

The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada)

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Martin, J.-L., Gaston, A. J. and Hitier, S. 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). – *Oikos* 72: 115–131.

We surveyed the vegetation and bird faunas of forests on 65 islands in the Gwaii Haanas archipelago of British Columbia, Canada, ranging in size from 1 to > 100 000 ha, using point counts at a uniform distance from the shore. Variation in habitat structure was correlated with variation in island area and isolation. Only among the smaller islands did the number of bird species recorded decrease with area. As some species became rarer with decreasing island size, others became more common. The distribution of bird species among the islands was correlated with the distribution of habitat features that were consistent with the biology and ecology of each species. In only a minority of species was their distribution related to area and isolation per se rather than to habitat features correlated with island size and isolation. Hence, we considered that variation in habitat structure mediated by area and isolation was the key factor involved in determining the local composition of the bird community. Only for a few species restricted to the largest islands, or missing from the very small islands, were high rates of extinction related to small population size the most parsimonious hypothesis explaining species distribution patterns. Our results emphasise how considering only the relationship between numbers of species and island area can mask all but the roughest species distribution patterns and prevent a deeper understanding of the biology of islands.

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The biology of islands has inspired biological and evolutionary thinking for over a century. As stressed by Kelly et al. (1989), citing de Candolle (1855), the strong correlation between island area and the size of its flora or fauna is one of the oldest and one of the few repeatable observations in ecology. Following efforts to quantify this empirical rule (e.g. Palmgren 1917, Arrhenius 1921, Gleason 1922), competing views for explaining species distribution patterns on islands took shape in the 1960s (Simberloff and Martin unpubl.). In accordance with the habitat diversity hypothesis developed by Williams (1943, see also Connor and McCoy 1979), Hamilton et al.

(1963), Hamilton et al. (1964), Hamilton and Armstrong (1965) suggested that area was correlated with habitat diversity, and the latter was the real determinant of species number. Other studies investigated the relationship between the species diversity of an island biota and the biotic diversity of the colonisation source, the size of the island and its distance from potential source areas (Whitehead and Jones 1969).

Another interpretation of the species-area relationship derived from the equilibrium theory of island biogeography, developed simultaneously by Preston (1962) and MacArthur and Wilson (1963, 1967). This theory sees the

Accepted 5 July 1994

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ISSN 0030-1299

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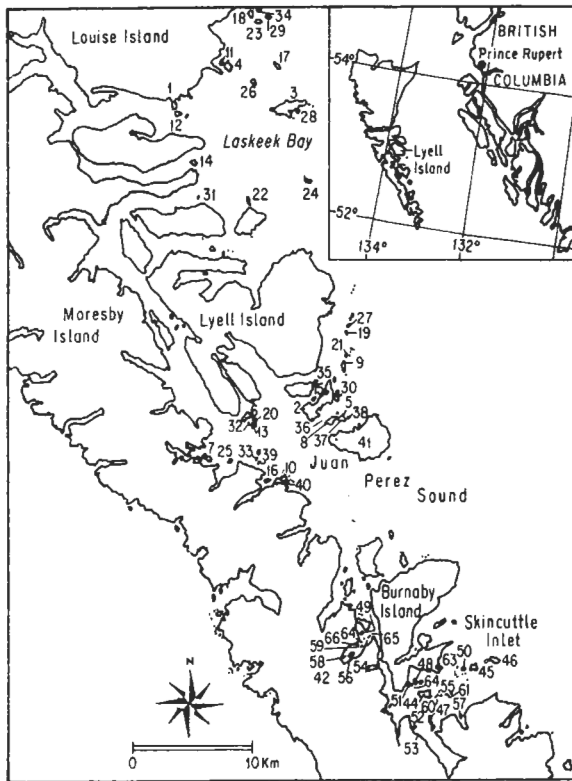


Fig. 1. Location of the islands censused in Gwaii Haanas. See Table 1 for island names.

number of species found on an island as the result of a dynamic equilibrium between immigration and extinction rates determined by island isolation and island size. At equilibrium there is a constant species turnover. In this hypothesis, the influence of island area on extinction operates through its effect on population size and hence on rates of extinction.

In contrast to the previous hypotheses that posit special processes at work in island biotas, the random placement hypothesis (Arrhenius 1921, Coleman 1981) suggests that larger islands support more species because they are simply samples from larger mainland communities where individuals are distributed at random.

Although a number of island biogeography studies have explored the correlation between island size, habitat feature and species richness (e.g. review in Nilsson et al. 1988) many others have been based on faunal lists or on general surveys. By doing so they implicitly considered that islands are otherwise comparable in terms of habitat diversity and structure and ignored between-island differences in species abundance. They also ignored the fundamental comments of MacArthur and Wilson that "area alone cannot be assumed in any particular case to be a precise predictor of species diversity"... "Area (does not exert) a direct role on numbers of species; rather (it is) related to other factors, such as habitat diversity, which in

turn controls species diversity" (MacArthur and Wilson 1967: 19, 20). MacArthur and Wilson in fact considered area only as a necessary stepping stone on the journey towards a real understanding of the species diversity within a given area (1967: 8). By concentrating on MacArthur and Wilson's dynamic equilibrium model as the ultimate theory rather than a necessary stepping stone, most of island biogeography ignored an essential part of their fundamental message.

Such considerations motivated us (Martin 1983, Martin and Lepart 1989) to study the variation in island bird faunas simultaneously with variation in island vegetation. We 1) considered sets of islands covered by a single type of macro-habitat (here coastal old growth forest of the Pacific Northwest) in order to limit the problem to variation in habitat structure with island area and not to analyse habitat turnover or habitat addition with changes in island area; 2) sampled the bird fauna so that variations in species abundance between samples can be estimated; 3) sampled habitat structure and birds simultaneously to estimate how much of the variation in bird species distribution and abundance was habitat-mediated.

In this study we analyse variation in forest habitat structure and in bird species richness, abundance and distribution in relation to variation in island area and isolation in three sets of islands of Gwaii Haanas (Queen Charlotte Islands, British Columbia, Fig. 1). We use these data to assess how bird species distribution patterns are related to patterns in vegetation structure that covary with island area and isolation. We examine the relevance of our results to theories relating to species diversity patterns on islands.

Study area, material and methods

Study area

Gwaii Haanas is part of Haida Gwaii (Queen Charlotte Islands), the largest and most isolated archipelago off the Northwest Pacific coast of Canada. Haida Gwaii is separated from the mainland by 80 km and from the nearest Alaskan islands by 50 km. The archipelago was almost completely glaciated during the Pleistocene, although refugia are believed to have existed that enabled the survival of various relict plants and animals (Heusser 1989). Forty species of land birds breed, of which at least 24 are resident (Godfrey 1986, McTaggart-Cowan 1989).

Haida Gwaii includes two large islands: Graham and Moresby. All our work was conducted on the islands of Haida Gwaii adjacent to Moresby Island (Fig. 1) and our further account refers only to that area. The lowland vegetation is rather uniform, consisting of a climax evergreen forest of western red cedar *Thuja plicata*, western hemlock *Tsuga heterophylla* and Sitka spruce *Picea sitchensis* with an admixture of alder *Alnus* spp. where disturbance has taken place (logging, landslides, etc.). On the larger islands, this forest, containing trees up to 60 m

Table 1. Name, area (ha), isolation (Isol.) (distance to reference islands in m) and number of point count censuses for each island censused in the three study areas (Laskreek Bay, Juan Perez Sound, Skincuttle Inlet, see Fig. 1). CL = area class, R = large reference islands; n = identification number of the islands on Fig. 1; N = number of point counts on an island; N total = total number of point counts per area class.

CL	Laskreek Bay				Juan Perez Sound				Skincuttle Inlet				N total			
	n	Name	Area	Isol.	N	n	Name	Area	Isol.	N	n	Name	Area	Isol.	N	N
R	1	Louise	35 000.0	0	24						42	Moresby		0	9	40
						2	Murchison	400.0	1 900	27	43	Burnaby	6 600.0	0	7	27
2	3	Reef	249.0	6 500	21											21
3	4	E. Limestone	48.0	500	5	5	House	44.0	800	5	44	Bolkus	52.2	1 200	4	33
						6	Bischof N	40.0	500	5	45	George	32.7	3 150	6	
						7	De la Beche	40.0	550	4	46	East Copper	24.7	3 750	4	
4	11	W. Limestone	16.0	350	2	8	Hotspring	21.0	600	3	47	Long I Jedway	17.0	50	2	30
	12	Haswell	13.3	150	3	9	Agglomerate	20.5	2 550	4	48	Swan	14.0	550	3	
	14	Helmet	10.4	500	2	10	Marco	20.0	150	4						
						13	Bischof SE	12.0	1 650	3						
						15	Murchison I	10.0	1 900	2						
						16	Hutton	10.0	350	2						
5	17	Low	9.6	5 400	2	19	Tar S	6.0	2 500	1	49	Island Bay 3	7.5	150	1	22
	18	Skedans W	8.2	1 350	3	20	Bischof C	6.0	1 500	2	50	Skincuttle	7.1	2 250	2	
	22	Titul	5.6	250	2	21	Kawas SW	5.6	2 650	1	51	Swan islet	6.0	150	1	
	23	Skedans S	5.6	2 400	2	25	Sivart	5.0	550	2	52	Boulder	5.6	150	2	
	24	Lost	5.3	1 100	1											
6	26	South Low	4.5	2 900	2	27	Kawas N	3.8	3 000	1	53	Sea Pigeon	4.2	150	1	30
	28	Little Reef	3.5	8 500	1	30	Hotspring I1	2.0	500	1	54	Island Bay 1	3.5	200	1	
	29	Skedans E	2.9	2 850	1	32	Bischof W	2.0	1 550	1	55	Bolkus I2	3.1	2 150	1	
	31	Flowerpot	2.0	550	1	33	Hoskins L	2.0	900	1	56	Island Bay 7	3.0	150	1	
	34	Skedans N	1.7	2 300	1	35	Faraday N	1.5	850	1	57	Harriet	3.0	150	1	
						36	Hotspring I3	1.5	500	1	58	Island Bay 8	2.5	200	1	
						37	Hotspring I2	1.0	550	1	59	Island Bay 5	2.2	250	1	
						38	House I1	1.0	800	1	60	Bolkus I1	2.1	2 350	1	
						39	Hoskins S	1.0	700	1	61	Bolkus I3	2.0	2 100	1	
						40	Marco S	1.0	150	1	62	Rock islets	1.7	1 350	1	
											63	Swan IS	1.5	400	1	
											64	Island Bay 4	1.2	150	1	
											65	Island Bay 2	1.2	600	1	
											66	Island Bay 6	1.0	300	1	

high, generally has a closed canopy, a sparse understorey, and a ground cover dominated by mosses. On the southern part of Moresby Island vegetation structure changes when going toward the interior of the island. There, the abundance of western red cedar and locally of lodgepole pine *Pinus contorta* tends to increase, and the abundance of western hemlock and Sitka spruce to decrease; canopy height becomes lower and scrub cover becomes denser. On Moresby we restricted our surveys to the coastal forest. On some islands, especially Reef Island, substantial areas of unmixed lodgepole pine, with a rather open canopy, occur on dry, south-facing slopes. Elsewhere, similar forests also grow on acid bogs. In such areas there is a dense ground cover of sedges. Except for where recent logging has taken place (Louise Island only), the only unforested areas occur on very small islands, on some headlands or near the summit of mountain peaks (Louise and Moresby islands). Where the forest meets the shore, especially on headlands and on exposed coasts (usually south and east exposures), the canopy tends to be more open and an understorey of grasses and forbs occurs. Shrubs, especially salal *Gaultheria shallon*, can occur densely when deer browsing is reduced or absent (Pojar et al. 1980, Pojar and Banner 1984).

Our study included most islands off the east coast of Moresby Island from Cumsheva Inlet south to Skincuttle Inlet (Fig. 1). The islands can be grouped in 3 separate sets: the islands of Laskeek Bay in the north, the islands of Juan Perez Sound in the middle and the islands of Skincuttle Inlet in the south. Average island isolation from the main islands and from adjacent islands decreases from the northern set of islands (Laskeek Bay) to the southern set of islands (Skincuttle Inlet) (Fig. 1). The latter islands are those which are the most clumped together and the best protected from the open sea by bays and inlets.

During spring 1989 we surveyed 15 islands in Laskeek Bay and 24 islands in the northern part of Juan Perez Sound, ranging from 1 to 400 ha, and also Louise Island 35 000 ha, as a reference (Fig. 1 and Table 1). As Louise Island is separated from the much larger Moresby Island by only a 50-m-wide channel we considered that it would probably support the same birds. Until the channel was dredged in 1967, the two islands were connected at low tide. During the spring of 1991 we used the same protocol to survey another set of 23 islands in Island Bay and Skincuttle Inlet and two large reference islands, Moresby and Burnaby, the latter again only separated from southern Moresby by a narrow channel that almost dries out at low tide (Fig. 1 and Table 1). Finally, in 1993 Murchison Island was partly recensused in order to replace censuses that we could not make under standard weather conditions in 1989.

In each set, islands were grouped according to 7 size classes (Class R: reference class made of very large islands: Burnaby (6 600 ha), Louise (35 000 ha) and South Moresby (Fig. 1), class 1: 400 ha, class 2: 250 ha, class 3: 40–50 ha, class 4: 10–21 ha, class 5: 5–9.9 ha,

class 6: 1–4.9 ha (Table 1)). Group size varies between 1 and 15 islands. We sampled more islands in the smaller size classes in order to obtain a similar sample size (number of point counts) in each area class.

Census method

Censuses were conducted from 22 April to 3 June 1989, from 19 May to 4 June 1991 and from 27 May to 12 June in 1993, using 20-min point counts with fixed radius. The same observer (JLM) performed all counts, recording the numbers and identity of each species observed within 50 m. All of our censuses were carried out in mature forest below 150 m a.s.l. However, the area of forest on the smallest islands is necessarily small, so that on those islands census points had to be close to the forest edge. We minimised any bias from this effect by ensuring that all point counts were made a similar distance from the shore, irrespective of island size. The distance to the forest edge rarely exceeded 150 m and was never below 50 m. To ensure that there was no overlap between observations, we left at least 200 m between adjacent points. Hence, the number of counts possible on an island was limited by the island's area. Species that occurred outside the 50-m radius covered by the point count were also noted separately as supplementary species. Point counts were performed exclusively in the morning before 11.00 under uniform weather conditions (absence of steady rain and of strong wind). Drizzle or a light breeze were tolerated as they did not have any noticeable effect on bird activity in the forest interior. There was no systematic variation in survey conditions associated with island area or island isolation.

For each point we recorded a standardised description of the vegetation within the 50-m radius. We estimated maximum vegetation height and canopy height (the height of the highest vegetation layer with >25% cover); the vegetation structure (% cover at 0–0.25, 0.25–0.50, 0.50–1, 1–2, 2–4, 4–8, 8–16, 16–32, >32 m); the proportion of the ground covered by herbaceous vegetation, moss, dead wood and bare soil and the proportion covered by the dominant plant species. Estimates of cover percentages were made using a reference chart (Prodon 1988). The chart provides patterns of black patches corresponding to patch covers of 1%, 5%, 10%, 20%, 30% etc. up to 90% respectively. For each island we also recorded its vegetated area and the distance to the nearest large island (>5 000 ha) which we used as an index of isolation. Each island was visited only once. In order to estimate the total number of forest bird species on a single island we used an approach inspired from the single-visit procedure defined by Haila and Kuusela (1982). On the smallest islands (area <40 ha) the whole island was covered by excursions before, after or between point counts. On the largest islands and on the reference islands only a portion of the island was covered by excursions. Haila and Kuusela (1982) demonstrate that

Table 2. Variation among sets of islands of mean values of the vegetation variables. Variables for which at least one significant difference was observed are listed first (5% level; t-tests). LB = Laskeek Bay islands, JPS = Juan Perez Sound islands, SI = Skincuttle Inlet islands; *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; n.s. = not significant. P values were corrected for multiple comparisons.

Vegetation variables	Acronym	LB-JPS	LB-SI	JPS-SI
Max. height (m)	MH	33.9 < 39.7**	34.1 < 41.9**	n.s.
Canopy height (m)	CH	28.1 < 32.0**	27.7 < 34.8**	32.0 < 34.8*
Cover above 32 m (%)	32	n.s.	21.9 < 19.8*	n.s.
Cover from 16 to 32 m (%)	16	38.0 > 26.1**	n.s.	n.s.
Cover from 4 to 8 m (%)	4	n.s.	5.4 < 8.8*	4.8 < 8.8***
Cover from 1 to 2 m (%)	1	9.1 < 20.2**	n.s.	n.s.
Cover of grasses (%)	GRA	17.2 > 3.5**	17.2 > 0.8**	n.s.
Cover of moss (%)	MOS	n.s.	38.3 < 60.5***	n.s.
Cover of dead wood (%)	DWO	n.s.	21.6 < 36.0***	n.s.
Cover of w. hemlock (%)	HEM	26.5 < 44.3***	26.9 < 47.4***	n.s.
Cover of Sitka spruce (%)	SPR	47.5 > 25.6***	47.2 > 32.7*	n.s.
Cover of alder sp. (%)	ALD	11.3 > 3.1**	11.2 > 1.4**	n.s.
Cover of salal (%)	SAL	5.8 < 17.0**	n.s.	n.s.
Cover from 0 to 0.25 m	0	n.s.	n.s.	n.s.
Cover from 0.25 to 0.5 m	025	n.s.	n.s.	n.s.
Cover from 0.5 to 1 m	05	n.s.	n.s.	n.s.
Cover from 2 to 4 m	2	n.s.	n.s.	n.s.
Cover from 8 to 16 m	8	n.s.	n.s.	n.s.
Cover of bare soil	BSO	n.s.	n.s.	n.s.
Cover of red cedar	CED	n.s.	n.s.	n.s.
Cover of elder	ELD	n.s.	n.s.	n.s.
Cover of willow	WIL	n.s.	n.s.	n.s.
Cover of crabapple	CRA	n.s.	n.s.	n.s.
Cover of salmonberry	SAB	n.s.	n.s.	n.s.
Cover of huckleberry	HUC	n.s.	n.s.	n.s.
Cover of <i>Ribes</i> sp. shrubs	RIB	n.s.	n.s.	n.s.
Cover of ferns	FER	n.s.	n.s.	n.s.

almost 90% of the breeding species are recorded during such single visits. We tested and confirmed their results for 5 islands for which we had an exhaustive knowledge of the bird fauna (Murchison Island, Reef Island, East Limestone Island, Hot Spring Island, South Low Island) (our unpublished data). These islands covered the entire area range.

Statistical methods

Variation in habitat structure in relation to area and locality. We did the Principal Component Analysis of the 27 habitat variables measured on the 203 censuses. The plots of the census' projections onto the plan of the first two axes of PCA, for each of the three study areas (Laskeek Bay, Juan Perez Sound and Skincuttle Inlet) and by area classes, allowed us to appreciate if there were differences in habitat structure with island area and/or island isolation. It also enabled us, with the comparison of the mean values observed for habitat variables among the three study areas (t-tests), to identify whether habitat structure differed among our three study areas. We transformed the variables to minimise the impact of outliers and of non-normality and to make variances less dependent on means. Log-transformations turned out to yield the best results for all variables including percentages.

Species richness, and abundance. We used the total number of forest bird species observed on each island during single visits as an estimate of the total number of land bird species present (S). The average number of species observed in a sample (s) is a measure of the average local species richness within a sample:

$$s = \sum s_i / N$$

where s_i is the number of species recorded at the i th point count and N the number of point counts in the sample. S and s are used to compare species richness among samples and to compare species-area relationships. We used rarefaction analysis (Simberloff 1978, James and Rathbun 1981, James and Wamer 1982) to illustrate the relationship between sampling effort and the number of species observed. Variation in species abundance among different samples was estimated by variation in the average number of individuals of that species seen per count.

Variation in bird species distribution in relation to habitat, area and isolation. In order to simplify the analysis, we selected 15 of the 27 environmental variables. First, we selected the 12 habitat variables that had a significant correlation with the PCA scores in the analysis of variation in vegetation structure. Maximum canopy height (MH) was eliminated because it was strongly correlated to canopy height (CH), another selected variable. Then,

Table 3. Comparison of mean isolation values (in m) for island area classes censused in all three archipelagoes. Significance level of t-test is 0.05 corrected for multiple comparisons.

Class	LB-JPS	LB-SI	JPS-SI
3	n.s.	500 < 2 700	617 < 2 700
4	n.s.	n.s.	n.s.
5	n.s.	n.s.	n.s.
6	3 420 > 950	3 420 > 750	n.s.

we added the percent of cover of Sitka spruce (SPR) and of red cedar (CED) to the selection in order to make the final results more explicit biologically. Lastly, we added the two log-transformed variables isolation (ISO) and area (AREA). The species matrix uses the number of individuals observed for a given species in each point count. We used Canonical Correspondence Analysis (CCA, Ter Braak 1986, 1987, Chessel et al. 1987, Lebreton et al. 1988a, b, 1991, BIOMECO software) to analyse the relationships among variations in species distribution on one hand, and variations in habitat structure and/or changes in island area and isolation on the other hand. A review of the advantages of Canonical Correspondence Analysis for ecologists is given by Palmer (1993).

Results

We carried out a total of 203 point counts, 128 on 40 of the 41 islands visited in 1989 (73 censuses in Laskeek Bay and 55 censuses in Juan Perez Sound), 55 on the 25 additional islands censused in 1991 in Skincuttle Inlet and 20 censuses on Murchison in Juan Perez Sound in 1993 (Table 1).

We observed and included twenty-four species in the point counts. We observed a further eight species during the counts or elsewhere in the islands: four raptors (peregrine falcon *Falco peregrinus*, bald eagle *Haliaeetus leucocephalus*, red-tailed hawk *Buteo jamaicensis* and sharpshinned hawk *Accipiter striatus*), tree swallow *Tachycineta bicolor*, Swainson's thrush *Catharus ustulatus*, pine grosbeak *Pinicola enucleator* (unusual in the coastal areas) and a newcomer to southern Moresby Island, the European starling *Sturnus vulgaris*. The first five were probably inadequately sampled by the point-count technique inside the forest and we therefore excluded them from the point-count data. The late arrival of the migrant Swainson's thrush accounts for its omission; no other late migrants can be expected in northern coastal British Columbia (Godfrey 1986, see Appendix). The only bird species occurring in lowland forests on the islands that was not observed was the Steller's jay *Cyanocitta stelleri*.

Variation in habitat features according to locality area and isolation

Analysis of individual variables. Canopy height differed significantly among the three study areas, being lowest in the Laskeek Bay area (Table 2). The islands in Laskeek Bay also had greater cover of grass, spruce and alder, with correspondingly less hemlock, than the other areas (Table 2). Differences in vegetation between Juan Perez Sound and Skincuttle Inlet were trivial or non-significant.

Paired comparisons among island area classes showed that, for class 3 islands, those in Skincuttle Inlet were the most isolated. For class 6 islands those in Laskeek Bay were the most isolated (Table 3).

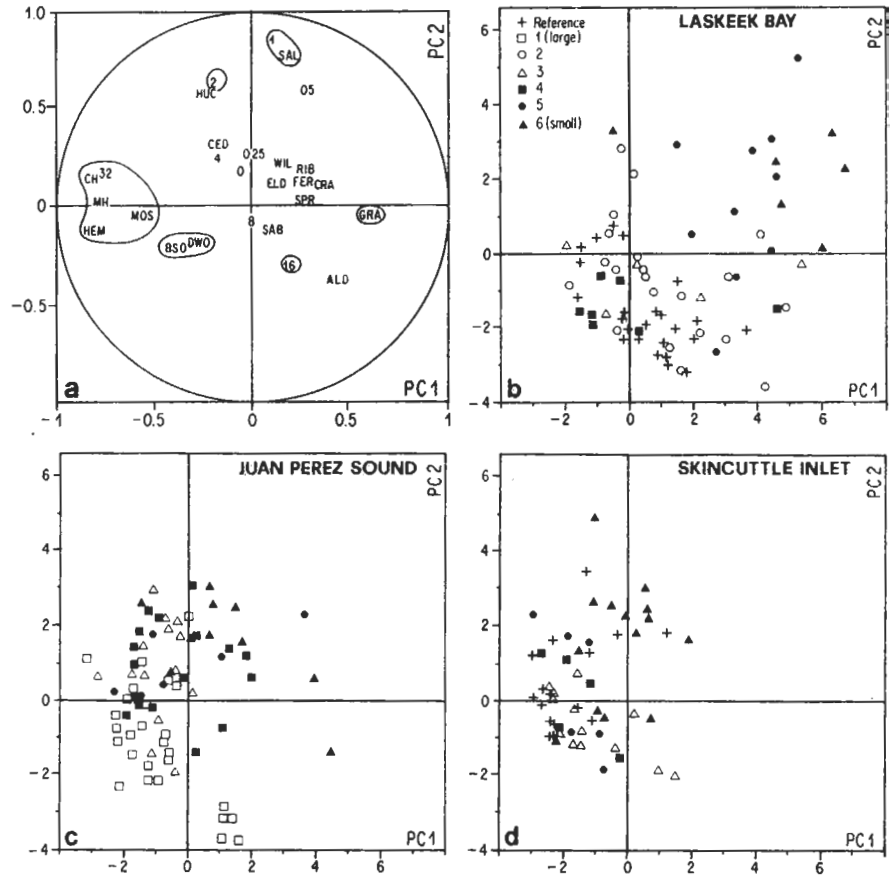
Habitat features, area and isolation. Island area was positively correlated with maximum canopy height (MH), the cover in the 16 to 32-m and 4 to 8-m layers (16, 4) and the cover of moss (MOS), of dead wood on the ground (DWO) and of western hemlock (HEM) (Table 4). Island area was negatively correlated with vegetation cover in the layers 1–2-m (1) and 0.5–1-m (05), and with the cover of salal (SAL), of huckleberry sp. (HUCK) and of Sitka spruce (SPR) (Table 4). Isolation was positively correlated with the cover of spruce (SPR), of grass (GRA), and of all the vegetation layers under 2 m (1, 05, 025, 0), suggesting that the higher average values observed for some of these variables on islands in Laskeek Bay may result from greater relative isolation. Isolation was negatively correlated with canopy and maximum heights (CH, MH), the cover of cedar (CED), western hemlock (HEM) and the cover of moss (MOS).

Thus, although we selected islands covered by the same type of macro-habitat we observe that the majority

Table 4. Correlation coefficients between area, isolation and the habitat variables. Only the 18 variables with significant correlations with area or isolation are listed ($P < 0.05$, $|r| > 0.15$, $n = 203$). 05 = cover from 0.5 to 1 m; BSO = cover of bare soil, CED = cedar, CRA = cover of crabapple. The other variables are explained in Table 2.

Habitat var.	Area	Isolation
MH	0.19	-0.25
CH	n.s.	-0.29
16	0.24	-0.15
4	0.16	n.s.
1	-0.42	0.17
05	-0.29	0.20
025	n.s.	0.16
0	n.s.	0.16
GRA	n.s.	0.27
MOS	0.19	-0.25
DWO	0.17	-0.15
HEM	0.16	-0.18
SPR	-0.15	0.28
CED	n.s.	-0.31
ALD	0.22	n.s.
CRA	-0.17	n.s.
SAL	-0.36	0.15
HUC	-0.20	n.s.

Fig. 2. PC1-PC2 plane of the Principal Component Analysis for vegetation variables. a) Correlation circle, variables with significant correlations with one or both axes are circled. For variable definitions, see Table 2. b-d) Census scores in the PC1-PC2 plane of the Principal Component Analysis on vegetation variables for each of the area classes in the three study areas. For definition of the island area classes, see Table 1.



(18 out of 27) of the measured habitat features varied with island area and/or isolation.

Principal component analysis. The two first principal components from the PCA on the 27 vegetation structure and composition variables summarise 27.1% of the data variance (respectively 15.7 and 11.4%). The third PCA summarises 7.7% of the variance and this proportion decreases regularly for the following components. These figures suggest that there is little covariance structure in the data. However, because we initially selected islands with similar habitat we expected no structure at all (if the habitat structure were rigorously homogeneous across the islands). Consequently, the observed variation and its possible relation to island area or isolation deserves attention.

We restricted our analysis to the PC1-PC2 plane. The correlation circle obtained for the PC1-PC2 plane shows that 12 out of the 27 original variables contributed significantly to the first two components (Fig. 2a). Census plots with negative scores on the first PC axis were in stands with a high canopy (CH, MH, 32), a high cover of hemlock (HEM) and mosses (MOS) plus, with lower correlation, a high cover of dead wood on the ground and

of bare soil (DWO, BSO). Census plots with positive scores on PC1 have the highest cover of grass (GRA).

Variables such as the vegetation cover between 1–2 m (1), 0.5–1 m (05) and 2–4 m (2) are positively correlated with PC2. They define stands with a dense understorey. The understorey is dominated by salal (positive correlation of variable SAL on PC2).

In all three sets of islands, scores on PC1 increased, on average, with decreasing island area (i.e. when going from island class R – the large reference islands – to island class 6 – the smallest islands, Table 1) (Figs 2b–2d). The spread of the scores on PC1 between large and small islands, as well as within island size classes, was highest in the Laskeek Bay islands and smallest in the Skincuttle Inlet islands. Average scores on PC2 increased as island size decreased.

Forest stands tended therefore to have a higher canopy and a more open understorey on large islands than on small ones (Fig. 2). The cover of hemlock was higher on large islands than on small ones where spruce was more dominant, together with alder (but without significant correlation with PC1 or PC2). Smaller islands also had, on average, a greater cover of grasses and a denser shrub layer of salal and huckleberry (Fig. 2). All these differen-

Table 5. Average number of individuals observed per point count for each bird species in the three local archipelagoes (LB = Laskeek Bay; JPS = Juan Perez Sound; SI = Skincuttle Inlet); S = total number of bird species observed in each archipelago. Slope = slope of the cumulative richness curve.

Archipelago		LB	JPS	SI
Number of point counts		73	75	55
Blue grouse	BGRO	0.01	0.01	0.02
Red-bellied sapsucker	SAPS	0.25	0.07	0.45
Hairy woodpecker	HAIR	0.10	0.13	0.16
Northern flicker	FLIC	0.00	0.05	0.05
Rufous hummingbird	HUMM	0.22	0.21	0.33
Western flycatcher	WFLY	0.38	0.76	0.91
Northwestern crow	CROW	0.42	0.68	0.82
Raven	RAVE	0.05	0.04	0.16
Chestnut-backed chickadee	CHIC	0.64	0.89	1.09
Red-breasted nuthatch	NUTH	0.01	0.04	0.09
Brown creeper	CREE	0.22	0.17	0.22
Winter wren	WREN	1.18	1.04	1.24
American robin	ROBI	0.03	0.00	0.02
Varied thrush	VARI	0.33	0.23	0.44
Hermit thrush	HERM	0.26	0.53	0.51
Golden-crowned kinglet	KING	0.36	0.35	0.35
Orange-crowned warbler	OCW	0.38	0.32	0.18
Townsend's warbler	TOWN	1.33	1.15	1.02
Wilson's warbler	WILS	0.00	0.03	0.05
Pine siskin	SISK	0.41	0.12	0.04
Red crossbill	CROS	0.60	0.57	0.56
Dark-eyed junco	JUNC	0.04	0.00	0.09
Fox sparrow	FOXS	0.30	0.29	0.22
Song sparrow	SONG	0.33	0.25	0.31
S		22	22	24
Slope		0.03	0.01	0.04

ces between large and small islands were greatest in the Laskeek Bay islands and least in the Skincuttle Inlet area (Figs 2b–2d). When large islands are considered (classes R to 4), the stands censused in Laskeek Bay (Fig. 2b) had, on average, more negative scores on PC2 than those censused in Juan Perez Sound (Fig. 2c) and in Skincuttle Inlet (Fig. 2d). This indicates a more open understorey on large islands in Laskeek Bay (reduced abundance of salal and huckleberry).

In summary, the PCA of habitat features revealed that variation in habitat structure among our samples mainly affected forest height, the relative proportion of hemlock and the density of the understorey. Comparing census scores among sets of islands and island size classes revealed that habitat features varied with island area and that the amount of area-related variation in habitat features differed from one set of islands to another.

Although, superficially, a similar type of forest occurs on all the islands sampled, we found a slight but meaningful habitat variation among samples, mediated by area and locality. The differences among large and small islands were strongest in Laskeek Bay, where the islands are the most isolated on average (Figs 1 and 2).

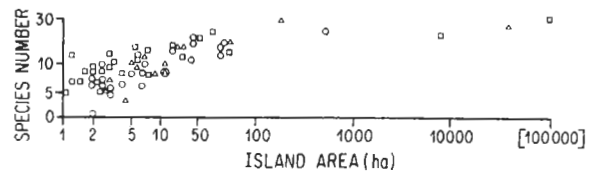


Fig. 3. Relation between the logarithm of island area and the logarithm of the total number of bird species observed on each island. For Moresby Island, 99 999 ha has been the default value used for its area. Triangles identity islands from the Laskeek Bay area, circles islands from the Juan Perez Sound area and squares islands from the Skincuttle Inlet area (see Fig. 1 and Table 1).

Variation in bird species distribution in relation to habitat, area and isolation

Bird species richness, island area and isolation. During census counts the same twenty-four species were recorded in different years (Table 5). Over the whole 203 counts, the slope of the cumulative species richness curve for the entire sample was zero, suggesting that our sam-

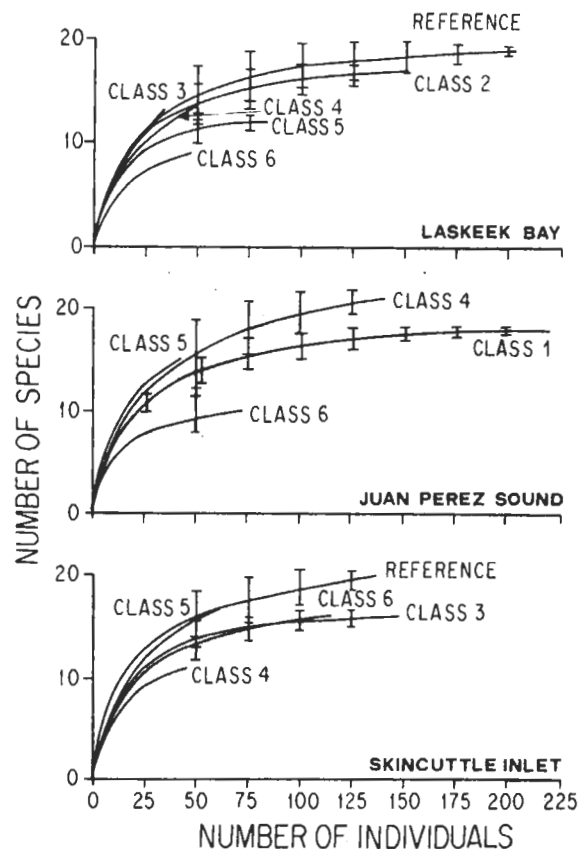


Fig. 4. Rarefaction curves for the different island area classes in the three sets of islands: Laskeek Bay, Juan Perez Sound, Skincuttle Inlet. Vertical bars refer to plus or minus 2 standard deviations. For area class definitions, see Table 1.

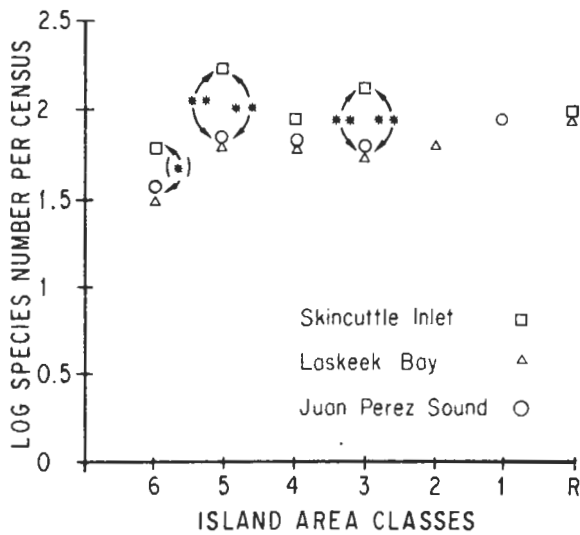


Fig. 5. Relation between island area (represented by the area classes defined in Table 1) and the logarithm of the average number of species observed per point count in each sample. Stars, circles and squares identify the three study areas as in Fig. 3.

pling recorded all available species. This slope varied between 0.01 and 0.04 among the three study areas (Table 5). The number of species recorded on individual islands increased with island area (Figs 3 and 4). However, there was little increase in species number with increasing area for islands larger than 100 ha suggesting an area threshold above which our samples include most of the lowland forest birds that are available within the archipelago.

Rarefaction curves (Fig. 4) reveal that the bird community of the smallest islands (class 6) is significantly poorer in species in Laskeek Bay and in Juan Perez Sound.

The average number of species recorded per point count remained relatively constant among island size classes within the three study areas (Fig. 5). However, the average number of species recorded per census in the smallest size class was significantly lower than on larger islands (*t*-tests). Values for *s* within an island size class were always higher for Skincuttle Inlet than for Laskeek Bay and Juan Perez Sound (Fig. 5, difference significant at the 0.01-level (*t*-test) for classes 3 and 5 and at the 0.10-level for class 6).

These results indicate that, although the classic pattern of decreasing species richness with decreasing area is generally confirmed, significant species impoverishment 1) is only observed for the smallest islands (Figs 3 and 5); 2) is locality dependant both within and between archipelagos (Figs 4 and 5) and 3) is highly variable among islands (some of the smallest islands have species numbers similar to those observed for the larger islands, Fig. 3). The smaller islands (class 6) in Laskeek Bay and Juan Perez Sound have less species than the smaller islands in

Skincuttle Inlet (Figs 3, 4 and 5) a feature possibly related with the more sheltered and more clumped (less isolated) localisation of the latter islands (see Fig. 1).

Seven species (northern flicker *Colaptes auratus*, western flycatcher *Empidonax difficilis*, northwestern crow *Corvus caurinus*, raven *Corvus corax*, chestnut-backed chickadee *Parus rufescens*, red-breasted nuthatch *Sitta canadensis* and Wilson's warbler *Wilsonia pusilla*) showed lowest abundance in the northern set of islands (Laskeek Bay) and highest abundance in the southern one (Skincuttle Inlet) (Table 5). Two species (orange-crowned warbler *Vermivora celata* and pine siskin *Carduelis pinus*) were much less common on the Skincuttle Inlet islands than in the other areas. Finally, at least three species (red-bellied sapsucker *Sphyrapicus ruber*, American robin *Turdus migratorius* and dark-eyed junco *Junco hyemalis*) had lower observation frequencies in Juan Perez Sound than in the other two areas.

Thus, area effect on species number per island and on abundance indices of individual species appears to be locality dependent.

Species composition and area. We examined variation in the abundance of individual species on islands of different size by comparing the mean number of individuals observed per point count. Species were ordered according to decreasing Spearman rank correlation coefficients, which varied from +0.97 to -1.00 (Table 6). In contrast to the expectations following from the species-area relationship some species show negative coefficients, i.e. higher observation frequencies on smaller islands than on larger ones. The three study areas show a considerable consistency in the species that display a negative Spearman rank correlation.

The different species-area patterns revealed by the Spearman rank correlation analysis explain why the average number of species observed per census remains constant in all except the smallest island size classes (classes 1 to 5) (Fig. 5 previous section). When island area decreases the decrease in abundance of the "large island species" is offset by the increase in abundance of the "small island species". Only for the smallest islands is the decreased abundance of some species sufficient to show up in a general decrease of the values of *s*.

Variation in species distribution in relation to habitat and area. The eigenvalues for the first four axes of the CCA were 0.279, 0.066, 0.055 and 0.049. Hence they account for 47.8%, 11.3%, 9.5% and 8.5% of the variance, respectively. Axis 1 explains almost 50% of the variance and is by far the more informative axis. Table 7 lists the correlation ratios of each environmental variable for each of the four first axes and confirms the dominance of axis 1. Indeed, strong ratios with axis 1 were observed for island area, cover of Salal, cover in the 1-2-m vegetation layer, cover of hemlock and cover of mosses as well as for isolation. Island isolation was the only variable with a strong correlation ratio for axis 2. All other variables had

Table 7. Correlation ratios on axes 1 and 2 of the Canonical Correspondence Analysis for the 15 habitat variables. Ratios are ranked according to decreasing values for axis 1.

Variables	Axis 1	Axis 2
Area	0.51	0.07
Cover of salal	0.48	0.07
Cover from 1 to 2 m	0.39	0.06
Cover of w. hemlock	0.33	0.05
Isolation	0.25	0.54
Cover of moss	0.24	0.03
Canopy height	0.18	0.03
Percent of dead wood	0.16	0.01
Cover of Sitka spruce	0.12	0.01
Cover above 32 m	0.11	0.00
Cover of grasses	0.09	0.18
Cover from 2 to 4 m	0.03	0.03
Cover from 16 to 32 m	0.02	0.04
Cover of bare soil	0.01	0.00
Cover of red cedar	0.01	0.02

correlation ratios lower than 0.10 on axis 2. Thus, axis 1 opposes censuses from large islands in high stands, closed canopy and open mossy ground cover to censuses from small islands in low more open stands with a denser undergrowth. Axis 2 essentially describes the effect higher or lower island isolation of the island will have on the pattern described by axis 1.

When variable vectors and average species scores for axes 1 and 2 were plotted, species fell into four fairly discrete clusters (Fig. 6). Cluster 1 includes species that

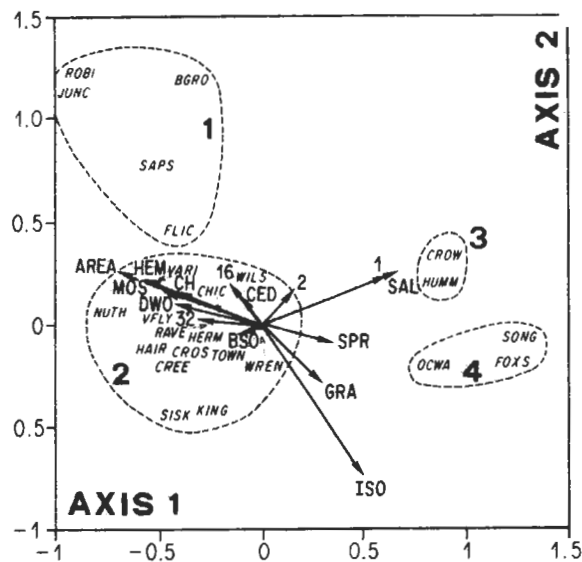


Fig. 6. Average scores of bird species in the axis 1-axis 2 plane of the Canonical Correspondence Analysis on species distribution with respect to area, isolation and habitat variables. The projections of the habitat vectors on these axes and their relative length are superimposed on the figure. For definition of species acronyms, see Table 5. For definition of habitat variable acronyms, see Table 2.

were mainly observed in censuses from large reference islands (which by definition have the lowest scores for isolation). The dark-eyed junco and the American robin are the best examples. The blue grouse *Dendragapus obscurus*, the red-bellied sapsucker and the northern flicker were observed on a wider range of island size. Many of the species in cluster 2 are widespread in the samples. The red-breasted nuthatch and the varied thrush *Ixoreus naevius*, are examples of species more frequently observed on large islands, or on smaller islands that are not too isolated. The lower the species' score on axis 1 and the higher its score on axis 2, the more its distribution is correlated to the distribution of tall open stands.

The pine siskin and the golden crowned kinglet *Regulus satrapa* were associated with stands that had an open understorey and that were equally dominated by hemlock or spruce (Fig. 7).

Clusters 3 and 4 include species with positive scores on axis 1 that are most frequently observed on the smallest islands (Table 6). The fox sparrow *Passerella iliaca*, song sparrow *Melospiza melodia* and orange-crowned warbler (cluster 4) are widespread and common on the small islands and are more frequently encountered on the more isolated of those islands (Fig. 7). The northwestern crow and the rufous hummingbird *Selasphorus rufus* (cluster 3), are also widespread on the small islands, but seem to be less affected by isolation than species in cluster 4. All these species have high scores for the habitat vector describing dense understorey (1) dominated by salal (Figs 6 and 7).

These results suggest that, if indeed species distribution is area-dependant, it is also strongly correlated with area and isolation-mediated habitat variation. They also show that complex species distribution patterns can be masked by simple species-area relationships. The focus of our discussion will be to evaluate how far the correlation between area, isolation and habitat is causal and how far area and isolation-mediated habitat variation should be considered as the ultimate factor explaining bird species distribution across the islands.

Discussion

Landscape pattern and habitat structure

We interpret the differences in habitat structure between large and small islands as caused by four major factors. First, on the smaller islands a higher proportion of edge habitat increases the amount of shrubs. But, as we distributed our point-counts so that they were the same distance from the shoreline, irrespective of island size, the pattern we observed was not caused by sampling closer to the shore on small islands. It rather reflected differences in habitat structure between large and small islands. On an island of a few ha, most of the vegetation will be subject to edge effects, whereas an area of the same size at the edge of a larger island will include both

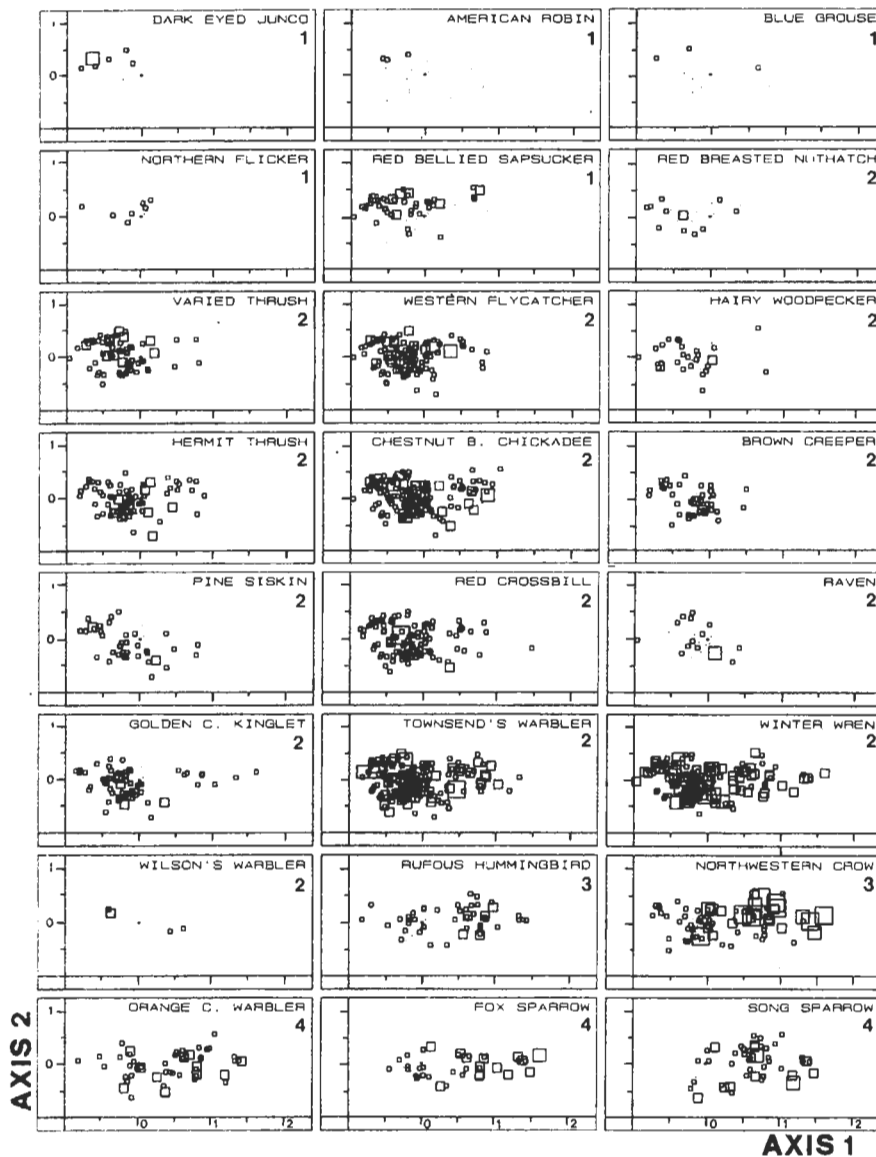


Fig. 7. Clouds of the abundance of the species in the axis 1-axis 2 plane of the censuses (Canonical Correspondence Analysis on species distribution relative to area, isolation and habitat). Squares identify the point counts where a given species was observed. The size of the square is proportional to the number of individuals observed for that species in the point count. The species are ordered along rows according to species clusters defined on Fig. 6. The number below the species name refers to the species cluster on Fig. 6.

edge and more interior conditions. Levenson (1981) reached a similar conclusion in his study of forest fragments.

Second, the smaller the island, the more it is exposed to storms that will increase windthrow. This explains the lower canopy and more open stands, favouring the development of the understorey and of broader edges. The impact of outside perturbation on vegetation structure will also depend on the island's position in the landscape: it will be stronger on exposed off-shore islands (e.g. the Laskeek Bay islands which are also the more isolated islands) and weaker on more sheltered islands (e.g. the Skincuttle Inlet islands). Such area-mediated mechanisms influencing the local environment have been discussed by

Ambuel and Temple (1983), Howe (1984), Rosenberg and Raphael (1986), Wilcove et al. (1986), Haila et al. (1987), Saunders et al. (1991), both for real islands and for habitat fragments in temperate forests and by Lawrence (1991) for fragments of tropical forest.

Third, local climatic variation related to landscape features can also affect habitat structure. We explain the negative correlation between moss cover and island isolation by the fact that the less isolated islands, being closest to the main island chain, receive more rain and moisture than more off-shore islands, which experience some rain-shadow from the large islands (Gaston 1992). Similarly, the higher canopy and greater moss cover recorded in Skincuttle Inlet (Figs 2 and 3) are partly the result of

higher rainfall there than on islands situated further north (Juan Perez Sound and Laskeek Bay), owing to the proximity of the Moresby mountain range.

Finally, the distribution of the black-tailed deer *Odocoileus hemionus* has also a significant impact on vegetation structure (Pojar et al. 1980, Pojar and Banner 1984) and is itself mediated by island area and island isolation (Martin unpubl. and Martin et al. 1994). The deer was introduced on the islands at the end of the last century (Osgood 1901) and it is widespread on the large reference islands. Browsing by the deer is reduced on the smallest islands, many of which, and especially the most isolated, do not support permanent deer populations. On larger islands deer may be common even when the island is isolated (e.g. Reef Island, Ramsay Island). By reducing the amount of shrub cover, the deer affect the distribution and abundance of some habitat features (Martin et al. 1994). Their lower incidence on small islands, where shrub cover tends to be increased by edge effect and by a more open canopy, exaggerates the influence of the above-mentioned factors on habitat differences between large and small islands.

Thus, island area and/or island isolation, by influencing island exposure to wind and storms, island accessibility to introduced browsers, or the local climate, affect habitat structure. We therefore suggest that the correlation we observed between habitat variation, island area and/or island isolation is to a great extent causal.

Variation in the distribution of bird species among the islands

Sampling effect and year effect on the distribution of land birds of Gwaii Haanas. Species that tend to be common on the large reference islands had their lowest observation frequency in Juan Perez Sound simply because no reference island was surveyed there (e.g. red-bellied sapsucker, dark-eyed junco, Table 5). Although the lower frequency of pine siskin at Juan Perez Sound, compared to Laskeek Bay, may partly result from the lower abundance of spruce in the Juan Perez Sound islands, the very low frequency of observations in Skincuttle Inlet was probably caused by an inter-year fluctuation in the population of this species. Numbers of pine siskin in the Laskeek Bay area were much lower in 1991 and 1993 than in 1989 (Laskeek Bay Conservation Society, unpubl.). No other between-year fluctuation in species abundance could be diagnosed.

Direct effect of area and isolation versus area and isolation-mediated habitat effect? Teasing out the respective role in the distribution of island forest bird species of 1) area and isolation, 2) of area- and isolation-mediated habitat variation and 3) of random sampling of the local avifauna by any given island presents a challenge.

The restriction, in our study, of the rarest species to the largest islands could suggest a random sampling of spe-

cies on islands reflecting their abundance on the large reference islands. However, because the overall number of point counts (and thus the sampling effort) is lower on large reference islands (40 point counts) than on the smallest islands (52 counts when classes 5 and 6 are pooled (Table 1)) the sampling hypothesis can be rejected.

The fact that 4 out of the 5 species almost exclusively restricted to the reference islands (species cluster 1 on Fig. 6) are either large species or the largest members within species guilds is consistent with the equilibrium hypothesis (i.e. for a given island, larger species, because they have larger territories and thus lower densities, will be more prone to extinction due to random population fluctuations than are smaller species). But the presence of robins on the large islands was always associated with the presence nearby of non-forested grassy edges (along small estuaries for instance) which were used by robins for foraging. Such habitat features are missing from smaller islands. For other species, large size and ecological specialisation go together, as in the woodpeckers, suggesting that rarity of resources on smaller islands, and not necessarily increased risk of random extinction, may be the ultimate factor explaining their distribution. In one case a flicker was observed using a nesting cavity on a small island and foraging on other islands situated nearby. The blue grouse is probably the species for which the equilibrium hypothesis is the most likely to apply. Considering the large size of that species, islands may become too small to house a viable population before their area affects the quality of the habitat available in a significant fashion.

For the remainder of the species that were more frequently observed on large islands (cluster 2, Fig. 6) the Canonical Correspondence Analysis revealed that they were more often observed in stands with a high canopy and an open understorey. Such stands were more common on large than on small islands, as shown by the Principal Component Analysis of vegetation variables (see Fig. 2). These observations are consistent with what is known on the ecology of the bird species involved (Godfrey 1986). The trunk and branch feeders, the red-breasted nuthatch and the brown creeper, were indeed more abundant in stands with the largest trees. An open understorey is a critical feature in the western flycatcher's habitat (Godfrey 1986) and this is confirmed by our results. The pine siskin and the red crossbill tend to move in flocks over relatively long distances while foraging for conifer seeds. The correlation between frequency of observation and island area for these species may relate to a decreased probability of flock visits on the smaller islands (and a reduced probability of finding these resources on smaller islands). The western flycatcher, the chestnut-backed chickadee, the pine siskin (but also the golden-crowned kinglet and the winter wren *Troglodytes troglodytes*) have been identified as forest interior species by Rosenberg and Raphael (1986) in their study of related habitats from the mainland.

The knowledge we have of the orange-crowned warbler's biology (Godfrey 1986) also is consistent with their high observation frequency in stands with a higher proportion of deciduous trees and grass cover, habitat features which are correlated to small islands. The high densities of the northwestern crow and of the rufous hummingbird on small islands were positively correlated to the abundance of salal. In the case of the hummingbird, salal flowers are an abundant food resource, and the shrub provides crows with a good cover for their nests (pers. obs.). Martin and Lepart (1989) studying an archipelago in the Baltic Sea found a similar relation between the abundance of the hooded crow *Corvus corone cornix* and island area. They attributed it to the increased proportion of shoreline available to crows for foraging near small islands, an interpretation that could also apply to the highly coastal northwestern crow (Godfrey 1986, Ehrlich et al. 1988).

Observations that some species are most abundant on smaller islands or in small habitat fragments have been made several times. They were mostly explained by the increased proportion of edges and edge-like habitat on small islands (Hogstad 1967, Haila et al. 1980, Helle and Helle 1982, Hansson 1983, Helle 1984). Rusterholz and Howe (1979) showed that song sparrows were abundant on small islands in a lake, but they were rare and localised along the shoreline on the mainland. Rosenberg and Raphael (1986) also found both the fox and song sparrows associated with the edges of forest fragments. The edge-like nature of small island habitat presumably explains the distribution of these species on the islands.

Decrease in the abundance of forest interior species and increase in the abundance of edge species have been found repeatedly in the study of mainland habitat fragments of decreasing size (Galli et al. 1976, Whitecomb et al. 1981, Humphreys and Kitchener 1982, Howe 1984, Opdam et al. 1985, Haila et al. 1987, Van Dorp and Opdam 1987, Opdam 1991). Distribution patterns of species shared with our study area in old growth fragments on the American mainland are generally consistent with those that we observed for real islands, but a few exceptions emerge. The American robin, northern flicker, American crow and song sparrow are usually equally present in all fragments (Forman et al. 1976, Rosenberg and Raphael 1986). All these species sometimes forage on the ground in open habitats and hence may use matrix areas adjacent to forest fragments.

We conclude that: 1) habitat structure is significantly influenced by the area and the isolation of an island at least for the smallest islands we considered; 2) the distribution of the bird species among the islands matches the distribution of habitat features that are consistent with the biology of these species, suggesting that area- and isolation-mediated variation in habitat structure is the ultimate factor involved in explaining the local diversity of the bird community; 3) only for a marginal number of species restricted to the largest islands or missing from the very small islands is a higher rate of stochastic extinction with

decreasing area the most parsimonious hypothesis explaining species distribution patterns; 4) there is no evidence in our example that supports the random placement theory (Connor and McCoy 1979) which presupposes habitat similarity among islands. Such a prerequisite might never apply to an area range including small islands; 5) the species-area relationship actually derives from processes that are more complex than the simple dropping off of species in a nested fashion as island size decreases. There are large and small island species, as well as species that are indifferent to variation in island area. Caution is required therefore in the analysis of summary statistics, such as species-area slopes, without a proper knowledge of single species distribution and biology. Simberloff and Martin (1991) called for similar caution when nested patterns of species distribution among islands or fragments are analysed and are used to draw principles for species conservation.

Such results emphasise, as pointed out by Haila (1986), how the restriction imposed by the Equilibrium Theory on species presence-absence matrices prevents a deeper understanding of the biology of islands. The intricate relationship between the habitat features of an island and its area, isolation and general geographical context are neglected. A full understanding of the local bird community needs a good knowledge of the general ecology of the islands, together with an understanding of how it is affected by area and isolation. (e.g. Martin 1992). These may be steps towards the ecological definition of an island called for by Haila (1990).

Thus, area and isolation-mediated habitat variation rather than island area or isolation per se explain the distribution of species on the islands of Gwaii Haanas. These islands may be too close together for there to be much barrier to dispersal between islands as far as birds are concerned. Furthermore, at least one third of the bird species are long distance migrants which have to recolonize the islands each spring. Consequently, the Equilibrium Theory may have little relevance to the local avian community structure in this archipelago.

Acknowledgements – We wish to thank the CNRS, the Pacific and Yukon Branch of the Canadian Wildlife Service, the Archipelago Management Board, the Canadian Parks Service, the Laskeek Bay Conservation Society, and the Queen Charlotte Islands Museum for logistic and financial support and for authorisation to work in Gwaii Haanas. K. Heise, A. Lawrence, S. Smith, J. Whitney and S. Blangy did not spare their efforts and sleep to help in the field. C. and T. Husband helped in keeping standards of cooking supplies high, and Guujaaw in exciting our interest for these islands beyond their Natural History. Finally we thank K. Moore for his helping presence on the other side of the phone and for handling the "mainland logistics" that kept us going. F.C. James and J.A. Wiens kindly provided comments and criticisms on the manuscript. Part of this work was done while JLM was a CNRS/NSF grantee at the Dept of Biological Science, Florida State Univ., Tallahassee, FL.

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Appendix

List of all the land birds recorded during or outside point count censuses on each of the 66 islands surveyed in Gwaii Haanas during this study. Islands are listed according to decreasing area. n = island identification number on Fig. 1. For definition of the acronyms of the species observed during point counts see legend of Table 5. BEAG = bald eagle; RTHA = red-tailed hawk; SSHA = sharp-shinned hawk; PFAL = peregrine falcon; TSWA = tree swallow; SWAI = Swainson's thrush; PGRO = pine grosbeak *Pinicola enucleator*; SVUL = European starling *Sturnus vulgaris*. * = island surveyed but not censused by point counts.

Island name	n	B E A G	R T H A	S S H A	P F A L	B T S W A	H I M W L	F I M W L	H I M W L	T S W A	W S W A I	C R A H U R R E N	C R A H U R R E N	N C H E N	C W R O B E R I	R V O A E R I	H S W I N S O N	S K O O I W L S O N	O T I W L S O N	W S C I R U G O S	C J P F S	J U G O O V	P R X N U	F O R S G	S V U L		
Moresby	42																										
Louise	1																										
Burnaby	43																										
Ramsay*	41																										
Murchison	2																										
Reef	3																										
Bolkus	44																										
East Limestone	4																										
House	5																										
Bischof north	6																										
De la Beche	7																										
George	45																										
East Copper	46																										
Hotspring	8																										
Agglomerate	9																										
Marco	10																										
"Long Island" Jedway	47																										
West Limestone	11																										
Swan	48																										
Haswell	12																										
Bischof south east	13																										
Helmet	14																										
Murchison islet	15																										
Hutton	16																										
Low	17																										
Skedans west	18																										
"Island Bay 3"	49																										
Skincuttle	50																										
Swan islet	51																										
Tar south	19																										
Bischof center	20																										
Kawas south west	21																										
Boulder	52																										
Titul	22																										
Skedans south	23																										
Lost	24																										
Sivart	25																										
South Low	26																										
Sea Pigeon	53																										
Kawas north	27																										
"Island Bay 1"	54																										
"Little" Reef	28																										
Bolkus islet 2	55																										
"Island Bay 7"	56																										
Harriet	57																										
Skedans east	29																										
"Island Bay 8"	58																										
"Island Bay 5"	59																										
Bolkus islet 1	60																										
Flowerpot	31																										
Hotspring islet 1	30																										
Bischof west	32																										
Hoskins large	33																										
Bolkus islet 3	61																										
Skedans north	34																										
Rock islets	62																										
Faraday north	35																										
Hotspring islet 3	36																										
Swan islet	63																										
"Island Bay 4"	64																										
"Island Bay 2"	65																										
Hotspring islet 2	37																										
House islet 1	38																										
Hoskins small	39																										
Marco small	40																										
"Island Bay 6"	66																										