

## THE INCIDENCE, FUNCTIONS AND ECOLOGICAL SIGNIFICANCE OF PETREL STOMACH OILS

JOHN WARHAM

*Department of Zoology, University of Canterbury, Christchurch*

**SUMMARY:** Recent research into the origins and compositions of the stomach oils unique to sea-birds of the order Procellariiformes is reviewed. The sources of these oils, most of which contain mainly wax esters and/or triglycerides, is discussed in relation to the presence of such compounds in the marine environment. A number of functions are proposed as the ecological roles of the oils, including their use as slowly-mobilisable energy and water reserves for adults and chicks and as defensive weaponry for surface-nesting species. Suggestions are made for further research, particularly into physiological and nutritional aspects.

### INTRODUCTION

Birds of the Order Procellariiformes (albatrosses, fulmars, shearwaters and other petrels) are peculiar in being able to store oil in their large, glandular and very distensible fore-guts or proventriculi. All petrel species so far examined, with the significant exception of the diving petrels, Fam. Pelecanoididae, have been found to contain oil at various times. The oil occurs in both adults and chicks, in breeders and non-breeders, and in birds taken at sea and on land. The oil is a light (specific gravity 0.88), low viscosity fluid, often solidifying to a wax in cool conditions, with a sweet, slightly fishy smell. It may be colourless or straw-coloured, but it is often darker — from amber to a deep reddish-brown. The colour is neither constant nor species-specific. For example, that from the cape petrel (*Daption capense*) is bright orange before egg laying but becomes duller during the birds 4 to 6 day incubation stints and at the end of these is normally dull green (Pinder, 1966). This green tinge is common also in oil samples collected from fasting adult petrels and may be due to the presence of bile pigments.

Many surface-nesting petrels spit oil in defense or offense, but copious amounts are often found in the chicks of burrowing species and these seldom spit oil. Northern fulmar (*Fulmarus glacialis*) chicks at St Kilda yielded about 280 ml of oil each; sooty shearwater (*Puffinus griseus*) chicks may contain 120 ml, while Murphy (1936) reports 200 ml of oil being taken from a short-tailed shearwater (*Puffinus tenuirostris*) chick: this would amount to about 30% of the adult's body mass.

Petrel oil has been used medicinally, as a lubricant and as an illuminant. The northern fulmar was a mainstay of the St Kildans' economy, supplying "oil for their lamps, down for their beds, a delicacy for

their table, a balm for their wounds, and a medicine for their distempers." In New Zealand, Travers and Travers (1873) described how the Chatham Island Morioris held young petrels over their mouths and allowed the oil to drain directly into them. In some years the St Kildans exported part of their oil harvest, as the Australian mutton-birders still do with oil from the chicks of *P. tenuirostris*. This has been used as a basis for sun-tan lotions, but most nowadays is used as a food stock supplement: a small quantity is said to impart a shiny coat to horses. Some 2796 gallons (12711 l) were sold after the 1976 season as a by product of the harvesting of 549 352 squabs (B. S. Simmonds, pers. comm.). It is also possible that fossil stomach oil has been used medicinally in the east for thousands of years.

A surgeon, John Scouler (1826), was among the first in modern times to discuss stomach oil from personal experience. He wrote of *Daption capense*, caught off Patagonia, which "never failed to vomit a considerable quantity of yellowish oily fluid on his enemy, and on dissection the source of this supply is easily detected. The first stomach is large and membranous and thickly set with numerous glandular follicles, which appear to be the organs which secrete this oily fluid, the only defensive weapon this animal possesses."

A number of papers describing aspects of the biochemistry of petrel oils appeared in the 1920's and 1930's, but the analyses were incomplete by modern standards. The investigators seem to have known little of the birds in life and so made erroneous deductions such as that of Otago chemists Carter and Malcolm (1927) who concluded that mutton-bird oil was ingested preen gland secretion. In some accounts the species from which the oil was drawn were misidentified e.g. oil from the Australian and

New Zealand mutton-birds (*P. tenuirostris* and *P. griseus*) was attributed to a quite different petrel *Pterodroma lessoni* (Serventy, Serventy and Warham, 1971).

In the early 1960's this writer circulated a review of current knowledge about petrel stomach oils among procellariiformists asking for samples of oil so that analyses using modern techniques could be run to establish, a. whether the oils were of similar composition and therefore probably of a secretory nature, or b. of varied composition and therefore more likely to be food-derived. These analyses have recently been published (Warham, Watts and Dainty, 1976; Watts and Warham, 1976) and with comparable analyses by other workers they provide information on oils from 25 petrels. There are about 100 species in the order.

## COMPOSITIONS

The main components of the oil samples so far analysed (by thin-layer and gas-liquid chromatography and infra-red spectroscopy) are summarised in Table 1.

In 24 of the species-samples either triglycerides or wax esters predominated. Many samples contained both. In a few oils there were no wax esters, in others no triglycerides. Oil from one species, *Oceanodroma leucorhoa*, had neither: instead, large quantities of glycerylether diesters were found. These were also present in oils from *Pterodroma mollis*, *Puffinus carneipes* and *Procellaria aequinoctialis* but in smaller proportions and only in association with wax ester or triglyceride.

In addition to the components shown in the table, most oils contained small quantities of di- and mono-

TABLE 1. *The main constituents of petrel stomach oils.*

(X = principal constituent, x = less abundant constituent, WE = wax ester, TG = triglyceride, Ch = cholesterol, DAG = diacylglycerol, S = squalene.)

| Species                           | WE | TG | Ch | DAG | S | Authority   |
|-----------------------------------|----|----|----|-----|---|---|
| Diomedeiidae                      |    |    |    |     |   |   |
| <i>Diomedea epomophora</i>        | X  | X  |    |     | X | Warham <i>et al.</i> , 1976                           |
| <i>D. exulans</i>                 | X  | x  |    |     | x | Lewis, 1969a  |
| <i>D. melanophris</i>             | x  | X  |    |     |   | Warham <i>et al.</i> , 1976;<br>Clarke & Prince, 1976 |
| <i>D. chrysostoma</i>             | x  | X  |    |     |   | Clarke & Prince, 1976                                 |
| <i>D. bulleri</i>                 |    | X  |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>Phoebetria palpebrata</i>      |    | X  |    |     |   | Warham <i>et al.</i> , 1976                           |
| Procellariidae                    |    |    |    |     |   |   |
| <i>Macronectes giganteus</i>      | X  | X  |    |     |   | Clarke & Prince, 1976                                 |
| <i>M. halli</i>                   | X  | X  |    |     |   | Warham <i>et al.</i> , 1976;<br>Clarke & Prince, 1976 |
| <i>Fulmarus glacialis</i>         |    | X  | x  |     |   | Cheah & Hansen, 1970a;<br>Warham <i>et al.</i> , 1976 |
| <i>Daption capense</i>            | X  |    |    |     | x | Warham <i>et al.</i> , 1976                           |
| <i>Pagodroma nivea</i>            | X  |    |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>Pterodroma macroptera</i>      |    | X  |    |     |   | Cheah & Hansen, 1970b                                 |
| <i>Pt. lessoni</i>                |    | X  |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>Pt. inexpectata</i>            | X  | X  |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>Pt. mollis</i>                 | X  | x  | x  | X   |   | Warham <i>et al.</i> , 1976                           |
| <i>Halobaena caerulea</i>         | X  | x  |    |     |   | Clarke & Prince, 1976                                 |
| <i>Pachyptila desolata</i>        | X  | x  |    |     |   | Clarke & Prince, 1976                                 |
| <i>Procellaria aequinoctialis</i> | x  | x  | x  | x   |   | Warham <i>et al.</i> , 1976                           |
| <i>Pr. westlandica</i>            | x  | X  |    |     | x | Lewis, 1969a  |
| <i>Puffinus griseus</i>           | X  | x  |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>P. tenuirostris</i>            | X  | x  |    |     |   | Cheah & Hansen, 1970a;<br>Warham <i>et al.</i> , 1976 |
| <i>P. carneipes</i>               |    | X  |    | X   | x | Lewis, 1969a  |
| <i>P. pacificus</i>               |    | X  | X  |     |   | Cheah & Hansen, 1970b                                 |
| Hydrobatidae                      |    |    |    |     |   |   |
| <i>Hydrobates pelagicus</i>       |    | X  |    |     |   | Warham <i>et al.</i> , 1976                           |
| <i>Oceanodroma leucorhoa</i>      |    |    | x  | X   |   | Lewis, 1966   |

glycerides and cholesterol, some free fatty acid and alcohols. However, one of two samples of oil from *Puffinus pacificus* contained substantial proportions of cholesterol (43% by weight), one from *Pterodroma macroptera* 30% of cholesterol ester, while oils from *Daption capense* and *Procellaria aequinoctialis* contained 23-43% of long chain alcohols.

#### ORIGINS

The origin of these oils has been the subject of some discussion since Scouler and later anatomists drew attention to the copious glands in the petrel proventriculus. One school believed that the lipids were food residues, even excretory products, of birds with an excess of fat in their diet; another that the oils were internal secretions of the proventricular glands. Harrison Matthews (1949) examined stained sections of proventricular epithelia and concluded that the glands were probably secreting lipid into the lumen of the stomach.

However, the intra-cellular fat that Matthews observed stained with Sudan Black but not with Sudan III or IV, and as Sudan stains pick out all neutral lipids whereas only Sudan Black stains phospholipids, it seems likely that the lipid Matthews detected was dietary phospholipid being taken up with the aid of an acid phospholipase (Watts, pers. comm.). There is very little phospholipid in the stomach oils so far examined, though a good deal in potential prey organisms.

All the analyses indicate that the oils are derived from the petrels' diets, for the following reasons:—

1. The intra-specific variations in the compositions of the oils are far greater than would be expected of a secretion, such as that of the proventriculus. For example, Clarke and Prince (1976) analysed the individual oils from 35 adult *Halobaena caerulea* and found a wide range in the proportions of the main constituents. The wax esters had a mean value with one standard deviation of  $68.9 \pm 21.7\%$  of total lipid, while the triglycerides at  $12.1 \pm 10.8\%$  were even more variable. Similarly Lewis (1966) found that the glycerylether contents of oils from four adult *O. leucorhoa* varied between 20% and 84% of the total lipid.
  2. The inter-specific variations in the compositions is even greater (Table 1) and there seems to be no correlation between composition and taxonomic status. For example, two of the oils of the six albatrosses contained mostly triglyceride, two others mainly triglyceride with lesser amounts of wax ester, one contained about equal proportions of tri-glyceride, wax ester and squalene while in the sixth wax ester predominated and there were smaller amounts of triglyceride and squalene.
  3. The constituents of the petrel oils show strong similarities to those of oils from crustacea, squid and fish either eaten by petrels or related to known foods of petrels. This also includes the hydrocarbons pristane and squalene: the latter could originate from shark's flesh or liver eaten by scavenging albatrosses, pristane from copepods and planktonic herbivores lower down in the food chain.
- An example of the correspondence in lipid constitutions is given by the fatty acid and alcohol components of the wax esters and the fatty acids of the triglycerides from marine animals and petrel stomach oils. Both show a preponderance of 16:0, 16:1, 18:1, 20:1, 20:5 and 22:6 carbon chain compounds. Oil from *Daption capense*, however, was unique in lacking 14:0 or 16:0 alcohols in its wax esters. This suggests that there is something special about this petrel's foods, at least around the Snares Islands where the birds were sampled.
- Imber (1976), who also believes in the dietary origin of stomach oils, emphasises that many petrels feeding at night take vertically migrating mesopelagic crustacea, fish and squid whose lipids contain much wax ester. He also draws attention to the similarity between the cephalopod diet of the albatrosses *Diomedea exulans* and *D. epomophora* and that of the sperm whale *Physeter catodon*. The whale's tissues are rich in wax esters as are their cephalopod prey. So too are the birds' stomach oils (Table 1).
4. The pigments of the oils are the same as natural lipid-soluble pigments in marine invertebrates. Thus carotenoid astaxanthins in oil from albatrosses, giant petrels and prions resemble those from decapods and euphausids (Lewis, 1969a; Clarke and Prince, 1976). One exception concerns the pigments of *P. tenuirostris* oil which were different from those of the euphausid *Nyctophanes australis* which forms this bird's main prey (Cheah and Hansen, 1970a).
  5. In the only analysis of organochlorine compounds in stomach oils so far published, Bogan and Bourne (1972) found that *F. glacialis* oil contained only 1.3 p.p.m. of polychlorinated biphenyls in contrast to 42 p.p.m. in the bird's body fat. The adults evidently did not pass on the high levels of PCB's to their young when they fed them oil and Dr Bourne (pers. comm.) points out that the oil's low PCB values provide further evidence of its non-secretory origin:

had the oil been synthesised in the bird a concentration of organochlorines would have been expected to occur, as in the fat.

6. Watts and Warham (1976) found that the intact lipids of the oils consist of randomly associated fatty alcohols and/or acids. These authors point out that this is what would be expected in oils of dietary origin, whereas with lipids synthesised by glands, e.g. mammalian mammary glands or liver, there are specific associations between particular fatty alcohols and/or fatty acids.
7. Variations in the compositions of oils from different members of the same petrel species are readily explained by mixed diets. Furthermore, even if the birds fed on the same prey, differences in the resulting stomach oils would be expected because the lipids of particular prey species are not of constant composition but may change during the annual cycle or with alterations of water temperature, so that their wax ester/triglyceride ratios vary in time and space.

#### WAX ESTERS, TRIGLYCERIDES, GLYCERYL ETHERS, PRISTANE AND SQUALENE IN THE MARINE ENVIRONMENT

Both wax esters and triglycerides are found in small to large amounts in many organisms which are eaten or likely to be eaten directly or indirectly, by petrels. For example, wax ester in the copepod *Calanus helgolandicus* composed 30-40% of total lipid; in mullet eggs 70%, and in *Latimeria* muscle 93% (Nevenzel, 1970). Whale blubber contains 50-80% wax ester, the remainder of the lipid being triglyceride. Some copepods contain up to 40% dry weight of triglyceride and others up to 50% dry weight of wax ester (Lee *et al.*, 1971). Spermaceti is mainly wax ester and this, and the mutton-bird oils referred to earlier, appear to be the only wax esters of animal origin sold commercially. One squid had 27% of its lipid as wax ester, 6% as triglyceride (Benson *et al.*, 1972). Triglyceride was the principal lipid in zooplanktonic ostracods, pteropods, euphausiids, amphipods and decapods collected in the Strait of Georgia, British Columbia (Lee, 1974).

Most marine animals so far analysed contain both wax ester and triglyceride, but with much inter-specific variation in their proportions. These proportions may also be dramatically different in the same species at different times. Thus the eggs and early nauplii of *Calanus helgolandicus* have 60% triglyceride in their lipid reserve but no wax ester, whereas the eggs are laid by adults containing largely wax ester (Benson *et al.*, 1972).

The quantities of lipid and the proportions of wax ester to triglyceride may not only vary with age and breeding status, but also with the animal's stage of starvation and with environmental factors. Polar and deep sea copepods tend to be rich in wax ester whereas those of sub-tropical seas are high in triglyceride (Lee *et al.*, 1971). The crustacean *Euphausia superba* lacks waxes but contains substantial quantities of triglycerides, whereas *E. crystallorophias*, which lives in colder water near or under the pack ice, lacks triglycerides but contains significant levels of wax esters (Bottino, 1975).

An important function of both wax esters and triglycerides in marine organisms is in energy metabolism (Nevenzel, 1970; Ackman *et al.*, 1970; Benson *et al.*, 1972). Also marine species, like arid zone land animals, tend to use lipid metabolism for the production of water. Copepods have been dubbed "camels of the sea" for this reason and polar species of copepods store great amounts of wax during the short summer and draw on this reserve to fuel moulting, mating and egg production during the dark part of the year (Benson *et al.*, 1972; Sargent, 1976.) These animals can use up their stores at controlled rates due to the actions of wax ester and triglyceride lipases. Triglycerides form the usual energy reserves in diatoms, dinoflagellates, teleosts and many pelagic crustacea (Benson *et al.*, 1972).

Starvation experiments have shown how these reserves may help marine animals to withstand bad feeding conditions. Lee (1974) starved four species of copepod for a month with little mortality occurring. The triglycerides were first utilised and only when these were nearly or completely exhausted were the wax esters slowly consumed. The ability to withstand long periods of starvation is also pronounced in deep sea copepods and has been interpreted in the light of their uncertain food supply (Benson *et al.*, 1972).

Large amounts of wax esters also occur in deep living fish (Nevenzel, 1970; Lee *et al.*, 1971), evidently derived from deep water copepods. These latter authors pointed out that for carnivorous species occupying regions where the standing stock of food is low, it would be advantageous to have an efficient digestive system, a low average metabolic rate and large energy reserves. Wax esters would supply the latter. Benson *et al.*, (1972) suggested that at least half of the earth's photosynthesis production is stored, for a time, as wax.

Petrels readily feed on fat and oil released onto the sea during whaling, sealing and fishing operations. Indeed fat has long been used as a lure for petrels. In the open oceans, oil slicks also occur naturally, like those containing wax ester and triglyceride

described by Lee and Williams (1974) which probably resulted from a massive mortality of *Calanus* species. Such slicks may provide yet another source of petrol stomach oil.

According to Nevenzel (1970), the wax esters in most marine species result from biosynthesis in the animal itself. He referred to experimental work with elasmobranchs and lantern fishes and suggested a route for the synthesis and breakdown of wax esters from and to fatty acids and alcohols. This scheme also allows for the transformation of wax ester to and from triglyceride via fatty acid intermediates. Benson *et al.*, (1972) thought that the unsaturated wax esters of *Calanus helgolandicus* were probably formed directly from triglyceride esters of their algal foods. Sargent *et al.*, (1974) also demonstrated the synthesis of wax esters by the copepod *Euchaeta norvegica*.

The other major components found in stomach oils are less widespread in the marine environment. Glyceryl ether diesters, found in four species of petrels (Table 1) occur also in squid, anchovies, chimaeras, elasmobranchs, penaid shrimps and pteropods (Lewis, 1966; Lee, 1974). Pristane is a prominent hydrocarbon in copepods which are near the base of food webs and it occurs particularly in marine herbivores (Ackman *et al.*, 1970). This substance probably originates from phytol in chloroplasts of phytoplankton and is also found in the liver oils of sharks and whales (Blumer *et al.*, 1963). Squalene is an intermediate in the biosynthesis of cholesterol. It occurs in shark liver oils (Lewis, 1969b) and is used by some deep sea elasmobranchs as a buoyancy agent (Corner *et al.*, 1969.)

#### FUNCTIONS OF PETREL STOMACH OILS

These oils probably serve a variety of functions, but few of the following possibilities have been confirmed by field or laboratory experiment, so that these ideas must be regarded as tentative.

1. It seems likely that the primary function of the oil is to act as an energy reserve. This was the initial hypothesis when the present investigation was started: it appeared improbable that birds capable of laying, at most, one egg annually, had access to so much food that they could be wasting what was clearly a high-energy resource—the material burnt. Lipid releases more heat per unit mass than either protein or carbohydrate and bomb calorimetry has confirmed the high energy contents. Thirty-one samples from 11 species had a mean calorific value with one standard deviation of  $9646 \pm 266$  cal/g (Warham *et al.*, 1976). This is slightly below the value for commercial diesel oil. I calculated

that the stomach oil contains from 5 to 35 times the energy content of the prey at the time of capture.

In this role the oil would supplement the more conventional energy reserves of subdermal and visceral fat that are laid down by petrels and other sea-birds and which are also drawn on during fasts.

The oil is certainly fed to the chicks and as these may have to go for days without meals, despite exposure to inclement weather, the ability to draw on a high energy resource would have obvious value. The protein needed for growth would be gained from the tissues of squid, fish and other prey that are normally fed with the oil. However, not only the chicks must fast; so too must many adults like breeding *Puffinus tenuirostris* during their 12-day stints on their egg. Many pelagic petrels also appear to fast at sea where their foods are patchily distributed. Thus both when at sea and ashore the availability of a rich energy store would have great survival value.

Ashmole and Ashmole (1967), who also postulated that the oil was an energy source, pointed out that the excretion of water from the prey and the concentration of the lipids as stomach oil would reduce energy expenditure by the parent birds during long flights back to the nesting grounds from the feeding places.

There is little direct evidence that the oils are assimilable in the birds, but there is some indirect evidence. For example, in highly migratory species like *P. tenuirostris*, the oil content falls as the chicks approach fledging time (Serventy *et al.*, 1971). This is certainly not due to excretion of the oil, as the ejection of large amounts in burrows or elsewhere could not be overlooked. The oil evidently can be metabolised in man and in rats and has been broken down experimentally with mammalian lipases (Carter and Malcolm, 1927; Gunstone and Sealey, 1964). Reptiles too can probably digest the oil: Fleming (1939) described how skinks (*Lygosoma dendyi*) drank from pools of oil ejected by *Diomedea cauta* chicks.

2. As a water source, particularly for land-based chicks which can normally only get water from their food. Combustion of the oil to carbon dioxide and water could provide heat and water for growth and maintenance during their long fasts between meals. This function was first proposed by Kritzler (1948) in the course of his work on captive fulmars *F. glacialis*.

Petrel chicks must need more water than other chicks of comparable size as their growth rates are low, nestling periods ranging from 47 days in small species to 278 days in giant albatrosses; the chicks' uncontrolled water losses will be correspondingly high.

3. As a device to help retard digestion. In laboratory experiments it was found that the oils had a significant preservative power for crustacea. Thus it seems possible that in the presence of stomach oil the digestion of food is slowed down. Such a facility would be beneficial for pelagic species dependent on patchy food sources and allow the birds to metabolise both food and oil slowly so that energy and nutrients were made available over an extended period instead of being rapidly consumed. Slow assimilation of lipids would also help to explain the ability of chicks to discharge oil many days after they have been fed.

Clearly these three roles could be complementary and they suggest interesting parallels with the ecological roles of lipid stores in the planktonic crustacea already mentioned. Significantly, *Pelecanoides urinatrix*, the common diving petrel, which is a coastal bird and feeds its chicks daily, is the only petrel not known to contain oil either as chick or as adult.

The defensive/offensive role for stomach oil seems to be a secondary development from the widespread habit among frightened seabirds of ejecting their stomach contents to lighten their bodies for escape (Matthews, 1964). Oil ejection is used almost exclusively by surface-nesting species, notably by fulmars of the genera *Fulmarus*, *Daption*, *Thalassoica*, *Pagodroma* and *Macronectes*, and also by chicks of *Diomedea* and *Phoebetria* albatrosses. Fulmars can squirt oil with some accuracy for one or two metres. They can make several discharges before the supply is exhausted, the first consisting of the lighter oil and subsequent ones containing an increasing proportion of food material, evidently representing the evacuation of the lower part of the proventriculus. Most albatross chicks have less control and tend to splatter the oil in the general direction of the stimulus. A few burrowing gadfly petrels like *Pterodroma macroptera*, *Pt. lessoni* and *Pt. inexpectata* and at least one shearwater (*Procellaria aequinoctialis*) may also discharge small quantities of oil, but usually quite ineffectively (Warham, 1956; 1967 and unpublished). The defensive discharge of oil is made through the mouth, not through the nostrils, as stated by some early authors. However, live storm petrels often allow oil to dribble from their nostrils when held in the hand.

Young petrels may discharge oil many days after their last meal. Murphy (1936) gave several instances. Warham (1956) recorded a nestling *Pterodroma macroptera* that had not been fed for 6 days spitting oil, while a chick of *Macronectes giganteus* spat 14 days after its last meal (Warham, 1962).

In young *Fulmarus glacialis*, the oil-spitting ability is well developed by the time the chick is large enough to be left nattended in the nest, freeing both parents to forage for food. In this species spitting has been stated to occur even from a chick not completely free from the egg (Lees, 1950). The suggestion by Clarke and Prince (1976) that this chick was actually spitting bile, seems likely, as more recent data suggests that several days elapse after hatching before oil spitting behaviour appears. Williamson (1965) never saw vomiting by the very many young and hatching *F. glacialis* he handled, nor did the writer when weighing many hatching and new-born *Macronectes giganteus* and *M. halli* chicks, which are notorious spitters. Conroy (1972) found that the young *M. giganteus* first spat oil at 6 days old.

The adult *F. glacialis* is one of the most proficient at repelling aggressors or potential competitors by spitting oil. I have seen this bird displace a kittiwake (*Rissa tridactyla*) from a nesting ledge and Fisher (1952) refers to a young herring gull (*Larus argentatus*) being drenched with oil by a sitting fulmar. Murdo A. Macdonald (pers. comm.) saw northern fulmars spitting at jackdaws (*Corvus monedula*), one of which became drenched, its feathers matted and their insulation evidently destroyed. He has also noted that these petrels may spit at alien conspecifics, but such reports are few. Brown (1966) described fighting between male *Pagodroma nivea* in which stomach oil was forcefully ejected during disputes over partners or nest-sites. The combatants' white plumage was stained orange and to clean the feathers the birds resorted to "bathing" in dry snow or pushed their bills into the snow and vigorously rotated their heads from side to side. Pinder (1966) noted that breeding *Daption capense* occasionally ejected oil at intruders which landed at or approached their nests, but that this appeared to be a last line of defence.

Until recently it had been thought that the effects of contamination by stomach oil were minor and temporary, though probably effective in deterring many natural predators. Recent evidence from free-living and captive birds shows that oil-spitting can be a formidable weapon. Substantial contamination may lead to death due to matting of the victim's feathers leading to loss of flying ability and of water repellancy.

The deadly effect of oil contamination was dramatically illustrated by the fate of a fledgling

white-tailed sea eagle (*Haliaeetus albicilla*) re-introduced to Fair Island, Scotland (Dennis, 1970). These eagles include northern fulmars in their prey but one of the eagle eaglings, although well fed, was found with its plumage matted and its feathers soaked with fulmar oil. It could no longer fly and was presumed to have been snatching fulmar chicks from their nesting ledges, but had been unable to avoid the oil salvos. This eagle is thought to have died and some 20 other species (raptors, crows, owls, herons, gulls, even a few passerines) are believed or known to have been killed as a result of stomach oil contamination (Dennis, 1970; Broad, 1974; Booth, 1976). At Fair Isle, cliffs are the main resting places for migrant birds, but these are also heavily populated by fulmars and it seems that many of the victims blundered into the petrels' individual distances and hence were repelled by oil: the passerines may perhaps have been caught in cross-fire!

Confirmation of the potential danger of oil contamination was given by Swennen (1974) who kept a single *F. glacialis* (fed on thawed deep-frozen fish) in captivity with gulls and auks. The fulmar killed 5 of its cage mates merely by spitting oil during aggressive attacks. Deaths resulted from chilling and/or drowning. Vigorous bathing by the soiled birds failed to restore feather structure whereas the fulmar appeared to be able to remove any self-contamination by bathing and preening.

Mammals are also attacked. The oils seem in no way harmful to man, have no burning action on the skin, but rabbits soaked with oil have been found dead where nesting northern fulmars were taking over rabbit-burrowed ground at the top of a cliff (Fisher, 1952). Shetland crofters are currently experiencing financial losses due to their sheep being soiled with fulmar oil. The sheep remain healthy but their fleeces are unsaleable owing to matting by the oil to which heather, grass and other debris adhere (Robertson, 1975).

I have only one report of an encounter between a cat and an oil-spitting petrel. Knowles Kerry (pers. comm.) saw a nestling *Phoebastria palpebrata* discharge oil at a feral cat at Macquarie Island. As the oil struck, the cat leapt out of the way and rolled over frantically on the grass as if trying to remove the contamination. If this reaction is typical, it is unfortunate that the chicks of burrowing species are unable to spit oil, for it is these that suffer the greatest losses from predation by introduced cats.

One obvious problem that arises from the discovery of the deadly results of oil contamination is how the petrels themselves achieve immunity. They appear to eliminate soiling by bathing in water or snow but as this fails with other seabirds, some special mechan-

ism must be operating with petrels—perhaps a difference in feather structure. Further study is clearly needed.

The readiness of *F. glacialis* to eject oil suggests not only that this species has adequate food resources but also that the offensive role of oil may be an important element in the birds' successful and continuing expansion of breeding range.

Like other anti-predator devices, oil spitting does not confer total immunity. Despite their dangerous armoury, surface-nesting petrels and their chicks are eaten by a variety of natural enemies. For example, chicks of *Daption capense* and of *Macronectes giganteus* are killed and eaten by southern skuas (*Catharacta skua*) (Pinder, 1966). Even northern fulmars are eaten by bald, white-tailed and golden eagles (*Haliaeetus leucocephalus*, *H. albicilla* and *Aquila chrysaetos*), by the falcons *Falco peregrinus* and *F. rusticolus* and by the fox *Vulpes fulva* (Fisher, 1952; Hawker, 1975). Large gulls also get some fulmar chicks. The falcons, striking on the wing, would be expected to take fulmars with impunity, but even peregrines seem to fall victim at times (Clarke, 1977).

#### "MUMIYO"

Snow petrels use oil-spitting to good effect in deterring predatory skuas and during intra-specific conflicts over nest sites. In the cold climate the spilled oil, usually mixed with the excreta of the chicks, sets as hard as stone and accumulates around the nesting places as these are used year after year. Up to 9 kg of this frozen oil has been recovered in a single lump.

Geologists examining this material determined its biological nature and thought that it was formed from the petrel's excreta (Ardus, 1964; Jones and Walker, 1964), but Winsnes (1969) realised that it was mainly stomach oil. Meanwhile Russian scientists had noted the Antarctic material's similarity to "mumiyo", a deposit of biological origin found in rocks in Iran, India and China. The infra-red and ultraviolet spectra of "mumiyo" and the Antarctic deposits were similar (Korotkevich *et al.*, 1967). Some samples of "mumiyo" are also known to contain waxes (Poroshin *et al.* 1964).

"Mumiyo" has been known from antiquity, was described by Avicenna and others, and is still believed to be a valuable aid in mending broken bones in some circles of oriental medicine.

There seems no doubt as to the origin of Antarctic "mumiyo", but that of the Asian substance is so far undetermined. It seems rather unlikely that it will prove to be fossilised stomach oil but if so would reflect nesting sites along the shores of some former

coastline, perhaps that of the Tethys Sea. However, even if Asian "mumiyo" proves to have a single origin and from animal rather than plant material, there are possible sources of fossil oils and waxes other than petrels. For example, at Bute Inlet, British Columbia, copious submarine deposits of wax have been found. Analyses suggest that these may be a consequence of massive kills of *Calanus* sp. through unknown causes (Benson *et al.*, 1972). Conceivably such deposits could be preserved under appropriate conditions to form "mumiyo".

#### FURTHER WORK

Although the origins of the oils seem clearly established, many unresolved problems remain concerning functions and particularly concerning the metabolic pathways involved in the birds' processing of the oils. Do the chicks manufacture it? How much of the energy actually available is used? How is the combustion of the stomach oils and the depot fats controlled? Is there any re-incorporation into protein which Lee (1974) suggested as a role for the wax esters from the copepods eaten by the ctenophore *Pleurobrachia* and by arrow worms of the genus *Sagitta*?

The course of digestion in petrels seems unknown. Presumably the fragile oil-sacs of small crustacea would be ruptured in the proventriculus as happens with calanoids which, when netted, release quantities of oil into the water. Cheah and Hansen (1970a) considered that the oil accumulated in the petrel because protein was digested more rapidly than lipid, but if so, how is the protein moiety able to pass into the gizzard and intestine leaving the low viscosity oil behind? This may be aided by the operation of the pyloric valve and by the unusual arrangement in which the duodenum ascends from the gizzard before looping around the pancreas: this will help to stop the oil draining down to the intestine. Also, being heavier, the food tends to lie at the bottom of the proventriculus and hence will be the first to pass into the gizzard.

Or is protein absorbed in the proventriculus itself? However, it is customary to consider that chemical digestion in birds occurs in the small intestine. In some species the proventriculus has been shown to be the site of acid gastrin production. This begins the breakdown of proteins which is completed further along the intestinal tract. In the small intestine bile and bile salts emulsify fats while pancreatic and mucosal secretions help neutralise the acid chyme and allow lipases, carbohydrases and proteinases to work.

Another possibility is that protein and carbohydrate are absorbed intestinally while lipids are taken up by the proventricular epithelium. Watts' suggestion

that phospholipids are absorbed here (particularly the 20:5 and 22:6 polyunsaturated fatty acid components) with the help of an acid phospholipase, has already been mentioned. Clarke and Prince (1976) noted that while oil from an adult *D. melanophris* was rich in wax esters, that from four chicks consisted mainly of triglyceride with some free fatty acid. They suggested that this might indicate some digestion in the proventriculus. However, the contents of the proventriculus seem to be highly acid, and this in an unlikely environment for normal lipase activity which needs alkaline or neutral conditions. Nor is there any special route for pancreatic or bile secretions to reach the proventriculus, although the last discharges of oil tend to be green in colour suggesting that bile can be regurgitated. An ability to transform wax esters into triglycerides in the proventriculus, with or without absorption there, would provide yet another source of variability in the ratios of these compounds in oils from different conspecifics.

Imber (1976) also speculates as to whether petrel stomachs can preferentially utilise triglycerides during fasting periods as in the crustacea experiments of Lee *et al.*, (1971), so that the wax ester moieties increase proportionately in the course of digestion.

On the other hand, if food and lipids are all mainly absorbed in the intestine, then the functions of the copious proventricular glands remain in question. Even if absorption of phospholipids from food occurs there, phospholipid is not a significant constituent of the oils, and the glands, which in some species are known to have different forms when the lumen is full than when it is empty, seem too numerous and specialised merely to be producing gastrin and absorbing phospholipid.

The ability of proventricular epithelium to break down or absorb stomach oils could be tested *in vitro*. This was attempted by Cheah and Hansen (1970b) who found some evidence of lipase activity in *P. pacificus* but only between pH 6.5 and 9.0. They concluded that under the acid conditions obtaining in the proventriculus there could have been little effective lipolysis. Additional *in vitro* work seems to be required together with some *in vivo* experiments using radioactively-labelled oil, and, in view of the absence of oil in *Pelecanoides*, a comparative examination of the morphology and metabolic activity of the proventricular epithelia of that petrel and others could prove rewarding.

One possible approach for following the progress of digestion in the proventriculus would be to analyse samples of oil extracted at regular intervals from a fasting adult or chick, perhaps using the pipette technique of Grubb (1971), and look for changes in

the proportions of wax esters to triglycerides with time.

Yet another problem concerns the mechanisms for breaking down waxes. These are usually regarded as highly indigestible and in only one other bird group, the passerine honey-guides Fam. Indicatoridae, is ceratophagy normal. Wax digestion in these birds is believed to be achieved through the lipolytic activity of an intestinal microflora (Friedmann and Kern, 1956).

#### CONCLUSION

The appearance of stomach oil in petrels may result from the slow digestion of an unusual food which the birds have learned to use with difficulty but which confers significant advantages in providing an energy and water reserve, food and water for chicks and an offensive/defensive weapon.

Storage and use of stomach oil appears to be another adaptation that helps procellariiform birds to exploit pelagic foods which are patchily distributed and which involve parents in long journeys to find food and both parents and chicks in substantial fasts. Utilisation of stomach oil as energy and water sources complement other energy-saving adaptations that fit petrels for this lifestyle, such as their low body temperatures (which presuppose low basic metabolic rates), and the ability of many species to travel by dynamic soaring.

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