THE ORIGIN OF PETREL STOMACH OILS—A REVIEW

M. J. IMBER

Among stomach contents of procellariiform birds, one of the commonest components is oil which varies in color from pale yellow to red. This oil occurs in greatest quantities in stomachs of young birds on the nest and may be regurgitated by them when disturbed. Regurgitation is apparently more frequent, and may be more voluntarily controlled, in chicks of surface nesters than in those of burrow nesters, thereby possibly serving as a defense mechanism for the former. Because the oil floats on top of the stomach contents it is ejected most frequently but solid and partly-digested food may follow it.

Early analyses of stomach oil from Sooty Shearwaters (*Puffinus griseus*; Smith 1911, Carter 1921, Carter and Malcolm 1927) and from a Fulmar (*Fulmarus glacialis*; Rosenheim and Webster 1927) revealed high concentrations of wax esters. In these lipids the fatty acids are esterified with long-chain alcohols, whereas in typical fats (triglycerides) they are esterified with glycerol. Because wax esters were then virtually unknown in marine animals, though known to occur in large quantities in Sperm Whales (*Physeter macrocephalus*; Smith 1911, Carter 1921), hypotheses were put forward to explain their origin. Carter and Malcolm (1927) considered that they might be indigestible residues from food but failed to find them in an analysis of fish and shell-fish fats (littoral and epipelagic species). They and Rosenheim and Webster (1927) independently made similar hypotheses, based on similar reasoning: the stomach oils might be secretions of the birds themselves, similar to preen gland wax but possibly originating near the nasal cavity (Rosenheim and Webster 1927), or actual preen gland wax accidentally ingested (Carter and Malcolm 1927). Matthews (1949) found evidence suggesting that the proventriculus could be the site of secretion but he emphasized that proof of a secretory origin was still required. No such proof appears to have been published but, until very recently, some ornithologists have given unwarranted credence to this hypothesis (see Ashmole 1971).

A number of biochemical studies (table 1) have now revealed that petrel stomach oils are not uniform: wax esters, triglycerides and glyceryl ethers have variously been found to be the predominant lipids, and proportions have varied widely even among samples taken from the same species at the same time. It was mainly this variability that cast doubt on the secretion hypothesis (Lewis 1969), for it seemed unlikely that a secretory mechanism would vary its product so much. The hypothesis, first advanced by Hagerup (1926), of a dietary origin for the oils seemed more likely. Kritzler's (1948) experiment with a captive fulmar, which regurgitated oil resembling pork fat after being fed fatty pork (but no biochemical tests were made) tended to support this hypothesis. On the basis of their studies of petrel stomach oils, Lewis (1969) and Cheah and Hansen (1970 a,b) independently concluded that the oils were not secretions but derivatives of the diet.

Earlier studies of lipids in the marine environment had revealed mainly triglycerides. However, Nevenzel et al. (1965, 1966) discovered in some deeper-living pelagic fish large amounts of wax esters that were characterized by a predominance of oleic acid. Then Lewis (1967) found that the concentration of oleic acid in marine animals increased with increasing depth of habitat. He suggested, after considering the findings of Nevenzel et al., that this indicated increasing amounts of wax esters in deeper-living animals. Among the animals whose lipids he analyzed were crustaceans of the genera *Gnathophausia* and *Acanthephyra*, and of the family Pasiphaeidae, and fishes of the family Myctophidae, all of which contained moderate to high proportions of oleic acid among their fatty acids. All of these groups of animals were subsequently found to be important prey of Grey-faced Petrels (*Pterodroma macroptera gouldi*; Imber 1973) and Cook's Petrels (*P. cooki cooki*; Imber unpubl. data). Further studies by Lee et al. (1971) and Lee and Hirota (1973) of the lipids of marine animals taken from varying depths have confirmed Lewis's hypothesis. Many of the animals whose lipids they analyzed belonged to groups which have recently been found to be important prey of Procellariiformes (table 2).

Evidence of wax esters in other marine animals was produced by Hansen and Cheah (1969), who found that both the body tissues and items of the diet of Sperm Whales contained large quantities of wax esters. The

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TABLE 1. Results of analyses of petrel stomach oils reported in the literature.

Species		Stomach oil analysis (% of total lipids) Wax esters	Triglycerides	Glyceryl ethers	Reference
Wandering Albatross (*Diomedea exulans*)		77	4	2	Lewis 1969
Fulmar (*Fulmarus glacialis*)	a.	*			Rosenheim and Webster 1927
	b.		*		Gunstone and Sealy 1964
	c.	0	89	0	Cheah and Hansen 1970a
Westland Black Petrel (*Procellaria westlandica*)		19	59	0	Lewis 1969
Flesh-footed Shearwater (*Puffinus carneipes*)	a.	tr	78	0	Lewis 1969
	b.	3	17	51	
Wedge-tailed Shearwater (*Puffinus pacificus*)	a.	0	23	0	Cheah and Hansen 1970b
	b.	0	83	0	
Sooty Shearwater (*Puffinus griseus*)	a.	*			Smith 1911
	b.	*			Carter and Malcolm 1927
Slender-billed Shearwater (*Puffinus tenuirostris*)	a.	85	9	0	Cheah and Hansen 1970a
	b.	76	13	0	
Great-winged Petrel (*Pterodroma macroptera*)	a.	0	61	0	Cheah and Hansen 1970b
	b.	6	79	0	
Leach's Petrel (*Oceanodroma leucorhoa*)				*	Lewis 1966

* Major lipid type. tr trace.

diet of Wandering Albatrosses (*Diomedea exulans*; Imber and Russ 1975) and Royal Albatrosses (*D. epomophora*; Imber unpubl. data) closely resembles that of Sperm Whales (Gaskin and Cawthorn 1967).

Gordon (1955) suggested that oceanic birds may feed on the fauna of the deep scattering layers at night when it migrates toward the surface. Akimushkin (1954, 1963) found that Black-footed Albatrosses (*Diomedea nigripes*) in the north-west Pacific Ocean fed on mesopelagic squids that came to the surface at night. Lewis (1969) suggested that diurnal vertical migration of mesopelagic fishes and crustaceans made these available to oceanic birds, hence providing a potential source of wax esters. Ashmole (1971) noted that the deep scattering layers were a potential source of food for oceanic birds but that precise data were very scarce. Harris (1973) found that the Waved Albatross (*Diomedea irrorata*) fed on a wide variety of cephalopods, fish and Crustacea, and most of those cephalopods and crustaceans were mesopelagic species. I have examined food samples from Grey-faced Petrels (Imber 1973), Wandering Albatrosses (Imber and Russ 1975), Cook's Petrels (unpubl. data) and Black Petrels (*Procellaria parkinsoni*; Imber 1976) and found that they were composed almost entirely of mesopelagic species, some even being considered primarily bathypelagic. Present knowledge of the main foods of those petrels whose stomach oil has been analyzed (table 1) is shown in table 3.

TABLE 2. Analyses reported in the literature of the lipids of some important prey of Procellariiformes.

Prey	Lipid analysis (% of total lipids) Triglycerides	Wax esters	Reference
Cephalopoda			
Oegopsida ?species	6	27	Lee et al. 1971
Cranchiidae sp.	18	32	Lee and Hirota 1973
Fish			
Myctophidae spp.	2–27	tr–15	Lee and Hirota 1973
Crustacea			
Gnathophausia spp.	12	69	Lee et al. 1971
	8–12	32	Lee and Hirota 1973
Euphausiacea	7–21	tr	Lee and Hirota 1973

tr trace.