Diet Studies of Seabirds: a Review of Methods

DAVID CAMERON DUFFY AND SUSAN JACKSON

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.

Abstract.—Methods of collecting, analysing and presenting data on the diets of seabirds are reviewed, with consideration of methods employed in diet studies of other organisms. Killing of birds continues to be the primary source of dietary information from birds at sea but is no longer necessary for studies on land. Stomach pumps obtain complete stomach evacuation with low mortality. Stomach samples should be examined as soon as possible after collection, to avoid biases caused by preservation. Presentation of data is best done by rank-order to facilitate comparison between studies, but as many data should be provided as possible. Future work on diets will be strengthened through knowledge of digestion rates and nutritional values of food.

Key words.—Colonial waterbirds, diet, food consumption, methods, seabirds.

The study of diets is central to an understanding of seabirds and their adaptations to the marine environment. Diet studies provide information on diet composition and overlap between seabird species (e.g., Ashmole and Ashmole 1967), energy and nutrition of food fed to young by their parents (e.g. Harris and Hislop 1978, Prince and Rickets 1981, Montevecchi and Piatt 1984); meal size, prey choice and the timing and frequency of feeding by adults at sea (cf., Darnell and Meierotto 1962, Eggers 1977, Brown et al. 1981, Durbin et al. 1983, Wilson 1985); information on the composition of fish and invertebrate communities in seabird foraging areas (Ashmole and Ashmole 1968); an assessment of the potential or current impact of commercial fisheries on seabird populations (e.g., Wiens and Scott 1975, Harrison et al. 1983); estimates of avian consumption of commercially-important fish stocks for fisheries management (Schaefer 1970, Furness 1978, Furness and Cooper 1982); and other data on the distribution, age, sex, reproductive state, stomach contents and body condition of prey species (e.g., Sunada et al. 1981, Vermeer and Westrheim 1984, Duffy et al. 1985a). Unfortunately, despite the importance of diet, diet methodology in seabird studies has received relatively little attention. It is likely that major biases might result from different methods, and terms such as 'volume' and 'mass' require standardization. New methods of potential use in seabird studies have been developed by investigators working on fish and marine mammals, although these are often little known to seabird-researchers.

Methods of studying avian diet have been reviewed by McAtee (1912), Hartley (1948), Ashmole and Ashmole (1967) and Ford et al. (1982). Although reviews have covered groups such as fish (Hynes 1950, Hyslop 1980), marine mammals (Fitch and Brownell 1968), and animals in paleoenvironments (Casteel 1976), there has been no recent, general review of methods used in seabird diet studies. This paper reviews existing methodology for the study of seabird diets. We have included methods employed on other animals when these techniques appear of potential use in seabird studies. We also suggest additional areas where research is necessary. While the examples and references are by no means exhaustive, they are included to give an idea of the range of approaches possible. We also hope to provoke critical examination of many of the methods used in the study of seabird diets and to stimulate further work on methodology itself.

SAMPLE SIZES REQUIRED

The methods used in and data obtained from diet studies must vary according to the purpose of each study. The intensity, focus, duration, and analysis of diet studies depend on the questions being asked, rather than being the result of some non-existent 'ideal' methodology for the study of diets (Steven 1933).

Sample sizes for diet studies depend on the purpose of each study, the variability of samples, and the degree of precision desired. At one extreme, presence/absence data require very small samples while attempts to determine the exact proportion of a particular prey type may require enormous and usually unrealistic sample sizes.

The probability of detecting a certain prey species or life stage of a species in a diet can be determined using the cumula-

tive binomial distribution: $P(X > r) = \Sigma p^x (1-p)^{n-x}$, where $P(X > r)$ is the probability of at least r occurrences in n samples, p is the probability per sample of an occurrence, assuming the samples are independent (Mosteller and Rourke 1973).

Detection will normally require relatively small samples. For example, if a species occurs in only 10% of the diet, then it has a 65% chance of occurring at least once in a sample of 10 and an 88% chance of occurring in a sample of 20. More frequent prey require an even smaller number of samples.

Collecting samples to allow comparison of diet between species, locations, or times can require enormous samples if 'accuracy' is required. Hanson and Graybill (1956), after Cochran 1953) showed that to determine the proportion 'p' of a prey species with a 95% chance of being within a percentage 'd' of the true value, the sample needed 'N' $= 4p/(100 - p)/ d^2$. The closer 'p' is to 50%, the larger the sample; so the food with a 'p' closest to 50% will determine the minimal sample size. For a food where 'p' $= 50$, if 'd' $= 25\%$, 'N' $= 16$; if 'd' $= 5\%$, 'N' $= 400$, and if 'd' $= 1\%$, 'N' $= 10,000!$ While such samples might be acceptable, albeit tedious, for visual observations or collections of pellets, they represent massive disturbance if collection methods require the handling or death of seabirds. Non-parametric rank statistics, although not as powerful, require fewer samples (Siegel 1956); and diets might be considered similar with respect to ranks of different prey, if there were relative agreement between samples.

Sample sizes as small as six may be sufficient for such tests. Samples of 30 or more have only a small probability of sampling error and statistical values derived from them will approach their underlying statistical distributions. Such sample sizes are far more realistic than those for parametric samples.

The sample size necessary to calculate the total number of prey types taken can be determined graphically; each additional sample has a proportionally smaller chance of adding new prey types to a species' diet (cf., Baltz and Morejohn 1977). A dietary analysis can be considered complete when the rate of accumulation of new species or its diversity reaches an asymptote. This can be determined subjectively (e.g., Baltz and Morejohn 1977) but quantitative approaches discussed by Holgate (1969), Hurtubia (1973) and Pielou (1977) are preferable.

For studies of food consumption and energetics, rank statistics will be insufficient and parametric statistics would be required. Sample sizes can be reduced by lowering confidence limits, decreasing the desired precision; sampling from a more homogeneous environment, displacing 'p' from 50% by splitting or lumping prey categories or selecting sample sizes based on prey types with relatively small variation (Hanson and Graybill 1956). Parametric statistics can also be employed when looking at characteristics of prey such as size or mass when prey are numerically abundant, even within a few samples. Measurements per stomach are also more amenable to parametric or non-parametric analysis such as analysis of variance, ANOVA, which could be used to determine the degree of variation within and between samples (Schneider and Hunt 1984).

Although minimum sample size may be set statistically, maximum size is likely to be imposed by logistics or ethics. A statistically-acceptable number of stomach samples from albatrosses might kill off an entire colony or at least disrupt nesting.

Another problem that requires consideration, after collection of a preliminary sample, is the degree of homogeneity of a sample. If diet varies during the day, from day to day, over longer time periods, between sexes, or between adults at different stages of the breeding cycle, sampling must be designed to sample each group equally or samples must be initially analysed separately. Similarly, samples taken from several colonies are likely to differ. This may also be true of subcolonies at a nesting site. If seabirds exploit each other as sources of information (Ward and Zahavi 1973), birds at contiguous nests may be more likely to have similar diets than those at nests farther apart. What appear to be suitably large samples may be inadequate if different sources are lumped together or if samples are taken disproportionately from single individuals.

METHODS OF COLLECTING SAMPLES

There are three basic ways of collecting diet samples from seabirds: killing them, sampling birds without mortality, and using waste products or observations without the necessity of handling birds. Different methods will be necessary depending on the question asked, the species studied, and the stage of life-cycle examined.

Collecting by Killing

Killing birds is usually the least preferred approach (e.g., Coleridge 1854). When killing is necessary, every effort should be made to maximize information and minimize numbers killed. Both objectives can be achieved only by careful planning, an understanding of the species' biology, and explicit goals. Preliminary sampling should be used to identify the best times or locations for the collection of suitable samples.

With the development of stomach pumps (see below), we believe that killing birds that can be caught at nesting colonies or roosts is unnecessary. We believe the only reasons for continuing to kill birds on land are 'validation' of other methods and determination of the extent of differential digestion of various prey types, through comparison of the contents of the proventriculus and ventriculus.

In contrast, collecting birds at sea is probably most efficiently done by shooting them. Other methods (see below) are often extremely time and labor-intensive. Unless the species is endangered or from an intensively-studied population, shooting will probably be easiest, although other methods should be explored first.

Random shooting of birds seems to us a waste of birds, ammunition and time and can be condoned perhaps only in studies of timing of seabird feeding, when collecting is used to monitor the incidence of full stomachs at different times of day. For most studies of diet, however, full stomachs are to be preferred. The best way to ensure these is to shoot birds actively feeding or just leaving an active feeding-area (e.g., Vogt 1942, Lumsden and Haddow 1946, Bradstreet 1976). Since many pelagic species sit on the water after feeding (Brown et al. 1981), perhaps to digest food and reduce mass before flying

Table 1. Stomach fullness related to behavior of pelagic seabirds shot off the southern Cape Province, South Africa[2].

	Sitting on water	Behavior Associated with or engaged in feeding activity	Flying
Stomach fullness			
0–4%	45.0	19.6	73.7
5–20%	28.3	35.3	15.8
21–100%	26.7	45.1	10.5
Total no of birds:	60	51	19

[1]Species represented are: White-chinned Petrels (*Procellaria aequinoctialis*): Pintado Petrels (*Daption capense*); Southern Giant Petrels (*Macronectes halli*); Sooty and Great Shearwaters (*Puffinus griseus* and *P. gravis*); Cory's Shearwater (*Calonectris diomeda*); Prions (*Pachyptila* spp.); Antarctic Skua (*Catharacta antarctica*) and Parasitic Skua (*Stercorarius parasiticus*).

(Ashmole 1971), birds shot on the water are most likely to have partially or totally full stomachs. Table 1 shows the percentages of full stomachs in birds shot in Benguela waters off southern Africa in 1983-1984.

Baiting is highly effective in attracting seabirds (Beck *in* Murphy 1936), but such birds are likely to have empty stomachs, in that they are seeking food (Brown et al. 1981, pers. obs.). The contents of the stomachs collected are likely to be the bait, thus making the exercise a circular one.

Finally, some authors (e.g., Ogi and Tsujita 1973, Baltz and Morejohn 1977, Ogi 1984) have obtained stomach samples from birds found dead in fishing-nets or on beaches. Although net kills may be a reasonable source of samples, diets of beached birds may be as likely to reflect what killed them as they are to provide valid information on normal diets.

Catching Seabirds

Methods of sampling birds at colonies include catching chicks or adults of 'tame' species on or near their nests (Ashmole and Ashmole 1967, Harrison et al. 1983), mist-netting (Prince 1980a, Vermeer 1981), corrals into which mobile young are driven (Walter et al. 1986a), drop-traps over nests, nets (Ashmole and Ashmole 1967), hooks or snares (Prince 1980b, Roby et al. 1981, Hunter 1983). Bright

lights and recordings may attract nocturnal species such as procellariids at nesting colonies, particularly cliff-nesting species whose nests may be difficult to reach. Away from colonies, most species are warier. Baits may be used to attract birds close enough to be netted (Gill et al. 1970). The bait itself may be used to deliver sedatives such as alphachloralose (Williams 1966) and Avertin (Smith 1967). Night-lighting with a powerful spot-light and landing nets on a maneuverable boat, may be used successfully, especially in calm conditions, but it appears less efficient than diurnal shooting (Jackson unpubl.). Cannon and mist-nets may be used to catch birds at roosts (e.g., Jarvis and Southern 1976). Waterfowl in flight can be captured with an expanding net shot from a gun (Mechlin and Shaiffer 1980), although this technique has yet to be tried on birds at sea. However, only one or two of these are likely to be appropriate for any one species.

Sampling Living Birds

Many species regurgitate 'spontaneously' when disturbed, handled, or caught in a net (e.g., van Dobben 1952, Harris 1973, Prince 1980a,b, Knopf and Kennedy 1981, Harrison et al. 1983). Spontaneous regurgitation can have several drawbacks. Individual birds may differ in their willingness to regurgitate, depending on stomach fullness or perhaps on stomach contents. Spontaneous regurgitation may not empty the proventriculus or ventriculus entirely, so unless at least a few birds are sacrificed to confirm the completeness of regurgitation, caution must be used when inferring meal size or amount being brough back to the nest, although stomach contents and amounts fed to the young can be compared (Prince 1980a).

For young birds of some species, food may be extracted by inserting fingers into the proventriculus without apparent harm to nestlings (Hunt 1972, Hunt and Hunt 1976). Ligatures tied around the necks of nestlings to prevent them from swallowing food have been used for Black Skimmers (*Rynchops niger*) (White et al. 1984) and this could perhaps also be done with tame adults of some species such as cormorants for certain research problems (cf., Egremont and Rothschild 1979). Hatch (1984)

used hoods to prevent nestling alcids in burrows from consuming food left by their parents. Stomach oils can be sampled from living birds without killing them, using a sampling device devised by Grubb (1971). Gastronomy (opening of the stomach) has been used unsuccessfully on a Gentoo Penguin (*Pygoscelis papua*). The method appears excessively labor-intensive (Reilly 1982).

Stomach pumps and emetics have the advantage theoretically of inducing regurgitation in most birds and, after confirmatory work, of ensuring complete clearing of the proventriculus and ventriculus. Stomach pumps work in several different manners (Meehan and Miller 1978). These include placing a tube down the esophagus and then creating a suction to evacuate material (Emison 1968, Cowan 1983), back-flushing by pushing water into the anus (Baker and Fraser 1976), or by pumping water into the anterior end of the digestive tract (Seaburg 1957, Aho 1976, Brensing 1977, Meehan and Miller 1978, Randall and Davidson 1981, Wilson 1984); or by pushing stomach contents through the digestive system with saline solution (Moody 1970).

Emetics have been used on only a few seabirds. Montague and Cullen (1985) used them successfully on Little Penguins (*Eudyptula minor*). Regurgitation was induced in 21 min by ipecacuanha (ipecac) and in 8 min by copper sulphate. Ipecac resulted in occasional mortality but copper sulphate did not. Horne (1985) found both emetics "unsatisfactory" for Royal (*Eudyptes schlegeli*) and Rockhopper (*E. chrysocome*) Penguins. Croxall and Prince (1980) found emetics unsatisfactory for Gentoo (*Pygoscelis papus*) and Macaroni (*E. chrysolophus*) Penguins because large stomach samples absorbed orally-administered emetics rendering them ineffective. Randall and Davidson (1981) found that doses of tartar emetic large enought to produce regurgitation sometimes killed Jackass Penguins. While more work (cf., Chaney and Kare 1966) under controlled conditions might identify useable emetics, doses would have to worked out for each species and mortality might remain a problem (e.g., Prŷs-Jones et al. 1974, Radke and Frydendall 1974, Randall and Davidson 1981). In practice many stomach pumps and emetics appear to cause a great

deal of suffering and incidental mortality without providing complete samples. We believe improved stomach pumps render these methods unnecessary for most species of seabird.

We prefer stomach pumps that displace food by introducing water into the proventriculus. The simplest design (Brensing 1977, Ford et al. 1982, Wilson 1984) appears to be the easiest to use. It operates by forcing water into the proventriculus through a plastic tube, after which the researcher inverts the bird, applies pressure to the stomach and aims the bird at a container. The process takes less than two minutes, and sedatives are not needed unless pumping birds such as courting pairs that are sensitive to any form of handling. Clearance of the proventriculus and ventriculus is total for Jackass Penguins (*Spheniscus demersus*) (Wilson et al. 1985), but the stomach may not be completely cleared when the pump is used on other penguins or on White-chinned Petrels (*Procellaria aequinoctialis*) with very full stomachs (Lishman 1985, Ryan and Jackson 1986). Pumping birds a second time should ensure clearance; however, the ventriculus is unlikely to be emptied in procellariids and other groups in which it is highly differentiated (cf., McLelland 1979). The pump has now been used on over 18 species of birds ranging from albatrosses to storm petrels. Only one known mortality has occurred in over 2,000 applications. We suggest this device be tried first before emetics or other stomach pump designs are employed.

Other Sampling Methods

The ideal methods of sampling diets for many purposes would be those with minimal disturbance to birds, ease of collection, and ease of replication. Such methods include diet analyses from: stomach casts or pellets (Jordan 1959, Schlatter and Moreno 1976, Ainley et al. 1981, Clarke et al. 1981, Clarke and Prince 1981, Walter 1984); hard parts of ingested prey recovered from faeces (Lumsden and Haddow 1946, Treacy and Crawford 1981, Ralph et al. 1985) and guano deposits (Hutchinson 1950, Clarke and Fitch 1975); mollusc shells and other hard parts of prey dropped at feeding sites or around nests (Hartley 1948); and direct observa-

tion of prey carried in bills (Hartley 1948, Pearson 1968).

TYPES OF SAMPLES

The most-commonly collected samples taken from birds are contents of digestive tracts. In many studies, particularly those involving regurgitation, contents of the proventriculus and ventriculus are not separated. If differential digestion occurs (Hartley 1948, Gannon 1976) such that some prey items are digested more rapidly than others, time since the last meal will determine whether food is in the proventriculus, where breakdown of prey structure occurs, or in the ventriculus and beyond, where few soft parts remain. The relative frequencies of squid beaks and fish otoliths in seabird stomachs may not reflect the true relative dietary importance of prey types because beaks persist longer than otoliths in ventriculi (Imber and Russ 1975, Furness et al. 1984). Birds which consumed identical meals may appear to have different digestive tract contents, if differing amounts of time have passed since ingestion (cf., Perret 1962 *in* Swanson and Bartonek 1970, Bartonek and Hickey 1969). Separate analysis of the contents of the proventriculus and ventriculus should be undertaken whenever possible (e.g., Brown et al. 1981). Small series of birds should perhaps be collected to check for differential digestion when using such techniques as induced regurgitations. Alternatively, digestion studies of captive birds would achieve the same objectives (e.g., Swanson and Bartonek 1970, Custer and Pitelka 1975, Lifjeld 1983), preferably without the need to kill birds (e.g., Wilson et al. 1985).

Individual prey can be measured, weighed, and even sexed when intact specimens are recovered. More typically, prey are partially or totally digested (e.g., Imber 1976). Species, size, age, season, and even environmental temperature can be determined or estimated from indigestible or digestion-resistant parts of prey such as fish otoliths (e.g., Lumsden and Haddow 1946, Devereux 1967, Fitch and Brownell 1968, Casteel 1976, Batchelor and Ross 1984, Jackson 1984), scales (Casteel 1972, Miller 1979), squid beaks (Clarke 1962a, b, Clarke 1980, 1985) or statoliths (Clarke 1978), skeletal or exo-

skeletal parts (White 1936, Pikhu and Pikhu 1970, Casteel 1974, Newsome 1977, Mann & Beaumont 1980, Harrison et al. 1983), ventriculi (Minckley and Paulson 1976), and body length in relation to state of digestion (Fickling and Lee 1981). Normal taxonomic keys may be of little use except for pristine specimens.

Prey species can also be identified using electrophoretic (Cowie 1968, Hume and Mackie 1980) or immunological techniques (Pickavance 1970, Healey and Cross 1975, Greenstone 1977, Calver 1984, Feller et al. 1985). Electrophoresis seems to be suitable only for relatively undigested prey since proteins lose their characteristic electrophoretic bands as digestion proceeds (Walter and O'Neill 1986). Immunological techniques are less sensitive to the state of digestion (Walter et al. 1986b).

Although much less commonly employed, other contents of stomachs or tissues of collected birds can be used to examine diet. Stomach oils of procellariids may be specific products of particular prey (Lewis 1969), thus facilitating diet studies (Warham et al. 1976, Bishop et al. 1983). Body lipids may also be 'traceable' in ecosystems (Ackman et al. 1970, 1980, Gatten et al. 1983, Horgan and Barrett 1985). Although little work has been done (but see, Rausch 1983), diets of seabirds may be traced through the alternative hosts of their internal parasites. Many of these methods only resolve diet to the level of phylum, but even this may be useful in cases where full stomachs are rarely encountered.

Sampling diet indirectly through by-products or by direct observation allows large sample sizes with minimal disturbance. However, faeces, pellets or stomach casts of indigestible material may be biased in favor of hard parts and under-represent other prey so that pellets need to be 'calibrated' against other information (Hartley 1948). Pellets containing large or relatively indigestible prey may be more visible than pellets resulting from relatively indigestible material. Otoliths in pellets or guano may be partially eroded and otoliths from smaller fish may be under-represented because they dissolve completely or pass through the digestive tract (Lumsden and Haddow 1946, Prime 1979, Duffy and Laurenson 1983). Fish sizes in such cases can not be determined from otoliths without making assumptions about the extent of digestion (cf., North et al. 1983). These problems can be assumed to occur with pellets, until proved otherwise. Experimental work using captive birds fed fish of known otolith size should be attempted before relying on otoliths from pellets or scats for information on the original sizes of ingested fish.

Molluscs and other prey dropped at anvils or other feeding areas can only be used to infer sizes of such prey. One can not determine total diet from anvils because softer prey will be consumed completely (Hartley 1948). Some prey types may also last longer than others after being broken at anvils. Even within a prey species at an anvil, size distributions may be biased if, for example, larger prey are likely to be broken up and eaten on the site while smaller prey are taken away or swallowed whole (Hartley 1948).

Atwood and Kelly (1984) found that fish dropped in Least Tern (*Sterna albifrons*) colonies generally reflected diet. This method may be biased toward larger prey items since these are more likely to be too large for nestlings to swallow (Randall et al. 1981, I. C. T. Nisbet pers. comm.). Direct observation of prey taken, either at feeding grounds or when birds return to the nest, is very suitable for species such as terns (*Sterna* spp. (Pearson 1968, Nisbet 1979) and (*Gygis alba*) (Ashmole and Ashmole 1967), Red-throated Loons (*Gavia stellata*) (Reimchen and Douglas 1984), and those Alcidae that carry their prey externally. Distinctive species can be identified at considerable distances and size of prey can be estimated by comparison with mandible length (cf., Nisbet 1979). Several biases may occur, however. Adult terns may bring larger or smaller prey back to their nestlings than they themselves consume (Nisbet 1979). Smaller prey may be harder to see or to identify. Distinctively-shaped or colored species of prey are more likely to be identified than others. Studies with large proportions of such unidentified species are thus likely to be useless for the determination of relative importance of prey species. More insidiously, observers may tend to identify species according to 'search im-

ages' and subconsciously assign unknown or unidentifiable specimens to a few known species. These possibilities need to be tested, preferably by supplementing observers's identifications with close-up photographs or video recordings (e.g., Reimchen and Douglas 1984) of prey brought to nests.

METHODS OF ANALYZING SAMPLES

Mechanics of Stomach Analysis

The actual mechanics of analyzing samples are rarely considered but they are likely to affect diet results. Most diet samples are not analyzed immediately but are frozen or preserved in alcohol or formalin. Delay in preserving samples allows continued digestion (Dillery 1965). Transportation of samples typically involves agitation during movement by boat or car. Frozen samples may endure travel better but will begin to decay when thawed, and freezing may destroy fragile specimens. Unbuffered formalin, while keeping soft parts of prey intact, quickly dissolves otoliths, making identification of fish or determination of their size difficult (McMahon and Tash 1979). Alcohol has no effect on otoliths, but does not preserve flesh very well. Preserving in alcohol or formalin causes prey specimens to shrink and to gain mass over time (Parker 1963, Howmiller 1972, Hay 1981), making length and mass data derived from preserved material not directly comparable to measurements of fresh specimens.

In all cases, diet samples should be analyzed as soon as possible after collection. Ideally, analysis should be done immediately after collection, without the use of preservatives. Voucher specimens of prey types can then be preserved in alcohol after fixing in buffered formalin, and otoliths can be extracted from digested fish and dried for future identification. Immediate analysis also allows use of prey characteristics, such as color and even smell, which are lost during freezing or preserving.

Measurements of Diet Data

All the types of samples mentioned above can provide one or more forms of information on diet: species taken, frequency per sample; the mass and volume of each prey type; numbers of each prey type; state of digestion of prey types; and life history parameters of prey (age, size, six, stomach fullness, body condition). The different measurements vary in their usefulness depending on the purpose of the study (Table 2). Diets of some species may simply be unsuitable for various forms of analysis, even if these are the preferred methods for the questions being asked.

Species Identification.—The level of taxa indentification will limit subsequent analyses. For most studies, divisions of prey into phyla may be too crude, but identification to species level, unless it can be done for most prey, may make niche-overlap or diet-diversity studies meaningless (Matthews et al. 1977): for example, if one prey type is identified to species while another is identified only to family, which may contain several or even many species. Problems of this sort should be considered when the relative abundances of the two prey types are compared. Similarly, if a large proportion of the diet is not identifiable because of advanced states of digestion, major assumptions must be made. Unidentifiable prey can be assumed to have the same composition as identifiable prey from the same stomach; the material can be ignored; or treated as a discrete

Table 2. Measurements and their uses in diet studies

Measurement	Purpose	Reference
Frequency of occurrence	variability of prey abundance	Ashmole & Ashmole (1967), MacDonald & Green (1983)
Numerical abundance	frequency of prey encounter	—
Volume and mass	approximate nutritional contribution of similar prey to diet	Richards (1963)
Mass	meal size and diel feeding patterns	Wilson & Leslie (1911) in Hartley (1948), Vogt (1942), Keast (1970), cf. Magnuson (1969).
State of Digestion	prey encounter frequency, prey patchiness	Wilson (1985)

prey type. The first is almost certain to be wrong since similar prey collected in the same place at the same time should have similar digestive states. Unidentifiable prey were either caught earlier, perhaps in a different location, or different species collected at the same time, but digested more rapidly. Ignoring unidentifiable matter is likely to bias against more rapidly-digestible material. Treating the material as a separate prey type makes the fewest assumptions but may invalidate later inter-sample comparisons. Finally, species lists may also contain stomach contents of prey (e.g., Ashmole and Ashmole 1967) which, while perhaps contributing to the nutrition of the birds, are usually irrelevant to their foraging ecology.

Frequency of Occurrence.—Frequency of occurrence has the advantage of being fast, each stomach being scored for the presence or absence of prey. Frequency may be the most appropriate method when only a few, similarly-sized prey items are taken or when samples are well-digested (Ashmole and Ashmole 1967). This measure will tend to emphasize overlap between diet samples (Hartley 1948). Attempts to score more complicated frequencies such as 'dominance by bulk' (Frost and West 1940) are less useful. Criteria for 'dominance' are highly subjective. Objectivity may be improved by using volume or mass to determine dominance, but this in turn makes the frequency method redundant, because mass or volume may provide more information if used directly (Hyslop 1980). Frequency of occurrence will also tend to over-represent prey that persist longer in stomachs or that are present in only small numbers. The first problem can be reduced by excluding prey that are present only as "traces" (Perez and Bigg 1983). The second problem is reduced by presenting data on both frequency of occurrence and volume.

Mass and Volume.—Volume (by water displacement or settled volume) and mass (wet or dry) are to be preferred when prey vary greatly in size, to avoid small but numerous prey appearing disproportionately important as might result from their numerical abundance alone. On the other hand, mass and volume are sensitive to single, very large prey items if these are rare components of the diet (Hyslop 1980). Both measures can also be mislead-

ing if prey containing much indigestible materials, such as chitin, occurs in diet samples. Such material adds to volume or mass without contributing to nutrition (Hyslop 1980). Where many small prey types occur, volume of each prey type will be difficult to measure since the volume of each prey type may be miniscule. In such cases, prey types may be lumped or areas measured for samples squashed to a uniform depth (Hallawell and Abel 1971).

Wet mass is the easiest of the volumetric and gravimetric measurements to use, particularly when working with many small prey items, but surface water on objects may be an important source of error for both mass and volume (Hartley 1948, Parker 1963). Preserved stomach materials may also be heavier than fresh material, so comparisons may be invalid (Parker 1963). Dry mass requires drying facilities and considerable time which may prohibit routine use with large or numerous samples. As an end to itself, dry mass is probably not worth measuring since it is highly correlated with wet mass (Glenn and Ward 1968, but see Bradstreet 1976). Dry mass will, however, be necessary for calorimetric determinations. Volume and mass can be further expressed in two ways (Martin et al. 1946; Swanson et al. 1974): as the average contribution of a prey type within each sample ('aggregate percentage'); or as the relative proportion of all samples summed ('aggregate volume'). These will be the same only if all samples have the same total volumes or masses. Diet studies should be explicit about which is being used. Very full stomachs will greatly influence 'aggregate volume' estimates and essentially ignore empty stomachs, while 'aggregate percentage' weights each sample equally, making empty stomachs relatively more, and full stomachs relatively less, important.

Where stomach samples are heavily digested, mass and volume may be poor measures of diet, especially if differential digestion occurs (Hartley 1948). One way around this is to reconstruct the original meal by counting undigested hard parts and correcting for pre-ingestion mass or volume, (i.e., use numerical abundance multiplied by correction factors (Hyslop 1980). However, unless the original abundance and volume/mass data are also presented, the 'corrected' masses or volumes,

compounding two different sets of errors and variances, may present as inaccurate a picture of diet as the two original measurements.

Numerical Abundance.—There are two forms of numerical analysis: number of items of a certain prey type per stomach, and percentage of prey items of one type out of all prey items. Numerical abundance is most suitable when prey are more or less the same size. It will, however, tend to emphasize differences between samples (Hartley 1948) and overestimate the importance of small prey when considerable size variation exists. It is useless for food that does not exist in discrete units such as scavenged blubber of offal (Hyslop 1980). The problem of counting individuals of small, abundant prey types such as krill (*Euphausia superba*) or water striders (*Halobates* spp.) can be overcome by subsampling, but care must be taken to avoid biased subsamples in certain groups (Bradstreet 1976). Counting individual prey is also difficult when digestion has begun. Counts of different body parts of prey in digestive tracts may yield differing total numbers of individuals, requiring an arbitrary counting protocol such as using only upper squid mandibles or dextral fish otoliths to determine the number of squid or fish in the stomach (e.g., Ashmole and Ashmole 1967, Baltz and Morejohn 1977, Harrison et al. 1983).

State of Digestion.—The state of digestion of prey can yield information about the foraging behavior of seabirds and the ecology of their prey (e.g., Wilson 1985). For example, if seabirds feed in bursts of activity followed by rest periods, prey should occur at several, discrete stages of digestion. If the predator feeds continually, prey should be at all stages of digestion. Digestion states could then be used to calculate encounter rates for studies of foraging behavior. State of digestion may also tell when and perhaps even where food was eaten. Distance to foraging ground might be calculated by determining when the 'least' digested prey item was ingested and how far the seabird could have traveled since that time, assuming that birds are sampled as soon as they return to the colony.

At present, state of digestion is very difficult to use, since few data exist on rates of digestion of different prey types (e.g., van Dobben 1952, Furness and Laugksch 1983, Duffy et al. 1985b, Wilson et al. 1985). Assumptions about differences between prey types are therefore necessary, but highly likely to 'determine' the results. Wherever possible, objective scales of digestion state of prey should be used (e.g., Bowmaker 1963, Magnuson 1969, Tjomlid 1973, Wilson 1985).

Life History Characters of Prey.—Life history parameters of prey, except perhaps length and mass, will usually require that little digestion has occurred. In species of seabirds which vary greatly in the amount of time spent away from the nest, presumably foraging, relatively undigested prey are likely to come from birds which foraged closer to the colony. This may introduce a bias, if generalizations about prey characteristics are to be extended to the entire foraging range of the seabird being sampled.

Derived Diet Data.—The initial diet data can be used to derive other information which may, for some purposes, be more useful. Volume, length, and mass data can be converted to preingestion values for prey before capture using otoliths, squid beaks, or other digestion-resistant body parts (e.g., Ricker 1937, Bradstreet 1976, Ross 1976, Jackson 1984, Croxall et al. 1985). These new values would be most appropriate when differential digestion occurs. They can also be used to derive nutritional and energetic values for different prey (Ashmole 1971, Ellison 1978, Wiens and Scott 1975). Care must be taken however since errors in length/mass or length/volume equations, can introduce biases into volume or mass estimates (Bradstreet 1976). These errors appear typically to be on the order of 5-10% (Nielsen and Schoch 1980) but may be larger if data from preserved and fresh specimens are used indiscriminately (see above).

Two methods can be combined. For example Perez and Bigg (1983) used a "two-step modified volume" method after finding that "non-trace" frequency was the best means of estimating the relative proportions of fish and squid, but that within either group, volume provided better information on the relative proportions' of fish or squid species.

Table 3. Indices of importance for individual prey types in diet studies.

Index	Formula[1]	Reference
Index of Relative Importance (IRI)	$IRI_i = (N + V) \times F$	Pinkas et al. (1971)
Absolute Index (AI)	$AI_i = F_i + N_i + M_i{}^2$	George & Hadley (1979)
Relative Importance Index (RII)	$RII_i = 100\, AI_i / \Sigma^n AI$	Harrison et al. (1983)
—	$(N + F + V)/3$	Welsh (1945), quoted by Reintjes & King 1953

[1]N_i = percentage by number of prey of type i, V_i = percentage by volume of prey of type i, F_i = frequency of occurrence of prey of type i, M_i = percentage of mass of prey of type i, n = number of prey types.
[2](or V_i)

PRESENTING AND COMPARING DATA

Presenting Data

Ideally, a researcher could present the original data in as many different forms as possible, following the theory that because each form has its own biases, all forms are necessary for a proper interpretation of the data. In practice, the types of data will be determined by the purpose of each paper, reducing the likelihood of easy comparability between studies. In addition, endless tables of such data and pages of discussion, comparing and contrasting the data for each diet taxon and study species, quickly lead to what may be called 'data narcosis', resulting in a stunned or bored reader. Even researchers who make a point of presenting multiple analyses of data often end up concentrating discussion of results on one form.

One solution is the use of some form of index which combines one or more measurements (Table 3). These vary, however, in their applicability, depending on prey types. The Index of Relative Importance (IRI: Pinkas et al. 1971) is most sensitive to F, which is a multiplicand, rather than V or N which are addends. This method reduces the biases introduced by numerous small or a few very large items occurring in only one or a few stomachs. The Absolute Index (AI), in contrast to the Index of Relative Importance, adds all the variables, giving them equal weight. This increases the effects of very large or very numerous prey, but also reduces the effect of frequently encountered, minor items. Welsh (1949, quoted by Reintjes and King 1953) used the average of N + F + V. When multiplied by three, this will give the same values as AI. The Relative Importance Index (RII) ranks prey items among themselves, rather than against a fixed scale.

The same values of a particular index may reflect very different prey composition; for example: IRI = 5000 when a) V = 1, N = 50, F = 100; b) V = 50, N = 1, F = 100; c) V = 50, N = 50, F = 50; and d) V = 100, N = 100, F = 25. Values of AI of 101-102 can be obtained where V = 1, N = 50, F = 50 or V = 100, N = 1, F = 1.

Indices have other problems. they "confound two sources of error and variation" (Hyslop 1980). While they might facilitate non-parametric comparisons of diets between studies (Hyslop 1980), these are rarely presented. Within studies, the two absolute indices (IRI and AI) mean nothing in themselves: an IRI of 7500 means little except in comparison with the values for other prey. The relative index (RII) overcomes this problem, but involves two stages of calculation rather than one, making it even less likely to be widely used. Finally, MacDonald and Green (1983) have shown that, at least for some fish communities, the various measurements of diet are highly correlated, so that compound indices are redundant. This needs to be tested for seabird communities.

Waldron and King (1963), Ashmole and Ashmole (1967), and Harrison et al. (1983) used a ranking system, scoring the relative importance of each prey taxon separately by N, V, and F. The ranks were then summed for each taxon and presented, accompanied by full data on V, F, and N. The results have the advantage of avoiding the appearance of spurious precision (Ashmole and Ashmole 1967). This index is also relative and easy to calculate. We recommend its use as a summary of other data.

Comparing Data

Diet data can be compared in five general ways: between locations; between times; and between species, sexes, or age classes. Five types of information can be compared: diet diversity, diet overlap, nutrition, energetics, and prey characteristics.

A variety of diversity indices exist, ranging from the Shannon-Weiner Information Index (Shannon and Weaver 1949, Herrera 1976), with its falsely reassuring aura of cybernetics, to more prosaic indices of evenness (May 1975). Simpler indices (e.g., Berger and Parker 1970) appear to have more biological validity and descriptive power (Hurlbert 1971, May 1975, 1981). One drawback of all such indices is that the values are essentially arbitrary and make sense only when compared to values from other samples. Even then, differences do not necessarily mean anything. To cope with this, several workers have developed confidence limits for indices (May 1975).

Simple evaluation of variability such as the Coefficient of Variation (CV) and Analysis of Variance (ANOVA, Sokal and Rohlf 1969) may also be useful, especially when looking at the predictability of a prey type appearing in a diet. Given their greater mathematical tractability, perhaps ANOVA and CV should replace diversity indices whenever possible, although care should be taken with underlying assumptions of ANOVA procedures (Sokal and Rohlf 1969).

Measurements of diet overlap between species, areas, or times can range from simple comparisons of the number of species common to two samples (e.g., Jaccard 1908) to sophisticated multivariate analyses (e.g., Sokal and Sneath 1963, Hockey and Underhill 1984). One of the most suitable measurements is probably the Spearmann Rank Correlations (Siegel 1956, Fritz 1974) which is easy to calculate and makes minimal assumptions or requirements of the data. Various forms of overlap index are reviewed by May (1975).

Overlap indices can be vulnerable to a number of problems arising from data collection. Small sample sizes may result in large variances: calculated overlaps of 0.5 may be indistinguishable from overlaps of 0.3-0.7 (Ricklefs and Lau 1980). If greatly differing taxonomic levels are used, overlap measurements may be meaningless (Matthews et al. 1977). For example, by comparing prey only at the family level, overlap might be far higher than if the samples were compared by prey species (Diamond 1984). Similarly, if different taxonomic levels were used for two samples, comparisons will be suspect. Overlap will also depend on the number of prey types; higher overlaps will tend to occur with fewer categories.

Comparison of diet in terms of nutrition or energetics has been relatively infrequent in seabird studies but even the few studies produced so far suggest the importance of this method (e.g., Harris and Hislop 1978, Prince 1980b, Clarke and Prince 1981, Batchelor and Ross 1984, Heath and Randall 1984, Montevecchi and Piatt 1984), especially in energy budget and growth studies.

There are two major problems in the study of seabird diets: digestion and nutrition. We know little of either, even though the former frequently determines what sort of diet information is available and the latter, what the diet means to the birds. Other diet information is relatively easy to collect and the methods reviewed here should facilitate such work. We would suggest that, while diet data may be routinely collected during studies of breeding biology, both the diet data and the breeding study will be most useful after additional research on digestion and nutrition.

Digestion rates can be determined experimentally under seminatural conditions whenever fresh prey can be obtained from commercial or ad hoc fishing. These prey can be placed in stomachs using reverse stomach pumps in aviaries or seminatural enclosures in the field and the adults stomach-pumped after varying lengths of time (e.g., Wilson et al. 1985). Differential digestion rates can be determined with relative ease. Captive birds can also be used to 'calibrate' pellet production with diet (cf., Duffy and Laurenson 1983, Furness et al. 1984). Even when food types are not available from independent sources, they can often be obtained by pumping adults and then giving the food to other adults or

chicks on nests. Even if prey samples are partially digested, such experiments could be used to determine how long digestion takes from 'partially' to 'entirely' digested. Repeated feedings could then be used to reconstruct a curve of digestion rate.

Finally, if feeding experiments are not possible, either because prey types are not available at isolated research sites or because the study species is rare or vulnerable to disturbance, in vitro studies using pepsin can provide some index of digestion rates (e.g., Bigg and Fawcett 1985).

There is also a need for further work on the digestive morphology, biochemistry, and physiology of seabirds. Given the wide variety of prey types taken by seabirds; evidence that some species change their digestive tracts in response to different prey (e.g., Cymborowski 1968); and the minimal amounts of carbohydrates in seabird diets, seabirds offer a fertile field for investigation. In vivo studies of digestion would also be helpful: do seabird species differ in their abilities to digest different prey? Do seabirds rapidly reduce water content or mass of prey consumed to facilitate flight (Ashmole 1971, Laugksch and Duffy 1986)? How are oils formed?

For nutritional studies, routine analysis of the protein, fat, and energy values of food items would immensely enhance the usefulness of diet sampling. Many of the problems of measuring volume, mass, and frequency fall away if these are converted to nutritional levels. Baseline values for nutritional status of different foods are often available from the literature.

When the diets and the nutritional values of foods may be known, the connecting link is usually missing: studies showing that different diets affect growth or survival of young or food intake and egg production of adults. Captive rearing of young and maintenance of adults in captivity using different prey types would provide insights into the effects of different diets in the wild (e.g., Gailey-Phipps and Sladen 1982, Batchelor and Ross 1984, Heath and Randall 1984). Further manipulation of diet would be possible, using nutritional supplements such as additional fats, proteins, vitamins, or even the feeding of semisynthetic foods (e.g., Murphy and King 1982). Species fed by regurgita-

tion might be especially suited for such experiments, using soy and fishmeal bases.

CONCLUSIONS

Killing, of seabirds for diet studies, particularly for long-lived, slowly-reproducing species, can be kept to a minimum by using methods now available, at colonies and roosting sites. Further work is urgently needed to find non lethal ways to sample birds efficiently at sea.

Methods of dietary analysis should be clearly spelled out in reports. For example, methods of collecting samples may preselect for certain apparent diets; analysis by "volume", "mass", or "numerical abundance" are not self-explanatory, in that these may be on a per bird basis or represent a proportion of the total population. Use of preservatives and the time that passes before sample analysis may affect results. Differences between studies of diets may result less from true differences in diet than from hidden differences in method.

There is no single "correct" way to study diet, and methods must depend on the goals of each study. Nevertheless, a few measurements such as frequency of occurrence and numerical abundance of prey per bird can be used routinely to facilitate comparison between studies. Mass and volume of prey per bird are worth presenting routinely only if the degree of moisture and state of digestion are detailed. Diet is best summarized by ranking prey separately for each method of analysis, and then summing the ranks.

LITERATURE CITED

Ackman, R. G., C. A. Eaton, and J. Dyerberg, 1980. Manic docosenoic acid isomer distribution in the plasma of Greenland Eskimos. Am. J. Clinical Nutr. 33: 1914-1817.
Ackman, R. G., C. A. Eaton, J. C. Sipos, S. N. Hooper, and J. D. Castell. 1970. Lipids and fatty acids of

two species of North Atlantic Krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*) and their role in the aquatic food webs. J. Fish. Res. Board Can. 27: 513-533.

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. M. S. thesis. Corvallis, Oregon: Oregon State University.

Ainley, D. G., D. W. Anderson, and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83: 120-131.

Ashmole, M. J. and N. P. Ashmole. 1968. The use of food samples from seabirds in the study of seasonal variation in the surface fauna of tropical oceanic areas. Pac. Sci. 22: 1-10.

Ashmole,.N. P. 1971. Seabird ecology and the marine environment. pp. 223-286 *in* Avian biology, Vol. 1. (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York: Academic Press.

Ashmole, N. P. and M. J. Ashmole. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Peabody Mus. Nat. Hist. Yale Univ. Bull. 24.

Atwood, J. L. and P. R. Kelly. 1984. Fish dropped on breeding colonies as indicators of Least Tern food habits. Wilson Bull. 96: 34-37.

Baltz, D. M. and B. V. Morejohn. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk 94: 526-543.

Baker, A. M. and D. F. Fraser. 1976. A method for securing the gut contents of small, live fish. Trans. Am. Fish. Soc. 105: 520-522.

Bartonek, J. D. and J. J. Hickey. 1969. Food habits of Canvasbacks, Redheads, and Lesser Scaup in Manitoba. Condor 71: 280-290.

Batchelor, J. D. and J. B. Ross. 1984. The diet and implications of dietary change of Cape Gannets on Bird Island, Algoa Bay. Ostrich 55: 45-63.

Berger, W. L. and F. L. Parker. 1970. Diversity of planktonic Foraminifera in deep-sea sediments. Science 168: 1345-1347.

Bigg, M. A. and I. Fawcett. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). Pp. 284-291 *in* Marine mammals and fisheries. (J. R. Beddington, J. J. H. Beverton, and D. M. Lavigne, Eds.). London: George Allen & Unwin.

Bishop, D. G., T. A. Ritz, G. W. Hosie, J. R. Kenrick, and J. Olley. 1983. Fatty acid composition of the lipids of *Puffinus tenuirostris* (Temminck) in relation to its diet. J. Exper. Mar. Biol. Ecol. 71: 17-26.

Bowmaker, A. P. 1963. Cormorant predation on two central African lakes. Ostrich 34: 1-26.

Bradstreet, M. S. W. 1976. Summer feeding ecology of seabirds in eastern Lancaster Sound, 1976. Toronto, Canada: LGL Ltd.

Brensing, V. D. 1977. Nahrungsökologische Untersuchungen an Zugvögeln in einem südwestdeutschen Durchzugsgebiet Während des Wegzugs. Die Vogelwarte 29: 44-56.

Brown, R. G. B., S. P. Barker, D. E. Gasking, and M. R. Sandeman. 1981. The foods of Great and Sooty Shearwaters *Puffinus gravis* and *P. griseus* in eastern Canadian waters. Ibis 123: 19-30.

Calver, M. C. 1984. A review of ecological applications of immunological techniques for diet analysis. Aust. J. Ecol. 9: 19-25.

Casteel, R. W. 1972. A key, based on scales, to the families of native California freshwater fishes. Proc. Calif. Acad. Sci. 39: 75-86.

Casteel, R. W. 1974. A method for estimation of live weight of fish from the size of skeletal elements. Amer. Antiq. 39: 94-98.

Casteel, R. W. 1976. Otoliths: fish remains in archaeology and palaeo-environmental studies. New York: Academic Press.

Chaney, S. G. and M. R. Kare. 1966. Emesis in birds. J. Amer. Vet. Med. Assoc. 149: 938-942.

Cheah, C. C. and I. A. Hansen. 1970a. Wax esters in the stomach oil of petrels. Int. J. Biochem. 1: 109-202.

Cheah, C. C. and I. A. Hansen. 1970b. Stomach oil and tissue lipids of the petrels *Puffinus pacificus* and *Pterodroma macroptera*. Int. J. Biochem. 1: 203-208.

Clarke, A. and P. A. Prince. 1976. The origin of stomach oils in marine birds: analyses of stomach oils from six species of sub-Antarctic procellariiform birds. J. Exper. Mar. Biol. Ecol. 23: 15-30.

Clarke, M. R. 1962a. Significance of cephalopod beaks. Nature 193: 560-561.

Clarke, M. R. 1962b. The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. Bull. Brit. Mus. Nat. Hist. Zool. 8: 421-480.

Clarke, M. R. 1978. The cephalopod statolith—an introduction to its form. J. Mar. Biol. Ass., U.K. 58: 701-712.

Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the Southern hemisphere and their bearing on sperm whale biology. 'Discovery' Rep. 37: 1-324.

Clarke, M. R. 1985. A handbook for the identification of squid beaks. Oxford: Oxford University Press.

Clarke, M. R. and J. E. Fitch. 1975. First fossil records of cephalopod statoliths. Nature 257: 380-381.

Clarke, M. R. and P. A. Prince. 1981. Cephalopod remains in regurgitations of black-browed and grey-headed albatross at South Georgia. British Ant. Surv. Bull. 54: 1-7.

Clarke, M. R., J. P. Croxall, and P. A. Prince. 1981. Cephalopod remains in regurgitations of the Wandering Albatross *Diomedea exulans* L. at South Georgia. Br. Antarct. Surv. Bull. 54: 9-21.

Cochran, W. G. 1953. Sampling techniques. New York: John Wiley & Sons.

Coleridge, S. T. 1854. The rime of the ancient mariner. *in* The poems, a new edition. London: Moxon.

Cowan, A. N. 1983. A modified penguin stomach tube. Corella 7: 59-61.

Cowie, W. P. 1968. Identification of fish species by thin slab polyacrylamide gel electrophoresis of the muscle myogens. J. Sci. Food Agr. 19: 226-229.

Croxall, J. P. and P. A. Prince. 1980. The food of Gentoo Penguins *Pygoscelis papua* and Macaroni Penguins *Eudyptes chrysolophus* at South Georgia. Ibis 122: 245-253.

Croxall, J. P., P. A. Prince, A. Baird, and P. Ward. 1985. The diet of the southern rockhopper penguin *Eudyptes chrysocome chrysocome* at Beauchêne Island, Falkland Islands. J. Zool. (London) 206.

Custer, T. W. and F. A. Pitelka. 1975. Correction factors for digestion rates for prey taken by Snow Buntings *Plectrophenax nivalis*. Condor 77: 210-212.

Cymborowski, B. 1968. Influence of diet on the histological structure of the gullet and glandular stomach of the Common Tern (*Sterna hirundo* L.). Zool. Pol. 18: 451-468.

Darnell, R. M. and R. R. Meierotto. 1962. Determination of feeding chronology in fishes. Trans. Am. Fish. Soc. 91: 313-320.

Devereux, I. 1967. Temperature measurements from oxygen isotope ratios of fish otoliths. Science 155: 1684-1685.

Diamond, A. W. 1984. Feeding overlap in some tropical and temperate seabird communities. Stud. Avian Biol. 8: 24-26.

Dillery, D. G. 1965. Post-mortem digestion of stomach contents in the Savannah Sparrow. Auk 82: 281.

Dobben, W. H. van. 1952 The food of the cormorant in the Netherlands. Ardea 40: 1-63.

Duffy, D. C., R. P. Wilson and A. Berruti. 1985a. Anchovy in the diets of Dyer Island penguins: toward a test of two models of anchovy distribution. S. Afr. J. Sci. 81: 552-554.

Duffy, D. C., B. L. Furness, R. C. Laugksch, and J. A. Smith. 1985b. Two methods of measuring food transit rates of seabirds. Comp. Biochem. Physiol. 82A: 781-785.

Duffy, D. C., and L. J. B. Laurenson. 1983. Pellets of Cape Cormorants as indicators of diet. Condor 85: 305-307.

Durbin, E. G., A. G. Durbin, R. W. Langton, and R. E. Bowman. 1983. Stomach contents of Silver Hake, *Merluccius bilinearis*, and Atlantic Cod, *Gadus morhua*, and estimation of their daily rations. Fish. Bull. U.S. 81: 437454.

Eggers, D. M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290-294.

Egremont, P. and M. Rothschild. 1979. The calculating cormorants. Biol. J. Linn. Soc. 12: 181-186.

Ellison, J. P. 1978. The use of discriminant analysis in the study of fish food habits. Pp. 80-84 *in* Fish food habit studies, 2nd Pacific North-West technical workshop. (S. J. Lipovsky and C. A. Simonstad, Eds.). Seattle, Washington: University of Washington Press.

Emison, W. B. 1968. Feeding preferences of the Adelie Penguin at Cape Crozier, Ross Island. Pp. 191-212 *in* Antarctic bird studies (O. L. Austin, Jr., Ed.) Antarct. Res. Ser. 12.

Feller, R. J., G. Zagursky, and E. A. Day. 1985. Deep sea food web analysis using cross-reacting antisera. Deep-sea Res. 32: 485-497.

Fickling, N. J. and R. L. G. Lee, 1981. Further aids to the reconstruction of digested prey lengths. Fish. Manage. 12: 107-110.

Fitch, J. E. and R. L. Brownell. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25: 2561-2574.

Ford, H. A., N. Forde, and S. Harrington. 1982. Nondestructive methods to determine the diets of birds. Corella 6: 6-10.

Fritz, E. S. 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 1974: 210-214.

Frost, W. E. and A. E. J. West. 1940. River Liffey Survey. III The growth and food of young salmon. Proc. R. Ir. Acad. Sect. B Biol. Geol. Chem. Sci. 46: 53-80.

Furness, B. L. and R. C. Laugksch. 1983. An attempt to use Barium meals and X-ray photography to determine gastric evacuation rate and gut retention time in Jackass Penguins *Spheniscus demersus*. Cormorant 11: 3-6.

Furness, R. W., R. C. Laugksch, and D. C. Duffy. 1984. Cephalopod beaks and seabird diet studies. Auk 101: 619-620.

Furness, R. W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47: 39-53.

Furness, R. W. and J. Cooper. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. Mar. Ecol. Prog. Ser. 8: 243-250.

Gailey-Phipps, J. J. and W. J. L. Sladen. 1982. Survey on nutrition of penguins. J. Am. Vet. Med. Assoc. 181: 1305-1309.

Gannon, J. E. 1976. The effects of differential digestion rates on zooplankton by Alewife, *Alosa pseudoharengus*, on determinations of selective feeding. Trans. Am. Fish. Soc. 105: 89-95.

Gatten, R. R., J. R. Sargent and J. C. Gamble. 1983. Diet-induced changes in fatty acid composition of herring larvae reared in enclosed ecosystems. J. Mar. Biol. Assoc., U.K. 63: 575-584.

George, E. L. and W. L. Hadley. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomievi*) young of the year. Trans. Am. Fish. Soc. 108: 253-261.

Gill, D. E., W. J. L. Sladen, and E. E. Huntington. 1970. A technique for capturing petrels and shearwaters at sea. Bird-Banding 41: 111-113.

Glenn, C. L. and F. J. Ward. 1968. "Wet" weight as a method for measuring stomach contents of Walleyes. *Stizostedion vitreum vitreum*. J. Fish. Res. Board Can. 25: 1505-1507.

Greenstone, M. 1977. A passive haemaglutination inhibition assay for the identification of the stomach contents of invertebrate predators. J. Appl. Ecol. 14: 457-464.

Grubb, T. C. 1971. Stomach oil in Procellariiforms: an extraction technique. Ibis 113-529.

Hallawell, J. M. and R. Abel. 1971. A rapid volumetric method for the analysis of the food of fishes. J. Fish Biol. 3: 29-32.

Hanson, W. R. and T. Graybill. 1956. Sample size in food-habits analyses. J. Wildl. Manage. 20: 64-68.

Harris, M. P. 1973. The biology of the Waved Albatross *Diomedea irrorata* of Hood Island, Galapagos. Ibis 115: 483-510.

Harris, M. P. and J. R. G. Hislop. 1978. The food of young Puffins, *Fratercula arctica*. J. Zool. (Lond.) 185: 213-236.

Harrison, C. S., T. S. Hida and M. P. Seki. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85: 1-71.

Hartley, P. H. T. 1948. The assessment of the food of birds. Ibis 90: 361-381.

Hatch, S. A. 1984. Nestling diet and feeding rates of Rhinoceros Auklets in Alaska. Pp. 105-115 *in* Marine birds: their feeding ecology and commercial fisheries relationships. Spec. Publ. Canadian Wildlife Service, (D. N. Nettleship, G. S. Sanger and P. F. Springer, Eds.). Ottawa, Canada: Canadian Wildlife Service.

Hay, D. E. 1981. Effect of capture and fixation on

gut contents and body size of Pacific herring larvae. Rapp. p.-v. Reun. Comm. Int. Explor. Mer. 178: 395-400.

Healy, J. A. and T. F. Cross. 1975. Immunoelectroosmophoresis for the serological identification of predators of the sheep tick *Ixodes ricinus*. Oikos 26: 97-101.

Heath, R. G. M. and R. M. Randall. 1984. Growth of Jackass penguin chicks (*Spheniscus demersus*) hand-reared on different diets. J. Zool. (London) 205: 91-105.

Herrera, C. M. 1976. A trophic diversity index for presence-absence food data. Oecologia (Berl.) 25: 187-191.

Hockey, P. A. R. and L. G. Underhill. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related segregation. S. Afr. J. Zool. 19: 1-11.

Holgate, P. 1969. Species frequency distributions. Biometrika 56: 651-660.

Horgan, H. F. and J. A. Barrett. 1985. The use of lipid profiles in comparing the diets of seabirds. Pp. 493-497. *in* Antarctic nutrient cycles and food webs. (Siegfried, W. R., P. R. Condy, R. M. Laws, Eds.). Berlin: Springer-Verlag.

Horne, R. S. C. 1985. Diet of Royal and Rockhopper Penguins at Macquarie Island, Emu 85:

Howmiller, R. P. 1972. Effects of preservatives on weights of some common macrobenthic invertebrates. Trans. Am. Fish. Soc. 1972: 743-746.

Hume, A. and I. M. Mackie. 1980. The use of electrophoresis of the water soluble muscle proteins *in the quantitative analysis of the species components* of a fish muscle mixture. Pp. 451-456 *in* Advances in fisheries science techniques. (J. J. Connell, Ed.). London: Fishing News Books Limited.

Hunt, G. L., Jr. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53: 1051-1061.

Hunt, G. L. Jr. and M. W. Hunt. 1976. Exploitation of fluctuating food resources by Western Gulls. Auk 93: 301-307.

Hunter, S. 1983. The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. J. Zool. 200: 521-538.

Hurlbert, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

Hurtubia, J. 1973. Trophic diversity measurement in sympatric predatory species. Ecology 54: 885-890.

Hutchinson, G. E. 1950. Survey of contemporary knowledge of biogeochemistry 3: the biogeochemistry of vertebrate excretion. Bull. Am. Mus. Nat. Hist. 96: 554 pp.

Hynes, H. B. N. 1950. The food of freshwater sticklebacks (*Gasterasteus aculeateus* and *Rygosteus pungituis*) with a review of methods used in studies of foods of fishes. J. Anim. Ecol. 19: 36-58.

Hyslop, E. J. 1980. Stomach content analysis—a review of methods and their application. J. Fish Biol. 17: 411-429.

Imber, M. J. 1976. Comparison of prey of the black *Procellaria* petrels of New Zealand. N. Z. J. Mar. Freshwater Res. 10: 119-130.

Imber, M. J. and R. Russ. 1975. Some foods of the Wandering Albatross *Diomedea exulans*. Notornis 22: 27-36.

Iverson, L. K. and L. Pinkas. 1971. A pictorial guide to beaks of certain eastern Pacific cephalopods. Calif. Dep. Fish Game Fish Bull. 152: 83-105.

Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. Bull. Soc. Vaudoise Sci. Nat. 44: 223-270.

Jackson, S. 1984. Predation by Pied Kingfishers and White-breasted Cormorants on fish in the Kosi system. Ostrich 55: 113-132.

Jacob, J. 1982. Stomach oils. Pp. 325-340 *in* Avian biology, Vol. VI. (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). London: Academic Press.

Jarvis, W. L. and W. E. Southern. 1976. Food habits of Ring-billed Gulls breeding in the Great Lakes region. Wilson Bull. 88: 621-631.

Jordan, R. 1959. El fenomeno de los regurgitaciones en el guanay (*Phalacrocorax bougainvillii* L.) y un metodo para estimar la ingestion diaria. Bol. Comp. Adm. Guano 35: 23-40.

Keast, A. 1970. Food specialization and bioenergetics interrelations in the fish larvae of some small Ontario waterways. Pp. 377-411 *in* Marine food chains. (J. H. Steele Ed.). Edinburgh: Oliver & Boyd.

Knopf, F. L. and J. L. Kennedy. 1981. Differential predation by two species of piscivorous birds. Wilson Bull. 93: 554-556.

Laugksch, R. C. and D. C. Duffy. 1986. Food transit rates in Cape Gannets and Jackass Penguins. Condor 88:

Lewis, R. W. 1969. Studies on the stomach oils of marine animals—II. Oils of some procellariiform birds. Comp. Biochem. Physiol. 31: 725-731.

Lifjeld, J. 1983. Stomach content analyses of the Dunlin *Calidris alpina*: bias due to differential digestibility of prey items. Fauna Norv. Ser. C 6: 43-46.

Lishman, G. S. 1985. The food and feeding ecology of Adelie (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antartica*) at Signy Island, South Orkney Islands, J. Zool. (London) 245-266.

Lumsden, W. H. R. and A. J. Haddow. 1946. The food of the Shag *P. aristotelis* in the Clyde Sea area. J. Anim. Ecol. 15: 35-42.

MacDonald, J. C. and R. H., Green. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Can. J. Fish. Aquat. Sci. 40: 635-637.

Magnuson, J. J. 1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98: 329-392.

Mann, R. H. K. and W. R. C. Beaumont. 1980. The collection, identification and reconstruction of lengths of fish prey from their remains in the stomachs. Fish. Mgmt. 11: 169-172.

Martin, A. C., R. H. Gensch, and C. P. Brown. 1946. Alternative methods in upland gamebird food analysis. J. Wildl. Manage. 10: 8-12.

Matthews, F. D., D. M. Damkaer, L. W. Krapp, and B. B. Collette. 1977. Food of western North Atlantic tuna (*Thunnus*) and lancetfishes (*Alepisaurus*). NOAA Tech. Rep. NMFS Circ. 706.

May, R. M. 1975. Some notes on estimating the competition matrix, α. Ecology 56: 737-741.

May, R. M. 1981. Patterns in multispecies communities. Pp. 197-227 *in* Theoretical ecology: principles and applications. Second edition. (R. M. May, Ed.) Oxford: Blackwell.

McAtee, W. L. 1912. Methods of estimating the contents of bird stomachs. Auk 29: 449-464.

McLelland, J. 1979. Digestive system. Pp. 69-181 in Form and function in birds, Vol 1. (A. S. King and J. McLelland, Eds.). London: Academic Press.

McMahon, T. E. and C. J. Tash. 1979. Effects of formalin (buffered and unbuffered) and hydrochloric acid on fish otoliths. Copeia 1979: 155-156.

Mechlin, L. M. and C. W. Schaiffer. 1980. Net-firing gun for capturing breeding waterfowl. J. Wildl. Manage. 44: 895-896.

Meehan, W. R. and R. A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. J. Fish. Res. Board Can. 35: 1359-1363.

Miller, B. 1979. Ecology of the Little Black Cormorant, *Phalacrocorax sulcirostris*, and Little Pied Cormorant, *P. melanoleucos*, in inland New South Wales. 1. Food and feeding habits. Aust. Wildl. Res. 6: 79-95.

Minckley, C. O. and L. J. Paulson. 1976. Use of gizzard weights to determine total length and weights of threadfin shad eaten by predators. Trans. Am. Fish. Soc. 3: 409-410.

Montague, T. L. and J. M. Cullen. 1985. Comparison of techniques to recover stomach contents from birds. Aust. Wildl. Res. 12: 327-330.

Montevecchi, W. A. and J. Piatt. 1984. Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*): implications for seabird predators. Comp. Biochem. Physiol. 78A: 15-20.

Moody, T. 1970. A method for obtaining food samples from insectivorous birds. Auk 87: 579.

Mosteller, F. and R. E. K. Rourke. 1973. Sturdy statistics: nonparametrics and order statistics. Addison-Wesley, London.

Murphy, R. C. 1936. Oceanic birds of South America. New York: Am. Mus. Nat. Hist.

Murphy, M. E. and J. R. King. 1982. Semi-synthetic diets as a tool for nutritional ecology. Auk 99: 165-167.

Newsome, G. E. 1977. Use of opercular bones to identify and estimate lengths of prey consumed by piscivores. Can. J. Zool. 55: 733-736.

Nielson, L. A. and W. F. Schoch. 1980. Errors in estimating mean weight and other statistics from mean length. Trans. Am. Fish. Soc. 109: 319-322.

Nisbet, I. C. T. 1979. Courtship-feeding and clutch size in common terns *Sterna hirundo*. Pp. 101-109 in Evolutionary ecology. (B. Stonehouse and C. Perrins, Eds.). London: MacMillan.

North, A. W., J. P. Croxall and D. W. Doidge. 1983. Fish prey of the Antarctic Fur Seal *Arctocephalus gazella* at South Georgia. Br. Antarct. Surv. Bull. 61: 27-32.

Ogi, H. 1984. Feeding ecology of the Sooty Shearwater in the western subarctic North Pacific Ocean. Pp. 78-84 in Marine birds: their feeding ecology and commercial fisheries relationships. Spec. Publ. Canadian Wildlife Service. (D. N. Nettleship, G. A. Sanger, and P. F. Springer, Eds.). Ottawa, Canada: Canadian Wildlife Service.

Ogi, H. and T. Tsujita. 1973. Preliminary examination of stomach contents of murres (*Uria* spp.) from the eastern Bering Sea and Bristol Bay, June-August, 1970 and 1971. Jap. J. Ecol. 23: 201-202.

Parker, R. R. 1963. Effects of formalin on length and weight of fishes. J. Fish Res. Board Can. 20: 1441-1455.

Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 621-552.

Perez, M. A. and M. A. Bigg. 1983. Food habits of northern fur seals (*Callorhinus ursinus*) off western North America. Pp. 15-24 in Marine mammal/fishery interactions. (J. Beddington, R. Beverton, and D. M. Lavigne Eds.). London: George Allen & Unwin.

Pickavance, J. R. 1970. A new approach to the immunological analysis of invertebrate diets. J. Anim. Ecol. 39: 715-724.

Pielou, E. C. 1977. Mathematical ecology. New York: Wiley-Interscience.

Pikhu, E. K. H. and E. R. Pikhu. 1970. Reconstruction of the sizes of fishes swallowed by predators from fragments of their vertebral column. J. Ichthyol. 10: 706-709.

Pinkas, L., M. S. Oliphant and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fish. Bull. Calif. 152: 1-105.

Prime, J. H. 1979. Observation on the digestion of some gadoid fish otoliths by a young common seal. Int. Counc. Explor. Sea Coop. Res. Rep. 1979/N: 14.

Prince, P. A. 1980a. The food and feeding ecology of the blue petrel (*Halobaena caerulea*) and dove prion (*Pachyptila desolata*). J. Zool. (London) 190: 59-76.

Prince, P. A. 1980b. The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and Black-browed albatross *D. melanophris*. Ibis 122: 476-488.

Prince, P. A. and C. Ricketts. 1981. Relationships between food supply and growth in albatrosses: an interspecies chick fostering experiment. Ornis. Scand. 12: 207-210.

Prŷs-Jones, R. P., L. Schifferli, and D. W. MacDonald. 1974. The use of an emetic in obtaining food samples from passerines. Ibis 116: 90-94.

Radke, W. J. and M. J. Frydendell. 1974. A survey of emetics for use in stomach contents recovery in the House Sparrow. Am. Mid. Nat. 92: 164-172.

Ralph, C. P., S. E. Nagata, and C. J. Ralph. 1985. Analysis of droppings to describe diets of small birds. J. Field Ornithol. 56: 165-174.

Randall, R. M. and I. S. Davidson. 1981. Device for obtaining food samples from the stomachs of Jackass Penguins. S. Afr. J. Wildl. Res. 11: 121-125.

Randall, R. M., B. M. Randall, and E. W. Klingelhoefer. 1981. Species diversity and size ranges of cephalopods in the diet of Jackass Penguins from Algoa Bay, South Africa. S. Afr. J. Zool. 16: 163-166.

Rausch, R. L. 1983. The biology of avian parasites: helminths. Pp. 367-442 in Avian biology, Vol. 7. (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York: Academic Press.

Reilly, P. 1982. What makes a Gentoo chuck? Aurora 3: 8-9.

Reimchen, T. E. and S. Douglas. 1984. Feeding schedule and daily food consumption in Red-throated Loons *Gavia stellata* over the prefledging period. Auk 101: 593-599.

Reintjes, J. W. and J. E. King. 1953. Food of Yellow-

fin Tuna in the central Pacific. U.S. Fish Wildl. Serv. Fish. Bull. 54: 91-110.

Richards, S. W. 1963. The demersal fish populations of Long Island Sound. III. Food of the juvenile from a mud locality. Bull. Bingham Oceanogr. Coll. Yale Univ. 18: 73-93.

Ricker, W. E. 1937. The food and the food supply of the sockeye salmon (*Onorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Biol. Bd. Can. 3: 450-468.

Ricklefs, R. E. and M. Lau. 1980. Bias and dispersion of overlap indices: results of some Monte Carlo simulations. Ecology 61: 1019-1024.

Roby, D. D., K. L. Brink and D. N. Nettleship. 1981. Measurements, chick meals and breeding distribution of Dovekies *Alle alle* in northwest Greenland. Arctic 34: 241-248.

Ryan, P. G. and S. Jackson. 1986. Stomach pumping: is killing seabirds necessary? Auk. 103: 427-428.

Schaefer, M. B. 1978. Men, birds, and anchovies in the Peru Current—dynamic interactions. Trans. Am. Fish. Soc. 99: 461-467.

Schlatter, R. P. and C. A. Moreno. 1976. Habitas alimentarios del Cormoran antarctico, *Phalacrocorax atriceps brandfieldensis* (Murphy), en Isla Green, Antarctica. Ser. Cient. Inst. Antart. Chileno 4: 69-88.

Schneider, D. C. and G. L. Hunt, Jr. 1984. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska. Pp. 86-95. *in* Marine birds: their feeding ecology and commercial fisheries relationships. Spec. Publ. Canadian Wildlife Service, (D. N. Nettleship, G. A. Sanger, and P. F. Springer, Eds.). Ottawa, Canada: Canadian Wildlife Service.

Seaburg, K. G. 1957. A stomach sampler for live fish. Prog. Fish-Cult. 19: 137-139.

Shannon, C. E. and W. Weaver. 1959. The mathematical theory of communication. Urbana, Illinois: Illinois University Press.

Siegel, S. 1956. Non-parametric statistics for the behavioral sciences. New York: McGraw-Hill.

Smith, N. G. 1967. Capturing seabirds with Avertin. J. Wildl. Manage. 31: 479-483.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. San Francisco: W. H. Freeman Co.

Sokal, R. R. and P. H. Sneath. 1963. Principles of numerical taxonomy. San Francisco: W. H. Freeman Co.

Steven, G. A. 1933. The food consumed by shags and cormorants around the shores of Cornwall (England). J. Mar. Biol. Assoc. U.K. 19: 277-292.

Sunada, J. S., P. R. Kelly, I. S. Yamashita, and F. Gress. 1981. The Brown Pelican as a sampling instrument of age structure in the northern anchovy population. CalCOFI Rep. 22: 65-58.

Swanson, G. A. and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of Blue-winged Teal. J. Wildl. Manage. 34: 739-746.

Swanson, G. A., G. L. Krapu, J. C. Bartonek, S. R. Serie, and D. H. Johnson, 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38: 302-307.

Tjomlid, S. A. 1973. Food preferences and feeding

habits of the Pied Kingfisher *Ceryle rudis*. Ornis Scand. 4: 145-151.

Treacy, S. C. and T. W. Crawford. 1981. Retrieval of otoliths and statoliths from gastrointestinal contents of scats of marine mammals. J. Wildl. Manage. 45: 990-993.

Vermeer, K. 1981. The importance of plankton to Cassian's Auklet during breeding. J. Plankton Res. 3: 315-329.

Vermeer, K. and S. J. Westrheim. 1984. Fish changes in diets of nesting Rhinoceros Auklets and their implications. Pp. 96-105. *in* Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service Spec. Publ. (D. N. Nettleship, G. A. Sanger, and P. F. Springer, Eds.). Ottawa, Canada: Canadian Wildlife Service.

Vogt, W. 1942. Aves guaneras. Bol. Comp. Admora. Guano Peru. 18: 1-132.

Walter, C. B. 1984. Fish prey remains in Swift Tern and Hartlaub's Gull pellets at Possession Island, off Namibia. Ostrich 55: 166-167.

Walter, C. B., J. Cooper, and W. C. Suter, 1986a. Analysis of Swift Tern chick regurgitations in the Saldanha Bay region, South Africa 1977-1984. Ostrich 57.

Walter, C. B. and E. O'Neill. 1986. Electrophoresis in the study of diets and digestion rates of seabirds. Comp. Biochem. Physiol. 83a.

Walter, C. B., E. O'Neill, and R. Kirby. 1986b. "ELISA" as an aid in the identification of fish and molluscan prey of birds in marine ecosystems. J. Exp. Mar. Biol. Ecol. 33.

Waldron, K. D. and J. E. King. 1963. Food of skipjack in the central Pacific. Pp. 1431-1432. *in* Proceedings of the world scientific meeting on the biology of tunas and related species. F. A. O. Rome Sect. 5. Exp. Pap 26. (H. Rosa, Jr., Ed.). Rome: F.A.O.

Ward, P. and A. Zahavi. 1973. The implications of certain assemblages of birds as "information centres" for food-finding. Ibis 115: 517-534.

Warham, J., R. W. Watts, and R. J. Dainty. 1976. The composition, energy content and function of the stomach oils of petrels (Order: Procellariiformes). J. Exp. Mar. Biol. Ecol. 23: 1-23.

White, D. H., C. A. Mitchell, and D. M. Swineford. 1984. Reproductive success of Black Skimmers in Texas relative to environmental pollutants. J. Field Ornithol. 55: 18-30.

White, H. C. 1936. The food of kingfishers and mergansers on the Margaree River, Nova Scotia. J. Biol. Bd Can. 2: 295-309.

Wiens, J. A. and J. M. Scott. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77: 439-452.

Williams, L. E. 1966. Capturing wild turkey with alphachloralose. J. Wildl. Manage. 30: 50-56.

Wilson, R. P. 1984. An improved stomach pump for penguins and other seabirds. J. Field Ornithol. 55: 109-112.

Wilson, R. P. 1985. Diurnal foraging patterns of the Jackass Penguin. Ostrich 56: 212-214.

Wilson, R. P., G. La Cock, M-P., Wilson, and F. Mollagee. 1985. Differential digestion of anchovy and squid in Jackass Penguins. Ornis Scand. 16: 77-79.