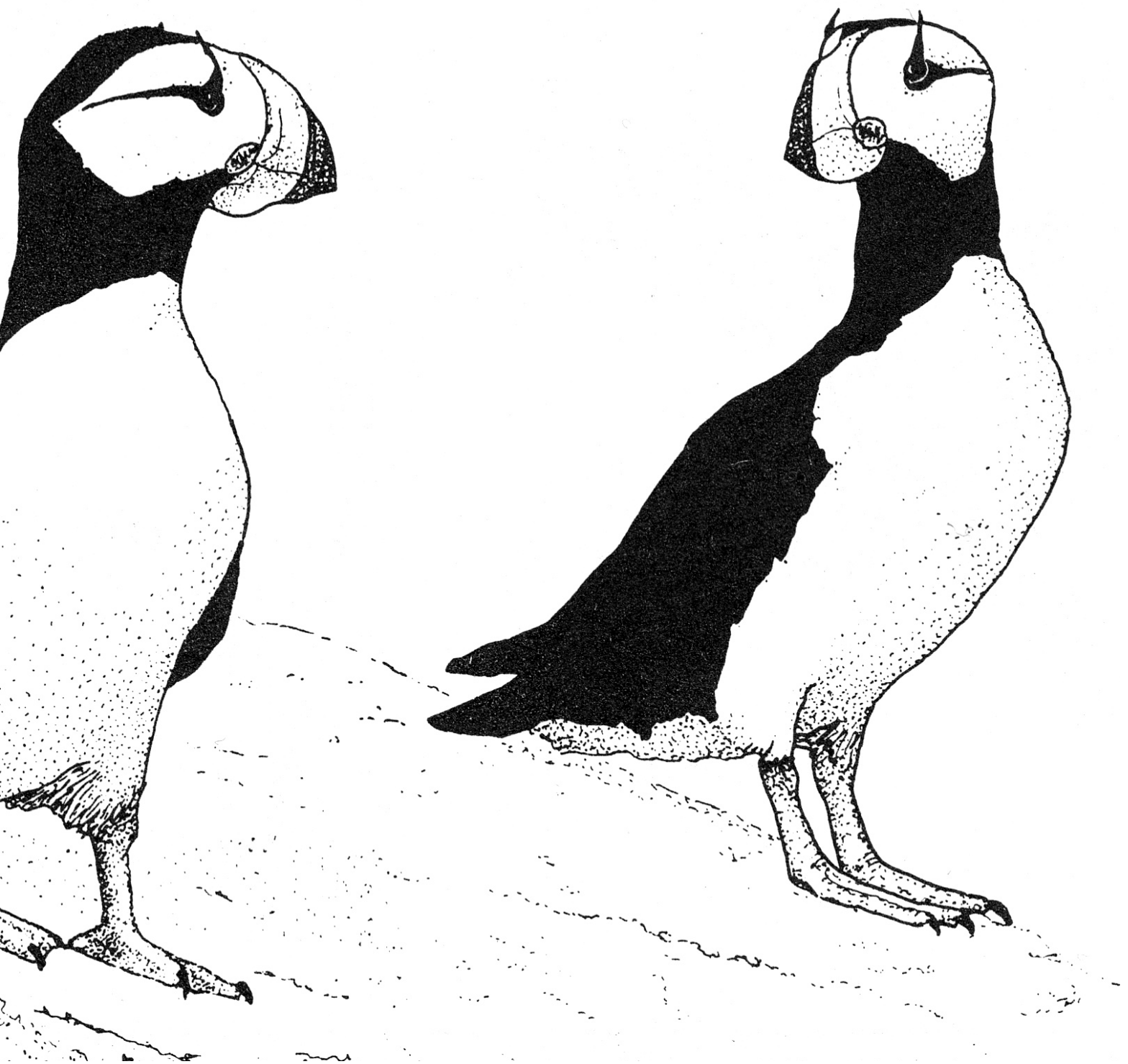


Attendance patterns and population monitoring of  
crevice-nesting Horned Puffins  
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A.M.A. Harding, J.F. Piatt, G.V. Byrd,  
S.A. Hatch, N.B. Konyukhov, and E.U. Golubova.

A.M.A. Harding, J.F. Piatt, S.A. Hatch  
Alaska Science Center,  
U.S. Geological Survey,  
1011 East Tudor Road,  
Anchorage, AK 99503  
USA

G.V. Byrd  
U.S. Fish and Wildlife Service,  
Alaska Maritime National Wildlife Refuge,  
2355 Kachemak Bay Drive, Suite 101,  
Homer, AK 99603  
USA

N.B. Konyukhov  
Institute of Animal Evolutionary Morphology and Ecology  
Laboratory of Bird Ecology  
Russian Academy of Sciences  
Leninsky Prospect 33  
Moscow 117071  
Russia

E.G. Golubova  
Lab of Ornithology  
IBPN DVO RAN  
Portovaya 18  
Magadan 685000  
Russia

*Cover and figure illustrations by Art SOWLS*

## **ABSTRACT**

It is difficult to monitor populations of crevice-nesting seabirds because nest sites are hard to identify and count. To complicate matters further, the number of adult birds attending a colony can be extremely variable within and between days. Horned Puffins and Parakeet Auklets generally nest in crevices throughout their range. There is no standardized method for censusing either species and consequently little is known about absolute numbers or population trends. This paper examines within- and among-year variation in the colony attendance of Horned Puffins and Parakeet Auklets at five breeding colonies in the North Pacific. Using 11 colony-years of data, we examined variance in attendance at colonies and consider the implications for detecting changes in population size. Due to breeding failure we were unable to suggest firm monitoring guidelines for Parakeet Auklets. We therefore focused on developing a population monitoring protocol for Horned Puffins, using the half-life of a puffin population at two rates of decline as a yardstick for measuring the performance of various monitoring protocols. In order to monitor Horned Puffins at individual colonies, we suggest that investigators a) first identify the colony-specific period of peak diurnal attendance, b) count birds once daily during the narrow window of peak diurnal attendance, c) count birds resting on the water adjacent to the colony, d) count birds daily during the census period, e) define the 30 days at the end of incubation as the census period, and, f) census colonies annually. Future research should focus on measuring interannual variability in Horned Puffin attendance.

## INTRODUCTION

Seabirds are vulnerable to a variety of anthropogenic threats. Oil and chemical pollution can cause mortality (Piatt *et al.* 1991), and commercial fishing operations can impact seabird populations directly via bycatch mortality, or indirectly through alteration of marine food webs (e.g., Barrett *et al.* 1987). In addition to their sensitivity to anthropogenic influences, seabirds are also valuable indicators of natural changes in marine ecosystems (Montevecchi 1993). Baseline evaluation of the status of seabird populations generally relies on the enumeration of population size by counting individuals or nest sites (e.g., Walsh *et al.* 1995). However, our ability to detect changes in population size depends on repeatable population census methods that account for species-specific variation in behavior and breeding biology (e.g., Hatch and Hatch 1989). Many studies have examined variation in colony attendance and developed standard methods for population monitoring of seabirds (e.g., Birkhead and Nettleship 1980, Slater 1980, Wanless *et al.* 1982, Harris 1987, Hatch and Hatch 1988, Jones 1992, Byrd *et al.* 1983).

Species breeding on exposed cliffs are relatively easy to census, while those that breed underground are more difficult to survey (Savard and Smith 1985, Bertram *et al.* 1999). It is difficult to accurately census some species of auk (Family Alcidae) because numbers of birds attending the colony can be extremely variable. For example, it is not uncommon to observe thousands of adult birds at a colony on one day, and none or very few the next day (e.g., Jones 1992). Due to such extreme variation in colony attendance, Atlantic Puffins (*Fratercula arctica*) are usually monitored by counting occupied burrows (e.g., Harris and Murray 1981, Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995). While such counts can provide an index of breeding population size for burrow nesting species, this method is not suitable for crevice-nesting members of the Alcidae because their nest sites are difficult to locate and monitor (e.g., Piatt *et al.* 1990, Jones 1992, Byrd *et al.* 1993).

This paper focuses on two species for which monitoring is especially difficult. Horned Puffins (*Fratercula corniculata*) and Parakeet Auklets (*Aethia psittacula*) almost always nest in cracks in cliff faces, amongst boulders, or in rock crevices. To complicate matters further, many crevice nest sites have multiple or shared entrances and are often deep within unstable piles of boulders, making it hazardous to access, identify and count nest sites. As a result, there is no standardized method for censusing either species and little

is known about absolute numbers or trends in population sizes. Developing census methods is a high priority for the conservation of these species (Piatt and Kitaysky 2001).

In crevice nesting species where counts of nest sites are not possible, counts of birds attending the colony can provide a useful index of population size (Ewins 1985, Piatt *et al.* 1990, Hildien 1994). In order for these counts to be used for monitoring population change, however, patterns of colony attendance must be examined to determine the optimum time of day and stage of breeding for censusing, and the number of counts required to detect prescribed levels of change (e.g., Hatch and Hatch 1989). This paper describes the colony attendance patterns of Horned Puffins and Parakeet Auklets at five breeding colonies in the North Pacific, and integrates historical attendance data from all available sources. The main purpose of this study was to examine diurnal, seasonal and annual variation in attendance among different colonies, consider the implications of this variation for population monitoring, and recommend methods for censusing that will be useful throughout the species' range.

## **METHODS**

### **Study Sites**

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) in 1997, 1998 and 1999; on Buldir Island (western Aleutian Islands: 51° 21'N, 175° 56'E) in 1988, 1991 (J. Williams and V. Byrd unpubl. data) and 2001 (Konyukhov and Juk 2001); on Chowiet Island (56 °N, 156°W; Hatch submitted) in 1977, 1993, and 1994; and on Suklik Island (56 °N, 156°W; Hatch submitted) in 1986. For the purpose of this study, Horned Puffin colonies on the neighboring islands of Suklik and Chowiet will collectively be called by the archipelago name, the Semidi Islands. Diurnal and seasonal patterns of colony attendance were examined at all four colonies (Buldir, Talan, Duck and the Semidi Islands; Fig. 1).

The colony attendance of Parakeet Auklets was recorded at Buldir Island (Konyukhov and Juk 2001) and Talan Island throughout the breeding season of 2001. Diurnal attendance was recorded for three days on St Paul in 2000 (Konyukhov and Juk 2001; Pribilof Islands: 57° 07'N, 170° 10'W, Fig. 1).

## **Study species**

### ***Horned Puffin***

Puffins spend the winter at sea, returning to colonies in spring to breed. Birds typically gather on the water during courtship and mating, with time on land spent maintaining pair bonds and selecting, defending, and maintaining nest sites (Piatt and Kitaysky 2001). Horned Puffins almost always nest in cracks in cliff faces, amongst boulders or in rock crevices. A single egg is laid in June, and is 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 attended only briefly during food delivery. Both parents feed the chick. Attendance at the colony during chick-rearing is highly variable. Birds spend time at the colony before and after food delivery to the chick, and adults synchronize time spent at the colony. These periods of peak attendance are often characterized with 'fly-bys' (Wehle 1980), where birds make synchronized circular flights above the colony before landing or joining rafts of birds on the water near shore. Chick development is slow, with a typical nestling period of 37 to 46 days (Peterson 1983). Offspring fledge over a period of about a month, with adult birds departing from the colony after their chick has fledged.

### ***Parakeet Auklet***

Parakeet Auklets return to colonies in spring to breed, nesting in rock crevices amongst boulders, talus and scree slopes or in dugout earth burrows (Hipfner and Byrd 1993). Incubation is about 35-36 days (Jones and Konyukov 2001), with both parents sharing incubation duties. The chick is brooded continuously for about the first week after hatching (Jones and Konyukov 2001). Both parents feed the chick, making several deliveries a day. Birds spend much time in small rafting flocks inshore; and fly to their nest sites in ones and twos (Gaston and Jones 1998). Most social behavior occurs in these staging areas (Manuwal and Manuwal 1979). Age at fledging is around 35-36 days (Sealy and Bédard 1973, Hipfner and Byrd 1993), with parents leaving the colony during late August/early September just after the chicks fledge.

## **Horned Puffin**

### ***Diurnal Attendance***

*Buldir Island 1988:* A land plot, with marked boundaries, measuring 2x10x12x12m was established. A movie camera (*Bell and Howell*) was set up about 10m from the plot. One to four photos were taken during each half hour period throughout the day (0700-2400). Data were collected for a total of 10 complete days during incubation (21, 25, 26, 29, 30 June; 1, 2, 5, 7, 22 July) and 13 complete days during chick rearing (23, 25, 29, 30 July; 4, 5, 14, 17, 18, 26, 16 August; 3 September). Numbers of birds present on the plot were later counted on the film images.

*Buldir Island 1991:* (J. Williams unpubl. data). A land plot, with marked boundaries, measuring 6x36x2x32m was established. A camera (Minolta 9000; 70-210mm) was set up 10m from the plot. One to four photos were taken during each half hour period throughout the day (0700-2330). Data were collected for a total of seven complete days during incubation (29 June; 3, 4, 8, 9, 16, 19 July). Numbers of birds present on the plot were later counted from the film images.

*Buldir Island 2001:* A land plot was established at the Main Talus sub colony (40m x 50m in size), and at the Crested Point sub colony (about 20m x 20m). A digital camera (*Nikon Coolpix 990*) connected to a timer (*digiSnap 2000*) was placed at each plot and used to take pictures of the plot every 15-minute, 24 hours a day. The camera at Main Talus was used on a telephoto setting with a 1.2x digital zoom, with images having 1024 x 768-pixel resolution and a compression ca. 13.5% of the original image. The camera at Crested Point was set at wide-angle with its images having 1024x768 pixel resolution and height compression being ca. 6.25% of the original size. Data were collected daily from 11 June to 4 September 2001 at Main Talus, with data missing from 12-13 July and from 4-5 August due to technical problems. Data was collected at Crested Point from 4 June to 11 July, with a gap 14-16 June. Numbers of birds present on images taken between 0615-2400 were later counted on a computer screen.

*Talan Island 2001:* A land plot (2530 m<sup>2</sup>) and a sea plot (150 x 100m = 1500 m<sup>2</sup>) were established at Talan Island. Both plots had well defined rock boundaries. Birds present within the plot boundaries were counted, at 15-minute intervals from 0800 to 2300, using binoculars from a fixed observation point. Counts were conducted daily from 20 June to 29 August 2001. Due to inclement weather conditions (heavy rain and/or fog) no data were collected on 16, 25 July and 3, 12, 21 August.

*Duck Island 1997, 1998, 1999:* Observations were made from a marked station overlooking North Cove, with 10 x 42 binoculars. Horned Puffins present in North Cove were counted from 0500-2300 at 30-minute intervals. Birds were counted separately on water and land at each half hour. Water counts included all birds on the water, inside the cove boundaries and within 200 m from shore; a set buoy was used for reference. Land counts included birds on all north-facing land visible from the observation station. Data were collected for a total of six days in 1996, 1997 and 1999; three days during the incubation period and three days during chick rearing.

*Suklik Island (Semidi Islands) 1986:* Three land plots were monitored, using time-lapse photography, from 8-29 June. Observations were made with 8 mm movie cameras mounted on a 2 m pole, with intervalometers set to take a frame every five minutes. An average of 12 images were taken per hour. Viewable plot area ranged from 25-55m<sup>2</sup>. Count frames were used as the sample unit, and separated into hourly blocks of time. See Hatch (submitted) for further details.

### ***Seasonal Attendance***

Daily count indices of birds attending the colony were used to assess seasonal patterns of attendance. A daily index was calculated from counts conducted during the daily peak in attendance. Since within-day attendance varied markedly with the time of day and between colonies, we first had to establish when peak periods of attendance occurred at each study site before we established the daily count window.

Although all indices were calculated from counts conducted during daily peaks in attendance, the frequency of counts around the peak, and therefore the calculation of daily indices, differed among islands. Indices were calculated at Buldir and Talan Island from the top five counts over a 3-hr daily peak; at Duck Island from five consecutive counts conducted over a 75 min daily peak; and at Chowiet Island from a single count conducted during a 2-hr daily peak. Detailed methods of data collection at each colony are presented below.

*Buldir and Talan Islands 2001:* A daily three-hour period of peak attendance was identified for both Talan and Buldir islands (Table 1). During the 3-h peak, we conducted 13 counts of birds on plots. Using these 13 counts conducted during the peak hours, we compared seven different calculations of the daily index in order to establish which method minimized the daily variation in counts (among-day CV) most effectively. Daily variation



in census counts across the breeding season on Buldir Island (n= 84 d) were compared using the index calculations based on: the median count (CV = 0.945); mean count (CV = 0.906); trim mean, using the middle five counts; (CV = 0.932); maximum count (CV = 0.843); a single random count, (calculated as the mean CV from 50 sets of seasonal data with one random count/day; CV = 1.037); trim mean, using the top five counts excluding the maximum count; CV = 0.868); and the mean of the top five counts (CV = 0.850). We decided to use the mean of the top five counts (CV= 0.850) as the daily index since among day variation was low and a single maximum count can be biased by extreme values or errors in counting (Bedard 1969).

The top five counts during the three-hour daily peak were therefore averaged to give a daily index of bird numbers attending the colony. A daily index was calculated across the breeding season; from 11 June to 4 September on the Main Talus plot, Buldir Island, from 4 June to 11 July on Crested Point plot, Buldir Island, and from 20 June to 29 August on Talan Island.

*Duck Island 1997, 1998, and 1999:* From all-day observations, an evening peak in colony attendance was observed on Duck Island (1900-2200h). Based on this timing, daily counts of birds on water and land were made at 15-minute intervals between 2030-2145 hr. Up to five counts were made during this peak period each day, and these were used to calculate mean daily values for the number of birds counted on water or land. Daily counts were made from 27 June to 31 August in 1997, from 26 May to 4 September in 1998 and from 23 May to 14 September in 1999. Due to shortening daylight hours, counts towards the end of the season were made earlier, starting at 2015h. Wind speed (knots) was measured once daily in 1999, using a hand-held anemometer (*Kestrel* brand), just prior to the first evening count.

*Chowiet Island (Semidi Islands) 1977, 1993, and 1995:* A single count of birds on water was conducted between 0700 and 0930 hr. daily, with the use of binoculars and a spotting scope, from a fixed location overlooking the bay adjacent to the main camp on Chowiet Island. The observed area measured approximately 1000 m linearly along shoreline and 500 m offshore, with defined shoreline features at the lateral boundaries. Counts were made from 28 April to 29 August in 1977, from 26 May to 20 August in 1993, and from 12 June to 8 August in 1995; see Hatch (submitted) for further details.

To boost our confidence that the single count conducted during the daily peak on Chowiet Island could be used to adequately describe attendance patterns, we used Buldir

Island data to generate simulated seasonal patterns by taking one random count during the daily 3 hr daily peak and using it as the daily index. We generated 30 sets of simulated daily single-count data. These 30 sets closely resembled each other and the seasonal pattern generated by the day index of the top five counts. We therefore feel confident that the single count on Chowiet can be used to adequately describe variability in the seasonal pattern of attendance.

*Breeding chronology:* Using known dates based on data collected on the timing of breeding events, we split the seasonal attendance data from each colony into two time periods: incubation and chick rearing. Details on the method and frequency of nest checks can be found in: Harding 2001 (Duck Island); Williams *et al.* 2000 (Buldir Island); Kitaysky and Golubova 2000 (Talan Island); Hatch and Hatch 1990 (Semidi Islands). Chick rearing was defined as the period from median chick hatching to median fledging. Median chick hatching date on Talan Island was 29 July (L. Golubova unpubl. data); Buldir Island, 25 July (Moore *et al.* 2001); and Duck Island, 25 July in 1997, 29 July in 1998 and 26 July in 1999 (Harding 2001). Since median hatch date was unknown for Chowiet Island, we based estimates of chronology on average mean lay date from 9 years of study (22 June: Hatch and Hatch 1990, S.A. Hatch, unpubl. data). Using 40.5 days (Piatt and Kitaysky 2001), as incubation duration, we defined incubation as the 41 days prior to the median chick hatch date, or 41 days post mean lay date for Chowiet Island.

*Among-day variation:* A two-tailed test for difference between two coefficients of variation (The Z test; Zar 1996) was used to compare CVs during the incubation and chick rearing period within each year and type of plot (land and water).

### ***Power analysis***

*Population change between years:* Estimates of within-year variation for water and land based counts (among-day CV) were used to estimate the statistical power to detect a population increase or decrease between two years using PASS 2000 statistical software (Hintze 2000). Within-year variation over a defined census period (30 days) was calculated for Buldir, Talan and Duck island's land and water-based counts, using two different calculations of the daily index based on: (a) mean of five counts/day during the daily peak in attendance ("top 5" counts at Buldir and Talan islands, and "consecutive 5" counts at Duck Island), and, (b) one count/day during the daily peak of attendance. The single count/day was chosen randomly from the daily counts conducted during the daily colony

peak in attendance (see above). This was repeated to generate 30 sets of simulated daily single-count data. Within-year variation (CV) was calculated for each set, and averaged to provide a mean CV. Mean estimates of within-year variation (CV) for land counts (one and five counts/day) and water counts (one and five count/day) were then used to estimate the sample sizes (number of daily counts per season) needed to detect a population change between two years of study. Desired power ( $1-\beta$ ) was set at 0.9 throughout, and 1-tailed tests were applied with a significance criterion of  $P < 0.05$ .

*Population trends over multiple years:* Inter-annual variations in attendance (CV of annual mean numbers counted during the census period) at Duck and Chowiet Island were used to estimate the power to detect population change across years using TRENDS statistical software (Gerrodette 1993, Hatch submitted). Such calculations are usually based on the residual variation of annual means remaining after the effect of any linear trend in population change is removed by regression (Hatch submitted). However, since it is difficult to separate the effect of true population change and inter-annual variation in colony attendance based on only three years of count data for each colony, we chose to use conservative estimates of inter-annual count variation, assuming no ongoing trend in population size, and thus eliminated the use of linear regression in estimating interannual CVs.

Estimates of inter-annual variation were calculated for Duck Island water-plot counts (using both one and five counts/day as a daily index; see above), and for Chowiet Island water-plot counts using the single count/day. Estimates of interannual variation on Duck Island were based on yearly indices calculated both from 10 sequential daily counts, and from daily counts over the duration of the census period (28-30 days). Yearly indices using 10 daily counts were calculated by randomly choosing 10 sequential days during the defined census period. The random selection process was repeated 30 times, and an average annual CV was calculated. Power ( $1-\beta$ ) was 0.9 for all analysis. We used 2-tailed tests and a significance criterion of  $P < 0.1$ .

### ***Autocorrelation***

An autocorrelation approach was used to test for periodicity in attendance and for serial correlation in counts among days (Brown and Rothery 1993). We calculated autocorrelation coefficients between pairs of daily counts (daily indices) separated by lag intervals of 1-40

days, and plotted an autocorrelation function (ACF) using the NCSS 2000 statistical software (Hintze 2000).

## **Parakeet Auklets**

### ***Diurnal attendance***

*Buldir Island 2001*: A water plot, approximately 380m long and 150m from shore, was established. Birds on water were counted every 15 minutes from a fixed observation point approximately 30m above sea level. Counts were conducted from 0630-2300 on five consecutive days during 3 separate periods: 28 May-1 June (incubation), 21-25 June (late incubation/early chick rearing), and 14-18 July (chick rearing).

*Talan Island 2001*: A land plot (60 m long and 25 m wide) and sea plot (100 m long and 100 m wide) were established at Talan Island. Both plots had well-defined rock boundaries. Counts of birds within both plots were made using binoculars from a fixed observation point. Birds on both the water and land plot were counted every 30 minutes from 0500-2400. A total of 4 daily counts were conducted; two days during incubation (21 June, 30 June) and two days during chick rearing (19 July, 29 July).

*St Paul Island 2000*: Four land plots were established at Reef Point, St Paul Island. Birds within each plot were counted at 30-min intervals from 0600-1900, using binoculars. All-day counts were conducted during late incubation (27 June), middle chick rearing (9 July), and late chick rearing (3 August). Counts were expressed as a percentage of the maximum plot count, and hourly means were calculated for all plot percentages.

### ***Seasonal attendance***

*Buldir Island 2001 and Talan Island 2001*: As for puffins, we had to establish the timing of daily peak attendance for Parakeet Auklets and use data from the peak attendance to examine seasonal trends. Birds within plot boundaries were counted every 15 mins during a 3-hour daily peak (Buldir Island: 0700-1000 during incubation and 900-1200 during chick rearing; Talan Island: 0630-0930 during incubation and 0830-1130 during chick rearing). The five highest 15-min counts across the 3-hour daily peak were averaged to give a daily index of the number of birds attending the colony (as for puffins, above). Counts were conducted daily from 28 May to 29 July on Buldir Island and from 21 June to 23 August on Talan Island.

*Breeding chronology:* Seasonal attendance data were split into two time periods: incubation and chick rearing. Detailed methods and frequency of nest-checks can be found in Williams et al. (2000) for Buldir Island and in Kitaysky and Golubova (2000) for Talan Island. Chronology was determined from first hatch (June 22 on Buldir Island, Moore et al. (2001); July 17 on Talan Island, E. Golubova, unpubl. data). The mean incubation period of Parakeet Auklets is 35-36 days (Jones and Konukhov 2001) and so the period of incubation was defined approximately as the 35 days prior to first chick hatch date.

## **RESULTS**

### **Horned Puffin**

#### ***Diurnal attendance***

Patterns of diurnal attendance were very different, both among colonies and between water and land counts. Attendance also differed between the incubation and chick-rearing periods (Fig. 2,3). Buldir Island was characterized by a gradual build-up of numbers to a strong evening peak between 1900-2200 (Table 1). The pattern of attendance during incubation was similar at the two Buldir sub-colonies (Main Talus and Crested Point: Fig. 2). Duck Island attendance was bimodal during both incubation and chick rearing, with a peak during the morning and a more pronounced peak during the evening. Attendance at the colony mirrored attendance at sea, except that peak numbers at the colony lagged peak numbers on water by 2-4 hours. In contrast to attendance at Buldir Island, attendance during incubation on Suklik Island peaked during the morning (0800-1100: Table 1). Attendance on Talan Island was characterized by a morning peak during incubation, whereas the daily peak in attendance was later in the day during chick-rearing (Fig. 2, 3).

#### ***Seasonal attendance***

*a) Pattern of attendance:* Three-day running means of the daily index counts were calculated to smooth out daily variability and help visualize the seasonal patterns in colony attendance (Figs. 4,5).

Data on pre-lay attendance are limited to 1998 and 1999 on Duck Island and Chowiet Island in 1977, 1993 and 1995. On Duck Island, the mean number of birds attending during pre-laying was lower (Table 2) than during incubation (two-way ANOVA on ranked data, Sokal and Rohlf 2000:  $H = 58.6$ ,  $df = 1$ ,  $P < 0.001$ ), but did not differ

between years ( $H = 3.13$ ,  $df = 1$ ,  $P > 0.05$ ). To allow comparison with results obtained on Duck Island (1998  $n = 22$  d; 1999  $n = 23$  d prior to the start of incubation), we confined analysis of Chowiet Island pre-lay data to 1977, since this was the only year with daily counts 23 days prior to the start of incubation. There was no significant difference between the mean number of birds counted on Chowiet Island in 1977 during prelay and the mean number counted during the incubation period ( $t = 0.54$ ,  $df = 41$ ,  $P = 0.59$ : pre-lay mean =  $193 \pm 37$ ,  $n = 23$ ; incubation mean =  $217 \pm 25$ ,  $n = 41$ ).

On Duck Island, the highest numbers of birds were present during the incubation phase of breeding in each year (Fig. 4, Table 2). After the onset of chick rearing, numbers of birds declined progressively, except for a sharp increase at the end of August 1999 (Fig. 4). Overall mean attendance (land and water counts combined) was higher during incubation than during chick rearing (two-way ANOVA on ranked data:  $H = 283.2$ ,  $df = 1$ ,  $P < 0.001$ ), but did not differ between years ( $H = 1.3$ ,  $df = 2$ ,  $P > 0.05$ ).

A seasonal increase in the numbers of birds counted on land occurred on Buldir Island (Fig. 5), with significantly higher numbers present during chick-rearing than during the incubation period ( $t = 4.79$ ,  $df = 58$ ,  $P < 0.001$ ). A significant positive correlation existed between the daily counts conducted at the two different subcolonies on Buldir Island (Crested Point and Main Talus) during incubation (correlation coefficient = 0.745,  $p < 0.001$ ,  $n = 24$  d).

The seasonal pattern of attendance on water at Talan Island exhibited two large peaks in the number of birds counted (Fig. 5). Land counts were generally depressed during late incubation. There was no difference, however, in the overall mean numbers attending the colony between the incubation and chick-rearing periods (land counts  $t = 0.26$ ,  $df = 41$ ,  $P = 0.8$ ; water counts  $t = 1.89$ ,  $df = 61$ ,  $P = 0.064$ ; Table 2). 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 2) in either 1977 ( $t = 1.26$ ,  $df = 66$ ,  $P = 0.21$ ) or 1993 ( $t = 1.2$ ,  $df = 22$ ,  $P = 0.24$ ).

*b) Autocorrelation:* Patterns of seasonal attendance were characterized by marked variation among days in the number of birds attending the colony (e.g., Duck Island, Fig. 4). Attendance was quasi-cyclic, with pronounced peaks and troughs at intervals varying from 1-10 days. However, the periods and amplitude of cycles were irregular and out of phase, eliminating statistically significant periodicity (Brown and Rothery 1993). Nonetheless, there was marked serial dependence between daily counts, and irregular

fluctuations at time scales of generally less than 10 days. Although the strength and duration of lagged correlations varied among colonies and also between time series of water and land plot counts (Fig. 6), significant positive correlations at lag intervals of one to five days were observed at Talan, Buldir and Duck Island, and all significant negative correlations ( $n = 45$ ) were of lag intervals of 10 days or less (Table 3).

*c) Among-day variation:* Coefficients of variation (CV) were calculated for 5-day running periods over the breeding season (Fig. 7) to show the differences in daily variation both across the season, and among colonies and years. CVs were generally high during prelay and early incubation and also towards the end of chick rearing. Overall, mean CVs were lower during the incubation period (prelay CV = 0.97, incubation CV = 0.68, chick-rearing CV = 0.78; Table 2).

Among 12 possible comparisons (Table 2), significant differences in CV between incubation and chick rearing were found only for Duck Island water counts in 1997 ( $Z = 2.26$ ,  $Z_{0.05(2)} = 1.96$ ,  $P < 0.05$ ) and 1999 ( $Z = 2.52$ ,  $Z_{0.05(2)} = 1.96$ ,  $P < 0.05$ ). CVs during both years were higher during chick rearing than during the incubation period. There was no significant difference between CVs calculated for incubation and chick rearing periods for the other 10 comparisons (Table 2:  $Z < 1.96$ ,  $P > 0.5$ ).

Because the period from mid/late incubation through early chick-rearing generally had the least variation among days, we compared CVs calculated for five different potential census periods (20-30 days) within this window (Table 4). Relative variability among the different census periods differed among colonies and among land and water counts, and no one census period had consistently lower variation (CV) for all colonies and years. Overall mean variability was lowest during the last 30 days of incubation (among day CV = 0.6). Given our definition for the start of chick-rearing (median hatch date) this period includes the beginning of the chick-rearing at the colony.

### ***Attendance and weather***

Although there was no relationship between wind speed (knots) and the daily index of birds counted on the water at Duck Island in 1999 ( $y = 74.0 + 1.67x$ ,  $F = 1.71$ ,  $df = 1,66$ ,  $P = 0.2$ ), there was a significant negative relationship between wind speed and the daily index of birds counted on land at Duck Island ( $y = 50.5 - 1.61x$ ,  $F = 9.84$ ,  $df = 1,66$ ,  $P = 0.003$ ).

### ***Power analysis***

*Detecting change between two years:* Within-year variation (CVs) associated with the two different protocols (one or five counts/day taken as the daily index) were calculated using the last 30 days of incubation as the ‘census window’ for Buldir, Duck and Talan water and land-plot counts (Appendix 1), and mean within-year variations (Table 5) were used to estimate the sampling effort needed to detect population change between two years of study. There is asymmetry in the minimum amount of population change that can be detected, depending on the direction of change (Fig 8). A decrease in numbers is easier to detect than an increase, because of the positive linear relation between the mean and standard deviation of counts (Fig. 9). For example, if five counts on water are conducted daily over the 30-day census period, it is possible to detect ca 37% decrease in population size but only a 75% increase.

Census effort (number of days counted within the 30-day census period) needed to detect change varied among the counting protocols. Within-year variation in water counts (mean CV = 0.62) was lower than the variation of land-based counts (mean CV = 0.8), and within year variation associated with five counts as the daily index (mean CV = 0.65) was lower than the CV (mean 0.77) arising from one daily count (Table 5). Z-tests indicated small differences between CVs calculated for one versus five counts per day ( $P = 0.048$  for water counts;  $P = 0.16$  for land plots). Differences in within-year variation associated with each of the four protocols are reflected in power curves and the estimated effort needed to detect population change. For example, the ability to detect a 60% decrease in population size between two years would require 12 days with five counts/day on water; 15 days with one count/day on water; 17 days with five counts/day on land or 23 days with one count/day on land.

*Detecting trends:* Estimates of interannual variation (CV) in mean numbers attending Duck and Chowiet islands are presented in Table 6. Interannual variation was higher on Chowiet (CV = 0.81), than on Duck Island (CV = 0.10) using comparable counting methods. On Duck Island, interannual variation differed among counting protocols, with less variation occurring on water plots (mean CV = 0.15) compared with counts of birds on land (mean CV = 0.39). There was little difference in the interannual variation observed using either one or five counts a day as the daily index. Interannual variation in water counts was higher when the annual index was based on 10 consecutive days of counting (mean CV = 0.2) rather than on 28-30 days (mean CV = 0.1).



Estimates of interannual variation using both types of daily index (i.e. one versus five counts per day) were averaged to yield four characteristic levels of variation among years: Duck Island water plot counts, with the annual index based on 28-30 days,  $CV \approx 0.1$ ; Duck Island water plot counts, with the annual index based on 10 days,  $CV \approx 0.2$ ; Duck Island land plot counts, average variation of counts resulting from both 10 and 28-30 days of counting,  $CV \approx 0.4$ ; and Chowiet Island water-plot counts, with the annual index based on 18-30 days,  $CV \approx 0.8$ . Using the option in TRENDS that assumes a linear relationship between means and SD (Fig. 9), i.e., assuming a constant CV, we examined the number of years required to detect given rates of population change under various sampling protocols. The four levels of interannual CV (0.1, 0.2, 0.4, and 0.8), and three different sampling intervals, were used as input to TRENDS. The resulting power curves are presented in Figure 10.

The effort (number of study years) required to detect a given rate of change depends on the sampling interval involved, with shorter studies required under a program of annual monitoring than a program in which birds are counted only at 2- or 5-year intervals. For example, detection of a 4% annual change in population size would require about nine years of study if a colony were censused annually; whereas 17 years are required using counts obtained every five years.

## **Parakeet Auklet**

### ***Diurnal Attendance***

The pattern of attendance differed among colonies (Fig. 11). Talan Island was characterized by a morning peak in attendance, with birds spending less time overall on the land plot than on the water plot. Attendance on Buldir Island (water) was also characterized by a morning peak in numbers, although there was also a lower evening peak in attendance. The peak in diurnal attendance on St. Paul was broader and generally less pronounced than the other two islands, with birds spending longer at the colony during the afternoon. The pattern of diurnal attendance at Talan and Buldir Island differed slightly across the breeding season, with the peak in numbers becoming slightly later in the day during chick rearing.

### ***Seasonal Attendance***

Parakeet Auklets on both Buldir and Talan Island had very poor breeding success in 2001, with the majority of chicks on Talan Island dying during the first two weeks of chick rearing and zero monitored fledging success (Golubova, unpubl. data). Birds on Buldir Island also failed; hatching success was low (0.35, n = 40 eggs) and monitored fledging success was also zero (Moore *et al.* 2001). The seasonal patterns of attendance during chick rearing on both islands therefore more accurately describes the attendance of failed breeders rather than provisioning parents. There was a noticeable increase in numbers counted on Buldir Island (water) after the majority of birds failed at the start of chick rearing (Fig. 12). The relative numbers of birds attending the colony on land and water changed over the season on Talan Island, with relatively more birds spending time on water as the season progressed (Fig. 12).

## **DISCUSSION**

Attendance by seabirds at their breeding colonies may be influenced by weather variables, tidal cycles and social behavior such as defense or acquisition of breeding sites and partners (e.g., Slater 1976, Stempniewicz 1986, Hatch and Hatch 1988, Hatch 1989, Jones *et al.* 1989, Piatt *et al.* 1990, Weimerskirch 1998). Such studies have also indicated that in some cases, patterns in colony attendance may be influenced by food availability; with the distance and density of prey influencing foraging time at sea and therefore time spent at the colony (e.g., Birkhead 1977, Gaston and Nettleship 1982). Numbers attending the colony may be high when food is abundant and foraging time minimal.

A few studies (e.g., Hatch and Hatch 1988, Jones 1992) have highlighted the difficulties of interpreting population count data, and discussed the effect that annual variation in food availability and reproductive performance have on colony attendance. In the present study, there were marked differences in the patterns of Horned Puffin seasonal colony attendance among colonies and years. These differences may be due to local or annual differences in food availability, foraging effort and the behavior of breeders, non-breeders and sub-adult puffins. For example, the decrease in Horned Puffin attendance after the onset of chick rearing at Duck Island may result from increased foraging time-budgets of adults after chicks have hatched at Duck Island, a colony where local food availability is

relatively low, and seabirds must work relatively hard (Kitaysky *et al.* 1999, Zador and Piatt 1999, Piatt 2002).

The proportion of non-breeding adults may also vary between colonies, and populations that are increasing in size may contain proportionately more non-breeders than stable populations. Patterns in Horned Puffin seasonal attendance may also reflect the presence of immature birds at the colony, for example, younger non-breeding Atlantic Puffins return to the colony later than breeders, and with younger and younger birds arriving progressively as the season advances (Ashcroft 1976, 1979, Davidsen 1994). Although numbers of immature birds and patterns of colony attendance may provide an indication of recruitment, direct linkage is complicated because sub adult birds may differ from older and actively breeding birds in their ability or willingness to spend time at the colony. Much of variation in counts may in fact be due to the variable presence of non-breeding individuals (e.g., Gaston and Nettleship 1982, Harris *et al.* 1986). Foraging efficiency increases with age in many seabird species (e.g., Burger 1980, Greig *et al.* 1983, Catry and Furness 1999), thus low food availability would be expected to have a marked effect on young pre-breeders. For instance, a study of colony attendance by prospecting pre-breeding Thick-billed Murres (*Uria lomvia*) indicated that older birds with higher feeding efficiency were able to spend more time at the colony than younger birds (Gaston and Nettleship 1982). The seasonal decline in numbers of Horned Puffins attending Duck Island over the season may therefore be explained partially by an inability of young pre-breeding birds to spend much time at the colony. However, there are currently no individually marked birds of known age with which to test this hypothesis.

Given the many influences on colony attendance and the complexities of count interpretation, population monitoring should be conducted during periods: a) of peak diurnal attendance, b) of minimal seasonal variability, c) with the maximum presence of breeders, d) with the minimum presence of immature and failed breeders, and, e) of least sensitivity to food supply. Based on the results from this multi-colony study we suggest the following approach.

#### Guidelines for monitoring populations of Horned Puffins

In this paper we examined: a) the power to detect an increase or decrease in numbers attending the colony between two years of study, and b) the power to detect population trends over multiple years. These are different problems that use different indices of

attendance variation (within-year variation and among-year variation, respectively). Variability determines the power to detect change, and census protocols should aim to minimize variation in colony attendance. Components of a census protocol (e.g., number of daily counts and the duration of census period) may influence within-year and among-year variation differently. A study aiming to detect change between two years of study may therefore require a slightly different protocol than that of one examining population trends among many years. Some of these differences are reflected in the guidelines below.

1) *Timing of Census Period*: Within-year variation in attendance was generally lower during the last 30 days of incubation. Field workers may adjust timing of census to local breeding phenology. Adult puffins carrying fish also provide a good indication that chicks are hatching and the census period is over. In addition to low among-day variation and an easily observed census end point, incubation may also be the better census period for two biological reasons:

- a) Young, prospecting individuals are known to arrive later in the season than breeders in a number of seabird species (e.g., Hatch 1989, Jones 1992, Warham 1990, Halley *et al.* 1995). Although there are no data on the return dates of Horned Puffin sub-adults, we assume that the pattern is similar to the Atlantic Puffin, with younger birds arriving later than breeders (Ashcroft 1979). Non-breeding four-year old Atlantic Puffins return to the colony during the incubation stage, three-year olds arrive about a month later during chick-rearing, and two-year olds arrive even later in the breeding season (Davidson 1994). Counts during the incubation period should therefore be more focused on the breeding population, whereas counts during chick rearing may include a high and varying proportion of sub-adults and non-breeders.
- b) Local feeding conditions are known to influence time spent at the colony (e.g., Gaston and Nettleship 1982). Although there are costs associated with egg formation and incubation (Monaghan and Nager 1997), parental time budgets should be especially sensitive to local food availability during chick rearing, because of the added foraging effort required for chick provisioning (Zador and Piatt 1999, Piatt 2002). Foraging behavior should be less constrained by local feeding conditions during incubation, and consequently less sensitive to annual variation in food availability.

2) *Duration of census period*: An optimal census protocol is one in which power to detect change is maximized. In practice, we seek a balance between survey effort and statistical power. Given the variability in attendance of common murrelets during incubation, for example, counts conducted on 40 consecutive days are needed to detect a 6-8% change in numbers between years, whereas counts conducted on only five days could detect a 20-26% change (Hatch and Hatch 1989).

Time series analyses suggested that daily counts of Horned Puffins were autocorrelated among days. There was marked serial dependence and irregular fluctuations at time scales of generally less than 10 days. In order to encompass this variation in attendance, we recommend that census counts should be conducted daily for a minimum of 10 days, or in multiples of 10 days.

Within-year variation in attendance was generally lowest during the last 30-days of incubation. Within-year variation also declined with the increasing number of daily counts conducted during this optimum 30-day census window, increasing our power to detect a change in numbers between two years of study. Moreover, estimates of inter-annual variation based on a 10-day census period were higher than those based on 30 days. Therefore, we suggest that for studies that examine either change in numbers between two years, and/or change in numbers among many years, the optimal population-monitoring protocol would consist of daily counts during the last 30 days of incubation. There would be no advantage to increasing counts much beyond these 30 days because seasonal variance in attendance would begin to erode statistical power.

3) *Time of day*: Evidence from Buldir Island suggests that diurnal attendance may be consistent both among years at the same colony and among sub-colonies on the same island. The timing of peak diurnal attendance, however, varied markedly among colonies. Given such differences, the window of peak attendance needs to be determined at each colony prior to the start of census by conducting all-day counts.

4) *Daily index*: Estimates of within-year variation in colony attendance were lower using a daily index based on five counts than those based on only one count. Five counts should therefore be used in studies comparing the number of birds between two years.

There was no difference in among-year variation at Duck Island using indices based on one or five counts a day, and therefore no difference in the power to detect a population

change among years. The less time-consuming and more practical method of conducting a single count per day and using this as the daily index should therefore be used for studies that monitor population trends over a multi-year time span.

5) *Land versus water counts:* Estimates of both within-year and among-year variation in colony attendance were higher from counts on land than from counts on water. Wind conditions at Duck Island also had less effect on the attendance of birds on water than those on land in the same cove. We therefore conclude that birds should be counted on water at colonies where plots can be established with defined natural boundaries. Boundaries must be easily recognized and remain consistent among years. Some sheltered bays may allow the use of buoys for demarcating plot boundaries.

6) *Weather:* There was no relationship between wind speed and the daily index of birds counted on water at Duck Island in 1999. Moreover, Hatch (submitted) found that although wind explained ca. 11% of the variation in counts of birds on water at Chowiet Island, wind had little effect on annual means. Daily counts, over a lengthy census period should therefore dampen any effects of weather on water-based counts (Hatch submitted), although poor weather may necessitate a longer census period.

7) *Monitoring effort required:* Analysis of differences in counts between two years of study may be useful for some questions, such as quantifying the effect of an oil spill on the number of birds attending a colony. The majority of such questions will predict either an increase or decrease in the number of birds, and therefore allow a one-tailed comparison test between the two annual means. Although the comparison of counts between two years of study is valid for answering such questions, more counts are needed during the daily attendance peak than would be true for long-term monitoring program, and the minimum amount of population change that can be detected is relatively high.

The majority of monitoring studies are long-term, requiring a multi-year approach to detect population trends. Ultimately, the power to detect population change depends on the level of residual interannual variation. At present, our knowledge of interannual variation in Horned Puffin colony attendance is limited to two colonies and only three years of data from each. Among-year variation on Duck Island was much lower than for Chowiet Island. However, since data on Chowiet Island were collected over a 20-year time span,

they are not directly comparable to Duck Island and it is impossible to determine whether the higher variability reflects an annual difference in attendance, or whether the population on Chowiet actually declined between 1977 and 1995. Until more knowledge of interannual variability is obtained, we assume that neither colony had changed in size over the three years of study. Interannual variability on Chowiet Island is therefore viewed as a worse case scenario for assessing the power to detect population change.

Following Hatch (submitted), we use the half-life of a puffin population at two rates of decline as a yardstick for measuring the performance or “success” of various monitoring protocols. 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. Combinations of interannual CV and sampling interval 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 in Fig. 10. Using an interannual CV of 0.1 (Duck Island counts of birds on water for 28-30 days as the annual index), sampling intervals of either one or two years would likely detect a population change of 6.7% year in less than the 10-year population half-life. By contrast, counts every five years would require about 14 years to detect the same rate of change—an inadequate effort if it is desired 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 for 10 days as the annual index), counts every one or two years would be likely to detect a 3.4% change 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.

*Summary:* A modest increase in interannual variability produces a large decrease in the power to detect population change. This clearly indicates the need to obtain better estimates of interannual variability in Horned Puffin attendance for use in power analyses of population monitoring. In the mean time, we suggest that long-term population monitoring programs for Horned Puffins should a) identify the colony-specific window of peak diurnal attendance, b) count birds once daily during peak diurnal attendance, c) count birds resting on the water adjacent to the colony, d) count birds daily during the census period, e) define the 30 days at the end of incubation as the census period, and f) visit and census colonies annually.

Detailed study of banded birds is also needed to determine the age of first breeding and return to the colony, as well as age-specific behavior and time allocation among Horned Puffins at a colony. Better knowledge of the underlying factors determining both within-year and among-year variability of colony attendance would aid with the interpretation of count data, both for purposes of population monitoring purposes, and as an indicator of local feeding conditions or colony recruitment.

Until more information is available, the interpretation of attendance patterns and the use of counts to assess population changes must be made with caution. For long-lived species, such as the Horned Puffin, adult survival is an important factor influencing population trends (Croxall and Rothery 1991). Thus, in addition to count data, effort should also be aimed towards establishing banded populations of Horned Puffins for monitoring of adult survival. Data on adult survival and reproductive performance should help distinguish true population trends from annual variation in food availability and behavior at the colony.

#### Guidelines for monitoring populations of Parakeet Auklets:

Since data collected during this study are limited to two colonies that experienced almost complete breeding failure, we have little knowledge of within-year variation in colony attendance and are unable to suggest firm guidelines for detecting change in Parakeet Auklet numbers between two years of study. Slight differences in the timing and duration of peak diurnal attendance among islands suggests that the window of peak diurnal attendance needs to be determined at each colony prior to census.

More knowledge of within-year variation in colony attendance during years of good or average breeding success is needed, but work should focus on increasing our knowledge of interannual variation in colony attendance among different colonies and over many years.



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## REFERENCES

- Anker-Nilssen, T. and Røstad, O.W. 1993. Census and monitoring of Puffins *Fratercula arctica* on Røst, North Norway, 1979-1988. *Ornis Scandinavica* 24: 1-9.
- Ashcroft, R.E. 1976. Breeding biology and survival of Puffins. Unpubl. D. Phil. thesis, University of Oxford.
- Ashcroft, R.E. 1979. Survival rates and breeding biology of Puffins on Skomer Island, Wales. *Ornis Scandinavica* 10: 100-110.
- Barrett, R.T., Anker-Nilssen, T., Rikardsen, R., Valde, K., Røv, N. and Vader, W. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980-1983. *Ornis Scandinavica* 18: 73-83.
- Bedard, J. 1969. The nesting of Crested, Least and Parakeet Auklets on St. Lawrence Island, Alaska. *Condor* 71: 386-398.
- Birkhead, T.R. 1977. Attendance patterns of Guillemots *Uria aalge* at breeding colonies on Skomer Island. *Ibis* 120: 219-229.
- Birkhead, T.R. and Nettleship, D.N. 1980. Census methods for murre, *Uria* species: a unified approach. Canadian Wildlife Service Occasional Paper no. 43.
- Brown, D. and Rothery, P. 1983. Models in Biology, mathematics, statistics and computing. Pub. John Wiley and Sons, New York.
- Burger, J. 1980. The transition to independence and post-fledging parental care in seabirds. *Behaviour of Marine Animals* 4: 366-447.
- Byrd, G.V., Day, R.H. and Knudtson, E.P. 1983. Patterns of colony attendance and censusing of auklets at Buldir Island, Alaska. *Condor* 85: 274-280.
- Byrd, G.V., Murphy, E.C., Kaiser, G., Kondratyev, A.Y. and Shibaev, Y.V. 1993. Status and ecology of offshore fish-feeding alcids (murre and puffins) in the North Pacific. In Vermeer, K., Briggs, K.T., Morgan, K.H. and Siegel-Causey, D. (eds) *The status, ecology and conservation of marine birds of the North Pacific*. Pp 176-86. Canadian Wildlife Service, Ottawa.
- Catry, P. and R.W. Furness 1999. The influence of adult age on territorial attendance by breeding Great Skuas *Catharacta skua*: an experimental study. *Journal of Avian Biology* 30: 399-406.

- Croxall, J.P. and Rothery, R. 1991. Population regulation of seabirds: implications of their demography for conservation. In Perrins, C.M., Lebreton, J.D. and Hirons, G.J.M. (eds.) *Bird population Studies. Relevance to Conservation and Management*. Pp 272-296. Oxford University Press, Oxford.
- Davidson, F. 1994. The ecology of the Puffin *Fratercula arctica*. Unpubl. Ph.D. thesis, University of Oxford, 323 pp.
- Ewins, P. 1985. Colony attendance and censusing of black guillemots (*Cepphus grylle*) in Shetland. *Bird Study* 32: 176-185.
- Gaston, A.J. and Jones, I.L. 1998. *The Auks*. Oxford University Press, Oxford.
- Gaston, A.J. and Nettleship, D.N. 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.
- Greig, S.A., Coulson, J.C., Monaghan, P. 1983. Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). *Animal Behaviour* 31: 1237-1243.
- Halley, D.J. Harris, M.P. and Wanless, S. 1995. Colony attendance patterns and recruitment in immature common murrets (*Uria aalge*). *The Auk* 112(4): 947-957.
- Harding, A.M.A. 2001. The Breeding Ecology of Horned Puffins *Fratercula corniculata* in Alaska. Unpubl. MSc. Thesis, University of Durham.
- Harris, M.P. 1987. Variation in the correction factor used for converting counts of individual Guillemots *Uria aalge* into breeding pairs. *Ibis* 131: 85-93.
- Harris, M.P. and Murray, S. 1981. Monitoring of Puffin numbers at Scottish colonies. *Bird Study* 28: 15-20.
- Harris, M.P., Wanless, S. and Rothery, P. 1986. Counts of breeding and nonbreeding Guillemots (*Uria aalge*) at a colony during the chick-rearing period. *Seabird* 9: 43-46.
- Hatch, S.A. submitted. Activity patterns and monitoring of Horned Puffins and Parakeet Auklets.
- Hatch, S.A. 1989. Diurnal and seasonal patterns of colony attendance in the Northern Fulmar, *Fulmarus glacialis*, in Alaska. *Canadian Field-Naturalist* 103: 248-260.
- Hatch, S.A. and Hatch, M.A. 1988. Colony attendance and population monitoring of Black-legged Kittiwakes on the Semidi Islands, Alaska. *Condor* 90: 613-620.

- Hatch, S.A. and Hatch, M.A. 1989. Attendance patterns of murrelets at breeding sites: implications for monitoring. *Journal of Wildlife Management* 53 (2): 483-493.
- Hatch, S.A. and Hatch M.A. 1990. Breeding season of oceanic birds in a subarctic colony. *Canadian Journal of Zoology* 68: 1664-1679.
- Hildien, O. 1994. Diurnal rhythm of colony attendance and optimal census time for the Black Guillemot *Cephus grylle* in the Baltic Sea. *Ornis Fennica* 71 (2): 61-67.
- Hintze, J.L. 2000. NCSS 2000 User's Guide-II. Number Cruncher Statistical Systems, Utah.
- Hipfner, J.M. and Byrd, G.V. 1993. Breeding biology of the Parakeet Auklet compared to other crevice-nesting species at Buldir Island, Alaska. *Colonial Waterbirds*, 16(2): 128-138.
- Jones, I.L. 1992. Colony attendance of Least Auklets at St. Paul Island, Alaska: implications for population monitoring. *Condor* 94: 93-100.
- Jones, I.L., Konyukhov N.B., Williams J.C. and Byrd, G.V. 2001. Parakeet Auklet. In *The Birds of North America*, No. 594 (A. Poole, and F. Gill eds.). The Birds of North America Inc., Philadelphia, PA.
- Jones, I.L., Gaston, A.J. and Falls, J.B. 1989. Factors affecting colony attendance by Ancient Murrelets (*Synthliboramphus antiquus*). *Canadian Journal of Zoology* 68: 433-441.
- Kitaysky, A.S. and Golubova, E.G. 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *Journal of Animal Ecology*, 69: 248-262.
- Kitaysky, A.S., Wingfield, J.C. and Piatt, J.P. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* 13: 577-584.
- Konyukhov, N.B., and Juk, K. 2001. Attendance patterns of Parakeet Auklets and Horned Puffins at Buldir Island, Alaska in 2001. U.S. Fish and Wild. Serv. Rep. AMNWR 01/10 Homer, Alaska.
- Manuwal, D.A. and Manuwal, N.J. 1979. Habitat specific behaviour of the Parakeet Auklet in the Barrens Islands, Alaska. *Western Birds* 10: 189-200.
- Monaghan, P. and Nager, R.G. 1997. Why don't birds lay more eggs? *Trends in Ecology and Evolution* 12: 270-274.

- Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. In Furness, R.W. and Greenwood, J.J.D (eds) *Birds as Monitors of Environmental Change*. Pp. 217-266. Chapman and Hall, London.
- Moore, H., Kappes, P. and Grindell, M. 2001. Biological monitoring at Buldir Island, Alaska in 2001: Summary appendices. U.S. Fish and Wildl. Serv. Rep. AMNWR 01/11. Adak, Alaska. 36 pp.
- Petersen, M.R. 1983. Horned Puffin (*Fratercula corniculata*). In Baird, P.A. and Gould, P.J. (eds) *The breeding biology and feeding ecology of marine birds in the Gulf of Alaska*. Pp. 401-426. U.S. Dept. Commerce, NOAA, OCSEAP Final Report 45 (1986).
- Piatt, J.F., Roberts, B.D. and Hatch, S.A. 1990. Colony attendance and population monitoring of Least and Crested Auklets on St. Lawrence Islands, Alaska. *Condor* 92: 97-106.
- Piatt, J.F., H.R. Carter, and Nettleship, D.N. 1991. Effects of oil pollution on marine bird populations. Pp. 125-141 in J. White (Ed.) *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, PA, 210 pp.
- Piatt, J.F. and Kitaysky, A.S. 2001. Horned Puffin (*Fratercula corniculata*). In Poole, A. and Gill, F. (eds) *The Birds of North America, No. 611*. The American Ornithologists' Union. The Academy of Natural Sciences; Washington D.C. Pp. 1-27.
- Piatt, J.F. (ed.). 2002. Response of seabirds to fluctuations in forage fish density. Final Report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Alaska Science Center, U.S. Geological Survey, Anchorage, Alaska. 406 pp.
- Savard, J-P. L, and Smith, G.E.J. 1985. Comparison of survey techniques for burrow-nesting seabirds. *Canadian Wildlife Service Progress Notes* 151: 1-7.
- Sealy, S.G. and Bédard, J. 1973. Breeding biology of the parakeet auklet (*Cyclorhynchus psittacula*) on St. Lawrence Island, Alaska. *Astarte* 6: 59-68.
- Slater, P.J.B. 1980. Factors affecting the numbers of Guillemots *Uria aalge* present on cliffs. *Ornis Scandinavica* 11: 155-163.
- Slater, P.J.B. 1976. Tidal rhythm in a seabird. *Nature* 264: 636-638.

- 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 (2): 247-263.
- Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W. and Tasker, M.L. 1995. *Seabird monitoring handbook for Britain and Ireland*. JNCC / RSPB / ITE / Seabird Group, Peterborough.
- Wanless, S., French, D.D., Harris, M.P. and Langslow, D.R. 1982. Detection of annual changes in the numbers of cliff-nesting seabirds in Orkney 1976-1980. *Journal of Animal Ecology* 51: 785-795.
- Warham, J. 1990. *The petrels, their ecology and breeding systems*. Academic Press Limited, London.
- Wehle, D.H.S. 1983. The food, feeding, and development of young Tufted and Horned Puffins in Alaska. *Condor* 85: 427-442.
- Weimerskirch H. 1998. How can a pelagic seabird provision its chick when relying on a distinct food resource? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. *Journal of Animal Ecology* 67: 99-109.
- Williams, J.C., Scharf, L. and Byrd, G.V. 2000. Ecological monitoring methods of the Aleutian Islands Unit, Alaska Maritime National Wildlife Refuge. U.S. Fish and Wildl. Serv. Rep., AMNWR 00/01. Adak, Alaska. 352 pp.
- Zador, S.G. and Piatt, J.F. 1999. Time budgets of Common Murres at a declining and increasing colony in Alaska. *Condor* 101: 149-152.

Table 1. Horned Puffin diurnal attendance. Time of daily 3-hour period of peak colony attendance during incubation and chick rearing (Fig. 2).

Colony	Year	Plot	Chronology	Peak Attendance
Buldir	2001	land	incubation	1900-2200
Buldir	2001	land	chick-rearing	1900-2200
Talan	2001	land	incubation	1030-1330
Talan	2001	water	incubation	0915-1215
Talan	2001	land	chick-rearing	1700-2000
Talan	2001	water	chick-rearing	1400-1700
Duck	1997-1999	land	incubation	1900-2200
Duck	1997-1999	land	incubation	1900-2200
Duck	1997-1999	water	chick-rearing	1900-2200
Duck	1997-1999	water	chick-rearing	1900-2200
Suklik (Semidis)	1986	land	prelay/early incubation	0800-1100





Table 3. The number of days over which Horned Puffin attendance was significantly autocorrelated at different colonies (see Figure 6).

Island	Year	Count	Correlation	
			Positive	Negative
Talan	2001	land	1	
Talan	2001	water	1	
Talan	2001	land and water	1,5	
Buldir	2001	land	6,4,7,5,3	
Duck	1997	land	7,2	
Duck	1997	water	1,3,4,5,2,6,8,9,10,7	
Duck	1997	land and water	3,1,4,5,2,7,6,	
Duck	1998	land	5	
Duck	1998	water	1,5,4,3	
Duck	1998	land and water	5,1,4,3	
Duck	1999	land	1	
Duck	1999	water	1,2,4,8,5,9,3	
Duck	1999	land and water		

Significant time lags are listed in order of increasing significance

Table 4. Coefficients of variation for five different potential census periods for Horned Puffins

Island	Plot	Year	Census Period *				
			1	2	3	4	5
Talan	land	2001	0.65	0.71	0.71	0.58	0.46
Talan	water	2001	0.58	0.65	0.68	0.68	0.76
Buldir	land	2001	0.70	0.70	0.65	0.8	0.86
Duck	land	1997	0.70	0.70	0.66	0.79	0.79
Duck	water	1997	0.43	0.52	0.43	0.37	0.23
Duck	land	1998	0.87	0.80	0.90	0.88	0.85
Duck	water	1998	0.73	0.86	0.76	0.37	0.49
Duck	land	1999	0.55	0.50	0.55	0.56	0.81
Duck	water	1999	0.56	0.70	0.35	0.38	0.21
MEAN			0.64	0.68	0.63	0.60	0.61

\* Census periods defined as:

1 = last 20 days of incubation

2 = last 20 days of incubation to first 20 days of chick rearing

3 = first 20 days of chick rearing

4 = last 30 days of incubation

5 = 20 days, ending 10 days before the end of incubation

Table 5. Estimates of within-years variation in Horned Puffin counts for power analysis of pair-wise comparisons of means.

Plot type	Counts/day	Mean count <sup>a</sup>	Mean CV <sup>b</sup>
Land	1	40.4	0.87
Land	5	48.7	0.73
Water	1	140.5	0.66
Water	5	170.0	0.57

<sup>a</sup> Unweighted average of mean counts for all colony-years with  $n = 1$  or  $n = 5$  counts per day (Appendix 1).

<sup>b</sup> Unweighted average of CV's for corresponding means in Appendix 1, i.e.,  $(SD_1 / \bar{X}_1 + SD_2 / \bar{X}_2) / 2 =$  unweighted average CV.

Table 6. Estimates of interannual variation in Horned Puffin counts for power analysis of multi-year trends.

Colony	Counts/day <sup>a</sup>	<i>n</i> (days)	<i>N</i> (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	--

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

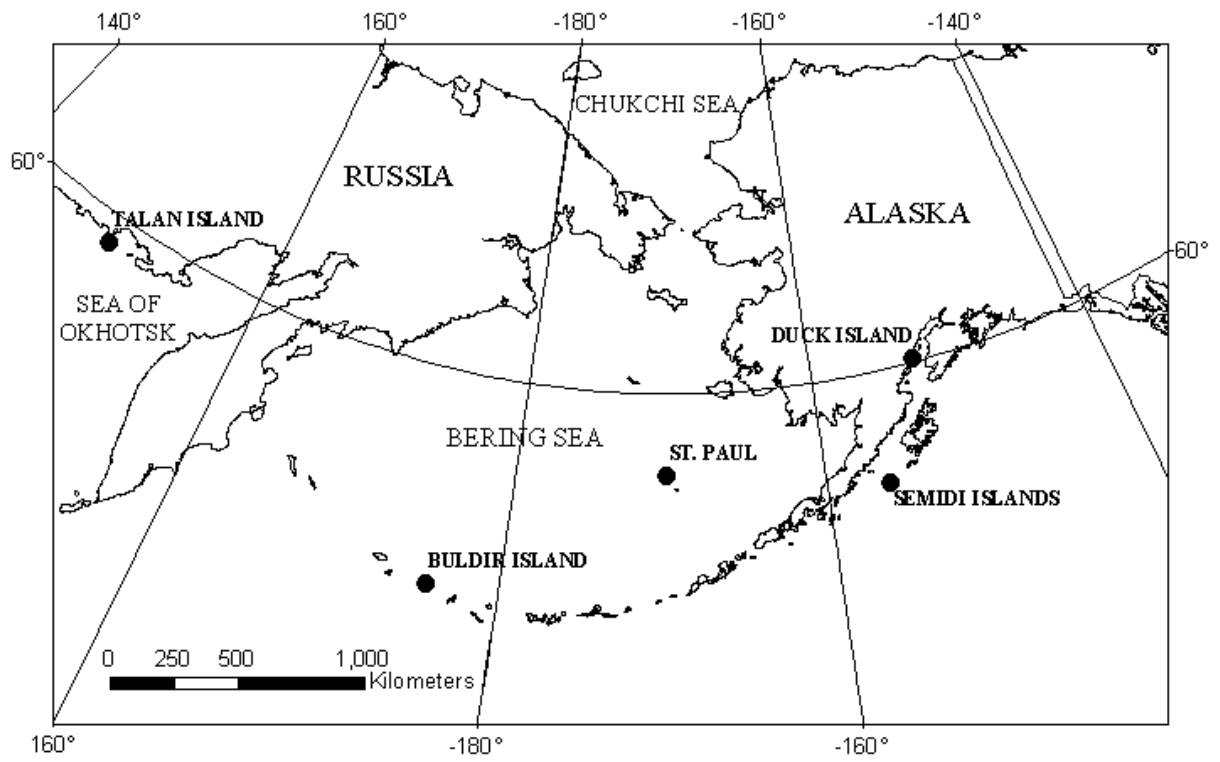


Figure 1. Location of Horned Puffin and Parakeet Auklet study colonies.

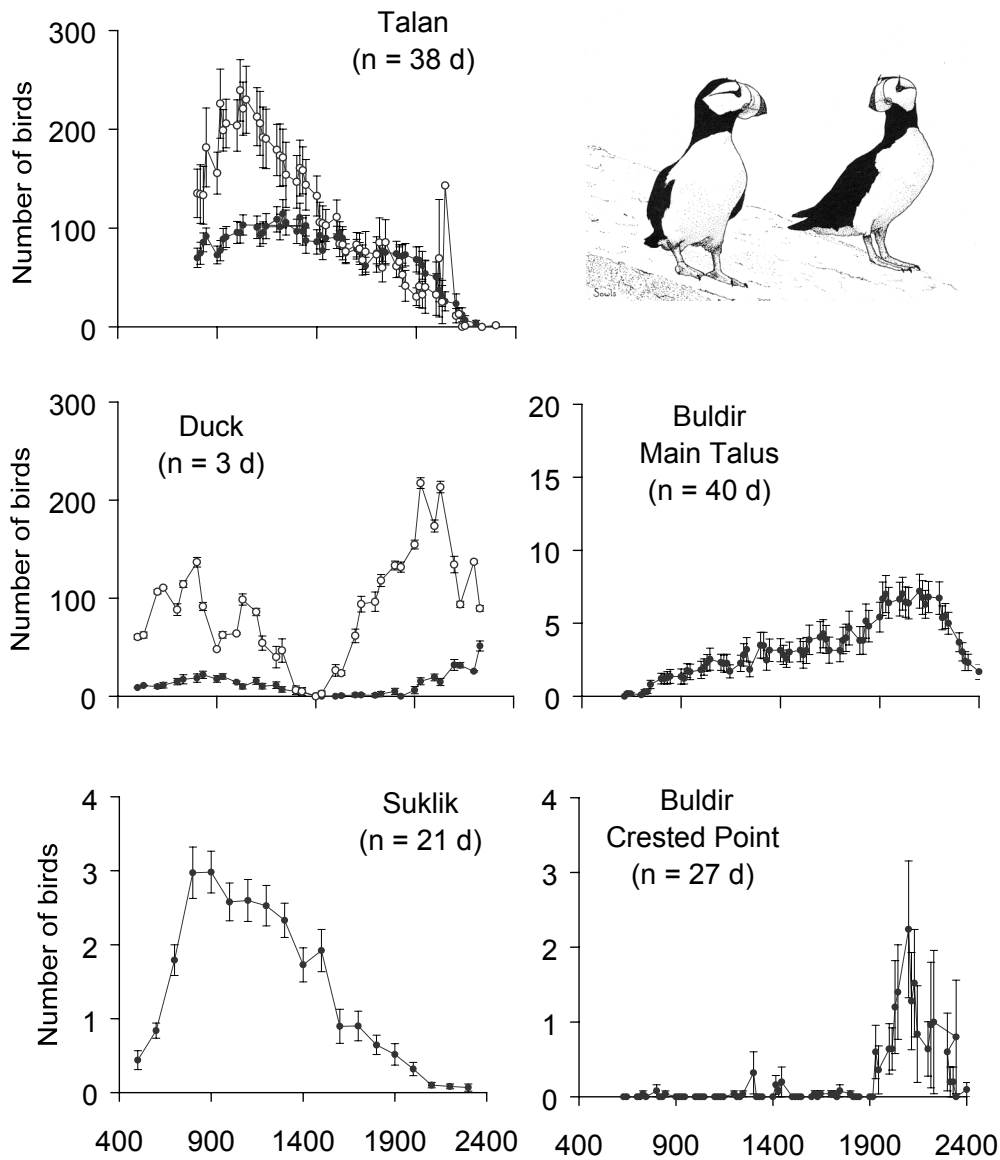


Figure 2. Diurnal colony attendance of Horned Puffins during the incubation period at different colonies. Mean number ( $\pm 1$  SE) of birds counted on water (open circle) and on land (closed circle). Sample sizes (days) are shown in parentheses.

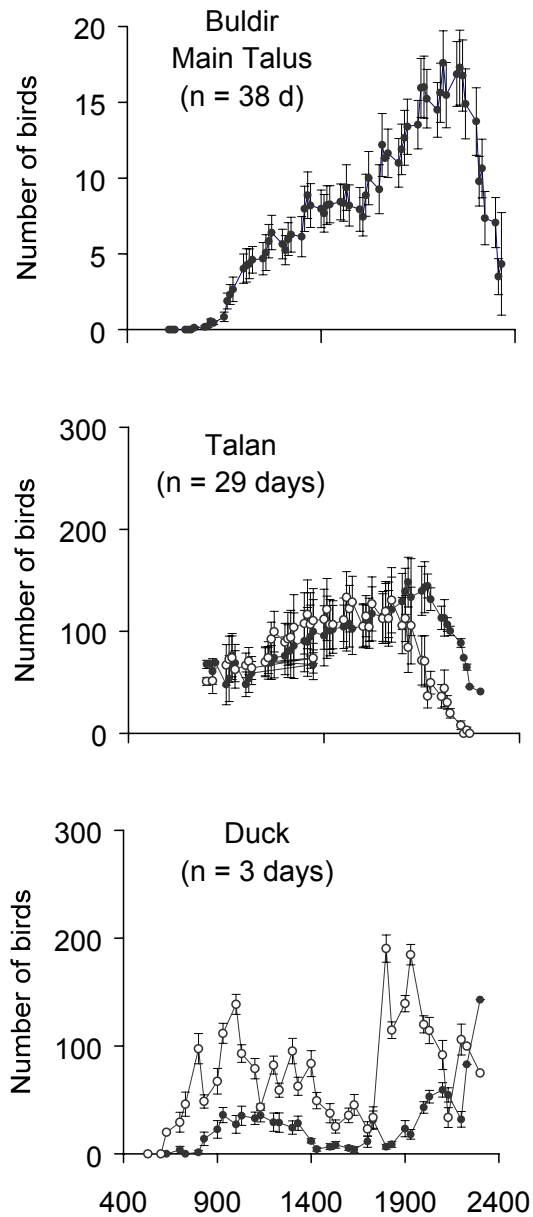


Figure 3. Diurnal colony attendance of Horned Puffins during the chick-rearing periods at different colonies. Mean number ( $\pm 1$  SE) of birds counted on water (open circle) and on land (closed circle). Sample sizes (days) are shown in parentheses.

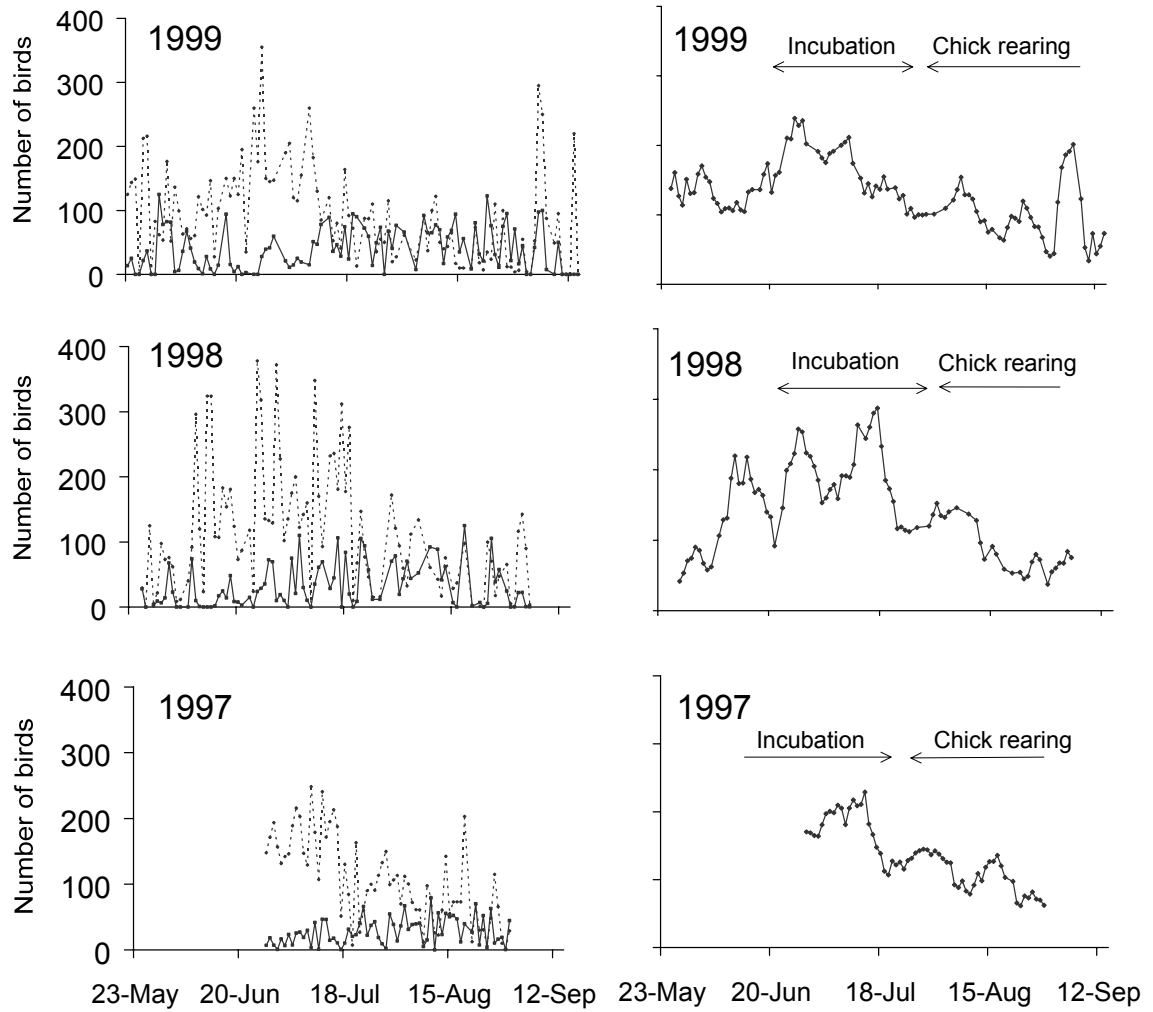


Figure 4. The seasonal colony attendance of Horned Puffins on Duck Island in three years. Daily index counts (see Methods) on water (dotted line) and on land (solid line) are presented on the left. Three-day running means of total birds (water and land combined) are presented on the right.



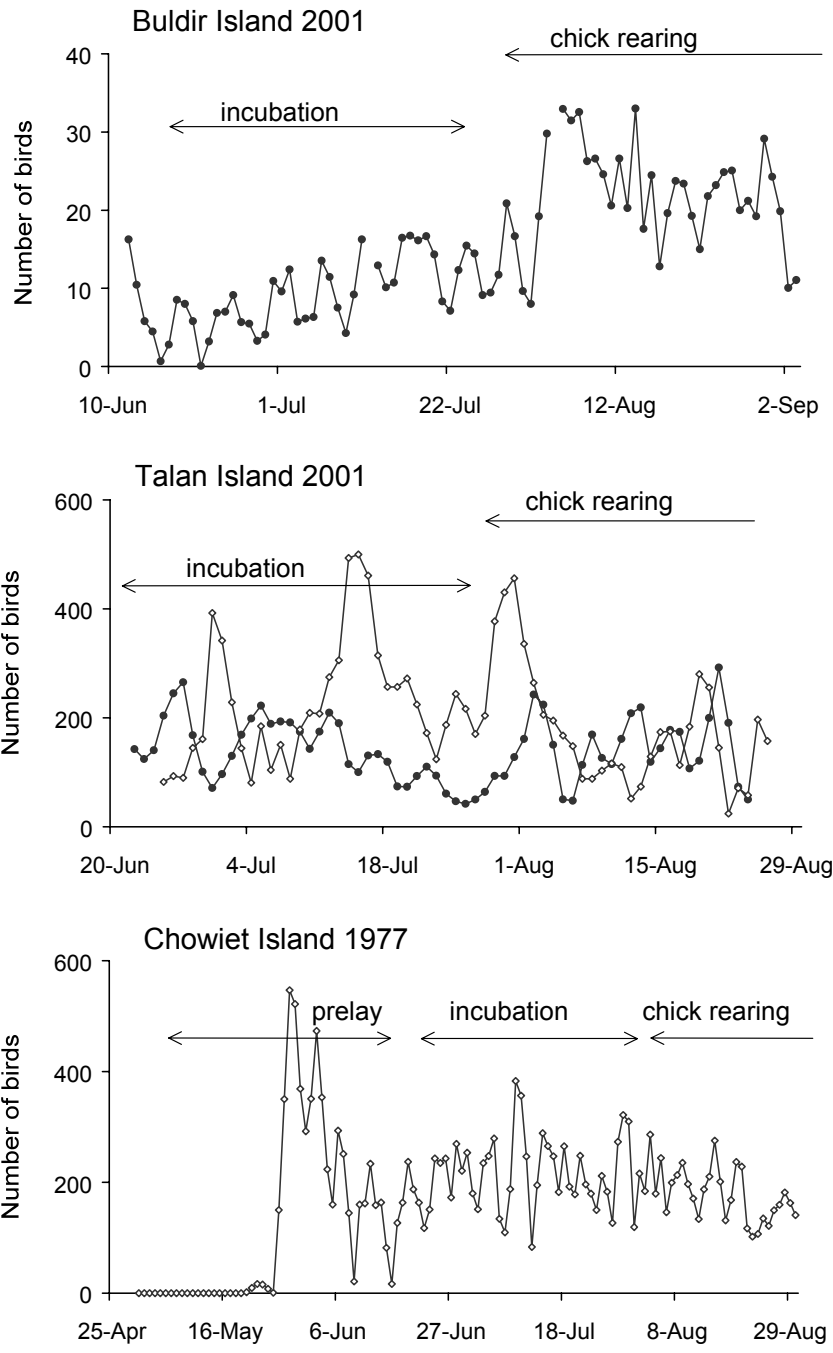


Figure 5. Pattern of Horned Puffin seasonal colony attendance at different colonies. Three-day running means of counts on water (open circles) and counts on land (closed circles).

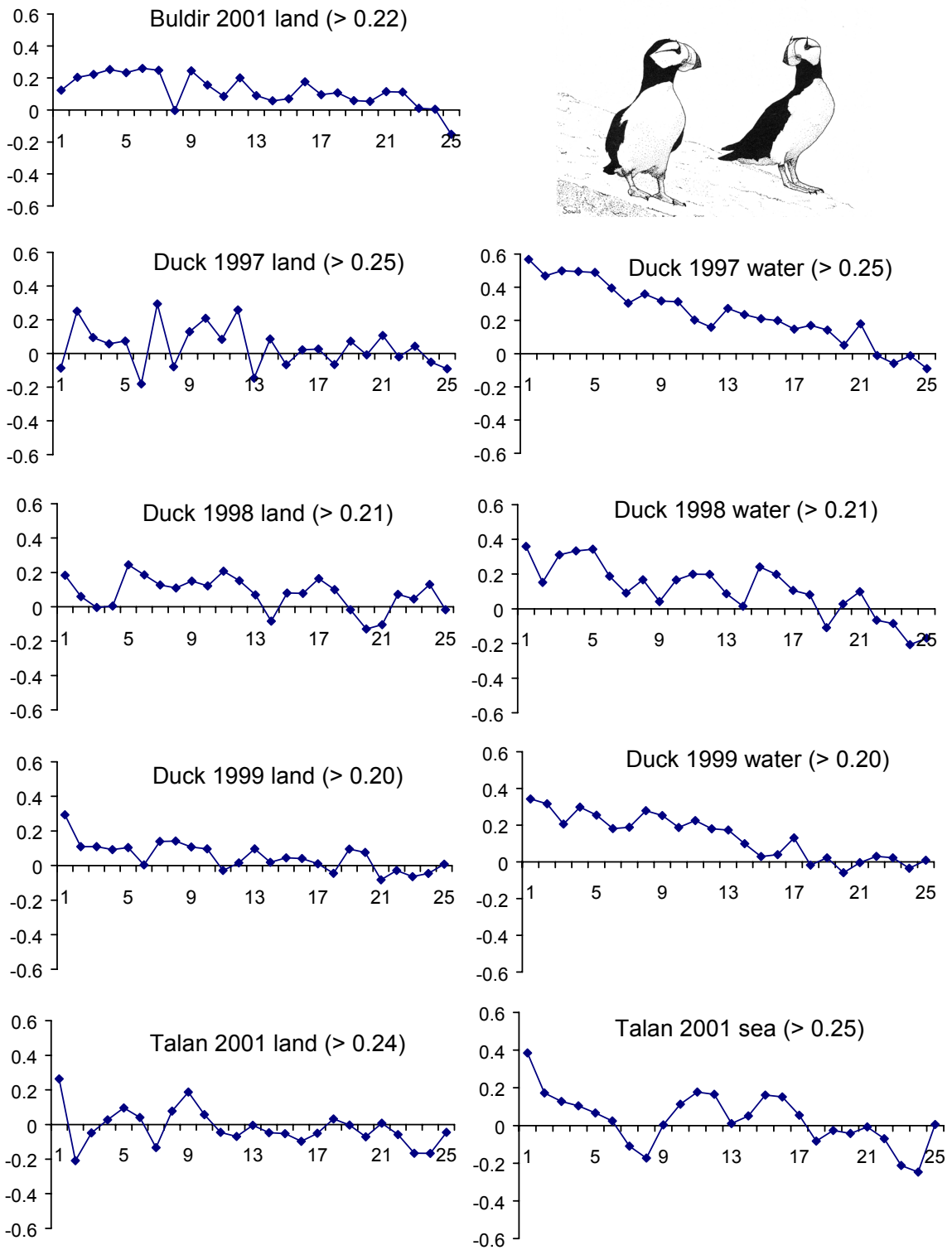


Figure 6. Autocorrelation functions (ACF): correlation between daily counts at different time intervals (days: X axis). Autocorrelation coefficients (Y axis) higher than those indicated in parenthesis are statistically significant.

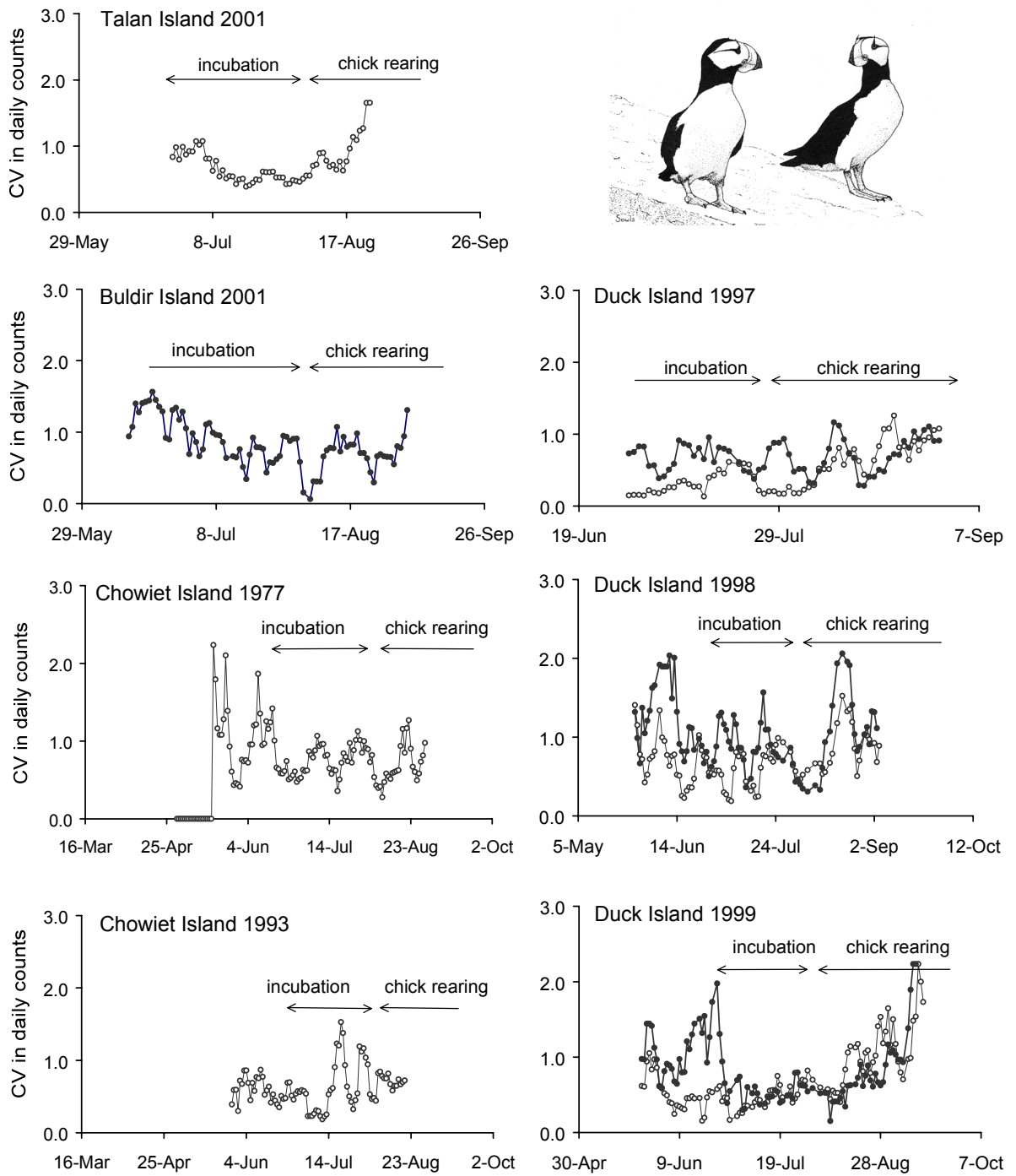


Figure 7. Seasonal changes in coefficient of variation (CV) in Horned Puffin attendance among colonies and years. Each value is the running CV calculated for a 5-day period. Counts on water (open circles), counts on land (closed circles).

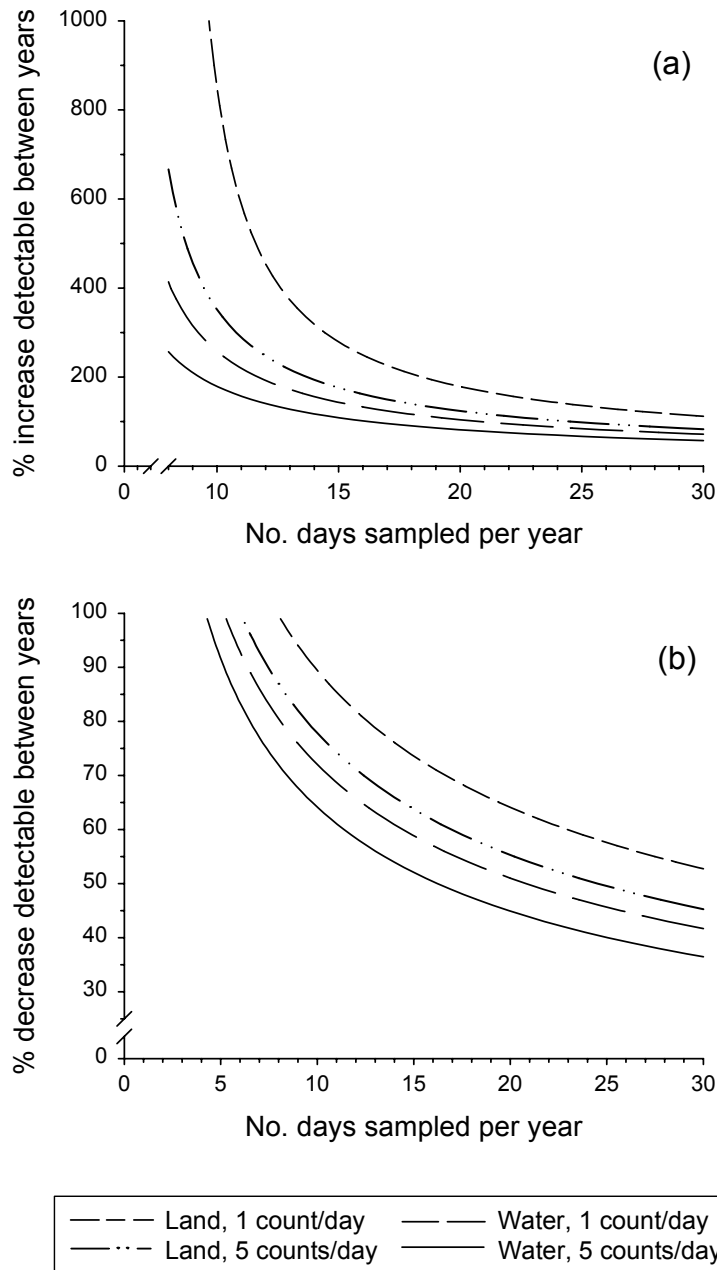


Figure 8. Relationship between sample size (counts/day and days/year within the census period) and proportionate changes in Horned Puffin numbers detectable between two years: (a) when numbers increase between year 1 and year 2, and (b) when numbers decrease between year 1 and year 2. Power ( $1-\beta$ ) is 0.9 throughout, using 1-tailed tests and a significance criterion of  $P < 0.05$ .

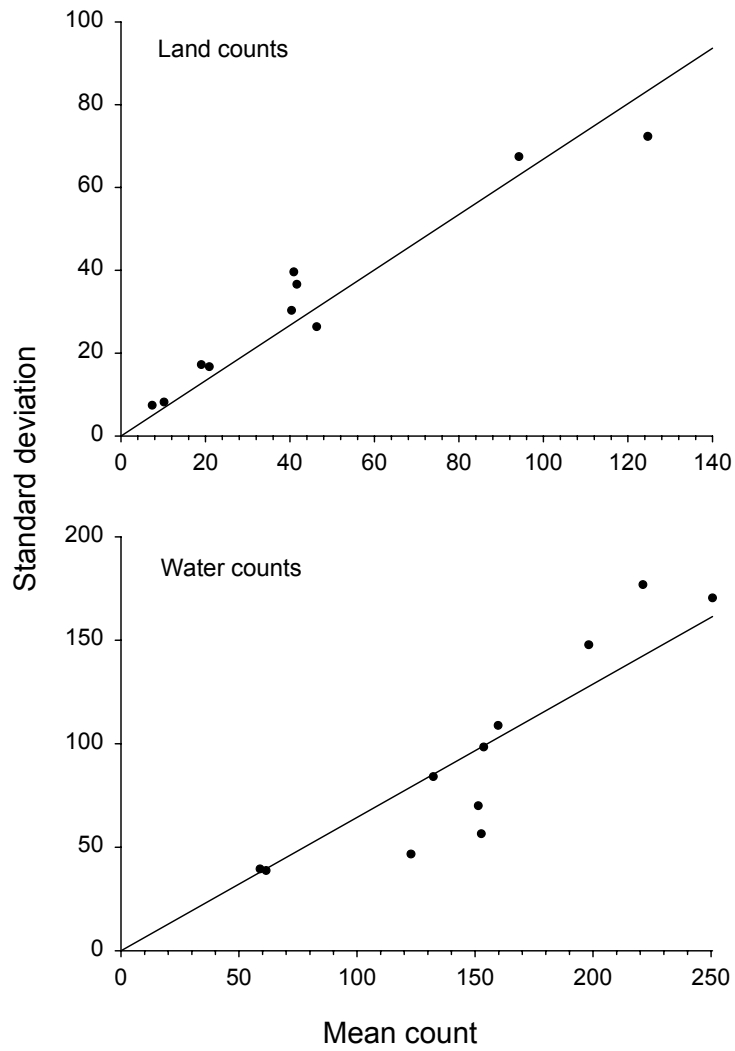


Figure 9. Illustration of linear dependence between standard deviation and mean counts of Horned Puffins obtained in several years at four study sites.

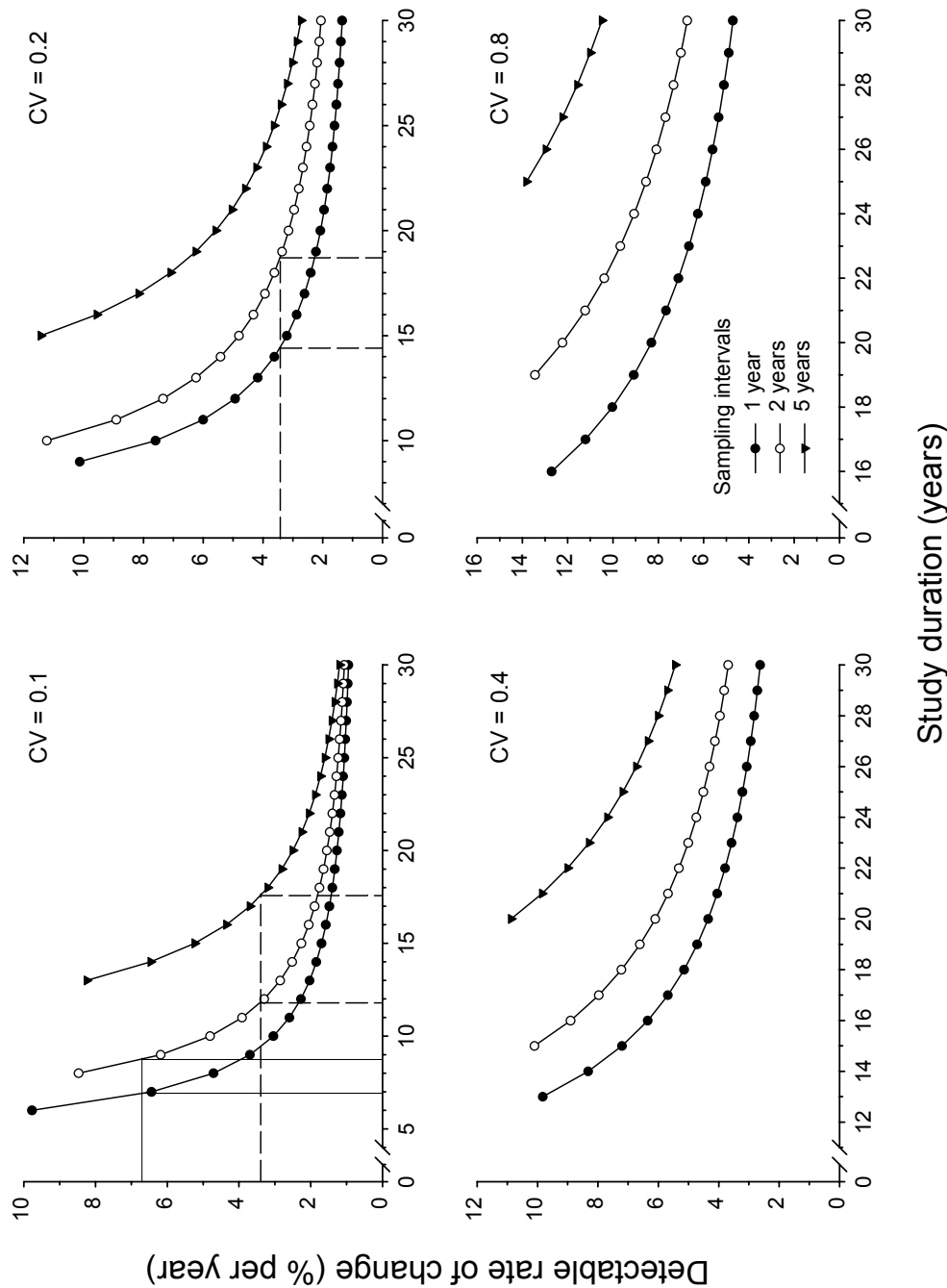


Figure 10. Power curves for detection of linear trends in log-transformed indices of Horned Puffin abundance under four assumed levels of variation among years. “Successful” combinations of interannual CV’s and sampling intervals are indicated by drop lines on the  $X$ -axis corresponding to trends of 3.4% of 6.7% per year. A successful protocol meets suggested program goals for seabird monitoring as described in the text. Power  $(1 - \beta)$  is set at 0.9 for all analyses, which evaluated 2-tailed tests of significance at  $P < 0.1$ .

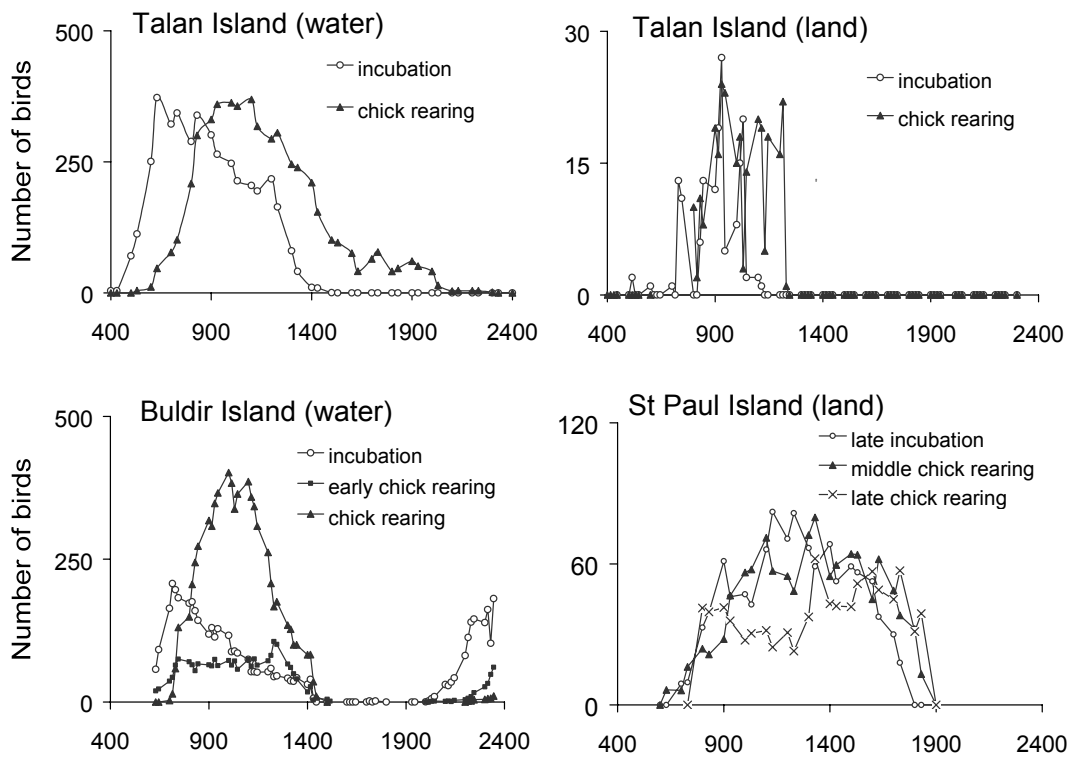


Figure 11. Diurnal attendance of Parakeet Auklets.

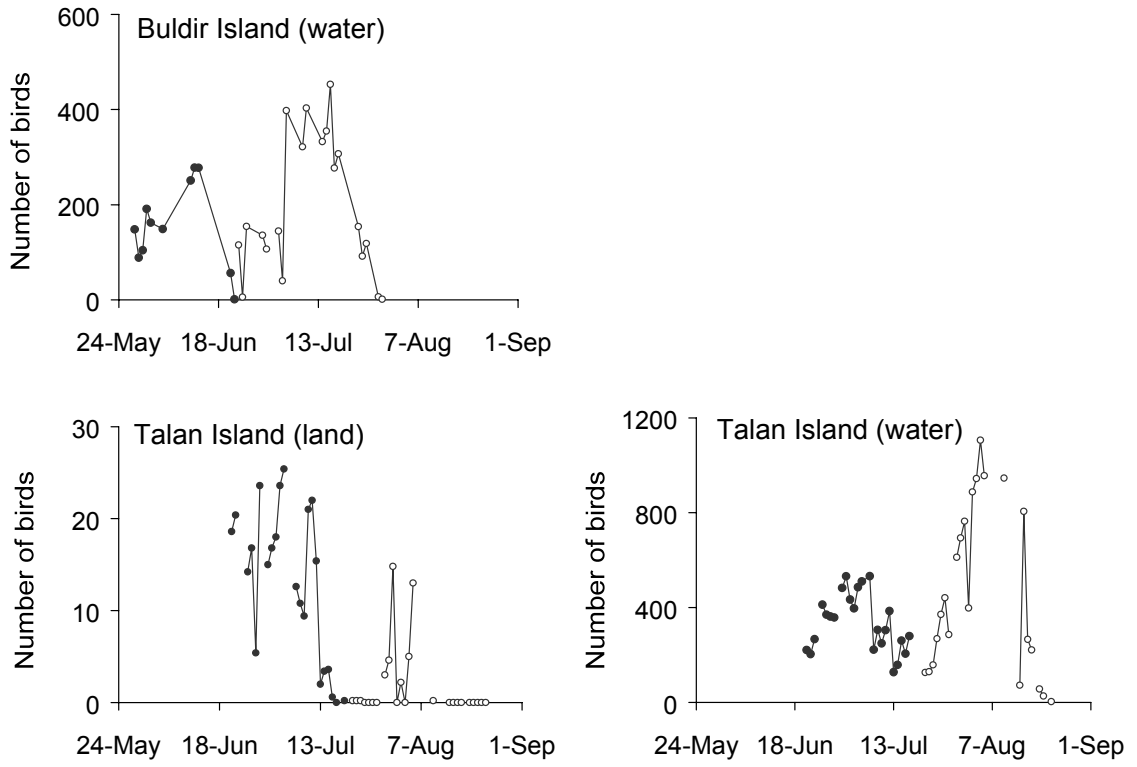


Figure 12. Parakeet Auklet seasonal attendance. Mean daily index counts during the incubation (closed circle) and chick-rearing period (open circle).



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

Colony	Plot type	Year	Counts/day <sup>a</sup>	<i>n</i> (days)	Mean count	SD	CV
Buldir	Land	2001	5	30	10.2	8.2	0.80
Talan	Land	2001	5	30	124.7	72.3	0.58
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	250.6	170.4	0.68
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

Appendix 1. Continued.

Colony	Plot type	Year	Counts/day <sup>a</sup>	<i>n</i> (days)	Mean count	SD	CV
Duck	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

<sup>a</sup> Studies with  $n = 5$  count per day included “top 5” counts at Buldir and Talan islands and “consecutive 5” counts at Duck Island (see Methods for explanation).