for birds, particularly those dependant on understorey vegetation (Allombert et al., 2005a; Gill and Fuller, 2007; Holt et al., 2010; McShea and Rappole, 2000). Where valued native species have declined under elevated browsing by deer

(Waller and Alverson, 1997; McShea and Rappole, 2000; Gonzales and Arcese, 2008), public pressure has occasionally led managers to consider reducing deer densities in an attempt to maintain viable populations of other species or to restore ecosystems (Gaston et al., 2008). However, the effects of high deer density can vary across ecosystems (Côté et al., 2004) and empirical estimates of historic deer densities, or densities likely to promote the persistence of particular valued species or processes, are rare (McCabe and McCabe, 1997). In this paper, we quantify relationships between deer abundance, forest vegetation structure and bird species abundance in a large island archipelago in western North America. We then use these data to estimate deer densities that are compatible with the maintenance of a diverse forest avifauna, ecosystem function and native species other than deer.

The Gulf and San Juan Island archipelagos of western Canada and the United States comprise over 600 islands of varied size. These archipelagos are ecologically unique lying in the Coastal Douglas Fir Bioclimatic zone (Meidinger and Pojar, 1991) and supporting many threatened species associated with the Garry oak savanna ecosystem (SARA, 2002). Black-tailed deer (*Odocoileus hemionus*) are endemic to the Gulf and San Juan Island archipelago

(Gonzales and Arcese, 2008). Predation by cougars (*Felis concolor*) and wolves (*Canis lupus*) and hunting by First Nations and then Europeans, probably kept deer densities low historically (Darimont et al., 2004; Gonzales and Arcese, 2008; MacDougall, 2008). Deer populations on islands can also be expected to have experienced periodic extinction events related to predator pressure and island size and isolation, suggesting browsing pressure has not been continuous (Darimont et al., 2004). By the late 1800s, European settlement of the islands resulted in the extirpation of cougars and wolves (Miller et al., 1935; Shackleton, 2000; Tremblay, 2004) and alienation of First Nation communities from their traditional deer hunting grounds (Arnett, 1999). More recently, human hunting pressure has also declined dramatically due to regulation and changing sentiment (Shackleton, 2000). As a result deer have become locally abundant, particularly where black-tailed deer co-occur with exotic fallow deer (*Cervus dama*, Shackleton, 2000). As a consequence, managers have become concerned about the effects of elevated browsing by unregulated deer populations on plant species and communities (Gonzales and Arcese, 2008), and on the viability of island songbird populations (Allombert et al., 2005a).

The Gulf Island and San Juan archipelagos provide an ideal landscape to test hypotheses about herbivore impacts on vegetation structure and bird species abundance because they provide many islands that vary in size, isolation and deer abundance. We conducted pellet, vegetation and bird surveys on 18 islands varying from 5 to 902 ha in size, and from 0 to over 1 deer/ha in density, to estimate the influence of deer on the relative abundance of bird species via its effect on vegetation structure. We predicted that understory vegetation cover would decline as deer density increased, leading to a range of positive and negative effects on the relative abundance of several focal bird species that vary in their reliance on understory vegetation for feeding or nesting. In addition, we describe how changes in the relative abundance of focal bird species, and the architecture of a widespread shrub, might be used as indicators of deer browsing impact in forest ecosystems, as well as targets for deer management and ecosystem restoration. Specifically, we tested if ocean spray, *Holodiscus discolor*, a palatable shrub of the Gulf and San Juan islands, could be used as an index of browsing level by recording variables that, cumulatively, described shrub architecture. Ocean spray recruits from seed but individual plants regenerate via coppicing, such that all mature stems arise from shoots developing from the base of older, broader stems. Thus, we expected individual ocean spray plants to approach an umbrella-like form, with one or more old stems supporting foliage above the reach of browsing deer (*c* 1.5 m) as deer density increased. We also tested if recruitment by ocean spray declined at high deer density, as predicted if herbivory limits seedling establishment.

2. Methods

2.1. Study location

Our study occurred in the Gulf and San Juan Islands of the Georgia Basin, western North America (48°35′36 57N; 122°59′46 79W, Fig. 1). The study region lies within the rain-shadow of the Cascade mountain range on the mainland resulting in a warm and dry climate between May and October (13 °C 43 mm) and mild and wet climate between November and April (5 °C 123 mm) (Gonzales and Arcese, 2008). The island landscape has been shaped by glacial ice over two glacial periods with the ice retreating around 12,000 years ago. The islands are underlain by sedimentary rocks with erosion resistant sandstone and conglomerate. Sampled forest were dominated by Douglas fir *Pseudotsuga menziesii* but typically included western red cedar *Thuja plicata*, grand fir *Abies*
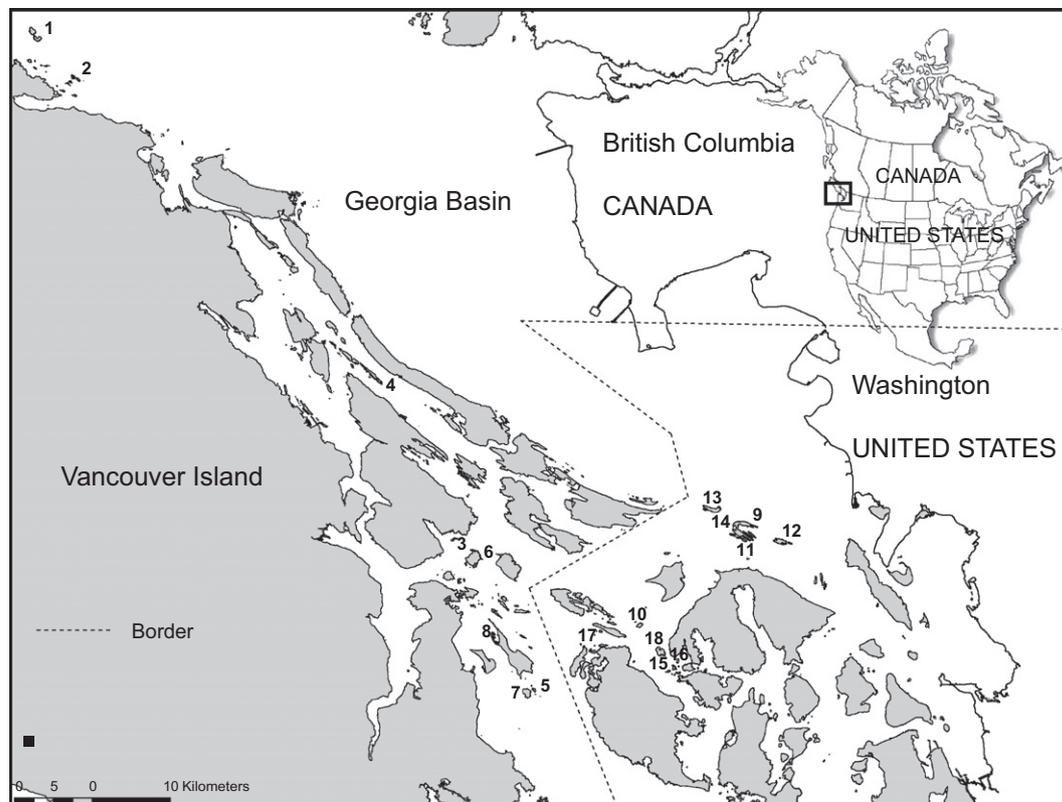
Fig. 1. Gulf Islands, Canada and San Juan Islands, United States study region. Locations of 18 study islands denoted with a number corresponding to island name listed in Table 1.

Table 1
Island features showing tenure, size, isolation from the mainland or Vancouver Island, number of bird, vegetation and faecal standing crop (FSC) plots, ocean spray shrubs sampled, estimated deer density per hectare, deer density category, and land tenure where GINP – Gulf island National park, MPP – Marine Provincial Park, WSMP – Washington State Marine Park and TNC – The Nature Conservancy, USFW – United States Fish & Wildlife Service.

Island no. and country	Island	Size (Ha)	Tenure	Isolation (km)	No. bird plots	No. veg. and FSC plots	No. ocean spray	Deer density (deer/Ha)	Deer density category
Canada									
1	North Ballenas	45.1	Private	4.05	6	9	2	0	Low
2	South Winchelsea	8.6	TNC	3.3	2	4	2	0	Low
3	Russel	13.4	GINP	0.63	6	0	0	0	Low
4	Wallace	80.7	MPP	1.47	21	25	13	0.13 ± 0.02	Moderate
5	Little D'Arcy	9.6	Private	2.03	4	0	0	0.21 ± 0.05	Moderate
6	Piers	101.6	Private	0.78	10	20	15	0.22 ± 0.04	Moderate
7	D'Arcy	85.9	GINP	1.97	20	23	21	1.05 ± 0.11	High
8	Sidney[*]	902.3	GINP	4.82	21	21	6	1.14 ± 0.10	High
United States									
9	Ewing	6.3	WSMP	5.59	2	3	2	0	Low
10	Flattop	23.9	USFW	2.92	6	7	7	0	Low
11	Little Sucia	9.8	WSMP	4.09	4	4	2	0	Low
12	Matia	64.1	WSMP	4.7	8	8	5	0	Low
13	Patos	85.5	WSMP	5.5	10	10	8	0	Low
14	Sucia	224.7	WSMP	3.58	10	10	9	0	Low
15	Yellow	5.4	TNC	1.85	2	6	1	0	Low
16	McConnel	13.2	Private	1.22	4	6	5	0.25 ± 0.05	Moderate
17	Sentinel	6.7	TNC	1.58	4	8	6	0.30 ± 0.04	Moderate
18	Jones	78.9	WSMP	0.8	10	13	7	0.38 ± 0.07	Moderate
	Total	1765.7			150	177	111		

[*] Only island to contain both exotic and native deer.

grandis, bigleaf maple *Acer macrophyllum*, arbutus *Arbutus menziesii* and less commonly garry oak *Quercus garryana*. Bird abundance and woody vegetation structure was surveyed across sites on 18 islands differing in size and isolation from the mainland or Vancouver Island and with varying histories of deer occupation and deer density (Table 1). Soil type and microclimate were similar across all study islands.

2.2. Estimating deer density

Estimates of deer density for each island were determined by calibrating the faecal standing crop (FSC) with known deer density on one island, Piers. Absolute counts of deer were obtained on Piers Island using a line of 12 observers traversing the island at dusk, counting each deer encountered. During the count, the sex, age, distinguishing features and location of each deer were recorded to minimize duplicate counting, and radios were used to maintain contact between groups of observers. Counts were conducted just prior dusk when deer on Piers Island congregate in meadows and are easy to observe. Counts were conducted twice (April and June 2007, yielding 20 and 24 deer, respectively).

On all islands the faecal standing crop (FSC) was measured by counting all pellet groups inside of one 100 by 2 m line transect (Marques et al., 2001) adjacent to each of 177 vegetation plots (Table 1). A pellet group was recorded when $\geqslant 18$ droppings occurred within an area $\leqslant 20$ cm^2 (Campbell et al., 2004). Using the mean number of deer counted on Piers Island along with its FSC estimate, we derived a calibration which was used to estimate the density of deer on all islands. Deer density (mean ± SE) for each island i was calculated as the average deer density on Piers Island (0.22 deer/ha) multiplied by the estimated faecal standing crop FSC_i per ha for island i divided by the FSC estimate per ha (42.2) for Piers Island (Table 1).

2.3. Measuring the impact of deer on vegetation structure

Location of forest vegetation plots and bird point counts were randomly stratified across each study island. Grids (100 × 100 m)

Table 2
Classification of vegetation strata and plant groups.

No.	Strata (m)	Plant groups
1	0–0.5	Grasses, shrubs, seedlings and saplings
2	>0.5–1.5	Shrubs, seedlings, saplings
3	>1.5–4	Tall shrubs, small trees
4	>4	Mature trees

were placed over digital maps of each island, and sites were then chosen using a random number generator to pick coordinates from the grid. Sites were located no closer than 15 m from the high tide line. In each (10 m radius) vegetation plot, three measurements were performed; forest structure, shrub structure (ocean spray) and recruitment. Because just one island (Sidney) supported exotic fallow as well as native black-tailed deer, we were unable to disentangle the relative impact of native versus exotic herbivores on vegetation structure.

2.4. Forest structure

To understand the influence of deer browsing on forest structure, we estimated the total percent cover of the forest strata and the main plant groups, namely trees, shrubs, herbs/grasses. Forest strata were divided into four categories (Table 2). Spot charts were used to estimate the cover of the different strata and plant groups along with two species of shrub, salal *Gaultheria shallon* and ocean spray *H. discolor*, both of which are known to be palatable to deer (MacTaggart-Cowan, 1945). We also counted the number of tree saplings (young trees $\leqslant 0.5$ m tall) of the following common tree species arbutus, douglas fir, grand fir, garry oak and western red cedar within each 10 m radius plot to estimate the influence of browsing on tree recruitment.

2.5. Shrub architecture – ocean spray

We quantified the architectural response of ocean spray shrubs to browsing. To do so, in each vegetation plot we selected the

north-most ocean spray for measurement, or if none were present, we measured the nearest individual to the plot. On each shrub we measured: total height; number of stems originating at the base without living foliage ('dead stems'); number of live stems ⩾20 cm tall that were >0–0.5 cm, >0.5–1 cm, >1–1.5 cm or >1.5 cm in diameter; and, finally, the diameter of the shrub at 1 and 2 m above ground level. Shrub diameters were used to estimate the ratio of foliage at 1 versus 2 m in height; e.g., with ratios below c 0.3 indicating a strong browsing impact and an umbrella-like architecture. We also estimated the effect of deer density on ocean spray seedling recruitment by counting the number of ocean spray seedlings within each 10 m radius vegetation plot.

2.6. Bird abundance and composition

Avian point counts were conducted on all islands between April and June 2007 by a single observer (TGM). At each point count all birds seen or heard within 50 m radius and 10 min interval were recorded. Aerial feeders and raptors foraging greater than 20 m above the site were not recorded nor were aquatic and pelagic species. Two counts on different days were made at each point. During our study, we estimated bird detection probabilities within our 50 m radius point count using distance sampling (Buckland et al., 1993). For each observation the distance between the centre of the point count and the observed bird was recorded. We found that the detection probabilities were not correlated with browsing pressure and therefore used our estimates of relative abundance for subsequent analyses. Bird surveys were conducted between 0500 and 1100 h. The location of each point count was recorded using a handheld GPS (Garmin60). Both vegetation plots and point counts were separated by a minimum distance of 200 m.

Prior to analysis, understory dependence scores were calculated using information on bird species foraging and nesting behaviour using information from Alsop (2001) and Allombert et al. (2005a). Note ground feeders were given an understory dependence vegetation score for foraging of 0. Foraging and nesting behaviour have been used successfully in other studies to predict impact of both deer browsing (Allombert et al., 2005a) and livestock grazing (Martin and Possingham, 2005).

2.7. Analysis

Modelling the number of individuals of a particular bird species, y_i recorded at the ith location was undertaken in a generalised linear mixed modelling (GLMM) framework using a Negative Binomial (NB) distribution where the mean, λ_i (on the log-scale) is represented as a linear function of deer browsing history, $b_{j(i)}$ j = low (L), moderate (M) and high (H) and an island random effect, l_i. We parameterise the model to have no intercept so we can estimate a separate parameter for low, moderate and high browsing levels. The overdispersion parameter ϕ is gamma distributed (Ga) with shape and scale parameters equalling 0.1. This informative prior was based on an initial exploratory analysis of the data in R using the glm·nb function from the MASS library (Venables and Ripley, 2002). The model is specified as

$$y_i \sim NB(\lambda_i, \phi) \quad (i = 1, \dots, n) \tag{1}$$

where

$$\log(\lambda_i) = \beta_L b_{L(i)} + \beta_M b_{M(i)} + \beta_H b_{H(i)} + l_i \tag{2}$$

with non-informative priors $\beta_j \sim N(0, 0.001)$ $(j = L, M, H)$, $l_i \sim N(0, \tau_l)$, $\phi \sim Ga(0.1, 0.1)$, $\sigma_l^2 \sim U(0, 2)$ where $\tau_l = 1/\sigma_l^2$.

In the above model, the prior chosen for the island random effect l_i was Normal (N) with mean 0 and precision τ_l and a uniform prior (U) was placed on σ_l^2. Analysis of similarities (ANOSIM) was used to test whether the variation in bird assemblage membership

was greater between islands with different deer densities than within islands with the same deer densities.

Modelling the effect of deer browsing on vegetation cover and ocean spray structure was also done using a Bayesian GLMM framework, where again three levels of deer density were considered fixed effects and island a random effect. In the following results, a significant difference between estimates is used in the Bayesian sense to mean that the 95% credible intervals of the estimates do not overlap.

3. Results

3.1. Deer density

Density of deer varied greatly across our 18 study islands; from those with deer currently and historically absent (e.g., Sucia, Patos, Matia), to those with moderate (e.g., Piers 0.22 ± 0.04, Sentenel 0.30 ± 0.04 deer/ha) or high deer densities (Sidney 1.14 ± 0.10 and D'Arcy 1.05 ± 0.11 deer/ha; Table 1). On Sidney Island, the high density estimate comprised predominantly exotic fallow deer, which expanded in number after being introduced to the island in the early 1900s. We found no clear relationships between deer density, island size and isolation despite a relatively large sample of 18 islands. For example, island size and deer density were positively related ($r = 0.63$) with Sidney Island included in the analysis, but not with this large island excluded ($r = 0.12$). Likewise, island isolation and deer density were negatively related ($r = -0.42$) with Sidney Island excluded, but not with it included ($r = -0.09$).

3.2. Effect of deer on forest strata vegetation cover

Islands with low deer densities supported a significantly higher cover of strata between >0.5–1.5 m, and to a lesser extent at >1.5–4 m, compared with islands with moderate and high deer densities (Figs. 2 and 3). Ground (0–0.5 m) and canopy-level strata (>4 m) varied markedly between islands with different deer densities overall, but not significantly so. Total tree cover was also similar among islands, but total shrub cover was lowest on high deer density islands (Fig. 4). Shrubs in this region vary in height from 0.2 to 4 m and thus represent a composite of the first three strata of Fig. 2. Percent cover of two common native shrubs, salal and ocean spray, varied little between islands, although the percent cover of ocean spray was reduced on high deer density islands (Fig. 4). The mean number of tree saplings varied widely across islands but was unrelated to deer density (low deer density island mean estimate 3.7, 95%CI 0.2–13.2; moderate 0.3, 95%CI 0–2.4; high 7.7, 95%CI 0–45.1).

Fig. 2. Percent vegetation cover for four strata across low (L), moderate (M) and high (H) deer density islands. Bars represent 95% credible intervals.

Fig. 3. Deer browsing impact on forest vegetation cover; (A) no deer (Patos Island), (B) moderate deer density (Wallace Island,) and (C) high deer density (Sidney Island).

Fig. 4. Percent vegetation cover for total trees, shrubs and herb/grasses as well as two common native shrubs salal and ocean spray across low (L), moderate (M) and high (H) deer density islands. Bars represent 95% credible intervals.

up to 140 stems per shrub on high deer density islands (Fig. 6). Likewise, the total number of stems 0–5 cm in diameter increased substantially with deer density (Fig. 6), reflecting ocean spray's coppicing response to browsing pressure. The number of stems at larger diameters was similar between islands grouped by deer density. The mean height of ocean spray was also similar across islands (low deer density, mean estimate 3.2 m (95%CI 2.4–4.0); moderate, 3.2 m (95%CI 2.3–4.4); high, 3.8 m (95%CI 2.2–5.9). We found too few ocean spray seedlings to relate recruitment of ocean spray to deer density.

3.4. Effect of deer on bird species

Of a total of 53 bird species recorded on 18 islands, 34 were detected often enough to undergo analysis. Equal numbers of resident and migrant species were classified *a priori* as strongly and moderately dependent on understory vegetation, whereas the majority of species classified as having a low dependence on understory vegetation were resident species (Table 3). As hypothesized, the indirect effects of deer density on bird abundance, via its direct effects on vegetation structure, were most evident in bird species that depend on understory vegetation for feeding or nesting (Table 3). We used *a priori* understory dependence scores (Table 3) to identify ten species likely to be most strongly reduced by deer browsing. As predicted, density estimates for all of these species were highest on islands with low density or no deer (Table 3). Fox and song sparrow, rufous hummingbird, spotted towhee, Bewick's wren and orange-crowned warbler showed the strongest preference for low deer density islands (see Table 3 for birds species scientific names).

We expected nine species to be moderately negatively affected by deer browsing, based on their reduced reliance on understory vegetation or use of both closed and open habitats (Table 3). The response for this group was variable. As predicted, golden-crowned kinglet, ruby-crowned kinglet, white-crowned sparrow and varied thrush, were all most abundant on islands with low to moderate deer densities. In contrast, Pacific slope flycatcher, chestnut-backed chickadee and American goldfinch were equally abundant across all deer densities (Table 3). Of the 15 species predicted to be indifferent to browsing based on having no clear link to understory vegetation, most varied little in abundance with deer density. Only one species, the dark-eyed junco, known to favor open-forest habitats, exhibited a strong preference for islands with moderate and high deer densities. Two species predicted to be indifferent

3.3. Effect of deer on ocean spray architecture

Deer browsing had a dramatic impact on the architecture of ocean spray, transforming shrubs from full-bodied plants with foliage distributed from near ground level to their tops, into umbrella-like shrubs with no foliage under *c* 1.5 m in height, above which foliage escaped browsing by deer (Fig. 5). We used the ratio of the diameter of the shrub at 1 m and 2 m in height to quantify this structural change and found that low deer density islands had the highest mean ratio of 0.65 (95%CI 0.44–0.89); whereas moderate and high deer density islands had mean ratios of 0.29 (95%CI 0.16–0.45) and 0.27 (95%CI 0.11–0.54), respectively.

The total number of dead stems also increased significantly with deer density, as did the number of browsed stems, reaching

Fig. 5. Impact of increasing browsing pressure on architecture of native shrub ocean spray; (A) no deer present (North Ballenas); (B) moderate deer density (Little D'Arcy); (C) high deer density (Sidney Island).

to browsing, Northwestern crow and Townsend's warbler, were more abundant on islands with low deer densities.

Bird species richness did not vary significantly between islands with different deer densities, although islands with low deer density did harbor the most species; 9.0 (95%CI 7.3–11.4); moderate 6.9 (95%CI 4.5–9.7); high 7.3 (95%CI 4.6–11). Species abundance, on the other hand, was twice as high on low deer density islands (21.7 95%CI 17.1–27.3) than on islands with either moderate (10.2 95%CI 7.3–13.6) or high deer densities (10.4 95%CI 6.0–17.4). Sørensens similarity index revealed that 32% of bird species were common to both low and moderate deer density islands, 34% to low and high, and 40% to moderate and high. Only 23% of species were common to all islands. Plotting the rank abundance of species across islands with low, moderate and high deer density

illustrated the similarity between moderate and high deer density islands with respect to species evenness and diversity, whereas islands with low deer density were strikingly different with a higher diversity and lower evenness of species (Fig. 7). The most abundant species recorded on low density islands was the orange-crowned warbler, whereas the American robin was the most abundant species on both moderate and high deer density islands. By comparison, the American robin was 7th most abundant on low density islands. Analysis of similarities (ANOSIM) confirmed that the bird assemblage of low and high deer density islands, while having some overlap in species, were clearly different, whereas the difference between moderate and high islands was marginal (Table 4). Plotting the proportional decrease in bird species abundance between low and high deer density islands against their understory vegetation dependence scores (Table 3 and Fig. 8) revealed a significant correlation $r = 0.51$, confirming that as deer density reaches high levels, bird species dependant on understory vegetation are disproportionately negatively affected.

4. Discussion

We show that deer regulate the amount and structure of vegetation in the understory of coastal Douglas fir forests of the Gulf and San Juan Island archipelagos. Deer simplified understory vegetation structure and reduced vegetation cover in the >0.5–1.5 m strata (Figs. 2 and 3). On the highest deer density islands (Sidney and D'Arcy) we observed large areas devoid of shrub cover (Fig. 3c). Changes in overall shrub cover contributed to this effect, but did not account for it entirely (Fig. 4). Instead, differences in vegetation cover among islands were driven largely by shrub architecture and the contribution of herbs and saplings to the understory. In ocean spray, for example, we found no difference in overall cover between islands, but enormous changes in architecture contributing to a significant reduction in cover at the >0.5–1.5 m strata (Figs. 2–6). In contrast, we found no effect of deer on sapling number, perhaps because we did not sample sufficiently to test if browsing affected each species similarly. For example, on Sidney Island, where deer density was highest, sapling density was sometimes high but comprised mainly of grand fir, perhaps indicating that deer selectively remove palatable species, but avoid those with high levels of phenolics or terpenoids (Vourc'h et al., 2002). Several other studies have shown that deer reduce recruitment in many palatable woody plant species (Alverson et al., 1988; Veblen et al., 1989; Vila et al., 2003b). Where high browsing pressure is sustained, we predict that managers will observe declines in the overall cover of palatable shrubs, including ocean spray, as old shrubs die and recruitment declines. Indeed, our observations suggest that most if not all ocean spray on islands with high deer densities are relatively old and that the recruitment of new individuals is limited by deer browsing. If correct, extant examples of highly palatable species on these islands now represent evidence of the island's outstanding extinction debt (Sax and Gaines, 2008; Vellend et al., 2006).

Although our study presents a single year of results, our findings are clear and support a growing body of evidence showing that deer can profoundly shape island forest flora, fauna and ecosystem processes (Côté et al., 2004; Gaston et al., 2008). Our results also support patterns reported from long term studies of the Haida Gwaii archipelago, 600 km north of our study area, and suggest that results from Haida Gwaii are applicable elsewhere. In Haida Gwaii, Vila et al. (2005, 2004) showed that individual salal shrubs were twice as old on average, and red huckleberry shrubs (*Vaccinium parvifolium*) 2–4 times older on islands with versus without deer. Overall, these and other studies indicate that the medium-term effects of high deer density on vegetation and bird
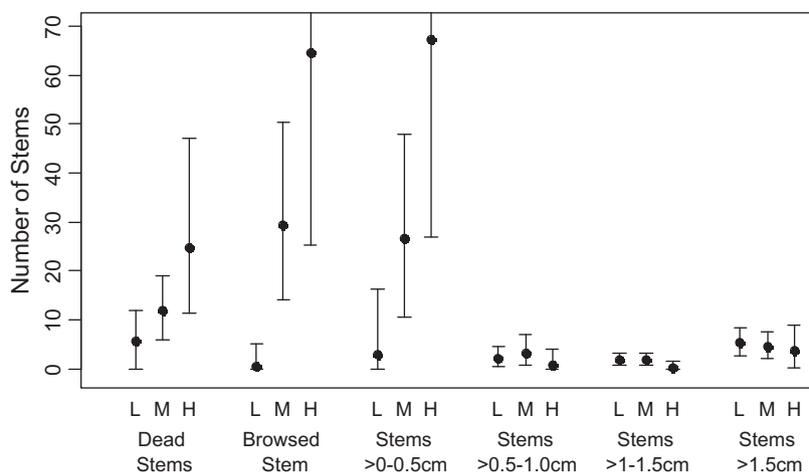
Fig. 6. Number of stems of ocean spray across three browsing levels low (L), moderate (M) and high (H). Bars represent 95% credible intervals.

community structure reported here are occurring across many temperate forest ecosystems (Allombert et al., 2005a,b; Côté et al., 2004; Gaston et al., 2008; Gonzales and Arcese, 2008; Stockton et al., 2005, this study), but that the full effects of high herbivore density on island ecosystem processes and biota may nevertheless take decades to unfold fully (MacDougall, 2008).

Mid-story vegetation cover (>1.5–4 m) tended to decline as deer density increased, perhaps indicating that browsing has begun to reduce recruitment in shrubs and trees on islands with moderate to high deer densities. Overall, these results are consistent with long-term changes in forest communities reported from the Haida Gwaii archipelago, where recruitment of western red cedar (*Thuja plicata*) and to a lesser extent yellow cedar (*Tsuga heterphylla*) has been directly impacted by deer browsing (Martin and Baltzinger, 2002), and where browsing stress has also been reported for sitka spruce (*Picea sitchensis*) (Vila et al., 2003a). Widespread declines in other palatable shrubs (e.g. *Vaccinium* spp.) and herbs (e.g. lady fern *Athyrium filix-femina*, spiny wood fern, *Dryopertis assimilis*, bunchberry *Cornus canadensis*) in this region have also been attributed to high deer density (Pojar, 2008).

4.1. Bird species response to deer browsing

Declines of North American forest birds have largely been attributed to the effects of habitat loss and fragmentation (Robinson et al., 1995; Villard et al., 1999). However, our current findings, those from Haida Gwaii (Allombert et al., 2005a,b; Martin et al., 2008) and others (deCalesta, 1994; Gill and Fuller, 2007; Martin and McIntyre, 2007; Martin and Possingham, 2005; McShea and Rappole, 2000) show unequivocally that native and exotic herbivores can moderate understory vegetation and in turn affect bird species community composition and relative abundance in habitats that we might otherwise assume are 'intact' and functioning to support bird populations. As predicted, the deleterious impacts of deer density weigh most heavily on understory and mid-story dependant bird species irrespective of migratory status (Table 3). Where browsing pressure is sufficient to eliminate or reduce understory vegetation to a low ground cover (e.g. our high deer density islands; Fig. 3c), substantially simplified bird communities develop as a consequence of the loss of the understory and mid-story species (Allombert et al., 2005a; deCalesta, 1994; Hino, 2006; Martin et al., 2005; Martin and McIntyre, 2007; McShea and Rappole, 2000).

Although bird species richness did not vary significantly between islands, twice as many individual birds were recorded on islands with low as compared to moderate or high deer density. We suggest that high bird species abundance is a predicted consequence of the effects of high understory cover on foraging and nesting opportunities and vegetation structural diversity (MacArthur and MacArthur, 1961). However, other indirect effects of deer, such as their impacts on invertebrate abundance, floral resources, and nest predation probably also contribute to this difference (Allombert et al., 2005b; Martin et al., 2008). Our results also show that islands with moderate and high deer densities were most similar with respect to their bird fauna. Rooney et al. (2004) reported that deer browsing contributed to the biotic homogenisation of understory vegetation in the mid-West United States. Our results suggest biotic homogenisation is also occurring in the bird fauna, as a result of changes in the understory vegetation brought about by deer browsing.

Bird species composition also differed between browsed and unbrowsed islands, with species such as the rufous hummingbird, song sparrow, fox sparrow, spotted towhee, orange-crowned warbler, winter and Bewick's wren most abundant on unbrowsed islands; whereas only one species, the dark-eyed junco was most abundant on browsed islands. Allombert et al. (2005a) found strikingly similar results for the same group of species co-occurring in Haida Gwaii. In both Allombert et al. (2005a) and our study, bird species diversity was highest on islands without deer (Fig. 7), whereas in eastern North America, where white-tailed deer (*Odocoileus virginianus*) dominate, McShea and Rappole (2000) found higher relative abundance of birds but similar bird diversity in unbrowsed than browsed sites, perhaps because species dependent on understory vegetation were replaced by those associated with other successional stages (McShea and Rappole, 2000). Two other studies reported that bird diversity peaked at moderate deer densities (Côté et al., 2004; deCalesta, 1994), suggesting that ecosystem-level responses to elevated deer densities may vary as a consequence of winter snow cover, which can prevent winter browsing of understory vegetation during much of the year.

Martin et al. (2008) suggested that one mechanism by which deer reduce abundance in understory birds on Haida Gwaii is by increased nest exposure and predation rate on islands with squirrels or raccoons present. Because racoons *Procyon lotor* were also present (but squirrels absent) on many islands we sampled, it is possible that variation in the demographic performance of birds in the presence or absence of deer contributed to our observation that understory bird abundance declined as deer density increased. If true, islands with high deer densities may represent 'population sinks' that reduce regional population growth in proportion to their prevalence at the landscape level (Jewell and Arcese, 2008). Alternatively, it is also possible that differences in bird species

Table 3

A-priori bird species dependence on understory vegetation scores and mean abundance and 95% credible interval estimates from Bayesian GLMM using field data collected across islands with three levels of deer density. Migratory status is defined as resident R, Migratory M (Lewis and Sharpe, 1987). Forage score: 3, complete dependence on understory for foraging; 2, majority of foraging in understory vegetation; 1, partial use of understory vegetation and/or foraging on the ground; 0, almost no foraging in understory. Nest score: 3, exclusive use of understory vegetation for nesting; 2, majority of nests in understory; 1, partial use of understory vegetation for nesting and/or nest on the ground; 0, no use of understory for nesting. Total score is the sum of forage and nest scores. A dash '–' denotes point count was zero.

Abbrev	Common name (scientific name)	Migratory status (R, M)	A-priori understory dependence scores			Dependence on understory vegetation	Mean abundance and 95% CI across three deer browsing levels		
			Nest	Forage	Total		Low	Moderate	High
FOSP	Fox sparrow *Passerella iliaca*	R	3	2	5	Strong	0.66 (0.2,1.86)	0.07 (0.01,0.3)	0.07 (0.01,0.6)
SPTO	Spotted towhee *Papilo maculatus*	R	3	2	5		2.13 (1.03,4.48)	0.45 (0.13,1.2)	0.09 (0.01,0.61)
WIWA	Wilson's warbler *Wilsonia pusilla*	M	3	2	5		0.66 (0.05, 2.26)	0.02 (0,0.22)	0.38 (0.03,3.0)
BEWR	Bewick's wren *Thryomanes bewickii*	R	2	2	4		0.41 (0.1,1.35)	–	–
HOWR	House wren *Troglodytes aedon*	M	2	2	4		0.87 (0.5,1.65)	0.67 (0.33,1.35)	0.38 (0.13,1.02)
OCWA	Orange-crowned warbler *Vermivora celata*	M	3	1	4		4.39 (3.0,6.05)	1.7 (1.07,2.77)	1.24 (0.58,2.44)
RUHU	Rufous hummingbird *Selasphorus rufous*	M	2	2	4		2.23 (1.54,3.0)	0.95 (0.63,1.42)	0.26 (0.11,0.56)
SOSP	Song sparrow *Melospiza melodia*	R	2	2	4		4.35 (2.92,6.23)	1.32 (0.78, 2.23)	1.04 (0.44,2.43)
YEWA	Yellow warbler *Dendroica petechia*	M	2	2	4		2.05 (1.11,3.32)	1.14 (0.61,2.0)	0.38 (0.14,1.0)
WIWR	Winter wren *Troglodytes troglodytes*	R	2	2	4		0.94 (0.24,2.46)	0.27 (0.03,1.05)	0.57 (0.06,5.87)
HETH	Hermit thrush *Catharus guttatus*	M	2	1	3	Moderate	0.06 (0.01,0.22)	0.02 (0.02,0.12)	0.01 (0,0.14)
CBCH	Chestnut-backed chickadee *Poecile rufesens*	R	1	1	2		1.25 (0.44,3.0)	1.34 (0.49,3.9)	1.27 (0.27,6.23)
GCKI	Golden-crowned kinglet *Regulus satrapa*	R	0	2	2		0.28 (0.07,0.93)	0.11 (0.01,0.57)	0.07 (0.01,0.68)
GCSP	Golden-crowned Sparrow *Zonotrichia atricapilla*	M	1	1	2		0.24 (0.01,1.49)	–	–
GOFI	American goldfinch *Carduelis tristis*	R/M	1	1	2		1.27 (0.84,2.01)	1.02 (0.55,1.75)	1.27 (0.64,3.67)
PSFL	Pacific slope flycatcher *Epidonax difficilis*	M	0	2	2		0.95 (0.41,2.1)	0.47 (0.15,1.26)	1.31 (0.2,6.05)
RCKI	Ruby-crowned kinglet *Regulus calendula*	M	0	2	2		0.24 (0.06,0.74)	0.1 (0.01,0.37)	–
VATH	Varied thrush *Ixoreus naevius*	R	1	1	2		0.29 (0.07,0.76)	0.01 (0,0.08)	0.01 (0,0.15)
WCSP	White-crowned sparrow *Zonotrichia leucophrys*	R	1	1	2		1.52 (0.74,3.0)	0.75 (0.33,1.65)	0.63 (0.2,2.01)
DEJU	Dark-eyed junco *Junco hyemalis*	R	0	1	1	Low	0.05 (0.01,0.2)	0.67 (0.18,2.0)	1.38 (0.18,8.76)
HAWO	Hairy woodpecker *Picoides villosus*	R	0	1	1		0.05 (0.01,0.32)	0.01 (0, 0.12)	0.03 (0,0.42)
PIWO	Pileated woodpecker *Dryocopus pileatus*	R	0	1	1		0.02 (0, 0.1)	0.13 (0.05,0.3)	0.01 (0,0.11)
PUFI	Purple finch *Carpodacus purpureus*	R	1	0	1		0.16 (0.05,0.67)	0.19 (0.04,0.74)	–
TOWA	Townsend's warbler *Dendroica townsendi*	M/R	0	1	1		1.34 (0.44,3.86)	0.13 (0.02,0.66)	0.41 (0.05,4.35)
AMRO	American robin *Turdus migratorius*	R	0	0	0		1.82 (1.11,2.77)	1.87 (1.15,3.1)	2.3 (1.04,5.31)
BHCO	Brown-headed cowbird *Molothrus ater*	M/R	0	0	0		0.45 (0.15,1.13)	0.47 (0.14,1.51)	0.39 (0.06,2.18)
BRCR	Brown creeper *Certhia americana*	R	0	0	0		0.09 (0.03,0.23)	0.34 (0.15,0.7)	0.21 (0.1,0.63)
CORA	Common raven *Corvus corax*	R	0	0	0		0.44 (0.22,0.82)	0.1 (0.03,0.27)	0.19 (0.06,0.61)
EUST	European starling *Sturnus vulagaris*	R	0	0	0		0.23 (0.02,1.35)	0.09 (0,0.9)	0.3 (0,9.97)
NWCR	Northwestern crow *Corvus caurinus*	R	0	0	0		1.78 (0.9,3.67)	0.38 (0.14,1.01)	0.1 (0.01,0.52)
NOFL	Northern flicker *Colaptes auratus*	R	0	0	0		0.27 (0.15,0.49)	0.16 (1.49,0.37)	0.21 (0.07,0.55)
OSFL	Olive-sided flycatcher *Contopus cooperi*	M	0	0	0		0.05 (0.01,0.15)	–	0.11 (0.03,0.5)
PISI	Pine siskin *Carduelis pinus*	R	0	0	0		0.1 (0.02,0.45)	0.14 (0.03,0.61)	0.34 (0.08,1.65)
RBNU	Red-breasted nuthatch *Sitta canadensis*	R	0	0	0		0.73 (0.3,1.65)	0.67 (0.27,2.01)	0.74 (0.12,3.0)
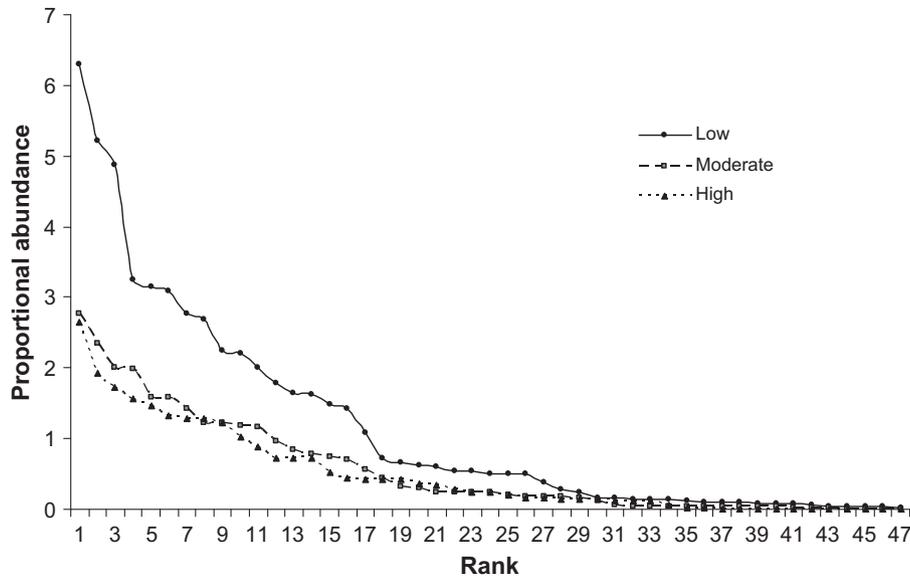
Fig. 7. Bird species rank abundance curves for low, moderate and high deer density islands.

Table 4
Analysis of similarities (ANOSIM), global $R = 0.329$.

Groups of islands	R statistic	Significance
Low, moderate	0.283	$P < 0.001$
Low, high	0.553	$P < 0.001$
High, moderate	0.156	$P < 0.001$
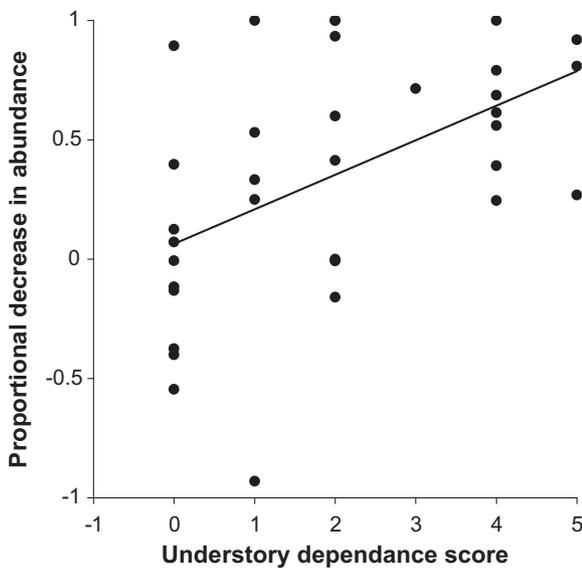
Fig. 8. Proportional decline in bird abundance between low and high deer density islands plotted against species understory vegetation dependence scores (Table 3), $r = 0.51$, $p < 0.001$.

abundance were a consequence of habitat selection for high foliage volume, nest site quality and concealment, or other factors. This scenario suggests deer reduce bird abundance mainly by reducing the amount of suitable habitat. Discriminating among these mechanisms will be necessary to reliably predict the long-term effects of deer density on the regional growth rate of understory bird populations (Jewell and Arcese, 2008).

4.2. Vegetation structure as a proxy for deer density

It is well-known that estimating deer density can be time consuming, costly and challenging to do precisely (Campbell et al., 2004). Simple measures of vegetation cover and shrub architecture can act as suitable indices of deer density when resources are scarce (McShea and Rappole, 2000). Such indices will become particularly useful when shown to co-vary with the abundance of other species of interest to managers or the public. For example, because browsing is the mechanism by which birds and other organisms are impacted by deer, vegetation keys derived from photos (Figs. 3 and 5) can depict growth forms diagnostic of particular deer densities. When linked to species abundances (Allombert, 2005a,b; this study), these keys should help managers determine which browsing state they are experiencing, and what changes to plant and bird communities are likely to occur if deer densities remain constant, increase or decline. Other useful indices of deer density include the estimates of the number of browsed stems (Balgooyen and Waller, 1995) and vegetation cover (McShea and Rappole, 2000). While tree regeneration was strongly reduced by deer browsing in Haida Gwaii (Martin and Baltzinger, 2002) and Wisconsin, United States (Alverson et al., 1988), McShea and Rappole (2000) did not find tight correlations between sapling number and deer density. We were unable to identify the relative effects of deer browsing on individual species of sapling due to small sample sizes.

4.3. Conservation deer management

In less than a century interest in deer management has moved from an emphasis on the recovery of exploited populations to controlling their abundance and expansion (Côté et al., 2004). The dramatic recovery of palatable native lilies protected from browsing suggests that black-tailed deer in the island archipelago also exist at much higher densities now than historically (Gonzales and Arcese, 2008), probably as a consequence of reduced predator pressure and human hunting, and increases in the extent of agricultural and edge habitats (MacDougall, 2008). Overall, therefore, our results and those of others on native plants (Gonzales and Arcese, 2008) indicate that high browsing pressure simplifies native plant and bird communities, reduces bird species abundance, and facili-

tates the introduction of exotic competitors, especially where human land uses isolate remnant patches of native vegetation.

Given the patterns above, at what densities should deer be maintained? Of the 18 islands we studied, those without deer supported the most abundant and diverse bird assemblages, whereas those with high deer densities were depauperate of iconic resident song and fox sparrows and migrant rufous hummingbirds. Islands with moderate deer densities (0.13–0.38 deer/ha) were similar in diversity and evenness to high deer density (1.05–1.14 deer/ha) islands, suggesting that even densities exceeding c 0.1 deer/ha were too high to maintain diverse bird communities. McCabe and McCabe (1997) estimated that densities of white-tailed deer prior to European colonization were between 0.031 and 0.042 deer/ha. In Haida Gwaii, Martin and Baltzinger (2002) suggested that densities above 0.04 deer/ha reduced tree recruitment. Given these assessments and our own findings, we suggest that a density of <0.1 deer/ha be adopted as one target within a wider, active adaptive management program to test the influence of different deer densities on plant and bird species persistence and ecosystem recovery. It is worth noting, however, that deer management alone may not ensure the recovery of an understory that promotes bird diversity. This is because severe browsing by deer can lead to recalcitrant understoreys (Royo and Carson, 2006), dominance by unpalatable shrubs and herbs (de la Cretaz and Kelty, 1999) and accelerated invasion by non-native species (Baiser et al., 2008; Best and Arcese, 2009; Gonzales and Arcese, 2008). In these cases, active restoration and deer management may both be required to promote diverse songbird assemblages.

Given the mythical status of deer and antipathy towards hunting by many humans (MacTaggart-Cowan, 1945), a general sense of stewardship for plant and bird communities will need to be developed alongside a public awareness of the deleterious impacts of deer if adaptive management of deer populations is to be successful. Acceptable methods of executing control in human populated areas must also be sought. At present, however, deer in the San Juan and Gulf Island archipelago are browsing down our natural heritage. In the absence of active management, high browsing pressure by deer can be expected to result in local extinctions of herbaceous flora as well as iconic island birds.

Acknowledgements

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