The Condor 97:1048–1052

REPEATABILITY IN LAYING DATE AND ITS RELATIONSHIP TO INDIVIDUAL QUALITY FOR COMMON MURRES[1]

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Abstract. We studied repeatability and annual variation in laying date and productivity of 37 color-banded female Common Murres (*Uria aalge*) on Southeast Farallon Island, California from 1986 through 1993 to investigate demographic aspects of individual quality. We substracted the mean population lay date from the lay date of individual females to produce a standardized anomaly statistic. Thirteen birds laid consistently before the population mean, 14 birds were intermediate (showed lay dates which varied earlier and later than annual population means over the study period), and 10 birds consistently laid after the population mean. Repeatability was estimated as 0.204 when excluding the El Niño year of 1992. Chick survival was significantly lower for females which were consistententy late relative to other members of the population, and for females that laid late within each season. Repeatability, as a measurement of between-individual variation in life history traits, is a useful index to individual quality.

Key words: Coloniality; Common Murre; ENSO; individual quality; laying date; repeatability; phenotypic variation; Uria aalge.

INTRODUCTION

The influence of timing of breeding and reproductive synchrony in colonially breeding seabirds has been of interest for many years (Darling 1938, Lack 1968). Reproductive success typically decreases for individuals which initiate nesting after the median population lay date (Perrins 1970, Perrins et al. 1973, van Nordwijk et al. 1981, Cooke et al. 1984, Newton and Marquiss 1984, Daan et al. 1988, Price et al. 1988, Sydeman et al. 1991, Spear and Nur 1994). Explanations include a seasonal decline in the quality or availability of food supplies (Hedgren and Linneman 1979, Gaston and Nettleship 1981, Ainley and Boekelheide 1990, Sydeman et al. 1991), and the possibly that late-laying birds are young, inexperienced or of inferior "quality" (Hedgren 1980, Coulson and Porter 1985, Coulson and Thomas 1985, Sydeman et al. 1991, Spear and Nur 1994). Variation between individuals, however, is difficult to document without extensive long-term studies, and between-individual effects on demography and fitness have been rarely assessed (but see Coulson and Thomas 1985, Clutton-Brock et al. 1989, Sydeman and Nur 1994). Very few studies have examined seasonal declines in productivity in relation to between-individual variation in laying date and environmental changes.

Common Murres (*Uria aalge*) nest in large, dense colonies (Wittenburger and Hunt 1985, Siegel-Causey and Kharitonov 1990), and exhibit considerable synchrony in egg-laying which has been related to productivity (Birkhead 1977, Gaston and Nettleship 1981, Wanless and Harris 1988, Hatchwell 1991). To investigate aspects of individual quality and coloniality in Common Murres we examine (1) consistency in the timing of breeding among individual females and (2) the effect of consistency and relative laying date on annual offspring productivity. We use repeatability (van Nordwijk et al. 1981, Boag and van Nordwijk 1987, Lessels and Boag 1987) as a simple index to assess and compare between individual consistency in laying date.

METHODS

We conducted this study on 37 color-banded females nesting on Shubrick Point, Southeast Farallon Island (SEFI; 37° 42′N, 123° 00′W), California, from 1986 through 1993 (see Ainley and Boekelheide 1990, Sydeman 1993, for details). The Shubrick Point colony is one of the largest colonies of breeding murres on SEFI, and in 1994 numbered about 3,000 breeding pairs (unpubl. data). Color-banded birds are interspersed throughout a group of about 1,500 pairs on the upper slopes of Shubrick Point. Additionally, a study plot has been monitored on upper Shubrick Point since 1973 (Boekelheide et al. 1990). The number of pairs breeding in the plot varied

[1] Received 14 April 1995. Accepted 13 June 1995.

annually during the course of this study from approximately 90 during the 1992 El Niño/ Southern Oscillation (ENSO) to approximately 140 in 1994 (Sydeman 1993, unpubl. data). Five color-banded females nested within the study plot.

We determined laying dates for pairs with color-marked females and pairs nesting in the study plot daily. For each female in each year, we calculated the number of days between its laying date and the overall average laying date for the population based on data from the study plot (Table 1). We then placed females into three groups; those laying consistently early, those consistently late, and those showing an inconsistent or intermediate pattern of lay dates relative to average values from the study plot, and related these groupings to productivity. We also evaluated the effects of "relative" and "absolute" laying date to productivity without grouping females. "Relative" laying date refers to the number of days difference between each individual female and the population average; this variable provides information concerning the adaptive value of reproductive synchrony. Positive anomalies in laying date reflect late laying relative to the population, whereas negative anomalies reflect early laying. "Absolute" laying date refers to the actual date of laying irrespective of other members of the population; this variable provides information on seasonal environmental changes presumably reflective of food availability.

We included females with 2–7 years of data in the analysis, generating an anomaly statistic for 129 "bird-years" from 37 individuals. There were a few cases when exact laying dates were unknown. For these cases, we estimated the individual lay date by back-counting 33 days from the exact date when the chick hatched, if this date was known. Between 1973 and 1992, the incubation period for first-clutch eggs was 32.58 days ± 1.62 SD (unpubl. data). We used logistic regression to investigate the effects of year, consistency in laying date, and relative and absolute laying date on fledging success. We selected logistic regression because reproductive success for Common Murres, which have a clutch of only one egg, is binomially distributed. We report the likelihood ratio statistic (LRS) generated by logisitic regression analysis in the text; the LRS statistic was used to test the hypothesis that regression coefficients differ from zero. Given anomalous food conditions during ENSO 1992, we examined relationships with and without this year. Statistical test were performed using STATA v. 3.1 (Stata Corporation 1993). Significance was assumed when $P < 0.05$.

TABLE 1. Annual variation in (a) laying date[1] and (b) reproductive success[2] of Common Murres.

Year	(a) Mean ± SE	(a) (*n*)	(b) Mean ± SE	(b) (*n*)
1986	135.65 ± 0.54	(111)	0.833 ± 0.152	(6)
1987	130.18 ± 0.47	(114)	0.867 ± 0.088	(15)
1988	119.87 ± 0.57	(119)	0.933 ± 0.065	(15)
1989	123.02 ± 0.83	(126)	0.933 ± 0.065	(15)
1990	123.19 ± 0.68	(135)	0.842 ± 0.084	(19)
1991	126.66 ± 0.41	(125)	0.956 ± 0.043	(23)
1992	149.34 ± 0.98	(93)	0.125 ± 0.083	(16)
1993	130.54 ± 0.79	(112)	0.894 ± 0.071	(19)

[1] Laying date is expressed as the number of days past 1 January each year (e.g., 130 = 10 May). Data are based on observations of pairs within the Shubrick study plot only.
[2] Reproductive success reflects annual values based on color-banded females only (n = 128).

RESULTS

CONSISTENCY IN LAYING DATE

Laying date varied significantly among years (Table 1; Two-way analyses of variance (ANOVA) $F_{7,126} = 59.61$, $P < 0.001$) and individuals ($F_{36,126} = 3.04$, $P < 0.001$); 51% of the varation in lay dates could be attributed to the between-individual effect (i.e., $r^2 = 0.51$). Quantitatively, 13 females laid consistently early (35.1%), 10 laid consistently late (27.0%), and 14 laid eggs on either side of the population average during the study period (37.8%). Using the methods of Lessels and Boag (1987), repeatability was estimated as 0.0018 (Table 2). However, this low value was mainly due to a delay in laying during ENSO 1992 (Table 1). Excluding 1992, we estimated repeatability in laying date as $r = 0.204$.

CONSISTENCY IN LAYING DATE AND REPRODUCTIVE SUCCESS.

Poor food supply during ENSO 1992 affected the relationship between consistency and breeding success. Reproductive success varied significantly by year (Table 1; LRS = 44.89, df = 7, $P < 0.001$), but not when 1992 was excluded from the analysis (LRS = 2.47, df = 6, $P = 0.872$). Due to the poor food conditions in 1992, most murres lost their eggs or chicks to Western Gull (*Larus occidentalis*) predation (Boekelheide et al. 1990, Spear 1993), irrespective of when they laid.

TABLE 2. Analysis of variance of laying date in female Common Murres (a) with and (b) without ENSO 1992.

	Source of variation	df	Sum of squares	Mean square	*F*-ratio	*P*-value
(a)	Between	36	5,796.45	161.01	1.00	0.4811
	Within	92	14,785.80	160.72		
	Total	128	20,582.25			
(b)	Between	35	2,651.61	75.76	1.81	0.0165
	Within	76	3,189.50	41.97		
	Total	111	5,841.11			

In relation to consistency in laying date, reproductive success of females that laid consistently early was greater than that of inconsistent females, or females that laid consistently after the population average (Table 3; LRS = 7.10, df = 2, P = 0.029, controlling for year). However, when excluding 1992, there was no relationship between consistency in laying date and reproductive success (LRS = 4.24, df = 2, P = 0.120).

EFFECTS OF RELATIVE AND ABSOLUTE LAYING DATE ON PRODUCTIVITY

Controlling for year, relative laying date was significantly related to reproductive success (LRS = 11.18, df = 1, P < 0.001, coefficient b = −0.184 ± 0.063 SE), showing no departure from linearity (LRS = 0.39, df = 1, P = 0.532). Laying earlier than the population mean was associated with higher productivity. However, this result could be due to the absolute effect of laying date, as reproductive success also declined with later laying date (controlling for year, LRS = 11.30, df = 1, P < 0.001, b = −0.183 ± 0.063). There was no departure from linearity between the absolute date of laying and reproductive success (LRS = 1.11, df = 1, P = 0.292).

DISCUSSION

This study has demonstrated significant differences among individual females in timing of breeding and a high degree of repeatability in laying date when excluding data from ENSO 1992. In addition to environmental effects on laying date, exemplified by likely food shortage during ENSO 1992, for some individuals there was a tendancy to lay progressively earlier throughout the study period, which may be related to age (cf. Saether 1990, Gaston et al. 1994).

Nevertheless, some individuals consistently initiated laying early, others were consistently late, and a third group was inconsistent relative to the population mean. Repeatability for Common Murres in Scotland was estimated at r = 0.488 (Wanless and Harris 1988), a value higher than our calculation of r = 0.204. Unfortunately, calculation of standard errors of repeatability is difficult and not routinely published, so we cannot statistically compare values of repeatability. Lower repeatability for murres in the California ecosystem and relatively large changes in our estimates of repeatability with and without data from 1992 may be related to the unpredictability of food resources in this environment (Ainley et al. 1995). Korpimaki (1990) suggested that the relatively low repeatability in laying date of Tengmalm's Owl (*Aegolius funereus*) in Finland reflected an adaptive response to fluctuating prey resources. This may also be true for Common Murres at SEFI, although the overall delay in laying during ENSO events in California should

TABLE 3. Reproductive success of female Common Murres in relation to consistency of laying date (a) with and (b) without ENSO 1992.

Timing class	(a) Mean ± SE (n)	(b) Mean ± SE (n)
Early	0.867 ± 0.051 (45)	0.974 ± 0.026 (38)
Intermediate	0.777 ± 0.057 (54)	0.875 ± 0.048 (48)
Late	0.759 ± 0.079 (29)	0.846 ± 0.071 (26)
Total	0.805 ± 0.035 (128)	0.902 ± 0.028 (112)

be viewed as a constraint imposed by poor food availability. These results also demonstrate that repeatability estimates change within species under differing environmental conditions. Additional studies on the same species in varying environments is needed to explore this idea more thoroughly.

We have provided evidence for variation between individuals in laying date, and documented how such variation may be related to fitness, via changes in annual reproductive success. It has been suggested for a variety of seabirds (e.g., kittiwakes *Rissa tridactyla,* Coulson and Porter 1985; Western Gulls *Larus occidentalis,* Sydeman et al. 1991, Spear and Nur 1994), that timing of breeding reflects individual quality. However, few studies have examined repeatability in laying date in relation to phenotypic variation in fitness. Our study supports the idea that timing of breeding reflects between-individual differences in fitness and also suggests that repeatability is a useful index to individual quality.

At SEFI, absolute date of laying, indicative of seasonal variation in food supply (Ainley and Boekelheide 1990), predation (Spear 1993), and perhaps genotypic variation between individuals, is an important component in determining breeding success. Notably, relative laying date was no better in explaining variation in productivity than absolute laying date, implying that synchrony was not important in determining reproductive success of Common Murres at SEFI. During severe ENSO conditions, however, both within-season and phenotypic components of breeding success have negligible effects because most pairs are unsuccessful regardless of when they initiate reproduction (Ainley and Boekelheide 1990, Spear 1993, unpubl. data). Further investigation of environmental and phenotypic determinants of demography will aid in understanding trade-offs and life history evolution in birds (Nur 1987, Stearns 1992).

ACKNOWLEDGMENTS

We thank the Farallon Patrol of the Point Reyes Bird Observatory for transportation to and from Southeast Farallon Island for the past 25 years. U.S. Fish and Wildlife Service–San Francico Bay National Wildlife Refuge manages the Farallon Islands National Wildlife Refuge, and provided financial support for many aspects of this project. Farallon biologists H. Carter, S. Emslie, E. McLaren, and P. Pyle deserve special recognition for supervising Farallon operations during the project as do many research assistants who collected data over the years. Support for data analysis and writing was provided by the California Department of Fish and Game–Office of Oil Spill Prevention and Response under contract FG-3483-OS. We thank D. Ainley, T. Gaston, N. Nur, and L. Spear for providing many helpful comments on earlier drafts of this manuscript. This is PRBO contribution no. 415.

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