FACTORS DETERMINING SEASONAL CHANGES IN ATTENDANCE AT COLONIES OF THE THICK-BILLED MURRE *URIA LOMVIA*

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ABSTRACT.—A comparison of the interyear variation in attendance patterns of Thick-billed Murres (*Uria lomvia*) with the variation in egg size and chick growth rates suggests that the number of birds in attendance at a murre colony at any time during the breeding season is determined principally by the availability of food in surrounding waters. This effect operates mainly through the behavior of a large floating population of prospectors. When food is abundant, numbers on the cliffs will be high because birds have plenty of time to spare. Conversely, when food is scarce, numbers will be low because birds must devote most of their time to feeding. Implicit in the hypothesis is the assumption that birds strive to maximize the amount of time that they spend at the breeding colony in order to improve their chances of acquiring and retaining a breeding site. *Received 31 March 1981, accepted 25 November 1981.*

A NUMBER of recent studies have described the attendance patterns of murres (*Uria* spp.) and other alcids at breeding colonies (Lloyd 1975, Birkhead 1978, Slater 1980, Gaston and Nettleship 1981). Such patterns have become of particular concern recently because of the problems they pose for the interpretation of census results. The overall pattern seen in all studies is a gradual increase from the initiation of egg laying to a peak early in the chick-rearing period, followed by a fairly sharp decline after the beginning of fledging. Two hypotheses have been advanced to account for this trend. Lloyd (1975) suggests, for alcids generally, that the pattern is determined by the number of nonbreeding birds visiting the colony, while Slater (1980) proposes, specifically for the Common Murre (*Uria aalge*), that the length of time spent by breeders at the colony is the most important determinant. In both cases the explanations beg the question of why either nonbreeders or breeders should spend more time at the colony at a particular stage of the breeding cycle.

Considerable information has been accumulated recently by the Canadian Wildlife Service on the attendance patterns of Thick-billed Murres (*Uria lomvia*) at colonies in Lancaster Sound and Hudson Strait in the Canadian Arctic. These observations were made concurrently with studies on all aspects of the species' breeding ecology. A comparison of interyear variation in attendance patterns with variation in egg size and chick growth rates enables us to propose a unifying hypothesis to account for the observed attendance patterns of Thick-billed Murres that may well apply to other alcids.

The hypothesis states that the number of Thick-billed Murres in attendance at a colony at any time during the breeding season is determined primarily by the availability of food in surrounding waters. When food is abundant, numbers on the cliffs will be high because birds have plenty of time to spare. Conversely, when food is scarce, or inaccessible due to weather or ice conditions, numbers will be low because birds must devote most of their time to feeding. Implicit in the hypothesis is the assumption that birds, particularly prospectors, strive to maximize the amount of time that they spend at a breeding colony in order to improve their chances of acquiring and retaining a breeding site. Superimposed on the pattern determined by food supplies would be fluctuations due to weather conditions, which may affect feeding success, but these would probably determine only short-term variation, not recurrent seasonal patterns.

Murres do not breed until they are 4–5 yr old, and prebreeding birds probably make up the bulk of nonbreeders attending the colony

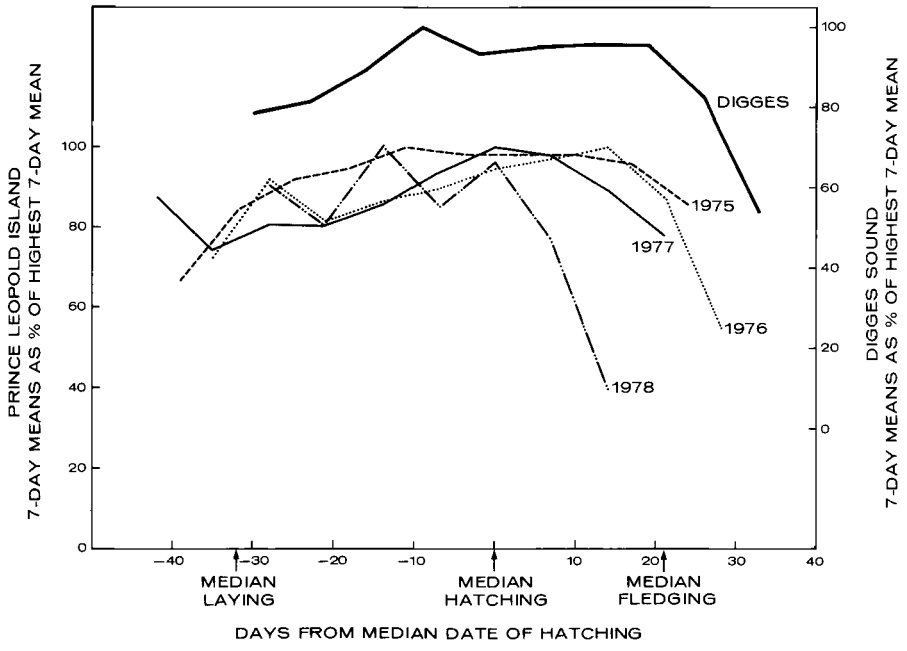

Fig. 1. Mean daily counts over 7-day periods at Prince Leopold Island in 1975–1978 and at Digges Sound in 1980, expressed as percentages of the highest 7-day mean.

(Birkhead and Hudson 1977). The numbers of these birds must be affected by recruitment during the previous 2–3 yr, a situation that affects interyear comparisons of attendance statistics. The proportion of prebreeding birds varies with the structure of the cliffs and the availability of suitable landing sites that are out of reach of breeders, which tend to attack them if they land too close to an occupied site (Gaston and Nettleship 1981). Although this variation will affect a comparison of different areas or colonies, it should not affect comparisons among recurrent observations of the same area of a cliff, because murres have a high annual survival rate (Birkhead and Hudson 1977) and are highly site tenacious, so that the ratio of breeders to nonbreeders probably varies little from year to year.

METHODS

Observations used in this analysis were made at Thick-billed Murre colonies in the Canadian Arctic on Prince Leopold Island (74°N, 90°W, ca. 90,000 pairs), Lancaster Sound, during 1975–1978 and on Eastern Digges Island (62°N, 77°W, ca. 125,000 pairs), Hudson Strait, in 1980. In all years the numbers of birds present on selected study plots scattered along the colonies were counted daily throughout the breeding season between 1600 and 1800 (solar time), except in 1975, when counts were made every 2–3 days, and in 1978, when counts were made only from the middle of the incubation period onwards. The counts at each colony were made at the same plots each year. The timing of laying, hatching, and fledging was recorded for a sample of the sites included in the daily counts [approximately 30%); see Birkhead and Nettleship (1980) for details of methods], while egg measurements (length and breadth) and chick weights, recorded every 2 days, were measured concurrently at another sample of sites, the same sites being used each year.

From egg laying onwards, all sites were permanently occupied by one member of the breeding pair, and a distinctive greeting display occurred on the arrival of the other (Gaston and Nettleship 1981). Birds involved in this arrival display were recorded as site holders, while all others were recorded as prospectors. A few birds that occupied sites throughout the season did not lay eggs and therefore constituted nonbreeding site holders. These made up less than 10% of the sites observed.

At one study plot at Prince Leopold Island, containing 100–150 breeding pairs of murres, periodic watches were made every 3 days in 1977 between 1300 and 1700 solar time in order to record the numbers of birds present each hour and the hourly rates

TABLE 1. Correlation coefficients between rates of arrival of site-holding and prospecting Thick-billed Murres and the numbers of birds counted on the study plot, where X = total number of birds arriving over 4 h, and Y = mean of hourly counts.

	Prince Leopold Island[a]	Digges Island[a]
Date	28 June–18 August	2 July–16 August
Number	18	8
Prospectors		
r	0.781**	0.567*
$R^2 \times 100\%$	60.9	30.9
Site holders		
r	0.522*	0.086
$R^2 \times 100\%$	27.2	0.7
Log_{10} prospectors		
r	0.851**	0.977**
$R^2 \times 100\%$	72.4	95.5

[a] * = $P < 0.05$; ** = $P < 0.01$.

of arrival of members of site-holding pairs and of prospecting birds. Similar watches were performed every 5 days at Digges Island in 1980. At a small sample of sites (ca. 20) the length of time spent at the site by both members of the pair simultaneously was also recorded. These behavioral observations were made in order to estimate the contribution of different segments of the population to variations in attendance.

RESULTS

Seasonal patterns.—A comparison among the 5 yr for which data are available shows that peak numbers occurred on the colony from 14 days before to 14 days after the median date of hatching (Fig. 1). The mean date of peak attendance at Prince Leopold Island over the 4 yr fell 5 days before the median date of hatching. Mean counts at the median date of hatching averaged 98% of the highest 7-day mean, compared to only 82% for counts at the median date of laying. Differences between 7-day mean counts at laying and at hatching were significant in all years ($P < 0.01$).

In 1975 at Prince Leopold Island and in 1980 at Digges Sound, numbers peaked comparatively early (12 and 10 days prior to median hatch, respectively), remaining fairly constant for about a month thereafter. In 1976, numbers rose steadily to a peak 14 days after the median date of hatching and then declined rapidly. The pattern in 1977 was intermediate, with a peak on the median date of hatching. In 1978, numbers peaked 14 days before the median date of hatching and declined sharply from the median date, probably because laying in this season was 2 weeks later than in any other. A decline in attendance after the start of fledging, seen in all years, was probably associated with adult birds accompanying chicks away from the colony, and from this time onwards the number of adults present in the vicinity of the colony probably falls continuously. Breeding success was similar in all years, and hence the proportion of failed breeders present is unlikely to have caused observed differences among years (see Gaston and Nettleship 1981).

The role of prospectors.—Evidence of the effect of prospectors upon attendance patterns was obtained by comparing the rate of arrival of prospectors with the total number of birds present on particular study plots. At Prince Leopold Island in 1977, the number of birds present on the study plot was positively correlated with the rates of arrival of both prospecting and site-holding birds during the period from the start of egg laying to the date when 25% of the young had fledged (Table 1), but a multiple regression analysis showed that the number of site holders did not significantly increase the amount of variation explained by prospectors alone (61%). Results at Digges Island in 1980 were similar, although only the correlation with the rate of arrival of prospectors was significant. In both cases log transformation of the number of prospectors arriving improved the correlation significantly, explaining 72% of the variation at Prince Leopold Island and 95% of the variation at Digges Island (Fig. 2 and Table 1). The length of the time spent together on the breeding site by both members of the pair decreased during the course of incubation and remained low during the chick-rearing period, offsetting an increase in the frequency of visits (Gaston and Nettleship 1981), so that the total length of time spent together per day remained more or less constant and did not contribute to the seasonal trend in attendance.

Attendance in relation to egg size and chick growth.—The maximum weight attained by chicks before leaving the cliffs was chosen as the best estimate of food availability during the growth period. Murres bring food to their chicks at a constant rate after the first 2 days

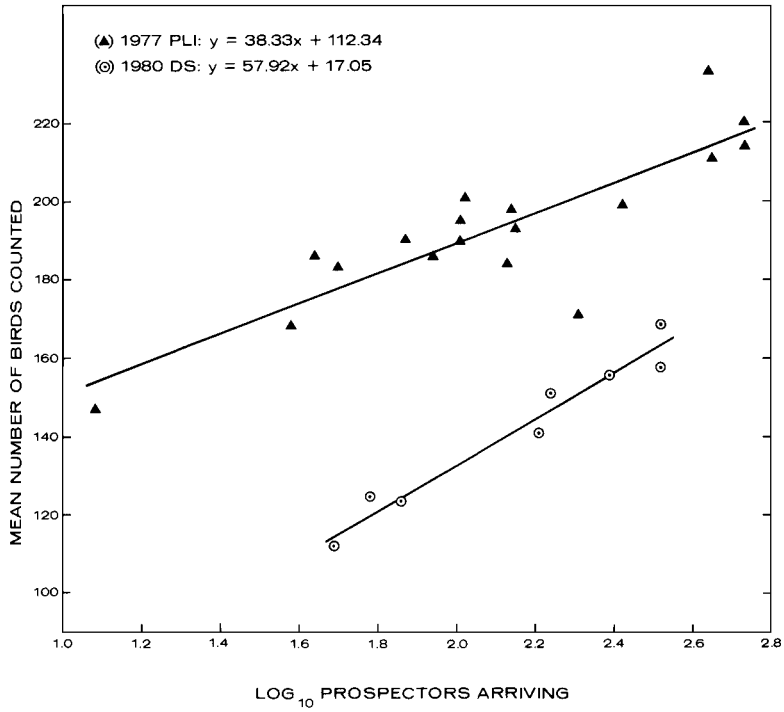

Fig. 2. Mean hourly counts during 4-h watches in relation to the rate of arrival of prospecting birds ($\log_{10}$ total number arriving over 4 h) for Prince Leopold Island in 1977 and Digges Sound in 1980.

beyond hatching (Gaston and Nettleship 1981), and hence the peak weight is more sensitive to fluctuations in food supply than is the rate of weight increase. The murres continued to increase their weight until they fledged in most years, and hence maximum weights were very similar to fledging weights. A comparison of maximum weights with attendance in the 15 days from the median date of hatching onwards [Thick-billed Murres begin to fledge at 15 days (Gaston and Nettleship 1981)] shows a positive correlation ($r = 0.93, P < 0.05$, Fig. 3). A comparison of egg volumes with attendance during the period 15 days prior to laying (egg formation takes approximately 15 days in the Thick-billed Murre) shows a similar positive, though insignificant, correlation.

DISCUSSION

The observed variation in the timing of peak attendance at the colony suggests that this is only loosely related to events of the breeding cycle, although changes in the behavior of breeders at different stages of the cycle may contribute to the overall pattern. From the start of laying to the beginning of fledging, the nonbreeding segment of the population appears to be the dominant factor in determining attendance.

The size of eggs and the growth rates of chicks are probably related to the availability of food in the vicinity of the colony. Although chicks are fed different food items from those eaten by the adults, the additional food required to feed a chick is only a small proportion of the adult's requirements (Gaston and Nettleship 1981). Growth rates of chicks must therefore be related to the amount of time that their parents can spare from their own maintenance requirements; hence, rapid chick growth is evidence of abundant food for adults as well as chicks. The relationship between light chicks and low attendance at the colony supports the initial hypothesis that the availability of food determines the amount of time spent at the colony.

The availability of food is determined not only by the abundance of food organisms but by their distribution in relation to the colony, because time spent travelling between the col-

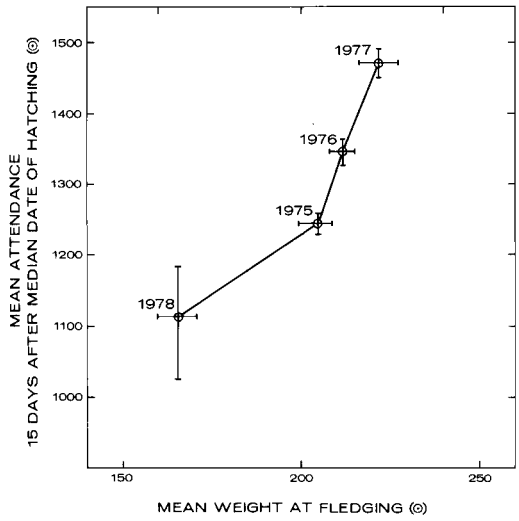

Fig. 3. Mean fledging weights of chicks in relation to mean daily counts during the 15 days following the median date of hatching. Bars represent standard errors.

ony and the feeding area probably constitutes a large part of the total time available for foraging. In a year when food is relatively easily available, this may mean that prey is moderately abundant close to the colony or very abundant further away. Unfortunately, no general measurement of regional production is likely to provide a simple indicator of the availability of food for murres, hence our reliance on the indirect measure of chick growth. Readily available food may increase attendance in two ways: by increasing the number of birds visiting the colony on a particular day and by increasing the length of time that they spend before departing again to feed.

The logarithmic relationship between arrivals of prospectors at the colony and numbers present suggests that, as the number of birds arriving at the colony increases, the additional birds spend shorter periods actually on the cliffs. If we assume that feeding efficiency increases with age, then, when feeding is poor, only older prospectors may be able to spare time to visit the colony. These birds have probably selected a breeding area within the colony and may spend long periods occupying potential sites. In contrast, younger birds, which visit the colony only when food is abundant, may not have selected a breeding area and must spend most of their time flying back and forth along the cliffs, landing briefly at many different sites (Gaston and Nettleship 1981). The increasing proportion of young prospectors as attendance increases probably accounts for the logarithmic relationship.

The contrast between our observations and Slater's finding that, for the Common Murre, attendance on breeding ledges is determined by the numbers of breeding birds present on the cliffs appears to be due to the fact that prospecting Common Murres spend little time on the breeding ledges, congregating instead in "clubs" on intertidal rocks at the foot of the colony. At the same time, at least at small colonies, breeding Common Murres spend a greater proportion of their time at their site than we observed for Thick-billed Murres (T. R. Birkhead, pers. comm.). Slater's observation that attendance increased during the season due to increasing lengths of time spent by breeders at their sites is compatible with our hypothesis, however, if we assume that the time spent at the site is related to the availability of food. We should expect breeding to be timed so that the maximum abundance of food occurs during the chick-rearing period (Perrins 1970), and, if so, the patterns observed by Lloyd (1975) and Birkhead (1978), who found that attendance in other alcids peaked during the chick-rearing period, can equally be accounted for by our hypothesis.

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