COLONY ATTENDANCE AND POPULATION MONITORING OF BLACK-LEGGED KITTIWAKES ON THE SEMIDI ISLANDS, ALASKA¹

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Abstract. Patterns of colony attendance in Black-legged Kittiwakes (*Rissa tridactyla*) were studied over 5 years on the Semidi Islands, western Gulf of Alaska. A census period of 50 days, extending from first egg laying through final hatching, was appropriate because counts made then were subject to the least amount of daily variation. Five counts during that period were sufficient to detect a 25% change in numbers between years; counts made on all 50 days of the census period would detect a 5 to 7% change. There was little evidence for seasonal trends or serial correlation of counts during the census period, but attendance was negatively correlated with wind speed. Half of an apparent 17% increase in population between 1980 and 1981 was due to birds spending more time at their nest sites in the latter year, thereby increasing the mean of attendance counts. Despite such difficulties in the interpretation of attendance counts, birds were considered to be better counting units for population monitoring than nests, because nest densities were subject to large annual fluctuations in breeding effort.

Key words: Black-legged Kittiwake; Rissa tridactyla; Alaska; colony attendance; census methods; population monitoring; time budgets.

INTRODUCTION

Black-legged Kittiwakes (Rissa tridactyla) have a circumpolar distribution in the northern hemisphere. Their colonies are conspicuous, relatively easy to census, and apparently sensitive to short- and long-term changes in the productivity of surrounding seas (Drury 1978). Efforts to determine the status and trends of kittiwake populations include studies in northern Europe (Coulson 1963, 1974, 1983; Barrett and Schei 1977: Stowe 1982: Wanless et al. 1982: Fleet 1984: Barrett 1985: Godo 1985: Richardson 1985), eastern Canada (Nettleship and Lock 1973, Brown et al. 1975), and Alaska (Craighead and Oppenheim 1985, Springer et al. 1985, Nysewander 1986). Long-term studies of breeding biology and population dynamics at one colony in the North Sea have provided a wealth of information relevant to monitoring methods and results (Coulson and Thomas 1985). However, there are indications that breeding productivity. and possibly other population parameters, differ greatly between Pacific colonies and the North Shields colony studied by Coulson and coworkers (Hatch 1987).

Two techniques have been used to census kittiwakes: counts of nests (e.g., Coulson and White 1956, Stowe 1982, Barrett 1985) and counts of birds (Barrett and Schei 1977, Hodges 1977, Wanless et al. 1982, Richardson 1985). A welltimed nest count indicates the number of birds breeding in a given year, whereas counts of birds measure the whole population of breeders and nonbreeders present. Because of daily and seasonal fluctuations in attendance at the nest site, multiple counts are essential when birds are the counting units. Nest counts are subject to little short-term variation, but can be misleading if they are poorly timed, or if intermittent breeding is prevalent (Barrett 1985).

Another sampling unit worthy of consideration is the occupied site, which may be defined as any site containing a single bird or pair during a count, whether or not nest material is present. Derivations could include the mean number of sites occupied daily during an appropriate census period, or the maximum number of sites occupied on any day in the prelaying period. The latter count should be little affected by the failure of birds to build nests, or the failure of nests after breeding has begun. For purposes of population monitoring, we seek an index that accurately re-

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FIGURE 1. Seasonal patterns of colony attendance in Black-legged Kittiwakes in 4 years on the Semidi Islands.

flects changes in the population of birds remaining alive.

Here we examine seasonal patterns of colony attendance, the effects of weather, the time budgets of individuals, and variations in breeding effort observed over several years in an Alaskan kittiwake colony. These data are considered in relation to the choice of methods and interpretation of annual censuses.

STUDY AREA AND METHODS

The work was conducted on the Semidi Islands (56°N, 156°W), where an estimated 70,000 to 100,000 kittiwakes bred annually from 1977 to 1981 (Hatch and Hatch 1983). Study plots were located along a 2-km expanse of cliffs on the west side of Chowiet Island, the largest (1,300 ha) of nine islands in the group. Seven plots containing a total of 400 to 500 nest sites were established in 1977 and used in all years from 1977 to 1981. Although plots were spatially well separated, no attempt was made to select them randomly from the available habitat. Observations in 4 years spanned the period from 5 to 9 weeks before egg laying (early April to early May) through midfledging (late August to early September). Studies were limited to the late prelaying and laying periods in 1978 (24 May to 29 June). Single birds and pairs on the plots were counted daily, generally between 09:00 and 16:00 Alaska Daylight Time (ADT), when diurnal fluctuations in attendance of kittiwakes at nest sites are minimal (D. B. Irons and S. A. Hatch, unpubl. data). A single count of nests (including all sites containing any nest material) was made at about the same time relative to kittiwake breeding phenology each year (27 June to 8 July).

One study plot with about 80 nest sites was used for detailed observations on reproductive performance in 1977 and 1978. Two plots, each containing 60 to 80 nest sites, were used for the same purpose from 1979 to 1981. These plots were visited at 3-day intervals in 1977 and 2-day intervals in later years to record the attendance of adults and the presence or absence of eggs or chicks.

The allocation of time to on-land and at-sea activities by birds of varied breeding status was estimated by assuming that the mean proportion of birds present in a series of spot checks (at 2-day intervals) was equivalent to the proportion of time spent on land at a given stage of the season. Although none of the birds we observed were banded, the absence of a large floating population and consistent patterns of site use and defense from prelaying through midchick stages suggested that most birds occupied only one site throughout the season.

Weather variables recorded two to three times daily included wind speed and direction (compass bearing), percent cloud cover, visibility, sea state, and the presence or absence of fog. Maximum and minimum air temperatures, precipitation, and barometric pressure were recorded daily. The use of a hand-held wind gauge on the island proved unsatisfactory for determining wind speeds over the ocean; prevailing wind speeds were therefore estimated in knots each morning and evening and while working near the cliffs. Statistical analyses were performed using the SPSSx package of computer programs (SPSS 1983).

RESULTS

WITHIN-SEASON PATTERNS OF ATTENDANCE

Daily counts of birds made during the prelaying period were highly variable, and therefore poorly suited for detecting population changes between years (Fig. 1). The variability dropped sharply when egg laying began, however, and remained



FIGURE 2. Average counts of Black-legged Kittiwakes on study plots in 4 years on the Semidi Islands, showing the absence of seasonal trends during the 50-day census period.

low through hatching. A period of 50 days, beginning when the first eggs appeared, was the best portion of the season for censusing. After 50 days, counts became more variable again and declined on average.

Series of counts in the recommended census period were not devoid of trends, but the patterns were inconsistent among years. Regressions of the number of birds against day during the census period were significantly positive in 1977 (slope 1.7 birds per day, P < 0.01), nonsignificantly negative in 1979 (slope -0.2 birds per day, P > 0.5), significantly negative in 1980 (slope -1.1 birds per day, P < 0.01), and significantly negative in 1981 (-0.7 birds per day, P < 0.05). Average counts showed no consistent departures from the overall mean during the census period in 4 years (Fig. 2).

Autocorrelation functions were calculated for series of counts from which the effects of seasonal trends, if any, were removed (i.e., analysis performed on residuals from regression analysis). There was little evidence for serial dependence of counts in any year (Fig. 3). Correlations were weak at all lag intervals from 1 to 20 days, and runs tests (Sokal and Rohlf 1981:782) failed to show significant departures from a random series around the median value in any year.

Once egg laying began, overall attendance remained fairly constant, both within and among years, despite wide differences in breeding performance (Fig. 4). A relatively large number of pairs failed to produce eggs in 1979 but still attended their nest sites throughout the season. Most failed birds continued to occupy their nest



FIGURE 3. Autocorrelation of daily counts (using residuals from linear regression) of Black-legged Kittiwakes during the census period in 4 years on the Semidi Islands. Upper and lower dashed lines define a range of ± 2 SE around the zero value.



FIGURE 4. Breeding status of Black-legged Kittiwakes in individually monitored nest sites from first egg laying through the late chick stage in 3 years on the Semidi Islands. Data summarized by 4-day intervals beginning on the dates indicated. Maximum possible attendance (100% on the ordinate) defined as the number of sites never seen to be occupied by more than a single bird, plus two times the number of sites used by pairs.



FIGURE 5. Mean counts of Black-legged Kittiwakes on seven study plots during the census period in 5 years on the Semidi Islands.

sites regularly after failure in all years. Figure 4 reveals that only about half of the birds that regularly visited the study plots were present during a typical count from June through mid-August.

EFFECTS OF WEATHER

Wind direction and speed, maximum daily temperature, barometric pressure, cloud cover, precipitation, and fog were examined for their possible effects on daily counts. The correlation between wind speed and count was weakly negative over the whole season (5 years' data combined, n = 525, r = -0.242, P < 0.001), and it explained 12% of the variation among plot counts during the census period (n = 223, r = -0.341, P < 0.001). No other variable was found to have any effect.

ANNUAL COMPARISONS

The mean number of birds on study plots during the census period varied widely in the years from 1977 to 1981 (Fig. 5). Parametric analyses of variance were inappropriate because sample variances were unequal (Bartlett-Box F = 5.15, P < 0.001). However, Kruskal-Wallis ANOVAs confirmed the decline from 1977 to 1978 (P <0.001), the increase from 1980 to 1981 (P <0.001), and the absence of significant changes between 1978 and 1980. The change from 1977

TABLE 1.	Qualitative summary of annual changes in
numbers of	kittiwakes on seven study plots during the
census perie	od.

Contrast	No. plots decreasing [*]	No. plots increasing*
1977-1978	7 (7)	0
1978-1979	4 (0)	3 (1)
1979-1980	3 (1)	4 (1)
1980-1981	0	7 (6)

• Values in parentheses are numbers of plots showing significant (P < 0.05) contrasts by Kruskal-Wallis ANOVA.

to 1978 was a decline of 96 birds, or 20% of the 1977 mean.

In a two-way analysis of variance of counts made during the census period, the interaction between plot and year was highly significant (P < 0.001). Thus, not all of the seven study plots followed the same pattern as depicted in Figure 5 with respect to annual changes in mean counts. Considering only the direction of change, the results were unequivocal from 1977 to 1978, when all seven plots decreased, and from 1980 to 1981, when all seven plots increased. Between 1979 and 1980, however, one plot showed a significant decline while another plot showed a significant increase (Table 1).

Coefficients of variation revealed alternative measures of population size, including numbers of nests constructed and mean or maximum numbers of occupied sites, to be more variable among years than counts of birds (Table 2). Breeding productivity was also variable during the study, ranging from zero to more than one young raised per egg-laying pair. Counts of nests were the census parameters most strongly correlated with measured rates of breeding success.

TIME BUDGETS OF INDIVIDUALS

Since breeders with eggs or chicks were constrained to have at least one member of the pair in attendance at all times, they spent a relatively constant 50 to 51% of their time at the nest site (Table 3: see Methods on the use of nest checks for estimating time allocation). Failed birds spent more time at their nest sites than active breeders in 2 years, but less time than active breeders in 1 year. Nonbreeders (including all single or paired birds that produced no eggs) spent consistently less time at the colony than either active or failed breeders, averaging 39% of time at their sites over 3 years. Taken together, mean site occupancy by birds of all categories increased nearly 9% between 1980 and 1981 (4.2/47.6), which would increase the daily attendance counts by a similar amount.

DISCUSSION

Attendance patterns of kittiwakes on the Semidi Islands indicated that daily counts of birds from first egg laving through final hatching were useful for detecting annual changes in numbers. Counts within a season neither increased nor decreased appreciably during that period, whereas a steady decline in adults present was evident once the voung began to fledge. There was no evidence for a large influx of prospecting birds during egg and chick stages as reported for kittiwake colonies in Britain (Coulson and White 1956, Coulson 1959).

Lower counts were associated with stronger winds, which suggests that corrections for wind speed might be warranted if counts were made on only a few days during the census period.

TABLE 2.	Comparison	of kittiwake	census	parameters	in 5	years	with	different	levels	of breeding	success	on
the Semidi I	Íslands.					-				_		

	Year							
Parameter	1977	1978	1979	1980	1981	x	CVa	r _{prod} b
Productivity (young/pair)	0.70	0	0.51	0.34	1.15	0.54	79.1	_
Attended nests ^c	426	229	243	345	387	326	26.7	0.70
Total nests ^c	—	256	305	381	411	338	20.9	0.79
Mean of daily attendance counts, census								
period	480	384	383	375	437	412	11.0	0.64
Mean no. occupied sites, census period ^d	463	344	355	352	407	384	13.2	0.64
Maximum no. occupied sites, May-June ^d	596	461	452	562	493	513	12.4	0.20

^a Coefficient of variation among years.
^b Pearson correlation coefficient for paired values of annual productivity and a given census parameter.
^c Attended nests were occupied by one or two adults at time of the count. Total nests includes sites with signs of nest building in the current year but unattended at time of the count. Dates of nest counts as follows: 3 July 1977, 27 June 1978, 8 July 1979, 3 July 1980, 4 July 1981.
^d Occupied sites defined as those with a single bird or pair during a count, whether or not any nest material was present.

All birds ⁴			Ac	tive breeder	S ^b	= <u></u>]	Nonbreeder	Sc	Fa	ailed breede	rs ^d	
Year	Atten- dance ^e	ne	%	Atten- dance [®]	n°	%	Atten- dance ^e	n•	%	Atten- dance ^e	ne	%
1979	3,487	6,975	50.0	1,772	3,516	50.4	937	2,025	46.3	355	660	53.8
1980	1,898	3,990	47.6	1,139	2,272	50.1	192	650	29.5	469	1,016	46.2
1981	3,680	7,101	51.8	2,959	5,826	50.8	328	793	41.4	251	412	60.9

TABLE 3. Average attendance at the nest site by Black-legged Kittiwakes of varying breeding status during the census period.

Includes breeding pairs observed prior to egg laying, therefore totals are greater than the sum of active breeders, nonbreeders, and failed breeders. Pairs with eggs or chicks in the nest.
Unmated singles and pairs that produced no eggs.

^d Attendance recorded after loss of egg or chick. • Attendance and sample sizes n expressed in bird-days: $n = (25 \text{ days of observation}) \times (number of birds in sample)$. Number of birds in sample was the number of sites with singles plus two times the number of sites with pairs.

Serial dependence of counts did not appear to be a serious problem in the present study, but routine examination of similar data sets for the presence of autocorrelation is advisable. Where nonindependence of counts proves to be a problem, it may be necessary to space the counts at greater than 1-day intervals in the field, or to subsample the data before performing statistical tests.

Spatial variability (Table 1) is a potentially serious problem in monitoring studies if, as is generally the case, the same plots are revisited each year. Whenever the interaction of study plot and year is found to be significant, the null hypothesis of no change between years cannot be rejected unequivocally. With the knowledge that spatial variability exists, it can only be said that a large number of smaller plots may be preferable to a small number of larger ones.

Kittiwakes build a conspicuous nest of mud and grass, so a well-timed count of nests would seem to offer a useful alternative to repeated counts of individuals for population monitoring. Nest counts have the advantage of being unaffected by daily variation in attendance, and they convey more information about the size of the breeding population than counts of birds. However, not all kittiwakes that build nests produce eggs, and the definition of a completed nest is subjective (Wanless et al. 1982). In the present study, only 99 (84%) of 118 pairs with wellformed nests produced eggs in 1979; an additional 12 pairs (9%) started building nests that were never completed. At other kittiwake colonies in Alaska, instances of widespread failure to lay eggs have been recorded in some years (Searing 1977, Drury et al. 1981).

The years from 1977 to 1981 were marked by wide fluctuations in breeding productivity on the Semidi Islands and, not surprisingly, census pa-

rameters were crudely correlated with overall reproductive performance (Table 2). The coefficient of variation among annual means was lowest for counts of birds, which suggests that properly timed attendance counts provide an index that tracks real population change more closely than the other census parameters considered. Nest counts were greatly affected by annual differences in breeding effort, including nest building, and deterioration of failed nests before the count. Mean counts of occupied sites performed better than nest counts for population monitoring, but seemed to offer no advantage over counts of individuals. The maximum number of occupied sites observed each year was little affected by variation in overall breeding performance, but annual variation was as least as great as annual variation in mean attendance counts. Presumably, that variation reflected, in part, the potentially large sampling error involved in choosing any single observation as the annual index of population size.

Given that a series of attendance counts during the census period appeared to be the most suitable measure of population size, it is useful to consider the effect of sample size on our ability to detect differences among means. These relationships are illustrated in Figure 6 (see Sokal and Rohlf 1981:262-264 for methods of computation). As few as five counts were adequate to detect a change of 25% between years on the Semidi Islands, with 95% confidence of finding a significant difference at the 0.05 level. Counts made on all 50 days of the census period would likely detect a difference of 5 to 7%. Greater sensitivity using present techniques is precluded by the inherent variability among daily counts.

The largest difference between consecutive years was a decline of 96 birds from 1977 to



FIGURE 6. Relationships between sample size (number of daily counts made during the census period) and proportionate change in kittiwake numbers detectable between years. Power is the degree of confidence that the difference between sample means would be significant at the 0.05 level.

1978, or 20% of the 1977 value. Much of the apparent decline observed in those first 2 years of study was recovered by an increase of 17% from 1980 to 1981 (Fig. 5, Table 2). The question arises whether we measured respective changes of 20% and 17% in the population of kittiwakes alive, or differences in collective breeding effort and behavior among years that differed greatly in breeding success (Table 2). Obviously, any differences in the allocation of time to on-land

and at-sea activity would be reflected in the means of daily attendance counts. Thus, about half of the apparent increase in population between 1980 and 1981 could be explained by a difference in time budgets, since birds spent 9% more time at their nest sites in the latter year (Table 2).

In Alaskan colonies, counts of nests and counts of individual kittiwakes are both subject to important sources of variability that bear little relation to actual population change. Regardless of the choice of methods for censusing populations, long-term studies will be required to establish trends against this background of wide annual variation in breeding effort and behavior.

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