Factors affecting survival of fledgling Manx Shearwaters *Puffinus puffinus*

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Abstract
During an 11-year period starting in the mid-1960s, large numbers of fledgling Manx Shearwaters *Puffinus puffinus* were ringed and recaptured on Skokholm Island, Pembrokeshire, Wales. Since it is unlikely that any more will ever be found, this paper summarises the factors that affected the chances of a fledgling surviving long enough to be recaptured on the island. Both the date on which they were ringed and their weight at that time influenced the probability that they would be recaptured. Some implications for the annual cycle are discussed.

Introduction

Skokholm Island, Pembrokeshire, Wales, is well-known for its large colony of Manx Shearwaters *Puffinus puffinus* (Smith *et al*. 2001; Newton *et al*. 2004). The colony is perhaps the third largest in the world, with only the adjacent island of Skomer (Smith *et al*. 2001; Newton *et al*. 2004; Perrins *et al*. 2012) and Rum, Scotland (Murray & Shewry 2002) having larger colonies. The pioneer studies of the breeding biology of this species were carried out on Skokholm by Ronald Lockley (Lockley 1942). On Skokholm the shearwaters nest in burrows in soft soil. These burrows are concentrated around the perimeter of the island, often in land that slopes towards the sea. Nesting in such places gives the birds easier egress to the sea than from the flatter, central areas of the island from where take-off is more difficult.

As with other procellariiforms, the Manx Shearwater has a long breeding season. The egg is laid in early May, incubation takes about 51 days and fledging about 70 days so the chicks do not leave until late August or early September. The whole breeding season is some 15 days longer than this because after pairing and before laying the female leaves the colony for two weeks to forage for the food for egg-formation (Brooke 1990; Warham 1990).

During the first 50–60 days of the nestling period as the chicks grow they also lay down large reserves of fat, reaching a peak weight which may be as high as 800 g or more, about double the adult weight. During the last fortnight or so in the nest the amount of food brought to the chick drops markedly and many chicks do not receive any food; they lose about 15 g per day. Often the parents leave the colony well before their chick. For the last few nights prior to departure the chicks come up onto the surface and exercise their wings (Perrins *et al*. 1973). Usually they only do this on dark nights since they are vulnerable to predation by gulls if it is light enough for the gulls to be able to hunt them.

During the years 1964–74, as part of studies of the pattern of return to the island by the pre-breeders, some 70,000 fledglings were ringed and much effort was put into recapturing them when they returned (Perrins *et al*. 1973; Brooke 1978a, 1990). Large numbers of non-breeding birds return to land on dark nights around the new moon periods in June and July. One-year old birds rarely come to land, but from the age of two, the cohorts become progressively more common until age 5–6 after which they become progressively scarcer (Perrins *et al*. 1973). This is thought to be largely because once they are paired or start breeding, usually about age 6–7 (Brooke 1990), they are too occupied with breeding to sit around on the surface.

Bird ringing (and recapturing) was stopped by the owner of the island after 1976 and so for the years 1972–74 progressively fewer recaptures were made. Since that date only a few birds found dead have been recorded. The island has recently become available for seabird studies again. Sadly, the shearwaters' shuffling gait rubs the rings against the ground and they abrade badly; the rings used at that time had a limited life-span and needed to be replaced from time to time. Since this could not be done, it is unlikely that any birds ringed prior to 1976 and still alive are carrying rings, even though a few of them are probably still alive; Manx Shearwaters have been recorded as living to the age of 50 (McKee 2003; Brown 2009). Extensive capturing in recent years has not yielded any birds ringed in 1964–74. This paper re-examines the recapture rates of the fledglings ringed during this period. At the time of the study, there were thought to be around 35,000 breeding pairs of shearwaters on the island (Harris 1966; Perrins 1968).

Methods and Results

Chick ringing: During the years 1964–74 teams of people staying at the island's Bird Observatory went out at night to catch and ring fledglings. Fledglings started to come to the surface around 20 August, with numbers peaking around the end of the month. Thereafter numbers decreased steadily (Figure 1). Actual numbers in the long tail are probably under-represented because with falling numbers less effort was put into searching for them. Since most chicks leave the island within 3–4 days of first coming to the surface (Perrins *et al*. 1973), the date of ringing has been taken as indicative of date of fledging. A small proportion of the birds ringed may have remained on the island for longer. When first found, these chicks were still carrying much down; they also tended to be above average weight, supporting the belief that they were younger. All chicks recorded as 'downy' have been omitted from the analyses.

By far the largest concentration of burrows occurs in the southwest corner of the island, around the lighthouse, in an area called the 'Main Colony'. Because it was more rewarding, ringing was disproportionately concentrated in the Main Colony (Perrins 1968) and so a higher proportion of the chicks raised there would have been ringed than was the case for other areas of the island (referred to in this paper as 'Elsewhere'). In the three years 1965–67, large numbers of the fledglings were weighed when they were ringed; weighing was also concentrated in the Main Colony.

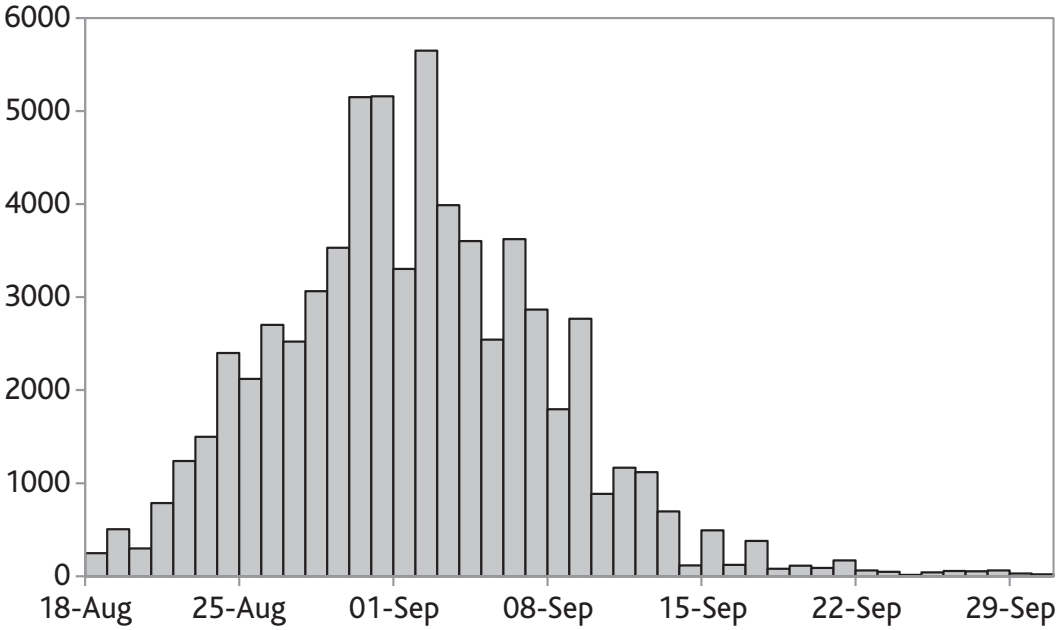


Figure 1. The numbers of fledgling Manx Shearwaters *Puffinus puffinus* ringed on Skokholm 1964–74 by date of ringing; 23 birds ringed before 18 August and 34 ringed after 30 September are excluded.

Recapturing the returning birds: The information presented in this paper is derived from the Observatory's ringing logs for the years 1964–74. Birds which were recaptured were recorded in the ringing logs; normally only the year (not the date) of first recapture was recorded and the site of recapture on the island was not recorded. For this study all recoveries of birds before the end of the calendar year of hatching were excluded, as were small numbers found on the island in the spring following the year of ringing; in these cases the logs usually recorded them as 'long dead' or 'presumed did not fledge'. As with the ringing of the fledglings, recapturing efforts were concentrated around the Main Colony with lower effort expended elsewhere.

The proportion of each cohort recaptured was remarkably similar, varying from about 22–28% (Table 1). The lower recapture rates in the last three years 1972–74 when the % recaptured dropped to 18%, 14% and then 5% was due to recapturing ceasing after 1976. In view of the very low percentage of recaptures from 1974 this cohort is omitted from the analyses below. Compared with birds ringed Elsewhere, birds ringed in the Main Colony were twice as likely to be recaptured on the island in a later year (Table 1, for 1964–1973, Main Colony: 8075/35135 = 22.98%, Elsewhere: 3519/32344 = 10.88%). This may have been due to a combination of both philopatry to natal site and to a higher intensity of retrapping in the Main Colony than Elsewhere. The difference was not, however, due to birds from the Main Colony having a higher probability of surviving than those ringed Elsewhere since the recoveries away from Skokholm, which eliminates any possible island area biases, were nearly identical (Table 2: $\chi^2 = 0.1874$, 1 df, P = 0.6648).

Fledging date: The likelihood of being found on the island in a later year was very strongly correlated with the date of ringing. Figure 2 and Table 3 show the relationship between chick recapture and ringing date for the areas Main and Elsewhere (2 level factor) using a generalised linear model with a binomial error distribution (events/trials) and logit link function. This analysis was performed on the total number of chicks recovered out of the total number of chicks that were ringed for different ringing dates summed over the ten years 1964–73.

Fledging weight: In 1965–67, when the chicks were weighed, fledging weights declined significantly with date (Figure 3). There were significant differences between years. The chances of a chick returning in a later year were strongly correlated with its weight (Figure 4, Table 4).

Table 1. Fledgling Manx Shearwaters *Puffinus puffinus* ringed and recaptured on Skokholm, 1964–74.

	Main Colony			Elsewhere		
Year	**Ringed**	**Recaptured**	**%**	**Ringed**	**Recaptured**	**%**
1964	3,014	760	25.22	2,297	290	12.63
1965	4,317	1,218	28.21	4,635	779	16.81
1966	3,928	846	21.54	4,698	506	10.77
1967	4,266	967	22.67	6,052	682	11.27
1968	3,724	999	26.83	4,859	571	11.75
1969	3,246	799	24.61	4,429	410	9.26
1970	2,650	711	26.83	652	80	12.27
1971	2,417	536	22.18	398	45	11.31
1972	3,838	699	18.21	1,377	92	6.68
1973	3,735	540	14.46	2,947	64	2.17
1974	3,053	153	5.01	689	10	1.45
	38,188	**8,228**		**33,033**	**3,529**	

Table 2. Recoveries away from Skokholm of Manx Shearwaters *Puffinus puffinus* ringed as fledglings on Skokholm, in relation to the area of ringing on the island (recoveries in year of ringing are omitted).

Area ringed	**No. Ringed**	**No. recovered**	**%**
Main Colony	35,135	134	0.38
Elsewhere	32,344	127	0.39

Table 3. Generalised linear model of variation in the proportion of Manx Shearwater *Puffinus puffinus* chicks surviving across the two areas of the island

Fixed Terms		**Parameter Estimate**	**SE**	**DF**	**F**	**P**
Ringing date		-0.07	0.006	1, 93	139.08	**< 0.0001**
Area	Main Colony	0.20	0.003	1, 93	1453.92	**< 0.0001**
	Elsewhere	0.09	0.002			
Ringing date*area	Main Colony	-0.30*	0.004	1, 92	15.97	**0.0001**
	Elsewhere	-0.42*	0.002			

Note: Significant values are shown in boldface type. n_{ringed} = 63,745, $n_{recovered}$ = 10,714. Parameter estimates are back-transformed. * = significantly different from 0.

Table 4. Generalised linear model of variation in recapture rates of Manx Shearwater *Puffinus puffinus* chicks ringed on Skokholm.

Fixed Terms		Parameter Estimate	SE	DF	F	P
Ringing date				1, 7331	0.81	0.37
Chick weight		0.04	0.01	1, 7331	33.95	**< 0.0001**
Year	1965	0.27	0.01	2, 7331	8.99	**0.0001**
	1966	0.22	0.01			
	1967	0.23	0.01			
Ringing date*chick weight				1, 7326	1.98	0.16
Ringing date*year	1965	-0.03*	0.01	2, 7326	5.61	**0.004**
	1966	-0.04	0.02			
	1967	0.02*	0.01			
Chick weight*year				2, 7326	0.21	0.81
Ringing date*chick weight*year	1965	0.02	0.01	2, 7324	4.10	**0.01**
	1966	-0.05*	0.02			
	1967	0.01	0.01			

Note: Significant values are shown in boldface type. $n_{observations}$ = 7,336. Parameter estimates are back-transformed. * = significantly different from 0.

We examined whether return rate was influenced by ringing date (covariate), chick weight (covariate) and year of ringing (3 level factor) using a generalised linear model with a binary error distribution and logit link function. This analysis was performed on individual ringing records ($N_{observations}$ = 7,336). To examine the significance of fixed effects we first tested interactions using full models with all terms included in models and then removed higher order interactions to test the main effects in each model. All analyses were conducted in SAS v9.2. Return rate was significantly affected by date of ringing, weight at ringing and year effects. In two of the years, but not the third, the effect of weight on return rate was independent of date.

Discussion

The results presented here indicate that some 22–28% of the fledglings survived to return to their natal colony.

The figures presented in this paper are for those chicks which survived and returned to the island and were recaptured. Although here it is assumed that the return rates are indicative of the relative survival rates of the types of chick, they are not survival rates for two reasons. First, it is most unlikely that all the birds returning to the colony — even in the Main Colony — were recaptured. Second, even in the extremely unlikely event that no survivors escaped being recaptured, the numbers in Table 1 would not represent the full number surviving. Brooke (1978b) showed that females were less likely to return to close to their place of birth than males. He estimated that, in the case of Skokholm, 50% of the females nested elsewhere, mostly in the larger colony on the adjacent island of Skomer (the nearest points of the two islands are only 3 km apart). Allowing for this, even if all the birds which returned were recaptured, the true survival of fledglings from leaving their nest to return to the breeding colonies might be nearer to 28–37%.

By no mean all these birds are going to survive to become members of the breeding population since the pre-breeders spend a lot of time on the surface in the colony and so are particularly susceptible to predation (Perrins *et al*. 1973).

There is an apparent contradiction in the data presented here: the chicks with the highest recapture rates were those which fledged at the very beginning of the season (around 20 August; Figure 3), but the peak fledging occurred about 10 days later than this (Figure 1); the large majority of the parent birds appeared not to be able to breed at the best possible time for raising chicks. Perrins (1970) suggested that this was because the females of many species of bird were unable to get sufficient food early enough to form their egg. Brooke (1978a) suggested that obtaining the energy to complete an incubation stint might be more difficult than obtaining the nutrients for the egg and so the birds delayed laying until this was possible. Similarly, Thompson (1987) calculated that the female shearwater had to acquire food at a faster rate during incubation than she did during egg-formation; hence waiting until food was sufficiently abundant for incubation might be necessary. Whichever is correct, it appears that resource limitations early in the season may prevent many of the birds from breeding at that time which would maximise chick survival.

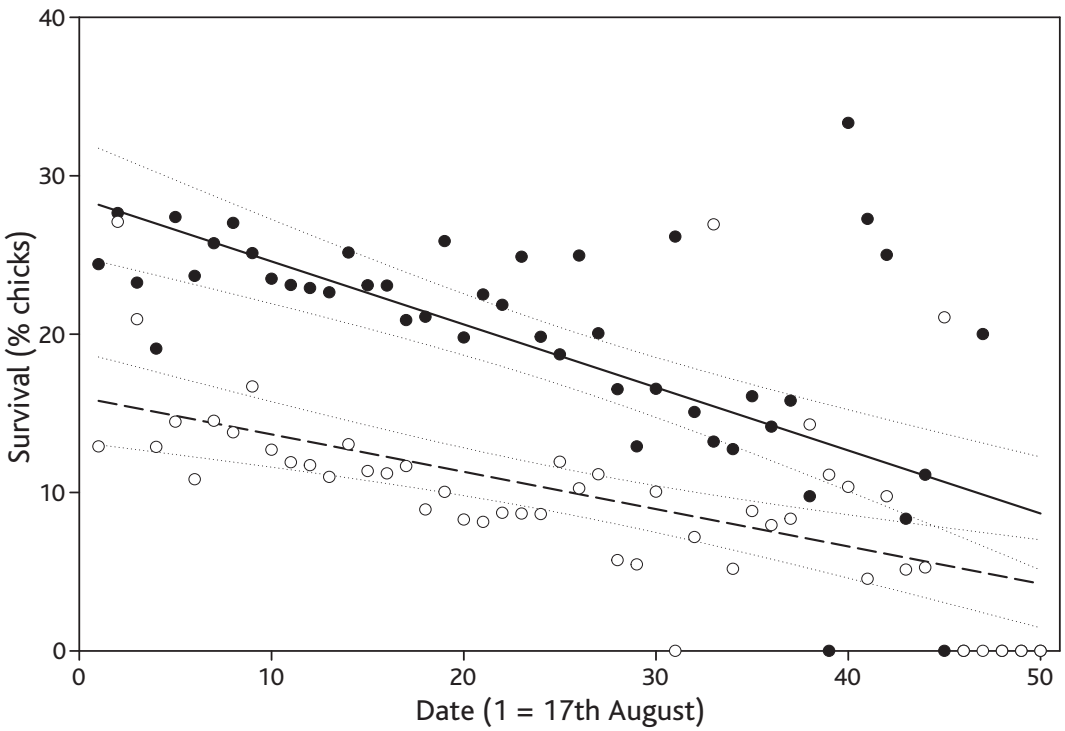
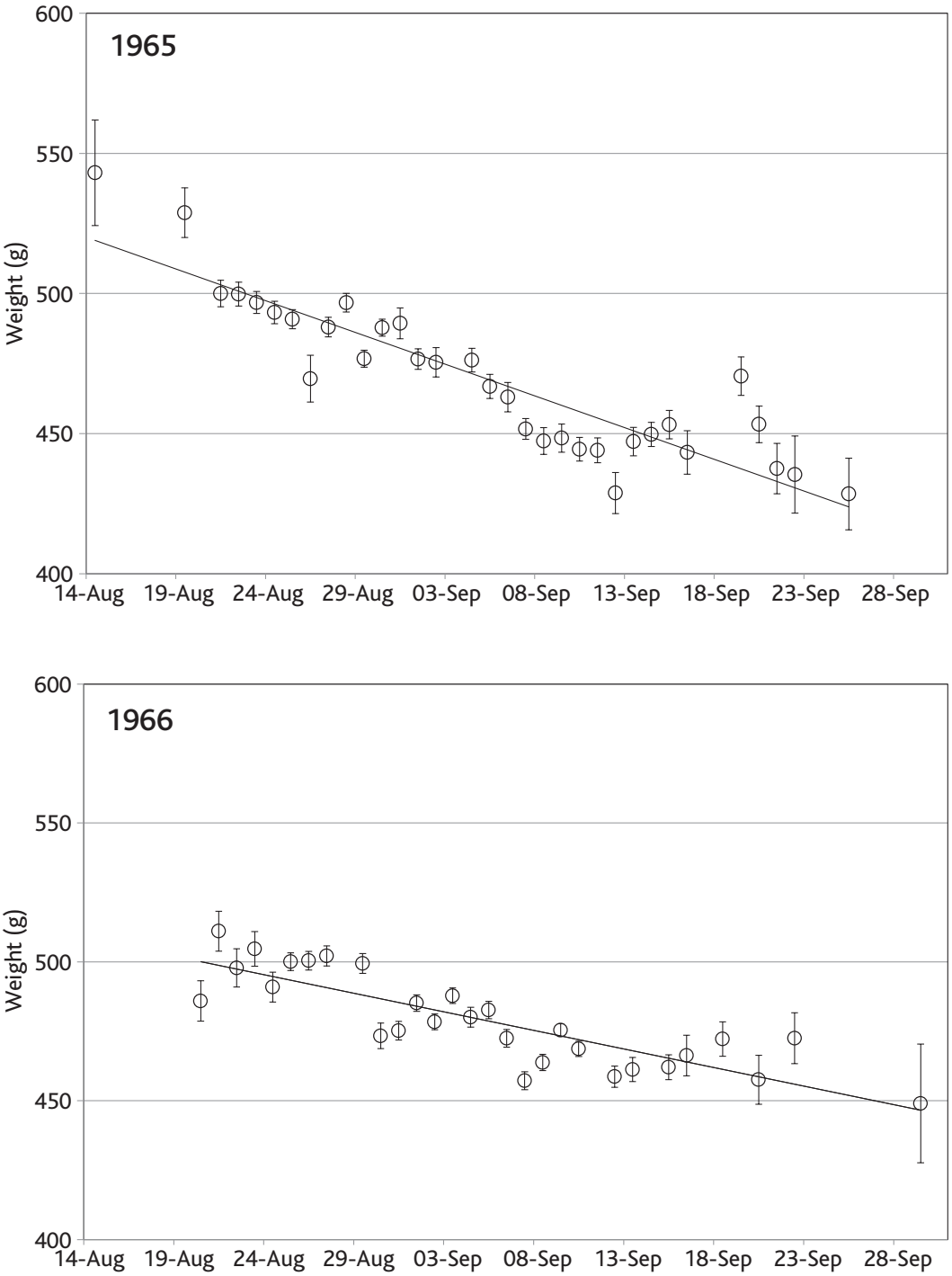
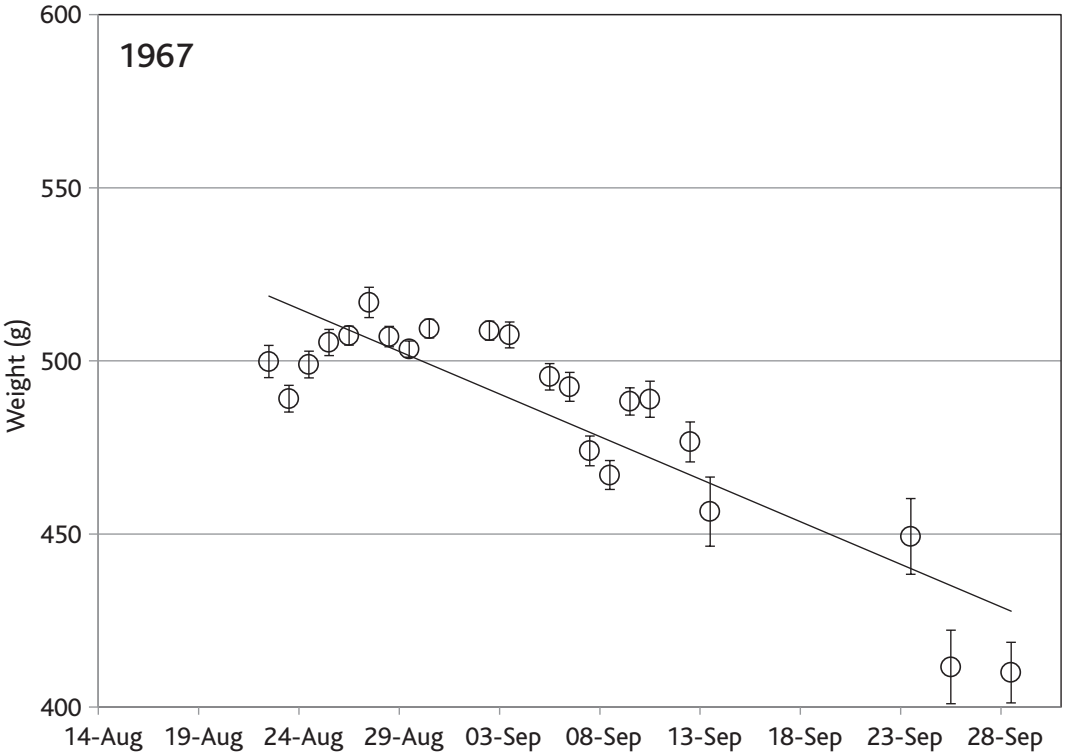


Figure 2. Percentage of Manx Shearwater *Puffinus puffinus* fledglings recaptured in later years in relation to date of ringing. Solid circles, continuous line = Main Colony; open circles, dashed line = Elsewhere. Lines are fitted lines for all data, dotted lines are 95% Confidence Intervals.

Figure 3. The mean weight of Manx Shearwater *Puffinus puffinus* fledglings in relation to date of ringing. Downy fledglings are excluded (see text). Lines are the regression lines through the data for each year (1965: n = 3,013, P = 0.000, r^2 = 14.2; 1966: n = 4,386, P = 0.000, r^2 = 6.1; 1967: n = 3,153, P = 0.000, r^2 = 6.8).





There are also resource constraints at the end of the season. As with many other procellariforms, the Manx Shearwater grows rapidly for the first part of the nestling period, reaching a peak weight some time before fledging. Although they lose much of this weight prior to fledging, about 3% of the birds caught on the surface weighed 600 g or more, 50% more than a parent.

A seasonal decline in fledging weight is observed in most seasons (Perrins *et al*. 1973 and in prep.). Since weight affects chick survival independently of fledging date this suggests that the parents find it increasingly difficult to collect as much food late in the season as they can at the beginning. If food availability starts to decline during August, the large fat store confers two advantages on the birds. It provides the chicks with a guarantee of the resources for its final two weeks in the nest and it enables the parents to migrate at an earlier date.

There are presumably advantages to the parents in being able to depart early. Little is known about the moult cycle of Manx Shearwaters, other than it takes place at sea when the birds are in their winter quarters in the South Atlantic (Hamer 2003). However, occasionally birds returning to the breeding colonies have been recorded as having not completed the moult in their flight feathers. Since one might expect the birds to try to complete their moult prior to the long flight northwards, this may indicate that they are under some form of time constraint to complete their moult in winter quarters and hence an early autumn departure may help them to do this.

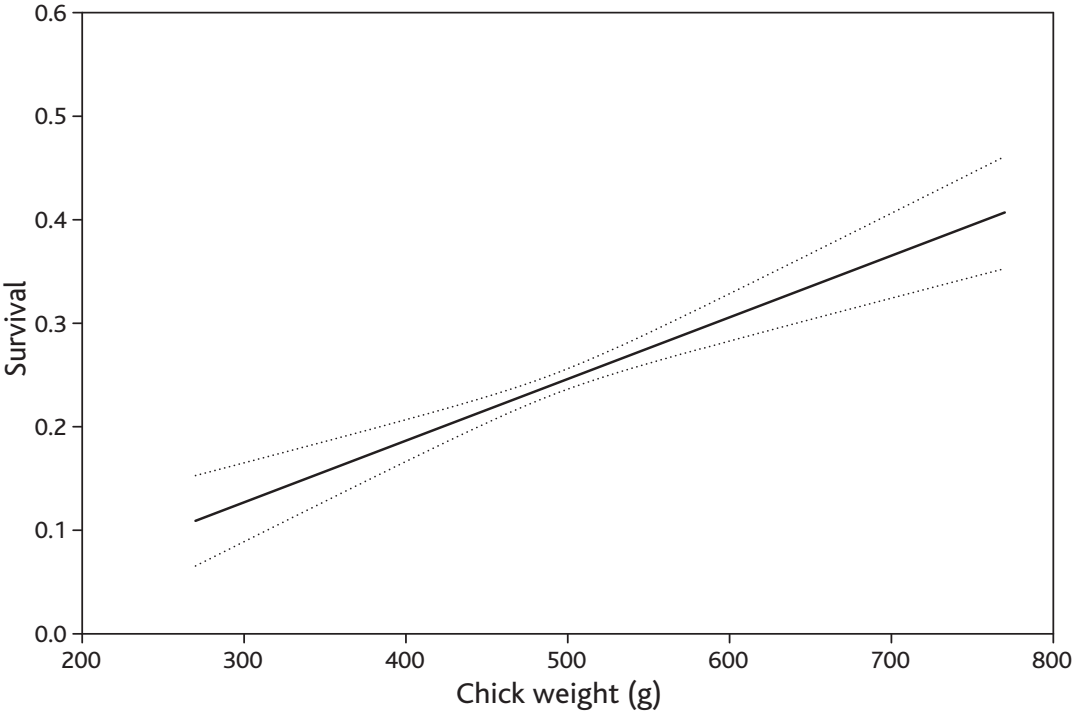


Figure 4. Probability of being recaptured in relation to weight of fledgling Manx Shearwaters *Puffinus puffinus*. The line is the fitted line for the data for the years 1965–67 and the dotted lines are the 95% Confidence Intervals.

The reasons for the differences in the rate of decline in weight in different years are unknown, but presumably relate to availability of food. Since 2000, smaller samples of fledglings have been weighed, largely on Skomer, and these show lower mean fledging weights than those reported here (in prep.). If these are reflected in reduced survival of the fledglings this would be a cause for concern.

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