SHORT COMMUNICATIONS

Mass-related survival of fledgling Sooty Shearwaters *Puffinus griseus* at The Snares, New Zealand

For atricial bird species, Lack proposed that there is a trade-off between the number and quality of nestlings that can be raised to fledging (Lack 1947). Growth rates of nestlings are assumed to indicate nestling quality; however, few studies have subsequently tested the hypothesis that birds that grow more rapidly as nestlings also survive better as juveniles and so are more likely to breed (Magrath 1991). A review of 21 studies which examined the assocation between nestling mass and juvenile survival showed approximately the same number of studies found no relationship as those that found larger nestlings had a higher probability of juvenile survival (Magrath 1991). However, six of the studies supporting the hypothesis were on one species—the Great Tit *Parus major* (Magrath 1991).

Seabirds are classic minimalists, many laying just a single egg each breeding attempt, which is not replaced if lost. This removes any interaction between growth rates of nestlings and brood size in any consideration of the effect on juvenile survival. In addition, seabirds tend to return to breed at the place where they were reared (Warham 1990). Consequently, seabirds provide opportunities to test further the relationship between nestling mass and survival, although because of their delayed maturity (Warham 1990), any such studies of necessity need to extend over several years.

The Sooty Shearwater *Puffinus griseus* is a burrow-nesting seabird which, in the New Zealand region, breeds in large numbers on several southern islands (Marchant & Higgins 1990). At The Snares (48°02'S, 166°36'E), there were an estimated 2.75 million Sooty Shearwater burrows on 328 ha in 1969 (Warham & Wilson 1982). These birds return to their burrows during September and lay in November, the eggs hatch in January and the young depart in late April and early May (Warham *et al.* 1982). Richdale (1954) was of the opinion that Sooty Shearwater chicks which left the burrow at a mass greater than 455 g would probably survive, but those of lower mass would not. However, he had no proof of the mass required for survival of chicks. The aim of our study was to test the hypothesis that survival of Sooty Shearwater chicks was influenced by their mass immediately before fledging.

METHODS

From 15 April to 7 May 1972, 500 fledgling Sooty Shearwaters were ringed at one site on The Snares; 119 were ringed between 15 and 23 April and 381 between 29 April and 7 May. To ensure that no adults were caught during April, only those birds that had some down on them were ringed, but from 5 May, all birds seen were ringed because no adult had been seen flying at dusk since 30 April. All birds were caught at night on the surface, fitted with a uniquely numbered stainless steel ring and weighed before release at the capture site.

Subsequently, searches were made for ringed birds on the surface within the study site during visits to the island in the austral summers of 1974–1975, 1976–1977, 1983–1984, 1985–1986, 1986–1987 and 1987–1988 (hereafter referred to by the year in which laying occurred, e.g. 1974 for 1974–1975). In the summers of 1974 and 1976, ringed birds were recaptured during ten early morning searches when birds were leaving the island. In the 1980s, early evening searches were made, and ringed birds were recaptured shortly after they landed back at the island after sunset. In all summers, we recaptured ringed birds with a hand net following detection of a ring by shining a light on the legs of the birds.

All statistics used in the analysis may be found in Zar (1984).

RESULTS

A total of 31 of the 500 birds ringed (6.2%) were recaptured as follows; 3 in 1974, 13 in 1976, 1 in 1983, 10 in 1985, 2 in 1986 and 2 in 1987. The mean mass at ringing of the birds recaptured two or more years later was 832 g (s.d. ±148 g, range = 564–1089 g, n = 31), significantly greater (t_{498} = 2.99, $P < 0.005$; Fig. 1) than the mean mass of 740 g (s.d. ±166 g, range = 224–1415 g, n = 469) of those birds ringed as chicks which were not recaptured. The minimum mass of a fledgling which was recaptured was 564 g; above this threshold, the proportion of birds surviving increased with fledging mass. Of the fledglings with a mass in the range 564–900 g, 5.4% (18/336) were recaptured compared with 13.0% (13/100) of fledglings in the range 901–1415 g.

The data were analysed to determine whether mass and recapture probabilities of fledglings were related to the date of ringing. The data were spilt into two time periods, 15–23 April (early) and 29 April–7 May (late). A two-way ANOVA showed that the probability of recapture was most strongly influenced by the mass at ringing ($F_{1,496}$ = 15.1, $P < 0.001$). Although the mean mass of birds ringed during the early period (698 g, s.d. ±195 g, n = 116) was less than that of those ringed later (761 g, s.d. ±153 g, n = 381), the effect was not significant ($F_{1,496}$ = 0.37, n.s.). The ANOVA showed a significant interaction between the mass of birds and date of ringing ($F_{1,496}$ = 6.28, $P < 0.05$). When we investigated further, we found that, for birds ringed during the earlier period, the mass of those subsequently recaptured (mean = 927 g, s.d. ±127 g, n = 6) was significantly greater (t_{117} = 2.96, $P < 0.005$) than the mass of those not recaptured (mean = 685 g, s.d. ±190 g, n = 113). However, for those ringed later, although the mass of birds recaptured (mean = 809 g, s.d. ±145 g, n = 25) was greater than the mass of those not recaptured (mean 757 g, s.d. ±153 g, n = 356), the difference was not significant (t_{379} = 1.65, n.s.; Fig. 2).

DISCUSSION

The results of this study support the hypothesis that the mass of Sooty Shearwater chicks immediately before fledging influences their chance of survival. Richdale (1954) considered that fledglings

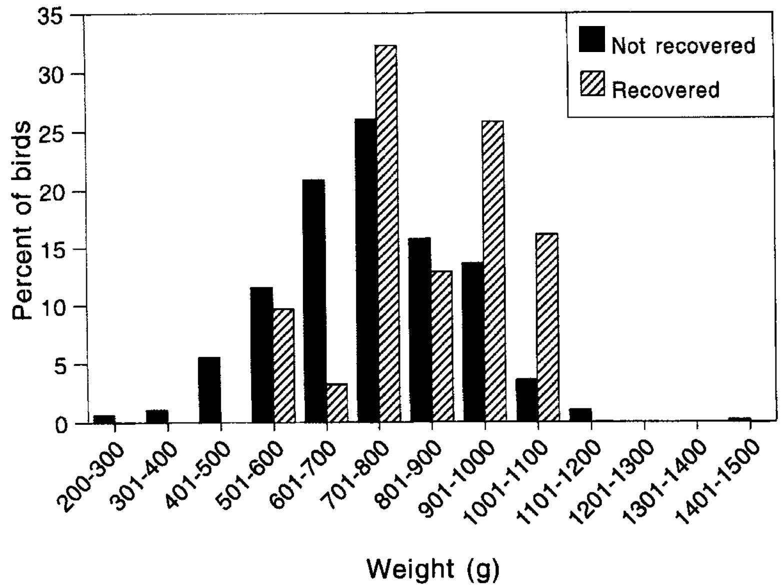

Figure 1. Frequency distributions of mass at ringing of fledgling Sooty Shearwaters.

must have a mass of at least 455 g in order to survive. However, our study indicates that they should have a mass of at least 564 g and that the proportion surviving increases with mass above this threshold. In this respect, Sooty Shearwater (this study), Manx Shearwater *Puffinus puffinus* (Perrins *et al.* 1973) and Kittiwake *Rissa tridactyla* (Coulson & Porter 1985) chicks are similar—those with greater fledging mass have a better survival rate. However, the trend may not be universal among all seabird species; no association has been recorded between fledgling mass and survival in Guillemot *Uria aalge* (Hedgren 1981) and Puffin *Fratercula arctica* (Harris & Rothery 1985). Heavier fledglings presumably have greater food reserves, so presumably once fledged they have a longer period to develop their own feeding ability than lighter fledglings. In addition, unfavourable wind conditions at the time of fledging may inhibit feeding (e.g. Dunn 1975) and so result in the death by starvation

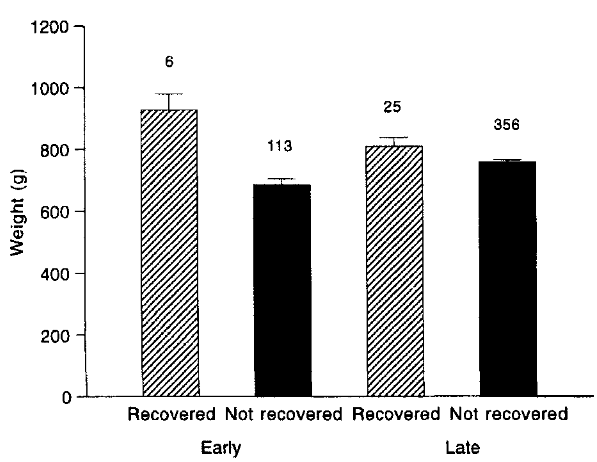

Figure 2. Mass (mean ± s.e.) of fledgling Sooty Shearwaters in two time periods. Numbers above error bars indicate the number of birds weighed.

of fledglings with lower food reserves. Such an instance was recorded by Stonehouse (1964), who reported the wreck of large numbers of fledgling Sooty Shearwaters along the east coast of the South Island, New Zealand, following a period of inclement weather at the time of fledging.

Richdale (1954) found that there was no significant difference in the dates at which light (<455 g) and heavy (>455 g) Sooty Shearwater fledglings left their burrows. Likewise in our study, the sample of birds which were found outside their burrows during the early period (15–23 April) were of lighter weight than those found later (29 April–7 May), but the difference was not significant. However, the difference in mass between the two periods probably explains the interaction between time and recapture probabilities, with recaptured birds significantly heavier than ringed individuals in the earlier but not in the later period.

Most Sooty Shearwater chicks have been deserted by their parents by 18 April (Richdale 1954, 1963), so continued feeding of chicks is unlikely to account for their higher mean mass in the later period. Warham *et al.* (1982) considered that light chicks which had been deserted emerged from their burrows sooner than heavy chicks because they were hungry.

One factor which may influence the results of our study is the degree of philopatry exhibited by males and females. In adult shearwaters, males tend to be larger than females, although the differences are slight (Warham 1990). In adult Sooty Shearwaters, male mass was about 95 g more than that of females (Marchant & Higgins 1990), although this finding was based on only three birds of each sex. In Manx Shearwaters, males have a higher degree of philopatry than females (Brooke 1978), but the philopatry in Short-tailed Shearwaters *Puffinus tenuirostris* is similar in both sexes (Serventy & Curry 1984). It may be that in Sooty Shearwaters, males have both a higher degree of philopatry than females and are heavier at fledging than females, which could account for the the result found in our study. However, data on sexual dimorphism in the mass of fledglings or the degree of philopatry by sex have not been reported for Sooty Shearwaters, so it is not yet possible to test the hypothesis that mass-related survival of fledgling Sooty Shearwaters is mediated by sex-related philopatry.

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Increased asymmetry of tarsus-length in three populations of Blackcaps *Sylvia atricapilla* as related to proximity to range boundary

The ability of individuals to thrive in a given region is considered to decrease towards the boundary of their range (Hengeveld & Haeck 1982, Brown 1984, review by Lawton 1993). The Mediterranean region is a peripheral area of the Palaearctic realm which shows pronounced droughts in summer, in contrast with more northern, mesic European sectors. Many forest passerines are scarce in Mediterranean forests and woodlands (Tellería & Santos 1993, 1994 for the Iberian Peninsula). Because most European forest passerines have a Palaearctic distribution (Blondel 1990a), such scarcity has been interpreted as a consequence of their decreased ability to thrive in this peripheral area. However, abundance may be a misleading indicator of habitat quality (Van Horne 1983). Thus, independent measures of the condition of individuals are required to confirm the unsuitability or otherwise of Mediterranean habitats for Palaearctic forest birds.

Blondel (1990b) has suggested that a critical season for bird survival in the Mediterranean region is the hot, dry summer, when high temperatures may cause nestlings to suffer hyperthermia and problems of water balance. This hypothesis may be tested by using the fluctuating asymmetry of bilateral traits as an index of the developmental stress experienced by birds. Fluctuating asymmetry is an indirect estimate of the fitness of individuals (Soulé 1967, Hoffman & Parsons 1991, Clarke 1995) that has been used to evaluate the increased stress of edge populations in other taxonomic groups (Parsons 1992). Because the growth of the tarsus is completed in passerines just before the fledging stage (Alatalo & Lundberg 1986, Potti & Merino 1994), its fluctuating asymmetry could be used as an index of environmental stress during the embryonic and early nesting periods.

Blackcaps *Sylvia atricapilla* occur throughout the western Palaearctic (Cramp 1992), inhabiting nearly all wooded habitats of the moist, northern Atlantic belt of the Iberian Peninsula (Fig. 1). In central Spain, however, they show a limited distribution, restricted to woodlands of moist mountains or river banks (Tellería & Santos 1993). Rainfall levels are, in fact, the best predictor of the distribution of Blackcaps in the Iberian Peninsula (Tellería & Santos 1993, 1994). Here, we suggest that the fluctuating asymmetry of tarsus length in breeding Blackcaps increases along the moist–xeric, latitudinal gradient of Iberian forests.

During 1995 and 1996, we studied breeding Blackcaps at three localities that cover most of the climatic gradient found in the Iberian Peninsula (Fig. 1): Alava (42°55'N, 2°29'W; altitude 620 m),