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SEASONAL DECLINES IN DURATION OF INCUBATION AND CHICK PERIODS OF COMMON MURRES AT BLUFF, ALASKA IN 1987-1991

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ABSTRACT.—The Common Murre (*Uria aalge*) produces a single-egg clutch, and the female may replace the egg if it is lost. Even at breeding colonies in highly seasonal environments, egg laying may span several weeks. For example, the mean range of egg-laying dates was 41 days in a five-year period at Bluff, a coastal colony in western Alaska. In each of those five years, incubation periods of eggs were negatively related to laying date (i.e. incubation periods of eggs laid later in season were shorter). This is the first documentation of a seasonal decline in the incubation period of this species, and one of the few for birds in general. Analyses of seasonal changes in weather patterns indicated that the seasonal shortening of the incubation period cannot be explained by changes in environmental conditions. The duration of the chick period also declined seasonally in all five years, similar to results reported elsewhere. Overall, duration of the period between egg laying and fledging averaged about six days less for the latest breeding pairs than for the earliest breeding pairs. There is no evidence of a seasonal decline in hatching or fledging success at this colony. Consequently, these results indicate that murres breeding later in the season at Bluff reduce the duration of both the incubation and chick periods well in advance of seasonal deterioration of environmental conditions. Chicks develop more rapidly than embryos in eggs, and chicks at sea likely grow and develop faster than chicks at the colony. As the time remaining for completion of development decreases through the summer, quicker hatching of eggs and sea-going of chicks will be advantageous. Formation of sea ice throughout the region in late fall likely is the primary time constraint selecting for accelerated developmental patterns of eggs and chicks of late-breeding murres at Bluff. In highly seasonal environments, seasonal time constraints may influence most or all phases of avian breeding cycles. *Received 18 April 1994, accepted 12 June 1994.*

ANIMALS LIVING in seasonal environments must initiate and complete their reproduction within a restricted period of favorable conditions. Within bird species, the duration of each phase of reproduction (egg formation, incubation, and chick rearing) is potentially variable, and intraspecific variability in the duration of each of these stages may be adaptively important.

The Common Murre (*Uria aalge*) produces a single-egg clutch and may produce one or more replacement eggs if the egg is lost during incubation. In both the Common Murre and the Thick-billed Murre (*U. lomvia*), a seasonal decline in egg size occurs (e.g. Gaston et al. 1985), and replacement eggs are smaller than first eggs laid by the same female, but similar in size to first eggs of other females laying on the same date (e.g. Birkhead and Nettleship 1982). Because the potential daily chick growth is about double that of maximum daily growth rate of the egg (Gaston and Nettleship 1981), Birkhead and Nettleship (1982) proposed that seasonal decreases in egg size in murres should be interpreted as adaptations of later-laying females to minimize the period of egg formation and the delay in laying, thus shortening the period between onset of formation and hatching of the egg.

Theoretically, murres could shorten the duration of egg formation, the incubation period, or the chick period as the time remaining for reproduction decreases or environmental conditions deteriorate in late summer. The duration of egg formation can be examined directly by counting the number of daily growth rings in the yolk (e.g. Grau 1976, 1984). In the only study of seasonal changes in the number of growth rings of murre eggs, Birkhead and del Nevo (1987) documented significantly fewer daily growth rings in the yolks of replacement eggs than in the yolks of first eggs.

Seasonal variability in the duration of egg formation also can be examined indirectly for females producing replacement clutches by examining the relationship between the date of loss of the previous egg and the date of laying of the replacement egg (e.g. Birkhead and del Nevo 1987). If there is a seasonal decline in the period of egg formation, the period between loss and laying of the replacement egg should become shorter as the season progresses.

Intraspecific variability in incubation periods has received little attention. Parsons (1972) documented a negative correlation between duration of the incubation period and laying date, and a positive correlation between the incubation period and fresh egg mass in Herring Gulls (*Larus argentatus*). Bryant (1975) found a positive relationship between incubation period and egg mass in Common House-Martins (*Delichon urbica*), and Martin and Arnold (1991) found a positive correlation of incubation period to fresh egg mass in artificially incubated eggs of Japanese Quail (*Coturnix japonica*). Based on the positive correlation of incubation period to egg size and the negative correlation of egg size with laying date in murres, seasonal declines in murre incubation periods would be expected; however, incubation periods of Common Murres do not vary with laying date at either Skomer Island, Wales (Hatchwell 1988) or the Isle of May, Scotland (Wanless and Harris 1988), two Temperate Zone colonies in the eastern Atlantic.

Numerous studies have shown that the duration of the chick period of murres declines seasonally (e.g. Gaston and Nettleship 1981, Birkhead and Nettleship 1982, Wanless and Harris 1988, Boekelheide et al. 1990, Hatchwell 1991, but also see Hedgren and Linnman 1979). Seasonal declines in duration of the chick period appear to represent a changing trade-off between continued development at the colony, which may be a considerable distance from foraging areas, and more rapid development at sea (e.g. Ydenberg 1989).

Here, I examine seasonal variability in the duration of the incubation and chick periods of Common Murres breeding at Bluff, Alaska, near the northern limit of their breeding range in the Pacific. I also examine seasonal changes in duration of the period between loss of eggs and laying of replacement eggs to indirectly test for seasonal changes in duration of egg formation. These results and previous studies permit quantification of the extent to which seasonal reductions in the periods of egg formation, incubation, and chick rearing result in shortening of later reproductive attempts.

STUDY AREA AND METHODS

The seabird colony at Bluff, Alaska (64°34'N, 163°45'W), on the north shore of Norton Sound, has been described in detail previously (Murphy et al. 1986; Murphy and Schauer 1994). W. H. Drury and his coworkers established seven plots for the study of murre reproduction in 1977 (Drury and Ramsdell 1985); data in 1987–1991 on the breeding status and performance of all murres on those plots, and some additional areas adjacent to those plots, provided the basis of this study.

The Common Murre is the most abundant cliff-nesting species at Bluff, numbering about 50,000 and outnumbering the Thick-billed Murre about 100:1 (e.g. Drury et al. 1981). About 10,000 Black-legged Kittiwakes (*Rissa tridactyla*), 100 Pelagic Cormorants (*Phalacrocorax pelagicus*), and 100 Horned Puffins (*Fratercula corniculata*) also breed on the cliffs (Drury et al. 1981, Drury and Ramsdell 1985, Murphy et al. 1991). Potential predators of murre eggs and chicks include the several nesting pairs of Common Ravens (*Corvus corax*) and about 150 Glaucous Gulls (*Larus hyperboreus*).

Field crews were present throughout the murre breeding season in 1987–1991, arriving before the first egg was laid in the colony and departing when most (1987–1990) or all (1991) chicks either had left the colony or were at least 15 days old and, thus, had reached sea-going (hereafter "fledging") age. A member of the field crew visited reproductive plots and recorded the status of each breeding pair daily, weather permitting, from the day the first egg was seen at the colony until completion of the fieldwork. Observations were conducted on all but 5 of 86 days in 1987, 2 of 93 days in 1988, 3 of 86 days in 1989, 16–21 of 84 days in 1990, and 4–8 days of 97 days in 1991 (ranges indicate differences in numbers of days particular plots were observed). In all years but 1988, I trained a new two- to three-member field crew early in the breeding season; the 1987 field crew returned in 1988 with each member studying the same plots as in 1987.

Each season two to several observers collected data on murre reproduction, following the protocols outlined by Birkhead and Nettleship (1980). Each individual was assigned to a particular plot or set of study plots for the entire field season. Observers used a combination of hand-drawn sketches and black-and-white (through 1988) or color (1989–1991) photographs to map and record the behavior of each adult maintaining a breeding site within each reproductive plot.

During each visit the observer coded the posture of each adult possibly tending an egg or a chick and recorded the presence of an egg or a chick, if seen. Murres do not build nests, and it is often difficult to see an egg or chick beneath them. However, adults assume distinctive incubating postures (body pressed horizontally with wings held symmetrically down and back, and outline of lower back forming angle rather than smooth curve) and brooding postures (wings held asymmetrically, with one wing held out and covering chick; sometimes with bill of chick protruding posteriorly near bend of adult's wing). If the observer recorded an adult as incubating or brooding on several successive visits without seeing the egg or chick, the observer spent additional time and effort to determine if an egg or chick was present. I have omitted any case where the adult's posture was recorded as "incubating," but the observer was never able to verify the presence of an egg, unless the observer later saw an adult at that site brooding a chick.

Egg-laying dates were categorized as "known" if an egg was observed at a site where no egg was present the previous day, "probable" if an adult in incubating posture was observed at a site where no egg was present the previous day and an egg was seen at that site on a later date, and "unknown" if either the egg could not be seen or the posture of the adult could not be unequivocally categorized on the day the egg could first be present. Similarly, hatching date was recorded as "known" if a chick was seen on the first date the adult was in a brooding posture, "probable" if it was the first day the adult was in a brooding posture and a chick was observed at that site on a subsequent day, and "unknown" if adult postures could not be unequivocally categorized as incubating and brooding on successive days but a chick was seen on a later date. Fledging date was coded as "known" if a 14-day or older chick was seen on one day and it was gone on the next day, which was recorded as the fledging date, "probable" if an adult in a brooding posture was recorded on one day and the chick was missing the next day, and "unknown" if postures of the adult could not be categorized unequivocally on successive days when the chick could have fledged. If a chick disappeared before it was 15 days or older, I assumed that it died before fledging.

If a change in status was recorded (e.g. egg to chick, incubating to brooding) after one missed day of observation, I coded the date as "probable" and used the date observations resumed as the probable date. If a change in status was observed after two missed days of observation, I also coded the date as "probable" and recorded the second missed date as the probable date. If a change of status occurred during periods when observations were not conducted on three or more successive days (three times during 1987-1991), I recorded the date as "unknown." Therefore, the maximum error in assigning laying, hatching, and fledging dates was one day.

If a pair loses its egg, the female may lay a replacement egg. If an egg or a chick disappeared from a site, monitoring of that site continued and data on replacement attempts were recorded as for first attempts. I assumed that an egg laid at a particular site after the previous egg at that site had been lost was produced by the same pair that had lost the previous egg (also see Harris and Wanless 1988).

Incubation period, chick period, and attempt duration were recorded as the number of days from egg laying to hatching, from hatching to fledging, and from laying to fledging, respectively. I coded them by "observation type" as "known" when start and end dates were "known," "estimated" when one or both dates were coded as "probable," and "unknown" when one or both dates were coded as unknown (see above).

The U.S. National Weather Service reports detailed climatic data for Nome, Alaska. Nome is 80 km west of Bluff and also is on the north shore of Norton Sound. Bluff and Nome have very similar weather (unpubl. data). I therefore examined relationships of incubation periods to weather conditions using daily average temperature and average wind velocity reported at Nome and also calculated the "wind-chill equivalent temperature" (e.g. Halfpenny and Ozanne 1989):

$$W = 33 - [(10.45 + 10V^{0.5} - V)(33.0 - T)]/22.04, \quad (1)$$

where W is the wind-chill equivalent temperature (°C), V is the wind velocity (m/s), and T is the temperature (°C). W is a measure of the combined effects of temperature and wind on the ability of murres to effectively incubate their eggs. For each egg, I calculated the mean temperature, wind speed, and W for the period beginning one day after the laying date and ending one day before the hatching date (although few eggs were observed as they were laid, it appears that laying typically occurred in late afternoon).

All statistical analyses were conducted using BMDP (Dixon 1990).

RESULTS

Interval between egg loss and replacement.—No direct data on the duration of egg formation have been obtained at Bluff. However, the interval between loss of eggs and laying of replacement eggs has been used to approximate the period of egg formation in murres (e.g. Birkhead and del Nevo 1987); therefore, I used this interval to estimate the duration of formation of replacement eggs. Overall, the interval between loss and replacement averaged 14.3 ± SD of 5.1 days ($n = 246$).

The hypothesis proposed by Birkhead and Nettleship (1982) predicts that the period of egg formation decreases for eggs laid later in the season. Therefore, the interval between loss of eggs and laying of replacement eggs should be negatively related to loss date. Correlation coefficients ranged from −0.08 in 1989 ($n = 79$, $P = 0.48$) to 0.16 in 1987 ($n = 45$, $P = 0.28$); overall, the relationship was insignificant ($r = -0.01$, $n = 246$, $P = 0.84$). Therefore, this analysis fails to support the hypothesis that egg formation is shortened later in the season at Bluff.

A second corollary of the hypothesis proposed by Birkhead and Nettleship (1982) is that incubation periods should be positively correlated with the number of days between loss of one egg and laying of its replacement because a longer period of egg formation should result in a larger egg. At Bluff the correlation between the incubation period of replacement eggs and days between loss of the previous egg and laying of the replacement egg ranged from −0.31 in 1991 ($n = 18$, $P = 0.21$) to 0.05 in 1989 ($n = 43$, $P = 0.77$) and, overall, was nonsignificant ($r = -0.10$, $n = 158$, $P = 0.20$). Because these analyses are based on the untested assumption that the onset of formation of replacement eggs does not vary in relation to timing of loss of previous eggs, they are not critical tests of the hypothesis that egg formation is accelerated as the breeding season progresses; however, they fail to provide support for it.

Incubation period.—Egg laying began in early to mid-June and ended in mid- to late July in the five years of study (Murphy and Schauer 1994). On average, eggs were laid during a 40.8 ± 3.4 day period; egg-laying periods ranged from 37 days in 1987 to 45 days in 1990. Overall, incubation periods averaged 33.6 ± 2.2 days ($n = 1{,}237$). Incubation periods were significantly and negatively correlated with laying date in all five years (Fig. 1); regression coefficients ranged from −0.023 in 1988 to −0.123 in 1990. Based on the regression coefficients, a 10-day delay in laying resulted in a shortening of the incubation period from 0.2 days in 1988 to 1.2 days in 1990 (see Table 1).

Duration of the incubation period could be related causally to several factors other than laying date (e.g. ambient weather conditions; MacRoberts and MacRoberts 1972, Parsons 1972, Nisbet and Cohen 1975). Below, I examine relationships of incubation period to attempt (first or replacement), observation type (see above), and weather conditions during incubation.

To compare incubation periods of first and replacement attempts, I used an analysis of covariance (ANCOVA), specifying laying date as a covariate, and year and attempt (first or replacement) as grouping variables. There was no effect of attempt on the incubation period ($P = 0.36$) and no interaction between attempt and year ($P = 0.15$). Therefore, I pooled first and replacement attempts in all other analyses of incubation periods. Similarly, to compare known and estimated incubation periods (see above), I used an ANCOVA, specifying laying date as a covariate, and year and observation type as grouping variables. There was no effect of observation type on the incubation period ($P = 0.10$) and no interaction between observation type and year ($P = 0.31$), so I pooled observation

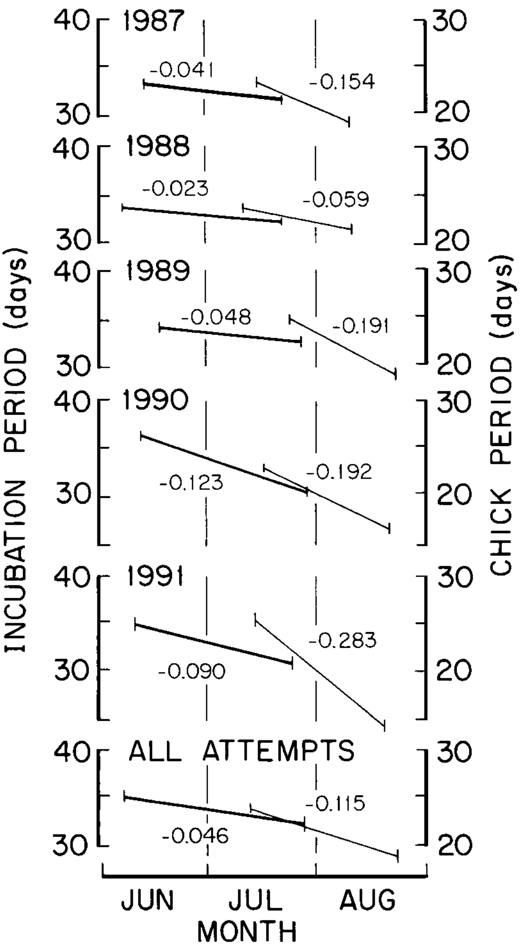

Fig. 1. Regressions (lines and regression coefficients) of duration of incubation and chick periods on laying and hatching dates, respectively. First and last egg-laying dates are endpoints of each line for incubation, and first and last dates of hatching are endpoints for each chick period line. Heavy lines indicate incubation; light lines indicate chick period.

TABLE 1. Results of linear regression analyses (correlation coefficient, regression coefficient, and sample size) of timing and duration of reproductive periods.

	Year					
	1987	1988	1989	1990	1991	Pooled
			Incubation vs. laying date			
r	−0.217	−0.132	−0.211	−0.346	−0.248	−0.197
b	−0.041***	−0.023*	−0.048**	−0.123***	−0.090***	−0.046***
n	246	279	209	168	335	1,237
			Chick period vs. hatching date			
r	−0.364	−0.147	−0.510	−0.312	−0.558	−0.299
b	−0.154***	−0.059*	−0.191***	−0.192***	−0.283***	−0.115***
n	221	217	175	140	307	1,090
			Attempt duration vs. laying date			
r	−0.299	−0.195	−0.582	−0.338	−0.591	−0.337
b	−0.127***	−0.081**	−0.245***	−0.250***	−0.345***	−0.144***
n	201	248	174	201	378	1,202

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Probability that coefficient equal to zero.

codes in all other analyses of incubation periods.

Parent murres alternate their attendance at the nest site to maintain constant incubation of the egg, except during the brief period when they exchange duties. Nevertheless, environmental conditions may vary seasonally (e.g. perhaps ambient temperatures increase seasonally so that murres laying later in season incubate their eggs more effectively, resulting in shortened incubation periods, than those laying earlier).

Summer temperatures at Nome for 1987–1991 showed no clear seasonal pattern (Fig. 2). Daily average temperatures between the first day of egg laying and the last day of egg hatching in each year generally were uncorrelated with calendar date (1987–1989, 1991), but were positively correlated with calendar date in 1990 ($r = 0.33$, $n = 81$ days, $P = 0.002$). The highest negative correlation between the duration of incubation and laying date occurred in 1990 (Table 1), suggesting that both calendar date and weather conditions during incubation may influence the duration of incubation (also see Parsons 1972).

Mean daily temperatures during each pair's incubation period (hereafter "ambient incubation temperatures") were highly positively correlated with laying date in 1988–1990 (1988, $r = 0.58$, $n = 279$, $P < 0.001$; 1989, $r = 0.38$, $n = 209$, $P < 0.001$; 1990, $r = 0.88$, $n = 168$, $P < 0.001$), but highly negatively correlated with laying date in 1987 and 1991 (1987, $r = -0.48$, $n = 246$, $P < 0.001$; 1991, $r = -0.76$, $n = 335$, $P < 0.001$). Thus, there were no consistent seasonal trends of ambient temperature during the incubation periods of murres among years. Incubation periods were uncorrelated with ambient incubation temperature in 1987–1989 (all $P > 0.5$), but negatively correlated with ambient incubation temperature in 1990 ($r = -0.19$, $n = 168$, $P = 0.015$) and 1991 ($r = -0.14$, $n = 335$, $P = 0.013$).

Results of an ANCOVA, grouping by year and specifying both laying date and ambient incubation temperature as covariates, demonstrated highly significant negative relationships between incubation period and both laying date ($F = 67.74$, df = 1 and 1,229, $P < 0.001$, $b = -0.07$) and temperature ($F = 18.65$, df = 1 and 1,229, $P < 0.001$, $b = -0.28$). Thus, ambient temperature during incubation, as well as laying date, influenced duration of incubation. However, incubation periods decreased seasonally in all five years despite inconsistent seasonal changes in ambient temperatures among years. There also was highly significant among-year variability in incubation periods ($F = 14.19$, df = 4 and 1,230, $P < 0.001$); annual means, adjusted for the effects of laying date and ambient incubation temperature, ranged from 32.8 days in 1988 to 34.3 days in 1990.

Increased wind velocity should cause more rapid chilling of eggs exposed even partially; therefore, incubation periods should be positively correlated with wind velocity. However, incubation periods were negatively correlated with wind velocity for 1987–1990, significantly so in 1989 ($r = -0.217$, $P = 0.002$) and 1990 ($r = -0.260$, $P < 0.001$), and positively correlated with wind velocity only in 1991 ($r = 0.298$, $P < 0.001$). These highly variable relationships are probably the result of inconsistent seasonal patterns of wind velocity among years; wind velocities were positively correlated with calendar date for 1987–1990, significantly so for 1988–1990 ($P = 0.006$, 0.043, and < 0.001, respectively), but negatively correlated with date in 1991 ($P < 0.10$). Thus, seasonal decreases in incubation periods occurred despite seasonal increases in wind velocity in 1987–1990. Wind-chill equivalent temperature accounted for less of the variability in incubation periods than temperature alone.

Egg viability and laying date.—Field crews at Bluff coded hatching failures as "losses," when eggs disappeared before they could have hatched, or as "duds," eggs failing to hatch despite apparent continuous incubation by the parents for 39 or more days. Because of the seasonal changes in the incubation period reported above and seasonal declines in egg volume reported for murres elsewhere (e.g. Birkhead and Nettleship 1982), I tested for seasonal changes in viability of eggs by conducting a two-factor ANOVA, grouping by year and hatching status (hatched vs. dud, eliminating eggs lost during incubation). Overall, dud eggs accounted for relatively few reproductive failures, and neither hatching success nor fledging success demonstrated seasonal declines (Murphy and Schauer 1994). In any year, sample sizes of dud eggs were small, ranging from 3 in 1991 to 20 in 1989, but the results of the ANOVA showed a significant difference in laying dates of eggs that hatched and dud eggs ($F = 8.50$, df = 1 and 1,124, $P = 0.004$); the hatching status by year interaction was not significant ($F = 2.11$, df = 4 and 1,124, $P = 0.077$). In 1989, the mean laying dates of dud eggs and eggs that hatched were similar (Tukey test, $P > 0.10$), but in all other years mean laying dates of dud eggs were significantly later than those of eggs that hatched (Tukey test, $P < 0.05$), particularly in 1990, when the mean laying date of dud eggs was 6.4 days later than that of eggs that hatched. These results suggest that viability of eggs laid later in the season was lower.

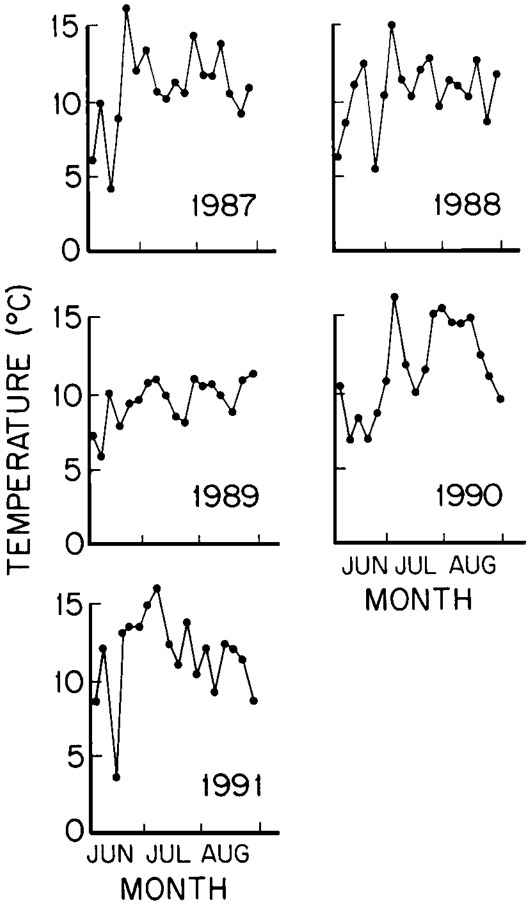

Fig. 2. Daily mean temperatures (five-day running means) at Nome, Alaska, for June through August, 1987–1991.

Duration of chick period.—Duration of the chick period averaged 22.0 ± 3.0 ($n = 1{,}090$) days (Murphy and Schauer 1994). In each year, the duration of the chick period was negatively correlated with hatching date (i.e. chicks from eggs hatching later in season fledged when younger). Regression coefficients ranged from −0.059 (in 1988) to −0.283 (in 1991); overall, the chick period decreased 1.2 days for each 10-day delay in hatching (Table 1).

Controlling for hatching date, there was no difference in duration of the chick period of first and replacement attempts (ANCOVA, grouping by year and attempt code with hatching date as covariate; attempt code, $P = 0.13$; attempt-by-year interaction, $P = 0.44$). Likewise, comparing chick periods calculated from known and estimated observations, I used an ANCOVA, specifying hatching date as a covariate and year and observation codes as grouping variables. There was no effect of observation code on the chick period ($P = 0.51$), and no interaction between observation code and year ($P = 0.14$). Thus, I pooled both attempt codes and observation codes in all other analyses of chick periods. Both year and hatching-date effects on the chick period were highly significant in an ANCOVA in which I specified hatching date as a covariate and grouped by year (year, $F = 36.73$, df = 4 and 1,084, $P < 0.001$; hatching date, $b = -0.17$, $P < 0.001$). The annual mean chick periods, adjusting for the effect of hatching date, ranged from 20.9 days in 1990 to 23.9 days in 1989.

Duration of successful attempts.—Fledging dates ranged between early August and mid-September in the five years of study (Murphy and Schauer 1994). Duration of successful attempts (hereafter "attempt duration") between egg laying and fledging averaged 55.6 ± 3.3 days (n = 1,202). Attempt duration was negatively related to laying date in all five years, with regression coefficients ranging from -0.081 (in 1988) to -0.345 (in 1991). Overall, for each 10-day delay in laying, attempt duration decreased 1.4 days (Table 1). Results of an ANCOVA, grouping by year and specifying laying date as a covariate, indicated that attempt duration varied significantly among years ($F = 23.94$, df = 4 and 1,196, $P < 0.001$) and was negatively related to laying date ($b = -0.21$, $P < 0.001$). Mean attempt duration, adjusting for the effect of laying date, ranged between 54.6 days in 1991 and 57.8 days in 1989.

DISCUSSION

Egg formation.—My study provides no evidence of seasonal declines in the duration of egg formation, but my analyses may not provide critical tests of the null hypothesis of no seasonal change in the duration of egg formation of Common Murres. On Fair Isle, Shetland, there were significantly fewer daily growth rings in the yolks of six replacement eggs ($\bar{x}$ = 9.3) than in the yolks of 20 first eggs ($\bar{x}$ = 11.5) of Common Murres (Birkhead and del Nevo 1987); both yolk mass and egg volume indices were less for replacement eggs than for first eggs. The mean interval between loss and replacement was 12.7 days, suggesting that the period of yolk formation was shortened 1.7 days ([10 × 2.2]/12.7) for a 10-day delay in laying.

Birkhead and del Nevo (1987) estimated that the lag between ovulation and laying averages 3.4 days in the Common Murre. No studies have quantified seasonal patterns in this lag, but it presumably does not vary seasonally (e.g. Grau 1984).

Incubation period.—At Bluff, murres breeding later in the season had shorter incubation periods in all five study years. Although the magnitude of this relationship was influenced by weather, unfavorable conditions for efficient incubation of later-laid eggs (cool temperatures or high winds) were insufficient to override this relationship. Overall, the reduction averaged about 0.5 days for each 10-day delay in laying. Within years, the laying period averaged 41 days; thus, the incubation periods of the latest breeding pairs averaged about two days less than those of the earliest breeding pairs.

How more rapid incubation is achieved in eggs laid later in the season at Bluff is unknown. Elsewhere, egg volumes and fresh egg masses of murres decline seasonally; late-season hatchlings are similar in size to those hatching earlier but have smaller yolk reserves (e.g. Birkhead and Nettleship 1982, 1984, Birkhead and Nettleship 1987a). Thus, embryos of eggs laid later in the season develop more rapidly, achieving equivalent size during a shorter incubation period than those laid early in the season. Similarly, the third egg of three-egg clutches of Herring Gulls (*Larus argentatus*) is smaller than the first two eggs, having less albumen but comparable yolk content (Parsons 1975); it develops more rapidly (Parsons 1972) and results in a hatchling of similar size, but with less yolk reserve than those hatching from the first two eggs (Parsons 1970). It is unclear how accelerated development is achieved by embryos in smaller eggs, particularly in three-egg clutches of the Herring Gull in which all three eggs are subjected to the same microenvironment during incubation. However, it appears that parents incubate smaller eggs more effectively, resulting in higher energy expenditure and accelerated development of the embryo. Thus, it is likely that late-breeding Common Murres at Bluff achieve shorter incubation periods by laying smaller eggs than early breeders.

Why do later-laying murres at Bluff have shorter incubation periods? Birkhead and Nettleship (1982) hypothesized that murres can more effectively provision chicks than eggs (the maximum daily growth rate of the chick is about double that of the yolk); thus, as time becomes a constraint later in the breeding season, murres should convert eggs to hatchlings as rapidly as possible. This can be achieved through a reduction in the duration of either egg formation, as emphasized by Birkhead and Nettleship (1982), or the incubation period, as occurs at Bluff, or both.

Why do not pairs that breed earlier in the season also have shorter incubation periods? At Bluff, egg viability decreased seasonally, suggesting a potential cost associated with a shorter incubation period. Elsewhere, as noted above, hatchlings from eggs laid earlier in the season hatch with greater yolk reserves than those hatching later in the season. Larger reserves at hatching may be beneficial if parents have difficulty provisioning the chick soon after hatching (e.g. during stormy conditions) and in other ways as well (e.g. Ricklefs 1992). Thus, early-season hatchlings are likely better buffered against adverse environmental conditions than late-season hatchlings, even though adverse conditions may be more prevalent later in the season.

Chick period.—At Bluff, murres breeding later in the season had shorter chick periods in all five study years, as reported for murres elsewhere (e.g. Gaston and Nettleship 1981, Birkhead and Nettleship 1982, Birkhead and Nettleship 1987a, Wanless and Harris 1988, Boekelheide et al. 1990, Hatchwell 1991, but also see Hedgren and Linnman 1979). Only Wanless and Harris (1988) reported regression coefficients; values ranged between −0.039 and −0.176, averaging −0.106, in their four-year study on the Isle of May. These values range somewhat, but not markedly, lower than those at Bluff (Table 1).

Why do chicks from eggs hatching later in the season typically fledge at younger ages? Wanless and Harris (1988) proposed that there is a progressive seasonal change in the costs and benefits of staying at the colony or going to sea, favoring younger ages of departure for later-hatching chicks. Potential increased costs of remaining at the colony that they discussed include seasonal decreases in food availability near the colony, higher predation rates at the colony on later-hatched chicks, and reduced time remaining for the parents to complete a full prebasic molt in the autumn. Ydenberg (1989) proposed that developing chicks face a trade-off between remaining at the colony, where, he suggested, they are less susceptible to predation, or going to sea, where they can achieve higher growth rates. However no data on the relative mortality rates of chicks on the colony and chicks at sea are available. Once at sea, chicks are relatively immune from aerial and terrestrial predators (e.g. Harris and Wanless 1988), and, indeed, predation rates may well be lower for chicks at sea. It is likely that the difference between slow growth at the colony, which may be 100 km or more from foraging areas (e.g. Swartz 1967), and more rapid growth, once the chick has accompanied its father to the foraging area, is pronounced, favoring a quicker transition to the sea when the time remaining for not only completion of growth and development of the chick, but also a complete prebasic molt of the parents, becomes more of a constraint.

Why do not chicks from eggs hatching earlier in the season fledge at younger ages? A chick fledging at a younger age may not have completed developmental processes that are critical to its ability to successfully jump from the cliffs and reach the sea, where it must rejoin and then accompany its father from the colony to foraging areas. Even though fledglings have limited gliding ability, sufficient development to glide, rather than plummet, may be important in reducing the likelihood of a debilitating or fatal injury on the cliff face or on the rocks below. Sufficient gliding ability to reach the sea directly also greatly reduces the probability of predation by gulls (Harris and Wanless 1988, Raygorodetsky 1993). Other aspects of development also may be important for successful fledging; for example, Harris and Wanless (1988) observed two downy fledglings that became waterlogged and died once reaching the water.

Attempt duration.—At Bluff, murres shortened their combined incubation and chick periods by about 1.4 days for each 10-day delay in laying (Table 1). Thus, the breeding attempts from egg laying to fledging of latest-breeding pairs were about six days less than those of the first-breeding pairs. This was achieved by shortening not only of the chick period, as widely reported (e.g. Birkhead and Nettleship 1982, Hatchwell 1988, Wanless and Harris 1988, Boekelheide et al. 1990), but also of the incubation period. If murres at Bluff also shorten the period of yolk formation similarly to those on Fair Isle (see Birkhead and del Nevo 1987), the duration of the attempt from the onset of egg formation to fledging could decrease up to 3.1 days for a 10-day delay in laying or by about 12 days between the very first and last breeders.

For a 10-day lag in laying of Common Murres at Bluff, the percentage reduction in duration of each stage of reproduction was lower for incubation, averaging 1.4% (decrease = 0.5 days, duration $\bar{x}$ = 33.6 days), than for the chick period, averaging 5.2% (decrease = 1.2 days, duration $\bar{x}$ = 22.0 days); the reduction could be highest for yolk production (17.3%), if Birkhead and del Nevo's (1987) results are applicable to murres at Bluff. Although the percentage decrease in the duration of the incubation period was relatively small, the incubation period is likely the least potentially variable phase of reproduction because eggs are incubated constantly (except during brief parental changeovers), and embryonic developmental patterns and rates are probably highly canalized.

Annual and geographic variability.—Both the incubation and chick periods varied significantly among years at Bluff, and these differences cannot be explained by annual differences in breeding chronology or weather conditions. Such annual variability is evident elsewhere in both the period of egg formation and the chick period. For example, Hatchwell and Pellatt (1990) documented laying dates and examined daily growth rings in yolks of eggs of Common Murres collected on Skomer Island. The mean laying dates were 16 May in 1986 and 11 May in 1987. Based on intraseasonal declines in numbers of growth rings (Birkhead and del Nevo 1987), higher numbers of growth rings would be expected in 1987, when laying was earlier. However, the mean numbers of growth rings were 16.1 in 1986 and 14.1 in 1987, probably reflecting annual differences in food availability during egg formation (Hatchwell and Pellatt 1990). Thus, annual variability in duration of one or more reproductive phases is not simply a consequence of annual differences in timing of reproductive events.

Geographic variability in seasonal changes of the incubation and chick periods is also evident. For example, neither Hatchwell (1988) nor Wanless and Harris (1988) found seasonal declines in the incubation period of murres at two Temperate Zone colonies in the eastern Atlantic, but there were significant declines in each year of study at Bluff, a subarctic colony in the eastern Pacific. Similarly, the duration of the chick period typically declines seasonally (e.g. Birkhead and Nettleship 1982, Hatchwell 1988, Boekelheide et al. 1990), but Hedgren and Linnman (1979) showed that the chick period does not change seasonally on Stora Karlsö, Norway.

There appears to be both annual and geographic variability in the effect of fledging date on juvenile survival. Hedgren (1981) found no relationship at Stora Karlsö, and Harris et al. (1992) documented significant relationships, with late-fledging chicks having lower post-fledging survival, in only two of six years of study at the Isle of May. Such variability suggests that the selection pressures on the duration of each reproductive phase of murres vary both annually and geographically.

Adaptation or environmental constraint?—Perhaps females breeding later in the season at Bluff produce smaller eggs because they are in poorer condition or environmental conditions are deteriorating, and the shorter incubation periods of later-laid eggs are simply a non-adaptive consequence of inability of later-laying females to lay eggs as large as those of females laying earlier. At many murre colonies, chick survival decreases seasonally. Hatchwell (1988) provided evidence that differences in the quality of pairs, with better-quality pairs breeding earlier, could account for the seasonal declines in chick survival on Skomer Island. At other colonies where seasonal changes in reproductive success have been studied, late-season declines in environmental conditions have been inferred from declining reproductive performance (e.g. Birkhead and Nettleship 1982, 1987b, Boekelheide et al. 1990). Reproductive success, growth rates of chicks, and fledging masses declined seasonally on Stora Karlsö, even for early breeding murres for which breeding was experimentally delayed by removal of their first eggs (Hedgren 1979, Hedgren and Linnman 1979, Hedgren 1980). At Bluff, however, there has been no evidence of seasonal deterioration in conditions for breeding; from 1987 through 1991 late-season attempts were as successful as earlier attempts and first and replacement attempts showed similar hatching and fledging success (Murphy and Schauer 1994). Thus, even the latest-breeding pairs began incubating their eggs long before environmental conditions could be deteriorating at Bluff.

Birkhead and del Nevo (1987) provided compelling evidence that the smaller size of replacement eggs is an adaptation to shorten the period of egg formation rather than a reflection of deteriorating female condition or environmental quality. They documented that daily growth increments of the yolks of replacement eggs were larger than those of first eggs; females terminated yolk formation earlier in replacement eggs, thus accounting for smaller yolks and smaller mass of replacement eggs.

Shortened incubation and chick periods of Common Murres breeding later in the season at Bluff probably are viewed most appropriately as time-saving adaptations to produce fledged chicks as rapidly as possible. Chicks fledge at about 20% of adult size (e.g. Ydenberg 1989). Potential developmental rates are successively more rapid for chicks than eggs (Gaston and Nettleship 1981, Birkhead and Nettleship 1982), and for fledged chicks at sea than chicks at their nest sites in the colony (Ydenberg 1989). Shortening the duration of those periods of development in which developmental rates are most constrained (i.e. the incubation period and the chick period at the colony) provides a quicker transition to the at-sea chick stage, where growth and development can proceed relatively rapidly and thus be completed before the local and regional environment becomes inhospitable in the fall. Sea ice forms abruptly throughout Norton Sound and the northern Bering Sea in the fall, making the region near Bluff uninhabitable for murres. For example, from 1987 through 1991 there was little or no sea ice in Norton Sound in early November, but there was complete ice coverage of the seas within 150 km (in 1987) to 250 km (in 1988) of Bluff by the end of November (Naval Polar Oceanography Center, Suitland, Maryland, unpubl. data). The quicker the egg hatches and the chick makes its transition to the sea, the sooner both the chick will complete its considerable remaining growth and development and the parents will molt, allowing them to depart the region before sea ice forms. A corollary of this hypothesis is that seasonal declines in incubation and chick periods should be more pronounced for murres breeding at higher latitudes where sea ice forms sooner in the fall or at colonies where environmental conditions near the colony deteriorate earlier than at Bluff.

Response to selection to shorten the period between the onset of egg formation and hatching has probably occurred primarily by reducing the period of yolk formation; this phase of reproduction appears much more labile than the incubation period. Shortening of both phases would be achieved by production of a smaller egg; thus, an adaptation to produce a hatchling more quickly could be achieved primarily by reducing the number of days of yolk formation but would be enhanced if the resultant egg is smaller and, therefore, can be incubated to hatching more quickly.

Shortening of the reproductive period may be a general response of birds to seasonal time constraints in seasonal environments. For example, reduced clutch sizes of birds breeding at high latitudes (e.g. Järvinen 1986) may represent adaptations to shorten the period between onset of breeding and completion of development of young (also see Hussell 1972). Typically, breeding adaptations have been interpreted with too little attention to seasonally varying time constraints.

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