OBSERVATIONS ON COLONY SIZE, BREEDING SUCCESS, RECRUITMENT AND INTER-COLONY DISPERSAL IN A TASMANIAN COLONY OF SHORT-TAILED SHEARWATERS *PUFFINUS TENUIROSTRIS* OVER A 30-YEAR PERIOD

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SUMMARY

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A programme to mark a small colony of Short-tailed Shearwaters, by means of monel leg-bands, was begun on Fisher Island during 1947-50 as part of a comprehensive study. Banding of all adults and their young has continued every year since (to 1980).

The number of breeding burrows occupied each year declined steadily during the first 25 years of the study, at the end of which numbers had been reduced by 71%. More recently, numbers have begun to increase again. No change has occurred in the relative sizes of three sub-colonies existing within the island. Annual rates of breeding success were usually lower than those reported from other less-studied colonies and have tended to be either relatively high (> 55%) or else poor (< 40%). Some chicks were raised every year; on average, the smallest sub-colony was as successful as the largest.

Nearly all breeding failures occurred before the chick-rearing stage and few successfully hatched chicks failed to fledge. No banded young were recaptured at the colony before age two and most not until three years and upwards. Age at first breeding for both sexes ranged from five to at least ten years. Forty-one per cent of chicks banded over 20 consecutive seasons were subsequently recovered alive on their natal island but only 35% of these were recruited as breeders. Losses of immatures and young adults through emigration were offset by an annual recruitment of unbanded immigrants, most of which could not have been bred on the island. After 30 years, the proportion of Fisher-bred breeders in the colony was stable at 41-46%. Band recoveries confirmed inter-colony dispersal by young adults. Fisher-bred birds found in nearby colonies were encountered mainly in the nearest breeding area on the closest neighbouring island.

Repeated disturbance of the colony during the course of the study is thought to have contributed to the decline of the colony, due to increased burrow desertion, decreased breeding success and decreased recruitment of young adults.

INTRODUCTION

This paper describes aspects of the dynamics of a colony of Short-tailed Shearwaters *Puffinus tenuirostris* breeding on Fisher Island in north-western Tasmania. Banding of the Shearwaters began in 1947, when young birds were fitted with copper leg-bands. More intensive banding, using highly durable monel bands, began in 1950 and has continued annually ever since under joint support by the Tasmanian National Parks and Wildlife Service (formerly the Fauna Board of Tasmania) and CSIRO Division of Wildlife Research. This is the first of a series of papers that will review long-term findings from the Fisher Island project in the light of 30 years' survey and recapture data. An earlier unpublished analysis indicated that 20 years' data were often insufficient to facilitate assessments of parameters in the life-history of this long-lived and commercially-exploited seabird.

Published findings on the species and the study area include Marshall & Serventy (1956, 1959), Serventy (1956a, 1957a, 1957b, 1958, 1961, 1963, 1967, 1974, 1977), Serventy & Farner (1959), Serventy, Serventy & Warham (1971), Naarding (1979-81), Norman (1970) and Skira & Wapstra (1980).

Short-tailed Shearwaters while on land are almost entirely nocturnal. Birds begin to arrive at their breeding colonies in late September. During October birds scratch out existing burrows or dig new ones, often close to and sometimes running into adjoining burrows. Pairs copulate on land and then depart to sea for about 20 days before they return to the burrow to lay in late November. The single egg is laid between 23 and 28 November in 85% of instances reported throughout the geographical spread of known colonies. Lost or unsuccessful eggs are not replaced. Incubation averages 53 days and is undertaken in shifts that are begun by males and often last more than 10 days. The chick hatches between 10 and 23 January, is brooded for about 2 days and is then left during the daytime. Together, parents feed the chick, nightly at first and then less often. The chick remains unfed for 3-15 days between the parents' last visits some time in late March or early April. Fledglings emerge from their burrows on April nights, exercise their wings and remain unfed until they fly to sea, usually in late April.

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Shearwaters other than those actually breeding or attempting to breed underground have been found to come to ground in and around the colonies. They do this at various times, landings most often occurring on nights of peak activity by the breeders. Visitors consist of immatures and young adults which have not yet begun to breed. Banding returns show that juvenile and immature birds, at least, leave the Bass Strait region in autumn and head east and then north into the Pacific Ocean, skirting Japan to reach the north Pacific during the northern summer. They return across the central Pacific and arrive on the eastern seaboard of Australia in spring.

In some ways, the Shearwater colony on Fisher Island is unusual. It is exceptionally small and supports less than 0.002% of an estimated 11.4 million breeders in Tasmania (Naarding 1979–81). Its small size has meant that a banding study could be undertaken on its entire breeding stock, enabling the life-histories of individuals to be followed. In this paper, we examine the record of the colony as a whole, prior to an analysis of the breeding lives of known individuals which is planned for future publication.

METHODS

Burrow occupation

Every burrow entrance found on the island was marked with a numbered peg. Burrows are sited in three sub-colonies, named Home Rookery, South Rookery and Potts Point. The sub-colonies are separated by areas of shallow soils that evidently prevent burrowing over much of the intervening ground. Descriptions of the sub-colonies are given in Serventy (1957a, 1977) and Gillham (1965).

The number of burrows in which one or more birds were found during daytime each breeding season has been taken as the rate of burrow occupancy. Although numbers of burrows in which an egg was laid would appear to be a more direct measure of the number of pairs actually breeding, later findings of chicks suggest that fieldworkers have had only moderate success in locating eggs in the longer or more convoluted-burrows. The efficiency with which eggs were found may also have varied with the skill, persistence and arm-length of different observers. By giving recognition to all birds found underground, we include with active breeders the failed pairs, and prospecting individuals, which together make up the overall 'burrow population'.

Every bird found in a burrow was banded and replaced, or, if already banded, its band and burrow numbers noted at each handling. Recapture data prior to 1950 are fragmentary because of the rapid wear and evident loss of the copper leg-bands used before that year. Adults were sexed by cloacal examination (Serventy 1956b); immatures could not be sexed in the field. We refer to any particular breeding season by the calendar year in which it began.

Inspections during the breeding cycle

Effective timing of the fieldwork carried out between November and April in each breeding season was made simple because of the extreme calendar precision and synchronization of breeding events.

Since 1947 each burrow has been inspected several times each summer to determine its occupants and contents. In the early years efforts were made to check burrows at frequent intervals, in some cases daily, in order to elucidate patterns of attendance prior to egg-laying, dates of laying, incubation strategies, parental attendance of the chick, feeding frequency and chick weights. In most years from 1960 onwards, burrows were first inspected in late November or early December, when an inventory of the incubating males was drawn up. A second inspection of all burrows followed in mid-December, when incubating females undertaking their first shift could be expected to be present. A third series of inspections was carried out each mid-March to early April, by which time chicks had grown sufficiently large to be relatively easy to locate underground and to retain a leg-band.

Above-ground recoveries of non-breeders

Birds that had not otherwise been recorded as members of the season's burrow population were found at night, when they landed in and around the sub-colonies at various times during each breeding cycle. Fieldworkers discovered that among such visitors were Fisher-bred immatures, often returning to the vicinity of the natal burrow, when aged 3 (rarely 2) years or over. By patrolling the surface of the island at night many early recaptures of known-age and sexually immature birds were made (Serventy 1967).

Before 1975 night patrols were made at any time when observers were present on the island. In recent years increasing concern that capturing and recapturing incoming and outgoing birds at night might disturb breeders led to a curtailing of night patrols until after the hatching period.

Sampling Shearwaters in the nearest neighbouring colony

The nearest of many larger colonies of Shearwaters on islands close by is that on Little Green Island, less than 2 km SE of Fisher (Fig. 1).

Each year from 1959 to 1971 visits were made to sample Little Green Island's Shearwaters to detect interchanges that the birds might make between adjacent islands. Shearwaters were caught above ground at night and in burrows by day, in various sections of the several thousand burrows on the island. Although birds were caught in virtually every part of Little Green Island at one time or another, most sampling effort was directed at the sub-colonies and headlands on the western end of the island, which faces Fisher Island.

In general, birds removed from burrows were banded but surface birds were merely checked for bands.

RESULTS

Number of occupied burrows

Some burrows were probably missed during the first census, in 1947. Over the course of the next 25 seasons, from 1948 to 1972, the number of occupied burrows on the island fell by 71% (Fig. 2). Since 1973, there has been no further decline, rather a slight increase to 32–37% of the 1948 total. The decline witnessed before 1973 affected all 3 sub-colonies equally; their relative numbers of occupied burrows have not changed appreciably in 30 years.

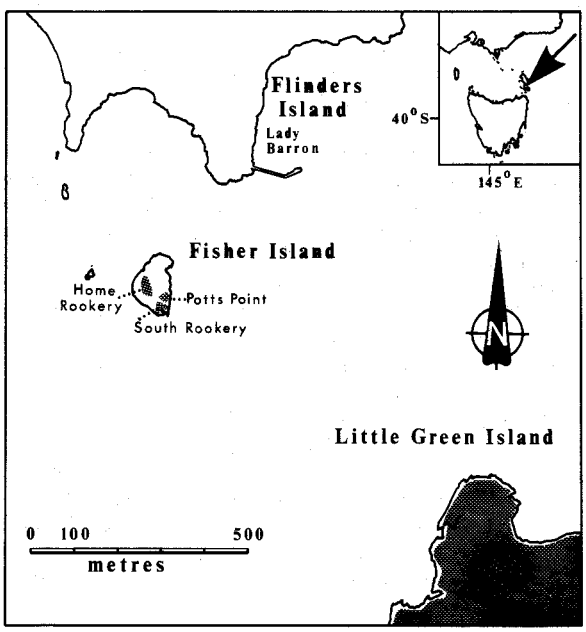

Figure 1. Map of part of Bass Strait, showing the position of Fisher Island and areas with burrows (hatched) on Fisher and Little Green Island.

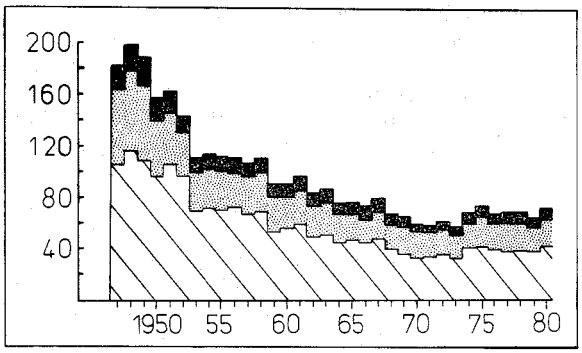

Figure 2. Numbers of occupied burrows, 1947–80. Upper section: Potts Point, middle section: South Rookery, lower section: Home Rookery.

Breeding evidence

Assessments of laying and hatching success are made more difficult because some eggs laid in burrows were evidently missed by observers; chicks are easier to locate and were fairly often found in burrows where no egg had been recorded during inspections made in the incubation period. The proportion of eggs not found can be estimated from the numbers of growing chicks later found and banded in burrows where no egg was recorded. As they grow, chicks become progressively easier to locate underground; it seems very unlikely that more than the occasional one could have avoided detection during burrow inspections made just before the fledging period. Chicks remain in their natal burrows until they are virtually full-winged and begin to emerge above ground at night. Eggs were found in 77% of burrows in which chicks were subsequently located. Actual rates of egg-detection may have been higher than this if the burrows in which eggs were found had their chances of success diminished by the more direct interference with the egg and the sitting bird.

Breeding success and failure.

Of 1,969 eggs found underground between 1950 and 1980, 965 (49.0%) gave rise to large chicks that were banded. The remainder failed at some stage. In the period from 1950 to 1969 when burrow records were most comprehensive, 54.3% of eggs were not successful and all but a small proportion of these failures occurred during incubation and hatching and were due to desertion by one or both parents, or the egg being physically damaged or both (Table I). The circumstances of many documented failures imply that burrow inspections, which were carried out daily in some instances, often alarmed the sitting bird. These disturbances were often linked with eggs becoming cracked or broken or were followed by desertion of the egg or hatching chick.

TABLE I

Circumstances of eggs that failed to give rise to banded chicks, 1950–69.

Evidence of failure	Number of cases	% of failures
Egg found damaged prior to any evidence of desertion	103	13.1
Cold, undamaged egg found deserted during incubation phase	247	31.4
Egg incubated to some stage but neither chick nor egg found during inspections for chicks	333	42.3
Unhatched egg found during inspections for chicks, and not previously known to have been deserted	82	10.4
Successfully hatched chick died or disappeared before reaching banding age	22	2.8
Totals	787	100

Another cause of egg-failure was the occasional flooding of burrows after unusually heavy summer rainstorms, such as those in 1966 and 1970. Burrows on lower ground, as are most of those in Home Rookery, tended to become waterlogged white those on elevations, notably at Potts Point, did not. As a result, in years of heavy summer storms the smallest sub-colony produced more young than the largest, although annual chick productivity at Potts Point correlates highly significantly with the island as a whole ($r_{29} = 0.76$, $p < 0.001$).

Over 32 consecutive seasons, chicks were reared to banding age in 44% of all occupied burrows. The number of occupied burrows per annum (mean 93) correlates significantly with the number of chicks reared per annum (mean 39, $r_{28} = 0.338$, $0.025 < p < 0.05$) and highly significantly with the number of eggs found in burrows per annum (mean 65, r_{28}, $p < 0.001$). Numbers of eggs located per annum correlate significantly with numbers of chicks reared per annum ($r_{28} = 0.325$, $0.025 < p < 0.05$) although there was variable annual success (Fig. 3). In most breeding seasons the colony as a whole has been either relatively successful (55–76% in nineteen seasons) or unsuccessful (17–37% in eight seasons). The presence of fieldworkers during the growth period did not correlate with the few chick failures observed, in fact no chicks are known to have died or disappeared in years when catching effort for surface birds was high after the hatching period.

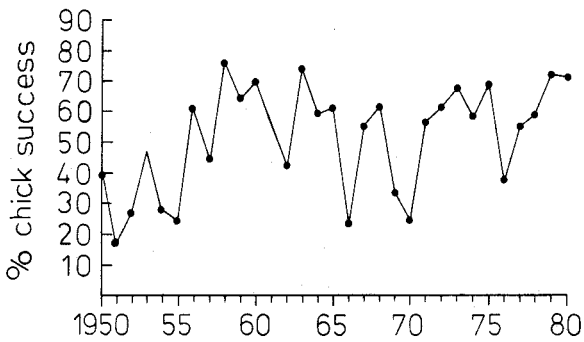

Figure 3. Annual breeding success, as percentage of eggs that produced banded chicks, 1950–80.

Dispersal and recapture of young

Almost all of the chicks banded in their burrows apparently fledged successfully, so numbers banded and fledging are similar. Fledglings derived from the monel-banded chicks during the first twenty seasons make up the sample on which we base an analysis of recoveries. The birds returning from later seasons may not all be known until ten years after fledging, so more recent cohorts are possibly incompletely known and have not been included here. Only one (0.1%) of the twenty seasons' young from Fisher Island (N = 922) was recovered far from the Furneaux Group: it was found dead in its fourth year at St. Lawrence Island, Alaska (Serventy 1961). Otherwise, 389 (42%) of those fledging returned and were recaptured on Fisher Island or nearby (Table II). Their ages at first recapture varied from 2 to 8 years. All but 16 of these were recaptured on Fisher Island at least once and 338 were recaptured nowhere else. The proportion of each season's offspring which was recaptured alive on the natal island varied from 16% (1955) to 61% (1951 and 1961; Table III).

During the study evidence accrued that inter-island visits and interchanges took place among immature birds and young adults not known to have begun breeding. On Little Green Island, recaptures of Fisher-bred Shearwaters were made almost routinely (see below) with those that had previously been recaptured on Fisher Island outnumbering those that had not by a ratio of 2: 1.

Recruitment

Only 35% (129/373) of the immatures that returned during the first twenty seasons bred (i.e. occupied a burrow in which an egg or chick was found) on Fisher Island in subsequent years. The recruitment rate was the same for both sexes. During the first 10 years in which locally-fledged birds of known age joined the breeding populations, females tended to begin breeding at a lower age than males (Serventy 1967). Figure 4 shows that, in a larger sample of individuals beginning to

TABLE II

Recoveries from 922 chicks banded on Fisher Island over 20 years, 1949–68.

Type of recovery	No. of birds	%
Total banded	922	100
Recovered alive	398	43.2
Recovered alive on natal island	382	41.4
Recaptured alive on Fisher Island and nowhere else	338	36.7
Recaptured alive on Fisher Island and subsequently at Little Green Island	34	3.7
Recaptured alive on Fisher Island after recovery on Little Green Island	4	0.4
Recaptured alive on Little Green Island without prior recovery	13	1.4
Recovered dead N. Hemisphere (Alaska)	1	0.1
Recovered dead before leaving birthplace	4	0.4
Not recaptured	519	56.3

TABLE III

Annual totals of chicks banded at the 3 sub-colonies over 20 years and numbers from each cohort subsequently recovered on Fisher Island (in brackets).

Season	Sub-Colony						Totals		% returning
	Home Rookery		South Rookery		Potts Point				
1949	8	(2)	7	(3)	5	(4)	20	(9)	45
1950	41	(14)	14	(1)	8	(2)	63	(17)	27
1951	16	(9)	5	(3)	2	(2)	23	(14)	61
1952	22	(10)	11	(1)	2	(1)	35	(12)	34
1953	50	(19)	21	(9)	10	(3)	81	(31)	38
1954	14	(10)	9	(3)	5	(1)	28	(14)	50
1955	15	(3)	11	(2)	5	(0)	31	(5)	16
1956	50	(27)	13	(2)	9	(2)	72	(31)	43
1957	34	(9)	17	(3)	7	(1)	58	(13)	22
1958	38	(11)	17	(7)	10	(3)	65	(21)	32
1959	31	(11)	15	(7)	5	(3)	51	(21)	41
1960	35	(14)	17	(8)	9	(5)	61	(27)	44
1961	34	(20)	14	(9)	8	(5)	56	(34)	61
1962	19	(10)	9	(7)	6	(2)	34	(19)	56
1963	39	(19)	18	(10)	6	(1)	63	(30)	48
1964	30	(16)	11	(5)	5	(1)	46	(22)	48
1965	24	(12)	15	(6)	4	(1)	43	(19)	44
1966	4	(2)	3	(1)	6	(2)	13	(5)	39
1967	24	(9)	12	(5)	4	(1)	40	(15)	38
1968	25	(16)	11	(6)	3	(1)	39	(23)	59
Totals over 20 y.	553	(243)	250	(98)	119	(41)	922	(382)	41.4

breed over a 20-year period, there is little difference in the range of ages at which males and females first bred, 5 years being the minimum age for both. These distributions, between ages 5 and 10 years, are not significantly different when tested by likelihood ratio tests against a log-linear model, or by the Mann-Whitney U test or the Wald-Wolfowitz runs test (Siegel 1956).

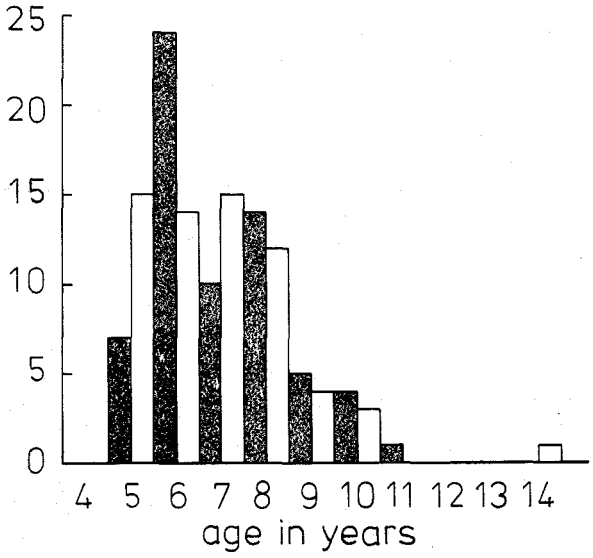

Figure 4. Age at first known breeding for recruits from 1949–68 fledglings males (shaded); females (open).

As expected, the proportion of known-age birds in the burrow population grew steadily and, by 1968, birds banded as chicks over the first fifteen seasons made up 40% of the total (Fig. 5). Since then, the proportion of known-age birds has remained steady at 41–46%. As well as locally-banded recruits of known age, individuals first found either as unbanded surface birds or as unbanded newcomers have continued to be recruited into the burrow population throughout the study period. Of 68 unbanded birds found in the burrows since 1954, 31 were males and 37 were females, so no difference in sex ratio is implied ($\chi^2_1 = 0.37$, $p > 0.05$).

Evidence of emigration and immigration

Large numbers of Shearwaters alighting on Little Green Island at night were checked for the presence of banded birds. Immatures and young adults that had been banded as chicks on Fisher Island were found among large numbers of unbanded non-breeders visiting this neighbouring colony. Between 1959 and 1971, over 16,000 'surface birds' were caught and checked for bands, mostly by C.A. Nicholls. Fisher-bred birds were

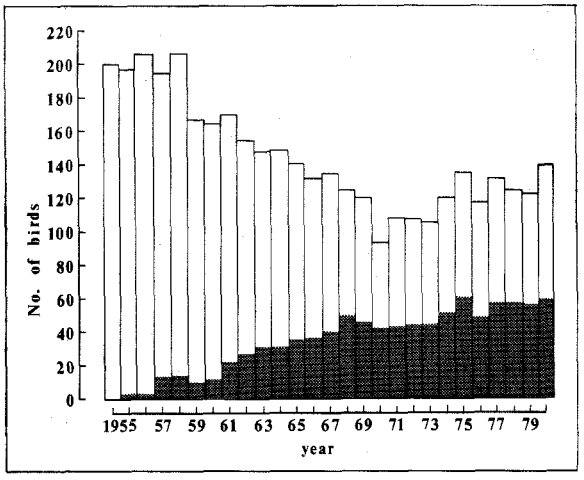

Figure 5. Numbers of Fisher-bred birds (hatched histograms) in the burrow population (open histograms), 1954–80.

found there every year but one, with an overall recapture rate of 1.0% of all birds picked up.

Conversely, six Shearwaters banded as chicks on nearby islands. Little Green, Little Dog and Great Dog were recaptured at Fisher Island, first appearing at ages between three and seven years. Two of these were subsequently recruited to the burrow population. No birds banded further afield have been recovered on Fisher. In all, approximately 73,000 individuals were banded at various colonies in Victoria, New South Wales, South Australia and elsewhere in Tasmania over 18 consecutive seasons beginning in 1956; numbers banded in the Furneaux and Kent Islands between 1950–74 represent 92% of the Tasmanian total (approx. 38,440) for that period.

Surveys of the burrow population on Little Green Island confirmed that some Fisher-bred Shearwaters took up residence in this adjacent colony. The incidence of Fisher-bred birds was evidently highest in the area of burrows nearest to Fisher Island, where 5 (2.5%) were found among a sample of 200 birds checked in early 1970 and 8 (3.2%) in 248 found in a similar sample in early 1972. Fisher-bred birds were less frequent in burrows sampled away from the north-western peninsula in early 1971: 2 (0.4%) in 517 birds ($\chi^2 = 9.6$, $p < 0.01$).

Age-structure of burrow population

The number of known-age birds has never exceeded 60 in any one year, so it is necessary to group data from successive years to compose a picture of age-frequencies occurring after 21–30 years of annual banding. In Figure 6, the upper limit of the age-distribution is 21 because that was the age of the recruits from the 1949 season in 1970. Shearwaters aged 22 to 30 years accounted for 10.6% of the known-age birds over a period when the proportion of known older birds was still rising steadily. The median age of this cumulative sample is 11.9 years, modes being 6 for males and 11 for females; overall, the age-distributions of the sexes are similar.

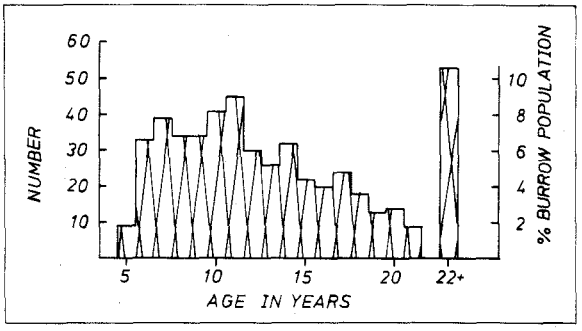

Figure 6. Numbers of each age group among the known-age birds occupying burrows, expressed cumulatively from ten breeding seasons (1970–79) 20–29 years after monel banding began.

DISCUSSION

Age-Composition

Recapture data show that 30 years after annual banding began, the average age of the breeding birds was still on the increase as birds recruited from the first breeding season lived on. In other words, the study had not yet outlived one generation of Shearwaters. Between 20 and 30 years after banding with monel bands began, birds aged 10 and 11 were, on average, the most numerous in the colony, although most individuals began breeding between ages 5 and 8. This implies that not all living members of the colony may have been breeding every year, at least during young adulthood.

Local and inter-island recruitment

Far from entirely replacing their parents, locally-bred banded birds made up less than 50% of the birds in burrows at the close of the 30-year period. The continued recruitment of unbanded birds could be accounted for if a large proportion of locally-bred birds lost their bands. However, examination of many long-lived breeders has shown that bands less than 10 years old rarely warrant replacement through loss of legibility, and they do not often wear to the point of actual loss in less than 20 years. Such losses as these would be of little consequence because all of the offspring that have

returned with their bands still fitted have been recaptured before the age of 10. The subsequent fitting of additional new bands acts as an insurance against the possible loss of a worn band.

Rather than being due to significant deficiencies, either in band durability or burrow survey technique, the continued recruitment of unbanded birds appears to be due to consistent immigration from outside the colony. After 21-23 years, banded Fisher-bred recruits made up approximately 40% of the breeders in the natal colony and also about 0.5% of the larger neighbouring colony, where emigrants were most in evidence in the section nearest to the natal island. It seems possible that, on average, roughly half of the surviving young adults emigrated, mostly to nearby colonies, while immigrants accounted for about the same proportion of recruits manifest as the unbanded birds found underground. From a 20-year sample, 14% of all fledgling Shearwaters were recruited to the natal colony. Dunnet *et al.* (1979) found that only 3% of Fulmars *Fulmarus glacialis* that fledged at Eynhallow were recruited to that colony, attributing this to a loss of 89-94% of surviving birds through emigration. Brooke (1978) detected a sex difference in the dispersive tendencies of Manx Shearwaters *P. puffinus* on Skokholm, where apparently few males but about half the females emigrated. On Fisher Island, the sex ratio of immigrant *P. tenuirostris* appears to be equal, which suggests that both sexes have a tendency to emigrate.

Causes of decline on Fisher Island

There is very good evidence that most of the Short-tailed Shearwater colonies in Tasmania that have been monitored have increased in area over recent years (Naarding 1979-81). The Shearwaters' decline on the Fisher Island over a 25 year period from the inception of the study is not consistent with the expansive trend in the Bass Strait region. Instances of colony decline are usually attributed to rather drastic local affects, such as from soil erosion or compaction, fire, predation by feral cats or excessive harvesting of mutton-birds. None of these is apparent on Fisher Island. Gillham (1965) gave botanical evidence to suggest that the small sub-colony at Potts Point was not as old as the other two but there has been no shift in the distribution of site preferences between the sub-colonies. Dunnet *et al.* (1979) detected a shift in the distribution of Fulmar nests around their study island over 28 years. We have no reason to think that suitable burrows, or sites for burrows, have been in short supply. Every year, some burrows have remained unoccupied, but unused burrows are said to occur in even the most rapidly expanding colonies of this species (Naarding 1979-81) and also in colonies of Sooty Shearwaters *P. griseus* (Richdale 1963).

Breeding success on Fisher Island has tended to be low compared to that found in other colonies during *ad hoc* surveys of burrows where no banding was involved (Table IV). High losses often incurred during incubation do not seem to be a function of the small size of the Fisher colony, and the smallest sub-colony has been at least as successful as its main part. On the whole, breeding seasons have tended to be reasonably successful or else poor. Even in 'good' years, success has been perhaps 5-30% lower than expected from rates observed in less-studied colonies. Ollason & Dunnet (1980) found that the presence of fieldworkers, particularly during the hatching period, was implicated with lowering overall breeding success in a Fulmar colony. Short-tailed Shearwaters seem to be unusually

TABLE IV

Comparisons of breeding success in Tasmanian colonies.

Year	Locality, success criterion* and study		%	% egg success Fisher Island
1965	Big Green Island; egg success		65	61
1966	" "		74	23†
1967	" "	(Norman 1970)	74	55
1978	Cape Queen Elizabeth; hatching		93	59
	Hunter Island		68††	
	Clifton Bluff	(Naarding 1979-81)	59††	
1979	Cape Queen Elizabeth; hatching		95	72
	Walker's Island		82	
1980	Cape Queen Elizabeth	(Naarding 1979-81)	92	71

* egg success denotes egg to large chick; hatching success denotes egg to small chick

† flooding implicated in losses
†† feral cats implicated in losses

sensitive to disturbances at the nest (Serventy *et al.* 1971, p 129); at any time these can cause one or both of a pair to abandon the nesting burrow at least temporarily, and the chances of this leading to failure appear greatest during incubation. Fledging success does not appear to have been similarly lowered, which suggests that neither night nor daytime surveys disrupt the post-hatching activities of parents in the same way. Observers engaged in examining other, scarcer, burrow-nesting seabirds, might, therefore, minimise the adverse effects of their fieldwork by timing their studies to avoid the incubation period whenever possible.

Disturbance of 'prospecting' birds caught either above or below ground early in the breeding season has probably contributed to the fall in numbers. Analysis of the recapture patterns for immature Manx Shearwaters returning to Skokholm led Perrins *et al.* (1973) to conclude that birds on the surface 'learned to avoid recapture'. Shearwaters returning as immatures and prospective breeders are presumably less likely to become recruited if they are recaptured, sometimes repeatedly, soon after coming to ground in a colony where they have little or no experience at landfall. More than two-thirds of the proven emigrants found on Little Green Island were originally recaptured as immatures on Fisher Island.

Night patrols made during the pre-laying weeks in earlier years may also have contributed to the start of some birds' breeding being delayed until later years. No males from the first ten year-cohorts to return to the island bred when aged 5, while small numbers did in later years.

It is especially interesting to note that in later years, when fieldworkers' visits have been restricted to monitoring attendance after laying, subsequent breeding success and banding the young, the colony has not become quickly repopulated to its former numbers. A greater understanding of lifelong breeding strategies and of the social factors that operate in mate-selection and recruitment may shed some light on this.

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