EVIDENCE FOR COLOR PHASE EFFECTS ON THE BREEDING AND LIFE HISTORY OF NORTHERN FULMARS[1]

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Abstract. About 15% of Northern Fulmars (*Fulmarus glacialis*) breeding on the Semidi Islands in 1979 had light-phase plumage; the remainder were dark. Fulmars of different plumage types mated indiscriminantly, but the lighter member of a mixed pair was more likely to be male than female. Pairs that included at least one light-phase member had lower breeding success than dark/dark pairs in one of six years. Constancy of breeding site use differed between light/dark and dark/dark pairs, suggesting dark birds skipped more breeding attempts or had lower over-winter survival than light birds. The apparent effect of breeding experience (assessed by site fidelity) on success also differed between pair types. The polymorphism on the Semidi Islands may result from light-phase fulmars immigrating from the Bering Sea, but there is also evidence to suggest it is maintained by balancing selection in a closed population.

Key words: Northern Fulmar; Fulmarus glacialis; polymorphism; color phases; breeding biology; life history.

INTRODUCTION

Plumage polymorphism is a well-known, although uncommon, phenomenon in birds. It occurs most frequently in raptors (Falconiformes), herons (Ciconiiformes), and tube-nosed birds (Procellariiformes), but examples are found in at least six other orders (Buckley 1987). Biological correlates of color phase have been studied in a few species (e.g., Murton et al. 1973, O'Donald 1983, Caldwell 1986, Cooke 1987), but in general the ecology and evolutionary significance of plumage polymorphisms remain poorly understood.

Among the Procellariidae (fulmars, prions, petrels, and shearwaters) plumage polymorphism occurs in at least six of 62 species (Harrison 1983). The Northern Fulmar (*Fulmarus glacialis*) is a familiar example in both the North Pacific and North Atlantic oceans. The distribution of fulmar color phases in the northeastern Pacific is fairly simple. Two large colonies in the Bering Sea contain light-plumaged birds almost exclusively (>99%), whereas dark-phase fulmars dominate (85–100%) colonies in the Gulf of Alaska and Aleutian Islands (Fig. 1). In some instances (e.g., Chagulak Island and the Pribi-

lofs), the dissimilarity of color phase composition between adjacent colonies suggests a virtual absence of gene flow.

I studied fulmars on the Semidi Islands, possibly the largest North Pacific colony and the only major one with a substantial mix of color phases. Judging from other accounts (Fisher 1952, Franeker and Wattel 1982), I believe the Semidi population includes examples of the lightest and darkest morphs known from any part of the Northern Fulmar's range. Plumage variation allowed individual recognition in many instances, which was useful for studies of life history and breeding ecology (Hatch 1987a, 1987b, 1990a, 1990b, 1990c). Here I examine some features of the polymorphism itself, including: (1) the occurrence and interbreeding of color phases, (2) evidence for differential breeding success and survival, and (3) the interaction of color phase and prior breeding experience as factors affecting breeding success. These topics are discussed in terms of alternative hypotheses to explain the origin and maintenance of plumage polymorphism at the Semidi Islands.

STUDY AREA AND METHODS

The Semidi Islands (56°N, 156°W) support the largest and most diverse assemblage of breeding seabirds in the Gulf of Alaska (Hatch and Hatch
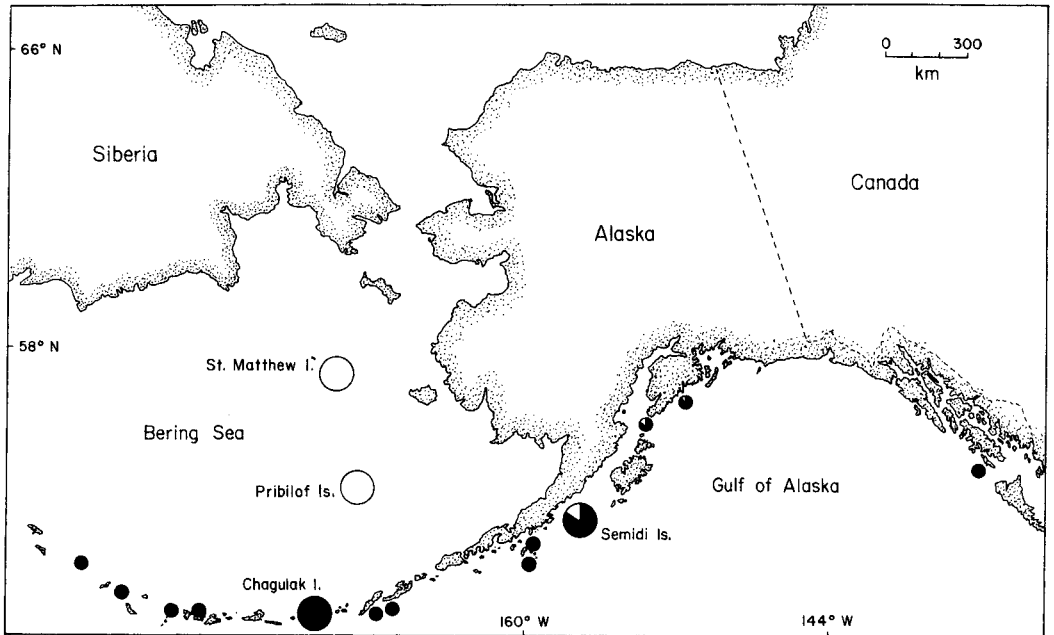
FIGURE 1. Locations and color phase compositions of Northern Fulmar colonies in Alaska. Shaded area of symbols indicates approximate proportion of dark-phase birds in each colony. Together, the populations of the Semidi Islands, Chagulak Island, the Pribilof Islands, and St. Matthew Island constitute more than 99% of the breeding population of fulmars in Alaska (Sowls et al. 1978). Information on the composition of colonies other than the Semidi Islands is from personal observations and unpublished data of the U.S. Fish and Wildlife Service.

1983). About 440,000 fulmars occupied 65 km of coastline on nine islands in 1979.

Although variation was continuous from the lightest to darkest fulmars on the Semidi Islands, birds were assigned to four discrete categories following Fisher (1952): (1) LL (double light)—head, neck, and underparts white; (2) L (light)—breast white; side of head, neck, and rest of underparts white, or lightly shaded or flecked with gray; crown, occiput, and nape light gray grading into gray of mantle; (3) D (dark)—head, neck, and underparts light or medium blue-gray, not as dark as wing tips; breast in most cases uniform with rest of underparts, sometimes lighter but never white; (4) DD (double dark)—almost uniformly dark or very dark blue-gray; wings as dark as their tips.

Inevitably, viewing distance and lighting conditions affect the use of this system. For instance, L birds examined in the hand often proved to have some pigmentation at the tips of breast or head feathers that appeared essentially white from a distance. With experience it is possible for one observer to become consistent in assigning birds

to categories, especially when repeated observations on the same individuals are possible, as was true in my study. Examples of the four major categories are depicted in Figure 2.

Once established, the pair-bond in fulmars usually persists for many years or until the death of one member of the pair; birds also use fixed breeding sites to which they return annually with a high degree of fidelity (MacDonald 1977, Ollason and Dunnet 1978, Hatch 1987a). The combination of plumage variation and strong mate- and site-fidelity allowed me to monitor the behavior and breeding success of many individuals over several years. I recorded descriptions of plumage characteristics for birds in the rarer LL, L, and D categories on audio tape and reviewed this information in cases of doubt about the identity of individuals between years. I made no assumptions about the identity of DD fulmars in the study, except for 10 such individuals that had unusual bill coloration (mostly black instead of yellowish).

For some analyses I classified L birds into three subcategories, denoted L^1, L^2, and L^3, based on
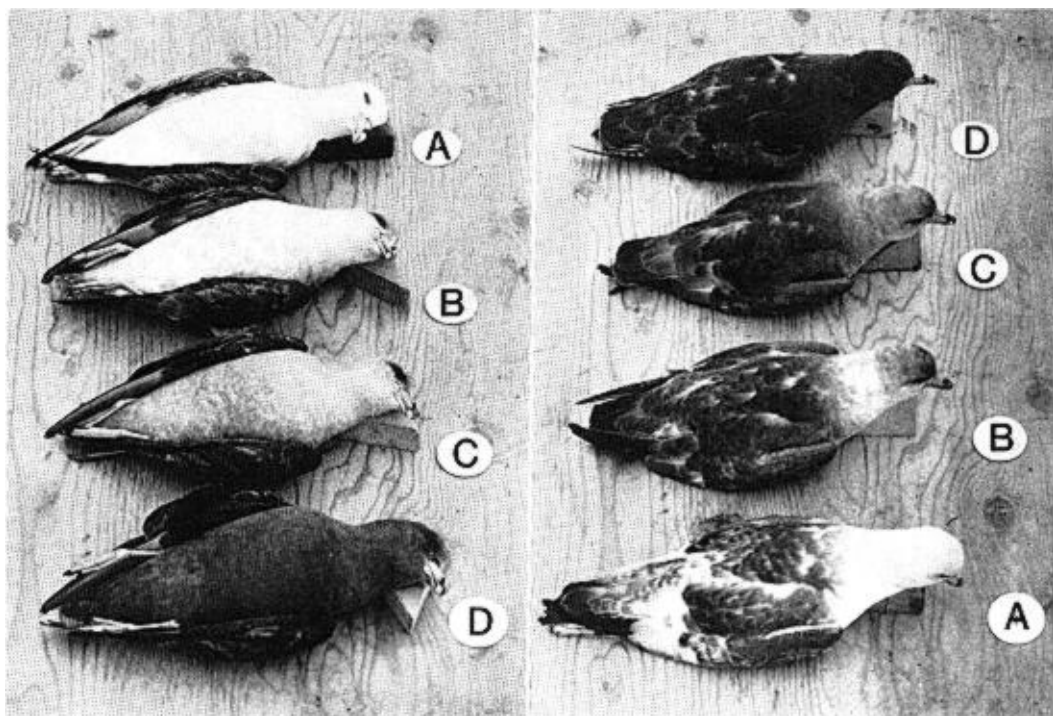
FIGURE 2.   Representative color phases of Northern Fulmars from the Semidi Islands. Specimens A, B, C, and D fall in the LL, L, D, and DD categories, respectively. Note that specimen B may not fit the strict definition of the L category (see text), because the existence of any clear white plumage on the breast, neck, or head is questionable in these photographs. At longer range and under most lighting conditions, however, the breast of specimen B would appear essentially white (L^3, or possibly even L^2).

the relative amount of dark shading on the forehead, crown, nape, belly, and flanks. L^1 birds had the least shading; L^3 birds had the most while still qualifying as L by having at least a small area of white plumage on the breast or side of the head. L^2 approximated the mid-point of the L category.

Unlike the other boundaries between major categories, there was no simple criterion for distinguishing between D and DD fulmars. To reduce confusion, I tended to make the D category a narrow one in practice. Only the lightest birds lacking clear white plumage on the breast were readily distinguished from the typical dark phase (DD) and so were assigned to the D category. Finally, I simplified some analyses by combining the two lighter classes and the two darker classes into "light" and "dark" categories, respectively.

To quantify the distribution of color phases in the Semidi population and to test for possible mating preferences, I classified 4,642 fulmars (2,321 pairs) at breeding sites on 12–13 May 1979.

I sexed a smaller sample by observing copulation in 224 mixed pairs.

Breeding biology was studied in six years (1976–1981) by observing daily the status of 540–550 sites (292 sites in 1976). The locations of sites were recorded on photographs to ensure continuity of the sample between years. Observations were made from 30–100 m using binoculars or a spotting scope. About half the observed sites contained pairs in which one or both birds were non-DD (LL, L, or D), the rest were used by DD/DD pairs. Sites containing light and dark-phase fulmars were dispersed among 17 different study plots. Most sites were selected in the first two years of study and reused in all later years. I usually began observations between late March and early May, 4–8 weeks before egg-laying, and continued through late August or early September.

In this paper the term "breeding" refers to individuals or pairs that produced an egg in a given year, whereas "nonbreeding" denotes the

TABLE 1. Color phases identified in 2,321 pairs of Northern Fulmars observed on the Semidi Islands, 12–13 May 1979.

	Color phase[a]				
	LL	L	D	DD	Total
No.	70	605	150	3,817	4,642
%	1.51	13.03	3.23	82.23	100.0

[a] See Methods for description of categories.

failure to lay (pairs) or the absence of an egg in the current year (sites). A breeding pair of fulmars produces only one egg a year, so the outcome of a breeding attempt is a dichotomous variable. I used contingency tests (chi-square or G statistics; Sokal and Rohlf 1981) to examine factors affecting the probability of success or failure to raise a chick. More specifically, I took the survival of young to the mid to late chick stage as an indicator of breeding success because I did not stay to witness young leaving the cliffs. Small differences between years in the timing of final nest checks were negligible because chick survival during the last two weeks of observed nest life was consistently high (>99%; Hatch 1987a).

I evaluated the effect of breeding experience on success by making use of the following information. First-time breeders are recruited to the adult fulmar population in either of two ways. Some recruits acquire similarly inexperienced partners and occupy a site for one to several years before producing an egg (Fisher 1952). Other inexperienced birds find experienced partners, but half of those pairs delay egg production at least

a year (Hatch 1987a). In contrast, pairs of known individuals that produced an egg during one year of this study rarely failed to lay the following year (2.8% of 71 observations; Hatch 1987a). Thus, the probability was high that a site known to have changed from nonbreeding to breeding status since the previous year contained a pair in which one or both members had no breeding experience. The comparison of pairs in that category with pairs from sites that had an egg the preceding year provides a qualified test of past experience as a factor affecting breeding success.

RESULTS

OCCURRENCE AND INTERBREEDING OF COLOR PHASES

There was a predominance of dark-colored fulmars on the Semidi Islands, more than 80% of the birds falling in the DD category (Table 1). LL birds comprised the smallest group, followed by D birds, although the latter category was artificially small for reasons explained above. Under a simple two-category classification, 15% of the Semidi birds qualified as "light" phase by having a measure of clear white plumage on the breast, while 85% lacked that distinguishing feature and therefore qualified as "dark" phase.

A comparison of observed and expected frequency distributions of pairs, under the null hypothesis of random mating, indicated that birds of different color phases mated indiscriminantly (Table 2). However, the lighter member of a mixed pair was more often male than female (Table 3). The tendency for light coloration to

TABLE 2. Tests for nonrandom mating among color phases of the Northern Fulmar on the Semidi Islands.[a]

	Expected occurrence				Observed occurrence
	Unadjusted		Adjusted for sex bias[b]		
Pair type	Proportion	No.[c]	Proportion	No.[c]	
DD/DD	0.6761	1,569.4	0.6748	1,566.3	1,566
L/DD	0.2143	497.4	0.2159	501.1	498
D/DD	0.0531	123.3	0.0534	124.0	122
LL/DD	0.0248	57.6	0.0255	59.3	65
L/L	0.0170	39.4	0.0165	38.2	44
L/D	0.0084	19.5	0.0083	19.2	14
L/LL	0.0039	9.1	0.0035	8.1	5
D/D	0.0010	2.4	0.0010	2.4	7
LL/D	0.0001	2.3	0.0001	2.1	0
LL/LL	0.0002	0.5	0.0001	0.3	0
Total	1.0000	2,321.0	1.0000	2,321.0	2,321

[a] No significant difference between observed and expected frequencies for unadjusted proportions ($\chi^2 = 5.531$, 7 df, $P > 0.5$) or expected frequencies adjusted for sex bias ($\chi^2 = 5.065$, 7 df, $P > 0.5$).
[b] See Table 3 and text on sex bias in the distribution of color phases.
[c] Cells with expected frequencies <5 combined for χ^2 tests.

TABLE 3. Color phases of sexed Northern Fulmars breeding in mixed pairs on the Semidi Islands.

Color phase[a]	Total	Males	Females	% males	G (1 df)[b]	P<
LL	36	30	6	83.3	9.09	0.01
L¹	33	26	7	78.8	5.38	0.05
L²	121	72	49	59.5	1.66	ns
L³	27	8	19	29.6	1.91	ns
All L	181	106	75	58.6	2.50	ns
D	29	16	13	55.2	0.07	ns
DD	202	72	130	35.6	8.50	0.01
Total	448	224	224	50.0		

[a] See Methods for description of primary color phases and subcategories L¹, L², and L³.
[b] G-test of departure from 50:50 sex ratio within each category.

indicate the male sex declined with increasing melanism.

The existence of sex differences in the occurrence of color phases altered the expected distribution of pair types, but reanalysis of the data to account for this bias again failed to reject the null hypothesis of random mating. Rather, the agreement between observed and expected frequencies was slightly improved (Table 2). The difference between the two expected distributions was small because the categories exhibiting the sex bias comprised only a small part of the population.

BREEDING PHENOLOGY AND SUCCESS

I detected no differences in laying dates among color phases. In 1979, pairs that included a light bird tended to have lower success than dark/dark pairs (Table 4). In other years, there was no significant effect. Combining data from all years, I found dark/dark pairs were not more successful than expected ($\chi^2 = 0.58$, 1 df, $P > 0.4$). Considering the results for 1979 in more detail, I found it made little difference whether the light bird was male or female, thus a highly significant difference in success existed that year between dark/dark pairs and the combination of light/dark, dark/light, and light/light pairs (Table 5).

USE OF BREEDING SITES

The conversion of sites from breeding to nonbreeding status between years was greater for sites occupied by dark/dark pairs than for sites occupied by light/dark pairs (Table 6). One explanation would be that dark/dark pairs changed breeding sites more frequently than light/dark pairs. Because a bird whose mate died usually retained the same site and acquired a new partner

TABLE 4. Breeding success of Northern Fulmars in relation to color phases within pairs.

Year	Overall proportion successful	Light/light			Light/dark (δ light)			Dark/light (δ dark)			Dark/dark			χ² (3 df)	P
		n	Success	Residual[b]	n	Success	Residual	n	Success	Residual	n	Success	Residual		
1976	0.153	3	0.000	-0.5	27	0.074	-2.1	20	0.250	1.9	120	0.158	0.6	—[c]	—[c]
1977	0.516	12	0.667	1.8	106	0.519	0.3	74	0.486	-2.2	190	0.516	0.0	1.35	0.717
1978	0.466	10	0.500	0.3	110	0.427	-4.2	69	0.507	2.9	204	0.471	1.0	1.20	0.753
1979	0.596	17	0.412	-3.1	107	0.551	-4.8	65	0.508	-5.8	210	0.662	13.7	9.18	0.027
1980	0.661	16	0.625	-0.6	100	0.610	-5.1	61	0.656	-0.3	212	0.689	5.9	1.99	0.576
1981	0.719	16	0.688	-0.5	98	0.704	-1.5	64	0.828	7.0	217	0.696	-5.0	4.53	0.209

[a] Light category includes LL and L; dark category includes DD and D.
[b] Residual is observed − expected number of successful pairs in a 2 × 4 contingency table.
[c] Some cells for 1976 had expected frequencies <5; no test performed.

TABLE 5. Differential breeding success of the color phases in 1979.

Effect tested	Groups compared[a]	n	Proportion successful	Residual[b]	χ^2 (1 df)	P<
♂, light vs. dark	light/light & light/dark with	124	0.532	−8.0		
					3.08	0.079
	dark/light & dark/dark	275	0.625	+8.0		
♀, light vs. dark	light/light & dark/light with	82	0.488	−8.9		
					5.07	0.024
	light/dark & dark/dark	317	0.625	+8.9		
♂ and/or ♀ light vs. ♂ and ♀ dark	light/light, light/dark & dark/light with	189	0.524	−13.7		
					7.88	0.005
	dark/dark	210	0.662	+13.7		

[a] First member of pair is male. Light category includes L and LL; dark category includes D and DD.
[b] Residual is observed − expected number of successful pairs in a 2 × 2 contingency table.

there (Hatch 1987a), a complete absence of use at a previously used site more likely indicated a move than the death of one member of a pair. Thus, I assessed the possibility of differential rates of site change as follows. Of the 83 sites with dark/dark pairs converted to nonbreeding status (1978–1981), 64 (77%) still contained a dark/dark pair, seven (8%) contained a dark single, and 12 (14%) were unattended in the year of nonbreeding. Of the 69 light/dark sites converted to nonbreeding, 44 (64%) still contained a light/dark pair, two (3%) contained a dark single, and 23 (33%) were unattended. The percentage of sites left unattended differed between dark/dark and light/dark pairs (G = 7.61, 1 df, P < 0.01), but the qualitative result is that, if anything, dark/dark pairs changed sites less, not more, frequently than light/dark pairs.

EFFECT OF EXPERIENCE

Between 1977 and 1981 the mean breeding success of dark/dark pairs in sites newly converted

to breeding status was 44%, compared with 64% in dark/dark pairs presumed to have at least one year of experience (Table 7). The difference between groups was significant in three of five years. In contrast, light/dark pairs with no known experience had reduced success in only one year (Table 8). Averaged over all five years, the rates of breeding success in the two groups of light/dark pairs were nearly identical. Curiously, the only year in which new and experienced light/dark pairs showed a marginally significant difference of the expected kind was the same year in which the effect was weakest in dark/dark pairs.

DISCUSSION

At least four evolutionary explanations for the plumage polymorphism of fulmars on the Semidi Islands are possible (Futuyma 1979). First, plumage variation is adaptively neutral—no differences in fitness exist among phenotypes, balanced or otherwise. Second, the polymorphism is not stable but changes due to natural selection

TABLE 6. Conversion of sites from breeding to nonbreeding status between years in relation to color phases of the pair present before the change.

Pair type[a]	Parameter	Year					Total 1978–1981[b]
		1977	1978	1979	1980	1981	
Dark/dark	n (sites)	125	159	169	177	176	681
	No. converted	33	26	18	20	19	83
	% converted	26.4	16.4	10.7	11.3	10.8	12.2
Light/dark	n (sites)	94	228	228	224	212	892
	No. converted	12	16	19	22	12	69
	% converted	12.8	7.0	8.3	9.8	5.7	7.7
	P<[c]	0.05	0.01	ns	ns	0.07	0.01

[a] Light/dark category includes LL/DD, L/DD, and D/DD pairs.
[b] Test of overall effect conservatively excludes 1977 because of inconsistent dark/dark : light/dark ratio and poor breeding success the preceding year.
[c] Probability of the difference between percentages (G-tests, 1 df).

TABLE 7. Presumed effect of breeding experience in dark/dark pairs.[a]

| Year | Overall proportion successful[b] | Status of site in preceding year | | | | Difference | χ^2 (1 df) | P |
| | | Breeding | | Nonbreeding | | | | |
		n	Success, current year[b]	n	Success, current year[b]			
1977	0.506	152	0.539	28	0.321	0.218	4.50	0.034
1978	0.471	146	0.486	43	0.419	0.067	0.61	0.434
1979	0.633	171	0.661	28	0.464	0.197	4.00	0.046
1980	0.703	170	0.747	25	0.400	0.347	12.56	0.001
1981	0.709	174	0.718	25	0.640	0.078	0.65	0.420
All years	0.607	813	0.637	149	0.443	0.194	19.91	0.001

[a] Dark category includes D and DD.
[b] Proportion of pairs laying eggs whose chick survived to mid or late nestling stage.

favoring some phenotypes over others (directional selection). Third, selection uniformly favors some phenotypes, but the difference is balanced by immigration (gene flow). Fourth, stability of the polymorphism results from a balance of selective forces acting differentially on the phenotypes. I can not definitely reject any of these hypotheses because the study did not continue long enough to establish whether the observed frequencies of the phenotypes are constant. Nevertheless, the effects I observed encourage some informed speculation concerning the origins and maintenance of this polymorphism.

The tendency of LL and L^J birds to be males suggests partial sex-linkage in the inheritance of plumage color in the Semidi Islands population. I see at least two alternative explanations, however. Light-colored females may tend to go unmated and were therefore under-represented in my sample, which included only paired birds. The evidence for random mating (Table 2), though not logically eliminating this possibility, makes it seem unlikely. The other possibility is that many of the lightest birds were recent im-

migrants from Bering Sea colonies and that males tend to emigrate from their natal colonies more than females.

The fulmar population on the Semidi Islands probably underwent a marked recession and expansion in historical times. In 1885, free-ranging arctic and red foxes (*Alopex lagopus* and *Vulpes vulpes*) were introduced to several of the islands for fur ranching (Bower and Aller 1917). Apparently, the predators died out after 1914, when caretakers ceased to provide winter food. In the interim, fulmar numbers were probably greatly reduced because much of the nesting habitat now used would have been accessible to foxes. If the response of fulmars to fox-free conditions involved immigration from the Bering Sea, that would explain why the Semidi Islands, alone among the major Alaskan colonies, has substantial numbers of both light and dark-phase fulmars. Fulmars coexist with native arctic foxes on Bering Sea islands (Pribilofs, St. Matthew) by nesting only in inaccessible sites. Chagulak Island (Fig. 1) is thought to be one of the few Aleutian Islands to which foxes were never introduced (Jones 1963, Bailey and Trapp 1984).

TABLE 8. Presumed effect of breeding experience in light/dark pairs.[a]

| Year | Overall proportion successful[b] | Status of site in preceding year | | | | Difference | χ^2 (1 df) | P |
| | | Breeding | | Nonbreeding | | | | |
		n	Success, current year[b]	n	Success, current year[b]			
1977	0.515	195	0.513	11	0.545	−0.032	0.04	0.833
1978	0.452	185	0.476	23	0.261	0.215	3.81	0.051
1979	0.554	188	0.548	14	0.643	−0.095	0.48	0.490
1980	0.619	174	0.603	20	0.750	−0.147	1.63	0.201
1981	0.730	183	0.727	13	0.769	−0.042	0.11	0.739
All years	0.572	925	0.572	81	0.568	0.004	0.01	0.945

[a] Light category includes L and LL; dark category includes D and DD.
[b] Proportion of pairs laying eggs whose chick survived to mid or late nestling stage.

Light-phase fulmars had lower breeding success than dark birds at the Semidis in 1979 (Table 4). One suspects the possibility of sampling error because the effect appeared in only one of six years. However, the probability of a Type 1 error was only 0.005 according to the analysis in Table 5, which suggests the difference was real. The effect may indicate an ecological disadvantage that light-colored fulmars have in a summer environment where the dark phase is predominant. The overall association of color phase and breeding success was weak, however, as pair types scarcely differed over the six-year term of this study.

If light-phase fulmars are at times disadvantaged breeders at the Semidi Islands, the hypothesis of balancing selection predicts offsetting factors such as differential survival of adults. Sites used by dark/dark pairs changed from breeding to nonbreeding status at a higher rate than sites used by light/dark pairs (Table 6), for which there are three possible explanations: (1) a greater incidence of nonbreeding (skipped years) among dark-phase birds, (2) more frequent changes of nest site by dark/dark pairs, or (3) lower overwinter survival of dark birds. Data on attendance at sites newly converted to nonbreeding status were inconsistent with the second possibility. Thus, the results in Table 6 imply that dark fulmars either skipped more breeding years or died at a higher rate than light birds.

These observations suggest a mechanism to maintain the polymorphism on the Semidi Islands in the absence of immigration from other colonies; namely, that light-phase fulmars are occasionally disadvantaged in rearing offspring but they live longer and make more breeding attempts. One difficulty with this is that even a small difference in survival rates would produce a substantial difference in the expected life spans of light and dark color phases. A much larger difference in breeding productivity than I observed would be expected if breeding success and survival were the only factors involved. Other potentially important parameters include the age of first breeding. Such data are not available for fulmars, but O'Donald (1983) found that sympatric light and dark-phase Parasitic Jaegers (*Stercorarius parasiticus*) differed by about 0.5 year in their average age at maturity.

The marked contrast between dark/dark and light/dark pairs in the apparent effect of breeding experience on success was unexpected and is difficult to explain. Ollason and Dunnet (1988) found that in fulmars breeding for the first time, breeding success was higher for those that were at least as old as the modal age of first breeding. If light-phase fulmars defer breeding longer than dark ones at the Semidi Islands, they may be more successful in their initial attempts and therefore fail to show the same influence of breeding experience as dark birds. A direct test of this idea would require extensive cohort banding and monitoring of known-age birds.

Fulmars in the North Pacific present an attractive system for detailed studies of population genetics—a small number of widely spaced colonies exhibit clear differences in genetic composition. Plumage polymorphism at the Semidi Islands may result from immigration of light-phase fulmars from other colonies (as in jaegers; O'Donald 1983), but there is also evidence to suggest a mechanism based on balancing selection within a closed population. Quantification of genetic differences between light and dark-phase fulmars from the four major colonies in Alaska may confirm the apparent absence of gene flow between the Aleutian Islands and Bering Sea and might also indicate whether light-phase fulmars on the Semidi Islands represent a recent influx of Bering Sea stock. Molecular genetic markers (mitochondrial DNA, nuclear DNA, allozymes) would be appropriate for such a study (Evans 1987, Quinn and White 1987, Shields and Helm-Bychowski 1988).

ACKNOWLEDGMENTS

LITERATURE CITED

BAILEY, E. P., AND J. L. TRAPP. 1984. A second wild breeding population of the Aleutian Canada Goose. Am. Birds 38:284–286.

BOWER, W. T., AND H. D. ALLER. 1917. Alaska fisheries and fur industries in 1915. Dept. of Commerce, Bureau of Commercial Fisheries, U.S. Gov't. Printing Office, Washington, DC.

BUCKLEY, P. A. 1987. Mendelian genes, p. 1–44. *In* F. Cooke and P. A. Buckley [eds.], Avian genetics. Academic Press, London.

CALDWELL, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. Auk 103:494–505.

COOKE, F. 1987. Lesser Snow Goose: a long-term population study, p. 407–432. In F. Cooke and P. A. Buckley [eds.], Avian genetics. Academic Press, London.

EVANS, P.G.H. 1987. Electrophoretic variability of gene products, p. 105–162. In F. Cooke and P. A. Buckley [eds.], Avian genetics. Academic Press, London.

FISHER, J. 1952. The fulmar. Collins, London.

FRANEKER, J. A. VAN, AND J. WATTEL. 1982. Geographical variation of the Fulmar Fulmarus glacialis in the North Atlantic. Ardea 70:31–44.

FUTUYMA, D. J. 1979. Evolutionary biology. Sinauer Associates, Inc., Sunderland, MA.

HARRISON, P. 1983. Seabirds. Houghton Mifflin, Boston.

HATCH, S. A. 1987a. Adult survival and productivity of Northern Fulmars in Alaska. Condor 89:685–696.

HATCH, S. A. 1987b. Copulation and mate guarding in the Northern Fulmar. Auk 104:450–461.

HATCH, S. A. 1990a. Time allocation by Northern Fulmars Fulmarus glacialis during the breeding season. Ornis Scand. 21:89–98.

HATCH, S. A. 1990b. Individual variation in behavior and breeding success of Northern Fulmars. Auk 107:750–755.

HATCH, S. A. 1990c. Incubation rhythm in the Fulmar Fulmarus glacialis: annual variation and sex roles. Ibis 132:515–524.

HATCH, S. A., AND M. A. HATCH. 1983. Populations and habitat use of marine birds in the Semidi Islands, Alaska. Murrelet 64:39–46.

JONES, R. D., JR. 1963. Buldir Island, site of a remnant breeding population of Aleutian Canada Geese. Wildfowl Trust Ann. Rep. 14:80–84.

MACDONALD, M. A. 1977. Adult mortality and fidelity to mate and nest-site in a group of marked Fulmars. Bird Study 24:165–168.

MURTON, R. K., N. J. WESTWOOD, AND R.J.P. THEARLE. 1973. Polymorphism and the evolution of a continuous breeding season in the pigeon, Columba livia. J. Repro. Fert., Suppl. 19:563–577.

O'DONALD, P. 1983. The Arctic Skua. Cambridge Univ. Press, London.

OLLASON, J. C., AND G. M. DUNNET. 1978. Age, experience, and other factors affecting the breeding success of the Fulmar Fulmarus glacialis in Orkney. J. Anim. Ecol. 47:961–976.

OLLASON, J. C., AND G. M. DUNNET. 1988. Variation in breeding success in Fulmars, p. 263–278. In T. H. Clutton-Brock [ed.], Reproductive success. Univ. Chicago Press, Chicago.

QUINN, T. W., AND B. N. WHITE. 1987. Analysis of DNA sequence variation, p. 163–198. In F. Cooke and P. A. Buckley [eds.], Avian genetics. Academic Press, London.

SHIELDS, G. F., AND K. M. HELM-BYCHOWSKI. 1988. Mitochondrial DNA of birds, p. 273–295. In R. F. Johnston [ed.], Current ornithology, vol. 5. Plenum Press, New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco.

SOWLS, A. L., S. A. HATCH, AND C. J. LENSINK. 1978. Catalog of Alaskan seabird colonies. U.S. Dept. Interior, Fish and Wildlife Serv., FWS/OBS-78/78.