CO-EXISTENCE IN THE *PHOEBETRIA* ALBATROSSES AT MARION ISLAND

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CONTENTS

1 Introduction

The family Diomedeidae, the albatrosses, contains two genera, Diomedea and Phoebetria. Phoebetria comprises the Sooty Albatross P. fusca (Hilsenberg 1822) and the Light-mantled Sooty Albatross P. palpebrata (Forster 1785). The two species are similar in size, but there are differences in the plumage and soft part coloration of adults and juveniles (Cox 1976). Phoebetria fusca and palpebrata have similar breeding biologies (Watson 1975), but there are slight differences in dispersion of nests (Van Zinderen Bakker 1971). The two species apparently take similar foods (Watson 1975). Phoebetria fusca and palpebrata are mainly allopatric in their breeding and pelagic ranges in the Antarctic and sub-Antarctic (Ozawa 1967, Watson 1975); they thus appear to be ecological counterparts inhabiting separate areas. However, the two species breed sympatrically at the Marion and Prince Edward islands, and at the Crozet islands (Watson 1975).

The aims of the present study are threefold. Firstly, the co-existence of the two closely related, normally allopatric, albatross species is investigated in their zone of overlap where interspecific competition for food resources and nesting space is likely to be most acute. Secondly, the genetic isolation of the two species is investigated, as co-existence implies increased interspecific social interaction with associated increased possibilities of hybridization. Thirdly, the two species' possible evolutionary histories are examined in relation to their ecologies. Logistical constraints prevented study of fusca and palpebrata on the feeding grounds, i.e. at sea, and feeding could be studied only indirectly.

The generally accepted principle of competitive exclusion holds that no two species inhabit the same ecological niche permanently (Lack 1971).

Thus, the existence of ecological differences between *fusca* and *palpebrata* can be expected, since the two species co-exist at Marion Island. The term "ecological niche" as used here, is defined as all the interrelationships between an organism and its environment (Hutchinson 1957). A species is characterized by a number of physiological, behavioural and morphological features. According to Mayr (1970): "Every recent investigation has confirmed the widespread conviction that a species is a unique biological system". Some of the morphological, behavioural and physiological differences between the two species may be indicators of ecological differences between the species. For example, beak size and shape are used commonly as indicators of ecological differences between bird species (Schoener 1974). Indeed, where two largely allopatric species occur sympatrically the differences are usually more marked. This phenomenon, termed character displacement (Brown and Wilson 1956), is thought to be a result of interspecific competition for the same resources, and tends to promote genetic isolation of the two species. However, Schoener (1974) warned that the existence of differences in the ecological niches of two similar species is not necessarily the result of interspecific competition, but may have evolved under the influence of other selection pressures, such as predation, and the maintenance of genetic isolation. Mayr (1971) stated that, "geographic speciation is the almost exclusive mode of speciation among animals". The procellariiforms breed in widely scattered discrete populations and generally slow a high degree of fidelity to the nest site and the natal colony (Fisher 1972, Richdale & Warham 1973). Such a situation would have promoted geographic speciation in both *fusca* and *palpebrata* in isolated populations of the *Phoebetria* ancestral stock. Thus, the ecology and species-specific characteristics were probably established in allopatric populations as the products of differing natural selection pressures. In summary, species-specific characteristics and differences in ecological niches between fusca and palpebrata at Marion Island may have been established in allopatric populations prior to co-existence, and possibly may have been exaggerated by interspecific competition, or may have resulted from interspecific competition.

Whilst studies of resource partitioning in animal species have been increasing at a rate four times that of biological studies as a whole (Schoener 1974), investigations of resource partitioning in the Diomedeidae and the Procellariiformes generally are few and poor in detail. This is a result partly of the practical difficulties of studying the birds at their feeding grounds. However, the breeding biology of the Procellariiformes is well documented, and adaptations for breeding by members of the group have been discussed by Lack (1967, 1968).

The comparative breeding biology of three sympatric Diomedeidae species pairs have been studied: Diomedea chrysostoma and D. melanophris at South Georgia (Tickell & Pinder 1975); D. nigripes and D. immutabilis at Midway (Rice & Kenyon 1962); and, fusca and palpebrata at the Crozet islands (Mougin 1970). Mougin's study is the least detailed of the three. Fisher (1972) investigated speciation, and the maintenance of genetic isolation in D. immutabilis and D. nigripes at Midway Island. The breeding biologies of allopatric populations of the species pair D. exulans and D. epomophora were compared by Tickell (1968). The breeding biologies of all the Diomedeidae, with the exception of D. albatrus, have been studied in varying detail. Apart from the above-mentioned studies, the more important accounts are as follows: D. cauta (Johnstone et al. 1975), D. chlororhyncos (Rowan 1951), D. exulans (Voisin 1969), D. epomophora (Richdale 1952, Westerskov 1963) and D. irrorata (Harris 1973).

The genus *Phoebetria* is less well known than *Diomedea*. *Phoebetria palpebrata* has received more attention than *fusca* in the past.(Sorenson 1950 and many brief accounts), and is currently being studied at Macquarie Island (Kerry pers. comm.). The most detailed study of *fusca* is in Mougin's (1970) comparative account of *fusca* and *palpebrata* at the Crozet islands. The Marion Island populations of both species have been mentioned briefly by Crawford (1952), Rand (1954) and Van Zinderen Bakker (1971).

The results of the present study are dealt with under five headings, followed by a synthesis and conclusions, and a summary. The first section describes the topography, climate and biota of Marion Island, and compares the avifauna of Marion and Prince Edward islands with other sub-Antarctic islands. The next section reviews the taxonomy, plumage coloration, distribution and numerical abundance of *fusca* and *palpebrata*, and presents new data on the plumage coloration, nesting distribution, numerical abundance, morphology and moult of the Marion Island populations. The succeeding three sections report on the two species' breeding biology, diet and ethology respectively. Thus, the species'general breeding biology, and ecological separation in diet and nest site selection are considered. As many species-specific characteristics as could be identified are, however, documented as potential indices of ecological differences, to allow deductions of key selection pressures fashioning these differences. The species' ethology is examined as a potential mechanism of genetic isolation.

2 Marion Island

2.1 Topography

The following synopsis is based mainly on Verwoerd (1971).

Marion Island is roughly circular in shape with a circumference of about 70km, and rises to 1 230m above sea level (Fig. 1). The island is volcanic in origin, and two successions of lava have been described. The older grey lava succession shows signs of glaciation and has a much smoother profile than the younger more broken black lava flows.

The land rises to a central highlands area, permanently covered with ice and snow. The summer snowline occurs at 610m (King 1952). The slope to the western and south-western coasts is interrupted by an escarpment, dropping steeply to a narrow coastal plain. This escarpment is cut in the south by a broad black lava valley, the Santa Rosa valley, and by Crawford's Bay whose sides rise several hundred metres above sea level. In anti-clockwise direction from Cape Hooker in the south east to Cape Davis in the north west, the slope is interrupted by several large grey lava ridges and faults, e.g., Long Ridge, Skua's Ridge, Stony Ridge and Piew Crags. Red and black scoria cones abound all over the island.

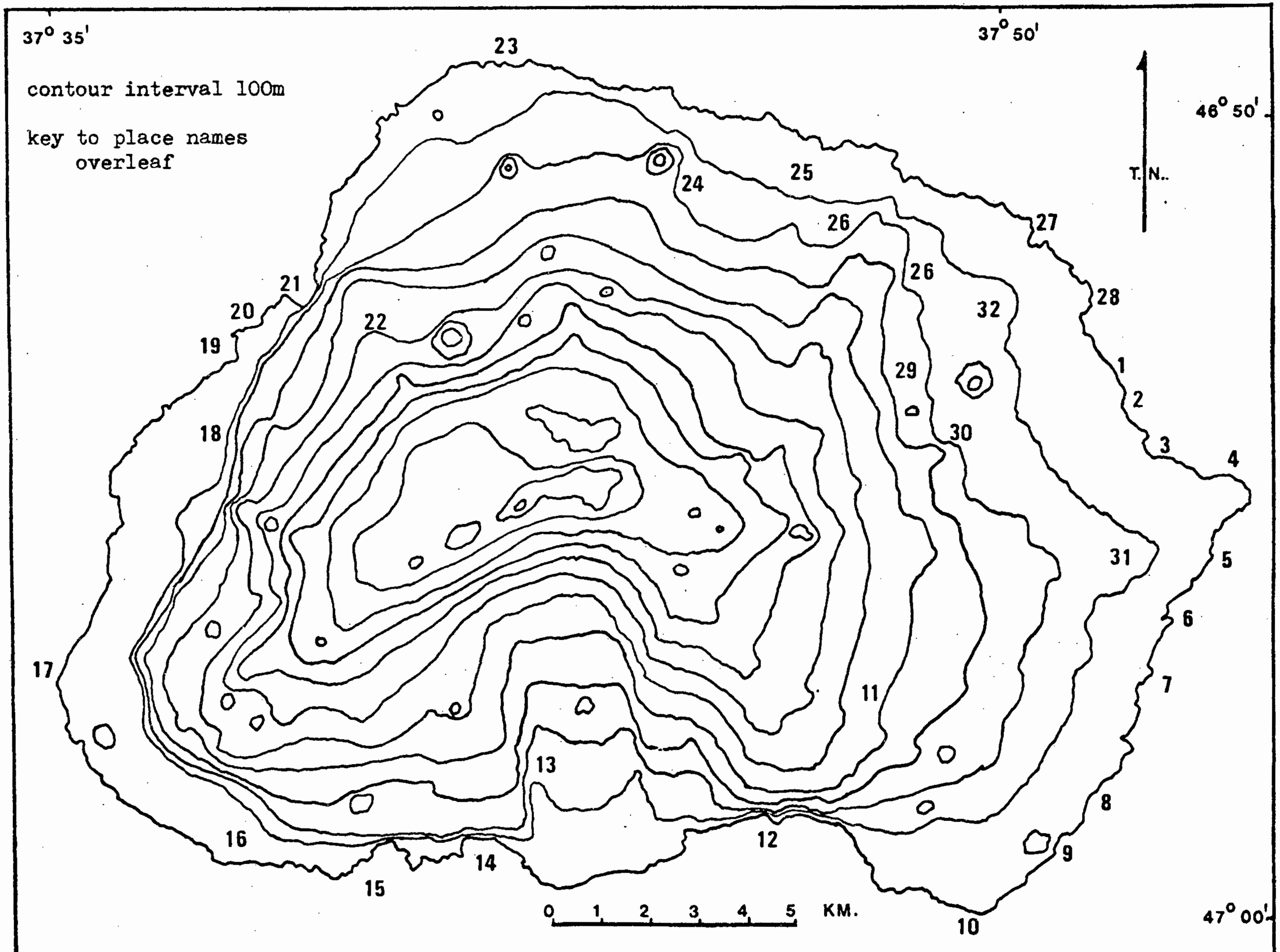
The coastline is irregular with numerous inlets, stony beaches and coves, but is mainly made up of black lava cliffs rising to 15m. The eastern coastline consists largely of grey lava cliffs which also occur at Crawford's Bay, Triegaardt's Bay, Cape Davis, Long Ridge, Skua's Ridge and Macaroni Bay. The grey lava cliffs are usually higher than the black lava cliffs.

2.2 Climate

The following synopsis is based mainly on Schulze (1971).

FIGURE 1

TOPOGRAPHICAL MAP OF MARION ISLAND. TAKEN FROM LANGENEGGER & VERWOED (1971)



PLACE NAMES FOR FIG. 1

1. Meteorological base
2. Trypot
3. Macaroni Bay
4. Archway Bay
5. Hansen Point
6. Bullard Beach
7. Killerwhale Cove
8. Haglet Stream
9. Kildalkey Bay
10. Cape Hooker
11. Black Haglet Valley
12. Crawford Bay
13. Grey-headed Albatross Ridge
14. Goodhope Bay
15. Rooks Bay
16. Penguin City
17. Swartkop Point
18. Kampkoppie
19. Fur Seal Bay
20. Mixed Pickle Cove
21. Triegaardt Bay
22. Azorellakop
23. Cape Davis
24. Repetto's Hill
25. Prinsloomeer
26. Long Ridge
27. Ship's Cove
28. King Bird Head
29. Tafelberg
30. Piew Crags
31. Stony Ridge
32. Skua's Ridge

The climate is typical of a sub-antarctic oceanic island. There is a high degree of cloud cover, coupled with high precipitation and relative humidity. Strong winds occur frequently. Air and sea temperatures are low.

Except for insolation, the parameters mentioned show little variation either seasonally or daily. Day-length varies from 8,6h in winter to 15,8h in summer. The sun shines on average 3,5h a day - only 29% of the possible maximum sunshine (Table 1). Only 50% of the possible total radiation is transmitted to the island's surface.

Precipitation is largely in the form of rain (Table 2), but snow and hail occur throughout the year. Winds blow strongest and most frequently from a north-westerly direction. Table 3 gives the monthly and annual frequency of moderate and full gales. Air and sea temperatures show little variation (Table 4 & 5). Sea temperatures indicate that the Antarctic Convergence approaches close to Marion Island in winter.

2.3 Biota

Marion Island has poorly developed soils, generally lacking in nutrients for plants. Plant and invertebrate life is relatively most diverse and abundant in the low-lying coastal areas where birds and mammals occur in greatest concentrations. Soil depth and vegetation generally decrease with increasing elevation. The broken malpais areas support little vegetation, even at the coast.

Marion Island has a tundra-like vegetation, limited to a few species of vascular plants of small form. The vegetation is thickest in low-lying areas, and only primitive plants, e.g., mosses and lichens, occur in the mountains. Dominant vascular plants include *Poa* spp., *Acaena adscendens*, *Blechnum penna-marina* and *Azorella selago*.

TABLE 1

MEAN ANNUAL SUNSHINE AT MARION ISLAND (1948 - 1965). TAKEN FROM SCHULZE (1971)

Percent possible sunshine	0	1-10	11-49	50-89	90-100
Frequency of days in year	79	54	151	81	0

TABLE 2

MEAN MONTHLY PRECIPITATION (mm) AT MARION ISLAND (1951 - 1965). ADAPTED FROM SCHULZE (1971)

Month	J	F	M	A	M	J	J	A	S	O	N	D
Precipitation	222	207	225	238	249	232	231	185	201	165	196	225

TABLE 3

MEAN MONTHLY AND ANNUAL FREQUENCY OF DAYS WITH FULL (66 km/hr) AND MODERATE (55 km/hr) GALES AT MARION ISLAND. BASED ON 10 YEARS OF RECORDS TAKEN FROM SCHULZE (1971)

Gales	Month												Year
	J	F	M	A	M	J	J	A	S	O	N	D	
Full	3,0	2,4	3,1	3,3	2,7	4,6	5,1	3,3	4,7	2,9	3,9	3,7	42,7
Moderate	8,7	6,2	6,5	8,0	8,6	9,5	10,7	10,3	11,4	8,4	8,4	10,1	106,8

TABLE 4

MEAN MONTHLY AND EXTREME MAXIMUM AND MINIMUM AIR TEMPERATURES (^{o}C) AT MARION ISLAND (1961 - 1965). ADAPTED FROM SCHULZE (1971)

Month	J	F	M	A	M	J	J	A	S	O	N	D
Mean max.	10,1	10,6	10,2	8,7	7,3	6,6	6,2	6,0	6,1	7,5	8,6	9,2
Mean min.	4,4	5,0	4,7	3,7	2,5	1,9	1,4	1,2	1,0	2,1	2,7	3,6
Extreme max.	22,2	22,3	20,4	17,8	17,8	14,0	13,3	16,2	13,4	17,7	21,4	18,3
Extreme min.	-0,8	-0,7	-0,8	-3,0	-3,0	-6,0	-6,0	-5,5	-6,8	-4,4	-2,6	-1,2

TABLE 5

MEAN MONTHLY AND EXTREME MAXIMUM AND MINIMUM SURFACE TEMPERATURES (°C) OF SEA AT MARION ISLAND (1951 - 1965). TAKEN FROM SCHULZE (1971)

Month	J	F	M	A	M	J	J	A	S	O	N	D
Mean	5,7	6,1	6,1	5,7	5,0	4,7	4,3	4,0	4,0	4,2	4,7	5,1
Extreme max.	6,9	7,9	8,0	7,7	6,4	6,4	6,3	5,1	5,7	5,4	5,9	6,5
Extreme min.	4,4	4,3	4,6	4,0	3,0	3,0	2,5	2,6	2,1	2,8	2,6	3,8

The mosses and liverworts occur in large variety, and more than 100 species have been recorded (Van Zanten 1971, Grolle 1971).

Terrestrial invertebrates are limited in species and abundance. In certain areas, earthworms and coleopteran and lepidopteran larvae are locally abundant in the soil.

The four breeding mammals are the Elephant Seal Mirounga leonina, Fur Seal Arctocephalus tropicalis and two introduced species, the House Mouse Mus musculus and the House Cat Felis domesticus (Anderson & Condy 1974).

Twenty-seven bird species breed on the island. The birds, which occur in great numbers, exert a major influence on the biota. An important source of nutrients for plants on the island is provided by the birds through the manuring of the soil.

2.4 The avifauna of Marion and Prince Edward islands

A total of 26 breeding bird species was recorded at Marion and Prince Edward islands by Van Zinderen Bakker (1971). Since then, the Antarctic Tern Sterna vittata has been recorded as an additional breeding species (Berruti & Harris 1976).

Winterbottom (1971) showed that the avifauna of Marion and Prince Edward islands had closest affinities with the avifaunas of the two nearest island groups - Crozet and Kerguelen islands. The only major avifaunal difference between the Marion and Prince Edward islands on one hand, and the Crozet and Kerguelen islands on the other, is that no member of the Oceanitidae (storm petrels) is known to breed at Marion and Prince Edward islands. However, several individuals belonging to two species (Fregetta tropica and Garrodia nereis) in the Oceanitidae have been recorded recently at Marion Island (pers. obs., Burger pers. comm.). These two species, which breed widely in

TABLE 6

NUMBERS OF PROCELLARIIFORM AND SPHENISCIFORM SPECIES BREEDING AT ISLANDS AT WHICH EITHER ONE OR BOTH SPECIES OF <u>PHOEBETRIA</u> SP. BREEDS. TAKEN FROM WATSON (1975)

	Spheniscidae	Diomedeidae	Procellariidae	Oceanitidae	Pelecanoididae	Total
Tristan da Cunha islands	1	3	9	2	1	16
New Amsterdam Island	1	2	2	0	0	5
St Paul Island	1	2	2	0	0	5
Gough Island	1	3	9	2	1	16
Crozet islands	4	4	11	2	2	23
Marion & Prince Edward islands	4	5	10	0	2	21
Kerguelen Island	4	4	10	3	2	23
Antipodes islands	2	3	9	2	1	17
Auckland islands	2	4	7	3	2	18
Campbell Island	2	5	4	0	1	12
Heard Island	5	3	4	1	2	15
South Georgia	4	4	6	3	2	19
Macquarie Island	4	4	6	0	0	14

TABLE 7

PROCELLARIIFORM AND SPHENISCIFORM SPECIES BREEDING AT THEIR SOUTHERNMOST OR NORTHERNMOST LIMITS AT MARION AND PRINCE EDWARD ISLANDS, CROZET ISLANDS AND KERGUELEN ISLANDS. TAKEN FROM WATSON (1975)

	Southernmost limit	Northernmost limit
Procellariiformes	Phoebetria palpebrata	Phoebetria palpebrata
	Diomedea chlororhynchos	Diomedea chrysostoma
	Pterodroma macroptera	Diomedea melanophris
	Pterodroma mollis	Pterodroma lessoni
	Pterodroma brevirostris	Pachyptila desolata
		Daption capensis
		Pelecanoides georgicus
Sphenisciformes		Aptenodytes patagonicus
		Pygoscelis papua
		Eudyptes chrysolophus

the Antarctic and sub-Antarctic (including Crozet and Kerguelen islands) might be breeding at Marion and Prince Edward islands as well.

The numbers of breeding sphenisciforms and procellariiforms (i.e., pelagic feeding species) on those islands which support at least one breeding Phoebetria species are shown in Table 6. The islands with the three highest numbers of breeding species are Crozet, Kerguelen, Marion and Prince Edward islands respectively. Five procellariiform species breed at their southernmost limits at these three island groups, while a further seven procellariiforms and three sphenisciforms species breed at their northernmost limits (Table 7) Only Halobaena caerula is known to be restricted, as a breeding species, to these three island groups. It is apparent that the three island groups support a comparatively rich avifauna in the transitional zone between cold and temperate sub-Antarctic waters.

3 The Bird

3.1 Introduction

Modern texts agree in treating Phoebetria fusca and P. palpebrata as distinct species (e.g., Watson 1975), in contrast to earlier accounts (e.g. Wilson 1907) which did not distinguish between the two forms. No races are recognized currently (Serventy, Serventy & Warham 1971, Watson 1975). Initial taxonomic confusion resulted from inadequate study of insufficient specimens. However, the literature dealing with plumage descriptions is still incomplete, and the difficulties in distinguishing juveniles have not been resolved (Serventy, et al. 1971).

A review of published descriptions of the morphology and plumage of fusca and palpebrata, with comparison of data obtained in the present study, is necessary to evaluate records of pelagic and breeding distribution. Moreover, it is necessary to determine which morphological and plumage characteristics are species-specific, as these may indicate ecological or genetic isolation of the two species.

Moult in birds is a period of increased energy demand, because of the metabolic cost of feather replacement. Thus, pattern of moult may differ in two sympatric species which are competing for energy sources.

3.2 Methods

The definition of various age classes is a necessary prerequisite to the discussion of plumage descriptions, breeding biology, morphological characteristics and ethology. Definitions of age classes are based on those of Tickell (1968). In the Diomedeidae, breeding is deferred for several years, and birds generally visit the breeding grounds one or more years before actually breeding (Richdale 1952, Tickell 1968, Fisher 1972, Richdale & Warham 1973). Tickell (1968,

1969) warned against placing birds at different stages of physiological development in the same age classes. Until more accurate data are available, it is sufficient for purposes of the present study to define only three age classes. Adult: A bird which has bred in a previous season, or subsequently in the same season. Subadult: A bird which has visited the breeding ground subsequent to fledging. Juvenile: A bird which has not visited the breeding grounds subsequent to fledging.

Adult and subadult members of fusca and palpebrata were captured during the 1974-75 breeding season at nesting colonies at Marion Island. The birds allowed a close approach, and were caught by hand. The head of each captured bird was covered with a heavy cloth bag. This greatly reduced the risk of injury to the handler by the bird's powerfully hooked beak. Before banding and release, each bird was weighed and measured; and plumage examined for wear and moult. Birds were weighed in a cloth bag with a hand-held 5 kg Pesola balance. The following linear measurements were taken: tarsometatarsus, culmen and tail length, depth of beak at the gonys, and wing length. Notes (supplemented by colour photographs) were made on plumage coloration. For fusca, 212 individuals were examined, of which at least 23 were known to be breeding. Eight fully-grown specimens of fusca were collected and sexed by examination of the sexual organs. Four of these specimens were examined for down and contour feather replacement over the entire surface of the body.

In 1976, I examined 17 fusca specimens and 21 palpebrata specimens in the collection of the British Natural History Museum, housed at Tring, England. Notes were made on plumage coloration, but it proved impossible to examine properly the study skins for moult without damaging them. Mensural data were not collected for several reasons. Museum specimens tend to shrink slightly with drying (Kinsky & Harper 1968), and the tarsometatarsus length is affected by the method of preparation (Clancey pers. comm.). The condition of some specimens was so poor, that even culmen lengths were not considered reliable. Many specimens had not been sexed. Most specimens were collected at sea, i.e., the birds' breeding status and population affinities were not known.

Counts of nests at breeding sites away from the study colonies at Marion Island were made at irregular intervals by myself, A. Burger, J. Mendelsohn and A.J. Williams.

3.3 Taxonomy

According to modern taxonomic convention, the family Diomedeidae is divided into two genera: Phoebetria, containing two species, and Diomedea with 11 species (Murphy 1936).

Distinctive characters assigned to Phoebetria include a long, cuneate-shaped tail; long, narrow wings; and, the sulcus - a long, lateral groove, containing a coloured skin-membrane dividing the lower mandible. The plumage of post-fledgling birds is dusky.

In Diomedea, only nigripes has a predominantly dusky, adult plumage, and in irrorata, the adult has a dark body and a light head. Juveniles of exulans and albatrus are dark, but become lighter with age. In most species of Diomedea, the adults have dark backs and wings, with light heads and underparts. The tail is rounded, and no sulcus is present. The wings of Diomedea species are relatively wider than those of Phoebetria species.

Formerly Phoebetria fusca and P. palpebrata were regarded as conspecific under Diomedea fuliginosa (e.g., Wilson 1907). Nichols and

Murphy (1914) provisionally recognized four races of palpebrata and two of fusca. However, individual variation in size and colour, and sexual dimorphism, were found to account for apparent differences between populations. Modern authorities accord full specific status to each form of Phoebetria but do not recognize any races within the species (Murphy 1936, Serventy et al. 1971, Watson 1975).

3.4 Plumage descriptions

3.4.1 Adults

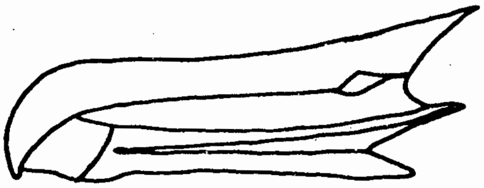
The general plumage characteristics of adult fusca and palpebrata are sufficiently distinct to allow easy separation of the species in the hand, and at reasonably close range in the field.

The plumage of fusca is a uniform, dark sooty-brown. The mantle and abdomen are lighter than the head, neck and wings, but the contrast is slight and never as marked as in palpebrata. In palpebrata, the mantle and abdomen vary from a pale ashy grey in the centre of the back and on the flanks, to a light sooty grey on the nape and abdomen. The shafts of the primaries are white in both species.

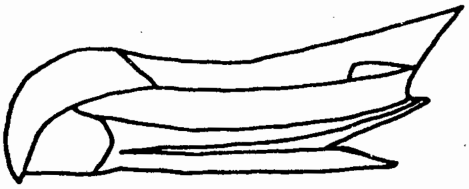
The culmen of fusca is relatively straight in profile, and the unguis is relatively weak (Fig. 2). The sulcus varies from yellow to very pale yellow, and is wider than in palpebrata. The culmen of palpebrata is concave in profile and the unguis is relatively strong (Fig. 2). The difference in culmen shape between the two species is only distinguishable at close quarters. The sulcus is bluish in palpebrata. The sulcus in fusca darkens slightly after death (pers. obs.), whereas Murphy (1936) states that the colour persists. The sulcus of palpebrata darkens after death (Nichols and Murphy 1914, pers. obs.), whereas Holgersen (1957) found that the sulcus turned

FIGURE 2

BEAK SHAPE IN PHOEBETRIA FUSCA AND P. PALPEBRATA. TAKEN FROM MURPHY (1936)



P. fusca



P. palpebrata

pale yellow a couple of months after collection. It is possible that changes in sulcus colour vary according to the method of preservation of the specimens.

Both species have an incomplete white ring of feathers immediately posterior to the eye. In _fusca_ the eye ring is slightly narrower, and extends farther forward along the anterior half of the lower and upper eyelids than in _palpebrata_ (Fig. 3).

In _fusca_, at Marion Island, the worn, aged plumage of adults is browner than normal, and individual feathers have buffy edges. A few very worn feathers attain a whitish edge, but these are neither prominent nor numerous. The occasional feather of the greater, median and lesser wing coverts is browner and more abraded than the surrounding grey feathers. Wear becomes particularly apparent on the forehead and crown, mantle and abdomen. The tip of the outermost primary is usually broken in old, worn plumage. Hagen (1952) describes buffy terminations on the body feathers of a Tristan da Cunha bird with especially worn plumage.

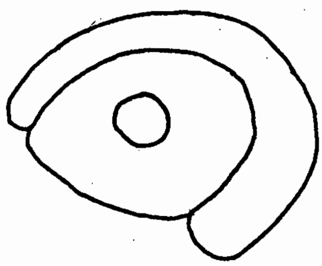
Only two _palpebrata_ were captured late in the breeding season at Marion Island when the plumage of _fusca_ showed most wear. No detailed evidence for plumage wear was noted, but colour photographs show that brown feathers occur in the greater, median and lesser wing coverts of _palpebrata_.

3.4.2 Subadults

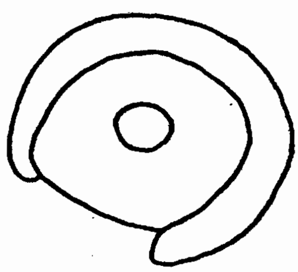
I was unable to differentiate between adult and subadult _fusca_, or between adult and subadult _palpebrata_, at Marion Island. There is no indication that subadult plumage differs from adult plumage in either species.

FIGURE 3

EYE-RING SHAPE IN <u>PHOEBETRIA FUSCA</u> AND <u>P. PALPEBRATA</u>



P. palpebrata



P. fusca

3.4.3 Juveniles

The scientific literature for <u>fusca</u> and <u>palpebrata</u> contains accurate descriptions of the plumage of juveniles at fledging only. Otherwise, birds described as "immature" were either observed and collected at sea, or found as beach-washed specimens, without any conclusive evidence for their age.

Tables 8 and 9 summarize the confusion and incompleteness of these age:plumage descriptions. Only those characters which distinguish adults and subadults between the two species, or indicate age differences within the species, are considered. Since subadults and adults of <u>fusca</u> and <u>palpebrata</u> are similar, all birds described in the literature as young, immature or juvenile are placed arbitrarily in the juvenile age group, as defined under Methods (3.2).

3.4.4 Synthesis

Reported morphological differences between <u>palpebrata</u> and <u>fusca</u> according to age are summarized in Table 10A & B. In both <u>fusca</u> and <u>palpebrata</u>, live adult birds are easily distinguished in the hand by sulcus colour, beak and eye-ring shape and general body coloration. In dead specimens the sulcus colour undergoes change and the shape of the eye-ring may alter, rendering these characters unreliable for identification of the species.

Subadults appear to be similar to adults in both species. Thus, for live subadults in the hand it is relatively easy to distinguish between species, but separation of subadults from adults within a species is not possible.

The juveniles of both species, but especially <u>fusca</u>, present the greatest difficulties in identification, because there is little de-

TABLE 8

MORPHOLOGICAL CHARACTERISTICS OF JUVENILE BIRDS IN PHOEBETRIA PALPEBRATA

Age group[1]	Characteristics				Source
	Sulcus colour	General body plumage	Eye-ring colour	Colour of primary feather shafts	
Immature	no data	mottled mantle[2]	no data	no data	Falla (1937)
Immature	pale grey	mottled scapulars[2]	no data	horn	Hitchcock (1950)
At fledging	brownish/bluish brown at base	as adult	grey-white	no data	Sorenson (1950)
Juvenile	brownish	no data	no data	no data	Serventy *et al.* (1971)
Juvenile	grey/pale yellow	barred mantle and breast	no data	dark	Watson (1975)
Immature	brownish	mottled mantle	dull	dark	Cox (1976)
At fledging[3]	grey	as adult	grey-white	dark	Present study
Juvenile[4]	dark	mottled mantle light abdomen	dull	dark	Present study

[1]Terms used by authors under "Source".

[2]Both authors state that the plumage initially resembles adult plumage but is subject to rapid fading giving a mottled effect.

[3]Birds examined at Marion Island.

[4]Study specimens in collection of British Natural History Museum.

TABLE 9

MORPHOLOGICAL CHARACTERISTICS OF JUVENILE BIRDS IN *PHOEBETRIA FUSCA*

Age group[1]	Characteristics				Source
	Sulcus colour	General body plumage	Eye-ring colour	Colour of primary feather shafts	
Immature	yellow[2]	pale nape and hind neck	no data	no data	Falla (1937)
Immature	violet	whitish buff nape and collar	no data	no data	Hitchcock (1950)
Juvenile	Bluish	light back	no data	no data	Serventy *et al*. (1971)
Juvenile	violet/grey/ yellow	buffy collar, whitish nape	no data	dark	Watson (1975)
Immature	bluish/grey/ yellow	brownish nape neck buffish white	dull	dark	Cox (1976)
At fledging[3]	grey-black	as adult	greyish white	dark	Present study
Juvenile[4]	dark	slightly mottled dark abdomen buffish neck	dull	dark	Present study

[1]Terms used by authors cited under "source".

[2]Sulcus colour recorded on only two occasions.

[3]Birds examined at Marion Island.

[4]Birds in the collection of the British Natural History Museum

TABLE 10A

VARIATION IN MORPHOLOGICAL CHARACTERISTICS ACCORDING TO AGE OF LIVE AND DEAD SPECIMENS OF PHOEBETRIA FUSCA

		P. fusca			
Age group	State of specimens	Sulcus colour	Beak shape	General body plumage	Eye-ring
Juvenile	alive	grey bluish	straight culminicorn weak unguis	whitish nape develops after fledging, dark abdomen	greyish-white
	dead	no data	no change	no change	shape possibly alters
Subadult	alive	yellow	straight culminicorn weak unguis	dark nape dark abdomen	whitish ring
	dead	no change or slightly darker	no change	no change	shape possibly alters
Adult	alive	yellow	straight culminicorn weak unguis	dark nape dark abdomen	white ring
	dead	no change or slightly darker	no change	no change	shape possibly alters

TABLE 10B

VARIATION IN MORPHOLOGICAL CHARACTERISTICS ACCORDING TO AGE OF LIVE AND DEAD SPECIMENS OF PHOEBETRIA PALPEBRATA

		P. palpebrata			
Age group	State of specimens	Sulcus colour	Beak shape	General body plumage	Eye-ring
Juvenile	alive	grey[1]	concave culminicorn strong unguis	mottled mantle develops after fledging light abdomen	greyish white ring less complete than in *fusca*
	dead	no change	no change	no change	shape possibly alters
Subadult	alive	bluish	concave culminicorn strong unguis	light mantle light abdomen	white ring less complete than *fusca*
	dead	changes[2]	no change	no change	shape possibly alters
Adult	alive	bluish	concave culminicorn strong unguis	light mantle light abdomen	white ring less complete than *fusca*
	dead	changes[2]	no change	no change	shape possibly alters

[1] Watson (1975) records sulcus as yellow.

[2] Hitchcock (1950) states the sulcus darkens after death, whereas Holgersen (1957) states the sulcus lightens after death.

finitive information on plumage succession. Tickell (1968, 1969) showed that plumage changes in Diomedea exulans, D. chrysostoma and D. melanophris were most rapid in the birds' first few years of life. For fusca and palpebrata many of the discrepancies in the descriptions of young birds are probably related to rapid change in sulcus colour, and general plumage coloration.

Fledgling palpebrata and fusca at Marion Island are easily identifiable by general plumage coloration and beak shape, which are similar to those of the adult. However, sulcus colour in both species is grey.

The conclusions of my study of museum specimens in the collection of the British Natural History Museum agree with the suggestions of Serventy et al. (1971) and Watson (1975), that the initial teleoptile plumage of fusca and palpebrata is subject to considerable wear, resulting in a mottled appearance in palpebrata and in a buffy or whitish nape in fusca. However, juvenile fusca have dark abdomens (with some buffy-edged feathers), whereas juvenile palpebrata have lighter abdomens. Juvenile fusca were slightly darker on the mantle, although worn buffy feathers resulted in a slightly barred effect. The nape and neck feathers were most worn, with buffy or whitish edges, resulting in the buffy collar referred to by various authors (Table 9). Juvenile palpebrata were markedly mottled on the mantle. Beak shapes are distinctive. Even if juvenile fusca possess blue sulci, they may be separated on the basis of these characteristics from all palpebrata. Sulcus colour is unreliable as an identifying characteristic, as fusca juveniles have been reported with blue sulci (Hitchcock 1950), and palpebrata juveniles with yellow sulci (Watson 1975). Sulcus colour of adult fusca and palpebrata is yellow and blue respectively.

My studies confirm the opinion of Cox (1976) who considered that, with care, most adults and juveniles can be identified within reasonable range in the field. However, Serventy et al. (1971) and Watson (1975) suggest that it may be impossible to identify some young Phoebetria, even in the hand. Definitive information from birds of known age are required from banding studies to settle conclusively these differences.

It is obvious that all sight records accumulated to date need careful and critical scrutiny. For example, the records of Phoebetria birds with blue sulci and dark backs in the Antarctic seas (Routh 1949), and of large numbers of so called palpebrata off Gough Island (Wilkins 1923) might have involved juveniles of fusca.

3.5 Distribution and numerical status

3.5.1 Marion and Prince Edward islands

The estimated total number of breeding pairs of fusca and palpebrata at Marion and Prince Edward islands is 2732 and 216 respectively. Estimated numbers of breeding pairs of fusca and palpebrata were based on counts in different areas of Marion Island and at Prince Edward Island (Tables 11 and 12). The distribution of breeding sites of both species at Marion Island is shown in Fig. 4.

An accurate census of fusca and palpebrata nests at Marion and Prince Edward islands is difficult for two reasons. Egg and pullus mortality is high, so that counts made after egg laying is complete underestimate total breeding populations. The broken terrain makes access to some coastal and most inland breeding sites difficult and time-consuming. In some areas, it is physically impossible to observe and count all the nests from the ground. Since actual counts usually underestimate the total number of breeding pairs, only the largest number of occupied nests recorded in each area is included in Tables 11 and 12. I was unable to apply standard correction factors

TABLE 11

ESTIMATED NUMBER OF BREEDING PAIRS OF *PHOEBETRIA FUSCA* AT MARION ISLAND, BASED ON NEST CENSUS DATA 1974-1976.

AREA	No. of occupied nests	Date of census	Estimated no. of breeding pairs
Macaroni Bay	110	12.10.76	115
Archway	1	7.5.76	2
Hansen Point - Bullard	4	25.10.76	6
Bullard - Killerwhale Cove	34	25.10.76	45
Killerwhale Cove - Haglet stream	135	25.10.76	180
Haglet stream - Kildalkey	152	25.10.76	200
Crawford's Bay	-	-	50
Grey-headed Albatross Ridge	1	24.2.75	4
Goodhope Bay	161	Nov.1974	250
Rooks Bay	89	Nov.1974	140
Penguin City	28	Nov.1974	35
Fur Seal Bay	98	Nov.1974	140
Mixed Pickle Cove	19	Nov.1974	30
Triegaardt's Bay	100+	Nov.1974	250
Cape Davis	78	28.2.75	200
Long Ridge - Ships Cove	34	15.2.75	85
Ships Cove - King Bird Head	239	3.12.76	300
	1 283		2 032
Prince Edward Island			700
	1 283		2 732

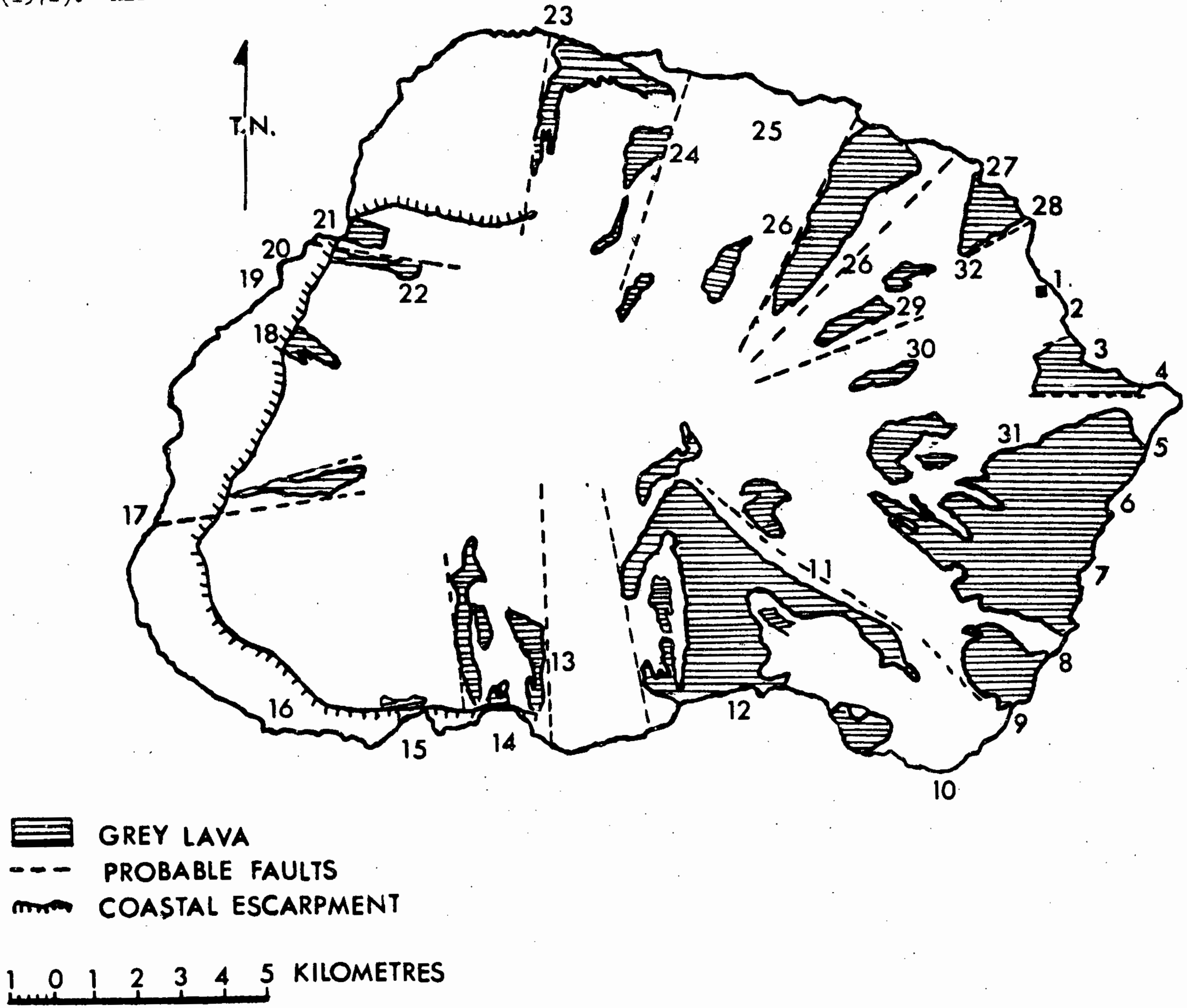
TABLE 12

ESTIMATED NUMBER OF BREEDING PAIRS OF *PHOEBETRIA PALPEBRATA* AT MARION ISLAND, BASED UPON NEST CENSUS DATA 1974 - 1976

AREA	No. of nests counted	Date of census	Estimated no. of breeding pairs
Tafelberg	2	17. 5.76	4
Piew Crags	10	23.11.74	12
Trypot	3	23.10.74	3
Macaroni Bay	2	25.10.74	2
Bullard - Killerwhale Cove	2	25.10.76	4
Haglet Stream - Kildalkey	3	25.10.76	3
Black Haglet Valley	4	Nov 1976	8
Crawford's Bay			10
Goodhope Bay	15	Nov 1974	20
Penguin City	1	Nov 1974	1
Swartkop Inland	3+	Nov 1974	6
Kampkoppie	2+	Nov 1974	5
Mixed Pickle Inland	5	Nov 1974	8
Triegaardt's Bay	4+	Nov 1974	15
Azorellakop			2
Repetto's Hill			5
Prinsloo Meer Cliffs	5	3.12.76	6
Long Ridge Inland	12	3.12.76	17
Long Ridge - Ships Cove			4
Ships Cove - King Bird Head	15	3.12.76	18
Unknown Inland Sites	—		23
	88		176
Prince Edward Island	0		40
	88		216

FIGURE 4

MAP OF MARION ISLAND SHOWING GREY LAVA AREAS, PROBABLE FAULTS AND COASTAL ESCARPMENT. ADAPTED FROM VERWOED (1971). KEY TO PLACE NAMES GIVEN OVERLEAF

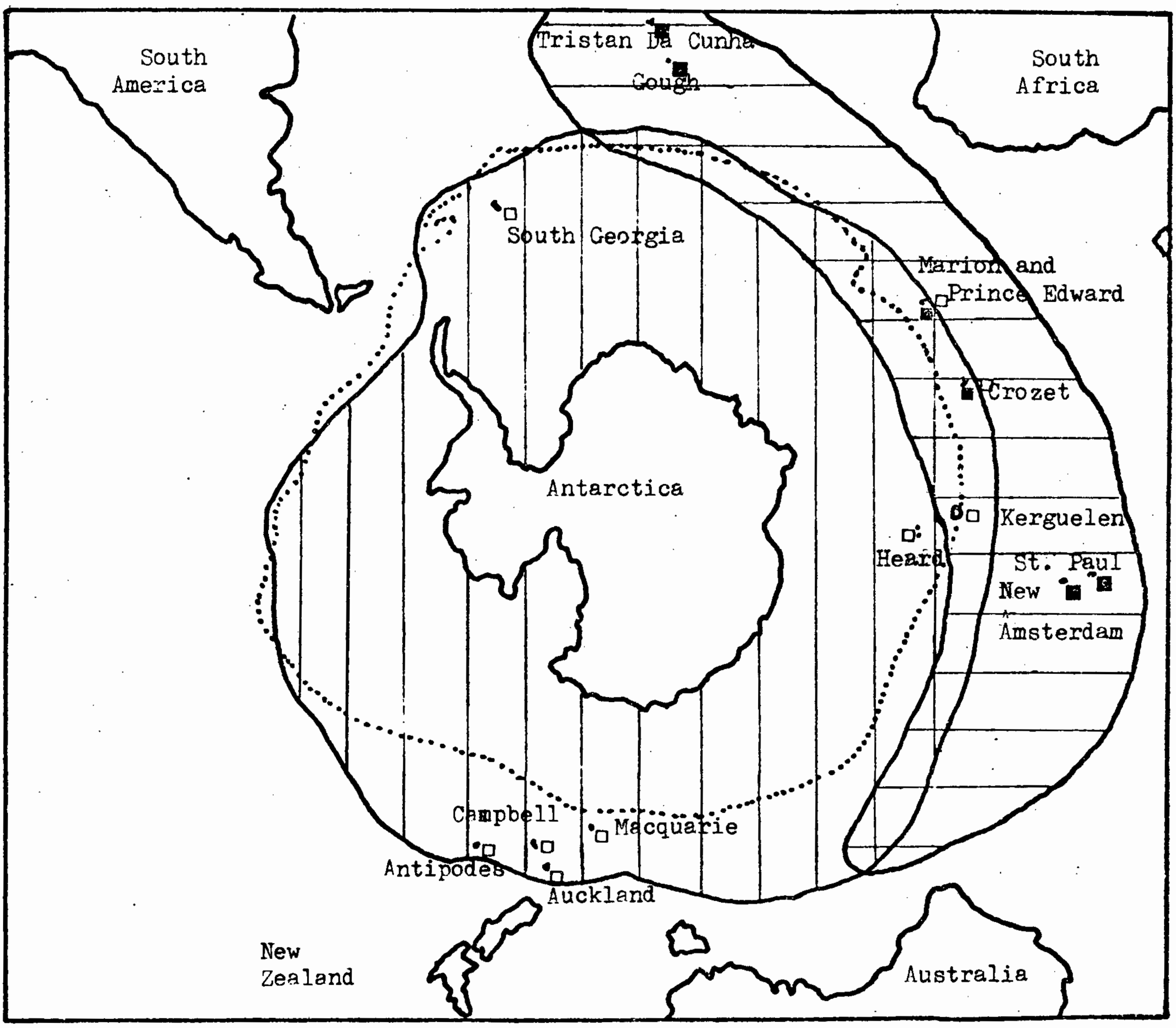


PLACE NAMES FOR FIG. 4

1. Meteorological base
2. Trypot
3. Macaroni Bay
4. Archway Bay
5. Hansen Point
6. Bullard Beach
7. Killerwhale Cove
8. Haglet Stream
9. Kildalkey Bay
10. Cape Hooker
11. Black Haglet Valley
12. Crawford Bay
13. Grey-headed Albatross Ridge
14. Goodhope Bay
15. Rooks Bay
16. Penguin City
17. Swartkop Point
18. Kampkoppie
19. Fur Seal Bay
20. Mixed Pickle Cove
21. Triegaardt Bay
22. Azorellakop
23. Cape Davis
24. Repetto's Hill
25. Prinsloomeer
26. Long Ridge
27. Ship's Cove
28. King Bird Head
29. Tafelberg
30. Piew Crags
31. Stony Ridge
32. Skua's Ridge

FIGURE 5

WORLD PELAGIC AND BREEDING DISTRIBUTION OF PHOEBETRIA FUSCA AND P. PALPEBRATA. ADAPTED FROM OZAWA (1967)



P. fusca breeding ■ pelagic (horizontal lines)

P. palpebrata breeding □ pelagic (vertical lines)

Antarctic Convergence ....

TABLE 13

BREEDING DISTRIBUTION AND NUMERICAL STATUS FOR <u>PHOEBETRIA FUSCA</u> AND <u>P. PALPEBRATA</u>

Locality	Co-ordinates	*P. fusca*	No. breeding pairs	*P. palpebrata*	No. breeding pairs	Source
Tristan da Cunha islands	37° 20'S 12° 45'W	X[1]	3 250	-[2]	0	Elliott (1957)
New Amsterdam Island	37° 47'S 77° 34'E	X	100	-	0	Segonzac (1972)
St. Paul Island	38° 42'S 77° 32'E	X	20	-	0	Segonzac (1972)
Gough Island	40° 15'S 10° 00'W	X	5 000	-	0	Swales (1965) and present study
Crozet islands	46° 25'S 51° 40'E	X	1 000+	X	?	Despin, *et al.*(1972) Segonzac (1972) Derenne *et al.* (1976)
Marion and Prince Edward islands	46° 50'S 37° 50'E	X	2 732	X	216	Present study
Kerguelen Island	49° 30'S 69° 30'E	-	0	X	thousands	Derenne *et al.*(1976)
Antipodes islands	49° 40'S 168° 45'E	-	0	X	?	
Auckland islands	50° 40'S 166° 10'E	-	0	X	5 000	Bell (1975)
Campbell Island	52° 33'S 169° 08'E	-	0	X	1 000+	Sorenson (1950)
Heard Island	53° 01'S 72° 23'E	-	0	X	200 - 500	Downes *et al.*(1959)
South Georgia	54° 00'S 38° 02'W	-	0	X	?	
Macquarie Island	54° 40'S 158° 50'E	-	0	X	500 - 700	Kerry (1972)

[1] X indicates presence of breeding population

[2] - indicates absence of breeding population

to allow for egg and pullus mortality, as this varied from colony to colony. Further, the proportion of hidden nests varied from colony to colony. Thus, estimated numbers of breeding pairs in each area are based on personal experience, usually involving two or more actual counts.

3.5.2 World breeding distribution

The distribution of the breeding grounds and the numerical status of Phoebetria breeding populations (where known) are given in Figure 5 and Table 13. It is virtually certain that all major breeding grounds of fusca and palpebrata have been found. The data for the Tristan da Cunha islands, Crozet islands and Gough Island warrant further discussion.

At the Tristan da Cunha islands, the fusca population has been reduced by the islanders through collection of eggs, pulli and adults. In 1816, when the islands were uninhabited, Carmichael (cited in Murphy 1936) counted more than 100 fusca nests in approximately 0,25 ha. In 1937-38 the largest number of nests found together at Inaccessible Island was four (Hagen 1952). Since the early 1950's, the collecting of eggs, pulli and adults has been controlled. Groups of up to 25 nests were recorded at Inaccessible Island by Elliott (1957), who suggested that the fusca population had increased since 1938. The present population at the Tristan da Cunha islands has presumably increased still further, because of stricter control of collection of eggs and pulli.

The breeding population of fusca for all islands in the Crozet group is not known, and data are available for Ile de L'Est (Despin, Mougin & Segonzac 1972), Ile de la Possession (Segonzac 1972) and Ile aux Couchons (Derenne, Mougin, Steinberg and Voisin 1976). The total breeding population of fusca could embrace at least 12 000 pairs. This is more than double the 5 000 pairs estimated by Segonzac (1972).

Different estimates for Gough, Marion and Prince Edward islands account for the large discrepancy in the total population estimate. Segonzac (1972) grossly underestimated the breeding population as 200 pairs at Marion Island, based on data in Rand (1954). The present study shows that the population is much larger (2732 pairs, see 3.5.1). Both Segonzac (1972) and I used Swale's (1965) information for the Gough Island population. My reason for estimating the Gough population as about 5 000 pairs, as opposed to 400 pairs by Segonzac, is based on my experience at Marion Island where I found it difficult to census breeding _fusca_ and _palpebrata_. The birds often nested on relatively inaccessible cliffs, and high mortality of eggs and pulli greatly decreased the number of occupied nests. These factors reduced the number of birds actually counted at Marion Island. It is probable that counts at other islands were similarly affected, and estimates of breeding populations at these islands should be viewed as conservative ones.

An estimate for the total breeding population of _palpebrata_ cannot be made, since potentially large and incompletely censused populations exist at Kerguelen, South Georgia, Antipodes and Crozet islands. The total breeding population at these four island groups is probably considerably more than the combined estimates given in Table 13.

Three _Diomedea_ species, _D. epomophora_, _D. exulans_ and _D. chrysostoma_ are known to breed biennially, if the pullus is successfully raised, or is lost late during the fledgling period (Tickell & Pinder 1967, Tickell 1968). However, if a breeding attempt fails during the incubation period, or early in the fledgling period, the pair will breed again the following season. Annual breeding has been reported in _D. immutabilis_ and _D. nigripes_ (Rice & Kenyon 1962), _D. melanophris_ (Tickell & Pinder 1967), _D. irrorata_ (Harris 1973) and _D. bulleri_ (Richdale & Warham 1973).

No data are available for _fusca_. Rice & Kenyon (1962) showed that although most _D. immutabilis_ adults breed every year, some birds did not.

Thus estimates of _fusca_ and _palpebrata_ populations, based on the number of nesting pairs, may be too low, as not all birds may nest every year.

The distribution of the islands used for breeding is clearly correlated with latitude. _Phoebetria fusca_ breeds mainly north of 45°S and _palpebrata_ mainly south of 45°S. However, both species breed sympatrically at Marion and Prince Edward islands, and at the Crozet islands. These islands are located between 46° and 47°S. The zone of sympatric breeding is therefore a narrow one.

3.5.3 World pelagic distribution.

The pelagic distributions of _fusca_ and _palpebrata_ are shown in Fig. 5. All records of _Phoebetria_ spp. in the northern hemisphere are rejected by Bourne (1967).

The pelagic distribution of _fusca_ is that of a temperate subantarctic species, concentrated in the southern Atlantic and Indian oceans between 30° and 50°S (Ozawa 1967). Serventy, _et al._ (1971) record fusca as "probably a fairly regular visitor to waters around Southern Australia, from Western Australia across the Bight to New South Wales (rarely) and Tasmania ..". The species has not been recorded on the Patagonian shelf area off the coast of Argentina, or off the coast of Chile (Jehl 1973, Brown, Cooke, Kinnear & Mills 1975). Two _fusca_ sightings are reported in the southern Pacific at 61°37'S 89°58'W (Holgersen 1957). The species has been recorded off Mauritius, between

19°50'S and 20°30'S (Watson, Zusi & Storer 1963). The type specimen was obtained in the Mozambique Channel (McLachlan & Liversidge 1970). However, individual birds probably wander regularly beyond the southern Atlantic and Indian oceans. There are no records of birds sighted visually, or recovered as beach-washed specimens, at New Zealand (based on sources given in Appendix 1).

Phoebetria fusca appears to range farther south in the austral summer, and to move to lower latitudes in the winter. Thus, it is recorded off South African coasts only in the winter (Liversidge 1959, McLachlan & Liversidge 1970).

Phoebetria palpebrata has a circumpolar distribution, and occurs at the edge of the Antarctic pack-ice. The species appears to be concentrated between 40 and 60°S, occurring regularly in the southern Pacific ocean (Ozawa 1967)and less regularly off the coasts of Argentina and Chile (Jehl 1973, Brown, et al. 1975).

In the austral summer, palpebrata has been recorded as far south as 77°50'S in the Ross Sea (Siple & Lindsay 1937). The whole pelagic range appears to shift farther north in winter, as the pack-ice edge moves north (Darby 1970, Hicks 1973). An analysis of sightings and beach-washed specimens recorded at New Zealand over the last 15 years indicates a northward extension of the pelagic range in winter (Table 14). Similarly, dated Australian specimens (Serventy, et al. 1971) were all obtained in the winter. It is possible that most of the Australasian winter specimens were juveniles in their first year at sea. The winter peak in mortality and sightings may reflect the inexperience and a tendency to wander in young birds during their first term at sea. A palpebrata pullus banded on 15 April 1969 at Ile de la Possession was recovered dead on 7 July 1970 at New Zealand (Barrat, Despin, Mougin, Prévost,

TABLE 14

NUMBER OF <u>PHOEBETRIA</u> <u>PALPEBRATA</u> SPECIMENS SIGHTED, OR RECORDED AS BEACH-WASHED SPECIMENS, AT NEW ZEALAND 1959 - 1974. BASED ON SOURCES IN APPENDIX 1

Month	J	F	M	A	M	J	J	A	S	O	N	D
No. birds	0	0	2	1	1	12	5	7	2	2	1	0

Segonzac & van Beveren 1971). To date, this is the only banding recovery for palpebrata.

Frost (unpublished) recorded hourly the numbers of fusca and palpebrata seen at sea during March-April 1976 in an area bounded by latitudes 21° - 49°S and 37° - 70°E which includes the Kerguelen, Crozet, Marion and Prince Edward islands. Phoebetria palpebrata occurred in numbers near these islands groups only, whereas fusca occurred in numbers throughout the area south of 40°S. The zone of overlap in pelagic distribution of fusca and palpebrata appears to lie in the southern Atlantic and Indian oceans between 40° and 50°S. The pelagic distributions do not conform rigidly to the zones of surface water temperature, but in general palpebrata occurs in regions of colder surface water than fusca (Fig. 5). Seasonal changes in the distribution may account for much of the reported overlap in the region 40° - 50°S. Pelagic ranges of fusca and palpebrata may be distinct at any given time.

3.6 Mass and linear dimensions

Table 15 presents mensural data for fusca and palpebrata. Phoebetria palpebrata is significantly heavier ($P<0,005$) and has a significantly longer wing ($P<0,001$), tarsometatarsus ($P<0,0125$) and tail ($P<0,05$) than fusca . However, fusca has a significantly longer culmen ($P<0,001$). Thus, palpebrata is a generally larger bird, but has a shorter culmen with a markedly concave culminicorn (Fig. 2).

3.7 Sexual size dimorphism

Five male fusca had significantly longer culmens ($P<0,005$), tails ($P<0,01$) and greater beak depths at the gonys ($P<0,001$) than four females (Table 16). All males, and three females, were sexed by

TABLE 15

MASS AND LINEAR DIMENSIONS OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA*, BASED ON LIVE BIRDS, CAPTURED AT MARION ISLAND, OCTOBER 1974 - MAY 1975

	P. fusca				*P. palpebrata*				Student's *t* test	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t value	significance
Mass (g)	2512	223,6	2100-3430	176	2823	344,4	2390-3250	6	3,29	P<0,005
Wing (mm)	516,5	12,9	490-551	101	541,8	17,4	508-559	7	4,90	P<0,001
Tail (mm)	265,5	10,6	245-294	118	279,0	4,3	274-282	3	2,19	P<0,05
Tarsometatarsus (mm)	82,7	2,3	77,5-90,0	212	84,4	2,2	81-88,7	10	2,29	P<0,0125
Culmen length (mm)	112,1	3,5	99,9-120,2	212	106,5	3,8	103,3-111,1	10	4,92	P<0,001
Beak depth at gonys (mm)	27,0	1,0	24,7-29,8	198	26,9	0,9	25,6-29,2	9	0,29	NS

TABLE 16

MASS AND LINEAR DIMENSIONS OF FIVE MALE AND FOUR FEMALE <u>PHOEBETRIA</u> <u>FUSCA</u> FROM MARION ISLAND

	Male				Female				Student's *t* tests	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t value	probability
Mass (kg)	2,56	0,2	2,30-2,75	5	2,38	0,2	2,31-2,63	4	1,34	N.S.
Wing (mm)	526,5	-	522-531	2	508,5	-	508-509	2	-	-
Tail (mm)	275,0	4,5	269-280	5	249,5	0,8	267-245	4	3,58	P<0,01
Tarsometatarsus (mm)	83,0	2,0	81,2-86,0	5	81,3	2,2	79,1-83,7	4	1,21	N.S.
Culmen length (mm)	114,9	1,8	112,4-116,5	5	109,9	1,0	108,5-110,5	4	4,93	P<0,005
Beak depth at gonys (mm)	28,4	0,4	28,1-29,0	5	26,2	0,8	25,3-26,9	4	5,42	P<0,001

examination of the sexual organs of collected specimens. The other female (measured during banding procedures, and subsequently identified by the colour bands) was the mate of a collected male which was sexed by examination of the sexual organs. This pair was captured while feeding a pullus.

A scatter graph of culmen length versus beak depth at the gonys of 198 unsexed and nine sexed _fusca_ shows a seperation of the sexes (Fig. 6). A discriminant analysis of the measurements of 203 unsexed and nine sexed birds was unsuccessful in separating the sexes. Complete separation of the sexes may be possible with a larger sample of positively sexed birds.

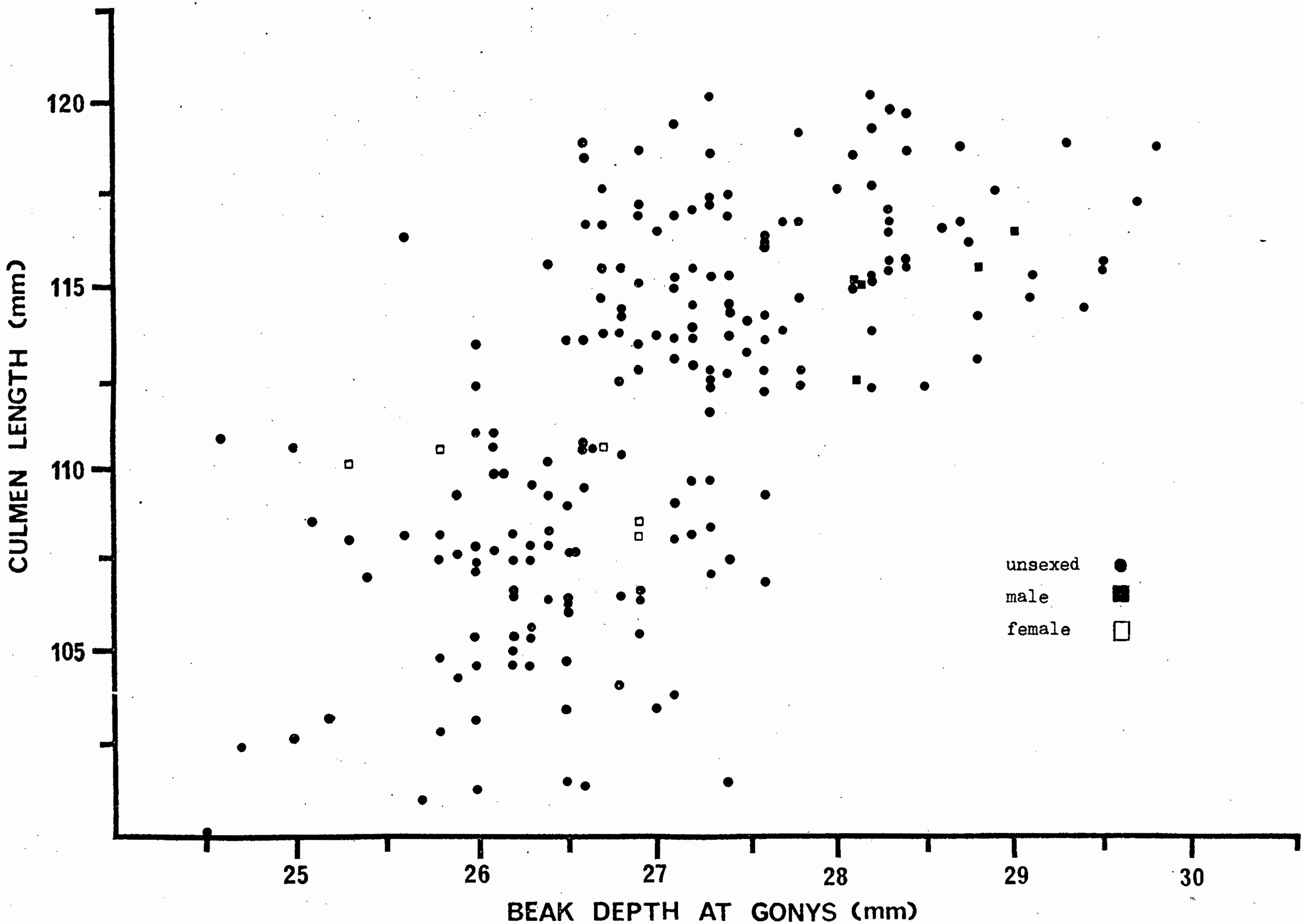
Males are significantly larger than females in _D. exulans_ (Tickell 1968), _D. nigripes_ and _D. immutabilis_ (Frings & Frings 1961) and in _D. irrorata_ (Harris 1973). Males tended to be larger than females in _D. chrysostoma_ and _D. melanophris_, but the only significant difference found was that male _melanophris_ were heavier than females (Tickell & Pinder 1975). However, the ratio of culmen length to beak depth provided good separation of the sexes in _D. melanophris_ (Tickell & Pinder 1975). Falla (1937) stated that male _palpebrata_ 'appeared' larger than females when observed together, and Serventy _et al._ (1971) stated that males are slightly larger than females.

3.8 Moult

Only one instance of active replacement of remige or rectrix feathers was found in the 212 adult and subadult _fusca_ examined. One of the central pair of rectrices of a presumed subadult bird captured on 25 March 1975, was two-thirds grown. This may have been the replacement of an accidentally lost feather. No other rectrix was

FIGURE 6

DIMORPHISM IN BEAK SHAPE OF 189 UNSEXED AND NINE SEXED PHOEBETRIA FUSCA AT MARION ISLAND



being replaced, or had been moulted. No active feather replacement was seen in the remiges and rectrices of free-flying fusca at the breeding cliffs. By comparison, active feather replacement and loss was clearly observed in similarly-sized Macronectes on the wing.

No active feather replacement was found in the 10 adult and sub-adult palpebrata examined. However, on 16 March 1975 I observed a trailing central rectrix feather in a flying bird. This may have been the beginning of moult in this individual.

The replacement of remige and rectrix feathers must take place during the pelagic stages of the life cycle in both species.

In D. irrorata some primaries are retained for two years, and occasionally three years, but none of the outermost four primaries are retained for longer than one year (Harris 1973). Harris (1973) suggested that the general pattern of rectrix moult in the Diomedeidae is by a wave, or waves of moult, progressing from the proximal to the distal primaries, starting from one or two centres. I found it difficult to evaluate the degree of feather wear in examining the primaries of six adult and subadult fusca. My impressions agree with the suggestions of Harris (1973) in that there appeared to be two moult centres, and that the outermost four primaries are replaced annually, while a few inner primaries appeared to be older than a year.

General wear on plumage increases as the season progresses. The plumage becomes paler and browner, and an increasing number of feathers develops the buffy edges characteristic of worn plumage, especially on the forehead, crown, mantle and breast. The occasional contour feather was extremely abraded and is probably retained for longer than a year. The incidence of broken outermost primaries in fusca increases as the season progresses (Table 17).

TABLE 17

INCIDENCE OF BROKEN TIPS OF THE OUTERMOST (TENTH) PRIMARY FEATHER IN ADULT AND SUBADULT *PHOEBETRIA FUSCA* AT MARION ISLAND, OCTOBER 1974 - MAY 1975

	Month							
	O	N	D	J	F	M	A	M
% Broken tips	20	21	38	31	71	97	100	88
No. birds examined	56	28	26	16	32	32	14	8

The moult of the down feathers of the single brood patch in <u>fusca</u> is associated specifically with incubation, and occurs independently of general down and contour feather replacement. I do not know when the brood-patch down feathers in either adult or subadult <u>fusca</u> are lost. Brood-patch down feather replacement of breeding birds had begun by the end of December, and was virtually completed by April. In presumed subadult birds, brood-patch down feather replacement was more irregular (Table 18) and active replacement was recorded in all months from October 1974 to May 1975.

Four specimens of <u>fusca</u> were examined for down and contour feather replacement over the entire body surface. A bird (presumed subadult) collected on 15 October 1974 showed slight replacement of down and contour feathers. Two birds collected on 27 January and 25 February 1975 respectively, showed active down feather replacement in the brood patch only, and no active contour feather replacement. An adult bird collected on 23 May 1975 showed moderate active down feather replacement and slight active contour feather replacement. It appears likely that in adult and subadult <u>fusca</u> moult of down and contour feathers spans the period of remige and rectrix moult, and may begin and end while the bird is present on the breeding cliffs.

Harris (1973) found that <u>D. irrorata</u> does not moult during the breeding period. Further, he stated that no Diomedeidae species moults rectrix or remige feathers during the breeding period, basing this statement on the study of museum skins of seven Diomedeidae species. However, moult apparently occurs in <u>D. melanophris</u> during the breeding season, as moulted feathers are found at the nest sites (Tickell & Pinder 1975). In <u>fusca</u> and <u>palpebrata</u> most feather replacement takes place at sea. Contour and down feather moult apparently begins at the

TABLE 18

INCIDENCE OF BARE (DEVOID OF DOWN FEATHERS) BROOD PATCHES IN PRESUMED SUBADULT PHOEBETRIA FUSCA AT MARION ISLAND, OCTOBER 1974 - MAY 1975

	Month							
	O	N	D	J	F	M	A	M
% Bare brood patches	49	43	71	25	10	0	0	0
No. birds examined	41	21	14	12	29	30	13	4

end of one breeding period and is completed at the beginning of the following breeding period.

4 Breeding Biology

4.1 Introduction

The breeding biology of the Procellariiformes shows several unusual characteristics which have been summarized by Lack (1968). The clutch size is one, and egg replacement occurs very rarely. The egg is proportionately larger, and the incubation and fledgling periods proportionately longer, than in most avian families. Pullus growth is slow. Pulli have to survive intermittent fasts, as successive feeds may be separated by intervals of several days. The pulli lay down large fat deposits, and attain peak masses 11 - 88% greater than adult masses. Pullus mortality through starvation may be high, whilst adult mortalities are low. Annual mortality rates for four Diomedea spp. range from 3 - 11% (Richdale 1952, Tickell 1968, Richdale & Warham 1973, Harris 1973. Breeding is generally restricted to scattered oceanic islands. Diomedea epomophora, which has a small breeding colony on the New Zealand mainland (Richdale 1952), is the only member of the family known to breed on a large land mass.

The breeding biology of the Diomedea species is well known, but that of Phoebetria is poorly documented. Phoebetria, like all Diomedeidae, is monogamous.

4.2. Methods

I studied the breeding biology of fusca in three nesting colonies at Marion Island, designated A, B and C. The colonies were situated at Macaroni Bay (Fig. 7). I began daily visits to colonies A and B on 8 October, and colony C on 10 October 1974 respectively. The nests of colonies A and C were situated on vegetated ledges of vertical and near-vertical slopes 10 - 20 m above sea level. Dominant plants were the grasses Poa cookii, P. annua and Agrostis magellanica. The nests of colony B were situated on the steeply sloping gradients of a semi-circular inlet which terminated in a sheer 5 m drop to the sea. All nests in colonies B and C were accessible to observers, but 12 nests in colony A were inaccessible. Egg-laying had begun before I started daily visits. Ninety-five nests and potential nest sites were marked individually with numbered wooden stakes, driven into the ground next to the nests. The 12 inaccessible nests were not marked.

Three palpebrata nests were marked on 23 October, when two contained eggs. A fourth nest containing an egg was marked on 28 October. Figure 7 shows the sites of these four nests and a fifth inaccessible palpebrata nest in Colony A.

All marked nests of both species were visited daily during the incubation and brooding periods, to determine incubation and brooding periods, and to monitor egg and pullus mortality. A pole was held behind the sitting adult bird's head to prevent attacks on the handler, while checking for the presence of eggs or pulli. Adults rarely left their nests during the observer's visits, and when they did leave, they invariably returned within 10 minutes after the observer had departed.

Twenty fusca adults from sixteen pairs nesting at Colony B, and six palpebrata adults of three nesting pairs were marked with red paint on the head or breast. Because most of the paint-marked feathers were removed during allopreening (Section 6), the birds were re-marked on the central rectrices. In neither species were birds observed to preen rectrix feathers.

Phoebetria fusca and palpebrata pulli were weighed daily from time of hatching until they were 110 - 117 and 90 - 100 days old respectively.

Thereafter, pulli were weighed at intervals of 1 - 4 days. Pulli initially were weighed in plastic bags using hand-held 300 g and 1 kg Pesola balances. Subsequently pulli were weighed in cloth bags with a hand-held 5 kg Pesola balance. The bags were weighed frequently in order to check and compensate for any mass of absorbed water. Pulli occasionally regurgitated stomach contents when handled, especially at the end of the brooding period. However, pulli habituated to regular handling and regurgitation occurred very seldom. Linear dimensions of fusca and palpebrata pulli were measured every second day during their first 3 and 6 weeks respectively. Thereafter, fusca and palpebrata pulli were measured every 4 - 5 and 3 - 4 days respectively. The following linear dimensions were taken: tarsometatarsus, culmen and wing. The wing was measured to the tip of the outermost primary, and measurements thus were made only after the outermost primary feather had emerged. Strong winds, low temperatures and frequent precipitation increased the difficulty of measuring pulli and recording data at nest sites on cliffs where, in addition, space is at a premium. Natural mortality reduced the number of measured fusca pulli from 22 to nine, and palpebrata pulli from three to two (see 4.6).

The growth data for nine fusca were averaged over five-day periods. (growth data from two pulli which were depredated when aged 128 and 134 days respectively were included). Growth data (except mass) for palpebrata pulli were averaged over five-day periods, and over 10-day periods when growth increments were small, i.e., when growth was nearing completion. Mass data for palpebrata pulli were averaged over 10-day periods because masses were highly variable, and the number of measured pulli was small.

While the fledging dates of some fusca pulli were noted, I left the island before all fusca pulli, and any of the palpebrata pulli, had fledged. Additional data on time of fledging, adult arrival, egg laying and incubation periods were provided by A. Burger, J. Mendelsohn and A.J. Williams during 1974 - 77.

4.3 Pre-egg period

4.3.1 Arrival of adult birds

In <u>fusca</u>, the annual arrival of adult birds at Marion Island occurs in late August. The first arrivals were recorded on 22 August 1974 (A. Burger pers. comm.), 25 August 1975 (J. Mendelsohn pers. comm.) and 15 August 1976 (A.J. Williams pers. comm.). In <u>palpebrata</u>, adults begin to arrive in early October. In 1974 the first arrivals were recorded on 4 October and in 1975 on 9 October (J. Mendelsohn pers. comm.).

In both species, the arrival times of adults breeding at some other islands are apparently similar to those observed at Marion Island, with two exceptions (Table 19A & B). In <u>fusca</u>, adults arrive at Tristan da Cunha over a month earlier than at Marion Island, but egg-laying commences only two weeks earlier at Tristan da Cunha (Elliott 1957). In <u>palpebrata</u>, adults arrive at the Crozet islands two weeks earlier than elsewhere (Mougin 1970).

4.4 Egg period

4.4.1 Egg-laying

The initial period of egg-laying was not observed for <u>fusca</u> in 1974. Eggs were found at colonies A and B at first inspection on 8 October 1974 and at colony C on 10 October 1974. The numbers of eggs present at first inspection and laid subsequently between daily checks are shown, as cumulative percentages, in Figure 8. Egg-laying was completed on 14 October 1974. The first <u>fusca</u> eggs in 1975 were recorded on 14

TABLE 19A

INITIATION OF BREEDING CYCLE OF PHOEBETRIA FUSCA AT VARIOUS LOCALITIES

	Arrival	Egg-laying	Hatching	Fledging	Source
Tristan da Cunha islands	Mid-July	Mid-Sept.	Mid-Dec.	Mid-May	Elliott (1957)
New Amsterdam Island			Mid-Dec.		Segonzac (1972)
St. Paul Island			Mid-Dec.		Segonzac (1972)
Gough Island	Late Aug.	Mid-Sept.	Early Dec.	Mid-May	Swales (1965)
Crozet islands		Early Oct.	Mid-Dec.	May	Mougin (1970)
Marion Island		Late Oct.	Mid-Dec.	April	Rand (1954)
Marion Island	Late Aug.	Early Oct.	Mid-Dec.	Late May	Present study

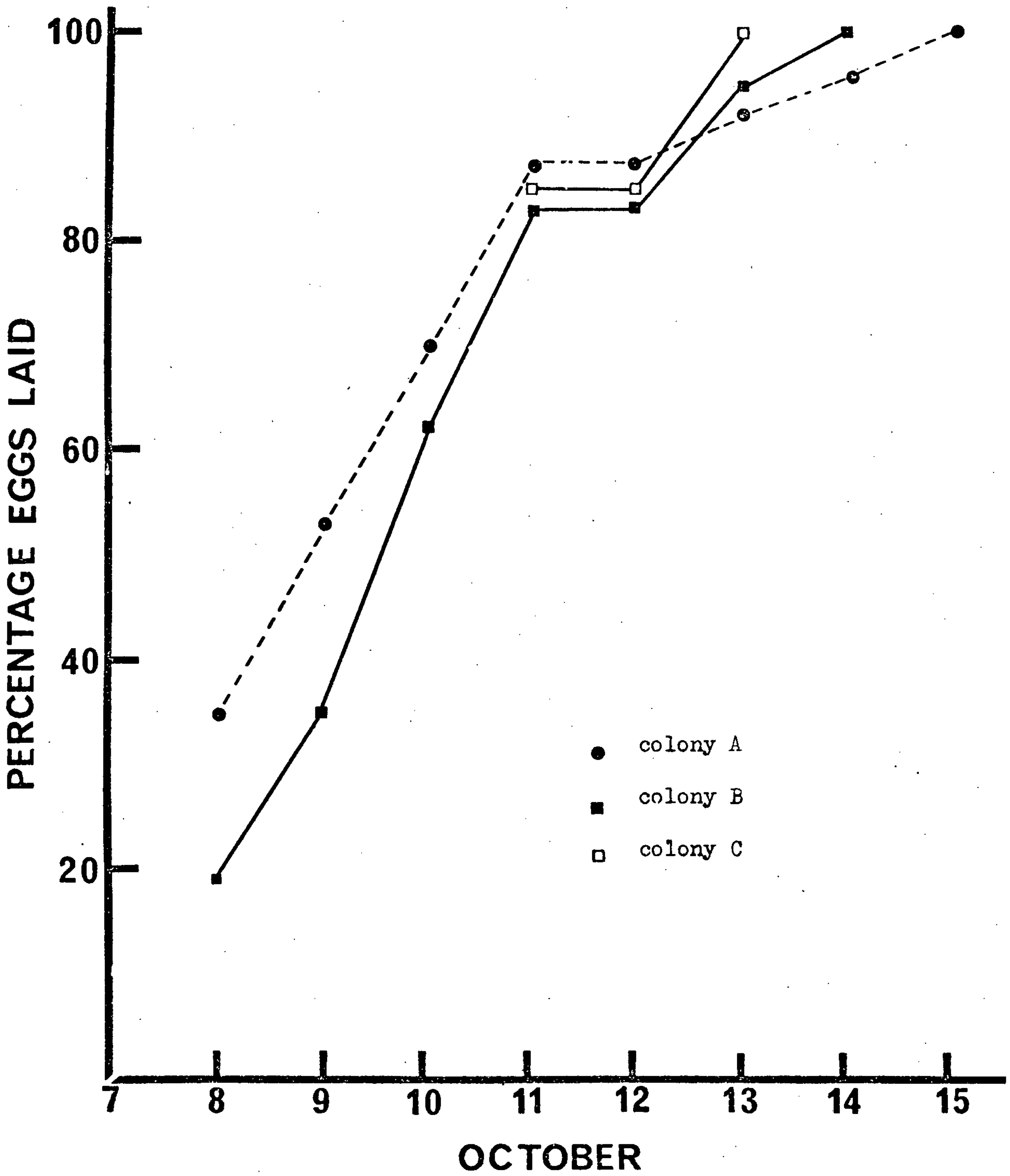
TABLE 19B

INITIATION OF BREEDING CYCLE OF *P. PALPEBRATA* AT VARIOUS LOCALITIES

	Arrival	Egg-laying	Hatching	Fledging	Source
Crozet islands	Mid-Sept.	Late Oct.	Late Dec.	Late May	Mougin (1970)
Marion Island	Early Oct.	Late Oct.	Early Jan.	Mid-June	Present study
Kerguelen island		Late Oct.	Late Dec.	Early June	Paulian (1953)
Campbell Island	Early Oct.	Late Oct.	Early Jan.	Late May	Sorenson (1950)
Heard Island	Early Oct.	Late Oct.	Early Jan.	Late May	Downes *et al.* (1959)
Macquarie Island	Oct.	Late Oct.	Early Jan.	Late May	Falla (1937)

FIGURE 8

CUMULATIVE PERCENTAGE OF EGGS LAID AT THREE *Phoebetria fusca* COLONIES AT MARION ISLAND, OCTOBER 1974



October (J. Mendelsohn pers. comm.). Thus, in 1975 apparently egg-laying started about two weeks later than in 1974. Onset of egg-laying in fusca at breeding stations other than Marion Island occurs during September-October (Table 19A). The egg-laying period (late October - early November) recorded by Rand (1954) for fusca at Marion Island appears to be incorrect. Rand reports pulli in mid-December, which means that egg-laying must have occurred in early October, since the incubation period is 69 - 73 days (Table 22).

At Marion Island, in 1974, the laying dates for two palpebrata eggs were determined as 25 and 30 October respectively. A third egg was laid between 19 and 23 October. In 1976, two eggs were laid within a day of 25 October, and a third between 25 and 30 October (A. Burger pers. comm.). In 1975, the two earliest eggs were found on 14 and 23 October respectively (J. Mendelsohn pers. comm.). At other breeding grounds onset of egg-laying in palpebrata occurs at the same time of the year as at Marion Island (Table 19B).

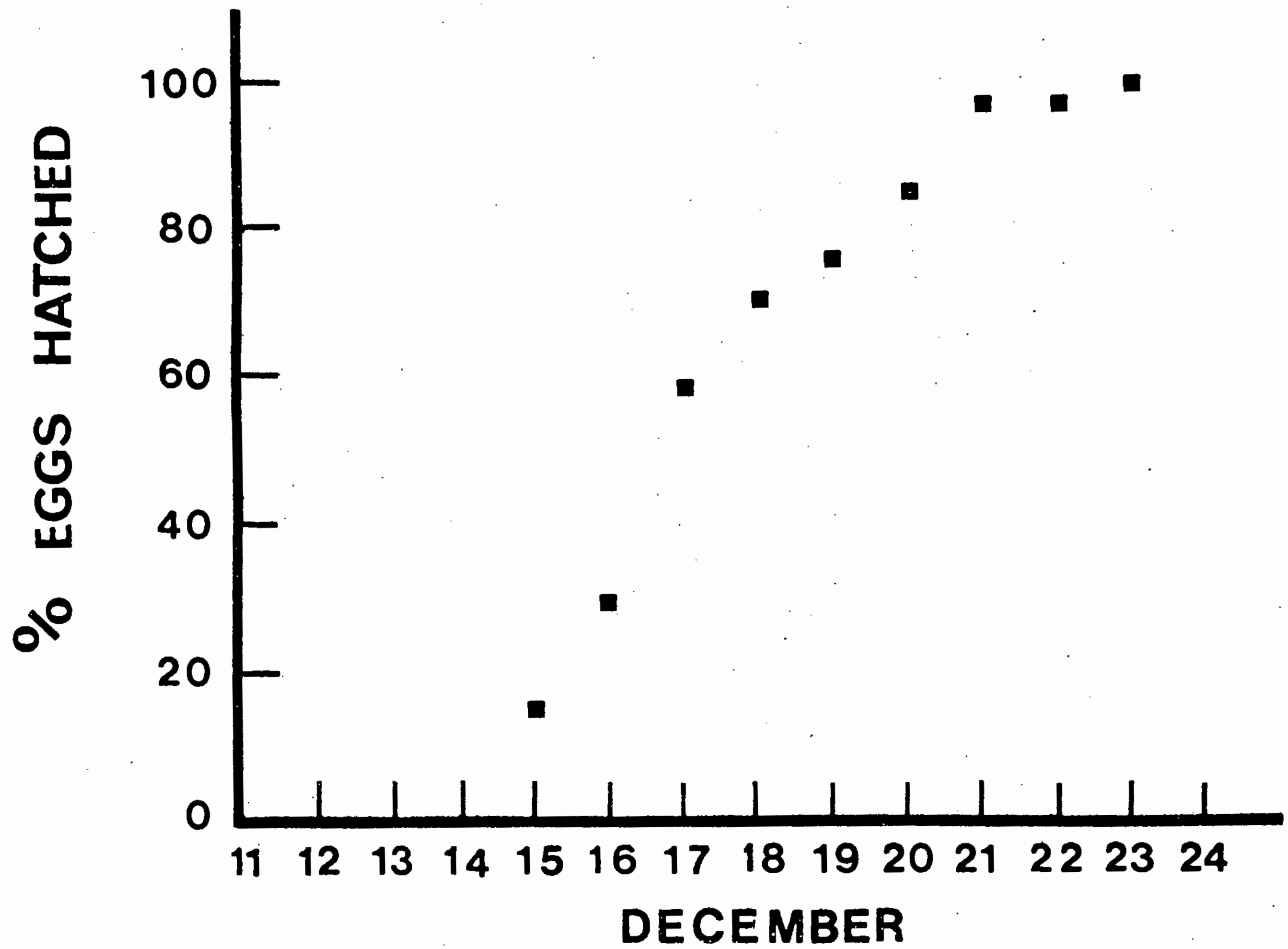
The period over which fusca eggs hatched at Marion Island in 1974 is shown in Figure 9. Hatching was restricted to 13-24 December, reflecting the highly synchronised temporal pattern of egg-laying. Four palpebrata eggs hatched during 1-4 January 1975.

4.4.2 Clutch size and egg-replacement

Only single eggs were found in 100 fusca nests and 22 palpebrata nests. A single-egg clutch is normal for all members of the Procellariiformes (Lack 1968). Replacement of eggs which are lost does not occur in fusca and palpebrata, and in this respect the two species again conform with all other members of the Procellariiformes (Lack 1968).

FIGURE 9

CUMULATIVE PERCENTAGE OF HATCHED EGGS OF <u>PHOEBETRIA</u> <u>FUSCA</u> AT MARION ISLAND, DECEMBER 1974



4.4.3 Egg mass and linear dimensions

At Marion Island, the egg of palpebrata is significantly heavier ($P<0,01$) and broader ($P<0,005$) than that of fusca (Table 20). There is no significant difference in egg length. The eggs of fusca and palpebrata represent 9,6 and 9,1% of adult mass respectively. Egg mass as a percentage of adult mass in eight Diomedea species ranges from 5,3 - 11,3% (Lack 1968, Richdale & Warham 1973, Harris 1973, Tickell & Pinder 1975).

I used Sorension's (1950) data to show that palpebrata eggs at Campbell Island are significantly lighter in mass than Marion Island eggs (Table 21). However, the Campbell Island eggs were weighed up to 10 days after having been laid. The lighter mass may be attributed partly to weight loss during incubation, since there was no significant difference in length or breadth of eggs from Campbell and Marion islands (Table 21).

4.4.4 Incubation period

The incubation period was determined for fusca and palpebrata eggs in respect to the period prior to pipping (termed pre-pip) and the period between pipping and actual hatching (termed pipped). The complete incubation period of 16 fusca eggs was significantly longer ($P<0,01$) than that of three palpebrata eggs. (Table 22). However, it must be noted that a palpebrata egg which hatched successfully was incubated for at least 72 days. The incubation period for palpebrata eggs has been reported variously as 63-67 days at Campbell Island (Sorenson 1950) and 68-70 days at the Crozet islands (Mougin 1970). The incubation period for fusca eggs has not been recorded previously.

In the Diomedeidae male and female parents alternate in incubating

TABLE 20

MASS AND LINEAR DIMENSIONS OF *PHOEBETRIA PALPEBRATA* AND *P. FUSCA* EGGS AT MARION ISLAND

	P. fusca [1]				*P. palpebrata*				Student's t Test	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t Value	Probability
Length (mm)	103,0	3,1	96,0-11,7	67	102,3	2,8	98,3-106,4	17	0,79	NS
Breadth (mm)	65,1	1,8	59,3-68,7	67	66,7	2,3	62,7-70,0	17	2,91	P<0,005
Mass (g)	243,5	14,1	204-270	31	258,2	15,3	234-280	10	2,79	P<0,01

[1] One egg measuring 65,0 x 49,1 mm, weighing 89g, was not included

TABLE 21

MASS AND LINEAR DIMENSIONS OF *PHOEBETRIA PALPEBRATA* EGGS AT MARION ISLAND AND CAMPBELL ISLAND (SORENSON 1950)

	Marion Island				Campbell Island[1]				Student's t Test	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t Value	Probability
Length (mm)	102,3	2,8	98,2-106,4	17	102,4	3,2	98-107	6	0,07	NS
Breadth (mm)	66,7	2,3	62,1-70,0	17	65,2	1,4	63-67	6	1,09	NS
Mass (g)	258,2	15,3	234-280	17	223,2	11,7	212-219	6	3,62	$P<0,005$

[1] One egg measuring 99 x 58 mm, weighing 170g, was not included

TABLE 22

INCUBATION PERIOD (DAYS) OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* EGGS AT MARION ISLAND

	P. palpebrata				*P. fusca*				Student's t Test	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t value	Probability
Pre-pip period	63,5	-	63-64	2	66,3	1,2	63-68	16	-	-
Pipped period	4	0	4	4	4,2	0,9	3-6	28	0,438	NS
Incubation period	66,6	1,5	65-68[1]	3	70,1	1,8	69-73	15	3,129	P<0,01

[1] A third egg, which hatched successfully, was incubated for at least 72 days, but is not included here because the date on which it was laid was not determined.

the egg which is covered continuously. The female, immediately after laying the egg, undertakes the first and all subsequent odd-numbered incubation shifts; the male undertakes all the even-numbered shifts (Richdale 1952, Rice & Kenyon 1962, Tickell 1968, Harris 1973, Mougin 1970, Tickell & Pinder 1975). The male, if present, may begin incubation immediately after the egg is laid (Harris 1973). This strategy has been reported for palpebrata (Mougin 1970). Complete incubation shifts were recorded for eight pairs of fusca and three pairs of palpebrata whose eggs hatched successfully, and for three pairs of fusca whose eggs failed to hatch (Tables 23 & 24). Both parents continued to incubate infertile and addled eggs well beyond the normal incubation period (Table 23). In successful parents of both species, shifts were fewer in palpebrata than in fusca (Table 25), but only the second and fifth shifts were significantly different ($P<0,001$ and $P<0,05$ respectively) in duration between the species (Table 23 & 24). However, incre·sed s·mple sizes will probably show significant differences in ·ll shifts between the species.

In fusca, the fem·le spent more time on the egg than the male (Table 26), but the difference is not significant. Since the mode number of incubation shifts is seven (Table 25), the female normally undertakes four incubation shifts to the male's three. The share of the sexes in incubation is not given for palpebrata, because complete incubation shifts were determined only for one palpebrata pair. However, the data suggest that in palpebrata, the male may spend more time on the egg than the female.

4.5 Pullus period

4.5.1 Brooding period

TABLE 23

AVERAGE DURATION (IN DAYS) OF PARENTAL INCUBATION SHIFTS IN

PHOEBETRIA FUSCA AT MARION ISLAND

Incubation shift no.	Sex of parent	Hatched successfully			Failed to hatch		
		Mean	Range	N	Mean	Range	N
1	F	6,6	3-10	5	5,7	1-8	3
2	M	12,8	9-17	8	10,6	9-13	3
3	F	14,4	11-17	8	13,3	10-15	3
4	M	12,8	9-16	8	14,3	10-17	3
5	F	11,6	8-13	8	11,0	10-12	3
6	M	7,4	5-10	8	9,7	8-13	3
7	F	4,5	3-8	6	4,0	1-7	3
8	M	3,0	2-4	2	3,0	2-5	3
9	F	3,0		1	2,0	1-3	3
10	M				3,7	2-5	3
					3,5	3-4	2
					3,0		1

TABLE 24

AVERAGE DURATION (IN DAYS) OF PARENTAL INCUBATION SHIFTS IN *PHOEBETRIA PALPEBRATA* AT MARION ISLAND, AND AT THE CROZET ISLANDS (MOUGIN 1970)

Incubation shift no.	Sex of parent	Marion Island			Crozet islands		
		Mean	Range	N	Mean	Range	N
1	F	13,0		1	3,7	1-8	3
2	M	24,3	19-29	3	9,3	9-10	3
3	F	16,3	13-22	3	15,3	12-19	3
4	M	12,6	10-16	3	17,7	17-19	3
5	F	5,0	1-10	3	13,7	10-17	3
6	M	4,0		1	14,0	12-17	3
7	F				7,0		1

TABLE 25

NUMBER OF INCUBATION SHIFTS UNDERTAKEN BY PARENTS IN *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND

No. of incubation shifts undertaken by parents	*P. fusca* clutches		*P. palpebrata* clutches
	Successful	Unsuccessful[1]	Successful
4			
5			2
6	2		1
7	4		
8	1		
9	1		
10		1	
11		1	
12		1	

[1] Failed to hatch within the normal incubation period.

TABLE 26

THE SHARE OF THE SEXES IN SUCCESSFUL INCUBATION IN *PHOEBETRIA FUSCA* AT MARION ISLAND

	Male	Female
Mean (days) [1]	33,4	37,4
S.D.	3,2	3,9
Range	28-36	32-42
N	7	7

[1] Difference significant at P<0,1

The brooding period is defined as the period between hatching (when the pullus is completely free of the eggshell) and when the pullus is first left alone by the parents. A parent will sometimes return to brood for one to two days after the pullus has first been left alone.

There was no significant difference in the duration of the brooding phase recorded for 23 fusca and four palpebrata pulli at Marion Island (Table 27). The duration of the brooding shifts in six pairs of fusca and three pairs of palpebrata is shown in Table 28. Phoebetria palpebrata apparently has fewer brooding shifts, of longer duration, than fusca. However, this conclusion is tentative, because data for both species are meagre. In fusca, the sexes apparently share brooding approximately equally, as both partners undertake many short brooding shifts (Table 28 & 29). In palpebrata, the female brooded for significantly longer ($P<0,05$) than the male (Table 28 & 29). The difference between the two species appears to be accounted for by the long first shift in palpebrata, apparently usually undertaken by the female. However, in one of the three palpebrata pairs brooding was shared equally by the sexes.

As the mode number of incubation shifts is odd in both species (Table 25), the female is usually present at hatching. For fusca, the female was present at hatching in six out of eight clutches. For palpebrata, the female was present at two out of three clutches.

4.5.2 Fledgling period

The duration of the fledgling period was determined for six fusca pulli as 149, 156, 159, 169, 162-166 and 160-164 days respectively. One palpebrata pullus fledged 170-175 days after hatching. Fledgling periods of 133-140 days have been reported for palpebrata at Campbell

TABLE 27

BROODING PERIOD OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND

	P. fusca	*P. palpebrata*
Mean (days)[1]	21,0	19,5
S.D.	±2,1	±1,3
Range	17-28	18-21
N	23	4

[1] Difference not significant

TABLE 28

AVERAGE DURATION (DAYS) OF PARENTAL BROODING SHIFTS IN *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND

Brooding shift no.	*P. fusca*			*P. palpebrata*		
	Mean	Range	N	Mean	Range	N
1	2,5	1-3	6	5,3	4-7	3
2	2,3	2-4	6	2,6	2-4	3
3	1,8	1-3	6	3,3	2-6	3
4	2,0	1-3	6	2,3	2-3	3
5	1,8	1-3	6	2,3	1-5	3
6	1,8	1-2	6	2,0	1-3	2
7	2,2	1-3	5	2,5	2-3	2
8	1,8	1-3	4	2,0		1
9	2,0	2	3	2,0		1
10	1,5	1-2	2	1,0		1
11	1,0		1			

TABLE 29

THE SHARE OF THE SEXES IN BROODING IN PHOEBETRIA FUSCA AND P. PALPEBRATA AT MARION ISLAND

	P. fusca		P. palpebrata	
	Male	Female	Male	Female
Mean (days)	10,0	11,5	7,3	12,7[1]
S.D.	-	-	3,1	2,5
Range	9-11	11-12	6-9	9-14
N	2	2	3	3

[1] Difference significant at $P<0,1$

Island (Sorenson 1950), and at least 150 days at the Crozet islands (Mougin 1970). For both species, the dates of hatching and fledging recorded at several breeding stations (Table 19) suggest that fledgling periods of about 160 days are normal at Marion Island.

4.6 Breeding success

Breeding success is computed by the equation:

$$\frac{\text{Total no. chicks fledged}}{\text{Total no. eggs laid}} \times \frac{100}{1}$$

In 1974, in the study colonies A, B and C only 13% of _fusca_ eggs (_n_ = 61) produced flying young (Table 30). In 1975, in the same colonies, 25% of _fusca_ eggs (_n_ = 36) produced flying young (A.Burger pers. comm.). However, breeding success in other _fusca_ colonies at Marion Island in 1974 apparently was higher, as proportionately fewer empty nests were observed there during the second half of the fledgling period. For _palpebrata_, 16 eggs produced five flying young. According to Mougin (1970), breeding success was 51% for _palpebrata_ at the Crozet islands. Since only four nests were observed regularly, details regarding loss of eggs and pulli are not known for _palpebrata_ at Marion Island.

For _fusca_, mortality of eggs and pulli in the three study colonies was relatively high during the incubation period and in the three weeks following hatching. Forty-three per cent of all eggs laid were lost in 1974 (Table 30). J. Mendelsohn counted all eggs in the three _fusca_ colonies on 26 October and 12 December 1975. Egg loss over the 47-day period was 36% (13 out of 36 eggs laid.) Egg losses of 28% have been recorded for _Diomedea exulans_ at South Georgia (Tickell 1968) and 29% for _palpebrata_ at the Crozet islands (Mougin 1970). In 1974, at

TABLE 30

BREEDING SUCCESS AND MORTALITY IN <u>PHOEBETRIA</u> <u>FUSCA</u> AT MARION ISLAND DURING THE SUMMER OF 1974 - 1975

No. Eggs	
Laid	61
Infertile	6
Lost due to unknown causes	20
No. pulli	
Hatched	35
Dead due to starvation and/or disease	5
Killed by predators (presumably Giant petrels)	18
Lost due to collapse and destruction of nest	2
Lost due to abandonment by parents (possibly induced by humans)	2
No. pulli fledged	8

least 10% of *fusca* eggs were found to be infertile at Marion Island. This incidence of infertility is similar to what has been found in other albatrosses: 7% for *D. exulans* at South Georgia (Tickell 1968); 3% for *D. epomophora* at Campbell Island (Westerkov 1963); and, 9% for *palpebrata* at the Crozet islands (Mougin 1970).

Although I was unable to determine all the causes of egg losses in *fusca* and *palpebrata* breeding at Marion Island, I believe that the Giant Petrels, *Macronectes* spp., played an important role in depressing breeding success. I have only indirect evidence in support of this, since I did not observe Giant Petrels actually killing albatross chicks. However in 1976, several killed a *fusca* fledgling (A. Burger pers. comm.). Giant Petrels have previously been suspected as predators of albatross pulli, having been observed feeding on freshly killed chicks of *D. cauta* at the Snares islands (Horning & Horning 1974).

At Marion Island, single Giant Petrels (species not identified) were observed either in the *fusca* breeding colonies or on their borders on four occasions. Pulli of *fusca* were found to have been killed by a predator either preceding or following each of the four sightings of Giant Petrels. Depredated pulli varied between six and 134 days of age, and weighed between 300 and 3000 g. Several pulli had been killed while being brooded, and up to five pulli were killed at a time.

Apart from Giant Petrels, other potential predators are the House Cats *Felis domesticus* and the Skua *Stercorarius skua*. I consider individuals of neither species to be capable of displacing brooding adult *Phoebetria* albatorsses, or of killing large *Phoebetria* pulli. Cooperative group action by cats or skuas theoretically could account for predation of brooded and nearly full-grown Phoebetria pulli. However, there is no evidence for suggesting that this actually happens. No Phoebetria feathers, including downy feathers, have been found in the stomachs of 120 House Cats examined on Marion Island (R. van Aarde pers. comm.). Similarly, House cats are not considered to prey on palpebrata at Macquarie Island (K. Kerry pers. comm.). Skuas apparently take only pulli weakened by, or dead from, starvation. On two separate occasions I witnessed single skuas feeding on carcasses of starved fusca pulli. Starvation of these two pulli was evident from their lack of visible body-fat deposits, retarded growth of the culmen, tarsometatarsus and primary feathers, and retarded general feather development. On five occasions I found starved fusca pulli dead on their nests, and I suggest that the only dead fusca pulli are normally available to skuas. Swales (1965) reported that skuas take eggs and pulli of fusca at Gough Island, but his statement lacks any further qualification. Skuas are considered unimportant in predation of eggs and pulli of palpebrata at the Crozet islands (Mougin 1970).

The fusca breeding colonies studed by me were selected because they were relatively accessible to a human observer. The colonies were presumably also more accessible to Giant Petrels than most other fusca colonies at Marion Island. In the study colonies, the most accessible pulli were depredated first. This is considered to be significant in relation to the agility of Giant Petrels - they are far less agile than skuas or cats. The relatively dispersed nests of palpebrata were generally more inaccessible (to the human observer) than fusca nests. Although the sample size (16 nests on coastal cliffs) is small for palpebrata, the apparently better breeding success (29%) of this species, compared to fusca, may be partly accounted for by the relatively greater inaccessibility of its isolated coastal nests to Giant Petrels.

4.7 Pullus growth

The culmen and tarsometarsus of palpebrata grew slightly faster than in fusca, although both curves had a similar form (Figures 10 & 11). In palpebrata eruption of the outermost primary took place on average eight days earlier than in fusca, but in both species primary growth was of similar rate and form (Figure 12). Mass increased more rapidly in palpebrata over the period 20 - 70 days after hatching. Mean fusca pullus mass decreased in mid - late February, 60 - 70 days after hatching (Figure 13). There was no equivalent decrease in mean palpebrata pullus mass over this period, about 45 - 55 days after hatching. The pattern of intermittent large meals resulted in large daily fluctuations in the mass of individual palpebrata and fusca pulli (Figure 14). Data from fusca pulli which starved to death were not included, since chronic starvation retarded growth (Table 31). Pulli of both species were observed to starve to death during the 1974 - 75 breeding season.

These comparisons rely on accurate adult asymptote estimation. Adult asymptote sample sizes for fusca are large, but small for palpebrata. If there was a marked predominance of one sex among the measured pulli, asymptotes of these pulli (when fully grown) would differ from the adult parent population. Additionally, sample sizes of measured pulli are small, and thus susceptible to chance variation. As the differences in growth are small, small changes in asymptotes could alter interpretation of results. Five fusca pulli, weighed and measured 1 - 5 days before fledging, had significantly shorter wings ($P<0,001$) and culmens ($P<0,001$) and were significantly lighter in mass ($P<0,001$) than adult fusca (Table 32). The difference in mean length

FIGURE 10

CULMEN GROWTH IN NINE PHOEBETRIA FUSCA PULLI, AND THREE P. PALPEBRATA PULLI AT MARION ISLAND, 1974-75

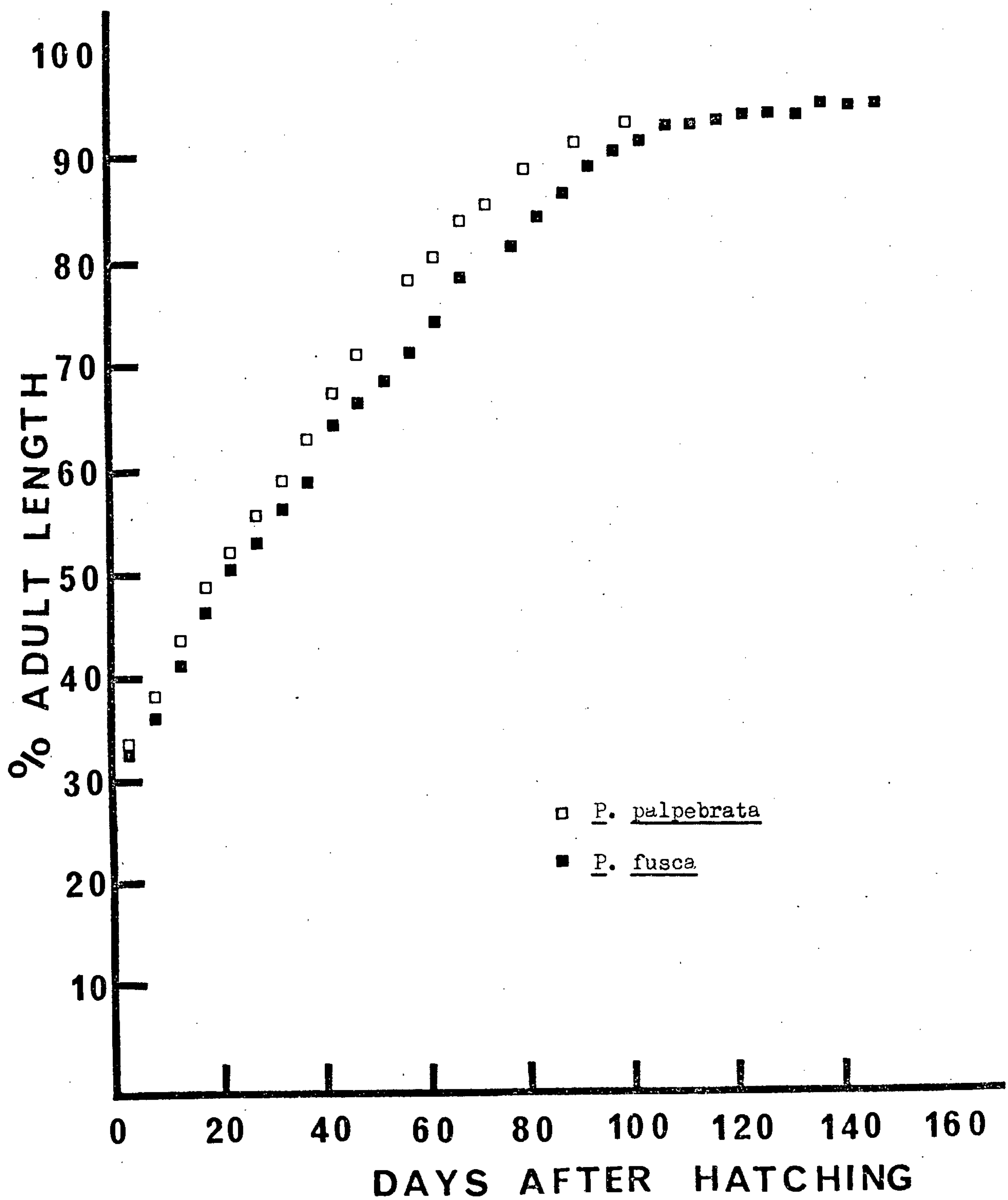


FIGURE 11

TARSOMETATARSUS GROWTH IN NINE PHOEBETRIA FUSCA PULLI, AND THREE P. PALPEBRATA PULLI AT MARION ISLAND, 1974-75

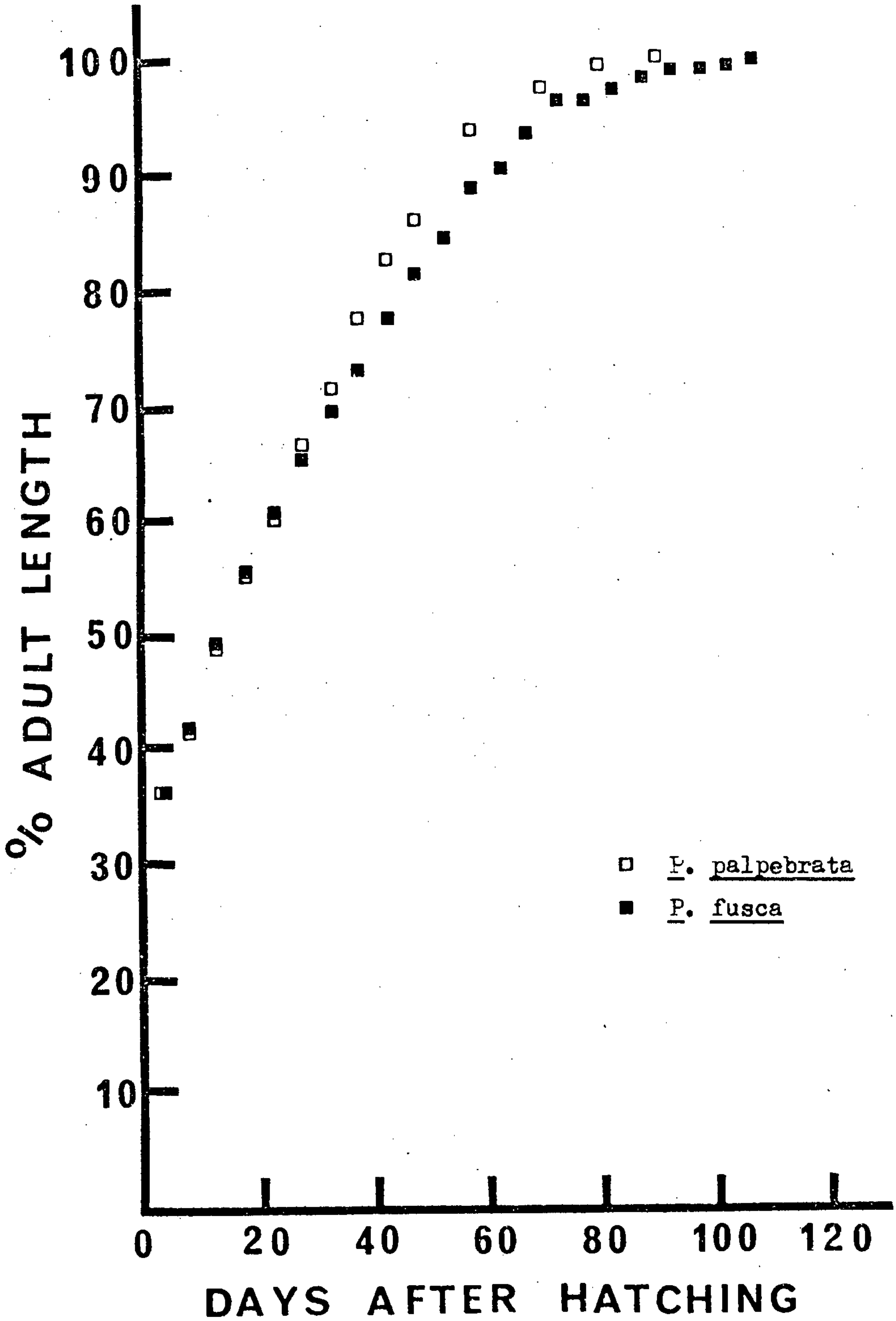


FIGURE 12

WING GROWTH IN NINE <u>PHOEBETRIA</u> <u>FUSCA</u> PULLI, AND THREE <u>P.</u> <u>PALPEBRATA</u> PULLI AT MARION ISLAND, 1974-75

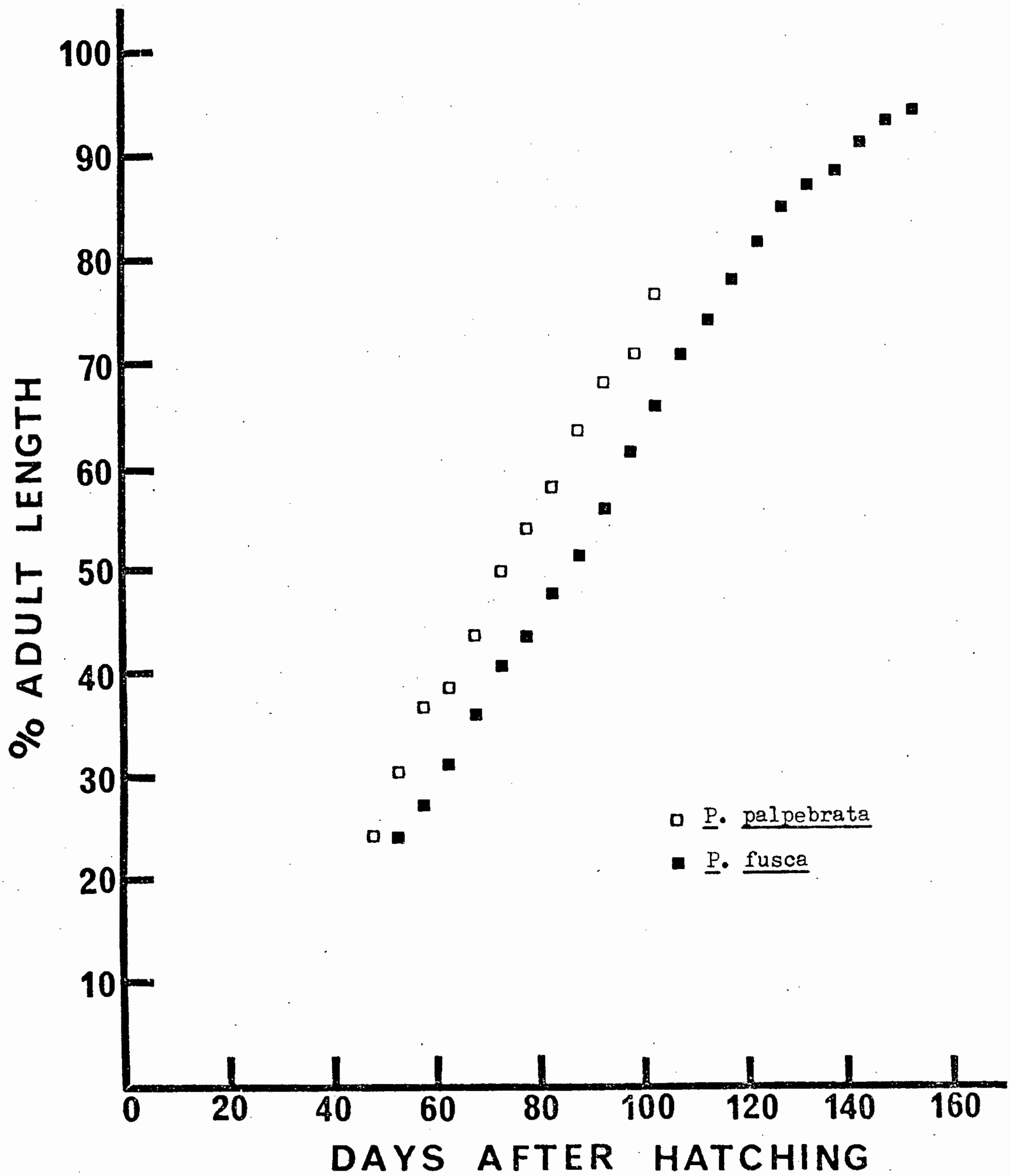
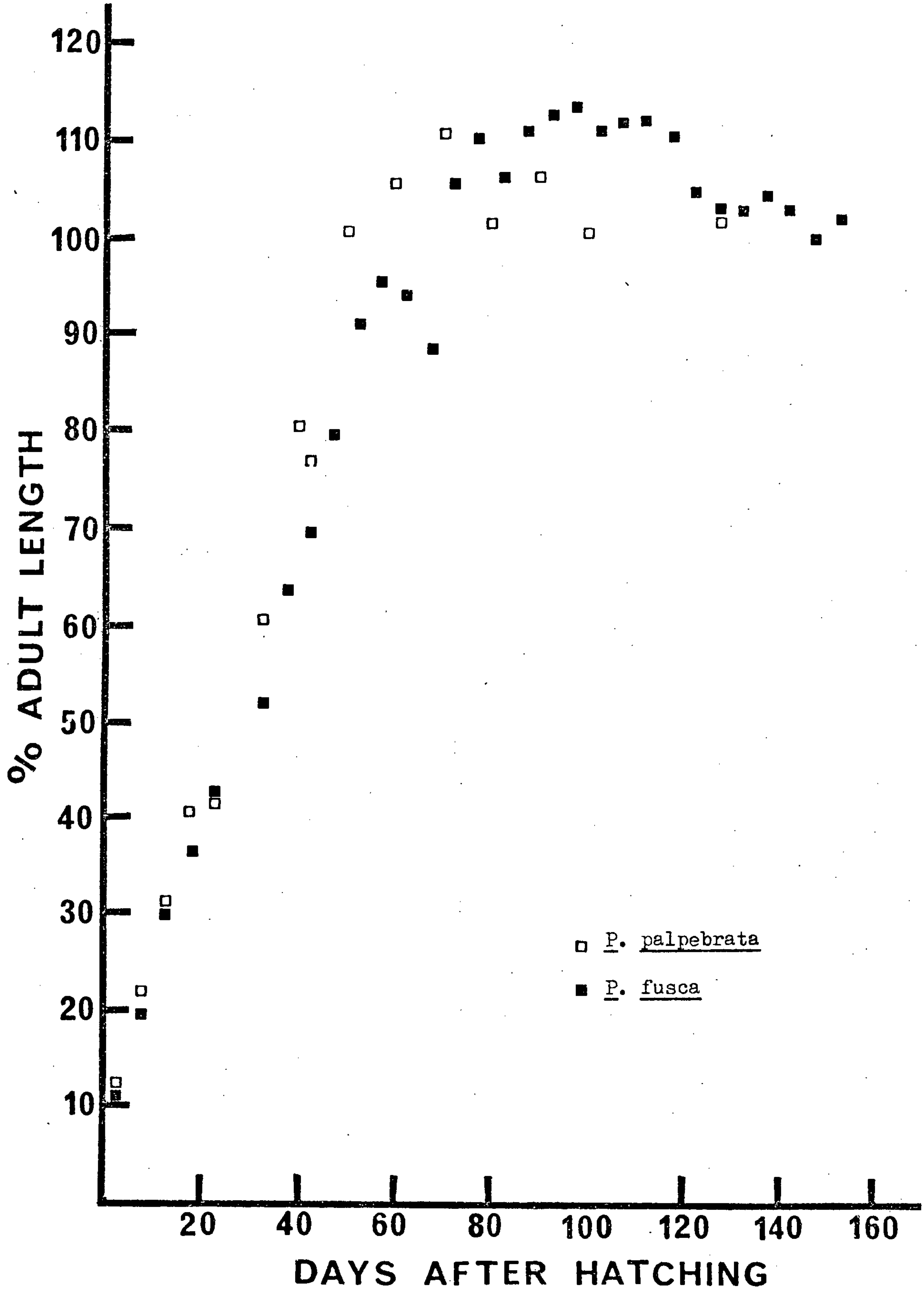


FIGURE 13

MASS GROWTH IN NINE <u>PHOEBETRIA</u> <u>FUSCA</u> PULLI, AND THREE <u>P. PALBEBRATA</u> PULLI AT MARION ISLAND, 1974-75



MASS GROWTH OF *PHOEBETRIA FUSCA* PULLUS NO. 84 AT MARION ISLAND, 1974-75

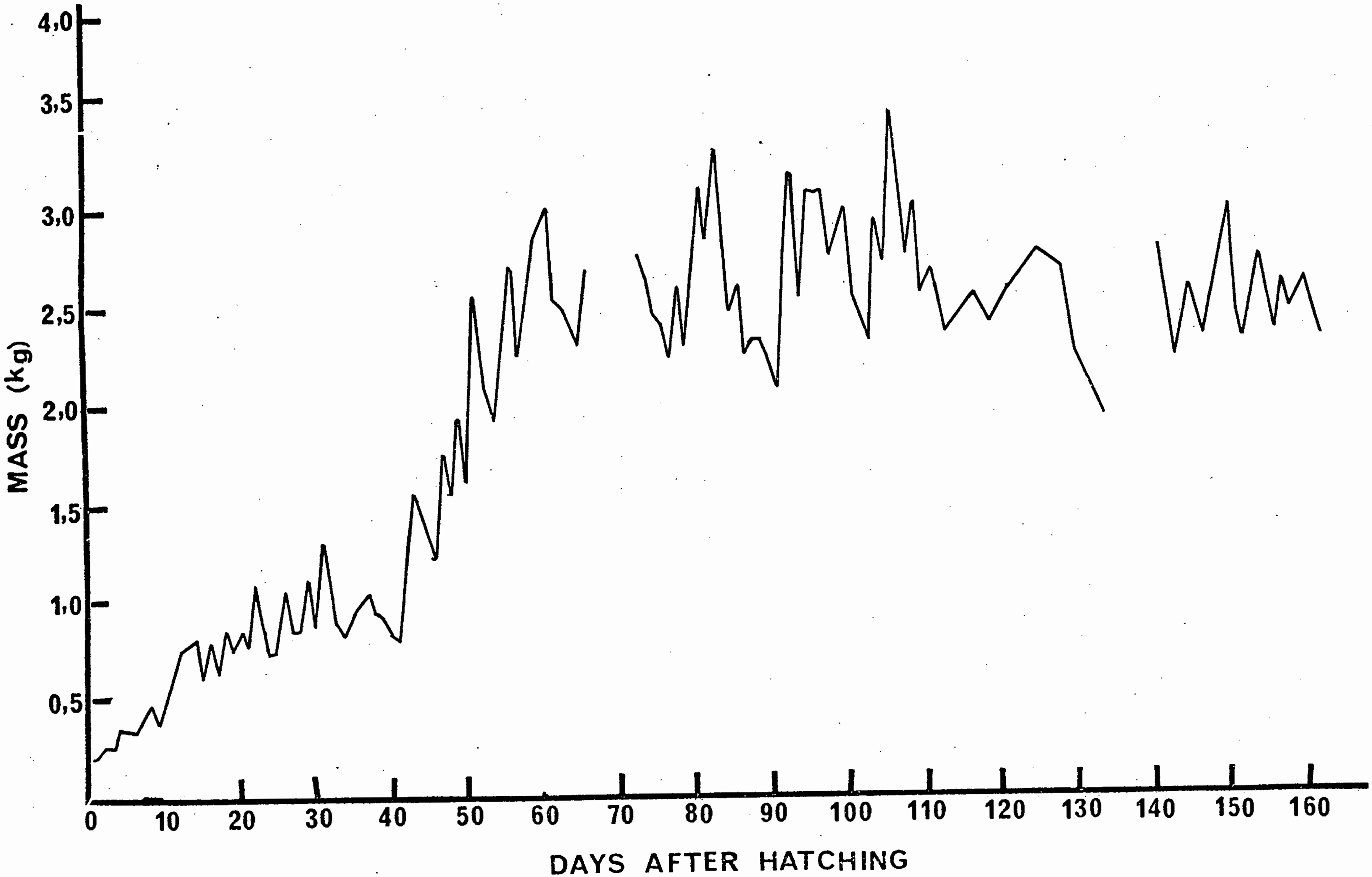


TABLE 31

DIMENSIONS AND WEIGHT OF THREE STARVED AND NINE HEALTHY *PHOEBETRIA FUSCA* PULLI AT MARION ISLAND

	Starved pulli[1]				Healthy pulli		
Age (days)	37	50	125		35-40	46-50	121-125
Weight (g)	540	1040	1220	Mean	1596	1999	2631
				S.D.	435	395	333
Culmen length (mm)	56,0	68,5	93,4	Mean	66,1	74,6	105,5
				S.D.	4,7	5,9	3,6
Tarsometatarsus length (mm)	48,4	61,6	77,2	Mean	60,0	66,7	82,0
				S.D.	5,2	5,2	2,4
Wing length (mm)	-	-	364	Mean	-	108	419,3
				S.D.		-	20,2

[1] Measurements of individuals at death.

TABLE 32

MASS AND LINEAR DIMENSIONS OF ADULT *PHOEBETRIA FUSCA* AND *P. FUSCA* PULLI PRIOR TO FLEDGING

	Adult				Pulli prior to fledging				Student's t Test	
	Mean	S.D.	Range	N	Mean	S.D.	Range	N	t Value	Probability
Mass (g)	2 512	223,6	2100-3430	176	2274	148,7	2050-2420	5	7,46	P<0,001
Wing length (mm)	516,5	12,9	490-551	101	483,2	15,5	470-503	5	1,82	P<0,1
Tarsometatarsus Length (mm)	82,7	10,6	77,5-90,0	212	80,8	2,5	77,4-83,9	5	4,00	P<0,001
Culmen length (mm)	112,1	3,5	99,9-120,2	212	105,8	3,1	102,8-110,2	5	5,50	P<0,001

of tarsometarsus ($P<0,1$) is not regarded as significant. It is apparent that fusca pulli fledge before growth is complete. Even assuming that all the measured pulli were female, and therefore were smaller than the mean population, it must be noted that the range for the whole pullus wing length does not overlap at all with that of the adult (male and female) population (Table 32). The growth of the tarsometarsus of fusca pulli is completed at about 110 days, and at about 100 days in palpebrata (Figure 11). Although the tarsometarsus length of the fusca pulli measured prior to fledging is not significantly ($P<0,1$) smaller than that of adults, the data suggest that the measured pulli were on average smaller than the average adult. There was no significant difference between the tarsometarsus lengths of fusca pulli, measured prior to fledging, and adult male fusca on one hand and adult female fusca on the other. However, sample sizes were small. There is thus no evidence to suggest that the measured fusca pulli were predominantly either male or female.

Data are not available to suggest whether palpebrata fledges before growth is complete.

Attempts to fit mass growth curves (Ricklefs 1967) were not successful, because this method does not anticipate pullus masses greater than 100% of adult mass halfway through the fledgling period.

The mean number of pullus feeds per day over the period 20 - 100 days after hatching, i.e., after the brooding phase is complete, are 0,42 and 0,39 for fusca and palpebrata respectively. A pullus was regarded as having been fed if its mass was greater than that recorded on the previous day's weighing. The data available are not adequate for determining a mean size of meal.

4.8 Nest sites

Phoebetria palpebrata nests at Marion Island, and at other breeding grounds, are usually found singly or in twos and threes, but occasionally in larger groups (pers. obs., Watson 1975). Phoebetria palpebrata nests on coastal and inland sites throughout its breeding range (pers. obs., Murphy 1936, Sorenson 1950, Downes et al. 1959, Mougin 1970, Kerry 1972). At Marion Island, 45% of the population breeds at the coast and 55% inland (total estimated population 216 pairs). Phoebetria fusca at Marion Island, and at other breeding grounds, breeds in loose groups of up to 40 nests, but occasionally nests singly (pers. obs., Watson 1975). Nesting is confined to coastal sites at Marion and Prince Edward islands, Crozet islands and St Paul Island (pers. obs., Mougin 1970, Derenne et al. 1976). At New Amsterdam Island, fusca nests inland only (Paulian 1953). At Gough Island and the Tristan da Cunha islands, birds nest inland and at the coast (Elliott 1957, Swales 1965).

Phoebetria fusca and palpebrata construct columnar nest mounds on vegetated ledges of vertical cliffs, or near vertical slopes. Four Diomedea species, D. melanophris, D. chrysostoma, D. bulleri and D. chlororhynchos, nest on relatively steeply sloping vegetated terrain and build columnar nest mounds. Diomedea chrysostoma and D. melanophris nest on open slopes, but the latter selects steeper, more rocky terrain at South Georgia (Tickell & Pinder 1975). Diomedea bulleri nests under scrub trees, or steep grassy slopes (Serventy et al. 1971). Diomedea chlororhyncos may nest of flat terrain, steep grassy slopes or under scrubby trees (Rowan 1951, Williams pers. comm.). Six Diomedea species, D. exulans, D. epomophora D. cauta, D. irrorata, D. immutabilis and D. nigripes, nest on flat or nearly flat terrain. The tropical and subtropical species do not construct columnar nest mounds. In fact, D. irrorata does not construct a nest at all, and the egg is laid on bare substrate (Harris 1973). The nest of D. nigripes and D. immutabilis is a shallow depression with a low rim in sandy substrate. The former nests on beaches, whereas the latter nests amongst inland vegetation (Fisher 1972). The nest of D. cauta is made of guanolike material, and is constructed on rocky substrate or occasional ledges (Richdale 1952, Serventy et al. 1971). I could find no information on D. albatrus. D. exulans and D. epomophora nest on open areas with a damp or wet soil substrate (Watson 1975).

The nest of both fusca and palpebrata is a low conical structure not taller than 20 cm, and is constructed from mud and vegetation. At Marion Island, the nest site is a ledge on a vertical cliff, or steeply-sloping gradient, with sufficient soil and vegetation to provide for nest construction. There is invariably a drop of at least three metres on one side of the nest. The older grey lava, interrupted by fault scarps and high coastal cliffs, provides the vegetated ledges suitable as nest sites. Cliffs only occur in the black lava flows at the coast, and these are generally low, and without vegetated ledges. Both fusca and palpebrata show a statistically significant preference ($P<0,0001$) for nest sites in grey lava regions (Table 33).

The nest of palpebrata is invariably backed by a bare earth or rock wall (Van Zinderen Bakker 1971, pers. obs.), whereas in fusca 20,1% (total N = 98 Macaroni Bay study colonies) of the nests had a similar backing wall. Thus the zone of overlap in nest site selection is confined to coastal sites with bare rock or earth backing walls. On this basis, all palpebrata coastal nest sites could be regarded as potential

TABLE 33

LAVA REGIONS USED FOR NEST SITES BY PHOEBETRIA FUSCA AND P. PALPEBRATA AT MARION ISLAND

	P. fusca			*P. palpebrata*					
	Coastal			Coastal			Inland		
	Observed	Expected[1]	Chi-square value	Observed	Expected[1]	Chi-square value	Observed	Expected[2]	Chi-square value
Grey lava	1772	503		90	24		88	15	
			4254[3]			241[3]			424[3]
Black lava	260	1529		7	73		6	79	

[1]Calculated as follows: $\dfrac{\text{coastline length of black or grey lava}}{\text{total coastline length}}$ X estimated number of coastal *fusca* or *palpebrata* nests

[2]Calculated as follows: $\dfrac{\text{area of black or grey lava}}{\text{total island area}}$ X estimated number of inland *palpebrata* nests

[3]Difference significant at P<0,0001

fusca sites. However, _fusca_ possesses a degree of coloniality not displayed by _palpebrata_. Of 16 _palpebrata_ coastal nests, five (31,25%) nests had two or more other nests (in this case _fusca_ nests) sited within three metres of themselves. These _palpebrata_ nests were designated here as "colonial". No coastal _palpebrata_ nest was found with more than one other _palpebrata_ within three metres. One group of six _palpebrata_ nests were found inland. Of 98 _fusca_ nests at Macaroni Bay, 92 (93,8%) nests had two or more other nests within three metres.

The number of _palpebrata_ nests on "typical" _fusca_ nest sites may be approximately as:

$$\text{proportion of "colonial" coastal } \underline{palpebrata} \text{ nests} \times \text{total estimated coastal } \underline{palpebrata} \text{ population}$$

$$0{,}3125 \times 97$$

$$= 30 \text{ nests}$$

The number of _fusca_ nests on "typical" _palpebrata_ nest sites may be approximated as:

$$\text{proportion of } \underline{fusca} \text{ nests with bare backing walls} \times \text{total estimated } \underline{fusca} \text{ population}$$

$$0{,}201 \times 2032$$

$$= 408 \text{ nests}$$

Assuming that interspecific competition does occur for nest sites, it is apparent that the _fusca_ population as at present would be virtually unaffected. The number of potential nest sites occupied by _palpe-_

brata represents 1,4% of the *fusca* nesting sites. However, the number of potential *palpebrata* nest sites presently occupied by *fusca* represents 231,8% of the sites occupied by *palpebrata*.

5 Diet

5.1 Introduction

Cephalopods were shown to be the most frequently taken food of *Phoebetria* albatrosses at the Crozet islands, based on the analysis of stomach contents of 18 *fusca* and 10 *palpebrata* adults (Mougin 1970). Other records of food taken by both species confirm that cephalopods are the most important of several food classes (Table 34 & 35). Similarly, cephalopods have been shown to be the most important items in the diets of four *Diomedea* species: *D. melanophris* and *D. chrysostoma* (Tickell 1964), *D. irrorata* (Harris 1973), and *D. exulans* (Imber & Russ 1975).

Since it is extremely difficult to determine the diet of procellariiforms by direct observation, studies have been based on the stomach contents of collected birds (Tickell 1964, Mougin 1970, Imber & Russ 1975, Imber 1976), regurgitated stomach contents (Ashmole & Ashmole 1967, Imber 1973, Harris 1973) and regurgitated casts of food remains (Imber 1973, Imber & Russ 1975).

5.2 Methods

The diets of *fusca* and *palpebrata* were not compared by analysing the stomach contents of collected adults or pulli, as the Marion Island *palpebrata* population (about 176 breeding pairs) was not considered large enough to allow adequate sampling.

It was not possible to compare the diets by collecting stomach contents of pulli disturbed during handling, as the small number of available pulli (i.e. outside study colonies but within reasonable distance of the base) soon habituated to disturbance. Further less than 1% of

TABLE 34

FOOD ITEMS RECORDED FOR *PHOEBETRIA FUSCA*

Food item						Source
Soft food	Crustaceans	Cephalopods	Fish	Penguin	Other bird	
	x	x	x	x	x	Hagen (1952)
		x			x	Mougin (1970)
x	x	x	x	x		Segonzac (1972)
	x	x	x	x	x	Watson (1975)
	x	x	x	x	x	Present study

TABLE 35

FOOD ITEMS RECORDED FOR <u>PHOEBETRIA PALPEBRATA</u>

Food item						Source
Crustaceans	Cephalopod	Fish	Penguin	Other bird	Mammal	
x	x			x	x	Falla (1937)
	x	x	x			Bailey & Sorenson (1962)
x	x	x			x	Mougin (1970)
x	x	x		x		Watson (1975)
x	x	x	x	x		Present study

captured adult birds regurgitated stomach contents during handling.

I based my comparison of the diets of fusca and palpebrata on the identification of undigested cephalopod beaks found in regurgitated casts. It is impossible to quantify the amount of fish, crustaceans, carrion or soft food from regurgitated casts. However, as mentioned, cephalopods are the most important food class taken by Phoebetria albatrosses. Since it is possible to estimate the mass of whole cephalopods by using beak measurements (Clarke 1962), the cephalopod material in casts can be analysed by mass and frequency of occurrence. However, volumetric estimation is not possible.

All regurgitated casts found at occupied nest sites during regular trips to the study colonies were collected and combined to give monthly samples. The lower beaks of cephalopods were identified tentatively to family, using the key and illustrations of Clarke (1962). The beaks were sent to Dr. M.J. Imber (Wildlife Services, Dept. of Internal Affairs, New Zealand) and Mr. D. MacLeod (Institute of Oceanographic Sciences, United Kingdom) for specific identification. The rostral length of the lower beak was measured within an accuracy of 0,3 mm, using calipers and a ruler. The masses of the cephalopods were estimated using regressions of lower rostral length versus mass, calculated for each cephalopod family (Clarke 1962). If the monthly sample of a cephalopod species exceeded 30 beaks, only 30 randomly selected beaks were measured. Monthly mean masses and standard deviations were then weighted according to sample size. Upper cephalopod beaks were not used in identification, or in estimating mass of whole animals.

5.3 Results

Monthly samples of cephalopod beaks were obtained from fusca regurgitation during October 1974 - May 1975. The range in number of beaks in the monthly samples was 66 - 1 725. Monthly samples of cephalopod beaks were obtained for palpebrata regurgitations during March - May 1975 only. The range in number of beaks in monthly samples was 49 - 191. A total of 58 cephalopod beak types was identified, of which 37 types were represented by five beaks or less out of a total of 3 188 beaks. Five species were identified by Dr. M.J. Imber. These five species accounted for 88% of the total number of beaks. Other tentative identifications to species or family taxon were made.

The frequency of occurrence of each cephalopod species, or group of species, varied monthly in the fusca material (Table 36). Thus, comparison in frequency of occurrence of cephalopod species in the casts of fusca and palpebrata was restricted to the period March - May 1975. Similarly, the mean mass of four cephalod species varied monthly from October 1974 to May 1975 (Table 37), and the comparison of mean masses of these cephalopod species between the two albatrosses was restricted to the period March - May 1975.

There was a significant difference ($P<0,001$) in the frequency of occurrence of cephalopod species found in the casts of fusca and palpebrata (Table 38). However, only one species (Histioteuthis sp. 53), which constituted more than 1% by frequency of occurrence in the casts of fusca, was not found in palpebrata casts. All cephalopod species which constituted more than 1% by frequency of occurrence of the beaks found in palpebrata casts were found in fusca casts.

Cephalopod mass estimation relies on accurate identification at the family level, since rostral length versus mass regressions are characteristic for each family (Clarke 1962). Thus, the masses of only the five species identified by Dr. M.J. Imber were estimated. Mean masses were not estimated for one of these five species, Kondakovia longimana,

TABLE 36

MONTHLY FREQUENCY OF OCCURRENCE OF CEPHALOPOD SPECIES IN THE REGURGITATED CASTS OF *PHOEBETRIA FUSCA* AT MARION ISLAND, OCTOBER 1974 - MAY 1975. ALL FIGURES ARE PERCENTAGES

	Months							
	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May
Histioteuthis eltaninae	1,3	2,3	6,4	12,0	18,9	15,5	40,7	46,2
Moroteuthis knipovitchi	0	0	0	0	3,0	1,3	2,6	9,2
Histioteuthis sp. 53[1]	0	0	0	29,6	19,6	9,9	8,0	0,8
Kondakovia longimana	68,9	64,7	75,8	8,3	0,4	4,2	8,3	5,4
Teuthowenia antarctica	1,3	0	0	2,8	33,0	56,1	24,7	4,2
Galliteuthis glacialis	2,7	2,3	1,6	5,5	3,7	5,3	6,5	4,6
Psychroteuthis glacialis[1]	0	0	0	0	0	0,1	0,8	0,4
Chiroteuthis spp.[1]	14,7	10,2	11,2	31,5	15,9	3,6	2,1	1,6
Taonius spp.[1]	4,1	4,5	1,6	1,9	0,7	0,7	1,8	10,9
Unidentified spp.	7,0	15,9	3,2	8,3	4,2	3,3	4,5	16,7

[1] Identification requires confirmation

TABLE 37

MONTHLY MEAN MASSES (g) OF FOUR CEPHALOPOD SPECIES IN REGURGITATED CASTS OF <u>PHOEBETRIA FUSCA</u> AT MARION ISLAND, OCTOBER 1974 - MAY 1975

		Months							
		Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May
Histioteuthis eltaninae	Mean	35	40	38	42	50	46	49	52
	S.D.	-	-	-	6,6	4,2	8,0	6,8	9,9
Moroteuthis knipovitchi	Mean	-	-	-	363	453	495	476	380
	S.D.	-	-	-	139,2	137,5	151,5	97,8	-
Teuthowenia antarctica	Mean	56	-	-	52	62	73	79	103
	S.D.	-	-	-	-	23,7	11,1	11,4	40,9
Galliteuthis glacialis	Mean	106	116	115	100	105	102	95	94
	S.D.	-	-	-	19,5	13,1	34,2	13,8	8,9

TABLE 38

FREQUENCY OF OCCURRENCE OF CEPHALOPOD SPECIES IN REGURGITATED CASTS OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND, MARCH - MAY 1975

	P. fusca		*P. palpebrata*	
	Observed	Expected	Observed	Expected
Histioteuthis eltaninae	714	711,82	102	104,18
Histioteuthis sp. 53[1]	68	59,32	0	8,68
Moroteuthis knipovitchi	239	231,17	26	33,83
Kondakovia longimana	156	181,45	52	26,55
Teuthowenia antarctica	1 183	1 123,57	105	164,43
Galliteuthis glacialis	157	203,25	76	29,75
Psychroteuthis glacialis[1]	10	23,55	17	3,45
Chiroteuthis spp.[1]	89	86,21	11	12,68
Taonius spp.[1]	52	47,28	2	6,92
Unidentified spp.	165	158,52	18	23,36

Z = 209,21 Differences significant at P<0,001

[1] Identification requires confirmation

because the beaks often were broken. The remaining four species made up 75,0 and 80,9% by frequency of occurrence of the beaks found in _palpebrata_ and _fusca_ casts respectively. _Phoebetria fusca_ took significantly larger _Moroteuthis knipovitchi_ ($P<0,001$), while _palpebrata_ took significantly larger _Teuthowenia antarctica_ ($P<0,025$) and _Galliteuthis glacialis_ ($P<0,01$ - Table 39). There was no significant difference in the mean masses of _Histioteuthis eltaninae_ between the two birds.

The process of digestion introduces bias favouring relatively resistant food items in analysis of albatross diet, based on stomach contents or regurgitated casts (Imber 1973). In the case of cephalopods, small and immature beaks are less resistant to digestion, and are less easily identified when damaged. The relatively small species _Spirula spirula_ (estimated mean mass 10g) represented 35% of the identifiable cephalopods in the stomach contents regurgitated by _Pterodroma macroptera gouldi_, but only 0,3% of the cephalopods found in regurgitated casts of the same species (Imber 1973). Imber (1973) suggested that cast formation is initiated when a large, ingested pair of beaks, too large to enter the gizzard, hinders the passage of other beaks into and through the gizzard. Both factors bias the determination of cephalopod diet from beaks in regurgitated casts by overestimating the importance of large beaks in the diet. This will result in an overestimation of mean cephalopod mass in the diet as a whole. Further, the bias will tend to hide any differences in the frequency of occurrence of small beaks, since they are largely eliminated. I assumed that the digestive abilities of _fusca_ and _palpebrata_ are roughly equal.

The estimated mean cephalopod mass (considering _M. knipovitchi_, _T. antarctica_, _G. glacialis_ and _H. eltaninae_ only) was 105 g and

TABLE 39

MEAN MASSES (g) OF FOUR CEPHALOPOD SPECIES IN REGURGITATED CASTS OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND, MARCH - MAY 1975

	P. fusca			*P. palpebrata*			Student's t test	
	Mean	S.D.	N	Mean	S.D.	N	t Value	Probability
Histioteuthis eltaninae	48,6	7,8	714	47,6	10,3	102	1,15	NS
Moroteuthis knipovitchi	488,8	137,9	239	410,5	177,8	26	2,66	P<0,01
Teuthowenia antarctica	74,3	11,7	1183	76,9	2,6	105	2,27	P<0,025
Galliteuthis glacialis	99,0	28,8	157	116,9	24,4	76	4,66	P<0,001

112 g for palpebrata and fusca respectively. As these four cephalopod species comprise a major portion of the cephalopods taken, the actual mean cephalopod masses are assumed to be close to these values. The estimated mean masses of cephalopods eaten by D. irrorata (Harris 1973) and D. exulans (Imber & Russ 1975) are 260 g and 400 g respectively. These means are overestimations, because of the bias favouring larger beaks (Imber & Russ 1975). The body masses of D. irrorata (Harris 1973) and D. exulans (Russ & Imber 1975) are 3,29 kg and 8,70 kg respectively. The lighter Phoebetria albatrosses apparently take smaller cephalopod prey. The three most important (in terms of proportion of cephalopod mass ingested) cephalopod families taken by fusca, palpebrata (this study) and D. exulans (Imber & Russ 1975) are the Onychoteuthidae, Cranchiidae and Histioteuthidae. The three most important cephalopod families taken by the tropical D. irrorata are Histioteuthidae, Octopodoteuthidae and Ommastrephidae.

Watson (1975) states that palpebrata normally feeds by alighting on the surface, but may plunge below the surface as well. No information is available for fusca. However, both species probably actively capture cephalopods on, or near, the surface of the sea at night; facilitated by the bioluminescent organs of the prey, as suggested for D. exulans by Imber & Russ (1975). Most albatross species probably feed mainly at night when prey is relatively readily available through vertical migration. Both fusca and palpebrata may scavenge dead or dying cephalopods on the surface, as do Pterodroma alba (Ashmole & Ashmole 1967), Pterodoma macroptera gouldi (Imber 1973) and D. irrorata (Harris 1973). The presence of penguin remains in the stomachs and casts of fusca and palpebrata, and mammal remains in palpebrata (Tables 34 & 35), indicates that both species readily take carrion

(Hagen 1952, Mougin 1970, Segonzac 1972, Watson 1975).

It appears that the cephalopod-based diets of fusca and palpebrata overlap, to a large extent, in terms of species and size of objects included, although significant differences have been shown to occur.

The distribution of oceanic cephalopods is poorly known (Clarke 1966) so that at present there are no known "indicator" species in the southern Atlantic and Indian oceans. Imber (1976) states "one will rarely be able to deduce information not already available about the range of a seabird from the range of its prey, but the converse does no apply."

6 Behaviour associated with social communication

6.1 Introduction

Phoebetria fusca and *palpebrata* are not spatially, nor temporally, isolated at Marion Island. The three-week difference in the breeding chronology of the two species probably is insufficient to maintain reproductive isolation, since, in the Diomedeidae, mates require at least one pre-breeding season in which to form pair-bonds (Richdale 1952, Tickell 1968, Fisher 1972, Richdale & Warham 1973). At Marion Island, non-breeding members of both *fusca* and *palpebrata* were observed performing ritualized pair-formation behaviour throughout the breeding season, suggesting that pair-bonding also occurs over a relatively long period in these two species. Mayr (1970) stated that behavioural barriers are the most common mechanisms maintaining genetic isolation between two similar, sympatric species.

Behaviour is subject to modification by changes in selection pressures concomitant with changes in ecological niche during the process of speciation, and subsequent evolution. Thus behavioural differences between two congeneric species such as *fusca* and *palpebrata*, may suggest ecological shifts that occurred in the evolutionary history of the two species.

I followed Moynihan (1955) in defining ritualized displays as being those peculiarly standardized and often exaggerated performances which have been specialized or modified as social signals, or releasers. The terminology of Richdale (1949, 1950), Sorenson (1950) and Johnstone *et al.* (1975) was used, where appropriate, for names of displays which are written in capital letters. Qualitative descriptions of the behaviour associated with breeding were recorded for *fusca* and *palpebrata*. Far fewer observation were made of *palpebrata*, than of *fusca*. Figures 15 - 24 were drawn from photographs.

6.2 Displays

6.2.1 THREAT (Fig. 15)

Synonyms: "Gulping" (Richdale 1949) and "Snapping" (Richdale 1950, Rice & Kenyon 1962).

Typical performance: In fusca the threatening bird stares at the spproaching bird; the feathers of the mantle, neck and crown are erected. If the bird is sitting on a nest, the wings are lifted slightly away from the body. The beak is held at 30° - 45° below the horizontal. With increasing aggression, the threatening bird lifts its beak, now opened, and may lunge at the other bird. THREAT can culminate with the beak being snapped several times in rapid succession, accompanied by guttural vocalizations and physical attacks on the intruder. With an increasing tendency to flee, the bird will break of THREAT, and with sleeked plumage and hunched posture, attempt to move away from the other bird.

THREAT in palpebrata is similar to that in fusca.

Variations: THREAT shows variability in feather erection, vocalizations and beak movement.

Contexts: A bird sitting on an occupied nest, or standing on a ledge, will threaten a conspecific landing at, or moving into the area. Individual fusca were seen to give THREAT to members of palpebrata, Brown Skua Stercorarius skua, Sheathbill Chionis minor, Giant Petrels Macronectes spp., feral House Cat Felis domesticus and human observers. P. palpebrata were observed to give THREAT to fusca, Brown Skua S. skua, and human observers.

The displays termed "Gulping" (Richdale 1949) and "Snapping" (Richdale 1950, Rice & Kenyon 1962) describe two of a number of actions which I consider collectively to constitute the spectrum of THREAT behaviour.

6.2.2 SKYCALL (Fig. 16)

Synonyms: SKYCALL (Richdale 1950, Rice & Kenyon 1962).

FIGURE 15

THREAT IN PHOEBETRIA, AND CHANGES IN POSTURE WITH INCREASING AGGRESSION OR TENDENCY TO FLEE

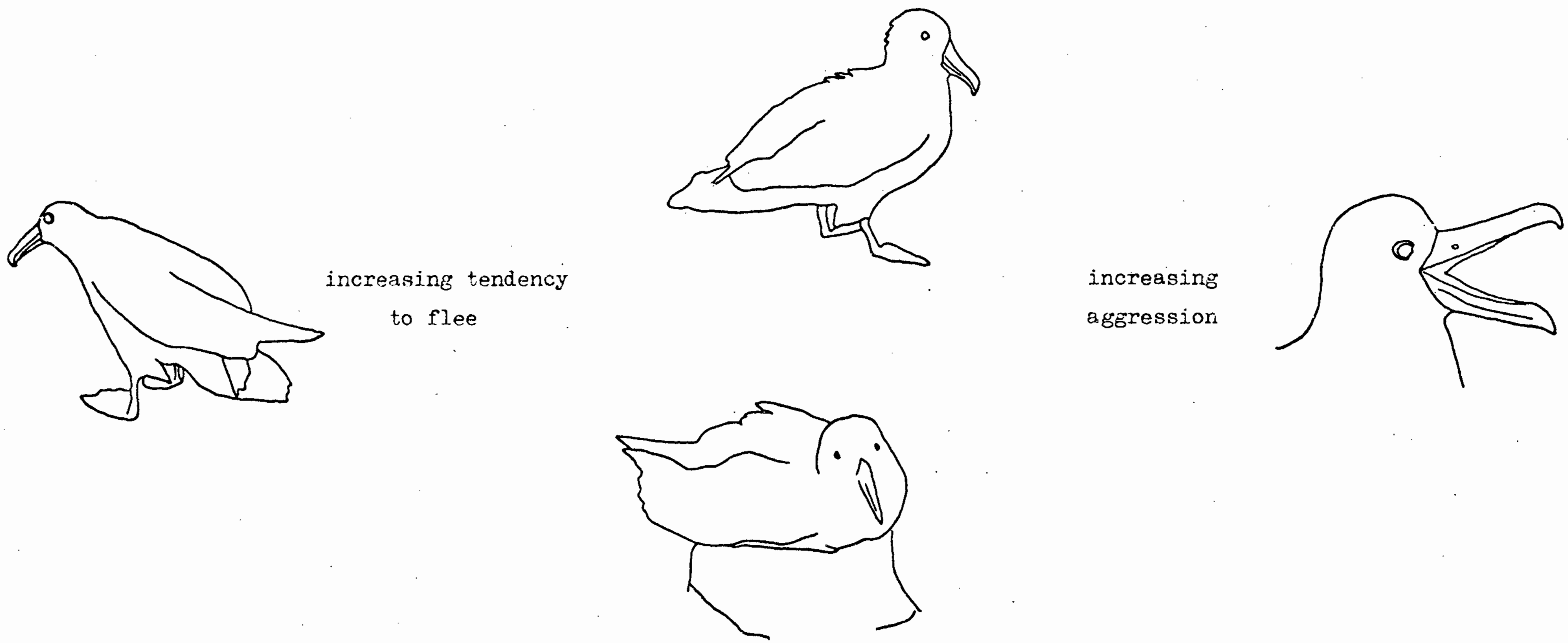
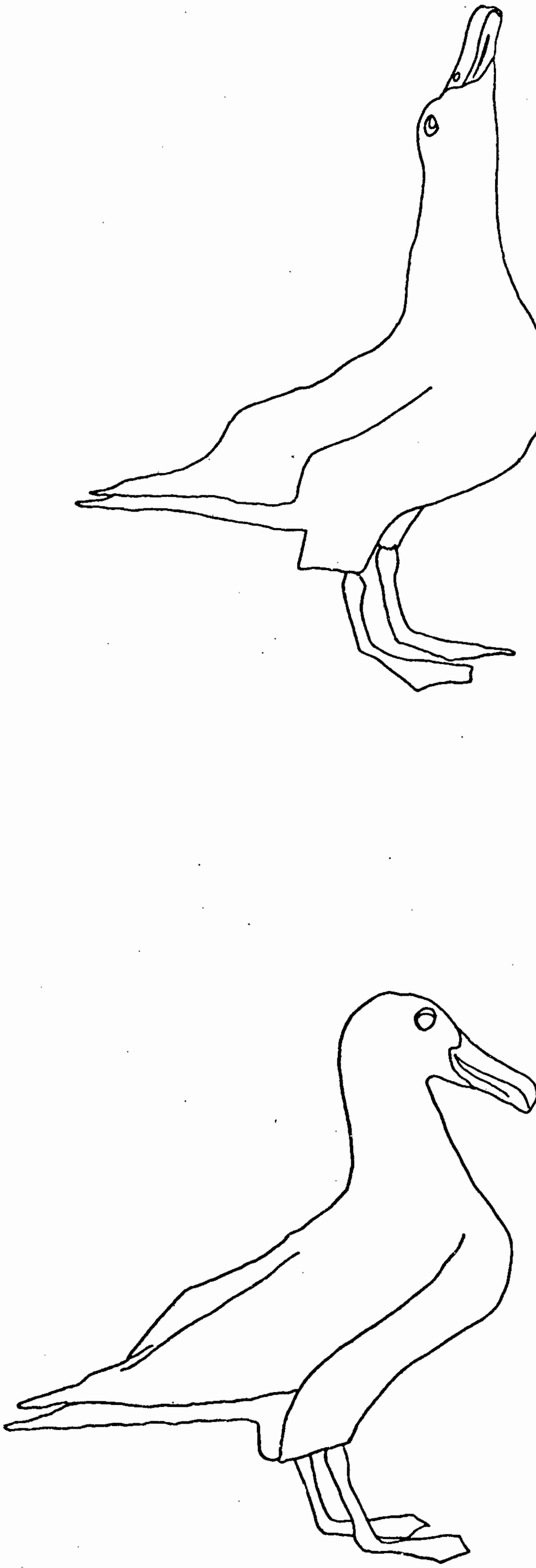


FIGURE 16

FULL SKYCALL IN <u>PHOEBETRIA</u>, SHOWING EXPIRATORY CALL (TOP) FOLLOWED BY INSPIRATORY CALL (BOTTOM)



Typical performance: There are two variants of this display. The first is termed "full" SKYCALL. In fusca, the bird stands erect with sleeked plumage. The head and beak are pointed vertically upwards with a brisk movement, and a loud, expiratory call is given. The beak is slightly opened. The head is rapidly lowered, and the beak is pressed against the breast, while an inspiratory, wheezing sound is uttered.

The "abbreviated" SKYCALL is given from a sitting position. The beak may not be raised to the fully vertical position, and the expiratory call is softer. The beak is not depressed onto the breast, and the inspiratory wheezing sound is softer.

The "full" and "abbreviated" SKYCALLS of palpebrata are similar to those given by fusca, except that the calls are apparently shorter and softer.

Variations: There is apparently little variation within the two variants of SKYCALL.

Contexts: Solitary birds give "abbreviated" SKYCALL from the nest, or "full" SKYCALL when standing, when a conspecific (thought to be a mate) flys past. Occasionally a second bird will land at the site, apparently in response to SKYCALL. Two birds (thought to be a mated pair, or in the process of establishing a pair-bond), give "full" and "abbreviated" SKYCALLS at the nest site, or at vacant ledges during prolonged agonistic encounters. Incubating or brooding fusca occasionally gave "abbreviated" SKYCALL at the approach of human observer, and after the human observer replaced an egg or pullus, removed from underneath the sitting adult. Incubating fusca gave "abbreviated" SKYCALL after expelling intruding conspecifics from the nest site area, on two occasions, and on one occasion when an adult palpebrata approached the nest.

Discussion: SKYCALL is associated with nest site, apparently as an advertisement display. Its performance during nest site defence is possibly a displacement activity, in a conflict situation.

The vernacular names for <u>Phoebetria</u> spp., variously given as Piew, Pio, Pee-arr and Peole (Murphy 1936) are derived from the two-syllabled call given in SKYCALL.

6.2.3 BILL POINTING (Fig. 17)

Synonyms: "Rapier Action" (Richdale 1949),"Billing" (Richdale 1950) and BILL POINTING (Johnstone <u>et al</u>. 1975).

Typical performance: In <u>fusca</u>, one bird reaches forward, pointing its beak at the head, neck, wing or breast region of a second bird. The bird performing BILL POINTING stares at the second individual. A slight, biting movement may be made, but actual contact with the other bird is seldom achieved. Any contact is brief and gentle. The beak is closed.

A similar display occurs in <u>palpebrata</u>.

Variations: The movements of BILL POINTING grade into movements performed during BILL CLASHING and ALLOPREENING in <u>fusca</u>, and BEAK THRUSTING and ALLOPREENING in <u>palpebrata</u>. There is variability in the movements, postures and duration of BILL POINTING, such that BILL POINTING is not generally an easily distinguishable display.

Contexts: BILL POINTING occurs during agonistic encounters between two birds (thought to be a mated pair, or birds in the process of establishing a pair-bond).

Discussion: BILL POINTING is variable. However, I have treated it as a distinct display, as it has been distinguished as such by other authors (Richdale 1949, 1950, Johnstone <u>et al</u>. 1975).

6.2.4 BILL CLASHING (Fig. 18)

Synonyms: BILL CLASHING (Richdale 1949)

Typical performance: This display occurs in <u>fusca</u> only. As one bird reaches forward with its closed beak pointing at the head of a second bird,

FIGURE 17

BILL POINTING IN <u>PHOEBETRIA</u> <u>FUSCA</u>. THE BIRD ON THE RIGHT IS BILL-POINTING TOWARDS THE SECOND BIRD, WHICH IS AUTOPREENING

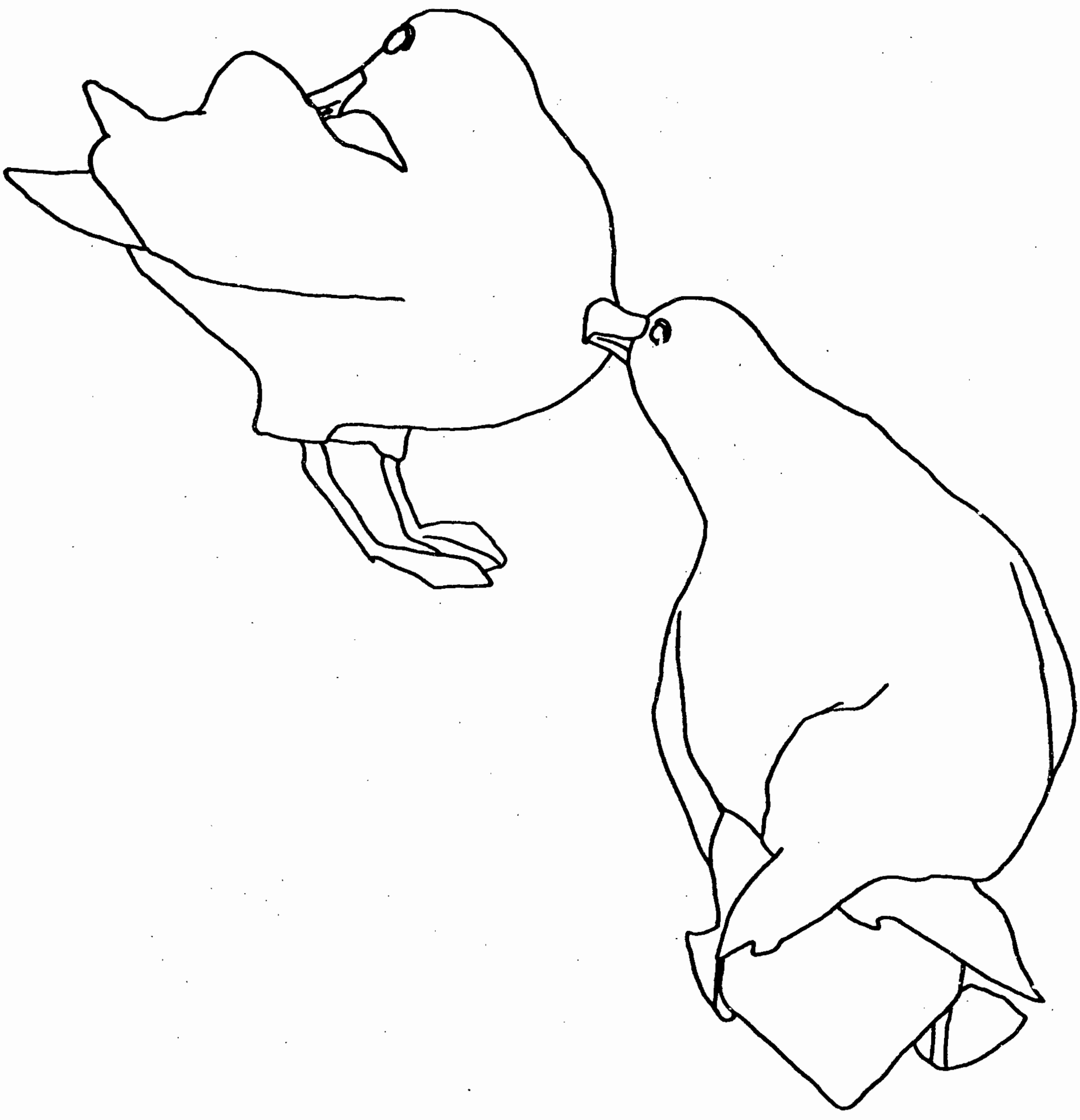
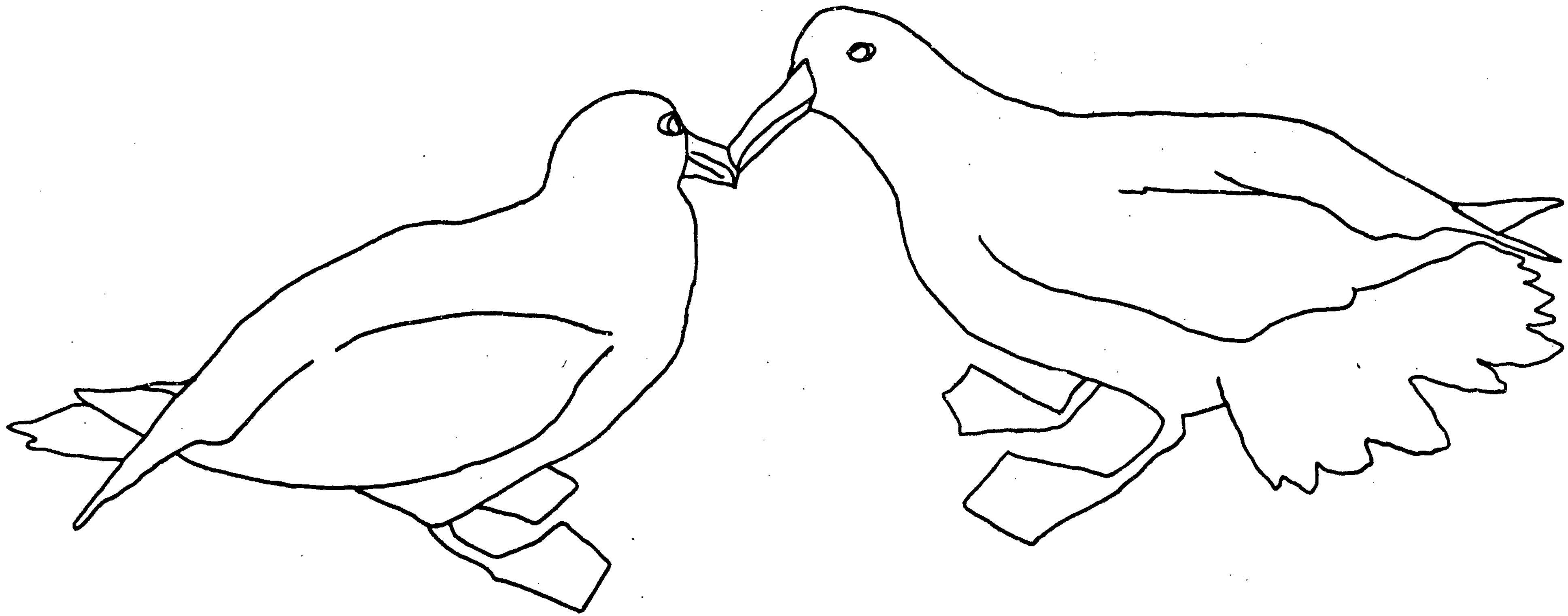


FIGURE 18

BILL CLASHING BETWEEN TWO *PHOEBETRIA FUSCA*



the recipient jerks its head sideways such that the beaks of the two birds make brief, light contact, accompanied by a clicking sound. Both birds continue to make beak contact up to 15 times in rapid succession, with jerky sideways movements of the head. Both birds are invariably standing, and the tail may be fanned at an angle of 45^{o}, and is skewed to one side.

Variations: The number of beak contacts is variable, and tail fanning apparently occurs in high intensity displays only. If the birds are standing close together, there is no forward reaching movement.

Contexts: BILL CLASHING is performed by two birds (thought to be a mated pair, or in the process of establishing a pair-bond) at the nest, or on a vacant ledge.

Discussion: This is usually the first mutual display, and physical contact between two birds engaging in prolonged social interactions. See discussion of section 6.2.5.

6.2.5 BEAK THRUSTING (Fig. 19)

Synonyms: BEAK THRUSTING (Sorenson 1950)

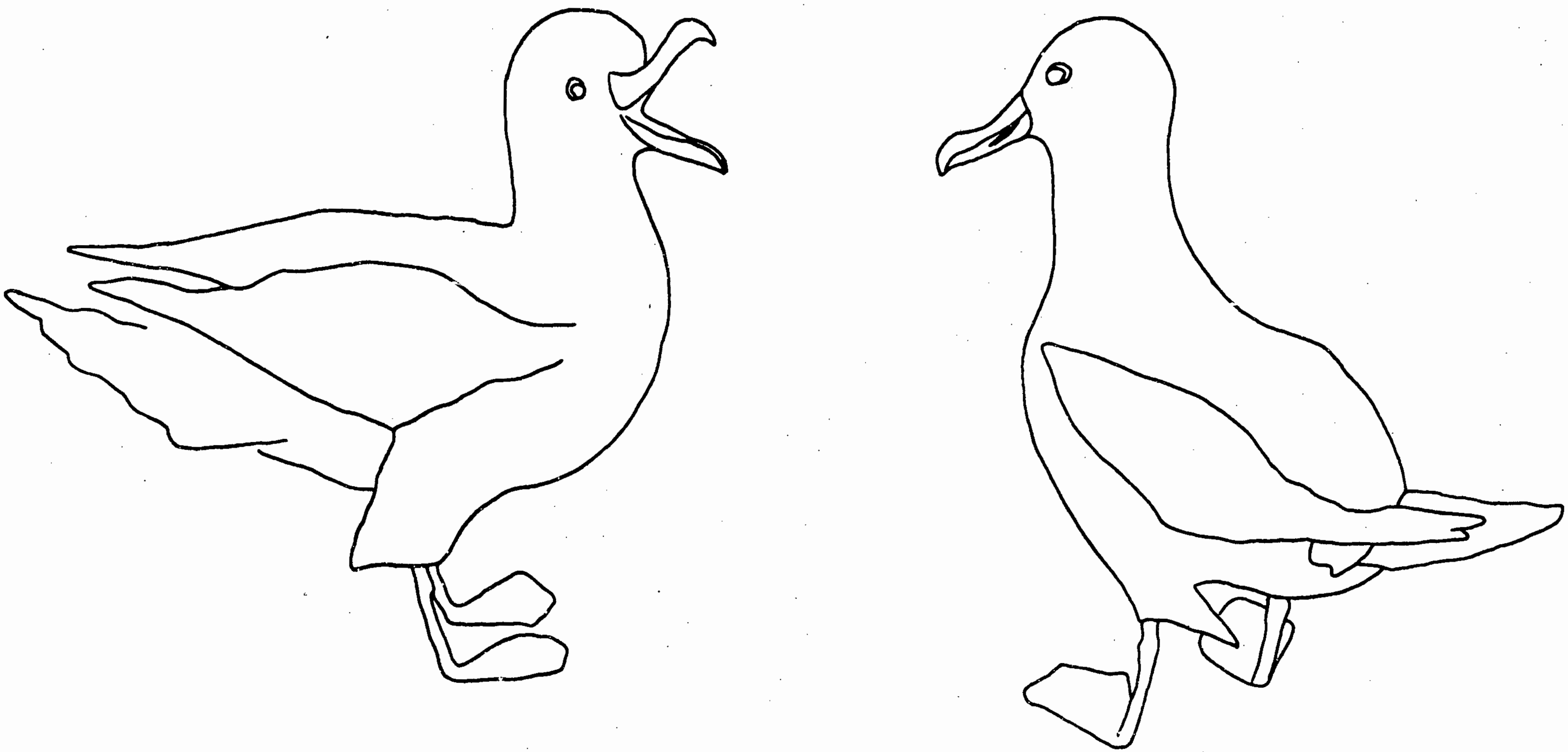
Typical performance: This display occurs in palpebrata only. Two birds stand facing each other with crests raised. Each bird moves its head from side-to-side. As the head of one bird directly faces the other during the side-to-side movement, the head is raised and the action of an exaggerated bite is performed, with the pink mouth interior showing conspicuously. The side-to-side movements are synchronized such that the birds make alternate biting movements. No actual physical contact is made. The tail is fanned at an angle of 45^{o} and skewed to one side.

Variations: The number of sideways head, and biting movements is variable.

Contexts: BEAK THRUSTING is given by two birds (thought to be a mated pair, or in the process of establishing a pair-bond) at the nest,

FIGURE 19

BEAK THRUSTING IN PHOEBETRIA PALPEBRATA



or on a vacant ledge.

Discussion: This is usually the first mutual display performed by two birds engaging in prolonged social interactions.

I consider that BILL CLASHING and BEAK THRUSTING are homologous displays given in the same context. The basic movements and postures are similar. I consider that BEAK THRUSTING is a more aggressive display than BILL CLASHING. A primary component of BEAK THRUSTING (palpebrata) is the ritualized bite, whereas the beak is not opened in BILL CLASHING (fusca). In fusca the members of a pair performing BILL CLASHING stand close together, and take part in highly ritualized physical contact, whereas in palpebrata, the two birds stand farther apart, and make no physical contact.

6.2.6 ALLOPREENING (Fig. 20)

Synonyms: "Mouthing" (Richdale 1950, Rice & Kenyon 1962) and "Mutual Preening" (Johnstone et al. 1975).

Typical performance: In fusca, one bird preens the other, concentrating attention around the head region, especially around the eye and base of the beak. The actual preening movements accord with McKinney's (1965) description of nibble-preening in ducks. The recipient responds by tilting the head, and partially closing the eye, and may actually be directing preening movements by changes in head orientation. One or both birds may be standing as the display commences, but one or both birds sit as the display proceeds. Birds may preen each other simultaneously.

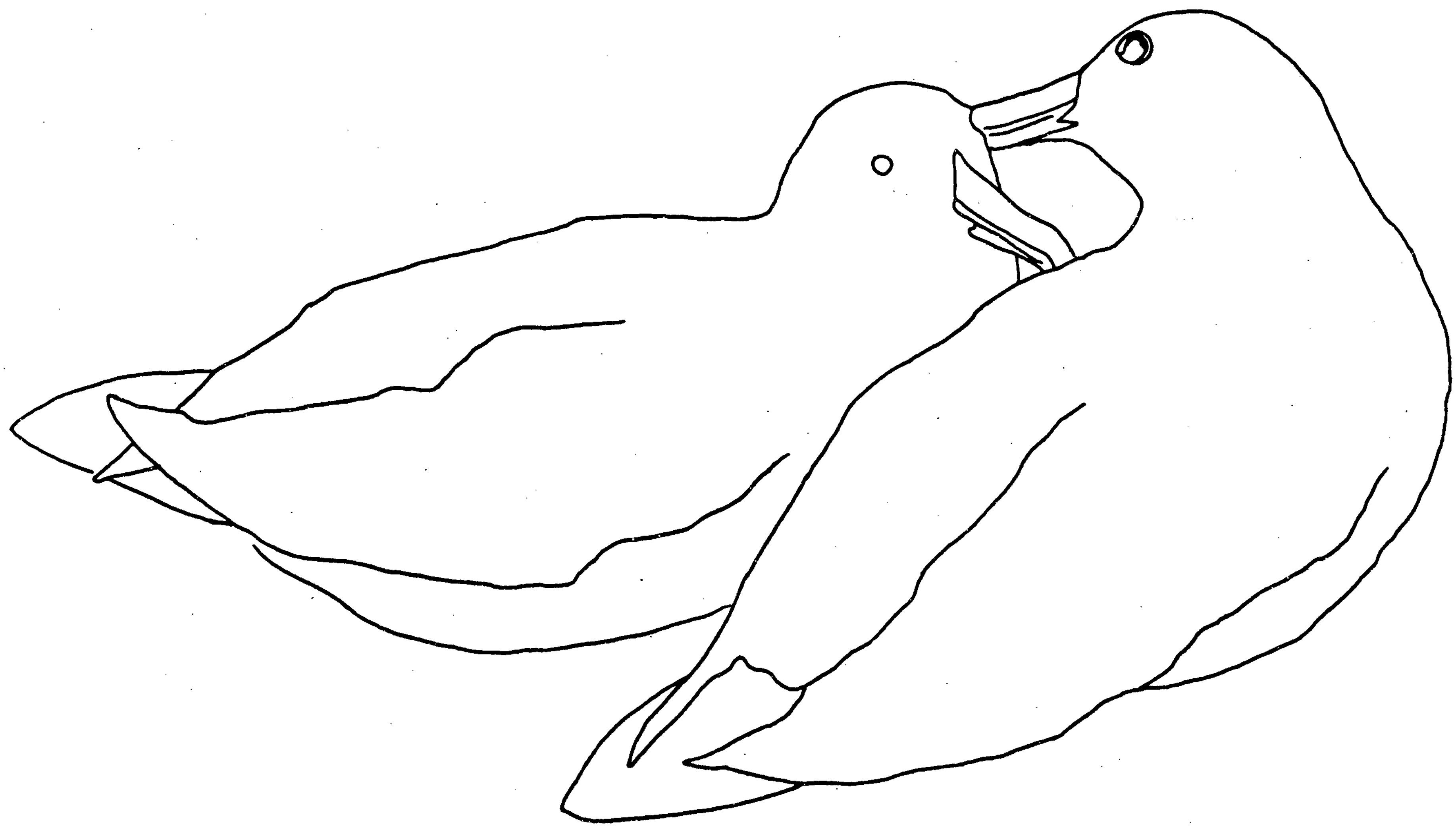
ALLOPREENING is performed in a similar way in palpebrata, but is apparently performed less frequently.

Variations: The duration, intensity and site of preening are variable.

Contexts: ALLOPREENING is performed by two birds (thought to be a mated pair, or birds in the process of establishing a pair-bond) during

FIGURE 20

ALLOPREENING IN <u>PHOEBETRIA</u> <u>FUSCA</u>



prolonged social interactions. After bouts of ALLOPREENING, birds often cease the performance of overt behaviour, and assume sleeping postures, or begin preening.

Discussion: The performance of ALLOPREENING apparently reduces aggressive tendencies between two birds to a minimum, such that the conflict situation no longer exists. The birds are then able to perform maintenance activities eg. autopreening and sleep, while in close proximity of a second bird.

ALLOPREENING appears to be functional in feather care, and in the removal of ectoparasites from body regions relatively inaccessible to the bird, as well as having a social function.

6.2.7 SCOOPING (Fig. 21)

Synonyms: SCOOPING (Richdale 1949).

Typical performance: This display occurs in palpebrata only. Two birds are present, one or both of which are standing. A standing bird bows slightly, lowers its beak while holding the head slightly to one side. The beak may touch the breast. The tail is fanned at an angle of 45°, and is skewed towards the second bird. The posture is held for two or three seconds.

Variations: There is apparently little variation in the display.

Contexts: SCOOPING is performed during agonistic encounters between two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

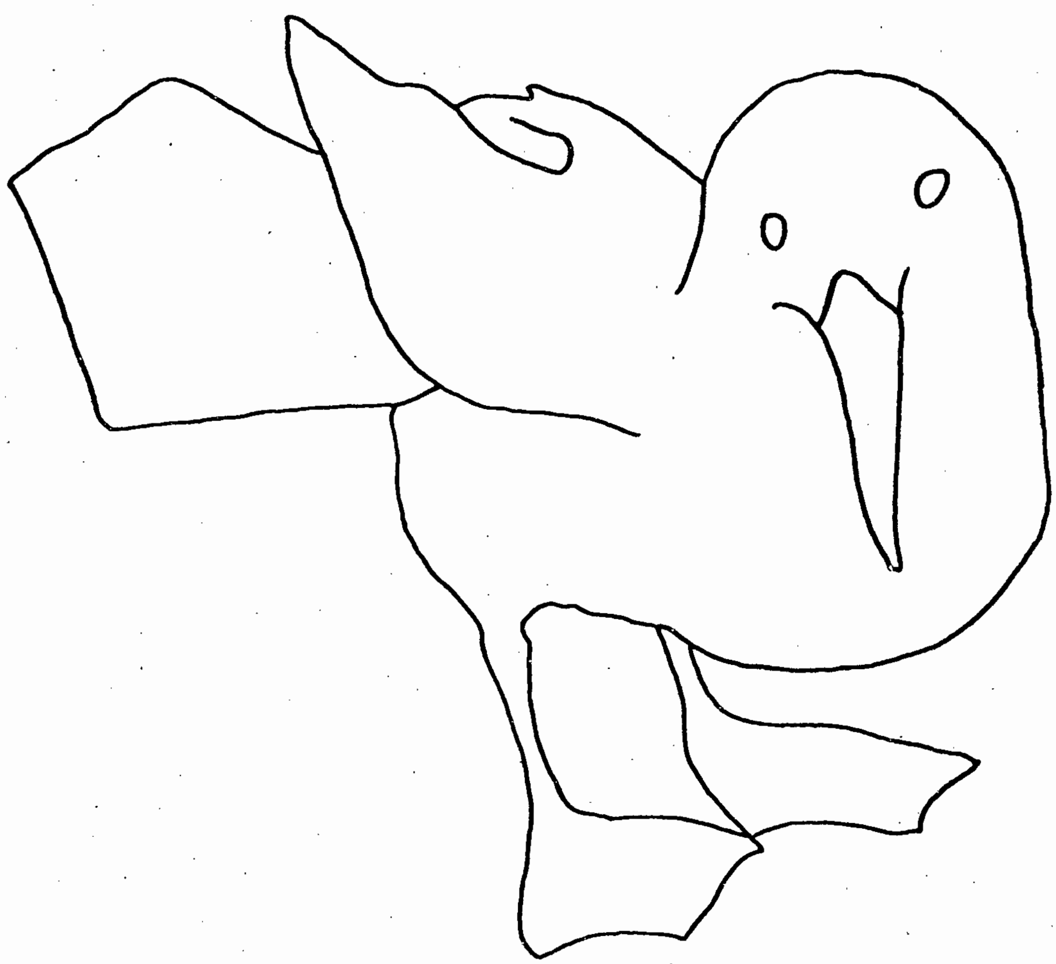
Discussion: Phoebetria fusca does not appear to have a display homogous with SCOOPING.

6.2.8 PADDLE-WALK

Synonyms: None.

FIGURE 21

SCOOPING IN PHOEBETRIA PALPEBRATA



Typical performance: This display occurs in palpebrata only. Two birds are present, one or both of which are standing. A standing bird moves toward the second bird, shuffling the feet and legs forward with brisk up-and-down "paddle" movements.

Contexts: PADDLE-WALK occurs during prolonged agonistic encounters between two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

Discussion: Phoebetria fusca does not appear to have a display homologous with PADDLE-WALK.

6.2.9 AUTOPREENING (Fig. 22)

Synonyms: "Leg Action" (Richdale 1949).

Typical performance: In fusca, a standing bird nibble-preens feathers on the flanks, or less often, on the breast or upperparts AUTOPREENING seldom lasts more than a few seconds. The bird occasionally makes preening movements without opening the beak, or touching any feathers.

AUTOPREENING is performed similarly in palpebrata.

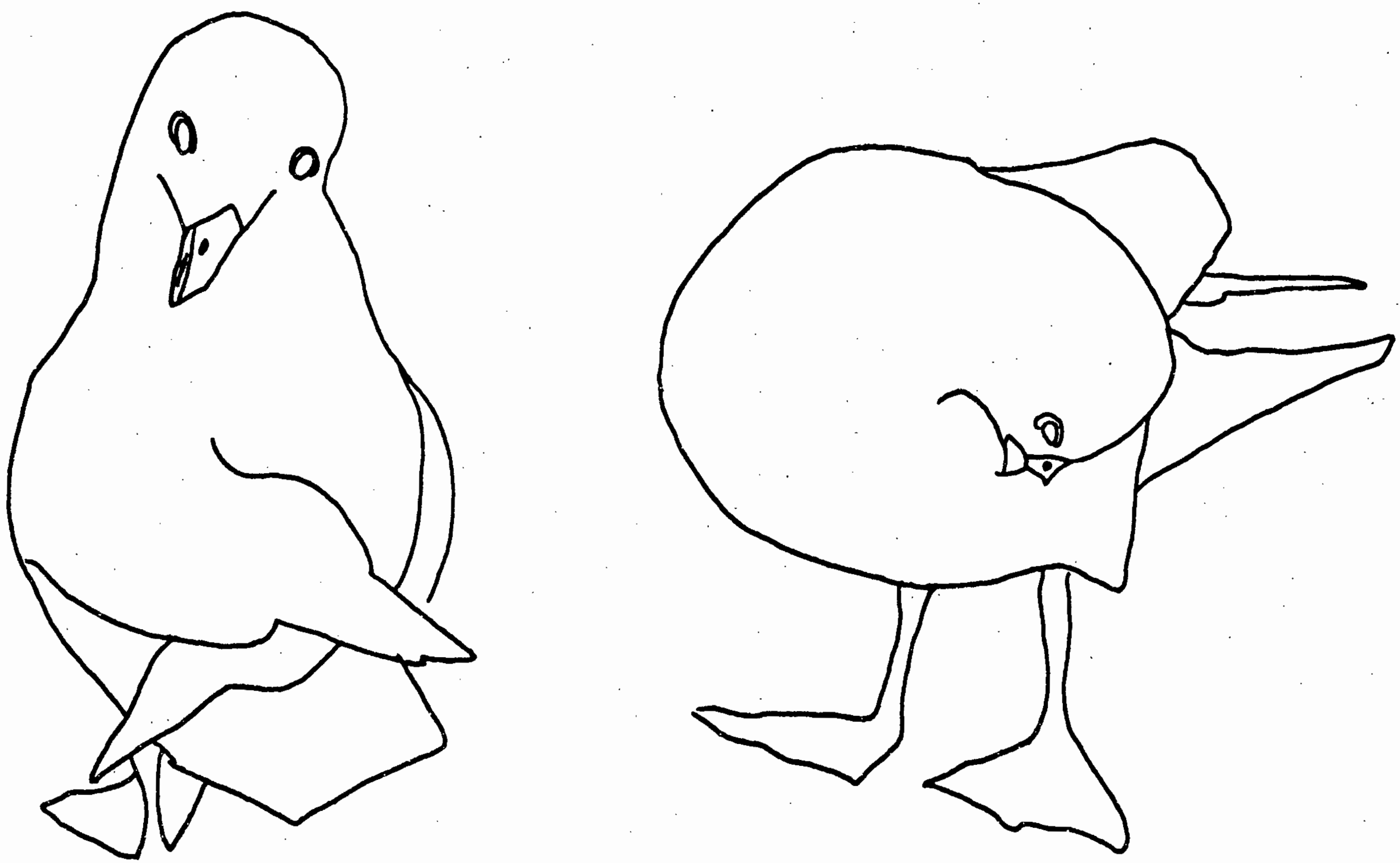
Variations: The site, duration and movements of preening are highly variable.

Contexts: AUTOPREENING occurs briefly during prolonged agonistic encounters between two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

Discussion: AUTOPREENING is apparently a displacement activity performed during agonistic encounters, which has become ritualized. Some preening movements appear to be functional, but others are rudimentary. Some of the more ritualized movements accord with Richdale's (1949) description of "Leg Action" in D. bulleri.

FIGURE 22

AUTOPREENING IN <u>PHOEBETRIA</u> <u>FUSCA</u>



6.2.10 SCAPULAR ACTION (Fig. 23)

Synonyms: SCAPULAR ACTION (Richdale 1949, Rice & Kenyon 1962)

Typical performance: In <u>fusca</u>, a standing bird turns its head and places the beak at the junction of the wing and body. The tail is fanned at an angle of 45°, and is skewed to one side.

SCAPULAR ACTION is performed similarly in <u>palpebrata</u>.

Variations: Variability was not recorded, as the display was rarely observed.

Contexts: SCAPULAR ACTION is given during prolonged agonistic encounters between two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

Discussion: SCAPULAR ACTION was observed rarely, and appears to be a highly ritualized preening movement.

6.2.11 FOOT LOOKING (Fig. 24)

Synonyms: "Nodding" (Richdale 1949).

Typical performance: In <u>fusca</u>, a standing bird bows its head, placing its beak between its legs, and occasionally touching the lower abdomen with its beak. A biting movement may be performed between the legs. FOOT LOOKING lasts two to three seconds.

FOOT LOOKING is performed similarly in <u>palpebrata</u>.

Variations: The bird may bow its head two or three times. There is variability in beak movement.

Contexts: FOOT LOOKING may be performed spontaneously apparently in isolation. It also occurs during prolonged agonistic encounters between two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

Discussion: FOOT LOOKING is apparently a nest-site orientated display.

FIGURE 23

SCAPULAR ACTION IN PHOEBETRIA FUSCA

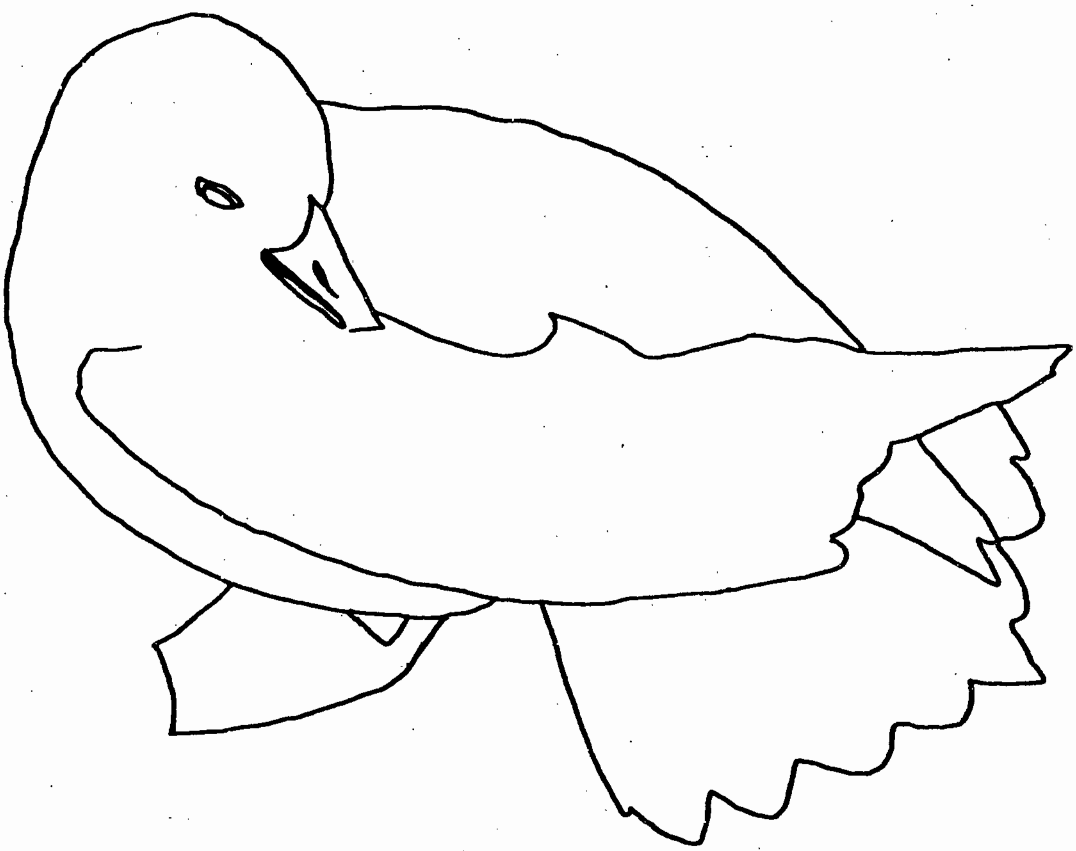
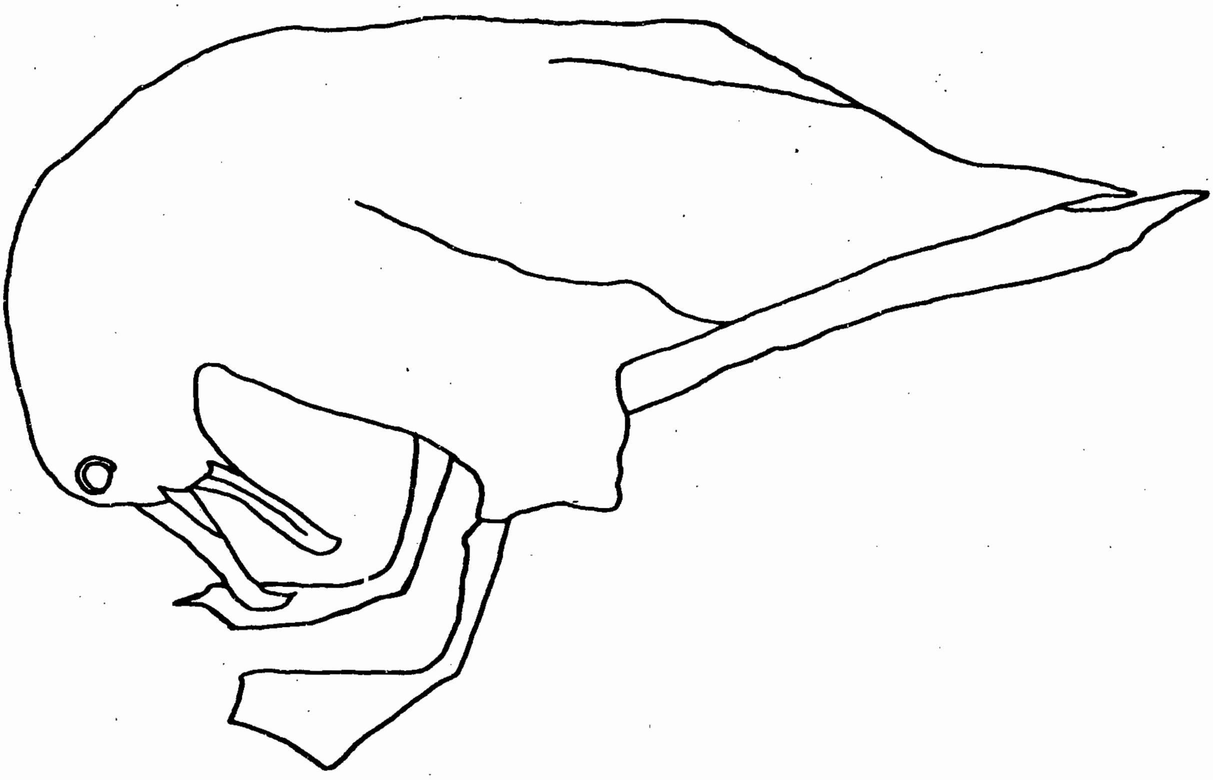


FIGURE 24

FOOT-LOOKING IN PHOEBETRIA FUSCA



6.2.12 SYNCHRONOUS FLYING

Synonyms: None.

Typical performance: In *fusca*, two birds synchronize flight manoeuvres to a marked degree, while flying back and forth past the breeding cliffs. The wings are seldom actively flapped, and the birds glide and soar in wind currents rising against the cliffs, or waves.

SYNCHRONOUS FLYING is performed in a similar way in *palpebrata*.

Contexts: SYNCHRONOUS FLYING is performed by two birds (thought to be a mated pair, or in the process of establishing a pair-bond).

Discussion: Complex aerial displays are not recorded in *Diomedea* (Richdale 1949, 1950, Rice & Kenyon 1962, Johnstone *et al.* 1975). The aerial display appears to be an important display in *fusca* and *palpebrata* which otherwise have smaller repertoires of displays than members of *Diomedea* (Richdale 1950).

6.3 Synthesis

I assume that behavioural differences between *fusca* and *palpebrata* are important in maintaining genetic isolation between the two species. Hybrids, mixed pairs or even prolonged interspecific encounters have not been observed at Marion Island, or elsewhere, despite the lack of temporal and spatial segregation that exists at places where the two species breed sympatrically. However, the sympatric populations are small, reducing the chances of hybridization. It is possible that hybrids have occurred in the past, but have not been recognized as hybrids because they have been identified wrongly as juvenile *fusca* or *palpebrata*, as the plumage descriptions of this age class are so confused.

There are three major differences in the social behaviour of *fusca* and *palpebrata*. Firstly, the homologous displays of BEAK THRUSTING (*palpebrata*) and BILL CLASHING (*fusca*) are markedly different. Secondly, palpebrata has two displays, PADDLE-WALK and SCOOPING, which apparently have no homologues or analogues in the behavioural repertoire of fusca. Thirdly, palpebrata apparently is more aggressive generally than fusca. The BEAK THRUSTING display of palpebrata has more aggressive components than the homologous BILL CLASHING of fusca. Phoebetria palpebrata usually supplants fusca in interspecific agonistic situations. On one occassion, an adult palpebrata attacked and chased two adjacent palpebrata, after having been attacked by one of these birds. Such aggressive contacts were not recorded for fusca, in spite of the relatively greater number of observations for the species.

Genetic isolation between fusca and palpebrata is apparently maintained by behavioural differences, which are emphasized by species-specific morphological characteristics. Fisher (1972) showed that behavioural differences, emphasized by morphological characteristics, maintained genetic isolation between sympatric populations of D. nigripes and D. immutabilis. If a fusca lands next to a palpebrata, or vice versa, the two birds appear to recognize immediately that the other is not a conspecific. It appears that the species-specific morphological characteristics (general plumage coloration, body size, sulcus colour, beak and eye-ring shape, presence or absence of a crest) provide the cues which allow the birds to distinguish conspecifics and other species. The usual social interaction between fusca and palpebrata was restricted to threat displays, with palpebrata usually supplanting fusca. Should a fusca and a palpebrata incorrectly regard each other as conspecifics (which was not observed) the performance of BEAK THRUSTING, PADDLE-WALK or SCOOPING by palpebrata, or BILL CLASHING by fusca, would presumably be malappropriate to the other bird, and interrupt any incipient pair-bonding sequence. The long courtship period (probably requiring a year or more for establishment of a pair-bond in either species) would provide apportunities for termination of "wrong" pair-bonds.

The complexity and types of social behaviour of the Diomedeidae are consistent with the amount of space available at the nest site. Species nesting on open, flat areas, e.g., D. exulans, D. epomophora, D. nigripes and D. immutabilis, have elaborate courtship dances, spread-wing postures and a greater number of displays than other Diomedea species (Richdale 1950, Rice & Kenyon 1962). Species nesting on slopes or uneven terrain with a corresponding decrease in nest site area, e.g. D. bulleri, D. chlororhyncos and D. cauta have less elaborate courtship dances, no spread-wing postures and a small number of displays (Richdale 1949, Rowan 1951, Johnstone et al. 1975). The behaviour of D. melanophris, D. chrysostoma, D. irrorata and D. albatrus has not been described in detail. The cliff-nesting fusca and palpebrata have a very small nest site area. Displays are reduced in number, and show a minimum of movement. There is no courtship dance, or spread-wing posture. However, both species have an elaborate aerial display. I suggest that in Diomedea, the birds have relatively more space and time for signalling intentions, and thus the opportunity exists for a relatively large variety of postures potentially available for ritualization. Since the nest sites of Phoebetria are small, conflict over space often arises suddenly when one bird lands next to another at the site. The situation demands quick, clear signals of intentions by both birds. It is possible that differences in signal quantity, rather than signal quality, are more important in Phoebetria than in Diomedea which has a larger repertoire of displays.

The behavioural differences between fusca and palpebrata are consistent with the difference in dispersion of nest sites between the two species. In palpebrata there has been selection for relatively dispersed nests (Section 7.2), associated with the birds' aggressive temperament. Nest-site area is presumably larger in palpebrata than fusca. In palpebrata, the initial mutual display BEAK THRUSTING is aggressive, and does not include physical contact between the birds. I suggest that the two displays SCOOPING and PADDLE-WALK, with no recorded homologues in _fusca_, are necessary to reduce aggressive tendencies in realizing close physical contact between members of a pair. It is perhaps significant that PADDLE-WALK involves movement, and actually reduces distance between birds.

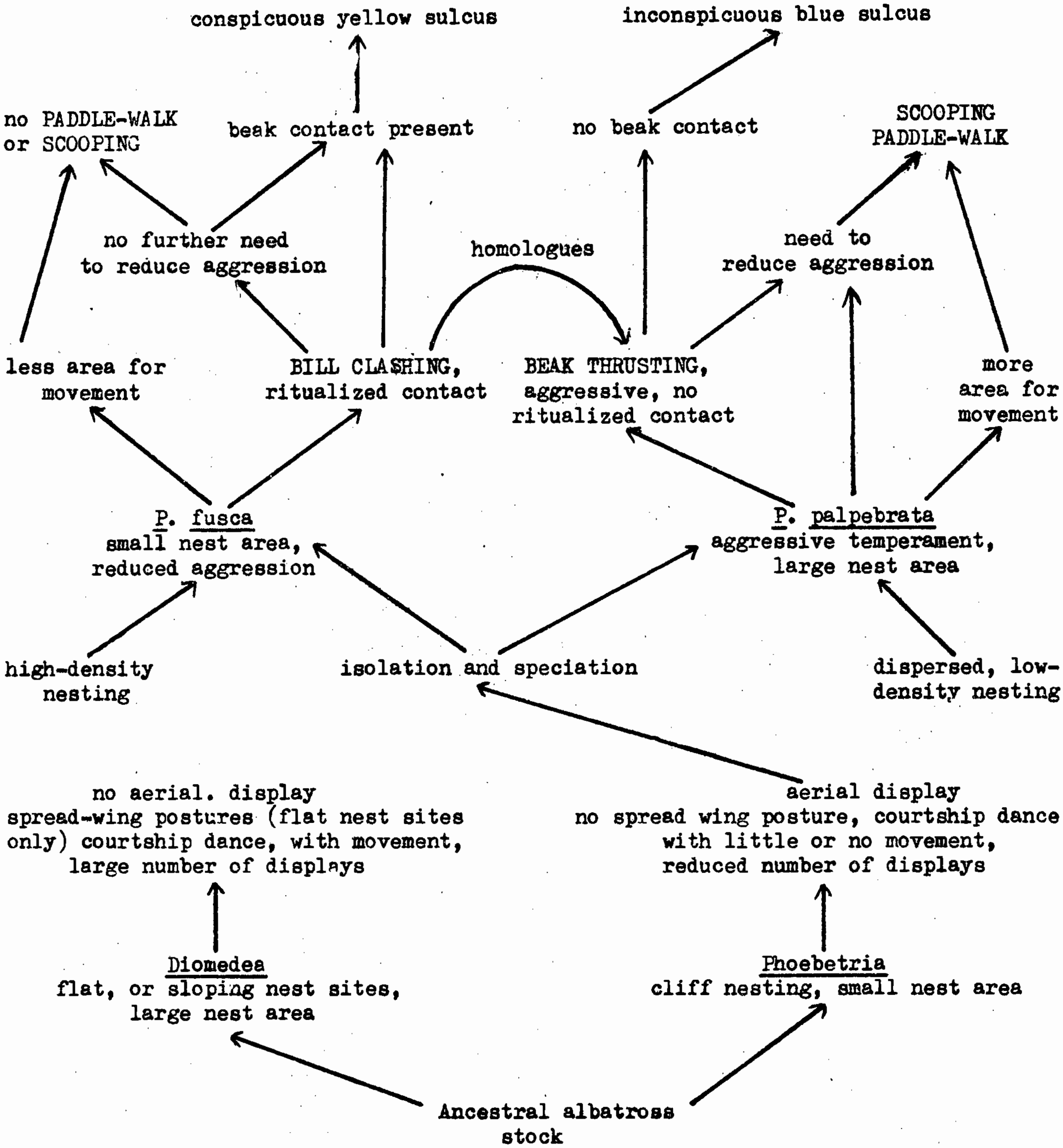
In _fusca_, there has been selection for relatively high nesting density (Section 7.2), associated with a reduction in intraspecific aggression. A relatively high level of aggression would tend to reduce breeding success, as eggs exposed during intraspecific fighting may be eaten within minutes by Brown Skuas _S. skua_, or Sheathbills _C. minor_. The energetic expenditure of intraspecific fighting may be too costly for a species which has difficulty providing sufficient energy to raise a single pullus. With decreased nest site area and reduced aggression, the birds make ritualized physical contact during BILL CLASHING, the initial mutual display of _fusca_. There is no need for further displays to reduce aggression and physical distance between birds.

In the sympatric _D. immutabilis_ and _D. nigripes_, the displays of the more aggressive _D. nigripes_ involve less beak contact than in _D. immutabilis_ (Fisher 1972). A similar trend is observed in _fusca_ and _palpebrata_. In _fusca_ and _palpebrata_, and in _D. nigripes_ and _D. immutabilis_, the species with little or no ritualized beak contact have inconspicuously coloured beaks (black in _D. nigripes_, blue sulcus in _palpebrata_), whereas the species showing more ritualized beak contact have conspicuously coloured beaks (yellow in _D. immutabilis_, yellow sulcus in _fusca_).

A summary of the suggested evolutionary history of the social behaviour in _fusca_ and _palpebrata_ is given in Fig. 25.

FIG. 25

SUGGESTED EVOLUTIONARY HISTORY OF SOCIAL BEHAVIOUR IN PHOEBETRIA FUSCA AND P. PALPEBRATA



7 Synthesis and Conclusions

The principle of competitive exclusion, formerly known as Gause's hypothesis (Lack 1971), holds that no two species inhabit the same ecological niche. In this light, the co-existence of two congeneric albatrosses with very similar morphologies and breeding biologies is apparently anomalous. However, the present study suggests that _fusca_ and _palpebrata_ at Marion Island partition food and nest-site resources, so allowing co-existence of the two species and concomitantly maintaining genetic isolation.

7.1 Food

Lack (1968) argued that the breeding biology of the Procellariiformes is adapted to a food resource irregularly, and often sparsely, distributed in space and time. Lack (1971) suggested that partitioning of food resources by spatial separation, or by feeding in the same area at different times, is common in seabirds. Further partitioning can be attained by selection of different prey species, or different prey size ranges, by temporal differences in the intensity of food source utilization and by differences in methods of prey capture. If it is normally difficult for procellariiforms to deliver sufficient energy for raising one fledgling (Lack 1968), then neither _fusca_ nor _palpebrata_ can afford to compete for the same food resources.

It appears that the cephalopod-based diets of _fusca_ and _palpebrata_ overlap to a large extent in species composition. Although non-cephalopod prey (especially soft foods such as tunicates) has not been studied, there was no indication in the present study, or in the literature, that either _fusca_ or _palpebrata_ takes a major food type not consumed by the other. However, in cold-water environments, species richness is low but species abundance is high, so that the species composition of the diets of the two albatrosses could be expected to overlap. Imber (1976) suggested that the diets of the procellariiforms differed relatively, rather than absolutely. The cephalopod diets of fusca and palpebrata were qualitatively similar, although the frequency of occurrence and mean size of cephalopod species taken tended to differ ie., the diets were quantitatively different. Diets of fusca and palpebrata were compared over three months in late summer, when prey presumably is still fairly abundant. Qualitative differences in the species of cephalopods taken by fusca and palpebrata may occur at other times of year, especially when food is less abundant. The food resources utilized by the Phoebetria populations at Marion Island are subjected to the same temporal pattern of utilization intensity. The three weeks difference in the chronologies of the two albatrosses' breeding seasons (which are eight months long) are not considered important in potentially reducing interspecific competition for the same food resources. Similarly, there appears to be no difference in moulting strategy between the two avian populations.

Recent studies suggest that many procellariiform species feed at the same time of day (Imber 1973, 1976, Imber & Russ 1975). Thus, the procellariiforms are generally nocturnal feeders, catching prey made available by night-time vertical migration to the ocean surface. There are very few records of actual prey-catching behaviour in the Diomedeidae. Murphy (1936) mentions five species of albatrosses which were seen to dive for prey, with only wing tips showing above the surface of the water. The similar morphologies of fusca and palpebrata do not indicate any potential interspecific difference in the method of prey capture.

Spatial separation of feeding areas of the Marion Island populations of breeding fusca and palpebrata has been suggested by van Zinderen Bakker (1971), who proposed that palpebrata foraged to the south of the Antarctic Convergence and fusca mainly to the north. The Antarctic Convergence lies to the south of Marion Island. Sea surface temperatures change markedly at the Convergence, and as such may constitute a barrier to pelagic birds in an otherwise homogeneous environment. The sea surface temperature might be used by seabirds as a cue to identify preferred feeding regions. The marine environment is essentially a horizontal habitat for pelagic procellariiforms which may be expected to partition the sea (and therefore food resources) interspecifically in the horizontal plane, similar to what Cody (1968) showed to be the case for grassland bird communities. Such pelagic spatial separation occurs in the sympatric species *D. immutabilis* and *D. nigripes* (Sanger 1974). Recoveries of *D. melanophris* banded at the Falkland Islands and South Georgia, and of *D. chrysostoma* banded at South Georgia have been discussed by Tickell (1967). Banding recoveries of juvenile and subadult *D. melanophris* showed that the South Georgia population occurs off South Africa, whereas the population of the Falkland islands occurs off eastern South America. Far fewer banding recoveries of *D. chrysostoma* were made, indicating that this species does not usually occur in either area. The two species have similar morphologies and nest site locations, but relatively large differences occur between the breeding biologies of the two species (Tickell & Pinder 1975). Although the banding recoveries do not demonstrate spatial separation at sea of sympatric breeding populations of the two albatross species, they do suggest that the juveniles and subadults, of two different island populations of the same species (*D. melanophris*), and of two sympatrically breeding species (*D. melanophris* and *D. chrysostoma*), are separated at sea.

The relatively high procellariiform and sphenisciform species richness at the Kerguelen, Crozet, Marion and Prince Edward islands suggests that there is either a relatively great diversity of nesting habitat, or that there is a relatively great diversity of feeding habitat, or both, in the vicinity of these islands; this would allow a relatively large number of avian species to co-exist. The fact that several of these species reach their northernmost or southernmost breeding limits at these islands may be correlated with the fact that the islands be close to, or on the Antarctic Convergence, a transition between cold and temperate sub-Antarctic waters. Thus, species (Such as palpebrata) breeding mainly in cold sub-Antarctic areas, and species (Such as fusca) breeding mainly in temperate sub-Antarctic areas can co-exist at Marion Island, as suitable feeding grounds exist there for both groups of species.

Lack (1968) suggested that the duration of the incubation shift, and the frequency of food delivery to the pullus, depend on the distance that the parent has to travel to find food or the difficulty experienced in finding food. Brown (1975) showed that increasing length of incubation shift in the Sooty Tern Sterna fuscata was correlated with increasing distance to feeding grounds. The relatively long incubation and brooding shifts of palpebrata at Marion Island indicate that this species travels farther to feed than fusca. The fact that the duration of the brooding and incubation shifts can vary according to local environmental conditions is demonstrated by the incubation shifts of palpebrata being shorter at the Crozet islands than at Marion Island, and the approximately equal incubation shifts of palpebrata at the Crozet islands and fusca at Marion Island.

Frost (unpublished) showed that fusca and palpebrata separate spatially at sea in the vicinity of Marion Island. During March-April 1976, Frost repeatedly observed palpebrata close to the Kerguelen, Crozet, Marion and Prince Edward islands only, whereas fusca occurred in numbers north of the Convergence. I suggest that the palpebrata birds observed in the immediate vicinity of the islands were subadults, visiting the cliffs to establish pair-bonds, and adult birds returning to feed pulli. Alternatively, deep colder waters well up to the surface against the island masses, creating suitable cold-water habitat for foraging palpebrata.

In either event, I suggest that breeding palpebrata and fusca are able to co-exist at Marion Island by partitioning food resources spatially, and that palpebrata feeds in cold-water areas south of the Antarctic Convergence and hence has farther to travel to feeding grounds than fusca which feeds mainly to the north of the Convergence.

Rowan (1965) argued that some southern temperate-zone seabirds are not limited by sparsely distributed food resources, since the birds are able to cover large distances between consecutive visits to pulli. Kenyon & Rice (1958) showed that D. immutabilis could cover 5,000 km in 10 days. Rice & Kenyon (1962) reported that an adult D. immutabilis banded on the nest was recovered 22 days later 3 700 km away. However, even if food does not regulate procellariiform populations, the hypothesis that feeding frequencies and duration of incubation and brooding shifts are correlated with the distance that adults must fly to obtain food is not invalidated.

If the characteristics of the food resource are important in shaping procellariiform breeding biology, the breeding strategies of fusca and palpebrata should be adapted to the spatial and temporal distribution of food resources in the temperate sub-Antarctic and the cold sub-Antarctic respectively. Generally, the cold waters have an abundant food supply over a short period in summer. Farther north, at warmer lower latitudes, the peaks of food abundance are lower, but food is available for longer periods of time (Watson 1975). Ricklefs (1973) suggested that the procellariiforms have difficulty in feeding their pulli sufficient energy. Thus, growth rate is slowed to reduce the amount of energy required for growth, as opposed to energy requirements for basal metabolism and maintenance activities. Thus procellariiform fledgling periods are long. At high latitudes, palpebrata parents should be able to provide their pulli with relatively large amounts of energy per unit time, since food is more abundant than farther north. Additionally, food resources are available for a relatively short period. Lack (1968) suggested that for those procellariiforms which experience more favourable conditions for feeding pulli (eg., palpebrata), natural selection has favoured the evolution of a more rapid growth rate instead of an increase in clutch size. Therefore, palpebrata should have a faster growth rate and shorter fledgling period than fusca. At Marion Island, palpebrata pulli grew slightly faster than fusca pulli over at least the first 100 days after hatching, but fledgling periods were approximately equal in the two species. However, the fledgling period of palpebrata pulli at the Campbell and Crozet islands is shorter than at Marion Island. This suggests that palpebrata pullus growth is more rapid at Campbell and Crozet islands than at Marion Island. In birds generally, there is a tendency for growth rate to decrease with increasing body size (Ricklefs 1973). Phoebetria palpebrata is larger than fusca, but apparently has a faster growth rate. This suggests that palpebrata has a more abundant food supply, and is able to deliver more energy per unit time to the pullus than fusca.

The evolution of a relatively slow pullus growth rate involves a slowing of the growth rate of the embryo in the egg as well (Lack 1968). This suggests that a species (eg., fusca) with a slow growth rate should have a longer incubation period than a species (palpebrata) with a faster growth rate. Lack (1968) showed that length of procellariiform incubation period is correlated with the length of flegling period, although he cited several exceptions. On this basis, palpebrata should have a shorter incubation period than fusca. This is, in fact, the case in spite of the larger egg of palpebrata. However, the tendency for the incubation period to increase in duration with increasing egg size is not constant in the procellariiforms (Lack 1968).

Lack (1968) argued that for seabirds generally the duration of the average incubation shift, and the interval between consecutive feeds delivered to the pulli corresponds to the distance the parent has to fly to find food (also shown by Brown (1975)), or the difficulty the parent has in obtaining food. Thus, palpebrata (with a faster growth rate and therefore requiring more energy per unit time) should have shorter incubation and brooding shifts than fusca, and should feed the pullus more frequently than fusca. However, the opposite appears to hold true at Marion Island. As argued above, a palpebrata parent has to fly farther to the breeding grounds, and thus does not feed its pullus as frequently as apparently occurs at other islands. The incubation shifts of palpebrata parents are shorter at the Crozet islands than at Marion Island, and they are approximately equal to fusca shifts at Marion Island. Phoebetria palpebrata is more numerous than fusca at the Crozet islands. I suggest that palpebrata parents at Marion Island are only just able to deliver sufficient energy per unit time to allow the pullus to fledge, and that the pullus would starve should the feeding frequency drop still further.

The procellariiform egg is proportionately larger than in most other avian families (Lack 1968). This functions to provide the pullus with a food reserve over the first few days of life, as feeding in the procellariiforms is intermittent, and there may be an interval of several days before the first feed, and between subsequent feeds (Lack 1968). It is advantageous for a species with a relatively low feeding frequency (ie., a species with a relatively slow growth rate) to have a proportionately large egg despite increasing difficulties of egg formation, since the intervals before the first, and between subsequent, feeds will tend to be relatively long. Thus, one would expect fusca to have a proportionately larger egg than palpebrata. This is the case at Marion Island. Further, if palpebrata at Marion Island has a slower growth rate and lower feeding frequency than elsewhere, then the egg at Marion Island should be larger than elsewhere. Eggs at Campbell Island apparently are lighter in mass and smaller than eggs at Marion Island.

A suggested outline of the evolutionary relationships of breeding adaptations in relation to food resources in the Diomedeidae is shown in Fig. 26. The characteristics of the breeding biology and diet of _fusca_ at Marion Island, and _palpebrata_ at Marion Island and elsewhere, is shown in Table 40.

I hypothesize, as argued above, that an albatross species with a relatively slow growth rate (as determined by the length of the fledgling period), should have a proportionately larger egg, a longer incubation period, longer incubation and brooding shifts, and a lower pullus feeding frequency than a sympatric, similarly sized albatross species with a faster pullus growth rate. Secondly, I suggest that the growth rate in albatrosses is related to the amount of energy delivered per unit time to the pullus, ie. the albatross pulli grow at the maximum possible rate.

Data presented in Tickell & Pinder (1975) show that the first hypothesis holds true for the similarly-sized sympatric, _D. melanophris_ and _D. chrysostoma_ at South Georgia. _Diomedea chrysostoma_ has a slower growth rate and is a biennial breeder, whereas _D. melanophris_ breeds annually. No data on pullus feeding frequencies are available for the two species. However, _D. chrysostoma_ pulli were fed a smaller amount of food than _D. melanophris_ pulli during their first 80 days after hatching (Tickell & Pinder 1975). The diets of the two species differ (Tickell 1964) and the smaller amount of food delivered to _D. chrysostoma_ pulli need not necessarily imply that relatively less energy was delivered. Thus, the second hypothesis cannot be tested.

Data presented in Rice & Kenyon (1962) show that the first hypothesis holds true for the similarly-sized, sympatric, North Pacific

FIGURE 26

SUGGESTED EVOLUTIONARY RELATIONSHIPS OF BREEDING ADAPTATIONS IN RELATION TO FOOD RESOURCES IN THE DIOMEIDAE

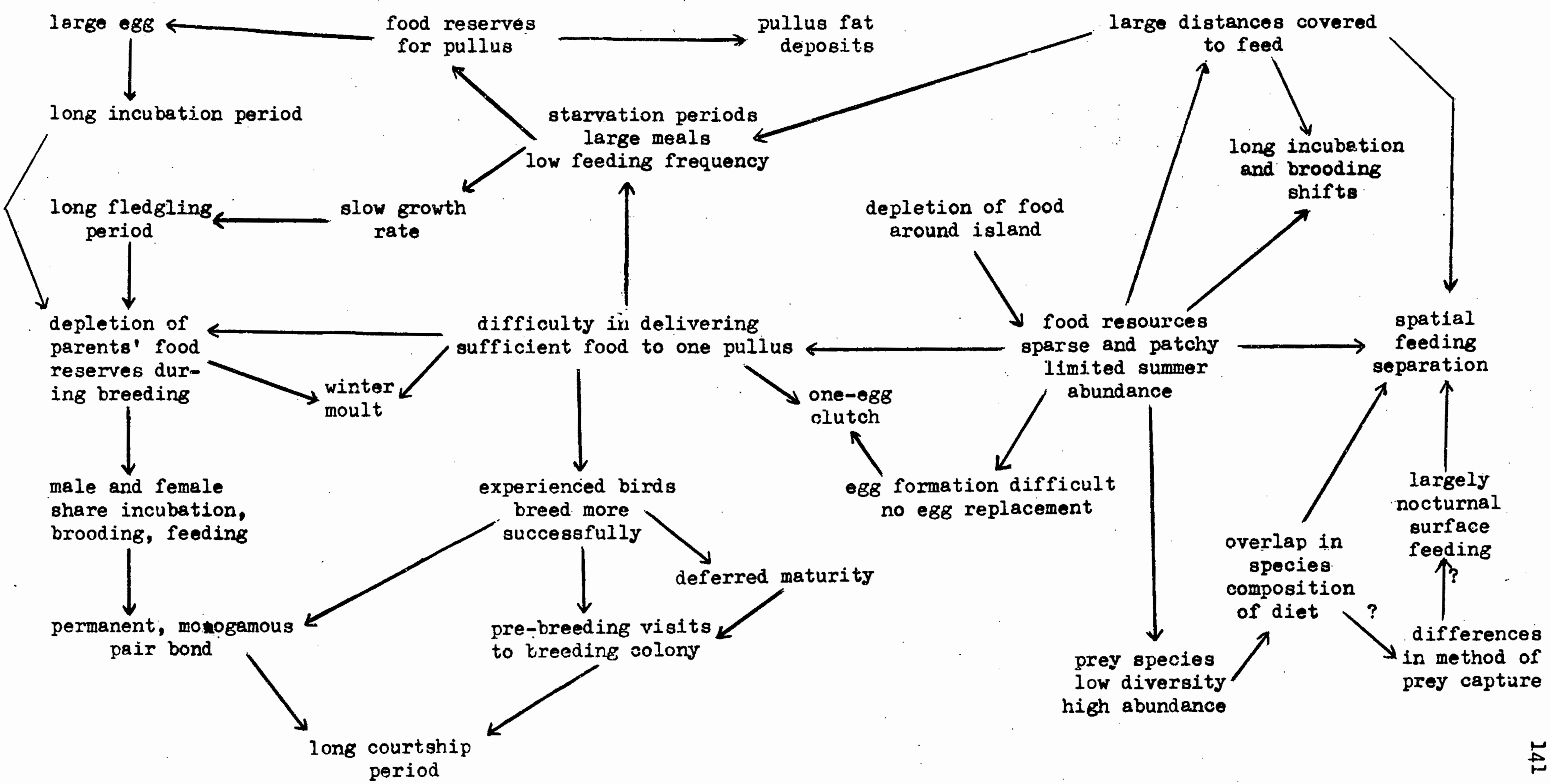


TABLE 40

COMPARISON OF CHARACTERISTICS OF BREEDING BIOLOGY AND DIET OF *PHOEBETRIA FUSCA* AT MARION ISLAND, AND *P. PALPEBRATA* AT MARION ISLAND AND ELSEWHERE

	P. fusca	*P. palpebrata*	
		Marion Island	Elsewhere
Egg size (% body mass)	9,6	9,4	>7,0[1]
Incubation period (days)	69 - 73[3]	65 - 68[3]	63 - 65[1], 65 - 67[2]
Incubation shift	equal to *P. palpebrata* at the Crozet islands	relatively long	equal to *P. fusca* at[2] Marion Island
Brooding period (days)	19[3]	21[3]	
Brooding shift	relatively short	relatively long	
Fledgling period (days)	about 160	about 160	135 - 140[1], 150[2]
Feeding frequency (feeds/day)	0,42	0,39	
Growth rate	relatively slow	relatively fast for first 100 days, then apparently slower	relatively fast
Major food types	similar	similar	similar
Cephalopod prey species	similar[4]	similar[4]	-
Cephalopod prey mean size (g)	about 112[5]	about 105[5]	-
Foraging areas	temperate sub-Antarctic	cold sub-Antarctic	cold sub-Antarctic

[1] Campbell Island (Sorenson 1950)

[2] Crozet islands (Mougin 1970)

[3] Significantly different (P<0,01)

[4] Significantly different in frequency of occurrence (P<0,001)

[5] Three of four cephalopod species significantly different in mass (P<0,025)

D. *nigripes* and D. *immutabilis*. The one exception to the rule is that the incubation period of D. *immutabilis* (which has a relatively slower growth rate) is shorter than that of D. *nigripes*. This may be attributed to the fact that the absolute size of the egg of D. *nigripes* is larger than that of D. *immutabilis*. No data are available to test the second hypothesis.

7.2 Nest site and reproductive isolation

Phoebetria palpebrata and *fusca* overlap in their use of nest sites, and the two species occasionally nest adjacent to each other. However, the two species do have slightly different nest-site requirements at Marion Island, such that most birds of the two populations do not compete interspecifically with each other. The differences in social behaviour which appear to maintain genetic isolation between the two species, are consistent with differences in dispersion of nest sites of the two species. Interspecific competition for nest sites is unimportant to *fusca*, in terms of the relatively small number of potential *fusca* nesting sites occupied by *palpebrata* at Marion Island. However, the *palpebrata* population theoretically could be trebled if all the potential *palpebrata* nest sites now occupied by *fusca* were to become available. It is possible that interspecific competition for nest sites is limiting the *palpebrata* population, since *fusca* occupies nest sites earlier in the season than *palpebrata* at Marion Island.

Several factors suggest that the *palpebrata* population is not limited by interspecific competition with *fusca* for available nest sites at Marion Island. Firstly, coastal and inland *palpebrata* populations are of approximately equal size (45% and 55% respectively of the total population). If interspecific competition with *fusca* for nest sites is limiting *palpebrata*, one would expect the inland nesters to constitute a far greater proportion of the palpebrata population, as fusca does not nest inland. It could be argued that at Marion Island, inland breeding sites are associated with relatively greater pullus mortality, due to relatively lower ambient temperatures and increased incidence of snow and ice. However, the bird frequently nests inland at more southerly islands, where the weather almost certainly is more inclement. Indeed, Watson (1975) states that generally palpebrata "prefers inland breeding sites rather than coastal cliffs". Inland breeding sites would probably be relatively free of Giant Petrels Macronectes spp. which are confined normally to the coastal plain at Marion Island. Thus, escape from the predatory activities of these birds would be achieved by these palpebrata breeders which select nesting sites inland. Secondly, palpebrata are able to nest and raise fledglings successfully in colonies of nesting fusca after these birds have laid eggs. The more aggressive behaviour of palpebrata apparently allows this species to nest in colonies otherwise occupied by fusca. Thirdly, there appears to be a large number of potentially available nest sites unoccupied every year, and not all coastal and inland nests may be occupied the following year at Marion Island. It appears, then, that nest-site availability does not limit the coastal or inland palpebrata population at Marion Island. However, the fusca population may be limited by density-dependent predation of pulli by Giant Petrels, and breeding success in fusca apparently varies with accessibility of the nest sites to these avian predators. Within the relatively large fusca population, some breeders are forced to use nest sites which are readily accessible to Giant Petrels.

I suggest that the differences in nest site dispersion are related to differential selection pressures of predation and exposure to climatic extremes during the speciation of isolated fusca and palpebrata populations. Phoebetria palpebrata presumably evolved in a colder zone than fusca, where more extreme weather conditions, e.g., lower ambient temperatures, higher incidence of snow and ice, occur. A potential nest site which is suitable further north under milder weather conditions, is too exposed for successful breeding in the colder regions, thus reducing the number of available nest sites. Phoebetria palpebrata may have evolved sympatrically with large populations of Giant Petrels. Predation would produce a spacing of nests, and a preference for inland sites, where Giant Petrels do not occur frequently. I suggest fusca evolved in a more temperate zone, where weather conditions would not restrict nest site selection as much as in colder regions. A high nesting density could have been selected for if fusca evolved where Giant Petrel predation was low or non-existent e.g., Gough Island, which has a total estimated Giant Petrel population of 200 birds (Swales 1965) and which lies in the temperate sub-Antarctic.

The differences in nest site characteristics of fusca and palpebrata at Marion Island are summarised in Table 41.

Nesting fusca and palpebrata apparently are able to co-exist on the coastal breeding cliffs at Marion Island, because each species has slightly different nest site requirements and there are sufficient nesting sites available to provide for both species. However, data on the breeding success of both species at the coast, and palpebrata inland, are needed for testing this hypothesis. Studies of the nesting requirements of the sympatric D. melanophris and D. chrysostoma at South Georgia (Tickell & Pinder 1975), and D. nigripes and D. immutabilis at Midway (Rice & Kenyon 1962), have revealed that the nesting requirements differed between the species in each of the two species pairs.

7.3 Conclusions

The food resources used by fusca and palpebrata are apparently partitioned spatially, with palpebrata feeding in cold sub-Antarctic waters

TABLE 41

COMPARISON OF NEST-SITE CHARACTERISTICS OF *PHOEBETRIA FUSCA* AND *P. PALPEBRATA* AT MARION ISLAND

	P. fusca	*P. palpebrata*
Nest site requirements	vegetated ledge on grey lava slope or cliff	vegetated ledge on grey lava slope, or cliff, with bare rock or soil backing wall
Location	coastal	coastal and inland
Nesting density	high	low, except when in *P. fusca* colonies
Nest site area	apparently relatively small	apparently relatively large
Onset of nest-site occupation	September	October
Macronectes pullus predation	apparently variable, high in some colonies	very low inland, possibly high at the coast

south of the Antarctic Convergence, and _fusca_ in the temperate sub-Antarctic region to the north of the Convergence. Considerable overlap occurred in the species and size range of cephalopod prey taken by the two albatross species. No differences are known in the time of feeding or method of prey capture, although these aspects were not studied. The food resources are subjected to the same temporal pattern of utilization intensity.

I suggest that in _palpebrata_ elsewhere than at Marion Island, parents can deliver more energy per unit time to the pullus than in _fusca_. Thus, the growth rate (ie., rate of development) in _palpebrata_ is faster and incubation and fledgling periods are shorter than in _fusca_. I suggest that since feeding frequencies tend to be higher in _palpebrata_ (because more food is delivered to the pullus than in _fusca_,(assuming equal calorific food values and meal sizes), incubation and brooding shifts are shorter. The egg is proportionately smaller in _palpebrata_, since the pullus, which is fed relatively more frequently, requires a smaller food reserve. These correlations between growth rate, duration of incubation and fledgling periods, and incubation shifts, and the proportionate egg size hold for two other species pairs of sympatric albatrosses.

I suggest that _palpebrata_ at Marion Island is unable to deliver as much energy per unit time to the pullus as elsewhere. Thus the growth rate of the pullus is slowed at Marion Island, and fledgling periods and incubation periods are longer than elsewhere. Since feeding frequencies are presumably lower than elsewhere, with resulting increases in the duration of the incubation shifts and proportionate egg size, I suggest that the food resources used by _palpebrata_ at Marion Island are not as abundant as elsewhere, or are located farther from the breeding site than elsewhere, and that the population is marginal because of this. No large difference was apparent in the breeding success of _fusca_ and _palpebrata_.

The difference in population size may result from increased mortality (possibly density-dependent) in palpebrata, of post-fledgling juveniles, which will tend to be underweight at fledgling and hence less fit to survive than fusca, or of breeding adults which have greater difficulty in obtaining sufficient energy for the pullus with a correspondingly greater depletion of their own body food stores associated with reduced capacity for survival. I suggest that fusca is more effeciently adapted to the temperate sub-Antarctic waters surrounding Marion Island, and that palpebrata is unable to compete on equal terms for food in this area. The mechanism by which fusca successfully excludes palpebrata is unknown.

There are differences in nest-site selection, allowing fusca and palpebrata to co-exist at Marion Island. As neither species is numerous enough to occupy all the potentially available nest sites, interspecific competition appears to be limited. The fusca population may be limited through predation of large pulli by Giant Petrels (Macronectes spp.). I suggest that the differences in nest-site requirements of the two species result from differing natural selection pressures of predation and relative weather conditions. Differences in social behaviour apparently maintain genetic isolation of fusca and palpebrata at Marion Island, and are consistent with the differences in dispersion of nest sites of the two species.

8 Summary

The two albatrosses *Phoebetria fusca* and *P. palpebrata* are largely allopatric in their breeding and non-breeding ranges. *Phoebetria fusca* occurs in the temperate sub-Antarctic zone, breeding on islands between 37° and 47°S in the Indian and Atlantic oceans, and has a pelagic distribution between 30° and 50°S in the Indian and Atlantic oceans. *Phoebetria palpebrata* occurs in the cold sub-Antarctic zone, breeding on islands between 46° and 55°S in the Indian and Atlantic oceans, and in the Australasian region, and has a circumpolar pelagic range between 40° and 60°S. Both species breed at the Marion and Prince Edward islands, and Crozet islands, which are situated in the Indian Ocean at 46°50'S and 46°25'S respectively. The numbers of breeding pairs of *fusca* and *palpebrata* at Marion and Prince Edward islands are estimated at 2 732 and 216 respectively. The world population of *fusca* is estimated at 12 000 breeding pairs. The world population of *palpebrata* is incompletely censused, but numbers at least 7 000 breeding pairs.

The two species are morphologically similar. However, adult and subadult *fusca* and *palpebrata* are easily distinguished by differences in plumage and sulcus coloration, and beak and eye-ring shape. Changes in plumage and sulcus coloration of young birds belonging to *fusca* and *palpebrata* are not clearly understood, but juveniles of the two species apparently may be distinguished by beak shape and abdomen coloration.

At Marion Island, *palpebrata* is significantly heavier with a longer wing, tarsometatarsus and tail than *fusca*. However, *fusca* has a significantly longer culmen than *palpebrata*. Although the size differences between the two species are statistically significant, they are not large.

Phoebetria fusca at Marion Island shows a slight degree of sexual dimorphism. The male has a significantly longer culmen, tail and greater

beak depth at the gonys than the female.

Adults and subadults of both species are present at Marion Island during the breeding season only. Breeding fusca return to Marion Island in late August, and egg-laying commences in early October. Breeding palpebrata return to Marion Island in early October, and commence egg-laying in late October and early December. Both species are monogamous. The clutch size is one, and there is no egg replacement. The palpebrata egg is significantly broader and heavier than that of fusca, although the palpebrata egg is proportionately lighter when it is expressed as a percentage of adult mass. At Marion Island, the incubation period of fusca (69-73 days) is significantly greater than that of palpebrata (65-68 days). The mean duration of the brood periods of fusca and palpebrata is 21 and 19 days respectively. At Marion Island, the incubation and brooding shifts of palpebrata tend to be longer in duration, and fewer in number than in fusca. The second and fifth incubation shifts of three palpebrata pairs were significantly longer than in eight fusca pairs. In fusca, the female tended to spend more time on the egg than the male. Brooding was shared approximately equally between the sexes. In palpebrata, the female brooded significantly longer than the male. The share of the sexes in incubation was not determined for palpebrata. The fusca fledgling period varied from 149 days to greater than 165 days. One palpebrata pullus fledged 170-175 days after hatching.

On average, palpebrata pulli grew slightly faster than fusca pulli over the first 60 days after hatching at Marion Island. During this period, the fusca pulli were fed more frequently (0,32 feeds/day) than the palpebrata pulli (0,29 feeds/day). Sixty-one fusca nests at study colonies at Marion Island produced 8 (13%) flying young during 1974-75. However, the overall breeding success of the fusca population was estimated at 30%. Sixteen coastal palpebrata nests produced five (29%) flying young during 1974-75 at Marion Island. The chief cause of pullus mortality was attributed to Giant Petrel _Macronectes_ spp. predation, although direct evidence for this was not obtained.

Adults and subadults of both species appear to moult during the non-breeding season (winter). In _fusca_, body feather moult is apparent at the end of a breeding season, and at the beginning of the following season when moult is nearing completion.

At Marion Island, _fusca_ and _palpebrata_ nested on vegetated ledges on sloping cliffs, or near-vertical cliffs, with a significant preference for grey lava areas. _Phoebetria fusca_ typically nested in groups at the coast. _Phoebetria palpebrata_ nests were situated inland and on the coast, and invariably were backed by a bare earth or rock wall. On only one occasion were more than two _palpebrata_ nests found in close proximity, although some _palpebrata_ nests were situated in _fusca_ colonies. It is argued that interspecific competition for nest sites is not important, and that the observed difference in dispersion of nest sites between the species resulted from differential predation and climatic selection pressures during speciation.

Both species take the same food types, of which cephalopods are the most important. _Phoebetria fusca_ and _palpebrata_ at Marion Island took the same cephalopod species (as determined from the beaks found in regurgitated casts, but the frequency of occurrence of cephalopod species in the two diets was significantly different. There were significant differences in the estimated mean masses of three or four cephalopod species which made up 80,9 and 75% by frequency of occurrence of the cephalopods taken by _fusca_ and _palpebrata_ respectively.

There are three major differences in the social behaviour of _fusca_ and _palpebrata_ at Marion Island. _Phoebetria palpebrata_ is more aggressive than fusca, and has two displays, SCOOPING and PADDLE-WALK, with no apparent homologues or analogues in the repertoire of _fusca_. BEAK THRUSTING (_palpebrata_) and BILL CLASHING (_fusca_), which apparently are homologous, but markedly different, are precursors to prolonged social contact. Interspecific behavioural contact was minimal, and usually aggressive. The behaviour of the Diomedeidae in general, and _Phoebetria_ in particular, apparently is related to the size of the nest site area and nature of the surrounding terrain.

It is suggested that speciation in _Phoebetria_ occurred through geographic isolation of ancestral populations, and that _palpebrata_ evolved in a cold sub-Antarctic zone, and _fusca_ in a temperate sub-Antarctic zone. It is proposed that _palpebrata_ is adapted to cold sub-Antarctic food resources which are abundant, but available for a short period of time in summer. The temperate sub-Antarctic food resources of _fusca_ are less abundant, but available for relatively longer periods of time. The _palpebrata_ pullus generally, elsewhere than at Marion Island, grows faster than the _fusca_ pullus. The shorter fledgling, and incubation periods, and proportionately smaller eggs of _palpebrata_ are correlated with this faster growth rate. It is argued that the Marion Island _palpebrata_ population is marginal, because the food resources exploited by this population are less abundant than elsewhere, or lie farther from the breeding grounds than elsewhere. It is suggested that the Marion Island _palpebrata_ population feeds primarily in the cold waters south of the Antarctic Convergence which lies south of Marion Island, whereas the _fusca_ population feeds primarily north of the Antarctic Convergence. Differences in the breeding biology between _palpebrata_ at Marion Island and elsewhere are explained in terms of relatively reduced availability of food to the Marion Island population.

The two species co-exist at Marion Island by partitioning available nest-sites and food resources, whilst genetic isolation is maintained by behavioural barriers.

9. Acknowledgements

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11 Appendix

List of sources for Table 14 referring to Phoebetria spp. in Notornis 1959-1974.

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5. Classified Summarised Notes 1959. Notornis 8, 197.

6. Classified Summarised Notes 1963-1970. Notornis 1970. Suppl. 10.

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