

Flight Behavior of the Procellariiformes.—There were about fifty Fulmars (*Fulmarus glacialis*) in Black Tickle, Labrador, on October 19, 1950. Most of these birds were flying—banking and gliding somewhat erratically about the harbor in their usual fashion. Rather suddenly, however, they began a different type of flight. One after another, the Fulmars started gliding unswervingly into the wind on stiffly outstretched wings. As they dropped closer to the water, they kicked in the water with alternate strokes of the feet, as though running across the surface. After doing this for a few seconds, a bird would acquire enough added speed to rise higher in the air. It would glide a little further before again descending to the water and repeating the performance. Most of the birds did this, over and over, at no time moving their wings. I cannot say what caused this behavior to appear almost simultaneously with so many birds. There had been no noticeable change in force or direction of the wind, a brisk, steady breeze from the northwest. Although I saw many Fulmars several other times under closely comparable conditions, I did not see this behavior again.

This action is very reminiscent of the flight of petrels, whose "water-walking" is well known. Accordingly, I have searched the available literature to determine whether other birds of the order Procellariiformes might not behave similarly. From this search has emerged a pattern of flight behavior which is very nearly order-wide. Most flying birds usually keep their legs directed back under their tails and pressed close to their bodies. It is true that some water birds, such as loons, grebes, coots, and diving ducks, paddle with their feet and flap their wings strongly as they take flight from water. Once they are air-borne, however, their legs are drawn up and kept out of the air stream. The Procellariiformes, on the other hand, may run on the water for long periods and without taking flight. At such times their wings are usually held motionless. There are differences in the exact details of such behavior, to be sure. Nevertheless, these differences do not seem very great when one considers the great diversity of birds in this order, ranging from giant gliders like the albatrosses to the relatively tiny petrels with a fluttering flight. This general type of behavior is common with some species; with others it is seen infrequently.

Nichols (1946: 19) has dealt briefly with the manner of flight of the Procellariiformes. He limited himself to rating about thirty species on the basis of four factors: elevation, flapping, rigidity, and twisting. Murphy (1936: 483) has discussed the various modes of flight found with the Procellariiformes. He gave several examples of the use of feet and legs in flight but he stopped short of suggesting that this might be general for the order. In what follows, I cite Murphy's observations, as well as all other pertinent references I could find.

The order Procellariiformes has been divided (Peters, 1931: 41) into four families. These are the Diomedidae (albatrosses), Procellariidae (shearwaters, Cape Pigeon, fulmars, whale-birds, and gadfly petrels), Hydrobatidae (storm petrels), and Pelecanoididae (diving petrels). These represent about one hundred species. In each of these families, except probably the last, we can find illustrations of the type of flight I have described.

Members of the Diomedidae show the behavior in several forms. Thus, Richards (1909: 7), with regard to albatrosses feeding on the water, has written: "Once on the water, the wings are kept partly expanded and raised high over the back, the wind's levitation thus bearing most of the weight. Actually, the birds now *walk on the water*, paddling with the big feet quite sufficing to lift the bodies clear." This passage deals with albatrosses as a group, not with any one species. Murphy's (1914: 441) description of a Wandering Albatross (*Diomedea exulans*) concerns some-

what different behavior: "It was a curious sight when he prepared to alight under our stern, and then, changing his purpose, ran heavily along the water for a hundred yards, before his stiffly set wings could raise his large body into the air." This is, of course, a prelude to flight, not flight itself. It is perhaps significant, however, that the feet and legs were the only mode of propulsion; there was no flapping of the wings. Still another aspect of this mode of flight was described by Murphy (1914: 446) when he wrote about Black-browed and Gray-headed albatrosses as follows: "Of eight 'Mollymokes,' our constant companions, six were *Diomedea melanophrys* and two *Thalassogeron culminatus*. As usual, when they saw bait on the hooks astern, they raised their heads comically, and often wiggled their feet with a running motion, halted in the air, and assumed extremely awkward attitudes while deciding whether to descend or fly on."

Among the Procellariidae, Cape Pigeons (*Daption capensis*) show a surprising mode of locomotion. Murphy (1936: 607) describes it: "Except in the teeth of a strong wind, the Cape Pigeons run foot after foot along the water when launching into flight. Sometimes when following a ship they will keep up this hydroplane style of progression for long distances, instead of mounting into the air. By this I mean that they set their wings as gliders and, keeping the breast barely above the surface of a quiet sea, they propel themselves with rapid, alternate running strokes of the feet. In this manner I have seen them trail my baits for an hour at a time." Interestingly enough, ashore the Cape Pigeon is almost completely helpless, being quite unable to walk in a normal manner (Murphy, 1936: 607). Murphy (1914: 451) observed that Cape Pigeons occasionally wriggle their feet with running motion as they fly, apparently at some height over the water.

Fisher, in his extensive study (1952) of the Fulmar, mentions no case where this bird uses its feet and legs during flight. Anthony (1895: 102), describing Fulmars hurrying to food on the water, has written: "Those that are on the water and have drifted away hasten to the spot with wings outspread and feet pattering along on the water." My own observations of Fulmars have already been described.

Murphy (1914: 451) has described Antarctic Whale-birds (*Pachyptila desolata*) wriggling their feet in air as though running while they flew. He has written further on this species (1936: 621): "The whale-birds . . . were progressing in the manner which I have called 'hydroplaning' in the preceding general account of the Procellariiformes. The birds worked along with an odd creeping motion, resting their bodies lightly upon the surface but holding the wings just above it, the feet apparently furnishing all of the motive power. Then, as they scurried forward quite rapidly, their heads would be thrust under water and the laminated bills would scoop for food."

Murphy's observation of the Shoemaker (*Procellaria aequinoctialis*) describes behavior which is rather unusual and which may be pertinent to the present subject. He wrote (1936: 647): "When flying thus over the nesting grounds, they often tuck one foot forward among the feathers of the belly and hold the other under the tail." Perhaps this is a vestigial remnant of the foot-wriggling habit shown by other species.

Lowe (1925: 68) regarded the flight of petrels as completely different from that of shearwaters or albatrosses. As we shall see, this view is not entirely correct. Thus, Bent (1922: 68) observes: "Like petrels the shearwaters occasionally skip along the surface of the water on their feet, using their wings to balance and support them." With respect to Greater Shearwaters (*Puffinus gravis*), Bent says: "they come skimming over the waves, alight softly on the water, and with head and breast held high and wings curved up and partly spread, they advance by rapid foot strokes to their feast." Regarding the Sooty Shearwater (*Puffinus griseus*), Audubon (1835: 555) said: "Like the small Petrels, it frequently uses its feet to support itself on the

surface, without actually alighting." Anthony (1896: 224) described Black-vented Shearwaters (*Puffinus opisthomelas*): "they chased each other, half running, half flying over the water." For Audubon's Shearwater (*Puffinus lherminieri lherminieri*) we find: "On approaching a mass of weeds, they raise their wings obliquely, drop their legs and feet, run as it were on the water, and at length alight in the sea" (Audubon, 1835: 620). Loomis (1918: 124) gives the following account of the Galapagos Shearwater (*Puffinus lherminieri subalaris*): "In rising from a calm sea they extend their wings and paddle rapidly forward for about two feet when they clear the water and are fairly a-wing. When feeding in windy weather, they often alight for a moment without closing their wings. One proved himself well worthy of the name of petrel while picking up food during a brisk wind. He would poise for a moment, with wings outspread and feet just touching the water, and then dart to the windward for a few feet without flapping his wings, which apparently served the same purpose as 'the sails of a vessel when close-hauled on the wind'."

Murphy (1914: 451) observed that Atlantic Petrels (*Pterodroma incerta*), like several other species, sometimes wriggle their feet with a running motion as they fly.

With the petrels of the family Hydrobatidae we find many instances of water-walking. Indeed, according to one explanation, the term "petrel" is derived from the name of St. Peter, who once walked on water. (This derivation of the name is not accepted by everyone, however.) The flight of Wilson's Petrel (*Oceanites oceanicus*) has been described several times. Several quotations can be given to illustrate the various aspects of its behavior. Thus (Bent, 1922: 169), "As a rule the petrels pick up the food as they skim over the water either bounding with both feet together or pattering lightly over the water running or walking with alternate feet. . . . The wings are often held motionless." Murphy (1914: 440) said: "Often as they pattered along for some distance on set, slightly depressed wings, they resembled small scurrying quadrupeds more than anything else. . . . In the strong wind I noticed that the petrels in our wake always faced the wind diagonally if not directly, with extended, motionless wings, whenever they pattered on the water." Murphy later (1936: 752) wrote, "When following a vessel, they skip along the surface as they approach, giving a vigorous kick on the lee side whenever they touch the water. When they 'stand' to feed, the wings are held rigidly and they face the wind; the momentum necessary to keep them from being blown away is furnished by the webs, the legs sinking to the heel as they work backward in unison." Roberts (1940: 175) has also described the flight of the Wilson's Petrel: "The feet are dropped only when the bird stalls or approaches the water closely, and they appear to lift the bird off the surface, steadying it and helping it along. As this downward beat of the feet occurs, the webs are spread out, and the bright yellow coloration becomes visible. Wilson's Petrels do not 'walk' on the water, but rather 'patter' on it, lowering both feet simultaneously, three or four times in quick succession, between each short stretch of gliding. When they touch the water with their feet, they do not necessarily pick up food; they pause for a moment, with body sloping upwards at about 45°, wings fully extended, and head turned down, presumably searching the surface for food." From these descriptions it appears that Wilson's Petrels may use their feet either alternately or together. As to the closely related Lowe's Storm Petrel (*Oceanites gracilis galapagoensis*), Loomis (1918: 181) says, "They usually pick up their food while fluttering close to the water with their feet dipping."

Several authors have commented on the flight of the White-faced Storm Petrel (*Pelagodroma marina*). Murphy (1936: 769) says, "their long dangling legs are conspicuous during the periods of their pattering upon the water. When they flit

over the land *en route* to their nesting grounds, they just 'tip' it with their toes, and bounce along, giving the impression of being full of springs." Again, "numbers were seen flitting along close to the surface of the sea, with their long legs dangling beneath them and just touching the water" (Ogilvie-Grant, 1896: 41). "The euphonious Maori name, Takahi-kare-moana, which means 'dancing on the waves,' . . . very aptly describes the behavior of the birds on the water" (Richdale, 1943: 97). "At sea they use the feet almost as much as their wings, as they go tripping along over the billows" (Campbell and Mattingley, 1907: 190).

Nichols (quoted by Bent, 1922: 175) says of the White-bellied Storm Petrel (*Fregetta grallaria*): "A little flock gathers [about food], pattering on the water with their feet, their wings extended fluttering over their backs." Beck (quoted by Bent, 1922: 175) reported that "An interesting characteristic of this bird is the manner in which it strikes the water with one foot. In a breeze or wind it was always the leeward leg that was used, the windward one being stretched out behind. . . . When the birds flew directly into the wind either one or the other or both legs might be used." Wilson (1907: 80) says, "We saw them continually dropping to touch the water with one foot, steadying themselves while they daintily took their minute crustacean food from the surface of the water." The congeneric Black-bellied Storm Petrel (*Fregetta tropica*) behaves somewhat similarly (Alexander, 1922: 263): "It mostly kept very close over the water near the stern of the ship, rarely flapping its wings, but hopping along over the surface with its wings spread out, gaining much of its impetus from its feet, which struck the surface simultaneously, not alternately as commonly depicted in pictures of Storm-Petrels."

Macgillivray (quoted by Bent, 1922: 128) has commented on the Storm Petrel (*Hydrobates pelagicus*): "It is only when picking up their food that, with upraised wings, they hover over the spot, and pat the water with their feet; although many persons have described this as their ordinary mode of progression."

Bent (1922: 135) says of Hornby's Petrel (*Oceanodroma hornbyi*): "The flight of this petrel, like others of its genus, is light, rapid and erratic, flitting hither and thither close to the surface of the waves, often with its feet extended as if walking on the water."

The literature contains very little indication that members of the family Pelecanoididae may use their legs and feet when flying. Coues (1903: 1021) referred to this group as "Sea-runners" but did not describe behavior warranting this name. His critical survey of the family (1866: 188) does not mention either the name or the behavior. No other writer seems to have described for the Pelecanoididae flight behavior of the type considered here. Indeed it appears that Coues' use of the name "Sea-runners" referred to behavior found frequently in other orders. Thus, Waite (quoted by Murphy and Harper, 1921: 538) says of *Pelecanoides urinatrix chathamensis*: "In rising from the water they used their legs with a paddling motion, flew a short distance with a seemingly labored or erratic flight, and then dropped to the water." This is not essentially different from the behavior of grebes or diving ducks. Murphy's (1936: 771) statements are worth quoting: "The diving petrels comprise a homogeneous, monogeneric, strikingly distinct group of Procelariiformes, the members of which exhibit few characters that might indicate their relationships with other divisions of that order. . . . Short-winged, characterized by 'whirr-flight,' like that of the auklets, rather than by gliding flight, and given to diving from above the surface of the water, the Pelecanoididae have little resemblance to typical petrels."

A fundamental feature of the type of flight considered here appears to be the use of stiffly set wings as gliders. This is accompanied by kicking or running in the

water with alternate strokes of the feet. In deviations from this basic pattern, birds may flutter their wings as they kick in the water, use both feet together when kicking, or wriggle their feet in a running motion when flying high above water. This behavior is very nearly order-wide, appears infrequently with some species and commonly with others, and has variations which seem of no utility. These facts suggest that such a manner of flight may be of genetic origin. Perhaps the ancestral Procellariiformes were birds for whom flapping flight was difficult and which glided about close to the surface of the sea, propelled largely by running strokes of the feet. With evolutionary divergence of the various groups of this order, this behavior was lost more or less completely with some birds and was modified with others. Dr. Ray H. Anderson has suggested (private communication) another useful aspect of this type of flight. It may have enabled ancestral gliding birds to stay at the surface of the water for feeding regardless of irregularities of the surface. Such advantages would still be attached to this mode of locomotion, of course.

SUMMARY

It appears that the Procellariiformes, with the probable exception of the Pelecanoididae, may use feet and legs while flying. In the most common form of this behavior, the wings are used as gliders, while the bird runs with alternate strokes of the feet along the surface of the water. With some species the wings may be flapped or both feet may be kicked simultaneously. Other forms of this general pattern are described, and possible origins of this behavior are mentioned.

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The Generic Allocation of the Green-tailed Towhee.—The Green-tailed Towhee, currently placed in the genus *Chlorura* Sclater, 1862, was originally described by Audubon (1839). The twenty-second supplement (1947) to the American Ornithologists' Union Check-List of North American birds designates the species as *Chlorura chlorura* (Audubon). The species breeds from central Oregon and south-central Montana to southern California, southeastern New Mexico, and central western Texas. In general it is a bird of the mountains or, in the Great Basin, of high plateau country. The purpose of the present paper is to present evidence to show that this species is a true *Pipilo* allied to the type species, *Pipilo erythrophthalmus*, by way of the closely related *Pipilo ocai*, the Collared Towhee, of Mexico.

Few species of North American birds have been moved about generically more than the Green-tailed Towhee. Ridgway (1901: 401-402) lists eight genera in the synonymy of the species and there have been two others in use since 1901. The species appeared most frequently in the literature under *Pipilo* prior to 1896 when Ridgway placed it in a new monotypic genus, *Oreospiza*. He proposed this separation in spite of his remarks favoring it as a *Pipilo*, which appeared in 1890 in a review of a work by Salvin and Godman. Salvin and Godman (1879-1887) had placed the species in *Embernagra*, and Ridgway correctly pointed out the line of relationship to the true towhees via the rufous-capped Mexican forms currently known as *P. ocai*.

The original use of the genus *Oreospiza* for the Green-tailed Towhee appears on page 439 of Ridgway's "Manual" (1896), and in the appendix (1896: 605) he writes as follows:

"Page 439, *Pipilo chlorurus* (= *Oreospiza chlorura*): This bird, which has been referred by different authors to the genera "*Embernagra*" (i. e. *Arremonops*) and *Atlapetes*, but which is really far more out of place in either than in *Pipilo*, I propose to make the type of a new genus, *Oreospiza*, whose characters are intermediate between, or rather a combination of, those of *Pipilo* and *Zonotrichia*."

This constitutes the original description of the genus.

Five years later Ridgway (1901: 399) wrote the following: "*Oreospiza* is inter-