

MANX SHEARWATER CHICKS: SEASONAL, PARENTAL, AND GENETIC INFLUENCES ON THE CHICK'S AGE AND WEIGHT AT FLEDGING¹

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Abstract. Manx Shearwater (*Puffinus puffinus*) pairs on Skokholm Island, Wales, typically breed together over several seasons, rearing one chick per year. There is a seasonal decline of chick fledging weight. Even after correction for this decline, pairs tend to rear chicks that are consistently heavier or lighter than predicted on the basis of the chick's hatching date. These deviations may reflect pair quality.

Weight and hatching date of a chick are not correlated with age of fledging. However, fledging ages of full siblings show significantly less variation than those of nonsiblings. The character appears highly heritable, with a heritability value around 0.84. This is the first study to address the extent to which the fledging age of wild birds is genetically determined.

Key words: Manx Shearwater; *Puffinus puffinus*; fledging age; heritability.

INTRODUCTION

There is apparent variation in the extent to which the age of fledging in birds mirrors environmental circumstances. In certain species, such as Audubon's Shearwater (*Puffinus lherminieri*) (Harris 1969) and the Common Swift (*Apus apus*) (Lack 1956), age of fledging is highly variable. When feeding conditions are favorable, chicks develop and fledge more rapidly than when food is scarce. In other species, for example, Sooty Shearwaters (*P. griseus*), fledging occurs at a similar age regardless of the fledgling's weight (Richdale 1963). Weight presumably reflects the food supply provided for the chick by the parents.

Perrins et al. (1973) have shown that, in the Manx Shearwater (*P. puffinus*) which naturally rears a single chick, experimentally twinned chicks fledge at a lighter weight than controls. Nevertheless, they fledge at the same age as controls and with a similar wing length. This resistance of fledging age to environmental influences suggests that it is a character at least partly under genetic control. The present study explores the suggestion further.

Studies of the heritability of avian morphology have mostly reported heritability values ranging from 40 to 90% (see Boag 1983). These high values probably represent heritable morphological variation, rather than the sharing of a common environment by parents and offspring (Smith and Dhondt 1980, but see also James 1983). Lower heritability values have generally been reported for other phenotypic characters, such as clutch size (Perrins and

Jones 1974) and laying date (Van Noordwijk et al. 1980). On the whole, "characters with the lowest heritabilities are those most closely connected with reproductive fitness, while the characters with the highest heritabilities are those that might be . . . the least important as determinants of natural fitness" (Falconer 1960).

There are few studies of heritability of growth rate and fledging age in wild birds. In one exception, Ricklefs and Peters (1981), using cross-fostering experiments, found a low heritability of growth rate in European Starlings (*Sturnus vulgaris*). No studies address genetic influences on fledging age, perhaps because in multi-young, nidicolous broods fledging is a process involving complex parent-chick interactions (Davies 1976). This problem arises less markedly in burrow-nesting Procellariiformes, since the chick is deserted by the parents sometime before fledging. (The Manx Shearwater desertion period averages 8.5 days [Harris 1966].) Fledging is then a singular event which occurs in the absence of contemporaneous parental influences.

METHODS

From 1973 through 1976 on Skokholm Island, Wales, I maintained a group of study burrows in which all breeding Manx Shearwaters were banded. Manx Shearwater pairs are normally faithful in successive years to each other and return to the same breeding burrow. As a result, faithful pairs raise in different years a series of chicks that are full siblings. The maximum possible number of chicks in each such "family" in this study is four, the number of years the study continued. Change of mate and burrow are both more likely after breeding failure (Brooke 1978).

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TABLE 1. Mean weight and age of Manx Shearwater chicks when fledging on Skokholm, 1973–1976.

Year	Mean weight (g) ± SE (n)	Mean age (days) ± SE (n)
1973	438.2 ± 5.4 (57)	71.3 ± 0.4 (53)
1974	455.2 ± 5.7 (57)	71.1 ± 0.4 (56)
1975	427.1 ± 5.1 (41)	71.4 ± 0.4 (39)
1976	444.7 ± 5.5 (54)	70.9 ± 0.4 (53)

Note: There are significant differences between years in fledging weight ($F_{3,205} = 4.27, P < 0.01$), but not in fledging age ($F_{3,197} = 0.22, n.s.$).

Burrows were inspected daily in the hatching period to determine the hatching date. Chicks were examined daily from 35 days of age until fledging at about 70 days. During the latter period chicks were weighed daily, at the same time each day. Peak weight, which occurs between Days 39 and 61 (Harris 1966), was therefore known, as were fledging weight, age when last fed, and age at fledging. As many as 55 chicks were reared in the study burrows each year. The sex of the chicks was not known.

RESULTS

Mean weight of chicks fledging from study burrows varied significantly between years (Table 1), but age of fledging did not vary. Since the chicks are reared by a random selection of breeding adults, these results imply that there are significant differences between years in environmental (feeding?) conditions.

In each year except 1976, there was a significant negative correlation ($P < 0.01$) between fledging weight and hatching date (Table 2). The decline in weight through the season could either be due to a deterioration in feeding conditions later in the season or to a tendency for pairs less proficient at feeding chicks to lay and hatch their eggs later. The fact that the rate of decline of fledging weight differed between years (Table 2) suggests that environment is at least partly responsible for that decline.

It is already known that female Manx Shearwaters, which remain paired to the same male in successive seasons, tend to lay on the same date, both absolutely and relative to the population (Brooke 1978). Their chicks therefore

TABLE 2. Correlation coefficients and slopes (g/day) of linear regressions of fledging weight on hatching date for Manx Shearwater chicks fledging on Skokholm, 1973–1976.

Year	<i>r</i>	Slope	SE	Sample size
1973	-0.415	-2.44	0.749	53
1974	-0.393	-1.57	0.501	56
1975	-0.469	-1.72	0.533	39
1976	-0.200	-0.96	0.659	53

Note: There are no significant differences between years in the regression coefficient.

TABLE 3a. Analysis of variance of fledging weight of chicks reared by 56 unchanged Manx Shearwater pairs that reared chicks in two or more of the years, 1973–1976.

Source	df	Sum of squares	Mean square	<i>F</i>
Between pairs	55	119,434	2,172	2.00
Within pairs	92	99,845	1,085	($P < 0.005$)
Total	147	219,279		

tend to hatch on the same date. Consequently, it would be expected that unchanged pairs would raise chicks of similar fledging weight in different years, and this was observed (Table 3a).

Knowing the regression of fledging weight on hatching date for a particular year (Table 2), it is possible to predict the fledging weight of a chick hatching on a particular date and then determine the magnitude and sign of the deviation from the prediction shown by any one chick. If unchanged Manx Shearwater pairs show consistent differences in their ability to feed chicks, then the within-pair variance in this residual value should be less than the between-pair variance. This was observed (Table 3b). Thus, after correcting for date, individual pairs tend to fledge chicks at a weight which is consistently greater or less than expected on the basis of the chick's hatching date.

There are insufficient data available to determine whether this result is in any way due to the fact that successful pairs typically breed in the same burrow in successive years (Brooke 1978). The result is not simply a reflection of body size, for example, large parents raising large heavy chicks. Although body size in shearwaters appears to be strongly heritable (Brooke 1977), there is no significant correlation ($r = 0.134, n = 197, n.s.$) between fledging weight and body size, as measured by 60-day tarsus length.

Multiple regression analysis of the age of fledging of chicks used four independent variables: the chick's age when last fed, the chick's age when at peak weight, the fledging weight,

TABLE 3b. Analysis of variance for residuals, from the regression of fledging weight on hatching date, of the fledging weights of chicks reared by 56 unchanged Manx Shearwater pairs that reared chicks in two or more of the years, 1973–1976.

Source	df	Sum of squares	Mean square	<i>F</i>
Between pairs	55	79,755	1,450	1.54
Within pairs	92	86,420	939	($P < 0.05$)
Total	147	166,175		

TABLE 4. Multiple regression of the age in days (Y) at which Manx Shearwater chicks fledge on four independent variables: X_1 = age (days) when last fed; X_2 = age (days) when at peak weight; X_3 = fledging weight (g); X_4 = hatching date (10 June = 0).

The regression equation			
$Y = 58.5 + 0.174X_1 + 0.102X_2 - 0.00916X_3 + 0.0254X_4$			
	Standard deviations of coefficients	t -ratio = coeff./SD	P
X_1	0.0498	3.49	<0.001
X_2	0.0394	2.60	<0.01
X_3	0.00502	-1.82	n.s.
X_4	0.0230	1.11	n.s.

Analysis of variance due to regression:

	df	Sum of squares	r^2
X_1	1	67.5	4.5
X_2	1	54.9	3.7
X_3	1	36.7	2.4
X_4	1	8.6	0.6
Total regression	4	167.7	11.2
Residual	190	1,332.4	
Total	194	1,500.1	

and the hatching date (Table 4). This analysis explained only 11.2% of the variance. The older chicks were when last fed and when reaching peak weight, the older they were at fledging; but the effects, though significant, were not pronounced. Hatching date had no significant effect on fledging age, and there was a weak, nonsignificant, negative correlation between fledging age and weight. Nevertheless the within-pair variance in fledging age was significantly less than the between-pair variance (Table 5). This is not due to siblings being of similar size and therefore fledging at similar ages, since there was no significant correlation between fledging age and chick size as measured by 60-day tarsus length ($r = 0.069$, $n = 197$, n.s.).

Is the result of Table 5 due to parental or chick effects? The multiple regression analysis above used four variables that are potentially under parental control. The results of the analysis show that the lower within-pair variance of fledging age is not a consequence of the known within-pair stability of fledging weight (Table 3a) or of hatching date. The other variables in the multiple regression, age when last fed and age at peak weight, are presumably partly under parental control, but together they explain only 8.2% of the variance in chick fledging age (Table 4). In toto the four variables used in the regression account for 14.8% (167.7/1,134.7) of the between-pairs sum of squares in chick fledging age. I conclude that factors intrinsic to individual chicks are important in determining the variance in chick fledging age.

Using Bulmer's methodology (1980:82), the repeatability of the fledging age of chicks of

TABLE 5. Analysis of variance of fledging age of chicks reared by 106 unchanged Manx Shearwater pairs in one or more of the years, 1973-1976.

Source	df	Sum of squares	Mean square	F
Between pairs	105	1,134.7	10.81	2.63
Within pairs	89	365.4	4.11	($P < 0.005$)
Total	194	1,500.1		

unchanged Manx Shearwater pairs is calculated from Table 5 as 0.470 (95% confidence range = 0.322 to 0.593). This calculation makes no correction for unequal family sizes, which ranged from one to four. Making the correction alters the repeatability estimate by less than 1%.

If this degree of repeatability between full siblings is entirely due to genetic determinants of fledging age, then the heritability is 2×0.470 , or 0.940. However multiple regression has indicated that nearly 15% of the between-pairs sum of squares could be due to identified parental effects on chick phenotype. If the between-pairs sum of squares is reduced to 967 (101 df), then the corresponding mean square becomes 9.57, the repeatability 0.419, and the heritability is recalculated as 0.838.

Since unchanged pairs only rarely move burrows, the possibility that the heritability value is elevated because of the effect of a common burrow environment remains open. To test this I divided the between-pairs variance component into two parts, that associated with different burrows and that associated with the 17 instances where a change of pair occurred within the same burrow (Table 6). Where there was a change of pairs within the same burrow, then the variance in fledging age was rather greater than for the error term ($F_{17,89} = 1.687$, $0.05 < P < 0.1$). There may be a slight burrow effect; but, overall, these limited data support the hypothesis that the within-pair constancy of fledging age is due to genetic factors. Furthermore, it does seem biologically more plausible that burrow effects (for instance poorer or better insulation) should influence fledging weight, which is unrelated to fledging age, rather than influencing fledging age itself.

DISCUSSION

Monogamous Manx Shearwaters lay a single egg from which breeding success is consistently high (Brooke 1978). Accordingly Manx Shearwaters of higher "quality" cannot readily translate that quality into greater production of young as can the most successful males of polygynous species (Clutton-Brock et al. 1982, De Vos 1983). However an alternative avenue

TABLE 6. Analysis of variance of the fledging age of chicks reared by unchanged Manx Shearwater pairs in one or more of the years, 1973–1976.

Source	df	Sum of squares	Mean square	F
Between pairs and between burrows	90	1,082.06	12.02	
Between pairs and within burrows	17	111.67	6.86	1.687
Within pairs and within burrows	89	362.58	4.07	(0.05 < P < 0.1)
Total	196	1,556.31		

Note: A slightly different data set from that handled in Tables 4 and 5 is used for two reasons: (i) Four instances where unchanged pairs reared chicks in two different burrows are deleted, and (ii) Pairs lacking one or other of the measurements X_1 , X_2 , X_3 and X_4 (Table 4) were excluded from Tables 4 and 5 but not from Table 6.

of raising fitness, that of rearing superior young, remains open. As heavier Manx Shearwater chicks survive better (Perrins et al. 1973), the ability to rear heavy chicks is biologically significant. The ability of certain Manx Shearwater pairs to raise chicks that are consistently heavier, both absolutely and when corrected for hatching date (Table 3), may reflect differences in parental quality.

About 47% of the variance in the age of fledging of Manx Shearwater chicks is due to between-pairs effects. It seems likely that this character is heritable, the heritability value not exceeding 0.94 and probably closer to 0.84. This value, within the range of heritability values for morphological characters, suggests selection for fledging age is not intense (Falconer 1960). Nevertheless, the fact that the age of fledging Manx Shearwaters does not differ in different years despite differences in fledging weight (Table 1) suggests that selection does act to keep the age at fledging within certain bounds. If the shearwater fledges after too speedy maturation, then the shift of resources from fat storage to development may prejudice the fledgling's survival chances. If the shearwater fledges slowly, then it may launch into a marine environment deteriorating during the autumn (Perrins 1966, Perrins et al. 1973).

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