The Condor 89:340–348

FACTORS INFLUENCING COLONY ATTENDANCE BY PIGEON GUILLEMOTS ON SOUTHEAST FARALLON ISLAND, CALIFORNIA[1]

DOUGLAS A. NELSON[2]
Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109 and
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970

Abstract. I studied colony attendance in a marked sample of Pigeon Guillemots (*Cepphus columba*) in 1979 and 1980 on Southeast Farallon Island, California. These observations were supplemented with sightings of known-age birds in 1977, 1981, and 1982. In 1979 and 1980 I compared the attendance of males and females from the time of colony occupation through the incubation and chick-rearing periods. Guillemots returned in early March in both years, but occupied territories earlier in 1979 than in 1980. Older, experienced birds arrived on land before young, nonbreeders. Males arrived earlier than females each year and spent more time on their territory each morning before and after egg laying. In 1979, colony attendance was higher for both sexes, egg laying began earlier, larger clutches were laid, and young chicks were fed at a higher rate. I suggest that the annual differences in attendance and egg laying dates may have been due to the greater availability of food in 1979, as measured by higher chick-feeding rates. Sex differences in attendance probably result from the increased energetic requirements associated with egg formation in females.

Key words: Pigeon Guillemot; Cepphus columba; *colony attendance; food availability; sex differences.*

INTRODUCTION

In many animals the time devoted to feeding conflicts with the time devoted to territory defense and other breeding activities (e.g., Ydenberg 1984). Thus, variation in food supply should influence the timing and success of breeding (Lack 1966, Perrins 1970, Ewald and Rohwer 1982) and time spent in breeding-related activities. This trade-off should be apparent for seabirds that often feed at great distances from their breeding territories. Thus the time spent in the colony should reflect the relative ease with which seabirds can find their food (Gaston and Nettleship 1982).

The prediction that annual differences in clutch size and breeding success are associated with differences in food abundance or availability has been amply documented in seabirds (e.g., Ainley and Lewis 1974, Boersma 1978, Manuwal 1979, Harris 1980, Vermeer 1980, Gaston and Nettleship 1981, Birkhead and Nettleship 1981). This study focuses instead on a corollary prediction: that differences in food availability influence the timing and frequency of colony attendance by Pigeon Guillemots (*Cepphus columba*). Although the general aspects of colony attendance by guillemots have been described (Storer 1952; Drent 1965; Ainley and Boekelheide, in press), there is little quantitative information on colony attendance. In this paper observations of marked individuals were used to study how attendance varied as a function of a bird's sex, age, and breeding status within and among years.

METHODS

STUDY SITE

I observed Pigeon Guillemots in 1977 and each breeding season from 1979 to 1982 on Southeast Farallon Island (SEFI), California (37°42′N, 123°00′W), a 44-ha island about 43 km west of San Francisco. Biological and physical features of the island are described by Ainley and Lewis (1974) and DeSante and Ainley (1980). Among the 12 species of marine birds breeding on SEFI is a population of approximately 1,000 pairs of Pigeon Guillemots (Ainley and Lewis 1974). I began observations in March 1979 and 1980 before guillemots had returned from their wintering areas, and continued until late July or August when chicks began to fledge. I visited for one month in April 1981 and May 1982.

My main study site was a surge channel (East

---

[1] Received 19 May 1986. Final acceptance 2 January 1987.

[2] Present address: The Rockefeller University, Field Research Center, Box 38B RR2, Millbrook, NY 12545.

Landing) on the island's southeast side where approximately 20 pairs nested in or near a rubble pile at the head of the channel. Three sections of sewer pipe (1 m long, 20 cm inside diameter) put at East Landing in the early 1970s by Point Reyes Bird Observatory (PRBO) biologists were used as nest sites by birds. In 1979 and 1980 I set out eight L-shaped wooden boxes and built one burrow of rocks to recruit more guillemots. By 1982 six of the nine artificial nest sites had been occupied by birds; only two (both nest boxes) had eggs laid in them in both 1979 and 1980. The boxes were dispersed throughout the study site to mimic the natural dispersion of nests. Nests were checked for eggs every other day beginning in early May.

I captured and banded 89 guillemots with leg nooses made of 50-lb test monofilament fishing line tied to hardware cloth (Nelson 1984). PRBO has banded between 2 and 272 chicks annually from 1968 to 1979 (1,418 total) with unique year-class color rings. Nine and seven of these birds were in my study plot as breeders or nonbreeders in 1979 and 1980, respectively. Birds were sexed by copulation position, assuming the male to be dorsal (Nelson 1984).

COLONY COUNTS

In March and April 1979 and 1980 I censused guillemots on the water at dusk from atop a hill in the island's center (see fig. 4 in Ainley and Lewis 1974:439). Evening counts could only be done in calm seas, thus sampling intervals were irregular (two or three days a week). In good visibility this point allowed a clear view of all but a small part of the surrounding ocean. I counted birds on land at dawn by walking a path that circled most of the island. The route followed the railroad track shown on the map in Ainley and Lewis (1974:439). At the eastern end of the track I went north to Shubrick Point. The dawn counts revealed relative changes in guillemot numbers occupying breeding areas. I terminated counts in April when many birds were ashore in the morning.

In April and May 1979, and April to July 1980, I counted all guillemots within a constant area at the East Landing site. One to four counts were made daily, between 07:00 and 10:00.

FOCAL SAMPLES OF ATTENDANCE

I observed birds from a blind 30 m from the rubble pile where most pairs nested. During 20-min focal samples (Altmann 1974) I noted arrivals and departures at one nest randomly chosen from the group (19 in 1979, 13 in 1980). I then calculated the amount of time each member of the pair spent on the territory, outside the nest. The frequency distributions of time spent on land were strongly bimodal with peaks at zero and 20 min for both males and females. This variable was reduced to a dichotomy by coding times of 0 to 9.9 min as "absent" and 10 to 20 min as "present." I then used a logit analysis (Fienberg 1980) to study how several independent variables affected the probability that birds were on their territories. The independent variables were: year (1979 versus 1980), time of year (prior to the population mean egg-laying date versus after), sex, and wind speed (rank-ordered in five categories from 0 to 45 km/hr). Breeding status (did or did not lay eggs) was also included in a second analysis using only the data from 1980, when four pairs defended territories but did not lay eggs. For reasons of parsimony, the logit model incorporating the fewest terms that fit the data was selected. The strength of association between attendance and each independent variable was assessed by a Concentration statistic (Norušis 1985). This expresses the proportional error reduction in predicting the dependent variable given knowledge of the independent variable(s).

ALL-MORNING WATCHES

Focal samples were supplemented by all-morning watches from dawn until 13:00 on six days in June 1980. Beginning at 15:00, I recorded guillemot numbers as they returned. Evening counts were not included in the analysis described below because it was difficult to identify individuals. Watches were done on 8, 10, 11, 13, 16, and 17 June. I did not include a nest after the first egg appeared, thus sample sizes were lower on 16 and 17 June. I recorded arrivals and departures, to the nearest minute, of all birds at eight nests, and also counted every 10 min all birds at those nests and on two "loafing" areas used by nonbreeders. I calculated the percentage of the total morning observation time each bird spent on land. The effects of sex, breeding status, and date on attendance were tested in a factorial analysis of variance.

CHICK-FEEDING RATES

Five 1-hr watches of food brought to chicks were made on four days in 1979 (between 29 June and

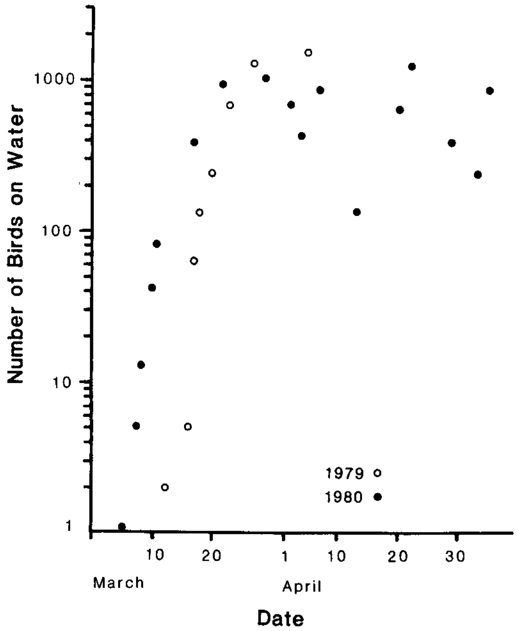

FIGURE 1. Numbers of Pigeon Guillemots counted on the water around SEFI at dusk in 1979 and 1980.

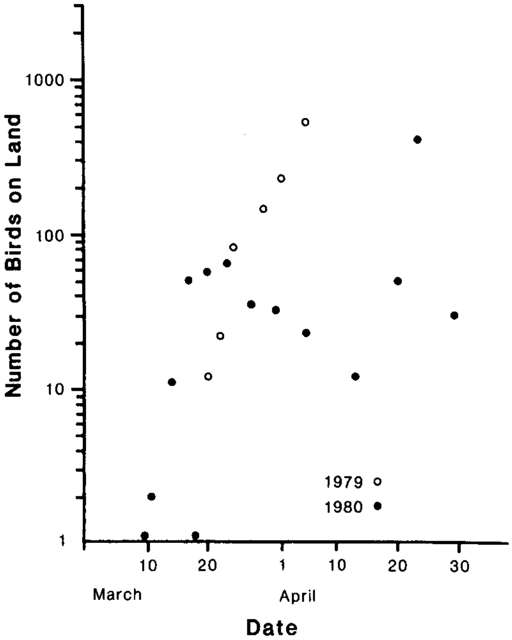

FIGURE 2. Numbers of Pigeon Guillemots counted on land at dawn in 1979 and 1980.

23 July) and 16 watches on 10 days were made in 1980 (8 July to 10 August). I recorded the identity of the parent and the times of arrival and departure. It was difficult to identify the food item precisely because birds darted into burrows immediately upon landing. Samples were evenly distributed among the morning and evening peak feeding times on days of moderate winds. Analysis of covariance was used to test for annual differences in chick-feeding rates. Chick age was the covariate used to adjust feeding rates.

Unless otherwise stated, statistics are reported as the mean ± standard error. For sample distributions that are non-normal, the median is given.

RESULTS

COLONY ATTENDANCE

The first guillemots returned to SEFI each year in the first week of March. Their numbers gradually increased until the entire breeding popu-

TABLE 1. Descriptive breeding statistics for 1979 and 1980.

	1979		1980	
	n	Mean ± SE[a]	*n*	Mean ± SE
Arrival date				
Males	18	6 April ± 2.5	16	18 April ± 5.8
Females*	17	10 April ± 3.4	15	1 May ± 5.6
Nonowners[b]	5	21 May ± 15.3	6	17 May ± 4.8
Laying date*	19	30 May ± 3.6	13	12 June ± 2.4
Pre-egg period (days)				
Males	16	55.8 ± 3.1	11	58.7 ± 4.9
Females	15	53.3 ± 3.5	11	45.1 ± 5.1
Clutch size*	19	1.84 ± 0.08	13	1.54 ± 0.14
Fledged/pair	17	0.82 ± 0.20	12	0.50 ± 0.15

[a] SE = Standard error of mean.
[b] Birds of either sex that did not defend territories.
* Denotes variables that differed significantly between years by Mann-Whitney *U*-Test, $P < 0.05$.

lation of about 2,000 birds had arrived in late March or early April (Fig. 1). The number of birds near the island at dusk was similar in both years (Fig. 1), but the birds occupied territories later (Fig. 2) and initiated egg laying significantly later in 1980 (Table 1).

In April and May 1979, the mean daily count at East Landing was independent of date as birds occupied their territories en masse early in April and attendance remained high throughout the pre-egg period (Table 2) (rho = +0.15, $n = 28$, $P > 0.25$). Mean daily counts increased significantly over the same period in 1980 (rho = +0.89, $n = 51$, $P < 0.01$). Count and wind speed were weakly negatively correlated in both years (1979: rho = −0.24, $n = 28$, $P = 0.10$; 1980: rho = −0.05, $n = 51$, $P > 0.3$).

Mean monthly counts are displayed in Table 2 along with calculated values of k, the ratio of the number of breeding pairs to number of individuals (Birkhead and Nettleship 1980). For counts made in May, for example, 100 individuals counted represent, on average, about 100 breeding pairs.

DAILY ATTENDANCE CYCLE

Early each evening guillemots formed large offshore rafts that persisted through the night and into the next morning. In early March rafts dispersed soon after dawn; as numbers increased, guillemots remained near the island later in the day and moved ashore to their nest sites for the first time in mid-March (Fig. 2). Early morning rafts disappeared as more birds occupied their nest sites in the morning. On windy days in late April and May guillemots formed rafts in the evening before moving ashore to their nests. Evening rafts were smaller on calm days.

The first nest visits were made at dawn, and only lasted a few minutes. At this time birds were wary and frightened by the slightest disturbance (e.g., gull alarms, loud noise from boats anchored offshore). As the season progressed, they increased the time spent ashore each morning until they left to feed during the afternoon (Fig. 3). Birds returned to the island in late afternoon, 16:00 to 18:00, and visited their territories and/or communal roosts near the water. Birds nesting at East Landing slept on a roost rock at the water's edge. Peak evening counts in Figure 3 were higher than peak morning counts because birds usually did not leave the roost in the evening, and the roost was probably used by birds that did not nest at East Landing.

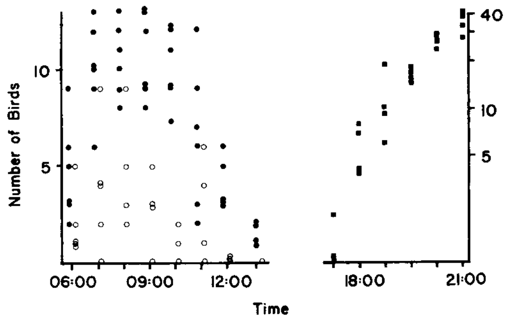

FIGURE 3. Numbers of guillemots at East Landing on six days in June 1980. Filled circles—territory-holders at eight nests, open circles—birds without territories, squares—total birds on communal roost and territories in evening. No counts were made at 14:00 and 15:00. Note that counts after 16:00 are plotted on a log scale.

SEX DIFFERENCES IN ATTENDANCE

Males arrived at nest sites before females. An average of four days (1979) and 13 days (1980) elapsed between arrival of males and females (Table 1). Birds that did not own territories arrived about 30 to 40 days later and visited territory owners. In general, older birds arrived before young birds (Table 3). The 1977 cohort was represented by three recognizable individuals. Their date of first arrival in the colony advanced

TABLE 2. Numbers of Pigeon Guillemots present at East Landing by month and year.

Year	April	May	June	July	August
1979	15.7 ± 6.2[a]	18.1 ± 6.3			
[19][b]	(17) *1.21*	(11) *1.05*			
1980	1.3 ± 3.1[c]	13.7 ± 7.9	18.1 ± 5.1	12.0 ± 5.1	8.2 ± 4.4
[13]	(20)	(31) *0.95*	(16) *0.71*	(28) *1.08*	(28) *1.58*

[a] The entry for each month consists of: Mean ± SD; on the line below: (n of daily counts), k. k is the number of breeding pairs/mean count.
[b] n of breeding pairs listed in brackets below year.
[c] Guillemots were on land only four days in April 1980 between 08:00 and 10:00. No k is listed.

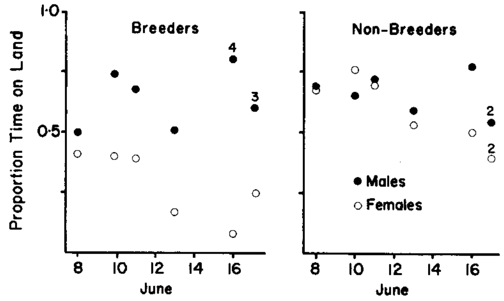

FIGURE 4. Mean proportion of time spent on land by territorial breeders ($n = 5$ pairs, except as noted) and nonbreeders ($n = 3$ pairs). Variances are homogeneous across groups, and are omitted for clarity. Data are analyzed in Table 5.

by about one month each year from 1979 through 1982 (Table 3). One three-year-old male acquired a territory and mate in 1980 but did not breed.

Guillemots visited their territories daily for about 50 to 60 days before the clutch of one or two eggs was laid in late May or early June (Table 1). In 1980 however, duration of the pre-egg period (the time between arrival on territory and date of clutch initiation) was not constant but decreased the later a female arrived (Spearman's rho = -0.84, $n = 11$, $P < 0.01$).

In the 20-min focal samples, time of year, year, and a bird's sex all influenced the probability that guillemots were visible on their territories. The simplest logit model providing a satisfactory fit to the data included the simple effects of all three independent variables ($G = 2.56$, df = 4, $P = 0.63$). That is, time of year, year, and a bird's sex had independent, additive effects on attendance. The three possible models that only included two factors at a time and more complex models that assumed interaction among the independent variables all failed to significantly improve the fit of the model.

TABLE 4. Percentage of 20-min focal samples that Pigeon Guillemots were visible on their territories.

	1979		1980		Mean	
Time of year	%	*n*	%	*n*	%	*n*
Males						
Pre-egg	82.1	56	73.9	134	76.3	190
Post-egg	43.2	44	28.8	125	32.5	169
Mean	65.0	100	52.1	259	55.7	359
Females						
Pre-egg	73.2	56	53.4	133	59.3	189
Post-egg	39.5	43	16.8	125	22.6	168
Mean	58.6	99	35.6	258	42.0	357

Time of year was the most important correlate of attendance, as it "explained" 16% of the variation in attendance (concentration statistic). Sex and year each explained 2% of the variation. Both sexes were more likely to be present in the pre-egg period than during incubation or chick-rearing, and were more likely to be present in 1979 than 1980. Males were on territory significantly more often than females, both before and after the mean date of clutch initiation (Table 4). Attendance of breeders and territorial nonbreeders did not differ in the 1980 focal samples. I could not compare breeders and nonbreeders in 1979 because only one pair in 1979 failed to lay eggs. Wind speed did not significantly affect attendance in the pre-egg period.

Differences between breeders (five pairs) and territorial nonbreeders (three pairs) emerged in the analysis of six all-morning watches in June 1980. Breeding status, a bird's sex and the date had significant simple effects on territory attendance in a factorial analysis-of-variance. Two of three possible two-factor interactions were significant: effect of sex depended on breeding status and date (Table 5, Fig. 4). Male breeders and both male and female nonbreeders had roughly similar day-to-day patterns of attendance. In

TABLE 3. The date on which known-age birds were first observed on land each year.

	Age (years)					
	1	2	3	4	5	6+
1977	13 July	10 July	12 May			
1979	none	16 June	11 May	24 March	9 May	2 April
1980	30 July	none	22 May	22 May	none	2 April
1981				22 April		4 April
1982			21 May	13 May	24 April[a]	

[a] The first day I visited the island in 1982.

TABLE 5. Analysis-of-variance of factors influencing percentage of time spent on land by Pigeon Guillemots at eight nests on six days in June 1980.

Effect	df	Mean square	F ratio[a]
Sex	1	0.931	34.49**
Breeding status	1	0.567	20.99**
Date	5	0.092	3.41**
Sex × Status	1	0.419	13.51**
Sex × Date	5	0.083	3.06**
Status × Date	5	0.015	0.57
Sex × Status × Date	5	0.019	0.69
Within cells	65	0.027	

[a] ** = $P < 0.01$. Test for homogeneous variances: Bartlett-Box $F_{23,1155} = 1.06$, $P > 0.30$.

contrast, female breeders spent considerably less time on land than did other birds, and three of five breeding females did not visit territories at all on the morning of 16 June; one, six, and eight days before they laid their first eggs. Winds were then the strongest, 35 to 45 km/hr, of any day in the sample. No tidal effect on attendance was apparent on these six days.

Guillemots left their territories periodically throughout the morning. Breeding males took about five supposed feeding trips per morning each with a median duration of 21 min ($n = 149$), while breeding females departed for 54-min-long bouts ($n = 87$). Visits to land by nonowners were significantly shorter (median = 15 min, $n = 134$) than were visits by territorial males (31 min, $n = 197$). As a consequence, the coefficient of variation for counts of nonowners ranged 65 to 100%, while counts of breeders varied 18 to 70%.

BREEDING SUCCESS

Females that arrived late relative to the mean date of clutch initiation laid smaller clutches than early arriving females (Spearman's rho = −0.67, $n = 32$, $P < 0.01$). In this analysis, the annual mean date of clutch initiation in 1979 or 1980 was subtracted from the arrival date in the respective year to correct for the 13-day mean difference in clutch initiation in the two years. The probability of fledging at least one chick decreased as females ($G = 4.5$, df = 1, $n = 32$, $P < 0.05$) and males ($G = 4.78$, $P < 0.05$) arrived later relative to mean annual clutch initiation date. The mean number of chicks fledged per nest did not differ significantly between years. Two pairs defended territories but did not lay eggs in 1979, while four pairs did so in 1980.

TABLE 6. Chick-feeding rates and foraging times in 1979 and 1980.

	1979 Mean ± SE	1980 Mean ± SE
Chick-feeding rate[a] (fish/chick·parent·hr)	0.81 ± 0.11 ($n = 53$)	0.55 ± 0.09 ($n = 85$)
Feeding trip duration* (min)	8.9 ± 1.4 ($n = 40$)	16.6 ± 1.2 ($n = 39$)
Time on land between feeding trips* (min)	3.3 ± 0.4 ($n = 61$)	2.0 ± 0.4 ($n = 80$)

[a] Differs between years. $F = 3.59$, df = 1, 135, $P < 0.06$. Rate adjusted for chick's age (<15 days) in an analysis of covariance. Regression slopes of rate on age are homogeneous, $F = 1.02$, df = 1, 134, $P > 0.5$.

* Differs between years by Mann-Whitney U-Test, $P < 0.01$.

CHICK-FEEDING RATES

The rate at which chicks were fed increased with chick age up to 15 days, and the mean rate was greater in 1979 than in 1980, despite the limited sample size in 1979 (Table 6). I had insufficient data for chicks older than 15 days in 1979, but in 1980 the feeding rate was independent of age (1.0 ± 0.14 fish/parent·hr·chick, $n = 64$). Feeding trips were significantly shorter in duration in 1979 than in 1980 and guillemots spent more time on territory between feeding trips in 1979 than in 1980 (Table 6). Guillemots feeding chicks in my study plot in 1979 often joined feeding flocks with Brandt's Cormorants (*Phalacrocorax penicillatus*) and Common Murres (*Uria aalge*) within one km of the island; guillemots feeding in these flocks usually returned with rockfish (*Sebastes* sp.) (Ainley and Boekelheide, in press).

DISCUSSION

This study has identified six factors that influence Pigeon Guillemot attendance at the breeding colony. Differences among birds in age, sex, and breeding status interacted with daily, seasonal, and annual variability in determining guillemot numbers on land.

An annual difference in food availability or abundance seems the likely cause of the annual difference in colony attendance documented here. The greater rate of feeding chicks in 1979 compared to 1980 provided an indirect measure of annual differences in food availability. Greater abundance or availability of food in 1979 may have led to the earlier occupation of territories, more frequent attendance on territories, earlier date of clutch initiation, and larger clutch size in 1979 (Tables 1, 4).

Ainley and Lewis (1974) and Manuwal (1979) have compared annual differences in reproductive success in Cassin's Auklet (*Ptychoramphus aleuticus*) breeding on SEFI to differences in the timing and extent of upwelling of cold, nutrient-rich waters along the California coast. Pierotti (1981) similarly explained differences in colony attendance and reproductive behavior of Farallon Western Gulls (*Larus occidentalis*). In years of strong upwelling, driven by consistent, strong northwest winds, auklets on SEFI have greater reproductive success than in years when warm waters remain in the area. Comparative studies of the breeding and feeding ecology of seabirds breeding on the Farallones suggest that food was more abundant near the island in 1979 than in 1980 (Ainley and Boekelheide, in press).

Guillemots returned to the vicinity of SEFI at about the same time in 1979 and 1980, as judged by counts of birds on the water at dusk (Fig. 1), but occupied territories later in 1980. This suggests that the timing of colony occupancy in these two years was less influenced by conditions experienced overwinter as it was by food conditions in waters nearby the colony. In both years, some birds (10 to 20% in mid-March 1980) in the offshore rafts had not yet completed their molt, and a few occupied territories while still in molt.

The first birds to return do not initiate breeding immediately, but defer egg laying 50 or more days. A return to the colony two months prior to the time when conditions permit breeding is apparently favored because there is competition among males and among females for territories and mates, and priority of residence is a major factor in determining the winner of disputes (Nelson 1984). Early arrivals, which tended to be older and more experienced, also had higher breeding success, however, this is not always the case for Farallon guillemots (Ainley and Boekelheide, in press). An early return gives females the time to acquire the food and nutrients required for a large clutch. In contrast, late-arriving females in 1980 spent less time in the pre-egg-laying period, and laid smaller clutches. Six of the last-arriving females in both years acquired territories and mates, but did not lay eggs. At least two of the six bred in a later year.

The daily attendance cycle with peaks in the morning and evening persists throughout the breeding season, although birds are more likely to be on land in mid-day during incubation and chick-rearing than they are in the pre-egg period (Storer 1952; Drent 1965; Ainley and Boekelheide, in press). Similar daily cycles have been reported for the Black Guillemot (*C. grylle*) in Shetland (Slater and Slater 1972, Ewins 1985) and Denmark (Asbirk 1979). On Mandarte, Island, British Columbia, Drent (1965) reported a single morning peak of attendance, and guillemots spent the night at sea, rather than on land. As Drent anticipated, different patterns of colony attendance reflect differences in the distance to the feeding grounds. At Mandarte, guillemots fed 4 to 5 km from the colony, whereas on SEFI they often fed within several hundred meters, and usually within 2 or 3 km (Ainley and Boekelheide, in press).

In addition to a daily cycle in attendance, guillemot numbers varied over the course of the breeding season. Breeders were on territory most frequently prior to egg laying. The decline in morning attendance after egg laying simply reflects that birds were incubating eggs or brooding chicks, or were at sea. The decreased postlaying attendance of breeders is partially compensated by the appearance in June of young nonbreeders. Thus, total counts in May, June, and early July of 1980 were comparable, and did not begin to decline until late July and August as chicks fledged and adults and young birds left the colony.

I did not count birds systematically in June and July 1979, but attendance by nonbreeders appeared higher than in 1980. On 23 July 1979 I counted 42 guillemots at East Landing, whereas the highest daily morning count in 1980 was 32 birds. Between 17 and 22 June 1979, guillemots were seen "loafing" in groups of 30 to 50 in areas near the intertidal not normally used as roosts. These were probably young birds recently returned to the colony. Guillemots were not present in these areas in 1980. Young Common Murres also congregate in clubs near the shoreline (Birkhead and Hudson 1977).

The attendance data summarized in Table 4 demonstrate that females were present less often than males, and suggest that attendance by females was depressed more than male attendance in 1980, when food was less available. The increased energy requirements associated with egg production may be responsible for the sex difference in attendance. A clutch of two 53-g eggs ($n = 15$) represents about 22% of female body mass (487 ± 6.6 g, $n = 9$ females caught in April). The eggs are laid within a three-day interval

(Drent 1965; Ainley and Boekelheide, in press), which spreads the female's energy requirements over several days (King 1973, Astheimer 1985). In order to acquire sufficient food to meet the demands of egg formation, breeding females must forage more than males, with the result that females may only visit territories for several visits each morning just prior to egg laying. It takes about 10 days for yolk formation in Pigeon Guillemots (Roudybush et al. 1979). The yolk may be held for a lag of unknown duration before albumen and shell are added, thus extending the time for egg synthesis by several days (Astheimer 1985). Most of the all-morning watches fell 12 days prior to clutch initiation for breeding females (median = 8, range = 1–16).

Low pre-egg-laying colony attendance by females has been documented in species that forage at large distances from the breeding colony (Manx Shearwater, *Puffinus puffinus,* Perrins and de L. Brooke 1976; Northern Fulmar, *Fulmarus glacialis,* MacDonald 1977; Common Puffin, *Fratercula arctica,* Ashcroft 1979; Common Murre, Birkhead et al. 1985). Decreased prelaying attendance by breeding female Pigeon Guillemots is not as pronounced as in these species probably because guillemots usually forage close to the colony. The lower colony attendance by females in the morning is not simply a result of sex differences in the diurnal pattern of colony attendance, as occurs in Blue-eyed Shags (*Phalacrocorax atriceps*: Bernstein and Maxson 1984). Male guillemots arrived at the colony in the evening before females.

These results documenting variation in colony attendance are also relevant to the problem of censusing Pigeon Guillemot populations. As in other auks, *k* values differed within and between years, thereby necessitating that *k* be measured for each colony and each year studied (Birkhead 1978, Cairns 1979, Birkhead and Nettleship 1980, Ewins 1985). Part of the variation in colony counts is due to the number of nonbreeders in attendance, which appears to be highly variable over the short and long term in auks (Lloyd 1975, Gaston and Nettleship 1982). Nonbreeding Pigeon Guillemots tended to arrive and depart synchronously, and tended to perch together on communal roosts.

Replicate counts made in mid-morning in the month prior to egg laying (May on SEFI) directly reflect changes in the breeding population. Counts made in April, when guillemots first return to the colony are variable, and are susceptible to annual differences in the timing of colony occupancy. There is a suggestion that annual variation in the food supply has similar effects on colony attendance of breeders and nonbreeders, so that a total count of all individuals accurately reflects the size of the breeding population.

ACKNOWLEDGMENTS

Logistic support was provided by PRBO and the Farallon Patrol of the Oceanic Society (San Francisco Chapter). The San Francisco Bay National Wildlife Refuge granted permission to work on the Farallones. Grants from the Society of Sigma Xi, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Division of Biological Sciences, Horace H. Rackham School of Graduate Studies and the Museum of Zoology of the University of Michigan, and a NSF graduate fellowship supported the work. Computer facilities were provided by The University of Michigan and Vassar College. During preparation of the manuscript I was supported by a NIH postdoctoral fellowship. I thank D. G. Ainley for comments on the manuscript. This is Contribution No. 252 of Point Reyes Bird Observatory.

LITERATURE CITED

AINLEY, D. G., AND R. J. BOEKELHEIDE [EDS.]. In press. Farallon Island Seabirds: community ecology, structure and dynamics in an upwelling system. Stanford Univ. Press, Stanford, CA.

AINLEY, D. G., AND T. J. LEWIS. 1974. The history of the Farallon Island marine bird populations, 1854–1972. Condor 76:432–446.

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:40–77.

ASBIRK, S. 1979. The adaptive significance of the reproductive pattern in the Black Guillemot, *Cepphus grylle.* Vidensk. Medd. Dan. Naturhist. Foren. 141:29–80.

ASHCROFT, R. E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. Ornis Scand. 10:100–110.

ASTHEIMER, L. B. 1985. Long laying intervals: a possible mechanism and its implications. Auk 102: 401–409.

BERNSTEIN, N. P., AND S. J. MAXSON. 1984. Sexually distinct daily activity patterns of Blue-eyed Shags in Antarctica. Condor 86:151–156.

BIRKHEAD, T. R. 1978. Attendance patterns of guillemots *Uria aalge* at breeding colonies on Skomer Island. Ibis 120:219–229.

BIRKHEAD, T. R., AND P. J. HUDSON. 1977. Population parameters for the Common Guillemot *Uria aalge.* Ornis Scand. 8:145–154.

BIRKHEAD, T. R., S. D. JOHNSON, AND D. N. NETTLESHIP. 1985. Extra-pair matings and mate guarding in the Common Murre *Uria aalge.* Anim. Behav. 33:608–619.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1980. Census methods for murres, *Uria* species: a unified approach. Can. Wildl. Serv. Occas. Pap. 43:1–25.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1981. Reproductive biology of Thick-billed Murres (*Uria lomvia*): an inter-colony comparison. Auk 98:258–269.

BOERSMA, P. D. 1978. Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. Science 200:1481–1483.

CAIRNS, D. 1979. Censusing hole-nesting auks by visual counts. Bird Banding 50:358–364.

DESANTE, D., AND D. G. AINLEY. 1980. The avifauna of the south Farallon Islands, California. Stud. Avian Biology 4:1–104.

DRENT, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba.* Ardea 53:99–160.

EWALD, P. W., AND S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in Red-winged Blackbirds *Agelaius phoeniceus.* J. Anim. Ecol. 51:429–450.

EWINS, P. J. 1985. Colony attendance and censusing of Black Guillemots *Cepphus grylle* in Shetland. Bird Study 32:176–185.

FIENBERG, S. E. 1980. The analysis of cross-classified data. MIT Press, Cambridge.

GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island. Canadian Wildlife Service Monograph Series No. 6, Ottawa.

GASTON, A. J., AND D. N. NETTLESHIP. 1982. Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre *Uria lomvia.* Auk 99:468–473.

HARRIS, M. P. 1980. Breeding performance of puffins *Fratercula arctica* in relation to nest density, laying date and year. Ibis 122:193–209.

KING, J. R. 1973. Energetics of reproduction in birds, p. 78–120. *In* D. S. Farner [ed.], Breeding biology of birds. Natl. Acad. Sci., Washington, DC.

LACK, D. 1966. Population studies of birds. Oxford Univ. Press, Oxford.

LLOYD, C. S. 1975. Timing and frequency of census counts of cliff-nesting auks. Br. Birds 68:507–513.

MACDONALD, M. A. 1977. The pre-laying exodus of the Fulmar *Fulmarus glacialis* (L.). Ornis Scand. 8:33–37.

MANUWAL, D. A. 1979. Reproductive commitment and success of Cassin's Auklet. Condor 81:111–121.

NELSON, D. A. 1984. Communication of intentions in agonistic contexts by the Pigeon Guillemot, *Cepphus columba.* Behaviour 88:145–189.

NORUŠIS, M. J. 1985. SPSSX advanced statistics guide. McGraw-Hill, New York.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

PERRINS, C. M., AND M. DE L. BROOKE. 1976. Manx shearwaters in the Bay of Biscay. Bird Study 23: 295–299.

PIEROTTI, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98:532–549.

ROUDYBUSH, T. E., C. R. GRAU, M. R. PETERSEN, D. G. AINLEY, K. V. HIRSCH, A. P. GILMAN, AND S. M. PATTEN. 1979. Yolk formation in some charadriiform birds. Condor 81:293–298.

SLATER, P.J.B., AND E. P. SLATER. 1972. Behaviour of the Tystie during feeding of the young. Bird Study 19:105–113.

STORER, R. W. 1952. A comparison of variation, behavior and evolution in the sea bird genera *Uria* and *Cepphus.* Univ. of Calif. Publ. Zool. 52:121–222.

VERMEER, K. 1980. The importance of timing and type of prey to reproductive success of Rhinoceros Auklets *Cerorhinca monocerata.* Ibis 122:343–350.

YDENBERG, R. C. 1984. The conflict between feeding and territorial defence in the Great Tit. Behav. Ecol. Sociobiol. 15:103–108.