Catastrophic events in natural environments are generally infrequent but may cause large adverse effects. Although many ecological models allow for the inclusion of catastrophic events, the necessary data are usually lacking to assess their importance. Both demographic and environmental stochasticity, on the other hand, is more common, so it is reported and modelled more regularly (Akcakaya et al. 1997). Observations of a natural phenomenon (e.g. a breeding season) that coincidentally includes a catastrophic event (e.g. a climatic extreme leading to breeding failure) may be biased, yet this may not be obvious to the researcher unless long runs of observations are available. An understanding of the frequency, context and consequence of catastrophes is rare (Strayer et al. 1986) because long-term data sets are rare (Bradley et al. 1991) or may not be sufficiently detailed to explain causes and effects.

In the 1960s, a study was set up to monitor the interaction between Short-tailed Shearwaters Puffinus tenuirostris and Wedge-tailed Shearwaters P. pacificus on Montague Island, New South Wales, Australia. Observations were restricted to an annual measure of fledgling production from selected plots within the colony in order to sustain a long-term study with minimal breeding disturbance. These surveys have been conducted in the last week of March every year since 1960 (Fullagar et al. 1993), but more intensive studies have been conducted on various aspects of the breeding ecology of the shearwaters on Montague Island since 1994 (Schultz & Klomp 2000, Tiller 2002).

This paper describes the influence of two extreme rainfall events on the breeding success of shearwaters on Montague Island. The events occurred 28 years apart, in the 1970–71 and 1998–99 breeding seasons, although the earlier event has remained unexplained until now. We also consider the likely frequency of such catastrophes.

METHODS

Montague Island (82 ha; 36°26′S, 150°23′E) is situated about 10 km off the coast of southern New South Wales. Short-tailed and Wedge-tailed Shearwaters breed in mixed colonies on the island in roughly equal proportions (Fullagar et al. 1993, Fullagar & Heyligers 1998). However, in the three long-term study areas, the proportions vary. Up to 15000 pairs of shearwaters commence breeding on the island in November each year in a colony of about 7 ha. Chicks fledge the following April (Fullagar & Heyligers 1998).

Although data have been obtained since 1960, systematic investigation of two permanent study plots (a total area of 690 m²) started in 1967, with another plot (293 m²) added in 1992. These three study plots are known to be representative of fledgling production within the colony (Fullagar & Heyligers 1998). The content of every burrow in each of these long-term study plots is recorded every year in the last week of March, and all chicks present are weighed, measured and banded. As it is unlikely that a breeding attempt would fail at such a late stage of the nestling period, the chicks then present are assumed to fledge successfully (Fullagar et al. 1991).

In the 1998–99 breeding season, in addition to the usual annual monitoring of the long-term study plots, we observed two other study areas daily from 15 January until 31 March. In these two areas, we observed 151 burrows (75 Short-tailed and 76 Wedge-tailed Shearwater burrows) containing an adult incubating an egg.

Rainfall data for Montague Island between 1956–2003 were obtained from the New South Wales Regional Office of the Bureau of Meteorology. Supplementary records were used for the years when Montague Island’s rainfall data were not available: for Moruya Heads (35°91′S, 150°15′E) from 1876–1910 and 1921–25, and for Narooma (36°22′S, 150°13′E) from 1911–20 and 1926–55.

RESULTS

On average, the proportions of shearwater fledglings present in the long-term study plots were 70% Short-tailed Shearwaters, 29% Wedge-tailed Shearwaters, with the remaining 1% made up by the few Sooty Shearwaters P. griseus that also breed on Montague Island (not further considered in this study). The number of shearwater
chicks produced each year on Montague Island varied considerably over the period 1967–2003. The 1970–71 and 1998–99 breeding seasons were unusually unproductive (Fig. 1).

There was a significant negative correlation between the number of fledglings of each species and summer rainfall (December–February) during 1967–2003 ($P. tenuirostris$: $r = -0.597$, $n = 37$, $P < 0.001$; $P. pacificus$: $r = -0.570$, $n = 37$, $P < 0.001$; combined: $r = -0.693$, $n = 37$, $P < 0.001$). The combined species correlation maintains significant after removal of the two extreme rainfall seasons ($r = -0.459$, $n = 35$, $P < 0.01$). In the 1970–71 and 1998–99 breeding seasons, Montague Island experienced a total summer rainfall of more than 600 mm, with more than 460 mm in a single month within each season. The extreme rainfall event of 1971 occurred in February, when chicks were about one month old, whereas the rainfall event of 1999 occurred earlier, shortly after most chicks had hatched.

The next highest monthly total of 263 mm occurred during the 1991–92 breeding season. The fledging rate was considerably greater in 1991–92 than in either 1970–71 or 1998–99, suggesting that, although damaging, the 1991–92 summer rainfall was not enough to devastate the breeding season.

A detailed, day-by-day mortality pattern is available only for 1999 (Fig. 2), when 77 breeding failures (51%) occurred immediately after a period of heavy rain (286.6 mm) on 29–30 January. Four days earlier, 10 breeding failures were recorded after 88 mm of rain fell over a two-day period (Fig. 2).

The collapse or partial filling of burrows with sand brought in by flowing water was the principal cause of egg and chick loss between 15 January and 31 March 1999 (Table 1). Only two fledglings were found in 1998–99 on the three long-term study plots, compared with an average of 137 (range 94–194) fledglings over the previous seven breeding seasons.

Summer rainfall was regressed against fledgling production for the period 1967–2003 and was found to explain 48.1% of the variation in annual fledgling production ($F = 32.411$, $P < 0.001$; density $= -3.049$ (Rainfall) + 2461.37). This relationship can be used to calculate the hypothetical annual production of fledglings from 1876–1967 (Fig. 3).

**DISCUSSION**

Flooding in heavy rain is probably the most widespread and common natural hazard for burrowing Procellariiformes (Warham 1990). Serventy and Curry (1984) reported occasional flooding of burrows after unusually heavy summer rainstorms on Fisher Island, Tasmania, that caused “egg-failure” in 1966 and 1970, with burrows on lower ground becoming waterlogged. It is possible that poor breeding success reported by workers monitoring colonies sporadically in a season (e.g. Bradley et al. 1991) may have been caused by heavy rainfall at a crucial time. Although heavy rainfall in February 1971 was suspected to be the cause of that season’s breeding failure on Montague Island, it was not until January 1999 that we found corroborating evidence to support this assumption.

A prediction of the frequency of heavy rainfall events causing catastrophic breeding failure in the past can be made using rainfall

**TABLE 1**

Causes of shearwater breeding failures on Montague Island, 15 January–31 March 1999

<table>
<thead>
<tr>
<th>Cause of breeding failure</th>
<th>Species (number of burrows monitored), breeding failures (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Short-tailed Shearwater (75)</td>
</tr>
<tr>
<td>Burrow collapsed or filled</td>
<td>42.1</td>
</tr>
<tr>
<td>Chick death (adult last recorded in nest, with dead chick)</td>
<td>26.3</td>
</tr>
<tr>
<td>Adult desertion of chick</td>
<td>14.0</td>
</tr>
<tr>
<td>Adult desertion of an apparently viable egg</td>
<td>14.0</td>
</tr>
<tr>
<td>Unknown reason</td>
<td>3.5</td>
</tr>
</tbody>
</table>

Fig. 2. The occurrence of breeding failures in 1999 (broken line) and daily rainfall (bars).

Fig. 3. Comparison of shearwater fledgling density and summer rainfall (bars) during 1876–2003. The solid line represents the actual fledgling production from 1967 to 2003; the broken line is an hypothetical fledgling production based on rainfall.
data since 1876 (Fig. 3). Such catastrophic breeding failures would likely have occurred at intervals of approximately 30 years over the period 1876–2003. The rarity of catastrophic breeding events is unlikely to affect significantly the lifetime reproductive output of long-lived seabirds such as shearwaters.

This paper highlights the value of long-term studies in revealing rare or irregular events in ecology, although more intensive short-term studies may be required to analyse the effect of specific factors.

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