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THE SHORT-TAILED SHEARWATER: A REVIEW OF ITS BIOLOGY

IRYNEJ SKIRA

Department of Parks, Wildlife and Heritage, 134 Macquarie St., Hobart, Tas 7000

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The life history of the Short-tailed Shearwater *Puffinus tenuirostris* has been well documented since it first came to the attention of naturalists. Approximately 23 million birds breed in about 250 colonies in southeastern Australia from September to April. The Short-tailed Shearwater commences to breed when 4 to 15 years. During their completed lifetimes 27 per cent of all individuals produce no young and 19 per cent only one chick. Mortality is age-related with the median survival time for breeding being 9.3 years after first breeding. Many areas remain open for study, with a particular need for interdisciplinary research that includes oceanography.

INTRODUCTION

The Short-tailed Shearwater *Puffinus tenuirostris*, commonly known as the Tasmanian muttonbird, is one of about 100 species in the Procellariiformes. The diagnostic feature of the order is the external nostrils produced into tubes extending onto the bill. Other distinctive features are the hooked and plated bill, and the glandular part of the stomach which is greatly extended and produces the well known 'oil', actually wax esters (Warham 1977). Most members in this order have a distinctive musky odour.

The family Procellariidae is the most diverse group in the order and contains 61 species of petrels and shearwaters (Serventy *et al.* 1971). The majority are nocturnal and nest in holes, burrows or crevices, which serve to protect them and their young from predators. The genus *Puffinus* consists of 15 medium-sized species that are among the world's most numerous seabirds. Their high nesting densities and their fidelity to a particular site has meant that they are highly vulnerable to exploitation (Serventy *et al.* 1971). The harvesting of Short-tailed Shearwaters, or muttonbirding as it is known in Tasmania, is one of the best documented instances of seabird harvesting (Skira 1987, 1990).

The Short-tailed Shearwater was one of the first Australian birds to be banded in large numbers (Serventy 1957, 1961) and to be subjected to a long-term scientific study (Guiler *et al.* 1958). This study was commenced on Fisher Island in the Furneaux Group of Tasmania in March 1947 by Dominic Serventy formerly of the CSIRO (Serventy 1977) and continues to the present, 42 years later. Due to the long-term nature of the study together with the banding of some 92 000 birds in Australia, the life history of the Short-tailed Shearwater is one of the best documented in the world of any bird (Bradley *et al.* 1989, 1990; Serventy 1974; Serventy and Curry 1984; Wooller *et al.* 1988, 1989, 1990).

EVOLUTION

The Procellariiformes are an ancient group of birds that probably originated from aquatic birds present at the end of the Cretaceous, some 64 million years ago. The phylogenetic history of shearwaters is little known (Kuroda 1954). According to Olson (1985 p.211), 'most of the modern species-groups, or subgenera, of *Puffinus* were in existence by the Middle Miocene, and there has been very little morphological change within these lineages in 15 million years or so'.

P. tenuirostris has not been found in any deposits apart from pre-historic archaeological sites (Bowdler 1984; Friedman 1934a and b, 1941; Vanderwal and Horton 1984). One of the fossil procellariids, *P. conradi* from the Middle Miocene of Maryland, USA, seems to have lived to the Pleistocene, one million years ago. *P. tenuirostris* may have evolved from a *P. conradi*-type ancestor through the *P. inceptor* line (Kuroda 1954). *P. inceptor* is known from the Middle Miocene of California suggesting that *P. tenuirostris* and its congener the Sooty Shearwater *P. griseus* which is abundant in New Zealand, were differentiated in the North Atlantic-North America areas. Having settled in the Southern Hemisphere, perhaps as late as the Pleistocene, their postbreeding migration may be an instinctive response to return to the Northern Hemisphere (Kuroda 1954; Marshall and Serventy 1956).

The fossil record left by seabirds in Australia is meagre compared to that of the Northern Hemisphere. It spans too short a period of time and is too low in diversity to test biogeographic hypotheses. The oldest petrel and shearwater fossils occur in the late Pleistocene or Holocene from coastal deposits around mainland Australia and Tasmania. In these deposits the genera *Pterodroma* and *Puffinus* predominate (Rich and van Tets 1982).

The interval from 25 000 to 10 000 years before present was a period of great faunal and climatic change in Australia. Climatic disruptions would have affected the location of Short-tailed Shearwater colonies through changes in sea levels. At times, the coastline was up to 50 km away from its current position (Blom 1988; Jennings 1971).

DISTRIBUTION AND ABUNDANCE

The Short-tailed Shearwater only breeds in Australia. There are known to be at least 167 colonies around the coast of Tasmania and its near offshore islands. The total area of these colonies is 1 522 ha and the number of burrows is estimated at 11.4 million (Skira *et al.* 1986). The largest colonies are in Tasmania, on Babel Island with 2.86 million burrows and Trefoil Island with 1.54 million burrows (Towney and Skira 1985a and b). Of other Australian States, Victoria has 1.45 million burrows in about 30 colonies (Harris and Norman 1981), South Australia 600 000 burrows in 33 colonies (A. C. Robinson, pers. comm.), New South Wales 25 700 breeding pairs in 13 colonies (Lane 1979) and Western Australia 10 000 burrows in several colonies (Johnstone *et al.* 1990a and b; Lane 1983). It is estimated that 23 million birds breed in about 250 colonies. Recent research by Japanese biologists has concentrated on mapping vegetation types in several colonies in Tasmania (Kuroda 1986).

MIGRATION

The Short-tailed Shearwater is a circum-Pacific migrant spending the boreal summer in the Northern Pacific region (Fig. 1). Sexually immature birds depart from Australia near the end of March, followed by the breeding birds around mid-April, with the fledged chicks leaving at the end of April to early May. The shearwaters migrate rapidly (Serventy 1956) and arrive in the Northern Hemisphere on a broad front across the central Pacific Ocean (Shuntov 1974; Maruyama *et al.* 1986).

Most arrivals to the northern part of the Pacific Ocean are from the end of April to the end of May or the beginning of June. The largest flocks can be observed in the eastern part of the Bering Sea in the Northern Hemisphere spring and the beginning of summer. In the second half of summer many pass into the Chukchi Sea, and while birds are still dispersing into the Chukchi Sea migration southwards begins. Some birds also migrate along the North American coast and others across the Pacific between the Hawaiian Islands and North America (Shuntov 1974). This results in very large flocks occasionally occurring off the west Canadian coast in May under certain wind conditions (Guzman and Myres 1983).

In the Gulf of Alaska, the Short-tailed and Sooty Shearwater are the dominant birds in spring and they prefer the continental shelf, which is between 100 and 150 km offshore (Harrison 1982). Numbers are greatest in May and by June their estimated density has dropped by half. In the north-east of the Gulf, the Kodiak area, Short-tailed Shearwaters outnumber Sooty Shearwaters by about 1.2:1 with flock sizes numbering 32 000 (Gould *et al.* 1982).

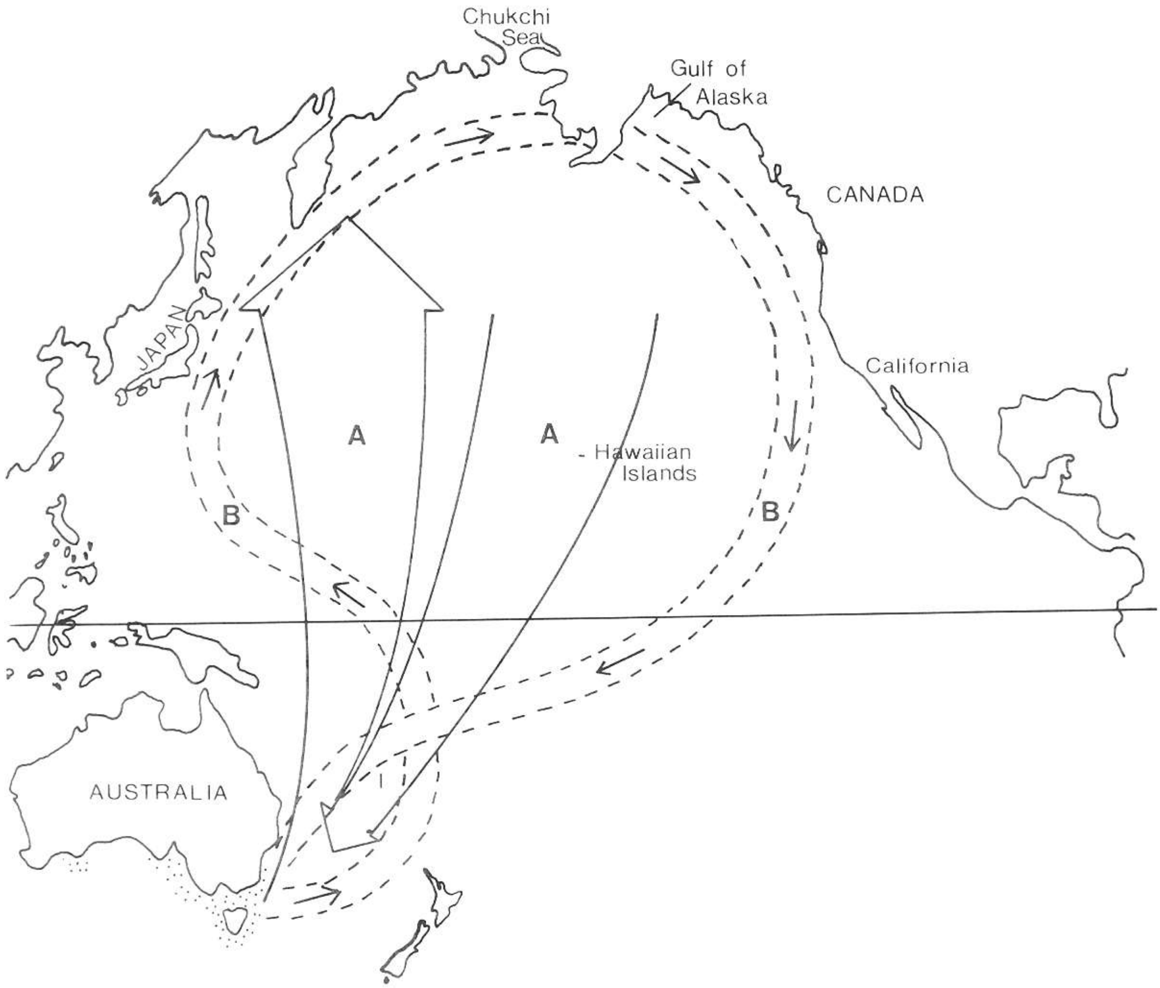

Figure 1. *Map comparing new migration route (A) of Short-tailed Shearwaters based on Japanese ship-board surveys to the figure-of-eight movement (B) of Serventy (1953). Breeding areas are stippled.*

The return journey commences at the beginning of September. Many Short-tailed Shearwaters have been observed moving through the western sector of the Pacific (Maruyama *et al.* 1986). Some flocks pass south and well offshore through the Gulf of Alaska to off California before heading across to Australia, but a lack of sightings indicate that there is no migratory movement along the Canadian coast after August. Some birds remain in the Northern Hemisphere during their first boreal winter (Forsell and Gould 1981). The presence of birds along the coasts of Japan and North America led Serventy to postulate a figure-of-eight migration (Serventy 1953). However, data from seabird surveys by Japanese ornithologists indicate that migration occurs on a broad front across the Pacific Ocean (Maruyama *et al.* 1986). Regardless of route, it is apparent that the movement of shearwaters between the two hemispheres occurs on a very broad front. It is possible that the route followed varies with the age or specific behaviour of the bird.

FEEDING

Shearwaters commonly form large aggregations on the sea surface called 'rafts'. These are common in calm weather and birds may thus assemble either when feeding or resting. Short-tailed Shearwaters are one of the most aquatic of the shearwaters and have a long narrow pelvis and compressed tarsum, well developed knee-joint process, long sternum, short thick compressed humerus and short smooth body plumage (Brooke 1990; Kuroda 1954). They have been seen up to 10 m below the surface pursuing prey (Skira 1979). Their feeding methods (after Ashmole 1971) ranked in order of importance are: pursuit plunging in which birds chase their prey after plunging into the water; surface seizing; pursuit diving; scavenging; hydroplaning; and bottom feeding (Morgan 1982; Morgan and Ritz 1982; Ogi *et al.* 1980; Skira 1979). During the breeding season the Short-tailed Shearwater is a neritic feeder obtaining its food close to the colony. Food, in order of importance (% frequency of occurrence), are the krill *Nyctiphanes australis*, the arrow squid *Notodarus sloani gouldi* and other squid, fish and crustaceans (Montague *et al.* 1986; Skira 1986). *N. australis* is abundant in large swarms particularly when breeding between October and December and is restricted to the continental shelf (Blackburn 1980). The diet of the birds changes from predominantly krill to a mixture of fish, squid and crustacea when eggs hatch in January. The transition could be due to reduced swarming of krill and an increase in the numbers of schooling post-larval fish (Montague *et al.* 1986).

Of seven water masses moving along the shores of northern and eastern Australia (Rochford 1957), four govern the food regime of the Short-tailed Shearwater. They are the Subantarctic derived from the Southern Ocean; the Southwest Tasman from the eastern approaches to Bass Strait; the North Bass Strait from the South Australian gulfs; and the East Tasmanian-West Tasmanian from the central Tasman Sea and Subantarctic. The mixing, during movement from the source regions, and changing patterns of distribution of these water masses determine the major physical and chemical characteristics of the region (Harris *et al.* 1987). These mixed bodies are subject to local weather effects such as heating and cooling which vary considerably with the seasons; their temperature range is 10° to 17°. They have high phosphorus levels and, thus, a high productivity. Factors that affect these water masses affect Short-tailed Shearwaters because the abundance and availability of their food is dependent upon the attributes of the individual water masses.

BREEDING BIOLOGY

On arrival from their migration in September-October, the birds clean out and refurbish their burrows. Breeding Short-tailed Shearwaters tend to occupy the same burrow as in previous years or one in close proximity. During October the colonies are a hive of noisy social activity. For three weeks in November prior to egg-laying, however, the colonies are deserted. This pre-laying absence enables female shearwaters to build up body reserves to produce the egg and males the reserves for incubation of the egg (Fitzherbert 1985).

Upon their return, eggs are laid from 19 November to 2 December with 85 per cent of the eggs being laid within three days on each side of the mean laying date 24–26 November (Serventy 1963). There is no annual variation in this pattern. Only one egg is laid and no re-laying occurs if the egg is lost. The incubation period varies between 52 and 55 days and averages 53 days. Both partners incubate the egg in alternative shifts, the male usually taking the first shift. The length of the shifts varies from 10 to 16 days and occasionally up to 20 days. Eggs can be left unattended for up to seven days and still remain viable as with other shearwaters, such as the Manx Shearwater *P. puffinus* in Britain (Brooke 1990; Matthews 1954). Nearly all breeding failures occur during the egg stage; only three per cent of successfully hatched chicks on Fisher Island die or disappear before banding (Serventy and Curry 1984).

The majority of chicks hatch between 10 and 23 January (Oka 1989). They are brooded by the parents for the first few days then left unattended during the day. The chick is fed nightly for the first week then at longer intervals with up to 16 days between meals and parents alternate in feeding. The final visit of the parents is from 1–23 days (mean 14) before the chicks depart (Serventy 1967). The time between the final feed and departure is termed the 'starvation' or 'desertion' period. The Short-tailed Shearwater chick is in the burrow for 88 to 108 days (mean 94 days). They grow quickly forming large fat deposits and attain a maximum mean weight of 800 g, nearly twice that of their parents, in the second week of April (Lill and Baldwin 1983).

In the second week of April, chicks begin to emerge from burrows at night and attempt to fly. They wander around and may enter any burrow during the day, generally moving closer to the sea prior to departure. This 'travel' phase is recognized by muttonbirders who may go over the same area up to three times during the season. Chicks leave from the third week in April to the first week in May. They leave at night working their way down to the sea shore and swimming out to sea. Strong prevailing westerly winds facilitate departure but also result in chicks that are not yet fully developed leaving too early and later perishing at sea.

Chicks tend to return to their natal colony (Serventy *et al.* 1989) but there is probably much exploration by young birds of other areas before they breed. For example, in any year only 40 per cent (range 16–61) of the breeding birds on Fisher Island were hatched on Fisher Island (Serventy and Curry 1984). However, once they begin to breed at a specific colony, Short-tailed Shearwaters have a very strong tendency to return to breed in that colony until death (Serventy 1967).

Short-tailed Shearwaters breed for the first time when 4–15 years of age, the mean for males being 7.3 and females 7.0 years. Mate retention appears to be related to reproductive performance. Some 33 per cent of all pairs which failed to produce an egg in the preceding season changed partners by divorce. However, the divorce rate was down to 23 per cent in pairs which produced an egg but which failed to hatch, and 15 per cent in birds which fledged young (Bradley *et al.* 1990; Wooller *et al.* 1988). During the completed lifetimes of 418 male and female shearwaters, 27 per cent of all individuals produced no young and 19 per cent only one young. Overall, 71 per cent of birds produced no offspring that returned to breed. In fact, 8 per cent of all birds that had completed their reproductive careers produced 53 per cent of all young that returned to Fisher Island to breed, and 26 per cent of all birds were responsible for all reproducing offspring. Shearwaters that formed known pairs produced on average 5.3 eggs, 3.1 fledglings, and 0.43 reproducing offspring each on Fisher Island (Wooller *et al.* 1988). The breeding success of shearwaters on Fisher Island from 1947 to 1984 is shown in Table 1. Annual banding of all chicks and adults found in burrows commenced in March 1947, and it took a minimum of 20 years for the percentage of banded birds in burrows which were fledged on Fisher Island to stabilize because of the longevity of Short-tailed Shearwaters.

TABLE 1

Breeding success of Short-tailed Shearwater recorded in burrows on Fisher Island between 1947 and 1984.

Years	Adult birds recorded in burrows total	Birds not associated with eggs %	Eggs resulting in chicks %	Adult birds in burrows which were fledged on Fisher Island %
1947–1957	1 965	19	41	1
1957–1966	1 619	17	66	16
1967–1976	1 163	21	58	43
1977–1984	1 009	14	68	45

The breeding success of young birds, 6-year-old or younger, during their first attempt (38%) was markedly lower than that of birds starting at seven or more years (58%) (Wooller *et al.* 1988). Thereafter, breeding success improved with increasing experience with a particular partner, and the number of previous mates (Wooller *et al.* 1989). The ratio of chicks fledged to eggs laid (termed breeding success) is about 60 per cent annually throughout Tasmania (Naarding 1979, 1980, 1981; Skira and Wapstra 1980).

MORTALITY

Mortality is age-related. Annual mortality (±SE) is 7.8 ± 1.5% in male and 10.6 ± 1.8% in female shearwaters in the year of first recorded breeding decreasing to 6.6 ± 2.1% and 7.6 ± 2.3% after nine years rising to 12.7 ± 1.9% and 15.6 ± 1.8% after 18 years. The median survival time is 9.3 years after first breeding (Wooller *et al.* 1988) although four birds on Fisher Island are known to have been at least 36 years old (Skira, unpubl. data). More vigorous birds, as measured by their survival and reproductive success, may tend to have a greater reproductive output earlier in life whereas individuals with lower vigour may produce fewer offspring and die earlier. However, among birds which have bred for 15 years, those which have fledged fewer young have a slight but significantly higher survival rate than those which have produced more offspring (Bradley *et al.* 1989; Wooller *et al.* 1990).

The greatest mortality (52%) occurs in the first year of life (Serventy 1967). In some years, large numbers of Short-tailed Shearwaters are washed onto Japanese beaches when easterly winds blow weakened birds off their normal route. Autopsies have established that death is due to starvation and that the majority are fledglings (Nishigai *et al.* 1981; Oka and Maruyama 1986). On the return trip annual mortalities are inversely proportional to fluctuations in plankton numbers in the Tasman Sea (Serventy *et al.* 1971). Autopsies on 14 shearwaters found dead along one Tasmanian beach in December 1983 showed that death was due to starvation (Skira, unpubl. data).

Natural causes of mortality are predation, disease, starvation and flooding of low-lying nesting areas. Quite severe mortalities are caused in some years by a condition known as 'limy-bird disease', which is associated with blockage of the lower part of the alimentary canal by concretions of sodium urate (Mykytowycz 1963).

Apart from muttonbirding which takes approximately 300 000 chicks each year, another human activity has had disastrous affects. Gillnet fisheries in the North Pacific operate using motherships and the Japanese enterprise drowns between 131 000 and 281 000 Short-tailed Shearwaters annually (King 1984; Ogi 1984). Korea and Taiwan also operate gillnet fisheries in the North Pacific. The effects of a salmon land-based fishery and a squid fishery are not known but they operate in an area through which large numbers of Short-tailed Shearwaters pass during migration. The United States and Canada are currently developing observer programmes with Japan, Korea and Taiwan to look at the 'by-catch' of squid gillnet fisheries in the North Pacific (Gould, pers. comm.).

Small plastic particles are commonly found in stomachs of seabirds (Azzarello and van Vleet 1987). A high proportion of Short-tailed Shearwaters contain plastic particles in their stomachs on their return to the Southern Hemisphere but lose them as the season progresses (Skira 1986). The effects of plastic ingestion are unknown but there is some suggestion of a link between high amounts of plastic ingested and decreased physical 'health' in Short-tailed Shearwaters particularly when in the Northern Hemisphere (Day *et al.* 1985). At the moment this 'impairment' has not been measured.

FUTURE RESEARCH

Much is known about the breeding biology of short-tailed Shearwaters while at the breeding colony. This is due to the long-term study on Fisher Island which has also made very important contributions to the ecology of vertebrate animals. Strayer *et al.* (1986) have reviewed the essential qualities of long-term studies and most of them are exemplified in the Short-tailed Shearwater research on Fisher Island.

There are many questions still to answer. For example, the roles of chance and other factors in determining which birds have long and productive lifespans have yet to be determined. Virtually nothing is known of the social behaviour and pelagic biology of shearwaters. The reasons for their great abundance is unclear. Advances in technological developments such as automatic burrow monitors and radiotelemetry will make some of the work easier. There is a need for interdisciplinary research that includes oceanography because of the dependence of Short-tailed Shearwaters on the marine environment.

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