

A MODEL APPROACH FOR ESTIMATING COLONY SIZE, TRENDS, AND HABITAT ASSOCIATIONS OF BURROW-NESTING SEABIRDS

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Abstract. We present a prototype monitoring strategy for estimating the density and number of occupied burrows of burrow-nesting seabirds. We use data and management questions from Washington State as an example that can be applied to burrow-nesting seabirds at single- or multi-island scales. We also demonstrate how habitat assessments can be conducted concurrently. Specifically, we compared the density and occupancy of burrows of the Rhinoceros Auklet (*Cerorhinca monocerata*) at nesting colonies in the California Current and the Salish Sea and in the 1970s, 1980s, and today. We estimated 36 152, 1546, and 6494 occupied burrows on Protection and Smith islands (Salish Sea), and Destruction Island (California Current), respectively. Our estimates for the Salish Sea are 52% greater than those from the 1970s and 1980s, while that for the California Current is 60% less than that of 1975. This suggests that the Salish Sea population has increased, despite greater human effects on that ecosystem. However, some of the estimated changes between the periods could be the result of methodological and analytical differences. To address these issues we recommend an unbiased and representative sampling approach (stratified random) and an approach for optimally allocating the samples among strata within and among islands, depending on the scale of the question being addressed. Optimally allocating the sample would save a great deal of field effort; using this approach, we achieve relatively high power (>0.80) to detect moderate changes (20%) sampling hundreds of fewer plots than in a sample not optimally allocated.

Key words: burrow-nesting seabirds, ecosystem health, habitat associations, monitoring, Rhinoceros Auklet.

Un Enfoque Modelo para Estimar el Tamaño de la Colonia, las Tendencias y las Asociaciones de Hábitat en Aves Marinas que Anidan en Madrigueras

Resumen. Presentamos un estrategia de monitoreo prototipo para estimar la densidad y el número de madrigueras ocupadas en aves marinas que anidan en madrigueras. Empleamos datos y preguntas de manejo del estado de Washington como un ejemplo que puede ser aplicado a diversas aves marinas que anidan en madrigueras a la escala de una isla única o de múltiples islas. También demostramos como las evaluaciones de hábitat pueden ser conducidas conjuntamente. Específicamente, comparamos la densidad y la ocupación de madrigueras de *Cerorhinca monocerata* en las colonias de anidación de la Corriente de California y del Mar de Salish en los años 70s, 80s y hoy. Estimamos 36 152, 1546 y 6494 madrigueras ocupadas en las islas Protección y Smith (Mar de Salish) y la isla Destrucción (Corriente de California), respectivamente. Nuestras estimaciones para el Mar de Salish son 52% mayores que aquellas de los años 70s y 80s, mientras que para la Corriente de California son 60% menos que la de 1975. Esto sugiere que la población del Mar de Salish ha incrementado, a pesar de los mayores efectos antrópicos en este ecosistema. Sin embargo, algunos de los cambios estimados entre los períodos podrán ser el resultado de diferencias metodológicas y analíticas. Para abordar estos temas, recomendamos un enfoque de muestreo no sesgado y representativo (estratificado al azar) y un enfoque para asignar óptimamente las muestras entre los estratos dentro y entre islas, dependiendo de la escala de la pregunta abordada. La asignación óptima de la muestra ahorraría un gran parte del esfuerzo de muestreo; usando este enfoque, alcanzamos un poder relativamente alto (>0.80) para detectar cambios moderados (20%), muestreando cientos de parcelas menos que en un muestreo no asignado de modo óptimo.

INTRODUCTION

Information from long-term monitoring is essential to making informed management decisions and to understanding relationships between animal populations and environmental conditions. For example, such information is used to describe changes in the

size of rare or declining populations (e.g., Miller et al. 2012), identify mechanisms for population changes (e.g., Chamberlain et al. 2000), assess changes in ecological conditions (e.g., Cairns 1987, Parrish and Zador 2003), and evaluate the effectiveness of management (e.g., Alexander et al. 2007). Marine birds, in particular, are often used as indicators of ecological conditions because

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of their ubiquity (Davoren and Montevecchi 2003), broad diet (Montevecchi and Myers 1995), and vulnerability to a range of human activities (Furness and Tasker 2000).

Precise and repeatable population counts are essential to estimating seabirds' population trends. Methods used to estimate seabird numbers include surveys at sea and counts at breeding colonies. Colony counts, which focus on numbers of adults attempting to breed, use mark-recapture methods (Sydeman et al. 1998), counts of birds in flight (Bretagnolle and Attie 1991), measurements of calling rates (Monteiro et al. 1999), and counts of nests and burrows (Rayner et al. 2007a). In the case of burrow-nesting seabirds, determining breeding activity can be problematic because not all burrows are occupied during any given nesting season. Thus accurate occupancy data for burrow-nesters are essential for colony estimates. Methods for obtaining occupancy information include playback response (Ryan et al. 2006), burrow scoping (Lawton et al. 2006), burrow excavation (Cuthbert 2004), and monitoring artificial burrows (Wilson 1991). Of these methods, burrow scoping is particularly effective because it causes little disturbance, can generate fairly large sample sizes quickly, and can be used on natural burrows throughout accessible areas on any given island.

For a monitoring program to achieve representative samples and statistically robust results, the monitoring methods need to be part of a larger sampling strategy. The strategy should consist of (1) a spatially and temporally defined question or objective, (2) an unbiased and representative sampling approach, (3) monitoring methods suitable to the species and environment (including the organism's spatial distribution), (4) methods that provide reasonably precise and repeatable results, (5) sample sizes sufficiently large to detect population changes with acceptable power, and (6) statistics appropriate for estimating temporal and/or spatial changes. Much of the literature on bird-population monitoring focuses on specific techniques (e.g., Bibby et al. 1992, Hutto et al. 1986). It is less common for the methods to be nested in a comprehensive monitoring strategy designed to address all of the components listed above (but see Gregory et al. 2004, Elzinga et al. 2001, Hayek 1994). Such strategies are necessary if seabirds are to be monitored comprehensively at large spatial scales, as called for in documents like the U.S. Fish and Wildlife Service's Pacific Region Seabird Conservation Plan (U.S. Fish and Wildlife Service 2005), and if we are going to directly address methodological and statistical issues that confound temporal comparisons and calculations of uncertainty for population estimates.

We present a colony-monitoring prototype for burrow-nesting seabirds by using data from the California Current (Destruction Island on Washington's outer coast) and two Salish Sea (Puget Sound and straits of Georgia and Juan de Fuca) islands (Protection and Smith islands). These field-tested methods and approach can be applied globally for many burrow-nesting seabirds. This strategy is well-suited for estimating population sizes and trends, burrow occupancy, precision of estimates, and statistical power. Specifically, we

present strategies at two spatial scales: (1) island-specific changes in the number of Rhinoceros Auklet (*Cerorhinca monocerata*) burrows between two periods of sampling (years) and (2) changes in the number of Rhinoceros Auklet burrows across multiple islands between the two periods. Finally, we demonstrate how habitat assessments can be conducted concurrently. This habitat information can be used to inform land management and restoration, to identify characteristics of critical breeding habitat, and to identify mechanisms potentially responsible for population changes within islands.

The data used in this approach were recorded during an assessment of an apparent decline in Rhinoceros Auklet populations in the Salish Sea since the 1970s (Wilson 2005). Rhinoceros Auklet colonies in the Salish Sea, a 16 925-km² inland sea that extends from Olympia, Washington, USA, north to the Campbell River, British Columbia, Canada (Fig. 1), are of global importance (Gaston and Deschesne 1996). The Salish Sea has been dramatically altered by human activities (Ruckelshaus and McClure 2007, Gaydos and Brown 2009, Pearson et al. 2011) that could affect colony size and trend. In this study, we assess whether or not this important component of the Salish Sea food web was in decline and also compared population trends spatially, using auklet colonies in the Salish Sea (Protection and Smith islands) and on the outer Washington coast (Destruction Island in the California Current, Fig. 1) to determine whether any population changes since the 1970s were unique to the Salish Sea, implying conditions for breeding there were poor.

METHODS

STUDY AREAS

Protection Island (48° 08' N, 122° 55' W) is a 143-ha island (approximate extent above mean high tide) located 3.2 km NNW of the mouth of Discovery Bay at the eastern end of the Strait of Juan de Fuca in the Salish Sea. Smith Island (48° 19' N, 122° 50' W), covering 15 ha, also lies at the eastern end of the Strait of Juan de Fuca. Destruction Island (47° 40' N, 124° 24' W), covering 15 ha, is located 4.8 km west of the Olympic Peninsula and 29 km SSE of La Push, Washington, in the northern California Current (Fig. 1).

STUDY DESIGN

We used stratified random sampling to estimate measures of the population including burrow density and burrow occupancy on all three islands. We qualitatively compared our estimates to previously published estimates to highlight some of the methodological and statistical issues associated with these types of comparisons. To identify habitat features associated with auklet burrows, we used the same study plots and habitat data collected at the same time as our burrow estimate to relate habitat variables with burrow density. Finally, we used our estimates of burrow density in a power analysis designed to inform future monitoring and to be used as a prototype for similar efforts at monitoring burrow-nesting seabirds.

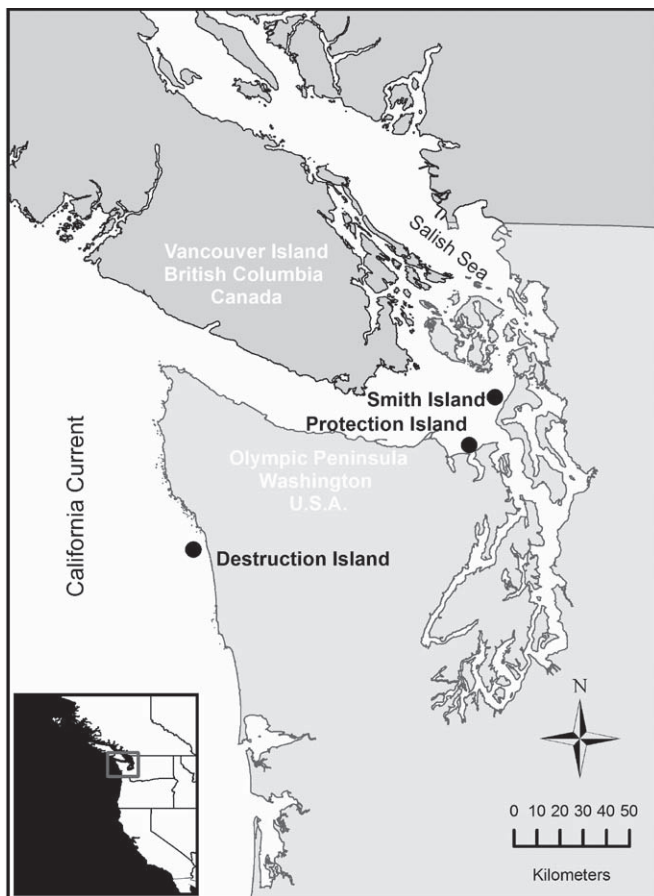


FIGURE 1. Map of the Salish Sea (Strait of Juan de Fuca, Puget Sound, and Strait of Georgia) and northern California Current (outer Washington coast) showing the islands studied (black circles).

DEFINING STRATA

Prior to sampling, we digitized strata by following natural geomorphic features known to be associated with varying levels of burrow density (slope breaks, changes in vegetation associated with changes in slope, and cliff edges; Thompson et al. 1985). The vertical cliff stratum on each island consisted of a single linear row of burrows at the upper edge of the cliff, and all burrows in this stratum on each island were counted as described below. We populated all other strata with random points in ArcGIS 9.2 (ESRI, Redlands, CA). We generated more random points in higher-density and larger strata to reduce variance associated with the overall estimate of burrow density; previous information on burrow density (Thompson et al. 1985, Leschner 1976) was invaluable for defining strata for Protection and Destruction islands. The strata for each island are identified in Table 1.

For Protection Island, we calculated the surface area of each stratum with digital elevation models by following Jenness (2004). For the island-top strata on Smith and

Destruction islands and the cliff-edge strata on Protection and Smith islands, we used the areal extent of these flat polygons (slopes generally around 1 to 2°). Because of the narrowness of the steep-slope polygon on Destruction Island and the large size of altitude raster cells (10 m) that would have been necessary to calculate the area of this stratum in ArcGIS, we decided to treat this polygon as a rectangular ribbon and calculated its area trigonometrically. To do this, we connected GPS reference points recorded along the upper and lower extent of burrows in ArcGIS to estimate the length of the ribbon. We estimated its width from its average elevation and slope. Elevation was provided by the Trimble GPS unit, and we measured the slope of random plots within this stratum as described below.

FIELD METHODS

Random points were generated in ArcGIS, and we then uploaded plot coordinates into the Trimble GPS unit, which we used to navigate to each point. We recorded the location of each plot sampled with the GPS unit and marked the plot's center. For each plot, we counted the total number of burrows within a 2.5-m radius of the center. For burrows on the edge of the plot, we included those for which the 2.5-m radius touched at least one entrance.

We defined burrows by characteristics determined with infra-red camera probes (Sandpiper Technologies Peep-A-Roo Video Probe) and/or by direct manual inspection. We considered any excavated hole that extended beyond the reach of our arm a burrow. In our experience, all or nearly all burrows longer than an arm's length have at least one nest chamber, and this method excludes "burrow starts," which tend to be very short (<0.5 m). Using the camera probe, we visually assessed the structure of a burrow, defining it as an entrance that led to both a tunnel and at least one nest chamber. We considered burrows with more than one entrance a single burrow unless there were two separate tunnels and two nest chambers. Collapsed burrows were not counted as burrows.

For each plot we used the camera probe to assess the occupancy of the burrows nearest the plot's center until either we had determined the occupancy of 6 burrows or all burrows had been probed (i.e., for plots with ≤ 6 burrows). In some cases, we could not determine the contents of a burrow (occupancy status) and excluded it from our occupancy estimate. A burrow with an adult, egg, or chick was considered occupied.

Within each 2.5-m-radius plot, we measured habitat variables at the center stake: slope angle with a clinometer; slope aspect in degrees with a compass, and elevation with the GPS unit. We estimated percent cover and height of grasses (perennial and annual), forbs, shrubs, and trees at three height classes: ≤ 1.5 m (grasses and forbs), 1.6–3 m (shrubs), and ≥ 3.5 m (trees). For the four vegetation classes, we estimated cover as: <1%, 1–5%, 6–25%, 26–50%, 51–75%, and 76–100%.

TABLE 1. Surface area, number of plots, burrow counts, density, occupancy rates and associated variance by stratum on Protection (2008), Destruction (2009), and Smith (2010) islands.

Island and stratum	Surface area (m ²)	Number of plots ^a	Total burrow count	Average number of burrows/plot	Sample variance	Burrow density/m ²	Burrow occupancy ±1.96 (SE)	Estimated total number of burrows ±1.96 (SE)
Protection								
Steep slope	156 251	79	406	5.1	16.33	0.26	64.3 ± 6.4	40 907 ± 7093
Cliff edge	31 560	44	165	3.8	21.68	0.19	69.7 ± 11.8	6029 ± 2212
Transitional	68 168	15	31	2.1	10.92	0.11	68.9 ± 25.4 ^b	7177 ± 5807
Island top	836 194	28	0	0.0	0.00	0.00	—	0
Vertical cliff	Linear feature	—	681	—	—	—	—	681
Totals	1 092 173	166	1,283				66.0 ± 5.3	54 794 ± 9390
Destruction								
Steep slope	55 473	54	213	3.9	18.36	0.20	55.1 ± 10.9	11 147 ± 3230
Island top	103 780	26	0	0.0	0.00	0.00	—	0
Vertical cliff	Linear feature	—	76	—	—	—	—	76
Totals	159 253	80					55.1 ± 10.9	11 222 ± 3199
Smith								
Cliff edge	9116	30	96	3.2	7.27	0.16	68.7 ± 12.8	1486 ± 448
Island top	115 540	30	1	0.03	0.033	0.002	100	200 ± 384
Vertical cliff	Linear feature	—	819	—	—	—	—	819
Totals	124 656	60					68.7 ± 12.8	2505 ± 577

^aPlots were 2.5 m in radius (19.6 m² in area).

^bThe sample size (25 burrows probed) for this stratum was lower than typically used for a confidence interval based on asymptotic standard error. The Clopper–Pearson exact 95% CI is 47–85% (SAS PROC FREQ, SAS Institute 2007).

STATISTICAL ANALYSES

We estimated the total number of burrows on an island

$$\hat{t}_{str} = \sum_{h=1}^H N_h \bar{Y}_h$$

where \hat{t}_{str} = estimated total number of burrows

rows among all strata, suffix h denotes stratum, N_h = total possible number of sampling plots in stratum h (area of the stratum divided by the area of the plot or 19.635 m²), and \bar{Y}_h = sample mean in stratum h (Lohr 2010, equation 3.1). Overall

variance was derived
$$\hat{V}(\hat{t}_{str}) = \sum_{h=1}^H \left(1 - \frac{n_h}{N_h}\right) N_h^2 \frac{s_h^2}{n_h}$$

where n_h = number of sample plots in stratum h , and s_h^2 = sample variance in stratum h (Lohr 2010, equation 3.4). To estimate the number of burrows on the vertical cliff we took the average count from three people counting independently from a boat (Protection) or from land (Destruction). The vertical cliff stratum on Smith Island was very long, so we counted the number of burrows in a series of high-quality digital photographs (taken with a Nikon D200 camera with an AF-S Nikkor 70–300-mm zoom lens). To estimate the total number of burrows on an island we added counts of burrows in the vertical cliff stratum to the estimate of total burrows in the other strata(um) on the island. On Protection and Destruction the island-top strata contained no burrows, so we

eliminated these strata from all estimates. Because there was only one occupied stratum on Smith (except for one burrow in the island-top stratum) and Destruction islands, we calculated a single occupancy rate for each island (Table 2). We also used a single occupancy estimate for Protection Island because occupancy rates did not differ significantly by stratum (see Results).

To estimate the total number of occupied burrows on an island, we multiplied the estimate of the total number of burrows by the estimate of occupancy for the whole island (total number of occupied burrows probed divided by the total number of probed burrows with definitive outcomes for each island). These two estimates (occupancy and total number of burrows) are not independent because they were measured in the same plots and include some of the same burrows. Therefore, we used a bootstrap approach to obtain confidence intervals for their product: the estimate of the total number of occupied burrows. For each island we drew 1000 bootstrap samples, preserving the stratum-specific sample sizes in each replicate. For each bootstrap replicate we (1) estimated the total number of burrows and the occupancy rate and (2) multiplied these two estimates to obtain an estimate of the total number of occupied burrows. From the resulting 1000 estimates of total number of occupied burrows, we took the 2.5th and 97.5th percentiles of the bootstrap samples to obtain 95% confidence intervals.

TABLE 2. Summary of burrow count (± 1.96 [SE]), occupancy (± 1.96 [SE]), and occupied burrow (95% confidence interval) estimates for Protection, Destruction, and Smith islands

Site and year	Burrow estimate	Occupancy estimate	Occupied burrows ^a	Source
Protection Island				
1961	1500–2000	—	—	Richardson (1961)
1977	27 549	62%	17 108	Wilson (1977), Wilson and Manuwal (1986)
1983	27 059	—	—	Thompson et al. (1985)
2000			12 000	Unpublished data cited in Wilson 2005
2008	54 797 (± 9390)	66% ($\pm 5\%$)	36 145 (29 602–43 084)	This report
Destruction Island				
1976	27 394	59%	16 162	Leschner (1976)
2009	11 222 (± 3199)	55% ($\pm 10\%$)	6498 (4493–8846)	This report
Smith Island				
1974	1194			Wilson and Manuwal (1986)
2010	2505 (± 577)	69% ($\pm 6\%$)	1548 (1157–2019)	This report

^aThis variable has also been described as the number of nesting Rhinoceros Auklet pairs on the island.

To examine associations between burrow density and the habitat variables listed above, we used overdispersed Poisson regression in SAS PROC GENMOD (SAS Institute 2007), restricting our analysis to occupied strata (potential habitat). In the model, “grass” included annual plus perennial grass and so could exceed 100% cover. For all variables, we used midpoints of the ranges cover classes (e.g., 1–5% = 3%). We tested the overall significance of the factor effect of island with a likelihood-ratio test, compared to a chi-squared distribution with 2 degrees of freedom. We centered the value of slope angle across islands and then squared that term (“centered-squared slope”) to reduce the correlation between slope and slope² (Neter et al. 1996). As trees and shrubs were rare within plots, we used the presence or absence of trees rather than cover classes in this analysis.

Finally, we examined the effects of sample size and sample allocation on precision of estimates and on the power to detect a population decline (Lohr 2010, equation 3.14). For the power analyses and precision (SE), we used finite population corrections to calculate the variance; we used a 1-tailed z -test with $\alpha = 0.05$ and 0.10 to evaluate the power to detect a 10, 20, or 30% decline in the total number of burrows relative to the estimated number of burrows for single islands or all islands combined. We conducted these analyses by (1) using the actual sample size and allocation of samples from this study compared to a future sampling date with optimal allocation and varying sample size and (2) assuming both time periods had optimally allocated samples with sample sizes varying but equal. For our power analysis, we assumed that sample variance within a stratum would remain constant even if the number of burrows declined. However, if burrow counts follow a Poisson distribution, the variance should decline as counts decline, so our estimate of power is conservative.

RESULTS

BURROW COUNTS, OCCUPANCY, AND POPULATION ESTIMATES

We established 166, 80, and 60 random sampling points on Protection, Destruction, and Smith islands, respectively; sampling points were allocated among strata as indicated in Table 1. Within the random plots, we probed 436 burrows on Protection Island 15–17 June 2008, 166 on Destruction Island 1–3, June 2009, and 89 on Smith Island 8–9 June 2010. On Protection Island, of the 435 burrows we could assess, 287 (66%) were occupied (we were unable to assess occupancy of one burrow). Of the occupied burrows, we observed chicks in 22 ($\cong 8\%$) and adults and/or eggs in all remaining burrows, indicating that our assessment was conducted at the end of the incubation period. On Destruction Island, of the 159 burrows we could assess, 92 (58%) were occupied (we were unable to assess occupancy of seven burrows). Of the occupied burrows, we observed a chick in one burrow and adults and/or eggs in all remaining burrows, so our assessment of that island took place the end of the incubation period as well. We surveyed the plots in the island-top stratum at Protection Island between 17 and 29 July and at Destruction Island on 15 July; none of the plots contained burrows. On Smith Island, of the 83 burrows that we could assess, 56 (65%; we were unable to assess occupancy of six burrows) were occupied. Of the occupied burrows, we observed adults and/or eggs in all burrows, indicating that our assessment was conducted during the incubation period.

We estimated that there are 54 794, 11 222, and 2505 burrows on Protection, Destruction, and Smith islands, respectively (Table 2). In occupied strata, burrow density varied from 0.002 to 0.26 burrows m^{-2} , depending on stratum (Table 1) and island (Table 2). On Protection Island, the average percent

occupancy rate per plot did not differ by stratum ($\chi^2 = 3.21$, $df = 2$, $P = 0.20$), with an overall average of 66% (Table 2). Occupancy rates for the steep-slope stratum on Destruction Island and the cliff-edge stratum on Smith Island were 55% and 69%, respectively. Only one plot in the island-top stratum had a burrow (it was occupied), and this burrow was located in a cluster of shrubs that extended inland from the cliff edge on Smith Island, suggesting the boundary of this stratum needed to be modified. From our fairly extensive coverage of this polygon while walking among random points we suspect that burrows in the island-top polygon are extremely rare.

Using the total number of occupied burrows divided by the total number of probed burrows with a definitive outcome, we estimated 36 145, 6498, and 1548 occupied burrows on Protection, Destruction, and Smith islands, respectively (Table 2). Assuming each occupied burrow represents a breeding pair, the overall estimates (95% confidence intervals) of breeding Rhinoceros Auklets are 72 291 (59 203–86 167) on Protection, 12 997 (8986–17 692) on Destruction, and 3096 (2315–4038) on Smith.

HABITAT VARIABLES ASSOCIATED WITH BURROWS

The effect of island was not significant in our regression model (likelihood-ratio test $\chi^2_2 = 3.68$, $P = 0.16$); therefore, we present only the model for all three islands combined (Fig. 2). Burrow density decreased with increasing forbs and grass and increased with increasing elevation and slope up to approximately 50°, then decreased with increasing slope. There was no effect of trees or shrubs (Fig. 2).

DEVELOPING A MONITORING STRATEGY

We present two different sampling strategies: in the first, we track changes in the number of burrows on each island between two periods of sampling (years); in the second, we track changes in the number of burrows across all three islands combined between two periods. At the all-island scale, the standard error of our estimates associated with our actual sample size ($n = 222$) decreased from 5065 to 4335 under optimal allocation. For individual islands, on Protection Island, the only island where multiple occupied strata were sampled rather than counted, the standard error of our estimate decreased from 4790 to 4313 when our sample size was allocated optimally (Fig. 3). Table 3 presents the optimal sample allocation for Protection Island only vs. all islands combined as well as the allocation of sampling effort from this study for comparison.

We compared the power for the sample allocation and number of plots from our study to scenarios of monitoring in which we varied sample sizes that were allocated optimally; we generally had very low power to detect small changes in the number of burrows for our multi-island example (adequate power to detect a 20% decline with $\alpha = 0.10$; Fig. 4) or our single-island example (adequate power to detect $\geq 30\%$ decline). However, allowing sample sizes to vary equally between periods of sampling and using optimal allocation for both periods increased power dramatically for both our multi- and

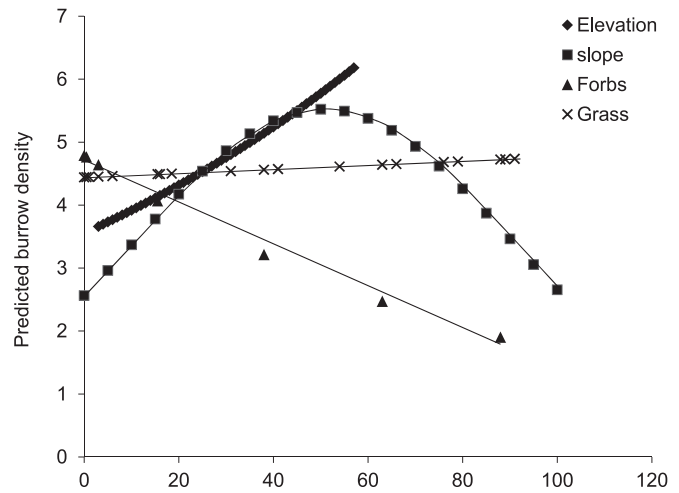


FIGURE 2. Relationship between burrow density and percent cover of grasses and forbs, percent slope, and elevation in meters. To generate curves, we used variable estimates from our Poisson linear regression and held all other variables to their median values.

single-island examples (Fig. 4). For example, as seen in Figure 4, with a sample size of 300 plots allocated optimally among strata and islands in both periods, at $\alpha = 0.05$, there is ≥ 0.80 power for detecting a $\geq 20\%$ decline in the number of burrows. This type of graph and associated tables can be used to determine sample sizes based on the desired precision and geographic scale of inference (e.g., single-island vs. all-island). For these comparisons, we are assuming that sample variance per stratum does not change even as the counts change; should the variance decline as the number of burrows declines (as is typical for count data), power would be even greater.

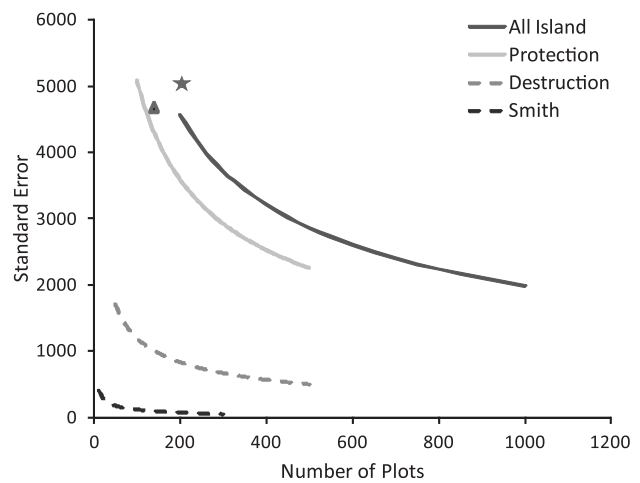


FIGURE 3. Relationship between the standard error and our estimate of total number of burrows for all three islands combined (all island) and for each island under optimal allocation (see Table 3) and various numbers of plots. The star indicates the sample size and standard error associated with all islands, the triangle the sample size and standard error associated with Protection Island.

TABLE 3. Proportion of total number of plots by stratum and island under optimal allocation for Protection Island, all three islands combined, and the allocation in this study.

Island	Stratum	Optimal allocation, Protection Island	Optimal allocation, all islands	Study allocation
Protection	Steep slopes	0.6291	0.487	0.356
Protection	Cliff edge	0.146	0.098	0.068
Protection	Transitional	0.224	0.213	0.198
Destruction	Slope		0.173	0.243
Smith	Edge		0.028	0.135

DISCUSSION

Counter to the population decline previously reported for the Salish Sea (Protection and Smith islands; Wilson 2005), our estimate of the Rhinoceros Auklet’s breeding population is 51% greater than previous systematic estimates (e.g., Thompson et al. 1985, Table 2), suggesting a growing

population. Moreover, our estimate for Destruction Island in the California Current was less than 50% of that made in the 1970s (see Table 2). Continuing studies of burrow occupancy, reproductive success, and diet quality and composition on Protection Island also indicate little to no changes in these measures since the 1970s (Pearson et al., unpubl. data)

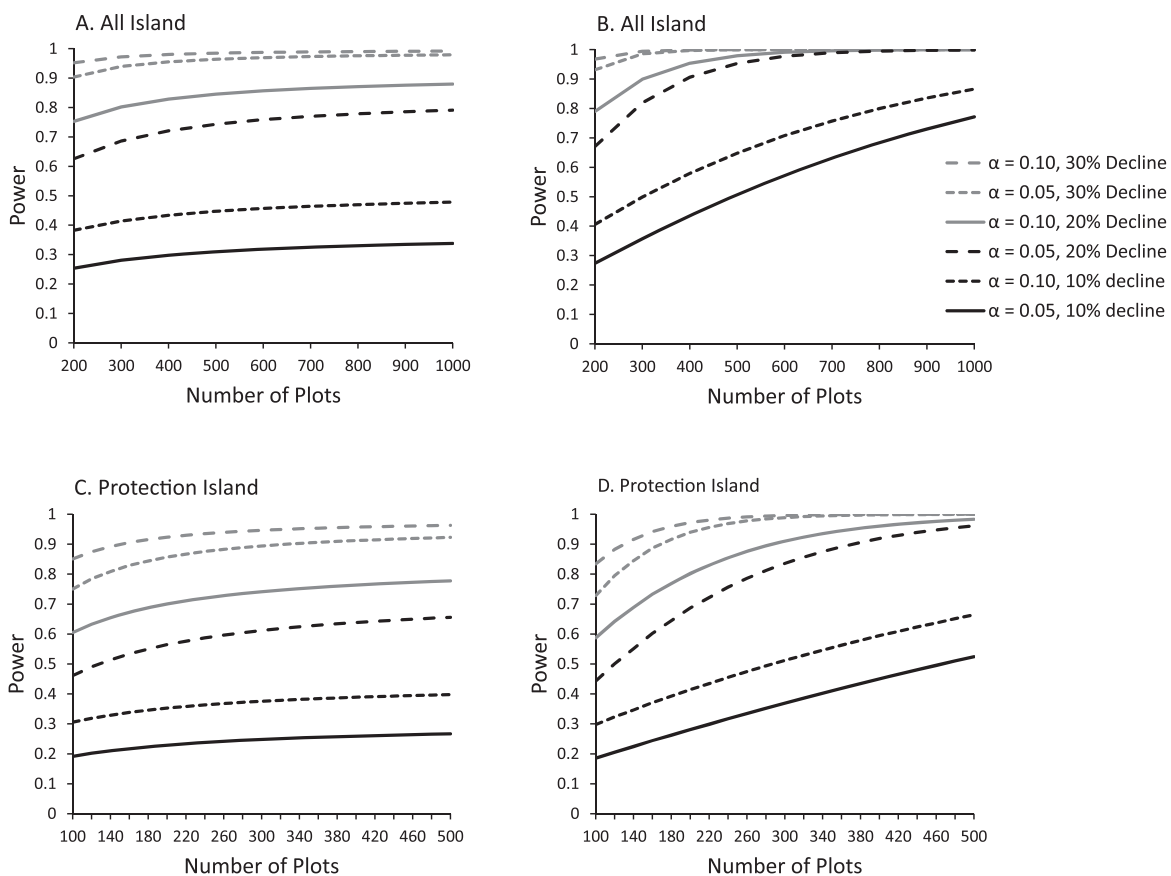


FIGURE 4. The relationship between power and sample size (number of plots) for different levels of α and different levels of burrow decline (% of the original estimate). The top panels (A and B) are for, all islands, the bottom panels (C and D) for Protection Island. The panels on the left (A and C) are based on the actual sample size ($n = 222$) and allocation to strata in this study for the first year of sampling while the sample size in the second sampling period is allowed to vary and the allocation is optimal. The panels on the right (B and D) show the results of calculations in which sample sizes vary but are equal for both sampling periods; both were optimally allocated. In all cases, we assumed that sample variances (per stratum) do not change even as the counts change. It would be reasonable to expect the variance to decline as the number of burrows declines, which would result in power higher than presented.

and suggest generally good conditions for successful auklet reproduction in the Salish Sea.

While it is likely that the population on Protection Island has indeed grown since the last systematic and published estimate in 1983 (Thompson et al. 1985), an increase from 27 000 burrows to somewhere between 44 000 and 64 000 burrows in 25 years would be fairly dramatic (annual growth of 1.95–3.45% if growth is exponential). The difference in estimates over the intervening period could reflect actual population changes or be due, in part, to methodological and statistical differences between the estimation procedures or variables. Previous estimates by Wilson and Manuwal (1986) and Thompson et al. (1985) employed a combination of subsampling within areas of high density and complete counts along cliff faces and areas of lower density. Even though subsampling was used to derive estimates, no associated variance was reported, so we cannot compare the lower bounds of our estimate to the upper bounds of previous estimates. If there was considerable variation among plots historically, the true difference between our estimate and previous estimates (Table 2: 27 059 vs. 54 794 burrows) may not be as great.

Finally, it is also possible that our random selection of plots on Protection Island was not truly representative of burrow distribution on the island. To test this possibility, we selected an additional 50 random plots on Protection Island in 2009 in the highest-density stratum (steep slope)—the area with the greatest influence on our overall estimate for the island. The average number of burrows estimated per plot in 2009 (6.1 ± 1.3 ; 95% CI) was even greater than the 2008 estimate (5.1 ± 0.9 ; 95% CI). These findings suggest that the population currently breeding on the island is in fact larger than was reported historically.

In contrast to Protection Island, the number of burrows on Destruction Island was less than half of the estimates from 1975 (Table 2). Leschner's (1976) burrow-density estimates ranged from 0.20 to 1.30 m^{-2} , and the stratum with the lowest density represented only 20% of the total area. Our overall estimate of burrow density was only 0.20 m^{-2} for the entire area the auklets occupied. If we weight Leschner's density estimates per stratum by their overall proportion of the area surveyed, the overall density estimate is approximately 0.80 m^{-2} , which is four times greater than our density estimate (0.20 m^{-2}). This comparison suggests that the population on Destruction Island has truly declined.

The statistical and methodological differences among studies and time periods, especially for Protection Island, illustrate the difficulties associated with assessing trends in colonies of burrow-nesting seabirds. To address these issues, we designed a burrow-sampling strategy that can be applied at the spatial scale of interest. First, the field methods can be applied quickly with relatively little disturbance to the colony. For sampling, we located study plots randomly within strata and allocated plots among islands and strata on the basis of published information on burrow density and our knowledge

of the sites (Rayner et al. 2007a, b). However, we lacked the preliminary data needed to determine sample sizes and sample allocation for a given effect size. This prior information would have allowed us to allocate our sample optimally among strata and islands. To address this issue and to inform future monitoring, we used the data from this study to develop recommendations for assessing future changes at the scales of both the individual island and all islands. This approach could easily be scaled up to assess changes in the North American breeding population of the Rhinoceros Auklet, for example.

Our power analysis indicates that at the all-island scale, over 800 plots optimally allocated among islands and strata and with equal sample sizes in each time period would be required for power high enough (≥ 0.80) for a relatively small (10%) population decline to be detected. However, with 300 plots optimally allocated, there is high power (≥ 0.80) to detect moderately large ($\geq 20\%$) declines (Fig. 4). At the island scale, power to detect small population declines is again low; on Protection Island, however, power to detect $\geq 20\%$ declines with 150–330 plots per island and optimal plot allocation is high (≥ 0.80) (Fig. 4).

There are many tradeoffs one might consider when allocating samples. For example, during future sampling, it may not be important to repeat vegetation measurements every sampling period or to survey island-top strata, allowing more time for sampling plots in occupied strata or probing additional burrows within plots. Also, by not repeating the island-top surveys (unoccupied strata that represent non-habitat) and allocating the sampling effort to the occupied strata, we would have increased our sample size considerably with the same amount of effort.

If we assume that the vast majority of effort (cost of sampling) is in probing burrows, we can then explore the tradeoff between increasing the number of plots in occupied strata vs. probing more burrows within a plot. If we hold the expected number of burrows to be probed constant, then the precision of the estimate of occupancy is also approximately constant. Therefore, to minimize variance of the estimate for total number of occupied burrows, we have only to minimize the variance for the total number of burrows (or, equivalently, the mean number of burrows per plot), which is accomplished by maximizing the number of plots. This suggests that the optimal sampling strategy may be to sample more plots but probe only one burrow per plot.

The option at the other end of the spectrum is to determine occupancy of all burrows in a plot, especially if density is low. Doing so would result in an estimate of the mean number of occupied burrows in a plot. Based on the stratified random sampling design, this estimate could then be used directly to obtain an estimate of the total number of occupied burrows on an island with associated standard errors that allow for a finite population correction (as opposed to using the bootstrap to estimate variance). This latter strategy does not work in our system because we were unable to assess

occupancy for the vertical-cliff strata. Furthermore, any burrows for which the occupancy status cannot be determined would be problematic.

Using this sampling approach, resource managers can make informed decisions about future monitoring based on the scale of inference and the desired effect size. For example, under an optimal allocation strategy and assuming managers are interested in assessing a change in the number of burrows for all islands combined, we would increase our sample in the Protection Island strata with the most burrows and decrease our sample size on Smith Island, which has fewer burrows. However, this choice would preclude our ability to assess changes in the number of burrows on Smith Island.

Regardless of the statistical approaches and scale of inference, these types of surveys should be conducted during similar oceanographic conditions, because of the dramatic effects that anomalous conditions can have on burrow-nesting seabirds' occupancy and reproductive rates. For example, during the spring and summer of 2005, warm sea-surface temperature and winds disfavoring upwelling (Schwing et al. 2006) resulted in Cassin's Auklets (*Ptychoramphus aleuticus*) abandoning breeding colonies *en masse* (Sydeman et al. 2006). Fortunately, both the surveys we report and those during the 1970s were done during favorable and similar oceanographic and weather conditions (relatively cool or neutral sea-surface temperature and winds favoring early upwelling; Peterson et al. 2010) and are therefore comparable.

The concentration of such a large portion of the North American Rhinoceros Auklet population on Protection Island (Gaston and Deschesne 1996) indicates that population status and trends on this island have significant implications for the species as a whole. Land management should therefore focus on maintaining suitable nesting habitat as well as addressing issues that inhibit successful nesting. To identify the habitat features associated with burrows, we present a habitat-assessment approach that can be accomplished fairly quickly and simultaneously with the burrow-occupancy assessment. Results of this assessment indicate that Rhinoceros Auklets use higher-elevation sites, that burrow density increases with slope to about 50° and then declines, and that burrow density declines with increasing forb cover (Fig. 2). Elevation and slope characteristics can be used to identify important nesting areas within islands and, consequently, areas in which to (1) focus management and restoration and (2) limit activities that might disturb nesting auklets.

CONCLUSION

We present a model monitoring approach to comparing island-specific or multi-island changes in the number of burrows between two sampling periods (years) depending on the scale of inference desired. We include an approach for allocating effort and choosing sample sizes that should allow managers to detect population changes. We also use this example to demonstrate some of the statistical and methodological issues

associated with historical comparisons. Finally, we provide an efficient method for simultaneously identifying the habitat variables that predict burrow density. This habitat assessment can provide valuable information needed for restoration and protection or provide insights into observed colony trends.

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