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WAX DIGESTION IN WILSON'S STORM-PETREL

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ABSTRACT.—Captive Wilson's Storm-Petrels (*Oceanites oceanicus*) fed a diet of pure wax (hexadecyl oleate) or triacylglycerol (olive oil) increased in body mass or lost mass more slowly than birds given only water, depending upon the quantity of lipid they were fed. Lipids extracted from the feces of wax-fed birds contained fatty alcohol and fatty acid, the products of wax hydrolysis. The data indicate the ability to digest waxes in this species. Waxes are abundant constituents of many marine organisms and form the majority of total lipid ingested by some seabird species. The ability to digest wax represents an important adaptation for marine birds that encounter waxy prey, allowing a vast source of potential energy to be utilized. *Received 9 July 1985, accepted 21 Oct. 1985.*

In terrestrial environments, animals typically store energy in the form of triacylglycerols (TAGs), and predators often derive much of their energy from the conversion of these lipids. In marine environments, however, many animals store energy in the form of wax esters (waxes), particularly in cold and deep water environments (Sargent et al. 1976). Waxes result from the esterification of a long-chain fatty alcohol with a single fatty acid. Many are liquid at room temperature, and all have an energy content similar to that of TAGs (40 kJ/g). It has been estimated that up to half of all the organic matter synthesized by the world's phytoplankton is converted at some time into wax (Benson and Lee 1975). There exists a huge standing crop of wax in the world's oceans. Wax storage is widespread at all levels of the food chain, and waxes are present in many marine organisms that are eaten by seabirds, including copepods, euphausiids, midwater cephalopods, and myctophid fishes (Sargent et al. 1976). Procellariiform birds accumulate dietary lipids in the proventriculus as stomach oil (Clarke and Prince 1976), and chemical analysis of these stomach

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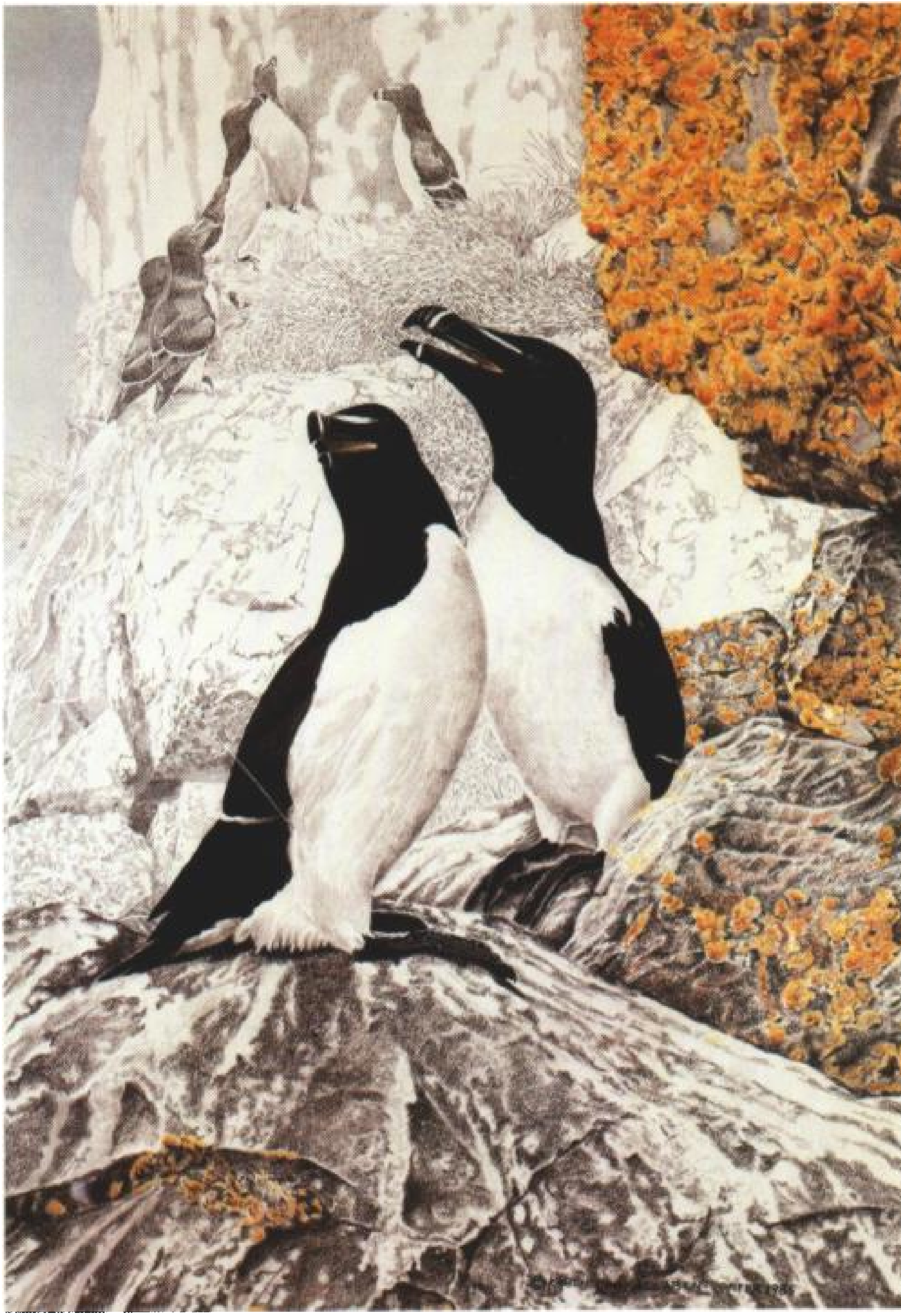

Razorbills *(Alca torda).* The painting, in pastels and pencil with watercolor, is by Karen Allaben-Confer, winner of the 1985 George Miksch Sutton Award for Ornithological Art.

TABLE 1

THE RELATIVE IMPORTANCE OF TRIACYLGLYCEROL (TAG) AND WAX ESTERS (WAX) IN STOMACH OILS OF 24 PROCELLARIIFORM SPECIES[a]

	TAG	Wax
Present in sample	23 (96%)[b]	20 (83%)
Most abundant constituent	11 (46%)	11 (46%)
Percent of total sample	0–80%	0–81%

[a] Data are taken from a summary of the chemical compositions of stomach oils in Jacob (1982).
[b] Number of species (% of species).

oils provides a convenient index of the types of lipids ingested by the birds. In 24 procellariiform species whose stomach oil constituents have been identified and quantified (Jacob 1982), waxes were of roughly equal importance to TAGs (Table 1). In almost half of these species, wax was the most abundant class of lipids present in stomach oil. Thus, if they can be digested, waxes represent a potentially important energy source for marine birds.

Waxes tend to be inert compounds metabolically, even within the marine organisms that synthesize them (Lee and Barnes 1975). Vertebrate lipases hydrolyze waxes at a fraction of the rate they hydrolyze TAGs (Mattson et al. 1970, Savary 1971, Patton et al. 1975). In laboratory mice, diets containing greater than 1% wax by weight result in diarrhea, weight loss, or death (Verbiscar et al. 1980). Although waxes are the primary constituents of blubber and spermaceti in odontocete whales (Hansen and Cheah 1969), waxes have not been found in the tissues of marine birds (Clarke, in press). Thus, the fate of these energy-rich lipids ingested by birds is of interest. An inability to handle dietary wax quickly and efficiently would increase the rates of prey capture needed to satisfy energy requirements of foraging seabirds, and possibly render whole species of prey inedible.

Among terrestrial birds, the ability to digest wax has been previously demonstrated for the honeyguides (Indicatoridae; Friedmann and Kern 1956). Here, I present evidence that the Wilson's Storm-Petrel (*Oceanites oceanicus*) is able to digest wax and use the chemical potential energy stored within wax molecules.

METHODS

Experiments were performed at Palmer Station, Anvers Island (64°46′S, 64°03′W), near the Antarctic Peninsula. Wilson's Storm-Petrels were captured at the nest and held in one-gallon containers fitted with a wire-mesh floor through which their droppings could fall. Birds were force-fed by packing a syringe with liquid or homogenized food (see below) and forcing it under slight pressure through a tube inserted past the glottis and into the stomach. Beginning one day after capture, all birds were fed 5 ml of homogenized krill (*Euphausia superba*) every 8 h. This feeding regime was maintained for 48 h to make certain that the birds had adjusted to the procedure and were maintaining body mass on a forced diet.

Four birds were then switched to experimental diets. One bird was fed 1 ml wax (hexadecyl oleate) with 4 ml water; a second bird was fed 1 ml of TAG (olive oil) with 4 ml water; and the remaining two birds were given 5 ml water. All birds were fed every 8 h. Each individual was weighed to the nearest 0.1 g immediately prior to feeding. After 56 h, the diets were again adjusted. The volume of lipid administered to both the wax-fed and TAG-fed birds was doubled; their new diets were 2 ml hexadecyl oleate with 3 ml water, and 2 ml olive oil with 3 ml water, respectively. The two birds previously given only water were switched to a diet including wax (2 ml hexadecyl oleate with 3 ml water). Thus, all birds received 5 ml of liquid every 8 h throughout the experiment, and only the composition of the liquids varied.

Droppings from each bird were collected daily and frozen. Fecal lipids were later extracted with methanol and chloroform according to the methods of Bligh and Dyer (1959). Extracted lipids were dissolved in ethyl ether (anhydrous), and the lipid families present were separated via thin-layer chromatography on silica-gel coated plates in a developing solution of petroleum ether, ethyl ether, and acetic acid (80:20:1). The plates were dipped briefly in a cupric acetate solution and charred at 130°C to make lipid bands visible. Bands were identified by comparison with a set of purified, commercial standards (Nu Chek Prep No. 18-5 C, containing cholesterol, cholesterol oleate, triolein, oleic acid, and lecithin, with hexadecyl oleate added).

RESULTS

Changes in body mass.—In the early part of the experiment, all four birds lost mass steadily (Fig. 1). However, the mean rate of mass loss in the birds receiving only water (3.85 g/day) was higher than that of either the wax-fed bird (2.19 g/day) or the TAG-fed bird (1.93 g/day). Rates of mass loss of the wax-fed and TAG-fed storm-petrels were very similar. When the volume of lipid administered was doubled, the decline in body mass was reversed; all four birds actually regained some of the body mass previously lost. The wax-fed storm-petrels showed a mean gain of 0.63 ± 0.28 g/day [SE] ($N = 3$) or 0.12 g body mass/g lipid fed, while the TAG-fed bird gained 2.29 g/day, or 0.42 g body mass/g lipid fed.

Fecal lipids.—In wax-fed birds, the total mass of lipid extracted from the feces averaged $3.2 \pm 1.4\%$ ($N = 3$) of the total lipid ingested. Mass of fecal lipids averaged $1.4 \pm 0.5\%$ ($N = 2$) of the lipid fed to TAG-fed birds. Analysis of fecal lipids (Fig. 2) from wax-fed birds revealed the presence of fatty alcohol and fatty acids, the end products of wax hydrolysis, as well as undigested wax. The prevalence of fatty alcohol in the feces was generally correlated with the quantity of wax fed to the bird during the 24-h period over which the feces were collected. Fecal lipids from TAG-fed birds included no fatty alcohols. However, the products of TAG hydrolysis, i.e., fatty acids and glycerol, were present, along with small quantities of TAG.

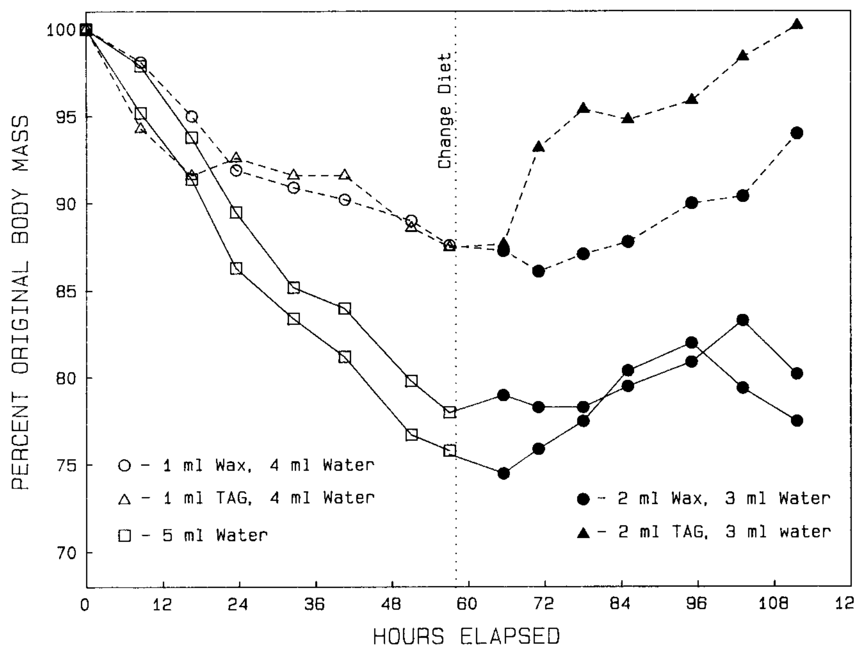

FIG. 1. Change in body mass of captive Wilson's Storm-Petrels fed diets of wax (hexadecyl oleate), TAG (olive oil), and water.

DISCUSSION

The Wilson's Storm-Petrel is an opportunistic feeder, taking such wax-rich items as myctophid fishes and midwater squids from the cold waters of its breeding range (Obst, unpubl. data). The ability to maintain or add body mass on a pure wax diet, along with the presence of the products of wax hydrolysis in the feces, indicates that the Wilson's Storm-Petrel can digest wax. The presence of fatty alcohols in the feces does not in itself establish that this species is capable of using waxes as food, since microbial hydrolysis of wax esters in the hindgut could presumably liberate fatty alcohols without making them available to the host. However, the ability to maintain body weight on diets of either wax or TAG demonstrates that both of these lipids represented an energy souce for the captive storm-petrels in this experiment. The ability to digest waxes would be an important adaptation for any seabird that commonly encounters wax-rich prey. It would prevent a large source of chemical potential energy from going unused, and allow such prey to pass through the gut without producing a laxative effect.

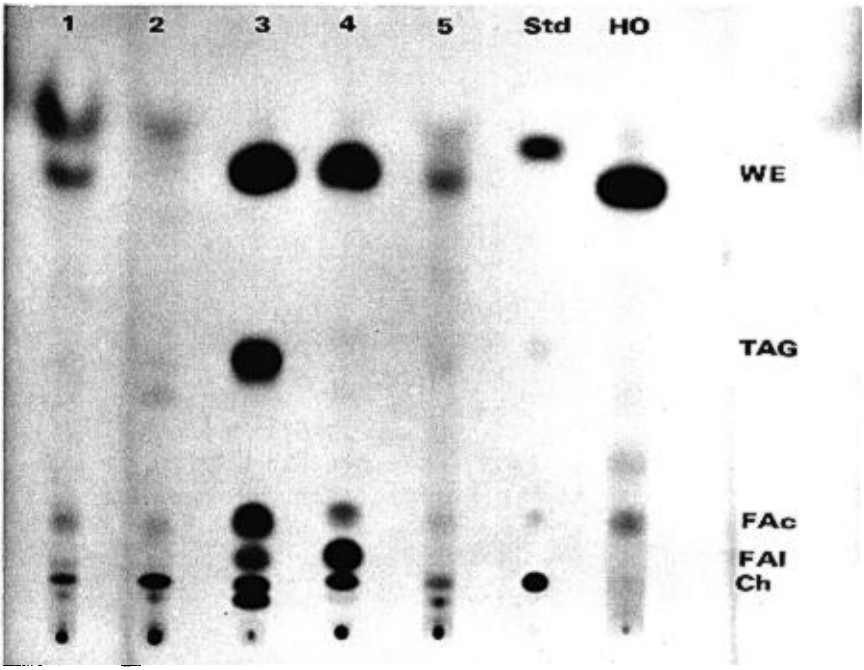

FIG. 2. Thin-layer chromatography of lipids extracted from feces of wax-fed and TAG-fed Wilson's Storm-Petrels. Lanes 1–5 represent individuals fed the following diets: Lane 1—3 ml wax/day; Lane 2—3 ml TAG/day; Lane 3—3 ml wax and 3 ml TAG/day; Lane 4—6 ml wax/day; Lane 5—3 ml wax/day, followed by a 24-h fast. Abbreviations are: WE = wax ester; TAG = triacylglycerol; FAc = fatty acid; FAl = fatty alcohol; Ch = cholesterol; HO = hexadecyl oleate (dietary wax); Std = standard, containing purified sterol ester, triacylglycerol, fatty acid, and cholesterol.

Rates of mass change appeared to be similar in wax-fed and TAG-fed storm-petrels when the birds were underfed, but TAG appeared to be used more efficiently than wax when provided in excess of the birds' energy requirements. Although the sample size upon which these observations are based is small, this interpretation is consistent with studies from other vertebrates that indicate that the hydrolysis of waxes proceeds at a slower rate than the hydrolysis of TAGs. Given a sufficiently long residence time in the gut, waxes might be digested completely, but rates of fat deposition would be relatively higher for birds on diets rich in TAGs if waxes are, indeed, digested more slowly. This could have important consequences for the growth rates of seabird chicks receiving wax-rich foods from their parents. However, conversion of wax to TAG requires a suitable source of glycerol, and the substrates normally converted into glycerol, glucose, and amino acids were not present in these experimental diets.

Although the majority of procellariiform species represented in Table 1 inhabit high latitudes, there is good reason to expect that low-latitude seabirds also ingest much wax. Midwater fishes and cephalopods known to be rich in wax are common prey for many tropical seabirds, which capture them as these prey are driven to the surface by other predators (e.g., tuna, porpoises) or as they migrate to the surface at night (Ashmole 1971, Imber 1976). Sphenisciform, pelecaniform, and charadriiform species, as well as the procellariiforms, undoubtedly encounter waxy prey. The ability or inability to digest wax could be a factor shaping patterns of prey selection, feeding rates, and growth rates of marine birds inhabiting waters where wax-bearing prey occur. In feeding experiments using radiolabeled lipid tracers, D. Roby et al. (unpubl. data) found evidence for wax digestion in 4 high-latitude, planktivorous seabird species (3 petrels and an alcid). Further work should be undertaken to determine how widespread wax digestion is among seabirds, using species representing a variety of families and oceanographic regions.

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COLOR PLATE

The Frontispiece painting "Razorbills" (*Alca torda*) has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by Karen Lynn Allaben-Confer, winner of the first George Miksch Sutton Award for Ornithological Art. (See announcement on page 333).