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# THE FOOD AND FEEDING ECOLOGY OF THE LIGHT-MANTLED SOOTY ALBATROSS AT SOUTH GEORGIA

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## SUMMARY

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The diet of the Light-mantled Sooty Albatross *Phoebetria palpebrata* breeding at South Georgia is described on the basis of quantitative analysis of thirty-seven food samples from chicks and nine from adults. Squid and krill *Euphausia superba* were the main components by weight and by frequency of occurrence, although fish were also taken.

Identifiable fish were chiefly myctophids; measurable krill were mature individuals. Of the eleven species of squid recorded, the most important were *Mesonychoteuthis* sp A (by numbers) and ?*Discoteuthis* sp (by weight). These species are hardly taken at all by the other two squid-eating albatrosses at South Georgia. There are few detailed similarities between the squid taken by *P. palpebrata* at South Georgia and those recorded in an analysis of regurgitated pellets at Marion Island.

Frequency of feeding of chicks and observations of birds at sea suggest that *P. palpebrata* can forage more widely during the breeding season than Black-browed and Grey-headed Albatrosses. Ecological segregation from these is thought to be achieved by a combination of differences in foraging range and area and by differences in the detailed composition of the diet.


## INTRODUCTION

The Light-mantled Sooty Albatross *Phoebetria palpebrata* has a circumpolar breeding distribution in sub-Antarctic latitudes, occurring at islands north and south of the Antarctic Convergence. At sea, it ranges from 45°S to the edge of the Antarctic pack ice (Johnstone & Kerry 1976; Thurston 1982; Watson *et al.* 1971) and is a species characteristically associated with the surface layer of cold Antarctic water.

South Georgia is one of the most important breeding sites for the species, with an annual breeding population of at least 5,000 pairs. Substantial numbers are also present during the breeding season on the Auckland Islands and Kerguelen Islands and up to several hundred pairs have been reported on Prince Edward, Crozet, Heard, Macquarie, Campbell and Antipodes Islands (Watson 1975; Williams *et al.* 1979).

Although the species is widely distributed, it does not breed in the large accessible colonies characteristic of many of the smaller *Diomedea* albatrosses. Instead, *P. palpebrata* prefers loose aggregates of pairs, on tussock-clad cliff ledges, and so the species has been little studied.

Aspects of the breeding biology of the species have been studied at Campbell Island by Sorenson (1950), at Iles Crozet by Mougin (1970) and at Marion Island by Berruti (1977, 1979). The only study of the diet, however, is an analysis of regurgitated squid beaks at Marion Island (Berruti & Harcus 1978).

This paper reports on the analysis of food samples obtained from adults and chicks at Bird Island and Elsehul, north-western South Georgia (lat. 54°S long. 38°W), during the austral summer of 1976-77 and in March 1978. Information on aspects of feeding ecology is also given.

## METHODS

Samples ought to be taken from adult birds returning to feed their chicks. However, because *P. palpebrata* is shy and nests in small well-dispersed groups and because it is difficult to handle full-grown birds on cliff ledges, this was possible only ten times. After a brief mutual recognition ceremony, which always precedes feeding, the single chick was fed by regurgitation. The adult was captured using a puffin hook, when about to pass food to the chick, and induced to regurgitate into a plastic funnel, 25cm in diameter, supported over a plastic beaker. Samples were transferred to Kilner jars for transport back to the field hut.

Most samples (37) were obtained from chicks, which were up-ended over a plastic funnel, and if sufficient material was regurgitated samples were dealt with as above.

In the laboratory, samples were weighed whole, the liquid portion decanted through a 250-$\mu$m-aperture sieve, excess oil washed away with water and the sample re-weighed. The solid material was then sorted into its component species or into unidentifiable residue. All components were weighed *separately and identified as far as possible.*

To supplement squid material, ten other regurgitations were obtained from chicks in March 1978, from which all squid material was extracted.

Cephalopod remains were identified by Dr M.R. Clarke and the approximate mass of whole animals was estimated from known relations between rostral length of lower beaks and biomass (Clarke 1962, 1980). I identified crustaceans and fish, using standard literature and some named reference material, with help from S. Jones.

## RESULTS

### *Timing of Sampling*

Figure 1 shows when the food samples were collected from the thirty-seven chicks and nine adults (one adult sample was lost before analysis) in relation to the breeding cycle on South Georgia.

More samples were obtained early in the nesting period because chicks rapidly became accustomed to handling and did not usually regurgitate a second time and because only a few pairs were accessible for sampling.

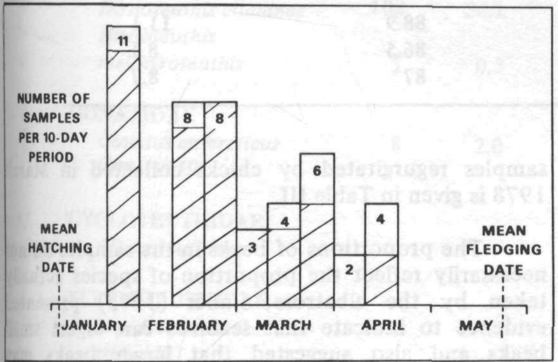


Figure 1. Date of collection of food samples from breeding Light-mantled Sooty Albatrosses. Samples from chicks are shaded.

### *Size of meal*

The fresh weight of ten food samples collected from adults about to feed chicks was 557 ± 175g (range 320-910g). With the Black-browed Albatross *D. melanophris* and the Grey-headed Albatross *D. chrysostoma* the mean weight of the sample was about 20% less than the true mean weight of the meal because birds, when handled, do not regurgitate all the material that they would deliver to the chick (Prince 1980). This is also likely to happen with *P. palpebrata*, the true average weight of whose meal would then be about 700 g.

### *Liquid material*

The liquid material is a mixture of water and oils, derived from the breakdown of solid food (Clarke & Prince 1976, 1980; Warham *et al.* 1976). As chicks regurgitate very variable amounts of liquid, the average proportion of liquid in each meal can only usefully be assessed for the nine adult samples, where it was 52%. This is very similar to values found by Prince (1980) for *D. melanophris* (48%) and *D. chrysostoma* (52%).

### *Solid material*

The composition of the solid components of the samples is shown in Tables I and II. For both adult and chick samples the analysis by weight shows crustaceans and squid to be of the greatest importance in the diet of *P. palpebrata* with fish being of less significance. Because fish, in particular, is rapidly digested, however, its quantity will be liable to underestimation. The frequency of occurrence shows a broadly similar picture, with fish still decidedly less important than squid or krill.

In samples from chicks this method of analysis is usually biased by the retention of items that resist digestion, particularly squid beaks and bones of large fish but perhaps also crustacean exoskeletons (Ashmole & Ashmole 1967; Imber 1973). Thus, there may be here some bias against recognition of the remains of small fish but other categories ought to be satisfactorily recognized. In general, there is good agreement, from both types of analysis and in both kinds of samples, that squid and crustaceans normally form the bulk of the diet.

Some further analysis was possible with the material of most prey.

### *Fish*

Most material was of myctophids Myctophidae and only two samples contained specimens of larger Nototheniidae. All material was too digested to permit more detailed identifications. The grey colour of much of the small proportion of unidentified material (see Table I) suggested that this was partially digested fish.

Fish never formed the dominant item in any one food sample and it would appear that myctophids are taken only incidentally, albeit regularly, in the course of feeding activities.

### *Crustacea*

Antarctic krill *Euphausia superba* formed the bulk of crustacea (90% by weight) and was the only species of euphausiid in the samples. A small number

TABLE I

*Percentage composition by weight of food samples from* P. palpebrata

| Food type | Squid | Fish | Crustacea | Carrion etc | Unidentified material |
|---|---|---|---|---|---|
| Sample type | | | | | |
| Adult (n=9) | 62.1 | 2.2 | 33.1 | 0.1 | 2.4 |
| Chick (n=37) | 41.4 | 13.0 | 41.1 | 0.5 | 4.0 |
| Combined (n=46) | 45.5 | 10.9 | 39.5 | 0.4 | 3.7 |

TABLE II

*Percentage frequency of occurrence of food items in food samples from* P. palpebrata

| Food type | Squid | Fish | Crustacea | Carrion etc |
|---|---|---|---|---|
| Sample type | | | | |
| Adult (n=9) | 100 | 55.6 | 88.9 | 11.1 |
| Chick (n=37) | 94.6 | 51.4 | 86.5 | 8.1 |
| Combined (n=46) | 95.6 | 53.3 | 87 | 8.7 |

of fairly undigested krill occurred in a sample collected on 30 January 1977. Their lengths from rostrum to telson were measured and averaged 5.25 ± 0.15 cm (n = 20), which indicates mature specimens.

Decapods were prevalent, occurring in 40% of the samples but composing only 4% by weight. The well-digested remains of one or two individuals were found in many samples but only two contained significant quantities. Both were collected at the end of February 1977 (from chicks) and 38 and 14% of the solid material present in the two samples was the undigested exoskeletons of *Acanthephyra* sp. Other samples contained at least one different unidentified decapod.

Two species of amphipod were identified; one specimen of *Cyllopus* was probably *C. lucusii*, and *Parathemisto gaudichaudii* occurred in small quantities (by number and by weight) in 10% of samples. Free-living amphipods are probably too small for *P. palpebrata* to take deliberately and they may have been obtained indirectly via the stomach contents of squid or fish. Two samples contained unidentified isopods.

*Squid*

The species composition of squid in the ten samples regurgitated by chicks collected in March 1978 is given in Table III.

The proportions of beaks in the samples do not necessarily reflect the proportion of species actually taken by the albatross; Imber (1973) presented evidence to indicate that seabirds can digest small beaks and also suggested that larger beaks may stimulate chicks to regurgitate more readily.

The principal species of squid in these samples were *Mesonychoteuthis* sp A and *?Discoteuthis* sp, which together made up 77% by number and 75% by weight of the lower beaks. Dimensions of beaks of *?Discoteuthis* sp suggest that, with an average individual weight of over 700g, this is the single most important species in the diet of *P. palpebrata* if it is caught whole.

*Carrion and other prey*

A piece of penguin skin with flesh attached must have been scavenged, perhaps killed by Leopard Seal *Hydrurga leptonyx* near South Georgia. Prions *Pachyptila* occurred in two samples and may have been scavenged. Small stones and penguin feathers were incidental items in 35% and 22% of samples, respectively.

TABLE III

*Composition of the squid component of the diet of Light-mantled Sooty Albatross from analysis of chick regurgitations (South Georgia) and chick pellets (Marion Island)*

| Squid species | MARION ISLAND | | SOUTH GEORGIA | | | | |
|---|---|---|---|---|---|---|---|
| | No. beaks | % | No. beaks | % | Est. mean wt. (Kg) | Total wt. (Kg) | % |
| CRANCHIIDAE | | | | | | | |
| *Taonius pavo* | 2 | 0.5 | | | | | |
| *Taonius cymoctypus* | 2 | 0.5 | | | | | |
| *Galiteuthis glacialis* | 76 | 19.4 | | | | | |
| *Teuthowenia antarctica* | 105 | 26.9 | | | | | |
| *Mesonychoteuthis sp A* | | | 107 | 56.9 | 0.081 | 8.7 | 17.0 |
| *Crystalloteuthis sp* | | | 3 | 1.6 | 0.270 | 0.8 | 1.6 |
| ONYCHOTEUTHIDAE | | | | | | | |
| *Moroteuthis knipovitchi* | 26 | 6.6 | | | | | |
| *Kondakovia longimana* | 52 | 13.3 | 1 | 0.5 | 1.000 | 1.0 | 2.0 |
| HISTIOTEUTHIDAE | | | | | | | |
| *Histioteuthis eltaninae* | 102 | 26.1 | 1 | 0.5 | 0.070 | 0.1 | 0.2 |
| *Histioteuthis meleagroteuthis* | 1 | 0.3 | | | | | |
| GONATIDAE | | | | | | | |
| *Gonatus antarcticus* | 8 | 2.0 | 9 | 4.8 | 0.300 | 2.7 | 5.3 |
| *Gonatus sp* | | | 14 | 7.4 | 0.150 | 2.1 | 4.1 |
| CYCLOTEUTHIDAE | | | | | | | |
| *?Discoteuthis sp* | | | 41 | 21.8 | 0.736 | 29.8 | 58.4 |
| LEPIDOTEUTHIDAE | | | | | | | |
| *Lepidoteuthis grimaldii* | | | 2 | 1.1 | ? | – | – |
| PSYCHROTEUTHIDAE | | | | | | | |
| *Psychroteuthis sp* | | | 9 | 4.8 | 0.569 | 5.1 | 10.0 |
| *Psychroteuthis glacialis* | 17 | 4.4 | | | | | |
| OMMASTREPHIDAE | | | | | | | |
| *Todarodes sagittatus* | | | 3 | 1.6 | 0.180 | 0.5 | 1.0 |
| LYCOTEUTHIDAE | | | | | | | |
| *Oregoniateuthis sp* | | | 1 | 0.5 | 0.21 | 0.21 | 0.4 |
| TOTAL beaks | 391 | | 191 | | | | |

Marion data from Berruti (1979)

## DISCUSSION

*Comparison with other albatrosses breeding at South Georgia*

Most albatrosses are primarily squid feeders (Harris 1973; Imber & Russ 1975; Prince 1980; Tickell 1968). Of the four species breeding on South Georgia, three eat mainly cephalopods; *D. melanophris* feeds mainly on krill and fish (Prince 1980). Analysis of the squid taken by the other albatrosses (summarized in Croxall & Prince 1980) has revealed marked differences in species composition and size of prey. Thus, *D. chrysostoma* mainly takes *Todarodes sagittatus* (84% by numbers, 95% by weight), which has a mean weight of 180g (Clarke & Prince 1981; Prince 1980). Both the Wandering Albatross *D. exulans* and *P. palpebrata* take a greater variety of species (and sizes) of squids than *D. chrysostoma* but only a few predominate. *D. exulans* breeds in the winter and, at this time, *Kondakovia longimana*, with a mean weight of 3,170g is the most important species (36% by numbers, 77% by weight) in its diet (Clarke *et al.* 1981). For *P. palpebrata*, although *Mesonychoteuthis* sp A forms 57% by numbers (but only 17% by weight) of the squids eaten, *?Discoteuthis* sp (21% by numbers but 58% by weight) is probably the most important component.

Therefore, different species and sizes of squid probably form the principal prey of the three albatrosses at South Georgia that rely significantly on this resource. The average weight of squid taken by *P. palpebrata* is about 270 g and, unless some of the large squid are scavenged, this is heavier than the average weight of squid (*c.* 180 g) taken by Black-browed and Grey-headed Albatrosses.

By taking much krill, *P. palpebrata* shows another difference from *D. chrysostoma* and more resembles *D. melanophris*. Both *P. palpebrata* and *D. melanophris* take 40% by weight of krill, a figure suggesting considerable dietary overlap, although squid and fish are of inverse importance in their diets.

*Comparison with other populations of* P. palpebrata

Berruti (1979) analyzed pellets from chicks of *P. palpebrata* on Marion Island as part of a comparison of the squid diets of *P. palpebrata* and the Sooty Albatross *P. fusca* and found much overlap in composition. The squid of most importance to both species, *Moroteuthis knipovitchi* (by weight) and *Histioteuthis eltaninae* and *Teuthowenia antarctica* (by numbers), were the same. Also, the distributions of sizes of these species were similar. Because they both feed chicks at the same time of year, Berruti suggested that inter-specific competition may be alleviated by differences in foraging range, *P. palpebrata* moving to feed south of the Antarctic Convergence while *P. fusca* forages north of the Convergence.

If *P. palpebrata* from Marion Island are indeed crossing the Antarctic Convergence on feeding trips, one might expect their squid diets to show similarities to those of *P. palpebrata* from the similar water zone round South Georgia. In fact, although four species are common to the diets of both populations of *P. palpebrata*, two of these, *Kondakovia longimana* and *Histioteuthis eltaninae*, are represented by only a single beak in the South Georgian samples. *Teuthowenia antarctica*, with *Histioteuthis eltaninae*, the squid most frequently taken by *P. palpebrata* at Marion Island (26.9% and 26.1%, respectively), does not occur in the South Georgian samples. It has, however, been identified from castings by *P. palpebrata* from Kerguelen and Macquarie Islands (Imber 1978).

Differences in the diets of Marion and South Georgian birds probably partly reflect geographical differences in distribution of squid. Nevertheless, unless *Kondakovia longimana* (the main squid in the diet of Wandering Albatrosses at South Georgia) is only common there in winter, its absence from the diet of *P. palpebrata* cannot be explained in this way and suggests that other factors, perhaps involving food selection, are involved.

The discrepancies might be due to differences in the source of the samples of squid (fresh regurgitations as opposed to castings). Small beaks are most likely to be preserved in fresh samples and more likely to have been digested by the time pellets are regurgitated naturally. In contrast, pellets ought usually to represent a much greater accumulation (and hence potential diversity) of beaks than forced regurgitations, especially as many of the latter were taken early in the period of rearing the chick. There is, however, no evidence for this in the data presented in Table III.

Other discrepancies may be artefacts resulting from identifications being made by different specialists in a difficult field with beak characteristics often poorly defined and species limits uncertain.

Krill forms a substantial proportion of the diet of *P. palpebrata* at South Georgia. Although there are no quantitative data, it appears that squid (and perhaps also fish) are more important and crustaceans less important, in the diet of the species at Marion Island than at South Georgia. This may simply reflect the greater abundance of krill near South Georgia and especially in the Scotia Sea.

*Feeding methods*

The small amount of information on the feeding technique of *P. palpebrata* indicates that, as with other albatrosses, they usually seize prey at the surface (Ashmole 1971) though plunging (Murphy 1936) has been recorded. Most observations refer to birds taking refuse from ships (e.g. Kock & Reinsch 1978) and as with the two mollymawks (Prince 1980), diving from the surface probably plays a role when the birds are exploiting natural food. The nature of the diet and possibly the lack of feeding observations suggest that *P. palpebrata* feeds mainly at night when krill, as a result of vertical migration, are more numerous at, or very near to, the surface. The bioluminescence of krill and of some squid species may help birds to locate prey at night, as has been suggested for some petrels and albatrosses (Imber 1973; Imber & Russ 1975).

Smell may be used to locate potential food by night and day as Grubb (1972) has demonstrated for the Great Shearwater *Puffinus gravis* and Wilson's Storm-Petrel *Oceanites oceanicus*, and Hutchison & Wenzel (1980) for a variety of other species. If so, this probably mainly facilitates the detection of dead or moribund animals floating on the surface.

Direct evidence for natural scavenging is only the occurrence of penguin flesh in one food sample. The remains of prions found might have been scavenged but the birds may have been captured alive at sea (although this implies considerable agility by *P. palpebrata*) or even on land where burrows are not uncommon near *P. palpebrata* nests.

That *D. chrysostoma* takes squid of mean weight c. 180 g yet the smaller and lighter *P. palpebrata* takes some squid (e.g. *?Discoteuthis*) of mean weight c. 730 g suggests that some of these large squid may have been scavenged from the surface. Also the presence of a few small, partially decomposed squid in some samples supports the contention that dead squid can be taken by *P. palpebrata*.

For *P. palpebrata*, opportunities for natural scavenging near South Georgia are probably restricted by the presence and dominance of the other larger albatross species and giant-petrels *Macronectes* spp.

*Feeding range*

The frequency with which an albatross chick is fed indicates the time spent by each adult in foraging and hence its potential feeding range at this stage of the breeding season.

At Elsehul in 1976-77, twenty-one chicks were weighed as part of a study of growth of chick *P. palpebrata* (Thomas *et al.* in press) These daily weighings have been used to derive an index of frequency of feeding chicks, comparable to that which can be calculated for *D. melanophris, D. chrysostoma* and *D. exulans* from data in Tickell & Pinder (1975) and Tickell (1968). All increases in weight over twenty-four hours were taken to show that the chick had been fed; all decreases, that it had not. On this basis, Table IV shows the percentage frequency of feeding for the four albatrosses at South Georgia.

Several authors (e.g. Ashmole & Ashmole 1967; Harper 1976; Tickell & Pinder 1975) have pointed out the errors in estimated feedings frequency arising from the use of chick-weighing data. Thus, a small loss of weight in twenty-four hours may mask a small feed and a large increase between successive weighings may disguise two feeds. In either case, frequency of feeding will be underestimated. Nevertheless, such an analysis is useful as a comparison between species.

At South Georgia, *P. palpebrata* chicks seem to be fed slightly less often than those of either *D. chrysostoma* or *D. melanophris*. Adult *P. palpebrata* may be able to travel farther from the breeding colony than the mollymawks. Seabird observations in the Scotia Sea during the summers 1976-79 tend to support this, and Figure 2 summarizes the data on the

TABLE IV.

*Mean frequency of delivery of feeds to albatross chicks at South Georgia, calculated from daily weighings (see text). 100% = 1 feed per day*

| Species | Chick age (days) | Feeding frequency (%) | Reference |
|---|---|---|---|
| Light-mantled Sooty Albatross | 21-80 | 42.6 | This study |
| Grey-headed Albatross | 21-80 | 48.5 | Tickell & Pinder 1975 |
| Black-browed Albatross | 21-80 | 49.7 | Tickell & Pinder 1975 |
| Wandering Albatross | 32-276 | 30.8 | Tickell 1968 |

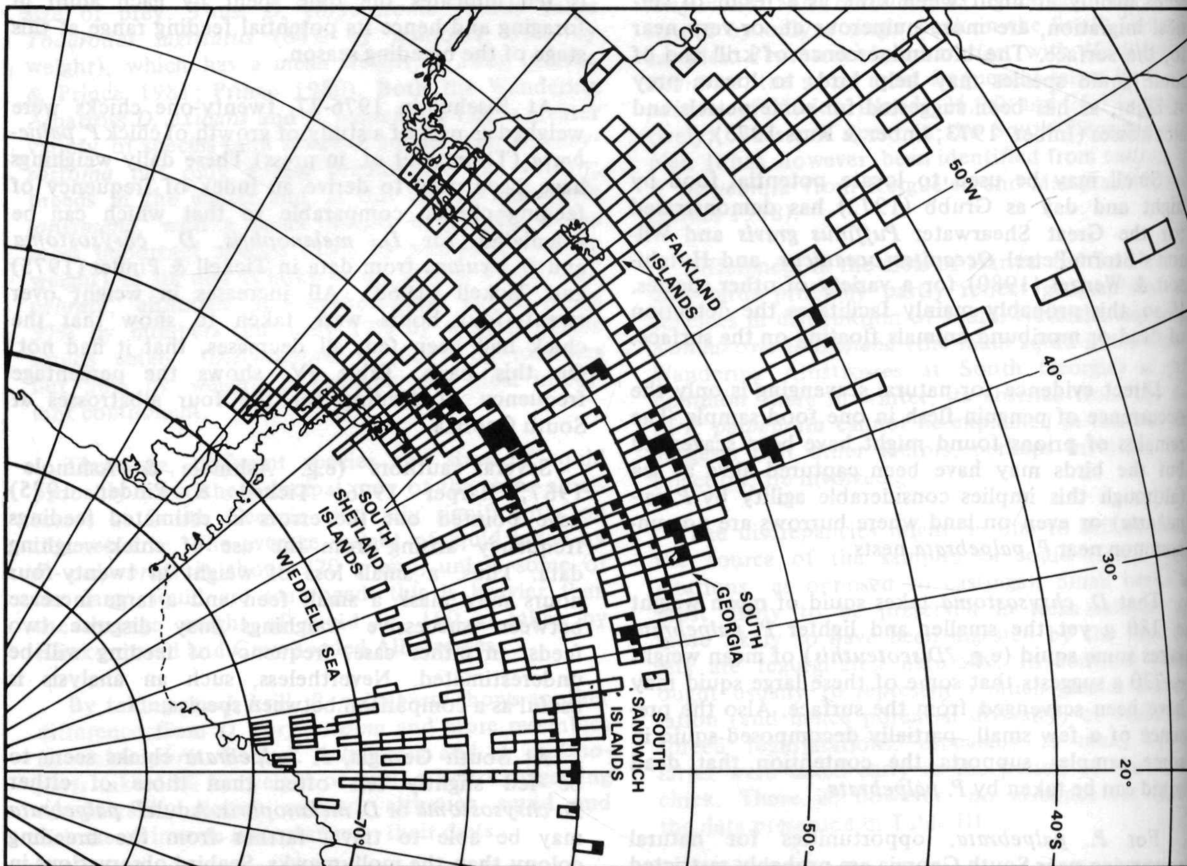


Figure 2. Pelagic distribution of *P. palpebrata* in the south-western Atlantic Ocean in summer (September-April). Data from British Antarctic Survey seabird record scheme "ten minute" cards. All degree squares (1° lat by 1° long) for which post-1975 data exist are outlined. For each square the proportion of cards with records of *P. palpebrata* is indicated by the extent of shading. A completely filled square indicates $>$ 50% cards with records; the lowest category ($<$ 5%) is slightly exaggerated in scale to permit recognition.

summer distribution of *P. palpebrata* in the south-western Atlantic Ocean. It seems particularly common just north of the South Shetland Islands and also near the South Sandwich Islands south-east of South Georgia. Neither area seems greatly frequented by the two mollymawks. The marked southerly distribution also appears to be characteristic of *P. palpebrata* in the Australian sector of the Southern Ocean during the summer, as Johnstone & Kerry (1976) and Ozawa *et al.* (1968) have shown it to be concentrated just north of the pack ice between 60-65°S and 120-140°E. Although *D. chrysostoma* and *D. melanophris* are widely distributed in the Scotia Sea, away from South Georgia they are most numerous near the Antarctic Convergence west of South Georgia. *D. chrysostoma,* though rather uncommon in Australian waters, also principally occurs round the Antarctic Convergence.

Croxall & Prince (1980), basing their calculations on theoretical minimum flight speed and chick feeding frequency estimates, suggested that breeding *P. palpebrata* might have a foraging range of about 1,250km. The concentrations of *P. palpebrata* round the South Shetland Islands are 1500 km from South Georgia. Therefore these birds could be on foraging trips to feed chicks. However, since *P. palpebrata* breeds once every two years (K.R. Kerry pers. comm.), any bird seen at sea is as likely as not to be a non-breeder.

*P.palpebrata* has a low wing-loading, high aspect ratio (Warham 1977) and high buoyancy index (Croxall & Prince 1980), compared with other albatrosses. These adaptations are probably associated with the ability to cover greater distances more efficiently, which would fit the observed distribution at sea and the longer intervals between successive feeds of the chick.

The reduced frequency of feeding the chick (compared with the two mollymawks) may be partly compensated for by an estimated true meal size (c. 700 g) that is greater than those of *D. chrysostoma* and *D. melanophris* (*c.* 600 g). The aerodynamic adaptations mentioned above may also be important in transporting a meal that is 25% of the body weight as opposed to 16% in the mollymawks.

Thus, *P. palpebrata* is probably the most pelagic of the three small albatrosses at South Georgia. Its wider distribution might enable it to exploit squid and krill outside the normal range of breeding *D. chrysostoma* and *D. melanophris* and so might partially explain some of the differences in the composition of squids in the diets of *D. chrysostoma* and *P. palpebrata*.

*P. palpebrata* is probably not in much direct competition with *D. chrysostoma* and *D. melanophris* in the breeding season because it can forage more extensively and has a diet broadly intermediate between that of the two mollymawks. It is uncertain to what extent the dietary differences result from different foraging areas or from differential selection of available prey in similar geographical areas.

The results of these analyses of food suggest that competition with *D. chrysostoma* is probably less direct, as quite different squid species are taken, than with *D. melanophris,* as krill appears equally important to it and *P. palpebrata*. In retrospect, however, 1976-77, when the samples of *P. palpebrata* food were obtained, appears to have been a season when krill was particularly available to albatrosses and penguins (Croxall & Prince 1979). Consequently, when krill is less readily available, squid may be still more important. The rate of growth of *P. palpebrata* chicks (Thomas *et al.* in press) is at least as slow as that of *D. chrysostoma,* (Ricketts & Prince 1981) and suggests that rather low energy foods (like squid, but not fish and krill) form the normal bulk of the diet of *P. palpebrata*.

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