Condor, 80:123–125

DIVING BY SHEARWATERS

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The anatomical studies reviewed by Kuroda (1954) have shown that a remarkable amount of morphological variation exists among shearwater species. At one end of the spectrum members of the genus *Calonectris* are lightly built, with long wings and a weakly developed sternum—features well adapted to effortless gliding flight but poorly adapted to the use of the wings in swimming under water. The weak pelvis and unstreamlined tarsus are also poorly adapted for swimming. At the opposite extreme, members of the genus *Puffinus* show a progressive trend towards a sturdy build, with short wings, well-developed sternum and pelvis, and streamlined, compressed tarsus. These features are well adapted for swimming under water with wings and feet, but they require a more laborious flapping rather than gliding flight when the bird is in the air.

Apparently, this morphological variation is related to differences in modes of feeding. Actual descriptions of hunting behavior, however, are few, and usually are given in general terms only (e.g., Bent 1922, Murphy 1936, Palmer 1962). The statement by Hutton (1865), quoted by Bent (1922:105) and Murphy (1936:652), for example, that Great Gray Shearwaters (*Procellaria cinerea*) "take a header into the water from the air" is hardly precise, and Hutton's claims that the species "remains under water for several minutes" and dives from "a height of about twenty or twenty-five feet" seem exaggerated and in need of confirmation. We therefore wish to describe the diving and underwater swimming of shearwaters watched under ideal conditions by a group of experienced observers off the Washington coast, and to compare these with observations of diving shearwaters that we have made elsewhere.

On 16 May 1975 we observed an assembly of several thousand seabirds (mainly Sooty Shearwaters, *Puffinus griseus*) following a fishing boat on the continental shelf at 46° 53′N 124°43′W, about 40 km W of Westport, Washington. We chummed them up with suet balls and watched them feed for about 45 min, often as close as 2 m. The birds' performances under water were also clearly visible. Wahl confirmed and amplified our observations at a similar assembly in the same general area on 16 May 1976.

Sooty Shearwaters dived either while sitting on the surface, or while flying by plunging in from heights of 3–5 m. Those diving from the surface usually put their heads under first, presumably looking for sinking bait, and held their wings raised above their backs. They then submerged very smoothly without any preliminary upward jerk of the head and breast. Most of the birds in the air came down at an angle of 45° with the wings about one-third extended sideways from the body and with the feet spread in front of the breast. They struck the water with the breast and feet and then instantly lowered the head and dived in the same way as sitting birds. A few dropped at an angle of about 40° above the horizontal, stalled very briefly about 0.5 m above the surface using the spread feet as air-brakes, and plunged in head-first at an angle of 60–75°. These "belly-flops" and stalls contrasted markedly with the direct, head-first, dart-like aerial plunges of sulids such as the Gannet (*Morus bassanus*), and presumably reduced the impact of the plunge. Once submerged, the birds descended at an angle of about 45°. They surfaced at a similar angle, often bursting out of the water almost directly into flight.

While the boat was stationary, the shearwaters swam around it under water using alternate kicks of their feet for propulsion. For most of the time they held their wings horizontally with the primaries folded and the rest of the wing about three-quarters extended. At this time the wings were beaten mainly on the ascent and descent. When the boat started to move slowly through the water at 1–2 m/s, they began to beat their wings as well as kick in level swimming in order to catch up. They had no difficulty in doing so; beating the wings seemed to give them almost instantaneous acceleration. Birds swam under the boat and so must have been diving at least 1–2 m deep. (Wahl has been told by fishermen that *P. griseus* will take bait from salmon hooks down to 5 m, and he has taken the closely-related Short-tailed Shearwater, *P. tenuirostris*, from gill-nets at this depth in the Ber-

ing Sea.) Individuals seemed to stay under for about 15 s, perhaps longer, but it was impossible to time this accurately. They were extremely agile under water; we saw several stop and spin around in tight 180° horizontal turns and observed no collisions. Even so, the birds were clumsy compared to more specialized divers such as the auks. We did not observe the agile, banking, underwater turns that have been described for the Common Murre (*Uria aalge*; Spring 1971:Fig. 4).

Brown is familiar with the behavior of *P. griseus* and the Greater Shearwater (*P. gravis*) diving for fish, bait, and euphausiids off Nova Scotia. Both species plunge from the air and dive from the surface in the ways already described (see also Murphy 1936:663, for a description of "belly-flop" plunging followed by the use of the wings under water by *gravis*). Both feed on euphausiid swarms at least as deep as 2 m, though the longest dive recorded for *gravis*, 12 s, does not suggest deep diving. In any situation *griseus* submerges more readily than *gravis* and, while *gravis* normally emerges directly ahead of its submersion point, *griseus* may emerge at almost any angle, suggesting that it is more agile under water. Bourne has seen both species behave similarly when feeding behind fishing boats off western Europe where, as Lockley and Marchant (1951) reported, their ability to dive gives them a slight advantage over competing scavenging species.

Kuroda (1954) regarded the smaller species of the genus *Puffinus* as morphologically even more specialized for swimming and diving than *P. griseus*, and our observations confirm this. Bourne (1976, see also King and Simmons 1976) has described "belly-flop" plunging followed by active feeding at and below the surface by flocks of Manx Shearwaters (*P. puffinus*) over schools of surfacing fish. Jones (1976) claimed that these birds also plunge head-first, but provided no description suggesting close observation. Bourne has seen an extreme form of the same behavior in the closely-related Fluttering Shearwater (*P. gavia*) in Australasian waters; the birds fed in a tight formation, with individuals continually flying up from the rear to plunge in again at the front of the flock. Brown (1972, and unpubl. data) has watched Little and Audubon's shearwaters (*P. assimilis* and *lherminieri*) diving readily from both the air and the surface in the western North Atlantic, though he did not note the precise form of the aerial plunge. If, as reported by Loomis (1918:125), *lherminieri* can stay submerged "for a full minute", it must indeed be a highly accomplished diver.

By contrast, other species of shearwaters dive much less readily. Small numbers of Flesh-footed (*P. c. carneipes*) and Pink-footed (*P. c. creatopus*) shearwaters were feeding among the *griseus* on 16 May 1975. These plunged breast-first to the surface from the air but never submerged completely. Wahl regards this as typical of these birds; he has occasionally seen *creatopus* dive from the surface for bait, but they remain submerged for only 2–3 s, and seem clumsy in comparison with diving *griseus*. Kuroda's (1954) and Norris's (1965) observations also suggest that *carneipes* is mainly a surface feeder. However, it appears to dive readily on occasion. Falla (1934) reported that it will follow baited hooks down to 3–5 m, and Cooper (*in* Baird et al. 1884, quoted by Bent 1922:64, and Murphy 1936:655–656) described how *creatopus* makes shallow dives when feeding on small fish. The statement by Serventy et al. (1971: 121) that *carneipes* "dives well and frequently" is rather general and needs refining.

Similarly Kuroda (1954) observed that the White-faced Shearwater (*Calonectris leucomelas*) does not submerge completely when it feeds. Bourne has watched the closely-related Cory's Shearwater (*C. diomedea*) feeding off Spain and Portugal; this species plunges briefly below the surface to take fish spilt from sardine boats but does not dive deeply. In this connection, Besson's (1973) statement that *diomedea* is never taken in the lobster pots set on the sea floor of the Mediterranean, and which regularly trap the deep-diving *P. puffinus*, seems significant. Bourne has also watched Wedge-tailed and Gray-backed shearwaters (*P. pacificus* and *bulleri*) in Australasian waters; they appear to be surface-feeding birds when compared with *P. gavia* in the same area (see above). Wahl has watched *bulleri* make clumsy, "belly-flop" dives from about 1 m above the surface, but the birds do not submerge completely.

Our observations agree with Kuroda's (1954) classification of the shearwaters on anatomical grounds. In this, the spectrum of variation from species adapted to an aerial mode of feeding to those adapted to an aquatic one runs from *C. diomedea* and *leucomelas* through *P. pacificus* and *bulleri*, the *carneipes* group, *gravis*, *griseus* and *tenuirostris*, *puffinus* and *gavia*, to *assimilis* and *lherminieri*. The mode that a species has adopted is probably determined by the type and availability of its food. Gliding surface-feeders tend to be

birds of relatively barren, warm subtropical waters (Palmer 1962, Serventy et al. 1971). Cory's Shearwater, for example, apparently relies on sporadic and erratically occurring schools of predatory fish to drive its prey up to the surface and into its reach (de Naurois 1969, Zino 1971). Under these circumstances energetically economical gliding may be the most effective form of hunting. Flapping flight would not only be less efficient, but the diving habit associated with it would probably expose the birds to the predatory fish. On the other hand, almost all the more specialized diving shearwaters (and all the even more specialized auks, penguins and diving-petrels, *Pelecanoides* spp.) are birds of richer, cold or cool-temperate seas, where food is abundant and where the birds can feed without having to associate with dangerous predatory fish. Here, energy-consuming diving and flapping flight would be better methods of locomotion.

Our observations were made in part on a pelagic trip following the conference on "Conservation of marine birds of northern North America" at Seattle, Washington, 13–15 May 1975. We thank the other members of the conference who contributed comments—in particular, H. J. Boyd, D. Paulson and G. A. Sanger. Brown's contribution is associated with the program "Studies on northern seabirds" of the Canadian Wildlife Service, Environment Canada (Report No. 54). Bourne was supported by a grant from the British Natural Environment Research Council to Professor G. M. Dunnet and the Seabird Group to investigate the ecology of birds at sea.

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