

# A natural experiment on the impact of overabundant deer on songbird populations

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## Abstract

Declines in songbird populations have been identified both in North America and in Europe. Several explanations have been proposed but few studies have evaluated the possibility that deer overabundance might affect songbird populations, and none have identified general rules to predict such an impact. We used a group of islands in the Haida Gwaii archipelago (British Columbia, Canada), where islands without deer co-exist near islands with deer, as a natural experiment to test if the dependence of each species on understorey vegetation was a good predictor of deer impact. Forest bird assemblages were compared on six islands that either had no deer, had deer for less than 20 years or for more than 50 years, and on an enlarged set of 31 islands for which vegetation data and an index of deer impact were available. In the six islands data-set, songbird abundance on islands browsed for more than 50 years was 55–70% lower than on deer-free islands. There was a significant decrease in alpha diversity on islands browsed by deer, but gamma diversity remained unchanged. Bird species with the highest dependence on understorey vegetation were most affected and their abundance decreased by 93%. Bird communities flipped from being 73% dependant on understorey vegetation on deer-free islands to 79% not dependant on understorey vegetation on islands with deer for more than 50 years. A canonical correspondence analysis on the 31 island data-set allowed us to further separate the interactions between bird abundance and distribution, vegetation features and deer presence. We propose that deer overabundance results in a decrease in songbird habitat quality through decreased food resources and nest site quality and may explain part of current continental-scale decreases in songbird populations. © 2005 Elsevier Ltd. All rights reserved.

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## 1. Introduction

There has been concern about the decline of common temperate bird species (BirdLife International, 2004) in North America (Robbins et al., 1989; Terborgh, 1989) and in Western Europe (Fuller et al., 1995; Siriwardena et al., 1998; Julliard et al., 2004). In Europe, most information available is about the decline of farmland birds, with agriculture intensification (Krebs et al., 1999) and

climate change (Julliard et al., 2004) being the main causes proposed. Declines in forest birds have been much less studied (Fuller, 2001). In North America, the decline of some forest songbirds has been mostly attributed to the direct (Robinson et al., 1995) or indirect effects of forest fragmentation such as increased nest predation (Wilcove, 1985; Böhning-Gaese et al., 1993; Schmidt, 2003) or increased cowbird parasitism (Brittingham and Temple, 1983), as well as to the deforestation and degradation of wintering grounds in the neotropics (Terborgh, 1989). In a study of the impact of high deer densities on songbirds, deCalesta (1994) suggested that increasing white-tailed deer (*Odocoileus*

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*virginianus*) populations could also explain bird population declines in some forest songbirds in the north-eastern US. Berger et al. (2001) also did suggest a connection between declines in neotropical migrants and high herbivore densities.

Increases in ungulate populations occur widely in North America (McCabe and McCabe, 1997; Crête and Daigle, 1999), where wild deer populations are reaching historic peaks (Waller and Alverson, 1997), and in Europe (Kuiters et al., 1996). The explanations usually proposed include the extirpation of large predators (Breitenmoser, 1998; Crête, 1999) and changes in silvicultural, agricultural and game management practices (Kuiters et al., 1996; Waller and Alverson, 1997). Elsewhere, and particularly in several countries from the southern hemisphere, high deer abundance resulted from the introduction of non-native deer species (Veblen et al., 1989; Bouchet et al., 1995; Nugent et al., 2001; Golumbia et al., in press).

High deer abundance has been shown to have strong effects on vegetation structure and composition in forest ecosystems (Whitney, 1984; Alverson et al., 1988; Stockton et al., submitted) and to cause decreases in abundance and diversity of many invertebrate taxa (Suominen et al., 1999; Wardle et al., 2001; Allombert et al., in press). Such changes suggest cascading effects on songbirds, as songbird abundance and/or diversity are dependent on the vegetation structural diversity (MacArthur and MacArthur, 1961; James and Wamer, 1982), and because most bird species use invertebrates for feeding (Ehrlich et al., 1988).

Several authors have discussed circumstantial evidence of an impact of deer on forest birds in North America (Boone and Dowell, 1986; Baird, 1990; McShea et al., 1995), as well as in Europe (Fuller, 2001; Perrins and Overall, 2001). However, only four studies have investigated the impact of deer population abundance on songbird assemblages (Casey and Hein, 1983; DeGraaf et al., 1991; deCalesta, 1994; McShea and Rappole, 2000). All studies suggested that deer had an impact on bird community composition, but no general rules enabling a prediction of deer impact was identified. Only two studies demonstrated an impact on overall population abundance (deCalesta, 1994; McShea and Rappole, 2000) and only one on species richness (deCalesta, 1994). Species characteristic of the shrub layer were those most often affected (deCalesta, 1994; McShea and Rappole, 2000). Ground dwelling species were affected in one study (McShea and Rappole, 2000) but not in two others (DeGraaf et al., 1991; deCalesta, 1994). All these studies took place in the north-eastern US in ecosystems heavily affected by human activities such as forestry, hunting, or supplemental ungulate feeding. They all focused on white-tailed deer. All but one used enclosures/exlosures protocols that do not always capture the full long-term effects of deer presence on forest ecosystem (Frellich and Lorimer, 1985).

Our objective in this study was to overcome some of the limitations of previous studies in order to get a clearer picture of the interactions between deer and forest birds and to evaluate the potential for deer overabundance to affect forest songbirds. The Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia, Canada), where Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced in the late 19th century (Golumbia et al., in press), provides a natural experiment to address this issue. It offers a collection of small islands covered with unmanaged temperate rainforest some of which were never colonized by deer, some of which were colonized less than 20 years ago and some where deer have been present for more than 50 years (Vila et al., 2004). This enabled us to compare bird assemblages at different levels of deer impact and to ask the following questions: (1) is there an effect of deer browsing history on bird population abundance, assemblage composition and structure? (2) Can the effect of browsing history on bird assemblages be predicted based on the dependence of each species on understorey vegetation? (3) What are the possible mechanisms of such an effect? (4) What conclusion can be drawn on the interaction between browsing history and songbird populations?

For each species, we developed an index of songbird dependence on understorey vegetation. We predicted that the higher the dependence of a particular species on understorey vegetation, the stronger the effect of browsing history. We tested this prediction in two ways: (1) we compared songbird abundance and species richness in a study of six islands of known deer browsing history, and (2) we revisited, in the light of current knowledge on deer effect, the data that had been collected on the bird assemblages of 31 islands on Haida Gwaii (Martin et al., 1995). We estimated an index of deer impact for each of these islands and verified, at this larger scale, the pattern disclosed in the six island study.

## 2. Study area and methods

### 2.1. Haida Gwaii and its introduced species

The archipelago of Haida Gwaii (Queen Charlotte Islands), situated off the coast of British Columbia, Canada, is 300 km long and comprises about 350 islands. The climate is temperate with a strong oceanic influence. Precipitation ranges from 1400 to 5000 mm (Golumbia et al., in press). The lowlands are mostly covered by temperate rainforests dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Where the effect of browsing by introduced deer is most severe the dense shrub layer dominated by salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*) and salmonberry

(*Rubus spectabilis*) has been replaced by an open understorey dominated by mosses (Pojar et al., 1980; Stockton, 2003).

There are 11 native land mammals on the archipelago. The caribou (*Rangifer tarandus dawsoni*) was the only native large herbivore before it became extinct. Its presence has only been documented in the north of Graham Island (McTaggart Cowan, 1989). Except for the river otter and the deer mouse (*Peromyscus maniculatus*) and the shrew none of these native mammals occur on the islands studied.

Fifteen mammal species were introduced since European colonization (Golumbia et al., in press), of which raccoons (*Procyon lotor*), red squirrels (*Tamiasciurus hudsonicus*) and black-tailed deer have colonized a large portion of the archipelago. All three have the potential to affect land bird populations. Red squirrel and raccoon affect birds directly by preying upon their nests (Martin and Joron, 2003, for squirrel on songbirds; Gaston and Masselink, 1997, for raccoon on seabirds). Raccoons were present on a few of the island studied but Martin and Joron (2003) did not report any predation on songbird nest in an extensive study monitoring the fate of natural and artificial nests.

Black-tailed deer, introduced in 1878, colonized the whole archipelago except a few small isolated islands (Golumbia et al., in press). Censuses, experimental deer culls and deer pellet counts in our study area yielded density estimates of 21–36 deer/km<sup>2</sup> (Daufresne and Martin, 1997; Martin and Baltzinger, 2002; Stockton, 2003; Gaston et al., in press). The impact of deer on the vegetation of the islands is extensive (Pojar, 1999; Martin and Baltzinger, 2002), affecting mainly the vegetation layer below 1.5 m. Intensity of effect is correlated with the duration of deer presence on a given island (Vila et al., 2004; Stockton, in press; Stockton et al., submitted).

## 2.2. Six islands of known deer browsing history

We studied six islands in the Laskeek Bay area (eastern side of the archipelago, Fig. 1). The two most isolated (Lost and Low islands) had no deer and no signs of deer presence has ever been found on them (Stockton, in press; Stockton et al., submitted; see Table 1). On two other, less isolated, islands (West and South Skedans) the analysis of age and frequency of rub scars and on age structure of shrub stems has shown that deer have been present for less than 20 years (Vila et al., 2004). On the remaining islands (Haswell and West Limestone islands), the largest and closest to one of the main islands of the archipelago (Louise Island) deer have been present for at least 50 years (Vila et al., 2004; Vila com. pers.). Together these islands represented a gradient of browsing history that we classified as three treatments: no deer, short browsing history (<20 years) and long browsing history (>50 years).

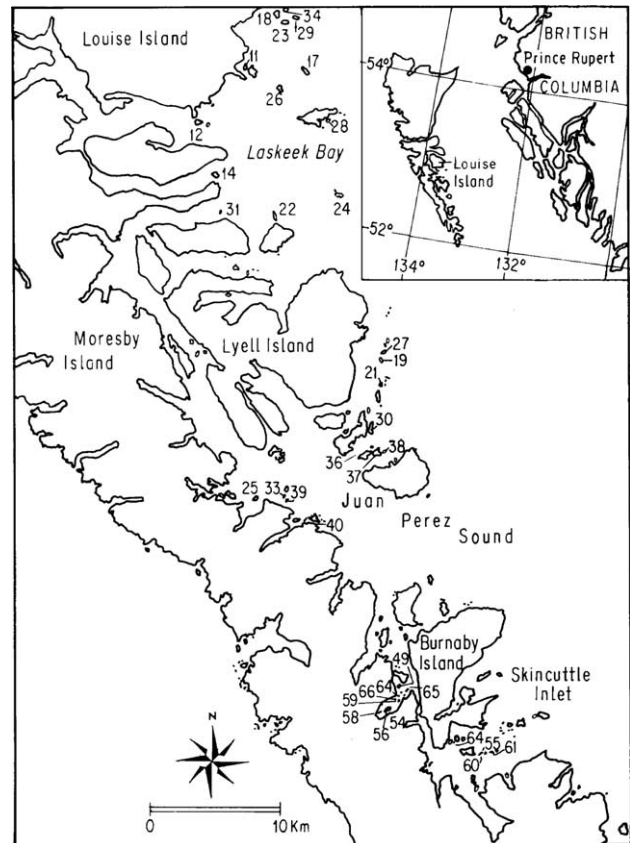


Fig. 1. Study area. Numbers next to islands refer to the island number in Table 1.

All six islands were relatively small (5.3–16 ha, Table 1), covered by primary forest dominated by Sitka spruce (Stockton, 2003) and situated within a maximum of 17 km of one another. A study by Stockton et al. (submitted) on the same six islands showed that the impact of deer browsing history on the vegetation resulted in a shift from a dense to an open understorey with a 96.8% reduction in percent of cover in the ground layer (0–50 cm) and a 99.8% reduction in the shrub layer (50–150 cm) on islands with a long browsing history when compared to deer-free islands. At the scale of the study plots, species richness decreased by 33.6% when comparing islands without deer to islands with a long browsing history. At the island scale species richness decreased by 10.9%. Values for islands with a short browsing history were always intermediate between deer-free islands and those with a long browsing history. In addition, Allombert et al. (in press) showed, on the same islands, a dramatic negative effect of deer browsing history on the abundance and diversity of invertebrates living on the vegetation. Ground-living invertebrates did not seem to be affected.

Finally, predators of forest birds and of their nests, such as corvids [common raven (*Corvus corax*) and north-western crow (*Corvus caurinus*)] and river otter (*Lutra Canadensis*) were present on all islands (Martin

Table 1

Name, area in ha and isolation (Isol.) in m (distance to the large reference island, both from Martin et al. (1995)), deer impact score (DIS), time since colonization by deer (Vila, Com. pers.), squirrel presence (1) or absence (0) and number of point-count ( $N$ ) censuses on each of the 31 islands studied in the Haida Gwaii archipelago

#	Name	Area	Isol.	DIS	Time since colonization	Squirrel	$N$
<i>Laskeek Bay</i>							
11	West Limestone	16.0	350	5	>50	1	2
12	Haswell	13.3	150	5	>50	1/0 <sup>a</sup>	3
17	Low	9.6	5400	0	0	0	2
18	West Skedans	8.2	1350	2.5	<20	0	3
23	South Skedans	5.6	2400	2.5	<20	0	2
24	Lost	5.3	1100	0	0	0	1
26	South Low	4.5	2900	0	–	0	2
29	East Skedans	2.9	2850	2.5	–	0	1
34	North Skedans	1.7	2300	2.5	–	0	1
<i>Juan Perez Sound</i>							
19	Tar S	6.0	2500	0	–	0	1
21	Kawas SW	5.6	2650	0	–	0	1
25	Sivart	5.0	550	4	–	0	2
27	Kawas N	3.8	3000	0	–	0	1
30	Hotspring Island 1	2.0	500	2.3	–	0	1
33	Hoskins L	2.0	900	0.2	–	0	1
36	Hotspring Island 3	1.5	500	2	–	0	1
37	Hotspring Island 2	1.0	550	2	–	0	1
39	Hoskins S	1.0	700	0.5	–	0	1
40	Marco S	1.0	150	4.5	–	0	1
38	House Island S	1.0	800	4.3	–	0	1
<i>Skincuttle Inlet</i>							
49	Island Bay 3	7.5	150	4.5	–	1	1
54	Island Bay 1	3.5	200	1.7	–	0	1
55	Bolkus Island 2	3.1	2150	4	–	1	1
66	Island Bay 6	3.0	300	0.5	–	0	1
56	Island Bay 7	3.0	300	2.5	–	0	1
58	Island Bay 8	2.5	200	3.8	–	1	1
59	Island Bay 5	2.2	250	1.6	–	0	1
60	Bolkus Island 1	2.1	2350	2.6	–	1	1
61	Bolkus Island 3	2.0	2100	2.8	–	0	1
65	Island Bay 2	1.2	600	2.1	–	0	1
64	Island Bay 4	1.2	150	1.5	–	0	1

A deer impact score of 0 and a colonization age of 0 refer to a deer-free island; # refers to the island number on Fig. 1. The first six islands were common to the two data-set.

<sup>a</sup> Squirrel present in 1989 but absent in 1999.

and Joron, 2003). Red squirrel occurred only on West Limestone Island.

We studied bird assemblages by two methods: point-counts and spot-mapping. Point-counts provided data suited for statistical comparisons of alpha diversity (species richness at the scale of a point-count study plot) and of abundances between samples (Hamel, 1984; Bibby, 1992). We used 50 m fixed-radius point-counts that lasted 20 min, following the methodology detailed in Martin et al. (1995). We chose the 20 min length to allow a better estimation of relative abundances and species richness (Hamel, 1984; Drapeau et al., 1999). On each island, we selected two stations among the five setup for vegetation sampling (Stockton et al., submitted) and invertebrate studies (Allombert et al., in press). They were at least 200 m apart to avoid overlap in bird counts (Bibby, 1992). To control for potential edge effect, the centre of all

study plots was situated between 50 and 95 m from the sea shore. Mean distance to sea shore did not vary between the three treatments (ANOVA,  $F_{2,9} = 1.29$ ,  $p = 0.32$ ). We repeated each point-count four times between the 25th May and the 22nd June 1999. For each repetition, all islands were censused in a sequence to avoid introducing temporal biases between different islands. The four repetitions were evenly spread over the whole period. Both repetition of point-counts and spreading through the season improve estimation of species richness and relative abundance (Dettmers et al., 1999; Drapeau et al., 1999). We counted birds in the morning and in the absence of rain or strong wind. We defined “plot” species richness as the number of species recorded on a census plot during the four repetitions of point-counts and abundance as the mean number of individuals contacted during the four repetitions.

Spot-mapping censuses were conducted over the entire area of each island, following the method used in the Common Bird Census in the United Kingdom (Marchant et al., 1990; Bibby, 1992). The method allows to estimate species population densities and provides better information on the presence and abundance of rarer species and on gamma diversity (e.g., species richness at the scale of an island; see Hamel, 1984; Bibby, 1992). We made four visits to each island. The entire island was covered during a visit and each bird seen or heard was located on a map and its behaviour recorded (singing, foraging ...). These visits were spread over the entire breeding season and were made on different days from the point counts. Because of their open understorey, the larger islands, those with deer for over 50 years, were the easiest to census, especially when compared to the smaller deer-free islands with their dense understorey. Thus, an average duration of about 4 h was necessary during each visit to properly census a larger or a smaller island. Island species richness was defined as the number of species recorded during the four mapping sessions. Breeding pair density was calculated by dividing the number of pairs identified during the mapping sessions by the area of the island (area data are from Martin et al., 1995). Point-counts and spot mapping sessions were all done by the same observer (SA).

### 2.3. Verifying deer impact patterns at a broader scale

To verify the generality of patterns determined from the six island study, we analyzed the distribution of land birds on an extended set of small islands in relation to vegetation structure and its modification by deer. We used data collected in 1989 and 1991 on 31 islands of the eastern side of Haida Gwaii (Martin et al., 1995). These islands included the six islands studied in Laskeek Bay and were in the same size range or slightly smaller (Table 1). On all of these islands, one to three 20 min, 50 m-radius point-counts were conducted by the same observer (JLM), leading to a total sample of 40 point-counts (see Table 1). Vegetation structure was measured as the percentage of cover in each of nine vertical strata in the 50 m radius plot (see Martin et al., 1995 for the detailed protocol).

In addition to the data on vegetation structure collected in 1989/1991, one of us (JLM) revisited the islands in 2000 to score current deer impact. To do so, we collected information on deer presence, on plant distribution and abundance, and on the percentage of the vegetation affected by deer browsing, this for a suite of plant species known to be indicators of deer browsing history (Stockton unpublished; Stockton, 2003; Stockton et al., submitted): three herbaceous flowering plants: goose tongue (*Plantago maritima*), Alaska saxifrage (*Saxifraga ferruginea*), fringe cup (*Tellima grandiflora*); two shrubs: red huckleberry (*Vaccinium parvifolium*) and salal (*Gaultheria shallon*) and two regenerating conif-

erous trees: Sitka spruce and western hemlock. This information was summarized for each of four different sections on each island as deer impact score running from 0 = no sign of deer presence to 5 = very heavy impact (impact comparable to the one observed on islands with over 50 years of browsing history). Segment scores were averaged for each island to give an overall island score. This information was compared with the data on vegetation structure collected on the same islands in 1989/91 to assess relative consistency between the two sets of information. Finally, we used these island scores to define three classes: 1 = islands with little or no deer impact (impact score  $\leq 1$ ), 2 = islands with an intermediate deer impact ( $1 < \text{impact score} < 4$ ), and 3 = islands with a high deer impact (impact score  $\geq 4$ ). These classes were considered equivalent to the three classes of browsing history used in the study using only six islands.

### 2.4. Data analysis

For both data-sets, we limited our analysis to songbirds, woodpeckers and hummingbirds. We excluded observations of raptors [bald eagle (*Haliaeetus leucocephalus*), peregrine falcon (*Falco peregrinus*), red-tailed hawk (*Buteo jamaicensis*) and sharp-shinned hawk (*Accipiter striatus*)], corvids (common raven and north-western crow), or of tree swallow (*Tachycineta bicolor*), pine siskin (*Carduelis pinus*) and red crossbill (*Loxia curvirostra*), as these species were poorly censused by the methods used (birds mostly seen flying over, see Bibby, 1992; Drapeau et al., 1999) and/or have life histories that make them irrelevant for the question addressed.

We used the literature especially as it applied to British Columbia and the Pacific Northwest (Godfrey, 1986; Poole and Gill, 2002), and our own observations, to score the expected dependence of each bird species on understorey vegetation for nesting and foraging, based on each species uses of this vegetation (see Table 2). A score between zero (no use of understorey vegetation) and three (exclusive use of understorey vegetation) was assigned for both nesting and foraging. The two scores were given equal weight and summed to yield an overall score of bird species dependence on understorey vegetation. Birds were split into three groups: species with a strong dependence on understorey vegetation (total score of three or above, see Table 2), species with a lower dependence (total score of 1 or 2) and species with no dependence on understorey vegetation (total score of 0).

We transformed bird abundance and species richness data by a  $\log(y + 1)$  function since there were typically greater variances for greater means and there were several null values (Sokal and Rohlf, 1995). We transformed percentages of plant cover with an arcsine function (Sokal and Rohlf, 1995) and log-transformed island area (ha) and isolation (distance to the large islands in meter).

Table 2  
Species dependence-scores on understorey vegetation

Species acronym	Species name	Dependence scores			Dependence on understorey vegetation
		Foraging	Nesting	Total	
RUHU	Rufous hummingbird <i>Selasphorus rufus</i>	3	1	4	Strong
OCWA	Orange-crowned warbler <i>Vermivora celata</i>	2	2	4	
WIWA	Wilson's warbler <i>Wilsonia pusilla</i>	2	2	4	
WIWR	Winter wren <i>Troglodytes troglodytes</i>	2	1	3	
FOSP	Fox sparrow <i>Passerella iliaca</i>	1	2	3	
SOSP	Song sparrow <i>Melospiza melodia</i>	1	2	3	
SWTH	Swainson's thrush <i>Catharus ustulatus</i>	1	2	3	Lower
DEJU	Dark-eyed junco <i>Junco hyemalis</i>	1	1	2	
HETH	Hermit thrush <i>Catharus guttatus</i>	1	1	2	
VATH	Varied thrush <i>Ixoreus naevius</i>	1	1	2	
GCKI	Golden-crowned kinglet <i>Regulus satrapa</i>	1	0	1	
PSFL	Pacific Slope flycatcher <i>Empidonax difficilis</i>	0	1	1	
BRCR	Brown creeper <i>Certhia americana</i>	0	0	0	None
CBCH	Chestnut-backed chickadee <i>Parus rufescens</i>	0	0	0	
HAWO	Hairy woodpecker <i>Picoides villosus</i>	0	0	0	
RBSA	Red-breasted sapsucker <i>Sphyrapicus ruber</i>	0	0	0	
TOWA	Townsend's warbler <i>Dendroica townsendi</i>	0	0	0	

Foraging scoring: 3, exclusive dependence on understorey vegetation; 2, most foraging dependent on understorey vegetation; 1, partial use of understorey vegetation for foraging, or/and foraging on the ground; 0, almost no foraging in the understorey. Nesting scoring: 3, exclusive dependence of understorey vegetation for placing nest; 2, Most nests placed in understorey vegetation or exclusive use of understorey vegetation for hiding nest; 1, possible use of understorey vegetation for placing nest or for hiding nest; 0, no use of understorey vegetation for nesting. Total scores is the sum of foraging and nesting scores.

For the six islands in Laskeek Bay, we analyzed four dependent variables: species richness at the plot and at the island scale, bird abundance at the plot scale, and data on breeding pair density using a general linear model procedure provided by SAS software (GLM procedure; SAS Institute Inc., 2001). Bird abundance was analyzed for all species combined as well as separately for each group of species relative to its dependence on understorey vegetation. Deer browsing history was used as a class explanatory variable (fixed effect) with three treatments, deer-free, short, and long browsing history. To analyze possible variations coming from inter-island differences, island was used as an explanatory variable nested within treatments for point-count data. In this case, statistical significance of browsing history was tested with the mean squares of the nested island effects as error terms, since island was considered to be a random effect (SAS Institute Inc., 2001). We also tested the significance of the differences between browsing treatments using contrast within the general linear model procedure, with the mean squares of the nested island effects as error terms in the case of point-count results.

We used Canonical Correspondence Analysis (CCA thereafter, CANOCO software; Ter Braak and Smilauer, 2002) to reanalyze the 31 islands data-set from Martin et al. (1995). CCA is especially recommended for the analysis of species–environment relationships (Lebreton et al., 1991; Palmer, 1993). The objective was to verify the general validity of our assumption on the interactions between song bird distribution, vegeta-

tion structure and deer browsing history and, in addition, to assess if island isolation or presence of squirrels were likely to influence these interactions. Species variables used were the number of specimen of each bird species recorded during each point-count. We included all species that were present in at least eight point-counts as active in the analysis. Species that were present in four to seven point-counts were added as supplementary species. We combined percentage of vegetation cover measured in nine strata into four environmental variables: ground which was the sum of the % of cover in the 0–0.25 and 0.25–0.5 m strata, shrub, the sum of the % cover in the 0.5–1 and 1–2 m strata, subcanopy, the sum of the 2–4, 4–8 and 8–16 m strata and canopy, the sum of the 16–32 m and above 32 m strata. In addition to these active vegetation variables, we included four supplementary variables in the analysis. These were: deer impact score, island area (area), island distance from the nearest large island (isolation) and presence of squirrels (squirrel). Following Palmer (1993), we used the linear combination of variables scores for plot scores.

### 3. Results

#### 3.1. Six islands of known deer browsing history

We recorded 14 species during the point-counts (Table 3). Both bird abundance and species richness at the plot scale decreased significantly when the length of

Table 3  
Abundance data for all species in the 6-islands data-set

Dependence groups	Species	Point-counts data			Mapping data		
		Deer-free	20 years	50 years	Deer-free	20 years	50 years
Strong	RUHU	1.06	1.13	–	1.53	1.56	–
	OCWA	2.19	1.56	0.13	2.44	1.99	0.07
	WIWA	0.19	–	–		(Non-breeding)	
	WIWR	1.38	0.69	0.38	1.58	1.03	0.62
	FOSP	1.31	1.06	–	1.89	2.41	–
	SOSP	0.69	0.25	–	2.06	1.29	0.13
	SWTH	0.19	0.31	–		(Late migratory)	
Lower	DEJU	–	–	–	–	0.11	0.13
	HETH	–	–	–	–	0.17	0.19
	VATH	–	–	–	–	0.06	0.08
	GCKI	0.94	0.88	0.69	0.83	0.64	0.19
	PSFL	0.69	0.38	0.50	1.14	0.41	0.53
None	BRCR	0.69	0.13	0.19	0.69	0.18	0.23
	CBCH	–	–	0.44	–	–	0.13
	HAWO	–	–	0.06	–	–	0.08
	RBSA	–	–	0.13	–	0.06	0.08
	TOWA	0.31	0.75	1.88	0.78	0.99	1.40

Point-counts data is expressed in mean number of individuals contacted per point-count. Mapping data is expressed in mean number of pairs per ha. Wilson's warbler is not included in mapping data as this species was not breeding. Swainson's thrush is not included in mapping data because of its late arrival in spring. See table 2 for species acronyms.

browsing history increased (Table 4). Total species richness decreased by 38% between deer-free islands and islands with a long browsing history and abundance by 51%. This resulted mainly from the 93% decrease in the abundance of species with a strong dependence on understorey vegetation. There was no significant impact of deer browsing history for species with a lower dependence or for species with no dependence. There was no island effect in any of the analysis.

We recorded 15 breeding species during spot-mapping (Table 3). As with the point-count results, there was a 70% decrease in breeding pair density on islands with a long browsing history when compared to islands without deer (Table 5). As before, the bird species that decreased significantly were those with a strong dependence on understorey vegetation (92% decrease). However, the average total number of species recorded per

island did not differ significantly between the three categories of islands.

Two common species with a high dependence on understorey vegetation, the fox sparrow (*Passerella iliaca*) and the rufous hummingbird (*Selasphorus rufus*), common on deer-free islands, were totally missing on islands with a long browsing history (see Table 3). Two other species with a high dependence on understorey vegetation common on islands without deer, the song sparrow (*Melospiza melodia*) and the orange-crowned warbler (*Vermivora celata*), were present in only one of the islands with a long browsing history and then only at a low density. The winter wren (*Troglodytes troglodytes*, high dependence species) and the golden-crowned kinglet (*Regulus satrapa*, lower dependence species) were also less abundant on islands with a long-browsing history than on deer-free islands. Finally, some species with

Table 4

Mean species abundance and plot species richness of birds obtained by point-counts for the three categories of islands and *F* statistic and *p* value for “Deer effect” and “Island effect” variables in the general linear model analysis

Variables	Deer-free	<20 year of browsing	>50 year of browsing	Deer effect		Island effect	
				<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species richness	9.50	7.75	6.00	15.50	0.026*	1.24	0.375 ns
Abundances							
All species	9.63	7.13	4.38	23.71	0.014*	0.65	0.611 ns
Strong dependence	7.00	5.00	0.50	59.41	0.003**	1.02	0.448 ns
Lower dependence	1.63	1.25	1.19	0.87	0.505 ns	1.17	0.397 ns
No dependence	1.00	0.88	2.69	3.84	0.148 ns	1.49	0.310 ns

Abundances are in number of individuals contacted per point-count (ns, not significant).

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

Table 5

Mean pair density and island bird species richness obtained by mapping censuses for the three categories of islands and *F* statistic and *P* value for “Deer effect” variable in the general linear model analysis. Density of pairs is expressed in number of pair per ha

Variables	Deer-free	<20 year of browsing	>50 year of browsing	Deer effect	
				F	P
Species richness	9.00	11.00	11.00	2.29	0.248 ns
Abundances					
All species	12.95	10.90	3.82	43.48	0.006**
Strong dependence	9.51	8.28	0.81	91.31	0.002**
Lower dependence	1.98	1.39	1.11	2.42	0.236 ns
No dependence	1.47	1.24	1.91	1.12	0.432 ns

Species richness is the number of breeding species recorded on average on an island (ns, not significant).

\*\*  $p < 0.01$ .

lower or no dependence on understorey vegetation were missing from remote deer-free islands [hairy woodpecker (*Picoides villosus*), red-bellied sapsucker (*Sphyrapicus ruber*), hermit thrush (*Catharus guttatus*), dark-eyed junco (*Junco hyemalis*), varied thrush (*Ixoreus naevius*), and chestnut-backed chickadee (*Parus rufescens*)] but present in low numbers on islands with a long browsing history.

For both census methods, when significant effects of browsing history occurred, values for islands with a short-browsing history were always intermediate between those from islands without deer and those from islands with a long browsing history. Contrasts showed that differences between islands without deer and islands with a long browsing history were significant, contrary to differences between deer-free islands and islands with a short-browsing history.

### 3.2. Deer, vegetation and bird assemblages at a broader scale

Ten bird species were observed in at least eight point-counts and were included in the CCA. Three additional species were observed in four or five point-counts and were added as supplementary species. The two first components of the CCA summarized, respectively, 73.1% and 14.1% of the variance of the species–environment relation. The third axis summarized 9.2%. We restricted the analysis to the two first axes.

Scores of vegetation structure variables (Fig. 2) show that the axis 1–axis 2 plane of the CCA opposes plots that have a dense understorey (positive scores on axis 1 and negative scores on axis 2) to plots with a very sparse understorey (negative scores on axis 1 positive scores on axis 2). Plots with a dense canopy have negative scores on both axes; plots with a dense subcanopy have positive scores on both axes. The supplementary variable deer impact score was well described by the two first axes. Plots with a low deer impact score (class 1 plots) were those with a dense understorey whereas plots most affected by deer (class 3 plots) had the more

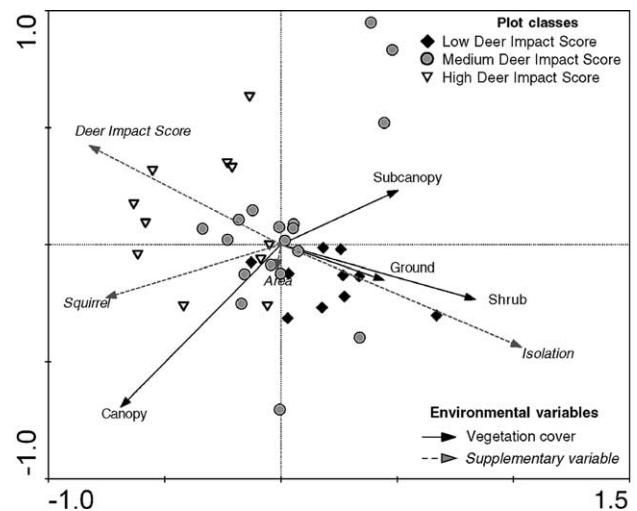


Fig. 2. Plot scores (linear combination of variables scores) in the axis 1 and axis 2 of the Canonical Correspondence Analysis on bird species distribution with respect to vegetation variables. The projection of the vegetation variables and the supplementary variables are superimposed on the figure. Class 1 islands have the lower Deer Impact Score (DIS < 1, little or no signs of browsing), class 2 intermediate DIS ( $1 \leq \text{DIS} \leq 4$ ), and class 3 the highest DIS (>4).

open understorey. Class 2 plots (medium impact) were in between and showed higher within class variability in vegetation structure (wider spread in axis 1–axis 2 plane). Isolation was inversely correlated with deer impact score. Island area was poorly described by the 2 first axes and was orthogonal to deer impact score. Plots with squirrel were associated with a dense canopy.

All bird species classified depending strongly on the understorey vegetation were positively correlated with a dense understorey and negatively correlated with deer impact score (positive scores on axis 1, Fig. 3). There was only one other species with a positive score on axis 1, the golden-crowned kinglet, a species classified as having a lower dependence on understorey vegetation. Three species, the Townsend’s warbler, and supplementary species varied thrush and red-breasted sapsucker showed slightly negative or no correlation with

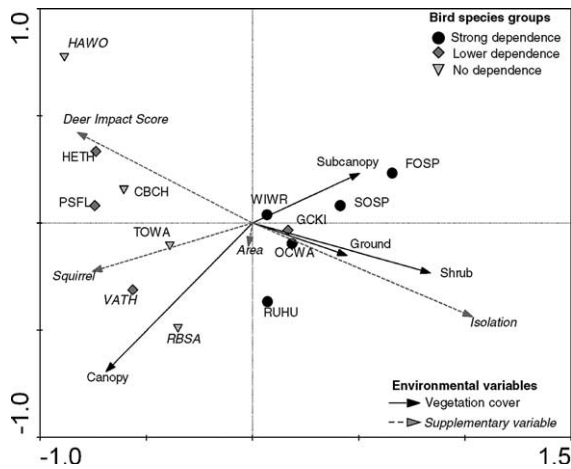


Fig. 3. Average scores of bird species in the axis 1 and axis 2 plane of the Canonical Correspondence Analysis. Bird species are represented according to their dependence on understory vegetation. The projections of the vegetation variables and of the supplementary variables are superimposed on the figure. DIS = deer impact score. See Table 2 for species acronyms. Species acronyms in *italic* refer to supplementary species.

understorey vegetation density and were positively correlated with a dense canopy. Finally hermit thrush, chestnut-backed chickadee and pacific-slope flycatcher, as well as hairy woodpecker (supplementary species) were associated with plots with an open understorey and a high deer impact score.

## 4. Discussion

### 4.1. Effect of deer browsing history on songbird abundance and species richness

A browsing history of more than 50 years was associated with major changes in the songbird assemblage. Overall there was a 70% reduction in breeding pair density when compared to deer-free islands. This reduction affected all bird species with a strong dependence on understorey vegetation, including those nesting and/or foraging in the understorey (orange-crowned warbler, rufous hummingbird, winter wren) and species foraging on the ground but hiding their nest in the vegetation (fox and song sparrows). The occurrence and density of species with lower dependence on understorey vegetation was not affected by browsing history. These species were typically species depending on the subcanopy and canopy for foraging or nesting (e.g., chestnut-backed chickadee, pacific slope flycatcher, Townsend's warbler) or species foraging on the ground in the open understorey and able to nest higher in the understorey or subcanopy (hermit and varied thrushes). The 92% reduction in breeding pair density we observed for species strongly dependent on the understorey vegetation when going

from islands without deer to islands with a long browsing history can be compared to the 83% reduction in understorey plant cover (Stockton et al., submitted) on the same set of islands and to the 87.5% reduction in the abundance of understorey-vegetation invertebrates (Allombert et al., in press). The strong reduction in the abundance of some songbird species probably explains why some species were not recorded on the islands with the longest browsing history. The Swainson's thrush, a common migratory species was absent from two data-sets because of its late arrival in spring, but data from a mist-netting program in the same area confirmed its abundance on deer-free islands and its scarcity or absence on islands with a long browsing history (Gaston et al., 2002, and unpublished data). Within all species highly dependent on understorey vegetation, only the winter wren was observed on all islands, even those with the longest browsing history, and this might be explained by its lower dependency on understorey vegetation for placing nests. As a result, the composition of the bird assemblage shifts from an assemblage dominated by species dependent on the understorey on islands without deer (73% of the individuals in the mapping data) to an assemblage dominated by species less dependent on the understorey on islands with a long browsing history (79% of the individuals).

The effect of deer browsing history on species richness was more complex. Alpha diversity decreased when browsing history increased. The 31% decrease in plot species richness for birds on islands with a long browsing history when compared to deer-free islands was similar to the one identified for plants (33%; Stockton, 2003), and has to be put in parallel with the 83% decrease in plot species richness found for invertebrates (Allombert et al., in press). Total species richness (gamma diversity) was comparable on all islands. This resulted primarily from the presence, on islands with deer, of species absent from the samples collected on deer-free islands. The biology of most of these species (red-breasted sapsucker, dark-eyed junco, pacific-slope flycatcher, chestnut-backed chickadee, hairy woodpecker and varied thrush) is little affected by understorey density. However, they are also species usually missing from the smallest and most remote islands (Martin et al., 1995). Hence, as our deer-free islands were the smallest and the most isolated, confounding factors make it impossible to draw conclusions on their interaction with deer presence.

As islands with a long browsing history were the larger and the less isolated ones, they should have the highest colonization rates and the lowest extinction rates according to the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). Thus, the absence of understorey species specifically from these islands would be difficult to explain in terms of equilibrium

island biogeography. Neither can the decrease of understorey bird abundance on islands with a long browsing history be explained by the higher frequency of predators such as squirrels. First, there was no difference in the bird communities between Haswell (island with a long browsing history and without squirrel) and West Limestone (island with a long browsing history and with squirrel) in the six islands study and, second, we observed no decrease in species with a low dependence on understorey vegetation, species which are also exposed to predation by squirrel. This leaves deer browsing history as the most parsimonious explanation for differences in understorey bird assemblages between island categories. This conclusion is further supported by the fact that songbird assemblages on islands with a short browsing history (six islands data-set) or with an intermediate deer impact score (31 islands data-set) always show characteristics intermediate between deer-free islands and islands with a long browsing history.

Differences in bird assemblages were larger between islands with a short and a long-browsing history than between islands with a short-browsing history and islands without deer. This may be explained by the persistence on islands with a short browsing history of patches of salal (Stockton, 2003), a shrub more resistant to deer browsing. These patches provide understorey-nesting songbirds with remnants of dense vegetation where to nest and forage. The patchiness of deer impact on the vegetation on islands most recently colonized by deer probably also explains the highest spread of census scores among censuses from islands with intermediate deer impact scores (Fig. 2).

#### 4.2. Mechanisms of deer impact

In both analyses, there was a strong difference between bird species most dependent on understorey vegetation and the other species. Moreover, the CCA analysis on 31 islands showed a good correlation between bird assemblage structure, vegetation structure and deer impact score, suggesting that deer impact on birds is directly mediated by its impact on the vegetation.

Among species which decreased in abundance on islands with a long browsing history, there were species that depended on the understorey vegetation primarily for foraging (e.g., rufous hummingbird) and those dependent on it for nesting (e.g., song sparrow), suggesting that deer may affect both nesting and foraging. For example, the rufous hummingbird, which feeds on nectar, gets most of its food from flowers of shrubs such as salmonberry, black twinberry (*Lonicera involucrata*), or from wildflowers such as red columbine (*Aquilegia formosa*) or fireweed (*Epilobium angustifolium*) (pers. obs.; Calder, 1993). All these species disappear or become rare on islands with a long

browsing history (Stockton, 2003). Species such as the orange-crowned warbler or the Swainson's thrush that forages for insects in the understorey (Sogge et al., 1994; Evans Mack and Yong, 2000) and a species such as the fox sparrow which digs for food in the thick litter of salal leaves (pers. obs.) are probably also directly affected by deer-caused changes in understorey vegetation. This hypothesis is reinforced by the reduction of abundance of invertebrates in the understorey vegetation on the islands with a long browsing history when compared to deer-free islands (Allombert et al., in press). The published observations of golden-crowned kinglet using the shrub layer foliage to glean insects (Ingold and Galati, 1997), may explain its lower abundance on deer-browsed islands (Table 2) and moderate association with islands with a low impact score in the CCA (Fig. 3), although this species, often associated to the canopy, can be locally common on islands with a long browsing history. A long browsing history is also likely to reduce the food resources for species such as Swainson's thrush and fox sparrow which, at the end of their breeding cycle, feed on the fruits and berries (Gervais et al., 1999; pers. obs.) produced by several shrub species (salmonberry, red huckleberry, thimbleberry (*Rubus parviflorus*)) heavily reduced by deer browsing.

By affecting vegetation structure deer probably also reduce the availability and quality of nest sites for species that put their nests in shrubs (reduced shrub density) or on the ground [reduced cover to hide nests from native avian nest predators (corvids) which use visual clues, see Martin and Joron, 2003]. Species such as the song sparrow, the orange-crowned warbler or the fox sparrow that depend heavily on ground vegetation for nest concealment (Godfrey, 1986; Ehrlich et al., 1988; Sogge et al., 1994) are examples. Where deer are present they tend to become restricted to regenerating patches of spruce or to steep slopes with rocks where remnants of vegetation persist for nest sites (pers. obs.).

Among the remaining species, the flycatcher favours an open understorey for foraging (Godfrey, 1986) and the hermit and varied thrushes commonly use open ground for foraging (Jones and Donovan, 1996; Luke George, 2000). Moreover, these two thrushes mostly feed on invertebrates of the litter which are little or not affected by deer presence (Allombert et al., in press). Although regularly observed on plots with an open understorey these species are also present in some of the plots with a dense understorey. Hence, as these three species are also sensitive to island isolation, it is difficult to evaluate the importance of deer related factors (open understorey) in their distribution. However, another study has already identified a positive impact of higher deer densities on the abundance of hermit thrush (DeGraaf et al., 1991).

## 5. Conclusion

Our results identified a strong indirect effect (*sensu* Strauss, 1991) of deer on forest birds through their effect on vegetation and associated insects. The reduction in songbird abundance was much stronger in our study (56% decrease in our point-count data and a 70% decrease in our mapping data) than suggested by other studies investigating deer impact on songbird abundance. Casey and Hein (1983) failed to find differences in bird abundance, DeGraaf et al. (1991) found a non-significant 14% reduction in forest stands with higher densities of deer, deCalesta (1994) observed a 37% reduction in understory bird density, and McShea and Rappole (2000) did not give any numeric information but observed higher abundances in their deer enclosure. The existence, in our study, of controls that had never been exposed to deer, instead of relatively recent enclosures, and/or the availability of different browsing histories spanning over a period of at least 50 years, against 10 years or less in most enclosure studies (deCalesta, 1994; McShea and Rappole, 2000), are probably enough to explain these differences.

The close fit in our study between relative decrease of understory vegetation cover and songbird abundance corroborates the suggestion by McShea and Rappole (2000) that understory vegetation cover and structure is an appropriate means to estimate the potential impact of deer overabundance on songbird populations. Hence, as several studies in both North America and Europe have identified decreases in understory vegetation similar to the one found in the islands we studied (e.g., Alverson et al., 1988; Rooney and Dress, 1997; Fuller and Gill, 2001), one should expect that the abundance of understory birds has been negatively affected in these forests. Moreover, our index of dependence on understory vegetation based on published information on the ecology of each bird species allowed us to predict which group of species would be affected by deer browsing. From a management perspective, this means that monitoring of understory vegetation density, combined with a careful analysis of bird species requirements should provide sufficient information to regulate deer populations for the conservation of bird populations.

White-tailed deer are estimated to be ecologically overabundant in 73% of their range and other North American deer species in between 14% and 41% of their range (Crête and Daigle, 1999). Similar trends of deer overabundance are observed in many parts of Western Europe (Kuiters et al., 1996). These trends, when put together with results from this and previous studies, underline the potential role of deer abundance as a factor explaining negative population trends in forest songbirds, a role probably still under-estimated.

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