

VARIABILITY IN COLONY ATTENDANCE OF CREVICE-NESTING HORNED PUFFINS: IMPLICATIONS FOR POPULATION MONITORING

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Abstract: It is difficult to survey crevice-nesting seabirds because nest-sites are hard to identify and count, and the number of adult birds attending a colony can be extremely variable within and between days. There is no standardized method for surveying crevice-nesting horned puffins (*Fraterecula corniculata*), and consequently little is known about abundance or changes in their numbers. We examined the variability in colony attendance of horned puffins at 5 breeding colonies in the North Pacific to assess whether variation in count data can be reduced to a level that would allow us to detect changes in the number of birds attending a colony. We used within-year measures of variation in attendance to examine the power to detect a change in numbers between 2 years, and we used measures of among-year variation to examine the power to detect trends over multiple years. Diurnal patterns of attendance differed among colonies, and among-day variation in attendance was generally lowest from mid- to late-incubation to early chick rearing. Within-year variation in water counts was lower than in land counts, and variation was lower using a daily index based on 5 counts per day than it was using 1 count per day. Measures of among-year variation in attendance also were higher for land-based than water-based counts, and they were higher when we used a 10-day survey period than when we used a 30-day period. The use of either 1 or 5 counts a day during the colony-specific diurnal peak of attendance had little influence on levels of among-year variation. Overall, our study suggests that variation in count data may be reduced to a level that allows detection of trends in numbers. However, more studies of interannual variability in horned puffin attendance are needed. Further, the relationship between count data and breeding population size needs more study before the number of birds present at the colony can be used with confidence as an index of population trend.

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Seabirds are vulnerable to a variety of anthropogenic threats such as oil pollution (Piatt et al. 1991) and commercial fishing operations (e.g., Barrett et al. 1987). They may also be valuable indicators of natural changes in marine ecosystems (Montevecchi 1993). Effective management of seabird populations requires reliable information on abundance and changes in the numbers of breeding birds. Without such knowledge it is impossible to quantify effects caused by natural changes in the marine environment or those arising from human impacts.

Detection of changes in the numbers of breeding seabirds generally relies on index counts of individuals and/or active nest-sites (e.g., Wanless et al. 1982, Walsh et al. 1995). Index methods are widely used to monitor population trends of avian species. Although indices cannot be used to

estimate population size, they may be used to estimate trend if we assume that (1) the index is correlated with population size, and (2) there is no temporal trend in the index ratio, which measures the relationship between actual population size and number counted (Bart et al. 1998). The precision of estimates of population change will depend on the interyear variability in the index ratio (Bart et al. 1998), and index methods are therefore designed to reduce the variation in counts associated with variability in behavior and detectability.

Many studies have examined variation in colony counts of seabirds and developed standard methods for population monitoring (e.g., Birkhead and Nettleship 1980, Hatch and Hatch 1989). Species breeding on exposed cliffs are relatively easy to survey because it is possible to count both active nests and birds and therefore estimate an index ratio (number of birds count-

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ed to the number of breeding pairs). Species that breed underground are more difficult to count (Savard and Smith 1985). Although counts of occupied burrows may provide an index of the number of breeding pairs of burrow-nesting species (e.g., Anker-Nilssen and Røstad 1993), this method is not suitable for crevice-nesting species because their nest-sites are difficult to identify and count (e.g., Byrd et al. 1983, Piatt et al. 1990, Jones 1992).

The horned puffin is an example of a crevice-nesting species of auk (Family Alcidae) that is especially hard to survey. Horned puffins typically nest in cracks in cliff faces, among boulders, or in rock crevices. Many crevice nest-sites have multiple or shared entrances and are often deep within unstable piles of boulders, making them hazardous for biologists to access, identify, and count. At present, there is no standardized method for surveying horned puffins, little is known about abundance or a change in numbers, and the development of survey methods is a high priority for the conservation of this species (Piatt and Kitaysky 2001).

Because it is difficult to count the number of nests directly, the number of breeding birds is unknown and there is no way of estimating an index ratio. Numbers of puffins attending the colony may provide an alternative estimate of abundance if we assume that the 2 are correlated (i.e., that the number of birds counted at the colony will decrease if the total breeding population is decreasing, and vice versa). Many crevice-nesting species of auk, however, have extremely variable colony attendance; it is not uncommon to observe thousands of adult birds at a colony 1 day and none or very few the next (e.g., Jones 1992). This variability in behavior and time spent at the colony might preclude detection of any trend unless count variability can be reduced below a level that will enable detection of change over a time scale that is biologically useful.

We collated historical data on the patterns of horned puffin colony attendance at 5 breeding colonies in the North Pacific. Although the retrospective nature of the data is reflected by the lack of uniformity among data sets, together they provide important information on the diurnal, seasonal, and annual variation in counts of horned puffins. We first analyzed variation in counts conducted on land and on water in order to determine (1) the least variable time of day and breeding season for counting, and (2) the number of counts required to detect prescribed

levels of change in the numbers of birds. Based on these results we suggest a potential monitoring protocol. Secondly, we provide guidance on what level of statistical power one might expect to have if the recommended protocol were applied to detect annual and longer-term changes in the number of birds attending the colony. Finally, we discuss whether there is enough biological evidence to suggest that the number of birds attending a colony is correlated with breeding population size.

STUDY AREA

Colony attendance of horned puffins was recorded at Talan Island (Sea of Okhotsk: 59°N, 149°E) in 2001; on Duck Island (western Cook Inlet: 60°09'N, 152°34'W; Harding 2001) during 1997–1999; on Buldir Island (western Aleutian Islands: 51°21'N, 175°56'E) in 1988, 1991, and 2001 (Konyukhov and Juk 2001); on Chowiet Island (56°N, 156°W; Hatch 2002) in 1977, 1993, and 1994; and on Suklik Island (56°N, 156°W; Hatch 2002) in 1986. Suklik and Chowiet are neighboring islands within the Semidi Island archipelago. Diurnal patterns of colony attendance were examined at Buldir, Talan, and Suklik, and seasonal patterns of attendance were examined at Duck, Talan, Buldir and Chowiet (Fig. 1).

METHODS

Puffins spend the winter at sea, returning to colonies in spring to breed. Horned puffins lay a single egg, incubated by both parents for an average of 41 days (Petersen 1983). After hatching, the chick is brooded constantly for the first 5–7 days (Wehle 1980). Once the chick has attained endothermy, it is left alone and is attended only briefly during food delivery. Both parents feed the chick over a typical nestling period of 37–46 days (Petersen 1983). Offspring fledge over a period of about a month, with individual adults departing the colony after their chick has fledged.

Using data on the timing of breeding events, we split the attendance data from each colony into incubation and chick-rearing intervals (Hatch and Hatch 1990; Harding 2001; Moore et al. 2001; E. U. Golubova, Laboratory of Ornithology, Institute of Biological Problems of the North, Magadan, unpublished data). Chick rearing was defined as the period from median hatching to median fledging. The period of incubation was defined as the 41 days prior to the median hatching date.

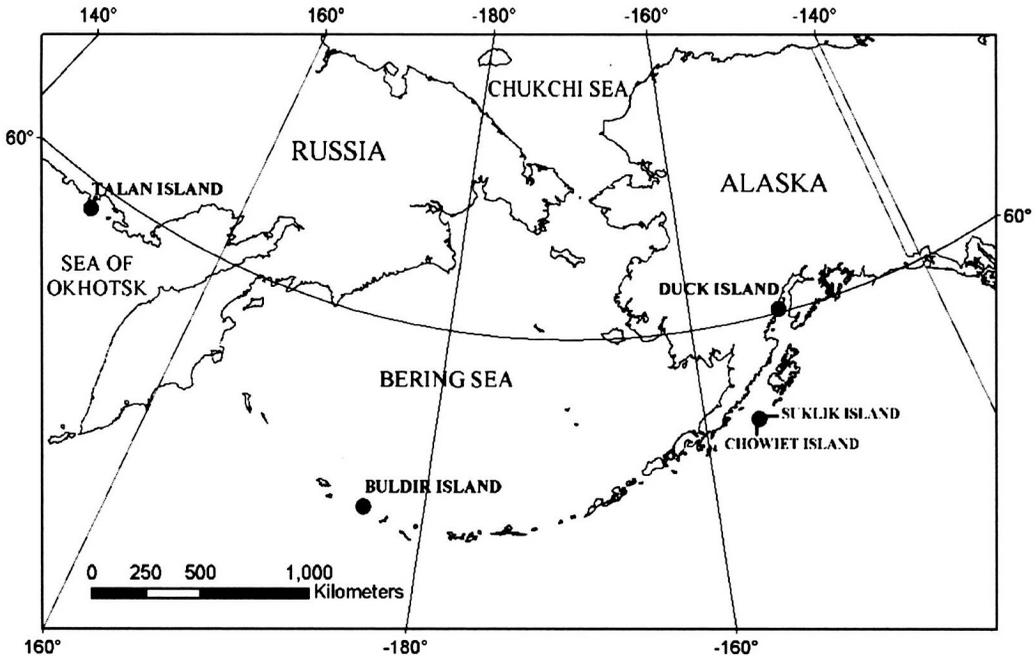


Fig. 1. Locations of the 5 horned puffin colonies.

Diurnal Attendance

Buldir Island 2001.—A land plot was established at the Main Talus subcolony ($\approx 2,000 \text{ m}^2$). A digital camera was used to photograph the plot every 15 min, 24 hr a day. Data were collected daily during incubation and chick rearing (11 Jun–4 Sep), with 4 days of data missing due to technical problems. Numbers of birds present in images taken 0615–2400 were later counted on a computer screen.

Talan Island 2001.—A land plot ($2,530 \text{ m}^2$) and a sea plot ($15,000 \text{ m}^2$) were established at Talan Island. Birds within each plot were counted at 15-min intervals from 0800 to 2300, using binoculars from a fixed observation point. Data were collected daily during incubation and chick rearing (20 Jun–29 Aug). Due to heavy rain and/or fog, no data were collected on 2 days in July and 3 days in August.

Suklik Island 1986.—Three land plots (viewable plot areas $25\text{--}55 \text{ m}^2$, comprising 15–33 burrow entrances) were monitored during incubation, using time-lapse photography from 8 to 29 June. An average of 12 frames was taken per hour. Birds per frame (hourly means) were plotted to ascertain diurnal patterns in attendance (Hatch 2002). Although the number of birds captured on film at any instant was small on average, the large number of observations yielded small SEs and an accurate depiction of temporal patterns.

Seasonal Attendance

Daily counts of birds attending the colony (Bédard 1969, Piatt et al. 1990) were used to assess seasonal patterns of attendance. Because within-day attendance varied markedly with time of day and colony, we determined the timing of peak diurnal attendance at each study site to establish the daily survey window.

We calculated a daily index of attendance from counts within the daily survey window at each colony, and we calculated 3-day running means of daily attendance indices to aid the visualization of seasonal patterns. Although all daily indices were calculated from counts conducted during peak attendance, calculation differed among islands according to the methods used. Indices were calculated at Buldir and Talan Island from the 5 consecutive counts conducted over a 3-hr diurnal peak, at Duck Island from 5 consecutive counts conducted over a 75-min diurnal peak, and at Chowiet Island from a single count conducted during a 2-hr daily peak. We present the detailed methods of data collection at each colony below.

Duck Island 1997, 1998, and 1999.—Duck Island diurnal attendance was bimodal during both incubation and chick rearing, with a peak in the morning and a more pronounced peak in the evening ($\approx 1900\text{--}2200$; A. M. A. Harding, Alaska Science Center, personal observation in 6 seasons of fieldwork;

Harding 2001). Counts (max 5 per day) of birds on water and land were made at 15-min intervals between 2030 and 2145 hr, and mean daily values were used as the daily index. Birds were counted separately on water and land, using binoculars from a fixed observation station overlooking North Cove. Water counts (sea plot) included all birds inside the cove boundaries and within 200 m from shore ($\approx 20,000 \text{ m}^2$); a set buoy was used for reference. Land counts (land plot) included birds on all north-facing land visible from the observation station ($\approx 100 \times 20 \text{ m}$). Counts were made daily between 27 June–31 August in 1997, 26 May–4 September in 1998 and 23 May–14 September in 1999. Wind speed (knots) was measured daily, using a hand-held anemometer (Kestrel brand) just prior to the first count.

Buldir and Talan Islands 2001.—A daily 3-hr period of peak attendance during the incubation and chick-rearing period was identified for Talan and Buldir islands (see RESULTS, Diurnal Attendance). A subset of daily counts from the period of peak attendance was drawn from the complete dataset at each island. For closer comparison with Duck Island, and with the aim of evaluating alternative monitoring protocols, we derived indices for Buldir and Talan using 5 consecutive counts obtained during the daily peak. We randomly chose 5 consecutive counts from the 13 counts conducted in the 3-hr peak interval, and the daily mean comprised the index. We repeated this process to generate 9 sets of daily indices. We calculated mean values and CVs for attendance during incubation and chick-rearing periods for each set, and then we averaged the 9 simulated means and CVs. Counts were made daily 11 June–4 September (Buldir Island), and 20 June–29 August (Talan Island).

Chowiet Island 1977, 1993, and 1995.—The preferred counting period on Chowiet was based on the time-lapse study of peak diurnal attendance on neighboring Suklik Island (see above). One count of horned puffins on the water was made between 0700 and 0930 hr daily (weather permitting), using binoculars from a fixed location overlooking the bay adjacent to the main camp on Chowiet Island. The observed area measured approximately 1,000 m along the shoreline and 500 m offshore, with conspicuous shoreline features at the lateral boundaries. Counts were made 28 April–29 August 1977, 26 May–20 August 1993, and 12 June–8 August 1995 (Hatch 2002).

To test whether the single count conducted during the daily peak on Chowiet Island would

adequately describe seasonal patterns, we subsampled Buldir Island data to simulate the protocol. Seasonal patterns reflected in 30 simulations closely resembled each other and the seasonal pattern based on our index of 5 consecutive counts on Buldir. We therefore concluded that the single count on Chowiet could be used reliably to characterize seasonal patterns.

Statistical Analysis

We used CVs to examine the daily variation in colony attendance during incubation and chick-rearing periods within each year and type of plot (land or water). We used a 2-way ANOVA to separate the effects of year and stage of breeding cycle (pre-laying, incubation, chick rearing) on the number of attending birds. We examined differences between the mean number of birds counted during pre-lay and incubation periods and during incubation and chick-rearing periods with an independent-sample *t*-test. We measured the strength of the relationship between wind speed and the numbers of birds attending Duck Island with a Pearson's product-moment correlation. We used a 2-tailed *Z*-test for the difference between 2 CVs (Zar 1996) to examine the variability in colony attendance. Unless otherwise indicated, values reported are means ± 1 SE and statistical significance was assumed at $P < 0.05$.

Autocorrelation.—We used autocorrelation to test for independence of counts among days and for possible periodicity in attendance (Brown and Rothery 1993). We calculated autocorrelation coefficients for pairs of daily indices separated by lag intervals of 1–40 days and plotted the autocorrelation functions using NCSS 2000 (Hintze 2000).

Power Analysis: Ability to Detect Difference Between 2 Years.—We used estimates of within-year variation (among-days CV) for water- and land-based counts in calculating the statistical power to detect an increase or decrease in the number of puffins attending the colony between 2 years using PASS 2000 software (Hintze 2000). We calculated within-year variation over a 30-day survey period (see below) for Buldir, Talan, Duck, and Chowiet Island counts (both water- and land-based) using 2 calculations of the daily index: (1) The mean of 5 consecutive counts conducted during the daily peak in attendance (Buldir, Talan and Duck Islands), and (2) 1 count per day during the daily peak of attendance (Appendix 1). In (2), we chose the single count randomly from counts obtained within the daily peak in

attendance. We repeated this to generate 30 sets of simulated single-count data. We calculated a within-year CV for each set, and we averaged the 30 simulated CVs. We then used mean CVs for land counts (1 and 5 counts per day) and water counts (1 and 5 counts per day) to calculate sample sizes (number of counting days per season) needed to detect a population change between 2 years of study. Desired power was set at 0.9 throughout, and 1-tailed tests were applied with a significance criterion of $P < 0.05$.

Power Analysis: Ability to Detect Trends Over Multiple Years.—We used interannual variation in attendance (i.e., CV of annual mean numbers counted during the survey period) at Duck and Chowiet Islands to estimate the power to detect change in the numbers of horned puffins across years using TRENDS (Gerrodette 1993, Hatch 2003). Ideally, such calculations are based on the residual variation of annual means remaining after the effect of any linear trend in actual population change is removed by regression (Hatch 2003). With only 3 years of count data available, it was not possible to separate the effects of true population change and random interannual variation in colony attendance. The mean number of birds attending Chowiet in 1977 was much higher than during 1993 and 1995, whereas indices of attendance calculated during the 3 consecutive years on Duck Island (1997, 1998, 1999) were quite similar. The reduction in attendance on Chowiet Island over 16 years could represent a decline in puffin numbers, or it could simply reflect high interannual variability in attendance and be unrelated to population change. Our aim was to use the values of interannual variation from these data sets to provide some illumination on the levels of statistical power one might achieve in attempting to detect trends in numbers of birds attending a colony. We decided to make the most conservative assumption of no change in population size in estimating the interannual CV on Chowiet. Therefore, our analyses comprise a worst-case scenario of high interannual variability (Chowiet Island) and a best-case scenario of low interannual variability (Duck Island), for purposes of calculating power to detect multiyear trends in a regression analysis.

To investigate the number of counts within days desirable for a monitoring protocol, we examined the power to detect trends in mean counts using both 1 and 5 counts as a daily index. We calculated estimates of interannual variation for Duck Island water and land counts (using both 1 and 5

counts per day as an index) and for Chowiet Island water counts using the single count per day. Estimates of interannual CVs for Duck Island were based on daily counts obtained: (1) over the entire survey period (28–30 days), and (2) during intervals limited to 10 consecutive days. In the latter case, we generated simulated data sets by randomly choosing intervals of 10 days within the 30-day survey period. We calculated the mean CV for 30 such subsamples. For the trend analysis, we used 2-tailed tests and a significance criterion of $P < 0.1$. Power was 0.9 for all analyses.

RESULTS

Diurnal Attendance

Diurnal patterns of attendance differed markedly among colonies, between water and land counts, and between incubation and chick-rearing periods. The pattern of diurnal attendance during incubation and chick rearing on Buldir was characterized by a gradual buildup of numbers to an evening peak between 1900 and 2200 (Fig. 2). Attendance during incubation on Suklik Island peaked in the morning hours (0800–1100). Attendance on Talan Island differed between incubation and chick-rearing periods, and between water- and land-based counts. A morning peak occurred on Talan during incubation (land, 1030–1330; water, 0915–1215; Fig. 2), whereas peak attendance occurred later in the day during chick rearing (land, 1700–2000; water, 1400–1700).

Seasonal Attendance

Pattern of Attendance.—Data on pre-laying attendance were limited to Duck Island in 1998 and 1999 and Chowiet Island in 1977, 1993, and 1995 (Table 1). On Duck Island, the mean number of birds attending the colony during pre-lay (125 ± 13 , $n = 44$) was lower than during incubation (176 ± 11 , $n = 72$; 2-way ANOVA on ranked data, Sokal and Rohlf 2000: $H = 58.6$, $df = 1$, $P < 0.001$), but it did not differ between years ($H = 3.1$, $df = 1$, $P > 0.05$). To allow comparison with Duck Island ($n = 22$ days in 1998 and $n = 23$ days in 1999), we confined analysis of Chowiet Island pre-lay data to 1977, the only year with pre-lay counts on consecutive days during the later part of pre-lay and up until the start of incubation. There was no difference between the mean number of birds counted on Chowiet Island in 1977 during pre-lay (197 ± 36 , $n = 33$) and the mean number counted during the incubation period (217 ± 25 , $n = 41$; $t = 0.54$, $df = 41$, $P = 0.59$).

Table 1. Numbers of horned puffins attending the colony during prelay, incubation and chick rearing at Talan, Buldir, Duck, and Chowiet Islands in the North Pacific.

Year	Prelay				Incubation				Chick-rearing				Z test ^a
	x (days)	\bar{x}	SD	CV	x (days)	\bar{x}	SD	CV	x (days)	\bar{x}	SD	CV	P
2001					39	135.4	78.2	0.58	26	141.0	111.7	0.79	>0.5
2001					33	248.4	158.5	0.60	28	155.8	138.2	0.89	>0.5
2001					46	9.4	8.4	0.89	38	21.6	13.8	0.64	>0.5
1997					27	20.9	16.4	0.79	38	32.6	21.7	0.66	>0.5
1997					27	152.7	56.0	0.37	38	71.7	46.2	0.64	<0.5 *
1998	21	13.9	21.0	1.5	37	36.1	34.1	0.94	27	40.0	36.7	0.91	>0.5
1998	22	103.7	99.5	1.0	37	155.2	101.7	0.65	27	64.6	64.6	0.76	>0.5
1999	23	29.8	34.6	1.2	35	38.4	29.9	0.78	37	51.6	33.7	0.65	>0.5
1999	23	97.8	59.5	0.6	35	130.5	71.1	0.54	37	55.5	63.6	1.15	<0.5 *
1977	33	197.0	203.8	1.0	41	217.0	159.8	0.74	28	175.6	112.2	0.64	>0.5
1993	22	237.6	240.0	1.0	38	62.3	39.6	0.64	14	47.0	41.0	0.87	>0.5
1995	10	97.4	47.3	0.5	28	60.0	42.0	0.70					

^a Z test (Zar 1996): Tests for difference between among-year variation (CV) during incubation and chick-rearing.

On Duck Island, counts were highest during incubation each year (Fig. 3). Attendance generally declined with the onset of chick-rearing, except for a marked rebound at the end of August, 1999 (Fig. 3). Whereas mean attendance (land and water counts combined) was higher during incubation (173 ± 8 , $n = 99$) than during chick rearing (103 ± 7 , $n = 102$; 2-way ANOVA on ranked data, Sokal and Rohlf 2000: $H = 283.2$, $df = 1$, $P < 0.001$), we found no difference among years ($H = 1.3$, $df = 2$, $P > 0.05$). A seasonal increase in attendance on land occurred on Buldir Island (Fig. 4), with significantly higher numbers present during chick rearing (21.6 ± 2 , $n = 38$) than during the incubation period (9.4 ± 1 , $n = 41$; $t = 4.8$, $df = 58$, $P < 0.001$).

Attendance of puffins on water at Talan Island exhibited 3 peaks (Fig. 4). Land counts were generally depressed during late incubation, but mean numbers attending the colony were similar during incubation and chick rearing (land counts $t = 0.26$, $df = 41$, $P = 0.80$; water counts $t = 1.89$, $df = 61$, $P = 0.06$; Table 1). Similarly, there was no difference in the mean number of birds counted on water during the incubation and chick-rearing periods on Chowiet Island (Table 1) in either 1977 ($t = 1.26$, $df = 66$, $P = 0.21$) or 1993 ($t = 1.2$, $df = 22$, $P = 0.24$).

Attendance and Weather.—At Duck Island, there was no relationship between wind speed (knots) and the daily index of birds on the water in 1999 ($r = 0.159$, $n = 69$, $P > 0.1$). There was, however, a weakly significant negative relationship between wind speed and the index of birds on land ($r = -0.36$, $n = 69$, $P < 0.05$).

Among-day Variation.—Coefficients of variation calculated for 5-day running intervals illustrate

the patterns of daily variation within years and among years and colonies (Fig. 5). Although patterns of seasonal variability differed among colonies and among land and water counts, CVs were generally high during pre-lay and early incubation and also towards the end of chick rearing. Among 11 possible comparisons (Table 1), we found significant differences in CV between incubation and chick rearing for Duck Island water counts in 1997 ($Z = 2.26$, $P < 0.05$) and 1999 ($Z = 2.52$, $P < 0.05$). Coefficients of variation in both years were higher during chick rearing than during the incubation period. There were no differences between CVs calculated for incubation and chick-rearing periods in the remaining 9 comparisons ($Z < 1.96$, $P > 0.05$). Among day variation was generally lowest from mid to late incubation through to early chick rearing (Fig. 5). We chose the last 30 days of incubation as a good potential survey period based on the relatively low variability in attendance from mid to late incubation through to early chick rearing and the easily identified survey end point (i.e., visual observation of adults carrying fish for chick feeding).

Autocorrelation.—Attendance at all colonies was highly variable (Figs. 3, 4) and often appeared to be somewhat cyclic, with pronounced peaks and troughs at intervals varying from 1 to 10 days. However, the periods and amplitude of fluctuation were irregular and out of phase, and they did not evince statistically significant periodicity (Brown and Rothery 1993). Marked serial dependence among daily counts and irregular fluctuations at time scales generally <10 days were present nonetheless (Fig. 6). Significant positive correlations at lag intervals of 1–5 days were observed at Talan, Buldir and Duck islands, and

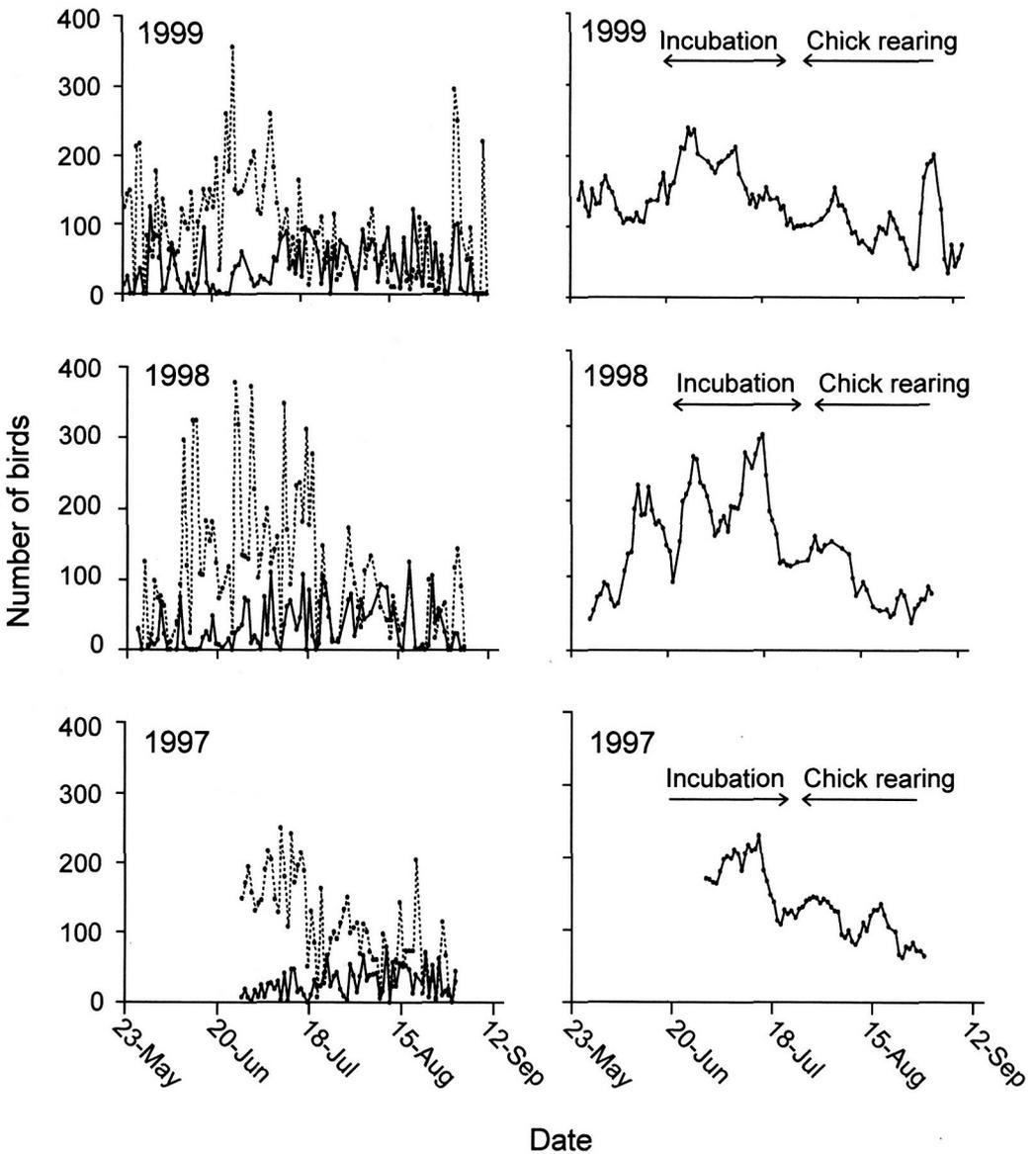


Fig. 3. Seasonal patterns of colony attendance by horned puffins on Duck Island, Alaska, USA, in 3 years. Daily index counts (see Methods) on water (dotted lines) and on land (solid lines) are presented on the left. Three-day running means of total birds (water and land combined) are presented on the right.

all significant correlations were of lag intervals of <10 days.

Power Analysis

Detecting Differences Between 2 Years.— The minimum detectable change in numbers between 2 years depended in part on the direction of change (Fig. 7). A decrease in numbers was easier to detect than an increase because of the posi-

tive linear relation between the mean and standard deviation of counts. For example, with 5 water-based counts conducted daily for 30 days, one is likely to detect a 33% decrease in population size, but only a 49% increase.

Within-year variation in water counts (mean CV = 0.59) was lower than the variation of land-based counts (mean CV = 0.81). Within-year variation for an index based on 5 counts per day (mean CV =

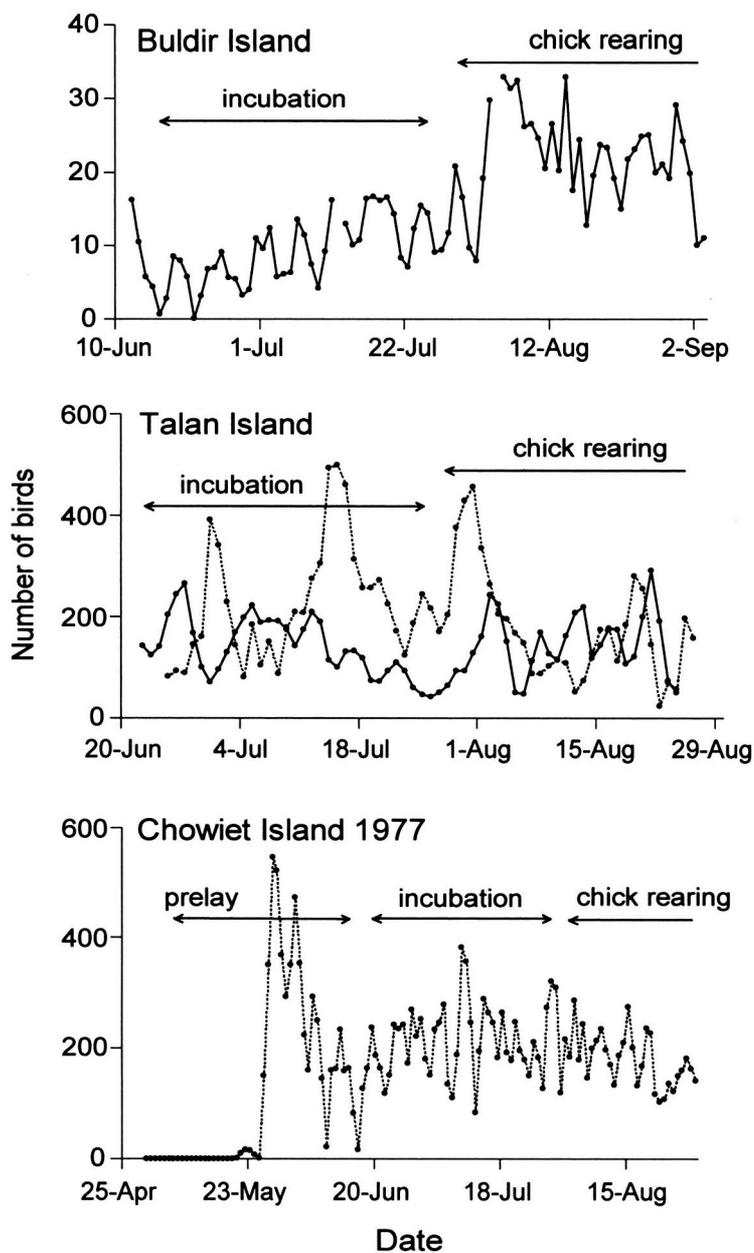


Fig. 4. Seasonal patterns of colony attendance by horned puffins at Buldir, Talan, and Chowiet Islands. Three-day running means of counts on water (dotted lines) and counts on land (solid lines).

0.64) was lower than daily variation (mean CV = 0.76) arising from 1 count per day (Table 2). Z-tests indicated small differences between CVs calculated for 1 vs. 5 counts per day (Table 2; $P=0.05$ for water counts; $P=0.16$ for land plots). Differences in within-year variation are reflected in power curves and the estimated effort needed to detect a given

amount of change (Fig. 7). For example, the ability to detect a 60% decrease in the number of puffins between 2 years probably would require 8 days with 5 counts per day on water, 14 days with 1 count per day on water, 16 days with 5 counts per day on land, or 22 days with 1 count per day on land.

Detecting Trends.—Discounting the possibility of population change on Chowiet between the 1970s and 1980s, interannual variation was higher (CV = 0.81) than on Duck Island (CV = 0.10; Table 3). On Duck Island, interannual variation differed among counting protocols, with less variation occurring on water plots (mean CV = 0.15) than on land (mean CV = 0.39). The choice of 1 or 5 counts per day, however, scarcely influenced the levels of interannual variation observed. Interannual variation in water counts was higher (mean CV = 0.2) for an annual index based on 10 consecutive days of counting compared with 28–30 days of counting (mean CV = 0.1).

We averaged estimates of interannual variation using both types of daily index (i.e. 1 vs. 5 counts per day) to yield 4 characteristic levels of variation among years: (1) Duck Island water plot counts, with a counting interval of 28–30 days and CV ≈ 0.1 ; (2) Duck Island water plot counts, with a counting interval of 10 days and CV ≈ 0.2 ; (3) Duck Island land plot counts, with counting intervals of either 10 days or 28–30 days and CV ≈ 0.4 ; and (4) Chowiet Island water-plot counts,

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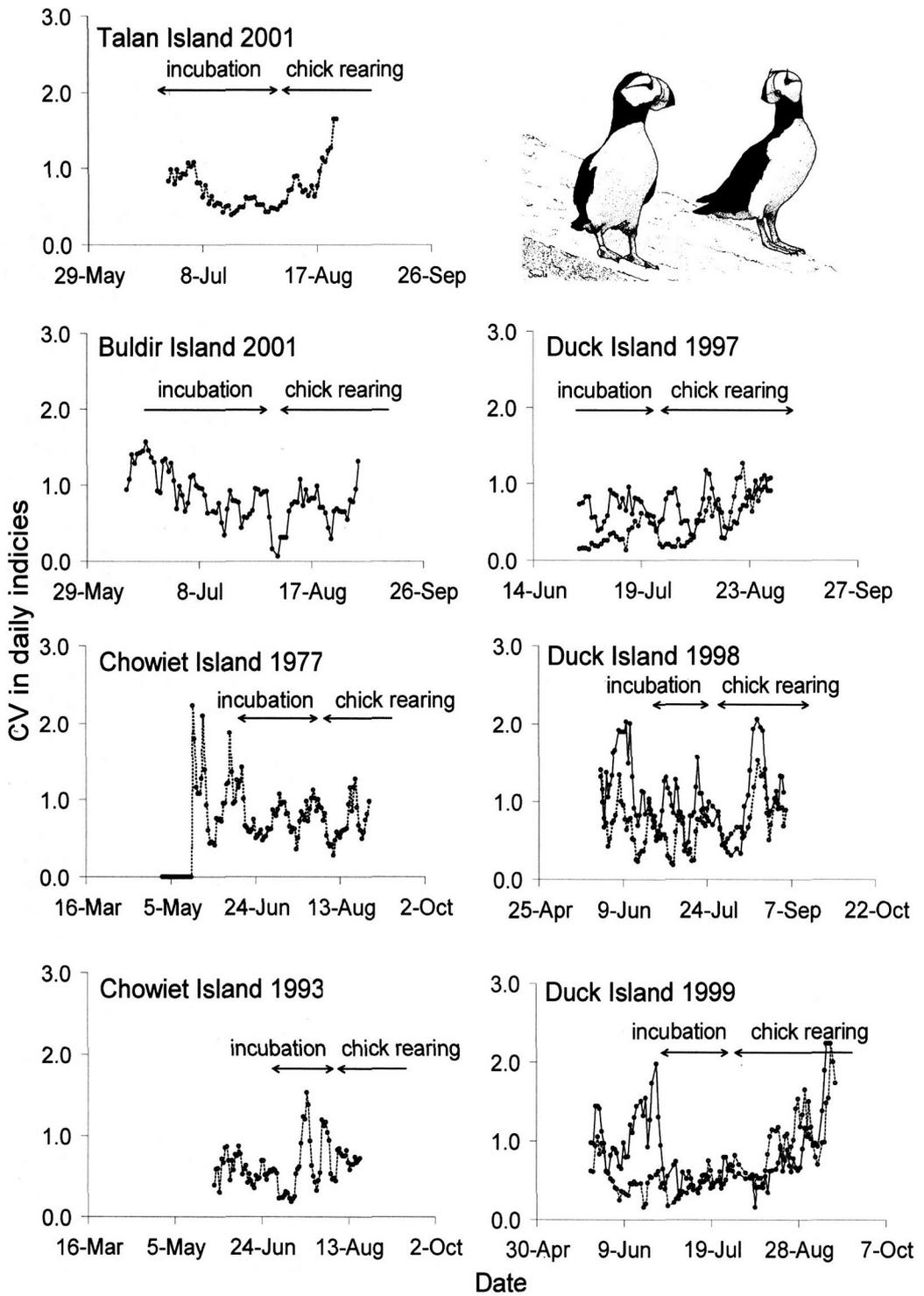


Fig. 5 Seasonal trends in the variability of horned puffin daily index counts on water (open circles, dotted lines) or land (solid circles, solid lines) at Talan, Buldir, Chowiet, and Duck Islands in the North Pacific in different years. Each value is a running CV calculated over a 5-day period.

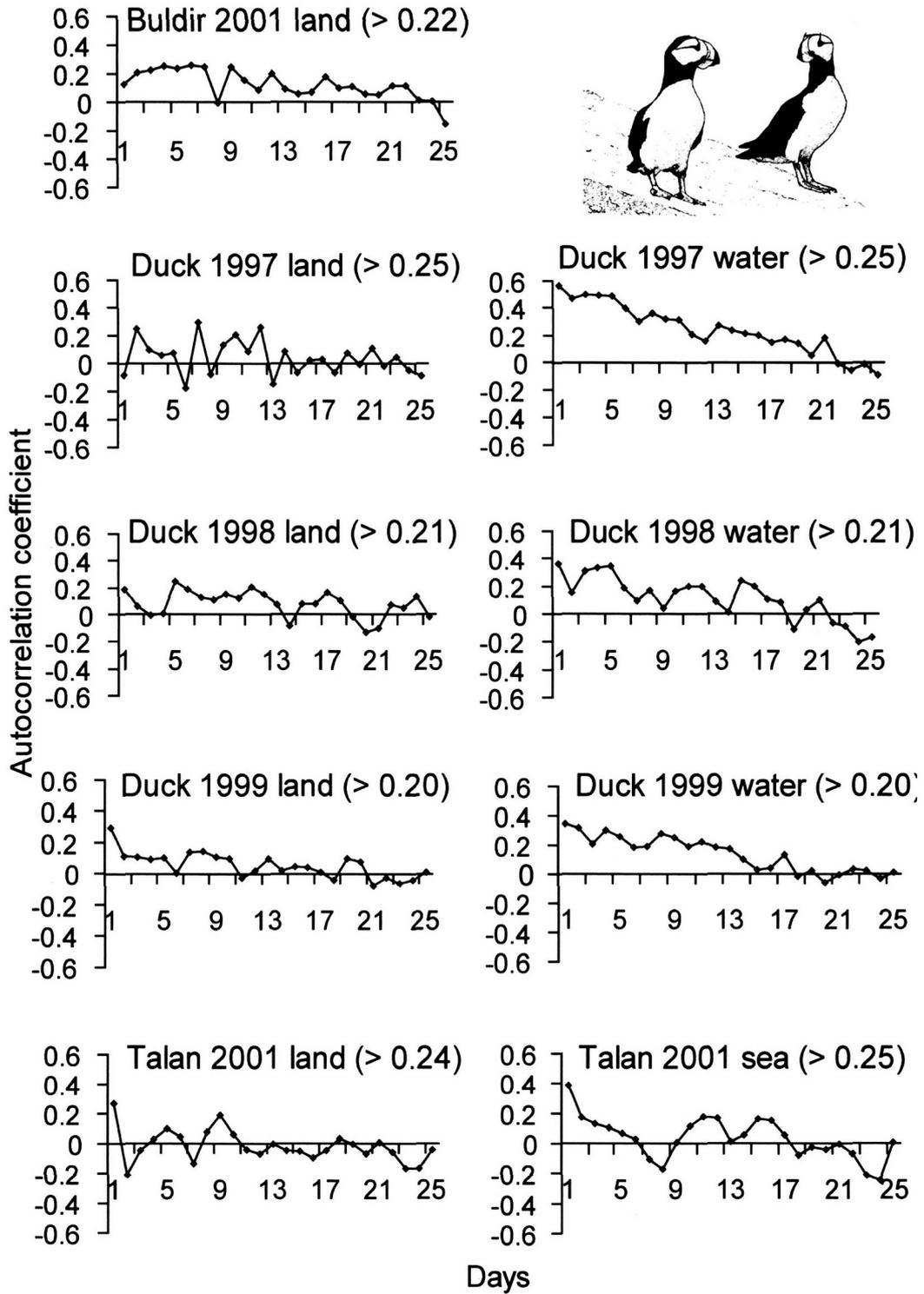


Fig. 6. Autocorrelation lag (days) of daily counts of horned puffins on water and land at Buldir, Duck, and Taland Islands, North Pacific, in different years. Autocorrelation coefficients (Y axis) exceeding the values indicated in parentheses are statistically significant.

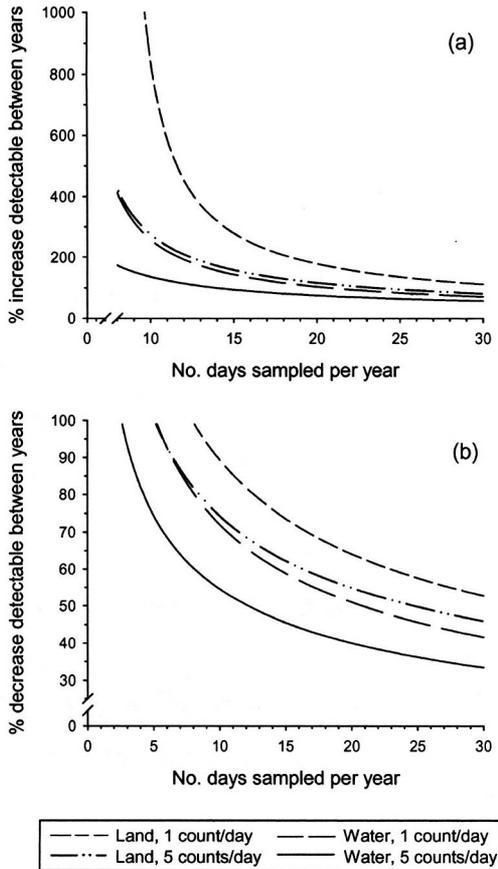


Fig. 7. Relationship between sample size (counts per day and days per year within the 30-day survey period) and proportionate changes in horned puffin numbers detectable between 2 years: (a) when numbers increase between year 1 and year 2, and (b) when numbers decrease between year 1 and year 2. Power ($1 - \beta$) is 0.9 throughout, using 1-tailed tests and a significance criterion of $P < 0.05$.

with a counting interval of 18–30 days and $CV \approx 0.8$.

Using the option in TRENDS that models a linear relationship between means and SD (i.e., a constant CV), we estimated the number of years required to detect given rates of change in the numbers of puffins under various sampling protocols. We used the 4 levels of interannual CV (0.1, 0.2, 0.4, 0.8) described above, plus 3 different sampling intervals (1-, 2-, 5-year frequencies) as inputs (Fig. 8). By way of an example of how to use these curves (Fig. 8), given an interannual CV of 0.1, detection of a 4% annual rate of change in the numbers of puffins attending the colony would require about 9 years if the colony were surveyed annually, or 17 years using counts obtained every 5 years.

Table 2. Estimates of within-year variation in horned puffin counts for power analysis of pair-wise comparisons of means. We calculated mean CVs for land and water counts using estimates of within-year variation over a 30-day survey period for Buldir, Talan, Duck, and Chowiet Island counts using 2 calculations of the daily index: (1) the mean of 5 consecutive counts conducted during the daily peak in attendance, and (2) 1 count per day during the daily peak of attendance (see Methods for more details).

Plot type	Counts per day	\bar{x}^a	Mean CV ^b
Land	1	40.4	0.87
Land	5	42.3	0.75
Water	1	140.5	0.66
Water	5	158.0	0.52

^a Unweighted average of mean counts for all colony-years with $n = 1$ or $n = 5$ counts per day

^b Unweighted average of CVs for corresponding means in Appendix 1, i.e., $(SD_1 / X_1 + SD_2 / X_2) / 2 =$ unweighted average CV.

DISCUSSION

Guidelines for Detecting Change in Attendance Counts

Patterns of colony attendance in horned puffins differed markedly in respect to geographic location, time of day, survey protocol, and stage of nesting. Optimally, attendance counts should be conducted during periods of (1) peak diurnal attendance, (2) minimal seasonal variability, (3) maximum attendance by breeding birds, (4) minimum attendance by immature and failed breeders, and (5) minimal sensitivity to fluctuations in food supply. With those considerations in mind, we offer the following guidelines for survey design.

Timing of Survey Period.—We suggest the last 30 days of incubation as an optimum survey period because variability is generally low, and incubation has an easily observed end point (i.e., adult puffins carrying fish to their chicks). Incubation may also be the appropriate survey period for 2 biological reasons: (1) counts during the incubation period may better reflect the breeding population, whereas counts during chick rearing may include a high and varying proportion of subadults and nonbreeders (Ashcroft 1979); and (2) foraging behavior may be less constrained by local feeding conditions during incubation (e.g., Benvenuti et al. 2002) and consequently less sensitive to annual variation in food availability.

Duration of Survey Period.—To encompass the variability and serial dependence among daily counts, we recommend conducting survey counts daily for a minimum of 10 days, or in multiples of 10 days, during the survey at any colony. Measures of interannual variation based on a 10-day

Table 3. Estimates of interannual variation in horned puffin counts for power analysis of multi-year trends. Estimates of interannual variation were calculated for Duck Island water and land counts (using both 1 and 5 counts per day as an index) and for Chowiet Island water counts using the single count per day. Estimates of interannual CVs for Duck Island were based on 10 consecutive days (see Methods for more details).

Colony	Counts/day ^a	n (days)	n (years)	Interannual variation (CV)	
				Water plots	Land plots
Duck	1	28-30	3	0.10	0.38
	5	28-30	3	0.12	0.37
	1	10	3	0.18	0.39
	5	10	3	0.21	0.43
Chowiet	1	18-30	3	0.81	

^aVariance estimates for 1 count/day and 10 days/year calculated from random subsampling of data obtained on Duck Island in 3 years (see Methods).

survey period were higher than those based on 30 days, so the best protocol would include daily counts throughout the 30-day survey period. There is little advantage to increasing counts beyond 30 days, however, because the larger variances encountered in doing so would limit the potential gain in statistical power.

peak diurnal attendance be identified annually at each subcolony that is monitored. Site-specific information on horned puffin diurnal patterns is essential for standardization and interpretation of survey data across the species breeding range.

Daily Index.—Five counts per day are preferred if the main objective is a comparison of numbers

Time of Day.—It is essential to determine the period of peak attendance at all colonies by conducting all-day counts prior to designing the protocol for long-term monitoring. Little is known about interannual patterns of diurnal attendance at the same colony, or the attendance patterns at different subcolonies. We therefore recommend that the timing of

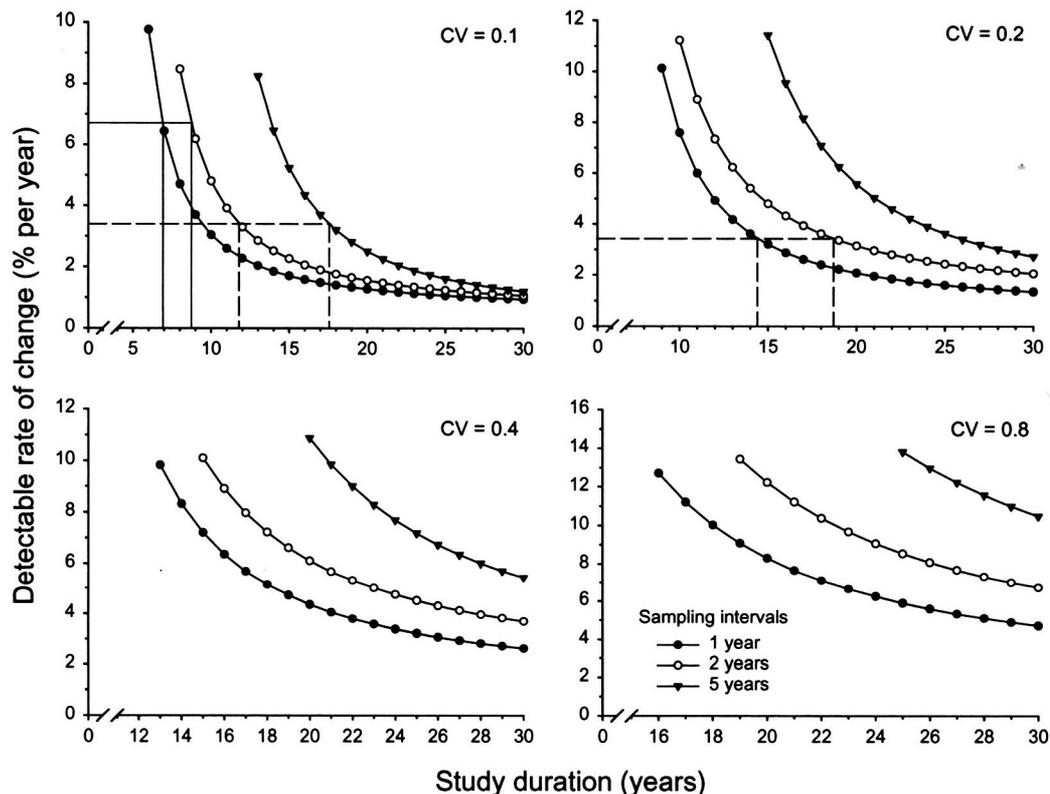


Fig. 8. Power curves for detection of linear trends in log-transformed indices of horned puffin abundance under 4 assumed levels of variation among years. Successful combinations of interannual CVs and sampling intervals are indicated by drop lines on the X-axis corresponding to trends of 3.4 and 6.7% per year. A successful protocol meets suggested program goals for seabird monitoring as described in the text. We used 2-tailed tests, with a significance criterion of $P < 0.1$. Power $(1 - \beta)$ was set at 0.9.

between 2 years, whereas the less intensive approach of making a single count per day and using this as the daily index would be suitable for studies intended to monitor trends.

Land vs. Water Counts.—Although the larger size of water plots may partially explain their lower within-year and among-year variability in colony counts, wind conditions at Duck Island had less effect on the attendance of birds on water than those on land in the same cove, and patrolling gulls (*Larus glaucescens*) disturbed birds on land more than birds on water (A. M. A. Harding, Alaska Science Center, personal observation). We therefore suggest that birds should be counted on water at colonies where plots can be established with well-defined boundaries on shore, or by use of buoys in sheltered bays. However, at colonies where water plot boundaries are hard to define, or nearshore waters are characterized by persistently rough conditions, land-based plots may be preferred.

Weather.—We do not consider it necessary to make corrections of counts for prevailing weather conditions, apart from excluding days with the most extreme weather conditions (when counting is generally impossible anyway), since wind has little effect on the number of horned puffins counted on water (Hatch 2002, this study).

Monitoring Effort Required.—Analysis of differences in counts between 2 years of study is often used to examine the effect of a local anomalous event, such as an oil spill. Most such questions will predict either an increase or decrease in the number of birds and therefore allow a 1-tailed test of the difference between means. Although pair-wise comparisons of years may be useful for addressing such questions in species where colony attendance is less variable, more counts of horned puffins are needed during the daily attendance peak than is true for purposes of longer-term monitoring, and the minimum amount of change that can be detected is relatively high. Furthermore, any conclusions about changes in numbers between 2 years should be made with caution because extreme differences in behavior and time at the colony will provide a large source of bias. For example, puffins are known to abandon their breeding attempt and leave the colony when food availability drops below a certain level (Vermeer et al. 1979). We recommend that other indices (such as adult survival) be used as corroborative evidence for any detected change in numbers between 2 years of study.

To examine the power to detect longer-term changes in numbers of horned puffins attending a colony, we used the half-life of a puffin population at 2 rates of decline as a yardstick for measuring the performance or success of various monitoring protocols (Hatch 2002). At a rate of 6.7% decline per year a puffin population would halve in size in 10 years, whereas 3.4% decline per year is equivalent to a population half-life of 20 years (Fig. 8). Combinations of interannual CV and sampling interval that are capable of detecting rates of decline over a span of years shorter than the population half-life are indicated by the drop lines on the X-axis (Fig. 8). Using an interannual CV of 0.1 (Duck Island counts of birds on water over 28–30 days), sampling intervals of either 1 or 2 years would likely detect a –6.7% rate of change in fewer than 10 years (i.e., before the population has halved in size). By contrast, counts taken every 5 years would require about 14 years to detect a trend given the same rate of change—an inadequate effort if one wishes to detect a 50% decline when it has occurred or predict such a decline beforehand. Given an interannual CV of 0.2 (Duck Island counts of birds on water over 10 days), counts every 1 or 2 years would likely detect a 3.4% rate of decline in fewer than 20 years. However, at higher levels of interannual variability, even annual monitoring is unlikely to detect a decline before a population has declined by half.

Further Work Needed.—The power to detect change in the number of birds attending the colony over several years depends on the level of residual interannual variation. At present, our knowledge of interannual variation in horned puffin attendance is limited to 2 colonies and 3 years of data from each site. Furthermore, interannual variation on Duck Island was much lower than on Chowiet Island. However, data from Chowiet Island spanned a 20-year period, and we do not know whether the higher interannual variability reflects simple fluctuations in attendance or a real population decline between 1977 and 1995. We chose to assume conservatively that interannual variability reflected variation in attendance vs. actual population change on Chowiet; although there is recent evidence from burrow distribution and densities on adjacent Suklik Island that suggests horned puffin abundance may indeed have declined substantially on the Semidis since the late 1970s (S. A. Hatch, Alaska Science Center, personal observation). If so, then the magnitude of interannual variability

in horned puffin attendance counts may be closer to that calculated for Duck Island.

Although interannual variability in count data may be lower than the worst-case scenario we suggest, better estimates of interannual variability are needed from more colonies and years to confirm our ability to detect trends in the numbers of puffins attending a colony. More work is also needed to determine the optimum number, size and distribution of attendance plots. Observations on banded birds are needed to determine the age of first breeding and return to the colony, as well as age-specific behavior and time allocation of horned puffins during the breeding season.

Attendance Counts as an Index of Abundance

Our study suggests that use of our protocol will reduce count variability enough to allow the detection of a 50% decline in attendance among years, but can numbers of puffins attending the colony be used as an index to estimate population trend? A detected change in the numbers of birds attending a colony could either represent a change in population size or changes in behavior and time spent at the colony unrelated to changes in abundance. Valid inference based on index counts is only possible if (1) the number of birds counted are related to population size, and (2) the detection probability or index ratio is constant (Bart et al. 1998, Schmidt 2003). The detection probability of horned puffins is unknown (because we are unable to count nests and it is impossible to count all individuals), and it is presumably highly variable among sampling periods (due to the variable time birds spend at the colony).

We must rely heavily on knowledge of the species' biology to assess whether counts are correlated with population size and to minimize temporal changes in the detection probability. Even though individual behavior may be influenced by different environmental and social factors (e.g., Slater 1976, Slater 1980, Gaston and Nettleship 1982, Stempniewicz 1986, Jones et al. 1989), breeding individuals must spend a minimum amount of time at the colony in order to incubate their egg, feed their chick, and maintain their nest site. Survey protocols can be designed to target the time of breeding season when the ratio of breeding to nonbreeding birds is maximized, and further variation in the detection probability can be reduced by counting birds at the least variable time of day and season, aver-

aging counts, reducing observer differences by using standardized methods, and by establishing permanent plot boundaries.

In comparison with many other avian species, horned puffins are highly visible, so if they are present at the colony surface, they should be seen. If counts can focus on breeding individuals, and the variation in count data associated with changes in behavior can be reduced, we may assume that long-term changes in the numbers of puffins attending the colony are correlated with breeding population trend. The low, interannual variability in attendance counts between consecutive years in our study (e.g., Duck Island 1997–1999) supports this assumption, and it suggests that count data based on the recommended protocol may be fairly sensitive to changes in the abundance of horned puffins vs. changes in behavior associated with different oceanographic and feeding conditions. Puffins at Duck Island were influenced by anomalous oceanographic conditions related to the El Niño–Southern Oscillation event of 1997–1998, and there is good evidence that birds were experiencing associated food shortage in 1998, with rates of chick mass increase lower in 1998 than in 1997 and 1990 (Harding et al. 2002). Birds generally spend more time foraging and less time at the colony when prey are far away or prey density is low (e.g., Birkhead 1977, Gaston and Nettleship 1982); however, we found very little interannual variation in the counts conducted on Duck Island in 1997, 1998, and 1999.

Although our study suggests that variation in count data may be reduced to allow detection of change in numbers vs. changes in behavior, more work is needed to verify the relationship between count data and breeding population size before the number of birds present at the colony can be used with confidence as a population index. This may be possible by visual observations of chick feeding (to determine the number of nest sites in a defined area of surface counts) or mark–recapture studies (Schmidt 2003). Transmitters may also be used to determine what percentages of birds attend the colony consistently during the time of peak diurnal attendance. Simultaneous collection of demographic and attendance count data may also confirm the reliability of attendance counts as a population index. Population trend is sensitive to small changes in adult survival of long-lived species such as horned puffins (Croxall and Rothery 1991). Thus, monitoring the survival of banded individuals, in addition to

recruitment and productivity, will help to determine the relationship between changes in attendance and changes in actual population size (Jones 1992).

MANAGEMENT IMPLICATIONS

Successful management procedures for monitoring seabird populations must be logistically feasible, reasonably precise, and cost effective. We suggest that a single daily colony-count of horned puffins for 30 consecutive days during the incubation period should allow detection of trends in the number of puffins attending a colony over multiple years. Data could be collected at colonies where fieldwork already is being conducted, or collected remotely using time-lapse photography. Because most horned puffin colonies are remote, the use of automatic time-lapse photography might be particularly cost efficient for monitoring colonies across their geographic range.

We identified sources of variability in counts of horned puffins and developed strategies for minimizing that variation to an acceptable level for monitoring purposes. This approach might be instructive in the design of monitoring protocols for a variety of other species that exhibit marked variation in numbers not attributable to real population change (Gibbs et al. 1998, Hyde and Simons 2001, O'Donnell 2002, Thompson et al. 2002). In all such cases, we recommend focusing efforts on the study of demographic parameters to determine the relationship between changes in attendance indices and actual changes in population size.

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LITERATURE CITED

- ANKER-NILSSEN, T., AND O. W. RØSTAD. 1993. Census and monitoring of puffins *Fratercula arctica* on Røst, North Norway, 1979–1988. *Ornis Scandinavica* 24:1–9.
- ASHCROFT, R. E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. *Ornis Scandinavica* 10:100–110.
- BARRETT, R. T., T. ANKER-NILSSEN, R. RIKARSEN, K. VALDE, N. RØV, AND W. VADER. 1987. The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980–1983. *Ornis Scandinavica* 18:73–83.
- BART, J., M. A. FLIGNER, AND W. I. NOTZ. 1998. Sampling and statistical methods for behavioral ecologists. Cambridge University Press, United Kingdom.
- BÉDARD, J. 1969. The nesting of the crested, least, and parakeet auklets on St. Lawrence Island, Alaska. *Condor* 71:386–398.
- BENVENUTI, S., L. DALL'ANTONIA, AND K. FALK. 2002. Diving behaviour differs between incubating and brooding Brunnich's guillemots, *Uria lomvia*. *Polar Biology* 25:474–478.
- BIRKHEAD, T. R. 1977. Attendance patterns of guillemots *Uria aalge* at breeding colonies on Skomer Island. *Ibis* 120:219–229.
- , AND D. N. NETTLESHIP. 1980. Census methods for murres, *Uria* species: a unified approach. Canadian Wildlife Service Occasional Paper Number 43.
- BROWN, D., AND P. ROTHERY. 1993. Models in biology, mathematics, statistics and computing. John Wiley and Sons, New York, USA.
- BYRD, G. V., R. H. DAY, AND E. P. KNUDTSON. 1983. Patterns of colony attendance and censusing of auklets at Buldir Island, Alaska. *Condor* 85:274–280.
- CROXALL, J. P., AND R. ROTHERY. 1991. Population regulation of seabirds: implications of their demography for conservation. Pages 272–296 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hiron, editors. Bird population studies: relevance to conservation and management. Oxford University Press, United Kingdom.
- GASTON, A. J., AND D. N. NETTLESHIP. 1982. Factors determining seasonal changes in attendance at colonies of the thick-billed murre *Uria lomvia*. *Auk* 99:468–473.
- GERRODETTE, T. 1993. TRENDS: software for a power analysis of linear regression. *Wildlife Society Bulletin* 21:515–516.
- GIBBS, J. P., S. DROEGE, AND P. EAGLE. 1998. Monitoring of plants and animals. *BioScience* 48:935–940.
- HARDING, A. M. A. 2001. The breeding ecology of horned puffins *Fratercula corniculata* in Alaska. Thesis, University of Durham, United Kingdom.
- , J. F. PIATT, AND K. C. HAMER. 2002. Breeding ecology of horned puffins (*Fratercula corniculata*) in

- Alaska: annual variation and effects of El Niño. *Canadian Journal of Zoology* 81:1004-1013.
- HATCH, S. A. 2002. Activity patterns and monitoring numbers of horned puffins and parakeet auklets. *Waterbirds* 25:348-357.
- . 2003. Statistical power for detecting trends with applications to seabird monitoring. *Biological Conservation* 111:317-329.
- , AND M. A. HATCH. 1989. Attendance patterns of murres at breeding sites: implications for monitoring. *Journal of Wildlife Management* 53:483-493.
- , AND ———. 1990. Breeding season of oceanic birds in a subarctic colony. *Canadian Journal of Zoology* 68:1664-1679.
- HINTZE, J. L. 2000. NCSS 2000 user's guide-II. Number Cruncher Statistical Systems, Kaysville, Utah, USA.
- HYDE, E. J., AND T. R. SIMONS. 2001. Sampling plethodontid salamanders: sources of variability. *Journal of Wildlife Management* 65:624-632.
- JONES, I. L. 1992. Colony attendance of least auklets at St. Paul Island, Alaska: implications for population monitoring. *Condor* 94:93-100.
- , A. J. GASTON, AND J. B. FALLS. 1989. Factors affecting colony attendance by ancient murrelets (*Synthliboramphus antiquus*). *Canadian Journal of Zoology* 68:433-441.
- KONYUKHOV, N. B., AND K. JUK. 2001. Attendance patterns of parakeet auklets and horned puffins at Buldir Island, Alaska in 2001. U.S. Fish and Wildlife Service Report, Alaska Maritime National Wildlife Refuge 01/10, Homer, USA.
- MONTEVECCHI, W. A. 1993. Birds as indicators of change in marine prey stocks. Pages 217-266 in R. W. Furness and J. J. D. Greenwood, editors. *Birds as monitors of environmental change*. Chapman and Hall, London, United Kingdom.
- MOORE, H., P. KAPPES, AND M. GRINDELL. 2001. Biological monitoring at Buldir Island, Alaska in 2001: summary appendices. U.S. Fish and Wildlife Service Report, Alaska Maritime National Wildlife Refuge 01/11, Adak, USA.
- O'DONNELL, C. F. J. 2002. Variability in numbers of long-tailed bats (*Chalinolobus tuberculatus*) roosting in the Grand Canyon Cave, New Zealand: implications for monitoring population trends. *New Zealand Journal of Zoology* 29:273-284.
- PETERSEN, M. R. 1983. Horned puffin (*Fratrercula corniculata*). Pages 401-426 in P. A. Baird, and P. J. Gould, editors. *The breeding biology and feeding ecology of marine birds in the Gulf of Alaska*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Outer Continental Shelf Energy Program Final Report 45 (1986).
- PIATT, J. F., H. R. CARTER, AND D. N. NETTLESHIP. 1991. Effects of oil pollution on marine bird populations. Pages 125-141 in J. White, editor. *The effects of oil on wildlife: research, rehabilitation and general concerns*, proceedings from the oil symposium, Washington D.C., October 16-18, 1990. Sheridan Press, Hanover, Pennsylvania, USA.
- , AND A. S. KITAYSKY. 2001. Horned puffin (*Fratrercula corniculata*). Pages 1-27 in A. Poole, and F. Gill, editors. *The birds of North America*, No. 611. The American Ornithologists' Union, Philadelphia, Pennsylvania, and The Academy of Natural Sciences, Washington D.C., USA.
- , B. D. ROBERTS, AND S. A. HATCH. 1990. Colony attendance and population monitoring of least and crested auklets on St. Lawrence Island, Alaska. *Condor* 92:97-106.
- SAVARD, J-P. L., AND G. E. J. SMITH. 1985. Comparison of survey techniques for burrow-nesting seabirds. *Canadian Wildlife Service Progress Notes* 151:1-7.
- SLATER, P. J. B. 1976. Tidal rhythm in a seabird. *Nature* 264:636-638.
- . 1980. Factors affecting the numbers of guillemots *Uria aalge* present on cliffs. *Ornis Scandinavica* 11:155-163.
- SCHMIDT, B. R. 2003. Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. *C. R. Biologies* 326: S119-S124.
- SOKAL, R. R., AND F. J. ROHLF. 2000. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, New York, USA.
- STEMPNIEWICZ, L. 1986. Factors causing changes in the rhythm of attendance of the little auk *Plautus alle* (L.) at a colony during the breeding season in Svalbard. *Ekologia Polska* 34:247-263.
- THOMPSON F. R., III, D. E. BURHANS, AND B. ROOT. 2002. Effects of point count protocol on bird abundance and variability estimates and power to detect population trends. *Journal of Field Ornithology* 73:141-150.
- VERMEER, K., L. CULLEN, AND M. PORTER. 1979. A provisional explanation of the reproductive failure of tufted puffins *Lunda cirrhata* on Triangle Island, British Columbia. *Ibis* 121:348-354.
- WALSH, P. M., D. J. HALLEY, M. P. HARRIS, A. DEL NEVO, L. M. W. SIM, AND M. L. TASKER. 1995. *Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds*. Joint Nature Conservation Committee/Royal Society for the Protection of Birds Institute of Terrestrial Ecology/Seabird Group, Peterborough, United Kingdom.
- WANLESS, S., D. D. FRENCH, M. P. HARRIS, AND D. R. LANGSLOW. 1982. Detection of annual changes in the numbers of cliff-nesting seabirds in Orkney 1976-1980. *Animal Ecology* 51:785-795.
- WEHLE, D. H. S. 1980. *The breeding biology of the puffins: tufted puffin (Lunda cirrhata), horned puffin (Fratrercula corniculata), common puffin (Fratrercula arctica), and rhinoceros auklet (Cerorhinca monocerata)*. Dissertation, University of Fairbanks, Alaska, USA.
- ZAR, J. H. 1996. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.

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(Appendix on next page)

Appendix 1. Within-year variation associated with different protocols for counting horned puffins on land and water.

Colony	Plot type	Year	Counts			SD	CV
			per day	<i>n</i> (days)	\bar{x} - count		
Buldir	Land	2001	5	30	7.9	6.7	0.85
Talan	Land	2001	5	30	94.7	60.9	0.64
Duck	Land	1997	5	28	20.9	16.7	0.80
	Land	1998	5	30	41.6	36.6	0.88
	Land	1999	5	30	46.3	26.4	0.57
Buldir	Land	2001	1	30	7.4	7.4	1.00
Talan	Land	2001	1	30	94.2	67.4	0.72
Duck	Land	1997	1	28	19.0	17.2	0.91
	Land	1998	1	30	40.9	39.6	0.97
	Land	1999	1	30	40.4	30.3	0.75
Talan	Water	2001	5	30	202.8	141.5	0.69
Duck	Water	1997	5	28	152.7	56.5	0.37
	Water	1998	5	30	153.7	98.4	0.64
	Water	1999	5	30	122.9	46.7	0.38
Talan	Water	2001	1	30	198.2	147.9	0.75
Duck	Water	1997	1	28	151.4	70.1	0.46
	Water	1998	1	30	159.8	108.8	0.68
	Water	1999	1	30	132.3	84.1	0.63
Chowiet	Water	1977	1	30	221.1	176.9	0.80
	Water	1993	1	28	58.9	39.5	0.67
	Water	1995	1	18	61.5	38.8	0.63