

INDIVIDUAL VARIATION IN BEHAVIOR AND BREEDING SUCCESS OF NORTHERN FULMARS

SCOTT A. HATCH

Museum of Vertebrate Zoology, University of California, Berkeley, California 94720 USA, and Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 USA¹

ABSTRACT.—In a sample of breeding Northern Fulmars (*Fulmarus glacialis*) observed in 4–5 years, up to 43% of the variability in 13 attributes of breeding behavior was consistent among individuals or pairs. Sample means for most attributes were correlated in a predictable way with annual levels of breeding success. Except for laying dates, there was little evidence that individual differences in these attributes contributed to variation in breeding success. A test of breeding experience as a contributing factor revealed an interaction between individual and annual components of variation. During years when the whole population did relatively poorly, pairs with no previous breeding experience were affected disproportionately. Late-nesting fulmars were more successful than early layers, possibly because delayed breeding ensured that food availability was adequate for successful incubation. Received 7 November 1989, accepted 15 May 1990.

If the same sample of breeding birds is monitored in several years, the observed variance in breeding success has annual and individual components. Annual variation arises from variability in environmental factors such as food supply, predation, disease, weather, or disturbance. Any added component of individual variation arises from differences in the quality of the habitats occupied by individuals (Nettle-ship 1972, Birkhead 1977, Hudson 1982), or from differences in the quality of the individuals themselves (Coulson 1968, Potts 1969, Reilly and Cullen 1981). Interaction between the two components of variation is expected because annual changes in the environment need not affect all individuals equally.

In a 6-yr study of breeding Northern Fulmars (*Fulmarus glacialis*), I found that young were more likely to be raised successfully in some sites than others (Hatch 1988). Fulmars are long-lived and have a strong fidelity to the same mate and nest site between years (Hatch 1987, Ollason and Dunnet 1988). Many of the birds in my sample were individually known from plumage differences, and all direct evidence indicated that few undetected changes of site ownership or pair bonds occurred during the study. I therefore hypothesized that the among-pairs component of variance in breeding success could be explained by individual differences in

breeding biology and behavior. Consequently, I assessed individual variation in laying dates and time allocation as factors that affect breeding success. I also considered the influence of breeding experience under the varying conditions that occurred during the years of study.

METHODS

The study was conducted from 1976 to 1981 on the Semidi Islands, western Gulf of Alaska (56° N, 156° W). The islands and their seabird populations are described elsewhere (Hatch and Hatch 1983). I usually arrived between 29 March and 3 May, 4–8 weeks before the first eggs were laid, and I departed 26 August to 9 September, 1–3 weeks before the first young fledged. In 1978 I was present only from 26 May to 29 June (egg laying) and on 30 August and 8 September to assess chick survival. Behavioral data were also incomplete for 1976; therefore much of the analysis pertains to observations from 1977 and 1979–1981.

By 1977 my sample of active breeding sites totaled ca. 400, and I monitored the same sites every year thereafter. I used a binocular or spotting scope to check sites once daily to record adult attendance and egg or chick survival. Laying dates were thus known to within ± 24 h. A pair of breeding fulmars produces only one egg a season. Chicks ranged from approximately 21 to 45 days old when last observed, but fledging does not occur until a mean age of 53 days (Mougin 1967). Thus, the measure of breeding success I use is the survival of chicks through the mid- to late chick stage.

Fulmars occurred in a wide range of plumage types, although most (85%) were dark phase (see Fisher 1952

¹ Present address.

or Hatch 1985 for a description of the color phases). Approximately half of the sites in my sample contained mixed pairs (i.e. the male and female were of different color phases). I sexed the birds from their position in copulation.

A bird whose mate failed to return in spring often skipped a year before it resumed breeding with a new—usually inexperienced—partner at the same site (Hatch 1987). Therefore I minimized the influence of undetected mortalities and mate changes by including in the analysis only sites that had a continuous record of breeding over 5 or 6 yr. Other recruits to the breeding population paired with similarly inexperienced birds and began to breed after one or more years of site occupation as nonbreeders, whereas experienced pairs rarely failed to lay (Hatch 1987). Thus, when a site changed to breeding status from nonbreeding, there was a high probability that one or both members of the pair had no previous experience. I tested the effect of breeding experience on success by comparing pairs from sites grouped according to whether or not an egg was or was not laid the year before.

I created three variables, all measured in days, to quantify individual attendance patterns during the prelaying period. First, I counted the number of days a bird was recorded as absent from its site during the 40 days immediately preceding its laying date. Second, I determined the longest period of continuous absence for each individual in the last 30 days before laying. Third, I defined a *pre-egg feeding interval* to include the days between departure of a bird on its longest absence (as above) and the start of its last uninterrupted presence at the breeding site before laying. The latter two values were frequently the same, especially in females. They are alternative measures of what is commonly called the "prelaying exodus" (see Macdonald 1977 and Hatch 1990a for details).

Most pairs had a well-synchronized rendezvous at the time of egg laying after an extended prelaying absence. Normally the female returned to find her mate waiting at the site or the male arrived soon afterward. The female often laid and departed within 24 h, leaving the male to take the first long shift of incubation (up to 2 weeks). I quantified behavioral coordination at egg laying by calculating the difference between male and female arrival dates. Male-female synchrony, so defined, ranged from -11 days (among early-arriving males) to +12 days (indicating late-arriving males).

The attributes of incubation behavior I considered included first shift durations for the male and female, mean shift length for the pair through 48 days of incubation, the overall ratio of male to female shares, and the number of days the pair was recorded at the site during incubation.

On the premise that variation in the amount of time spent at sea reflected differences in food availability (between years) or foraging efficiency (between in-

dividuals), I expected all three measures of time allocation in the prelaying period to vary inversely with breeding success, both within and between years (Hatch 1990a). By the same reasoning, I expected attendance by pairs during incubation to be correlated positively with success (Hatch 1990b). I expected synchrony at laying to be inversely related to success, because a late-returning male risked nest desertion and egg loss by the female. Principles of central place foraging (Orians and Pearson 1979) predict shorter incubation shifts in successful pairs and better years. I had no predictions concerning the ratio of male to female shares in incubation or the effect of annual variation in laying dates. However, I expected laying date to be negatively correlated with breeding success within years, as reported for many other species (Burger 1981, Perrins and Birkhead 1983).

I tested the significance of annual variation in behavior using a repeated measures ANOVA, an extension of the paired observations *t*-test (Sokal and Rohlf 1981). Individual differences were modeled as random effects and estimated from the ratio of between- to within-pairs variation in a one-way ANOVA. Both types of analysis were performed on a balanced subset of the data that consisted of all pairs observed in all years.

RESULTS

Annual and individual variation in behavior.—There was significant variation among years in 10 of 13 behavioral attributes examined (Table 1). Because 4 years' data were included in most of the analyses, it is necessary to determine whether the deviations of annual means from their grand means followed the expected patterns (i.e. whether higher annual breeding success was associated with more time spent on land in the prelaying period, shorter incubation shifts, etc.). Pearson correlation coefficients had the predicted sign, with two nonsignificant exceptions involving attendance patterns of the female.

There was significant variation among pairs in 11 of the 13 variables examined. This component ranged from approximately 7% to 43% of the total variance (Table 1).

Time allocation and breeding success.—Repeated measures ANOVA failed to show significant relationships between breeding success and any of the 12 measures of time allocation (Table 1), with the following exceptions. Synchrony of attendance at egg laying was significantly related to hatching success (but not to overall breeding success) in 1980 and 1981 ($F_{1,188} = 11.2$, $P < 0.001$ in 1980; $F_{1,193} = 18.8$, $P < 0.001$ in

TABLE 1. Annual and individual components of variation in breeding behavior of Northern Fulmars.

Variable	Source of variation						Correlation of annual mean and success ^a		Predicted sign?	Among-pairs variance component (%)
	Among years			Among pairs			r	P		
	F ratio	df	P	F ratio	df	P				
Laying date	7.80	3, 165	0.000	3.01	55, 168	0.000	-0.47	0.257	—	33.4
Cumulative prelaying absence, ♂	6.97	3, 162	0.000	4.03	54, 165	0.000	-0.96	0.014	yes	43.1
Pre-egg feeding interval, ♂	2.64	3, 132	0.052	1.38	44, 135	0.081	-0.49	0.249	yes	8.8
Longest prelaying absence, ♂	3.28	3, 162	0.023	3.35	54, 165	0.000	-0.84	0.066	yes	37.0
Cumulative prelaying absence, ♀	11.86	3, 162	0.000	2.45	54, 165	0.000	0.56	0.211	no	26.6
Pre-egg feeding interval, ♀	0.83	3, 162	0.480	1.87	54, 165	0.001	-0.97	0.009	yes	17.8
Longest prelaying absence, ♀	0.57	3, 162	0.636	2.50	54, 165	0.000	-0.88	0.047	yes	27.3
Synchrony at laying, ♂, ♀	17.12	3, 150	0.000	1.38	50, 153	0.069	-0.34	0.326	yes	8.7
First incubation shift, ♀	6.26	4, 372	0.000	1.37	93, 376	0.023	0.15	0.404	no	6.8
First incubation shift, ♂	22.48	4, 276	0.000	2.10	69, 280	0.000	-0.12	0.422	yes	18.0
Mean incubation shift length	8.21	3, 132	0.000	3.32	44, 135	0.000	-0.93	0.008	yes	36.8
Pair present during incubation	2.86	3, 183	0.038	2.61	61, 186	0.000	0.80	0.087	yes	28.6
Incubation ratio, ♂:♀	1.46	3, 129	0.230	3.29	43, 132	0.000	-0.82	0.040	—	36.4

^a Data points for correlations are annual means for all pairs observed plotted against breeding success ($n = 4-5$ yr). A significant correlation is possible in spite of a nonsignificant component of variation among years because tests for annual variation were limited to the sample of pairs observed during all years of study (repeated measures ANOVA).

1981). The sign of both relationships was as predicted (i.e. males that arrived after their mates had laid had a higher risk of egg loss). Duration of the pre-egg feeding interval in males was significantly related to hatching success in 1977, but in the opposite direction from my expectation (i.e. males that spent more time at sea before laying were more successful than males that spent less; $F_{1,172} = 8.2, P < 0.01$).

Effect of laying date.—There is no significant correlation between annual breeding success and mean laying dates (Table 1), but the probability of success within years is related to a pair's position in the laying distribution. Pairs that laid early had lower success than pairs that

laid in the middle or late portions of the distribution, a significant effect in 2 of 6 yr (Table 2). When I combined the data for all years, there was a substantial increase in success in middle layers over early layers (57% vs. 46%), and an additional small increase among late layers (59% success overall).

Considering only pairs that failed, there was a significant tendency for early-breeding pairs to fail early in the breeding cycle (within the first 14 days), whereas those in the middle group tended to fail at a later stage ($\chi^2 = 6.3, df = 2, P < 0.05$). Failure in the late-laying group was distributed about as expected between early and late stages.

TABLE 2. Effect of laying date on breeding success.

Year	Over-all breeding success ^b	Relative laying date ^a									χ^2	P
		Early			Middle			Late				
		n	Suc-cess	Residu-al ^c	n	Suc-cess	Residu-al ^c	n	Suc-cess	Residu-al ^c		
1976	0.143	47	0.085	-2.7	117	0.128	-1.7	25	0.320	4.4	7.89	0.019
1977	0.510	59	0.458	-3.1	254	0.492	-4.6	73	0.616	7.7	4.28	0.118
1978	0.461	78	0.321	-11.0	233	0.502	9.6	86	0.477	1.4	7.87	0.020
1979	0.594	79	0.570	-1.9	249	0.602	2.2	73	0.589	-0.3	0.28	0.872
1980	0.661	109	0.587	-8.0	208	0.697	7.6	72	0.667	0.4	3.87	0.144
1981	0.719	41	0.634	-3.5	290	0.728	2.5	64	0.734	1.0	1.64	0.440
All yr	0.550	413	0.462	-36.1	1,351	0.565	20.2	393	0.590	15.9	16.56	0.000

^a Middle group includes all eggs laid 3 days before to 3 days after the mean laying date within each year; early group includes all eggs laid earlier, late group includes all eggs laid later.

^b Proportion of chicks surviving to the mid- to late-chick stage.

^c Residuals are observed - expected numbers of successful pairs in a 2×3 contingency table.

Effect of breeding experience.—Pairs thought to include at least one member with no breeding experience had consistently lower success than pairs with at least one year of experience, although the difference was significant only in 1978 (Table 3). Only a small sample of newly converted pairs was available each year, and the effect was highly significant when the data from all years were combined.

Phi (Table 3) measures the strength of relationship between two variables in a contingency analysis (Nie et al. 1975). In this instance it measures the association between breeding success in year *i* and nonbreeding in year *i* - 1. Although none of the five phi values calculated is large, there is a significant negative correlation between phi and annual breeding success (Fig. 1). That is, in years when the whole population had a high level of breeding success, the importance to individual pairs of prior experience was diminished.

Breeding experience had a small effect on laying date. Pairs newly converted from nonbreeding to breeding status laid 1.4 days later on average than pairs with known breeding experience ($F_{1,2155} = 20.9, P < 0.001$). A two-way ANOVA indicated a significant interaction between year and experience. That is, the effect of experience on laying date was greater in some years than in others ($F_{4,1958} = 5.1, P < 0.001$). The mean difference between new and experienced pairs ranged from 0.3 day in 1977 to 4.0 days in 1980.

DISCUSSION

It is clear that differences in behavior among years accounted for most of variation I observed, but a sizable component of individual variation was present in some instances. Potentially,

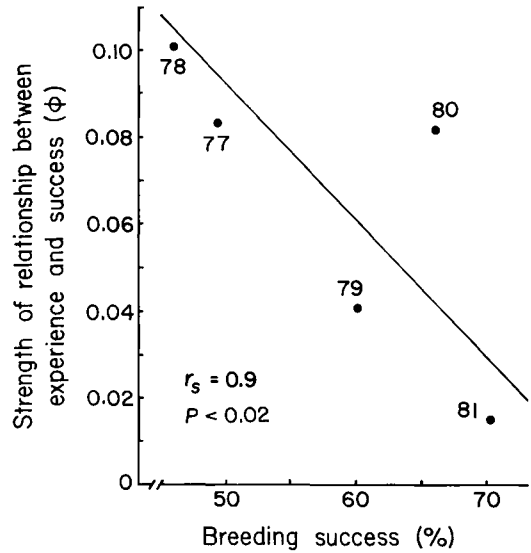


Fig. 1. Relation between overall breeding success of fulmars and the influence of breeding experience on individual success during 5 yr, 1977-1981.

tially, the relationships between breeding success and the two components of variation in behavior could take any of three forms: (1) within-year variation in behavior related to success, but no concordance between annual means of behavior and success, (2) annual variation in success correlated with annual means of behavior, but no relationship within years, or (3) both within-years and between-years variation in behavior predictably related to success. Laying date appeared to be an attribute of the first kind—a pair's position in the rank order of laying dates mattered, but annual differences in mean laying dates were unimportant. I expected most other variables to be in the third category—annual differences in time allocation re-

TABLE 3. Comparison of success rates in sites that were and were not used in the preceding year.

Year <i>i</i>	Overall breeding success	Breeding year <i>i</i> - 1		Nonbreeding year <i>i</i> - 1		Difference	χ^2	<i>P</i>	Phi (ϕ)
		<i>n</i>	Success year <i>i</i>	<i>n</i>	Success year <i>i</i>				
1977	0.497	143	0.517	34	0.412	0.105	1.23	0.268	0.08
1978	0.461	340	0.482	57	0.333	0.149	4.36	0.037	0.10
1979	0.603	356	0.610	37	0.541	0.069	0.68	0.414	0.04
1980	0.661	352	0.673	37	0.541	0.132	2.63	0.105	0.08
1981	0.720	363	0.722	33	0.697	0.025	0.09	0.761	0.02
All yr	0.599	1,554	0.614	198	0.485	0.129	10.57	0.002	0.08

flecting variation in the food supply and the time budgets of individuals reflecting differences in foraging efficiency. In some instances (e.g. male prelaying attendance, pair attendance during incubation, mean shift lengths), I found consistent individual variation and a strong relation between annual means and success, but was unable to show the expected relations between individual scores and breeding success. To be sure, many individual behavior patterns (probably some important ones, such as rates of food provisioning during chick-rearing) were not considered in this study. Also, consistency per se may be important for all breeding activities if it helps to promote behavioral coordination within the pair (Coulson 1972, Coulson and Thomas 1983).

Most of the behavior I examined, such as patterns of incubation and attendance at the nest site before laying, have been rarely studied from the standpoint of individual variation. However, the tendency of females to lay at the same time each year relative to other females has been noted in other species (e.g. Serventy 1963, Nelson 1966, Brooke 1978). The higher breeding success of late-nesting fulmars was surprising in view of the opposite effect reported in most other studies of colonial birds (Burger 1981), including two studies of Northern Fulmars in Scotland (Macdonald 1975, Ollason and Dunnet 1988). Why fulmars in Atlantic colonies and the Semidis should differ in this respect is unclear, but in any case fledging rates could be a misleading indicator of reproductive success (number of young surviving to breed). Some studies reported a negative correlation between post-fledging survival and hatching dates (Perrins 1966, Nisbet and Drury 1972, Parsons et al. 1976), whereas others have not (Hedgren 1981, Harris 1984).

Lack (1954) hypothesized that an optimal time for laying exists such that young are hatched when the food supply is at a seasonal maximum. On that hypothesis, the effect of laying date on breeding success should appear mainly in the chick stage, and both early- and late-hatched young should be disadvantaged relative to those in the middle. Neither condition was true in my study. Late layers were, if anything, more successful than middle layers, and the additional failure among early layers tended to occur early in incubation.

Certain features of the breeding biology of fulmars and other petrels suggest a different

interpretation. When their egg is laid, fulmars abruptly switch from spending an average of 76% of their time foraging to spending only approximately 50% of their time foraging (Hatch 1990a). There can be no corresponding increase in the food supply for every pair, and the early failures found in early breeding pairs may result because foraging conditions are still marginal for maintaining incubation during the first part of the laying period. This would select for later nesting, but lower postfledging survival of late-hatched young would provide stabilizing selection. On this hypothesis, the survival of offspring from fledging to recruitment should be highest for the earliest breeders, but survival from laying to recruitment would be highest for birds near the center of the laying curve. Brooke (1978) expressed a similar view of selection acting on laying dates in the Manx Shearwater (*Puffinus puffinus*).

The roles of age and experience have received considerable attention in studies of seabird breeding biology (Ryder 1980), and the Northern Fulmar is no exception (Ollason and Dunnet 1978, 1988). The effect of experience seemed weak in my study, but my data illustrate one little-studied aspect. There is an interaction between annual and individual components of variation. The effect of breeding experience on success was strongest during years in which the whole population did relatively poorly. A similar interaction was indicated for the effect of breeding experience on laying dates. The study covered only portions of the two seasons with the lowest productivity (1976 and 1978), an unfortunate coincidence because those years might have revealed most clearly the behavioral difference among individuals.

ACKNOWLEDGMENTS

I thank my wife, Martha Hatch, for assistance in the field. Barry Grand and Bay Roberts made constructive comments on an earlier draft of the manuscript. The fieldwork was funded in part by the Outer Continental Shelf Environmental Assessment Program (OCSEAP), administered by the U.S. Bureau of Land Management and National Oceanic and Atmospheric Administration.

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