

The vocal and homing behaviour of the Manx Shearwater *Puffinus puffinus* with additional studies on other Procellariiformes

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Dedicated to my wife Becky,
without whose love, patience
and encouragement this thesis
would not have been possible,
and to my sons, Nicholas, Matthew
and Neil, without whose innocence
I would be incomplete.

'Look after the genus of birds
called Petrels; they are very
peculiar in their way of life....'

G. White (1770)

'Spirits of darkness! - Ghouls of the night!
Now to the left of you, now to the right!
Silent as shadows, and swift in their flight -
Underfoot, overhead, everywhere round.
Fates from the heavens! - Ghosts from the ground!
Everywhere! Everywhere! Everywhere round.
Dark winged and sudden - they shiver and go,
As if from the Pit - lost spirits of woe -
Infectious, unholy, in hideous night
Twixt Midsummer gloaming and morning grey light.'

R. Drane, cited in Howells (1968)

ABSTRACT

The vocal and homing behaviour of the Manx Shearwater Puffinus puffinus with additional studies on other Procellariiformes. Paul Clive James, Wolfson College and Edward Grey Institute, D.Phil. thesis, Trinity term 1984.

The marine birds comprising the order Procellariiformes are an ancient and diverse assemblage. A large proportion are both nocturnal and burrow-nesting at their breeding colonies, where in sharp contrast to their behaviour at sea, they are highly vociferous. Virtually nothing is known regarding the adaptive features of this process. Various aspects of vocal behaviour have therefore been investigated from 1981 to 1983 for seven species at breeding stations in both the boreal and sub-tropical North Atlantic Ocean. In addition, the problem of how these birds return to their correct burrows at night has been considered.

A detailed study was conducted on the Manx Shearwater Puffinus puffinus. Various approaches showed that immatures contribute most to the calling heard. Males establish and defend burrows, but both sexes partake in aerial calling. Calling at ground level serves both sexual and territorial functions, whereas aerial calling is probably mainly concerned with sexual advertisement. Some males are more silent in flight than others. These probably represent birds as yet without burrows, perhaps the youngest age classes. Flighting activity probably expedites the acquisition of burrows and mates in these birds which are awkward on land, and aerial calling probably improves signalling efficiency in attracting mates.

Six other species (Bulweria bulwerii, Calonectris diomedea, Puffinus assimilis, Hydrobates pelagicus, Oceanodroma castro, Pelagodroma marina) were studied. As with Puffinus puffinus, sexual differences in voice exist for all except Bulweria and Pelagodroma, which also lack aerial calls. Thus a functional link exists between flight calls and their sexual divergence. Selection probably favours such divergence in species where males leave burrows to display in flight; the sexual identity of those species whose males do not is unambiguous as they remain in burrows and call.

The calls of Puffinus puffinus and Hydrobates pelagicus were compared at local and regional levels. Divergence exists between but not within islands. Vocal drift in Puffinus puffinus is also apparent after several years.

The calls of the nocturnal Procellariiformes are reviewed and discussed in relation to their systematics. The potential use of calls in petrel systematics is also evaluated and shown to be useful.

Observations on Puffinus puffinus showed that olfactory and auditory cues are not used for burrow homing. Experiments also confirmed this, and point to sufficient visual development in this species, although other senses may be emphasised in different ecological situations.

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CHAPTER ONE

General Introduction

General Introduction

Research activity on marine birds has mushroomed over the last few decades. In a brief review of the avian literature, Burger et al. (1980) noted that the proportion of papers published about them had steadily increased from 4% in 1930 to 15% in 1979. Yet, marine birds comprise only 3% of the known avian species in the world. Traditionally, a species is considered to be marine if it is a member of the Spheniscidae (penguins), Diomedeidae (albatrosses), Procellariidae (fulmars, petrels, shearwaters), Hydrobatidae (storm petrels), Pelecanoididae (diving petrels), Phaethontidae (tropicbirds), Pelecanidae (pelicans), Sulidae (gannets, boobies), Phalacrocoracidae (cormorants), Fregatidae (frigatebirds), Chionidae (sheathbills), Stercorariidae (Skuas), Laridae (gulls, terns), Rynchopidae (skimmers) or Alcidae (auks).

Because the majority of these birds nest in large colonies, thereby increasing their accessibility, they have afforded good opportunities in which to investigate fundamental problems in behaviour, ecology and evolution. Applied research has also increased, as seabirds have been viewed more and more as reflecting changes in environmental quality (Bourne 1976), and as being potential competitors with humans for food (Furness 1982, Bourne 1983). Interest has also focused on the plight of those species threatened with extinction (Bourne 1972, King 1981).

However, because most of this research has been concentrated at the breeding colonies, large gaps exist in our understanding of marine bird ecology and behaviour when they are at sea. In addition, the vast majority of behavioural research conducted at the colonies has considered the diurnal species only. For obvious reasons, the nocturnal species lend themselves less well to detailed observations. Yet they constitute a significant proportion of the marine avifauna, and as such, offer potentially

rewarding (and, as the writer believes, interesting) situations in which to study behavioural adaptation, not only for its own sake, but also to apply its understanding to practical problems, such as counting these birds, or clarifying their taxonomy.

The Procellariiformes, or tube-nosed swimmers are an ancient, large and diverse group of oceanic birds, the majority of whom are nocturnal at the breeding colony. They are divided into four families: the albatrosses (13 species), the fulmars, petrels and shearwaters (61 species), the storm petrels (21 species) and the diving petrels (4 species) (Nelson 1980). In addition to the tubular nostrils, they are distinguished by their stomach structure, the proventriculus of which produces an oily secretion. The order is distributed throughout the world's oceans, but is particularly well-represented in the southern oceans. All species are monogamous, and have extended pair bonds. Other features of their reproductive biology include a relatively large single egg, lengthy incubation periods and slow chick growth (Lack 1968). The annual adult mortality is very low, and sexual maturity is deferred for up to several years. During the years before breeding, these immatures visit the colony and prospect for burrows and mates.

Their adaptations for life at sea (legs well to the rear and long wings) have made them clumsy on land and they have difficulty taking off. Hence, their breeding colonies are usually situated on mammal-free islands. Predation pressure from other avian groups has probably led to all but the larger species to be burrow-nesters as well as nocturnal. During these nightly visits, in sharp contrast to their behaviour at sea, these birds are highly vocal. It is this dramatic shift of behaviour which forms the focus of this thesis. In the 10 years from 1971 to 1980, the Zoological Record lists only 15 papers giving any information on the vocal behaviour of these species out of a total of many hundreds published on the Procellariiformes and the vocal behaviour of birds in general. It is hoped

that the information researched and presented here will go some way in redressing the imbalance.

A large part of the work was conducted on the Manx Shearwater Puffinus puffinus, a member of the Procellariidae. The Puffinus shearwaters comprise the second largest group in the order (following the Pterodroma gadfly petrels) with about 14 species. They occur in both hemispheres with several species, including the Manx Shearwater, undertaking extensive trans-equatorial migrations. The Manx Shearwater is found in both the Atlantic and Pacific Oceans, as well as in the Mediterranean (Murphy 1952). The present study is devoted to the nominate race which breeds on islands off the British and Irish coasts (Cramp et al. 1974).

Despite being a nocturnal, burrowing seabird, the Manx Shearwater lends itself well to research activities. While on land, it is easy to catch and ring, and breeding pairs are tolerant of disturbance at the nest. As a result, its population biology is reasonably well understood. Lockley (1930, 1931) published the first basic information on incubation and fledging periods, We now have good information on breeding biology (Matthews 1954, Harris 1966a, 1966b, Brooke 1978a, 1978b), movements and dispersion (Lockley 1953, Thomson 1965, Harris 1972, Perrins & Brooke 1976, Brooke 1978c) and survivorship (Perrins 1966, Perrins et al. 1973). Aside from two papers (Brooke 1978d, 1978e), accounts of the behaviour of the Manx Shearwater (or indeed of any of these species) have been largely anecdotal and speculative.

Aims of the Study

Although in its infancy, the study of the behaviour and vocalizations of nocturnal seabirds during the breeding season seemed a challenging project. For almost no species do we have adequate accounts of call variability, either sexual or geographical. In addition, no one has attempted a general

explanation of the adaptive value of such vocal activity. With this in mind, the writer has set out to describe and interpret the vocal behaviour of the Manx Shearwater at the colony (Chapter two). Opportunities arose to study the vocal behaviour of six other nocturnal species in the north and sub-tropical Atlantic Ocean (Chapter three). This has permitted an evaluation of calling behaviour from an evolutionary perspective. Several colonies of both the Manx Shearwater and British Storm Petrel Hydrobates pelagicus were visited, and a large number of tape recordings collected. This has enabled an analysis of how calls vary geographically (Chapter four). Time and other constraints have not permitted the writer to study many other species first hand. However, copies of their calls tape recorded and held at the British Library have been used to give a brief review (Chapter five). Related to this is the potential use of these species' calls in their systematics, a much neglected area of research. The possibilities for their use as such are also evaluated. Another aspect of their behaviour which has drawn much speculation is their burrow homing ability. Observations and experiments on the Manx Shearwater are presented on this aspect of their nocturnal behaviour (Chapter six).

Study Areas and timing of visits

Skomer Island

Skomer (51°45'N, 5°18'W) lies at the southern end of St. Bride's Bay, Wales just 1 km from the mainland. In extent, it is about 292 ha including islets, and is largely a tableland some 60 m above sea-level. The island is composed mainly of volcanic rocks.

The Manx Shearwater colonies have been estimated at 95,000 pairs (Corkhill 1973), and could be slowly increasing (Alexander & Perrins 1980). The numbers of breeding British Storm Petrels have been estimated at up to 1000 pairs (Scott 1970), although a current census revealed only about 100 pairs (Appendix B).

Much of the research presented in this thesis was conducted on Skomer Island. In 1981, visits were made from 26 March to 11 April, 17 April to 19 May and 24 May to 1 September. In 1982, from 15 March to 10 April, 24 April to 14 May and 24 May to 25 August, and in 1983 from 14 March to 24 March, 1 April to 20 April, 29 May to 11 June and 31 July to 11 August. Over the three field seasons, this amounted to a total of about 330 nights spent on the island.

Skokholm Island

Lying about 3 km from the mainland and 4 km south of Skomer, Skokholm Island (51°42'N, 5°16'W) has an area of about 100 ha. It is also principally a plateau, though at a somewhat lower elevation than Skomer. In contrast to Skomer, it consists mainly of old red sandstone.

The Manx Shearwater colonies have been estimated to hold 35,000 pairs (Harris 1966a, Perrins 1967). The British Storm Petrels are much more numerous than on Skomer with an estimated 6,200 pairs (Scott 1970). The island was visited from 17 April to 24 April, 1982 and from 21 May to 28 May, 1983 for a total of 14 nights.

Rhum

The island of Rhum (57°00'N, 6°20'W) lies 24 km to the west of the Scottish mainland. It is large (about 10,700 ha) and mountainous, and is composed mainly of sandstone.

The majority of Manx Shearwaters breed at over 600 m above sea-level, and their numbers have been estimated at 116,000 pairs (Wormell 1976). There are no breeding British Storm Petrels. For the present study, the colonies on the northwestern slope of Hallival peak were visited for 7 nights from 15 May to 23 May, 1982.

Puffin Island

Lying just 0.5 km off the southwestern Irish coast, Puffin Island (51°50'N, 10°23'W) is about 54 ha in area, and is composed mainly of old red sandstone. Its principal feature is a long, narrow twin-peaked ridge with steep sides, although the bulk of the Manx Shearwaters nest in a much lower, flat area. Their numbers have been estimated at between 10,000 and 20,000 pairs (Evans & Lovegrove 1974). The British Storm Petrel colonies there are thought to contain about 4,000 pairs (Evans & Lovegrove 1974). The island was visited for 4 nights during 1983 from 20 July to 25 July.

Great Salvage Island

Largest of the three Salvages (about 162 ha), Great Salvage Island (30°08'N, 15°55'W) lies 300 km south of Madeira. A dry rocky plateau some 60 m above sea-level, it has two low peaks, and is partly covered with a crumbling phosphatic soil.

The island holds significant populations of Cory's Shearwater Calonectris diomedea, Little Shearwater Puffinus assimilis, Bulwer's Petrel Bulweria bulwerii, Madeiran Storm Petrel Oceanodroma castro and White-faced Storm Petrel Pelagodroma marina (LeGrand et al. in press), making it one of the most important seabird breeding stations in the sub-tropical Atlantic Ocean. It was visited for a total of 23 nights from 17 June to 11 July, 1983.

CHAPTER TWO

The vocal behaviour of the Manx Shearwater

The vocal behaviour of the Manx Shearwater

Introduction

Concerning the vocal behaviour of Manx Shearwaters, Brooke (1978d) has described three basic features:

(1) Males and females are sexually dimorphic in voice.

(2) Within pairs, individual recognition by voice exists.

(3) Counts over six nights showed that male calls predominated at ground level, and female calls predominated in flight.

The present chapter builds on this knowledge by describing the vocal activity at the colony in more detail, and supplementing these observations with experiments, to determine the biological functions of the calling.

General Methods

The work described in this chapter was carried out on Skomer Island. As with previous shearwater studies (Harris 1966a, Brooke 1978a), study nesting burrows were prepared and maintained. In contrast to other work, two types of study burrow were distinguished: Breeding and Immature. A breeding burrow was defined as one occupied by a pair of shearwaters in March each year and subsequently used for breeding. An immature burrow was defined as one not occupied until the new moon period in June each year and consequently not used for breeding. During this latter period large numbers of prospecting immatures visit the colony (Perrins et al. 1973).

All shearwaters in study burrows were sexed either by cloacal inspection (Serventy 1956) or voice (Brooke 1978d) and ringed. Following egg-laying, the cloaca of the female is swollen and bluish. Her mate may then be assumed to be a male. Sexing by voice involved either listening at burrow entrances and removing the caller for ringing, or by eliciting a vocal

response using the playback of male or female calls on a Sony M9 micro-cassette tape recorder. The male call has a combination of clear notes, which the females lack. Their calls consist entirely of harsher sounds (Brooke 1978d, see Figure 4.3). The difference was sufficient to enable me to easily assign by ear calling birds to one sex or the other.

Birds were also sexed by discriminant function analysis of bill and tarsus measurements (Brooke 1978c). Birds in breeding burrows were sexed either cloacally or vocally and their bill lengths measured with Vernier calipers to the nearest 0.1 mm along the dorsal mid-line, from the edge of the feathers at the base of the culmen to the tip of the hook. The tarsi were similarly measured from the middle of the mid-tarsal joint to the distal end of the tarso-metatarsus. Fifty males and 50 females were measured, and as Brooke (1978c) found, significant differences were noted between the sexes (Table 2.1). A discriminant function was then generated to distinguish male and female shearwaters using bill and tarsus measurements (Figure 2.1). As neither statistics change with age (Brooke 1978b), it was possible to sex immatures which could not be sexed vocally. As the percentage error in mis-sexing males and females was similar (males 28%; females 24%), the discriminant function was usefully applied to groups of birds. All measurements in the study were taken by myself in order to reduce observer variation.

Unlike other studies (Perrins et al. 1973, Brooke 1978b), there were very few birds of known age available for investigation. However, it was possible to assign birds into breeder and immature age classes by their weights. Data from Brooke (1978b) showed that the weights of birds aged 2-5 years (immatures) were significantly lower than those aged 6+ years (breeders). This difference remained throughout the summer (Figure 2.2). In the present study, weights of breeders in study burrows were taken through the breeding season to the nearest g using a Pesola spring balance.

Table 2.1

The mean ± s.d. bill and tarsus measurements (mm) of 50 male and 50 female Manx Shearwaters

	Male	Female	t	P
Tarsus	46.6 ± 0.97	45.3 ± 1.19	5.99	< 0.001
Bill	35.6 ± 1.20	34.6 ± 0.95	4.62	< 0.001

Figure 2.1

Discriminant analysis of tarsus and bill lengths for 50 male and 50 female Manx Shearwaters. The dashed line is the calculated discriminant function 0.92 Tarsus + 0.59 Bill = 63.05.

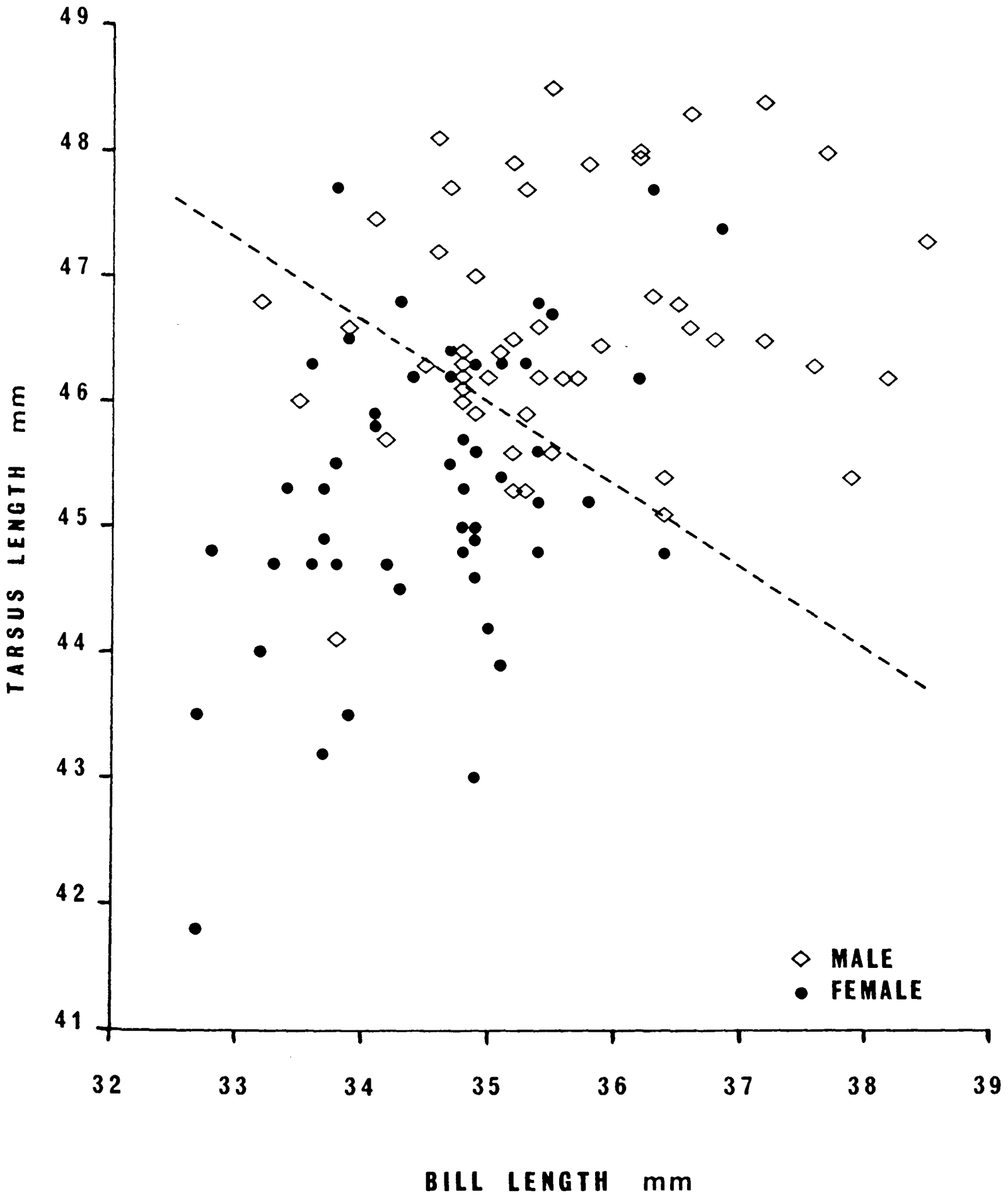
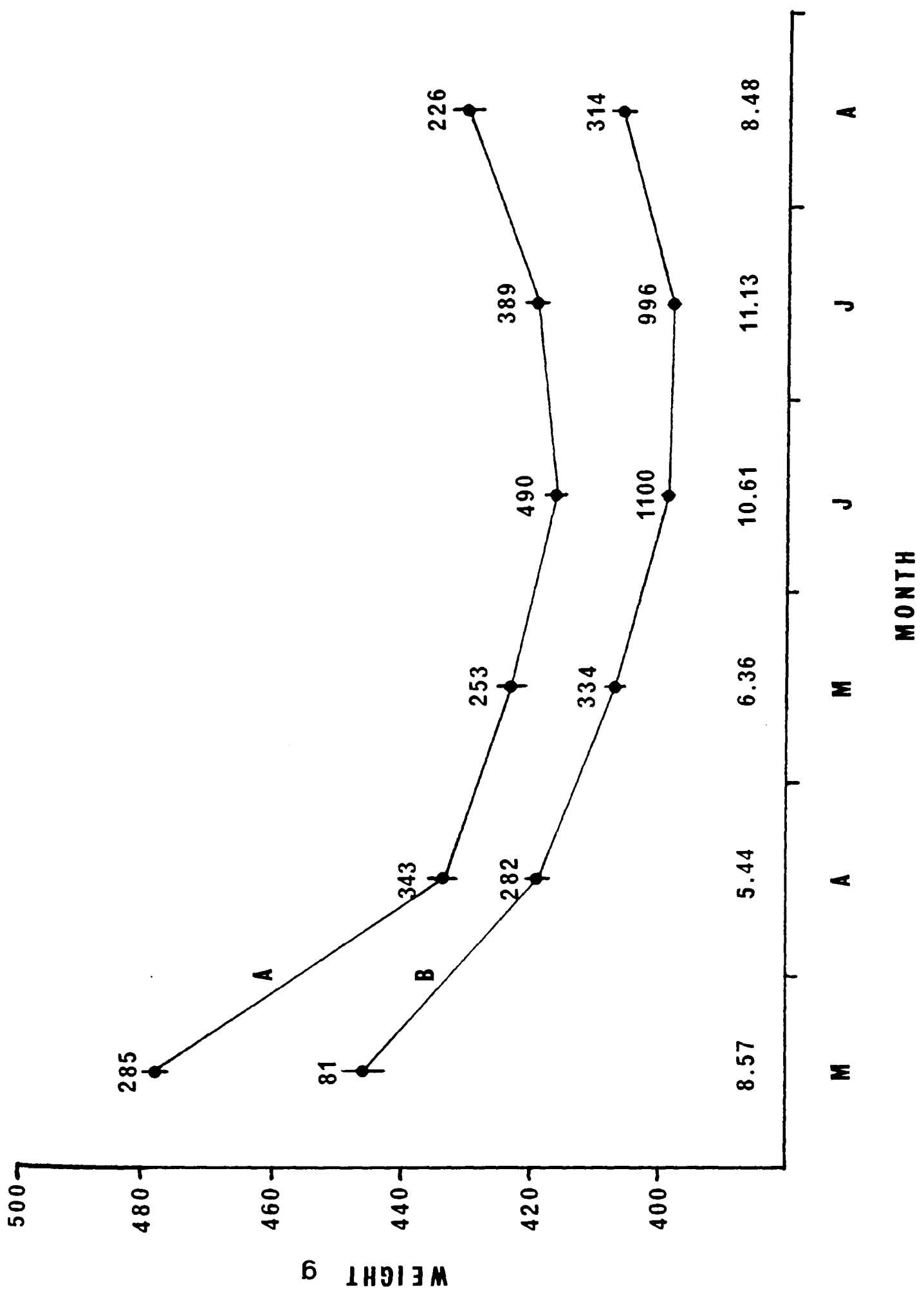

49
48
47
46
45
44
43
42
41
TARSUS LENGTH mm
32
33
34
35
36
37
38
39
BILL LENGTH mm
MALE
FEMALE

Figure 2.2

The mean $\pm$ s.e. monthly weights of (A) breeding (aged 6+ years) and (B) immature (aged <6 years) Manx Shearwaters. Data modified from Brooke 1978b. Numbers along ordinate are t values; all are significant. Sample sizes shown at each point.


WEIGHT g
500
480
460
440
420
400
MONTH
M
A
M
J
J
A
8.57
5.44
6.36
10.61
11.13
8.48
p<0.001
A
B
285
343
253
81
282
334
490
389
226
1100
996
314

These weights were then used as a baseline for comparison with other birds. It was not possible to definitely classify any one individual, since too much population variation existed, but the technique was useful for comparing groups of birds.

Vocal activity at the colony

Before describing experiments designed to aid interpretation of vocal activity, it is first necessary to describe the seasonal variation in both calling intensity and sex ratio at ground level and in flight.

'Call' as used in this chapter refers to call bout, i.e. a string of repeated call units(see Figure 4.3)

Methods

Counts were made during ten minute periods of male and female calls heard in flight at the same site through the season. As activity is affected by moonlight, counting was always carried out one hour after the first flight calls were heard on dark nights, i.e. with the moon below the horizon. Vocal intensity at ground level was counted by walking a standard path through the colony for 20 minutes, again through the season. No attempt was made to differentiate between birds calling on the surface and from below ground. As with the flight calls, counts were conducted one hour after vocal activity had begun, and when the moon was below the horizon.

The number of birds counted more than once was believed to be small in relation to the total counted.

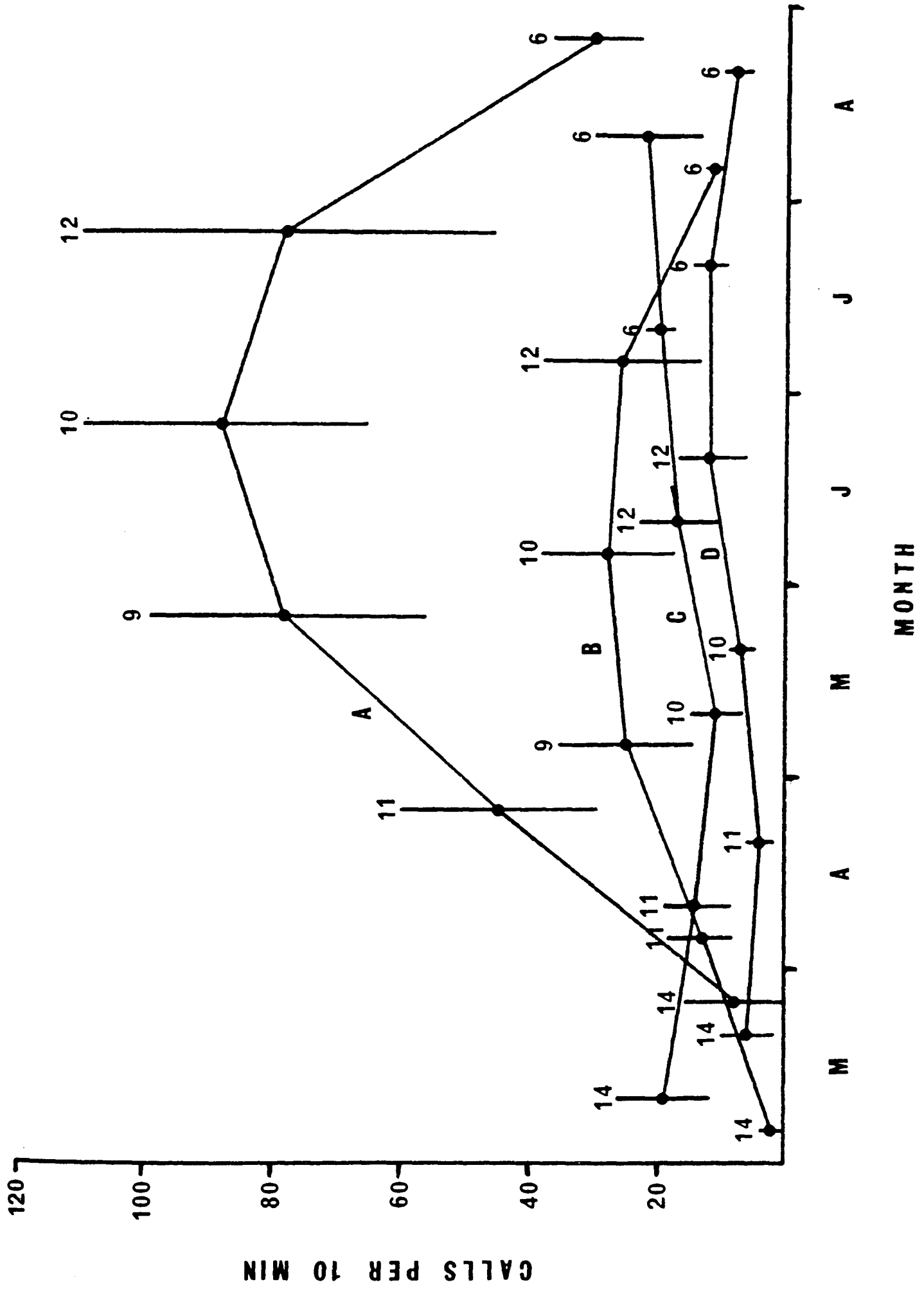
In addition, an instantaneous sampling method was used by visiting breeding birds (and from June onwards, immatures) in burrows through the season and scoring them as either calling or not calling.

Results

Male and female calling intensities both at ground level and in flight show highly significant ($p < 0.001$) seasonal changes (Figure 2.3). The numbers of male and female calls heard in flight reached their peaks in

Figure 2.3

The mean $\pm$ s.d. female flight (A), male flight (B), male ground (C) and female ground (D) call intensities heard each month. All show significant seasonal changes: F (ANOVA) = 39.38, 40.58, 11.34 and 12.15 respectively. Numbers above each point are the number of counts per month.


CALLS PER 10 MIN
120
100
80
60
40
20
MONTH
M
A
M
J
J
A
A
B
C
D
9
11
10
12
12
12
10
12
6
6
6
6
6
6
6
9
10
10
11
11
11
14
14
14
14

June, whereas the numbers heard at ground level showed less significant seasonal changes. Overall, aerial calling intensity was weakly but significantly correlated with ground calling intensity ($r = 0.319$, d.f. = 38, $p < 0.05$). The intensity of calling (as determined by the call counts) was significantly correlated between flying males and females, ground females and flying males, and ground females and ground males (Table 2.2).

Expressing the counts of calls heard at ground level and in flight as a seasonal $\frac{\text{call}}{\text{sex}}$ ratio (Figure 2.4), it can be seen that the male calls predominated at ground level, but female calls predominated in flight. Both sex ratios showed significant seasonal changes, especially the ground sex ratio with a decreasing proportion of male calls heard to May and then an increase to August.

Based on the instantaneous burrow checks, there was significantly more calling heard from immature burrows than from breeding burrows for both June and July (Table 2.3). Furthermore the frequency in which breeding burrows held calling birds declined significantly from March to June and July (Table 2.3).

Discussion

The significant seasonal changes that occurred in calling intensities at ground level and in flight (Figure 2.3) requires explanation, bearing in mind that the breeders arrive in March (Harris 1966a), and that the largest influx of immatures occurs in June and July (Perrins et al. 1973, Brooke 1978b). Calling intensities at ground level and in flight all peaked during this latter period suggesting that at this time of year at least, the majority of calling is by immatures. This is further borne out by the burrow checks (Table 2.3), which showed immatures contributing more than breeders to ground calling in June and July, and also a decrease in breeder calling from March onwards.

Table 2.2

Correlation matrix of male and
female Manx Shearwater calling intensities
in flight and at ground level

	Ground male	Ground female	Flying male	Flying female
Ground female	0.542* (40)	-	-	-
Flying male	0.029 (38)	0.567* (38)	-	-
Flying female	0.016 (38)	0.574* (38)	0.947* (52)	-

* $p < 0.01$; d.f. in parentheses

Figure 2.4

The mean $\pm$ s.d. proportion of calls heard each month at (A) ground level and (B) in flight that were male. Both show significant seasonal changes: H (Kruskal-Wallis) = 33.48 and 12.18 respectively. Numbers above each point are the number of counts per month.

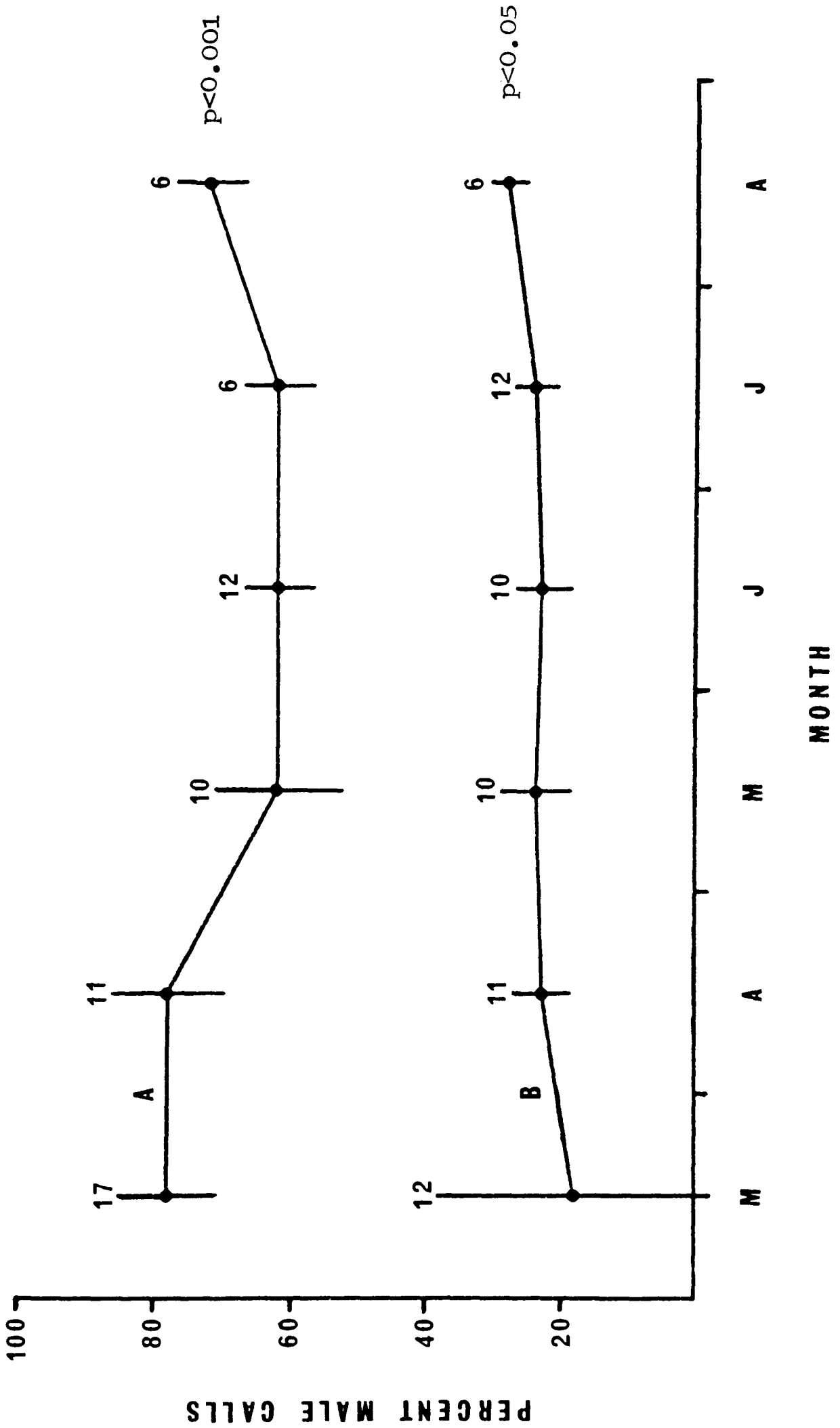

p<0.001
p<0.05
6
6
12
10
11
17
A
6
12
10
11
12
B
A
M
J
J
A
M
MONTH
100
80
60
40
20
PERCENT MALE GALLS

Table 2.3

The frequency of calling heard in breeding and immature Manx Shearwater burrows in different months

	Calling	Silent	X^2	P
Breeding (March)	8	53		
Breeding (June)	14	145	4.07	< 0.05
Immature (June)	12	54		
Breeding (July)	2	98	13.84	< 0.005
Immature (July)	7	27		

X^2 (Breeding March, June, July) = 7.47, d.f.=2, $p < 0.025$

Vocalizations in the Manx Shearwater serve three possible functions. Firstly, calling may be a form of sexual advertisement adapted to low light levels (Brooke 1978d). Secondly, it may function as a territorial signal (Brooke 1978d), or lastly and more speculatively, it may facilitate the homing process of incoming birds in the darkness, either by echolocation (Lockley 1967) or mate recognition (Lockley 1942, Brooke 1978d). As Manx Shearwaters have extended pair bonds, most of the breeders are already paired at the beginning of the season, so calling in them is more likely to serve territorial and/or mate recognition functions. Paired breeders apparently do not call in flight, since in March when most are already present, the level of aerial calling is extremely low (Figure 2.3). At this time too, very few immatures are present at the colony (Perrins et al. 1973, Brooke 1978b). If aerial calling is performed mainly by immatures, then it is more likely to be serving a sexual function. The significant correlation of male and female flight call intensities would seem to support this (Table 2.2). The very low level of aerial calling in March would also seem to dismiss the idea that it serves a homing function for breeders.

If breeder calling is associated more with territorial behaviour, and occurs mostly at ground level, then there should be less significant seasonal changes in overall calling intensity at ground level, compared with aerial calling, particularly if breeder calling declines when immatures begin occupying their own burrows (Table 2.3). This is indeed the case (Figure 2.3). Of course, there is no reason to believe that ground calling is solely concerned with the territorial defence of burrows. Female ground calling intensity was significantly correlated with male ground calling intensity (Table 2.2) suggesting also a sexual function to such calling, presumably mostly among immatures, and a mate recognition function among the breeders.

Despite the large seasonal variations in calling intensities, the segregation of male and female calling is distinct (Figure 2.4), with male calls predominating at ground level, and female calls predominating in flight. Brooke's (1978d) impression that this dichotomy occurred throughout the season is thus confirmed. Visits to Rhum and Puffin Island also showed that other colonies possess the same phenomenon. Brooke (1978d) suggested that this dichotomy arose as a result of the different roles of the sexes, with males being responsible for burrow establishment and defence. However, this explanation does not explain why some male calls are heard in flight, or why aerial calling exists in the first place.

Experiments on calling behaviour

The following experiments were designed to test some of the ideas generated from the observations made in the last section.

Calling at ground level

Methods

Twenty-five galvanized steel treadle traps (63 x 16 x 18 cm) were buried throughout the main study area in the centre of the island, and each made to look like a shearwater burrow by covering with grass sods. Each night, 21 were left as they were, and four had Blaupunkt car loudspeakers placed in the far end of them. These were connected to a Sony reel-to-reel tape recorder playing a continuous loop for the night of either a male or a female call. Each trap was checked at half-hourly intervals through the night, and each shearwater caught was weighed, measured (bill and tarsus) and ringed before release. Traps were only opened on nights without moonlight. All were reburied in new locations twice each season, and the four traps with

calls were rotated through the trap positions at weekly intervals. Loops were also replaced weekly with new individuals' voices. In order to obtain some idea of the seasonal sex ratio of shearwaters on the surface at night, samples of birds were caught by hand, and each bird measured and ringed as before.

Results

Numbers of shearwaters trapped

Table 2.4 shows the monthly distribution of birds caught in each trap type and the monthly trapping effort. Both male and female calling traps were significantly more attractive to shearwaters than silent traps (Figure 2.5). On average, traps with calls playing were six to seven times more effective at catching shearwaters than silent traps, whereas male and female calling traps caught shearwaters at the same rate (Figure 2.5). The rate of catching birds was highest from May to July when most immatures are present. The peak of catching shearwaters in female calling traps occurred one month ahead of the silent trap peak and two months ahead of the male calling peak.

Weights of shearwaters trapped

From April onwards the mean monthly weights of birds trapped was significantly lower than those of breeding shearwaters (Figure 2.6).

Sex of shearwaters trapped

Significantly more males than females (as determined as discriminant function analysis) were caught in both silent and female calling traps, and significantly more females than males were caught in male calling traps (Table 2.5). In addition, significantly more males entered male calling

Table 2.4

Number of Manx Shearwaters caught in each trap type in each month with trapping effort (hours) in parenthesis

	March	April	May	June	July	August	Totals
Male calling trap	0 (55)	0 (82)	11 (93)	23 (86)	22 (63)	10 (56)	66 (435)
Female calling trap	0 (28)	9 (80)	23 (94)	18 (114)	5 (54)	0 (50)	55 (420)
Silent trap	6 (1915)	23 (2560)	61 (2435)	95 (2509)	80 (2486)	44 (2315)	309 (14220)
Total birds	6	32	95	136	107	54	430

Figure 2.5

The number of Manx Shearwaters caught each month per 100 hours trapping effort in (A) female calling traps (B) male calling traps and (C) silent traps. Female and male calling traps are significantly more attractive than silent traps: G (Multiway Independence Tests) = 82.96 and 118.20 respectively. $p<0.005$ Male and female calling traps are equally attractive: G = 0.70. All d.f. = 1.

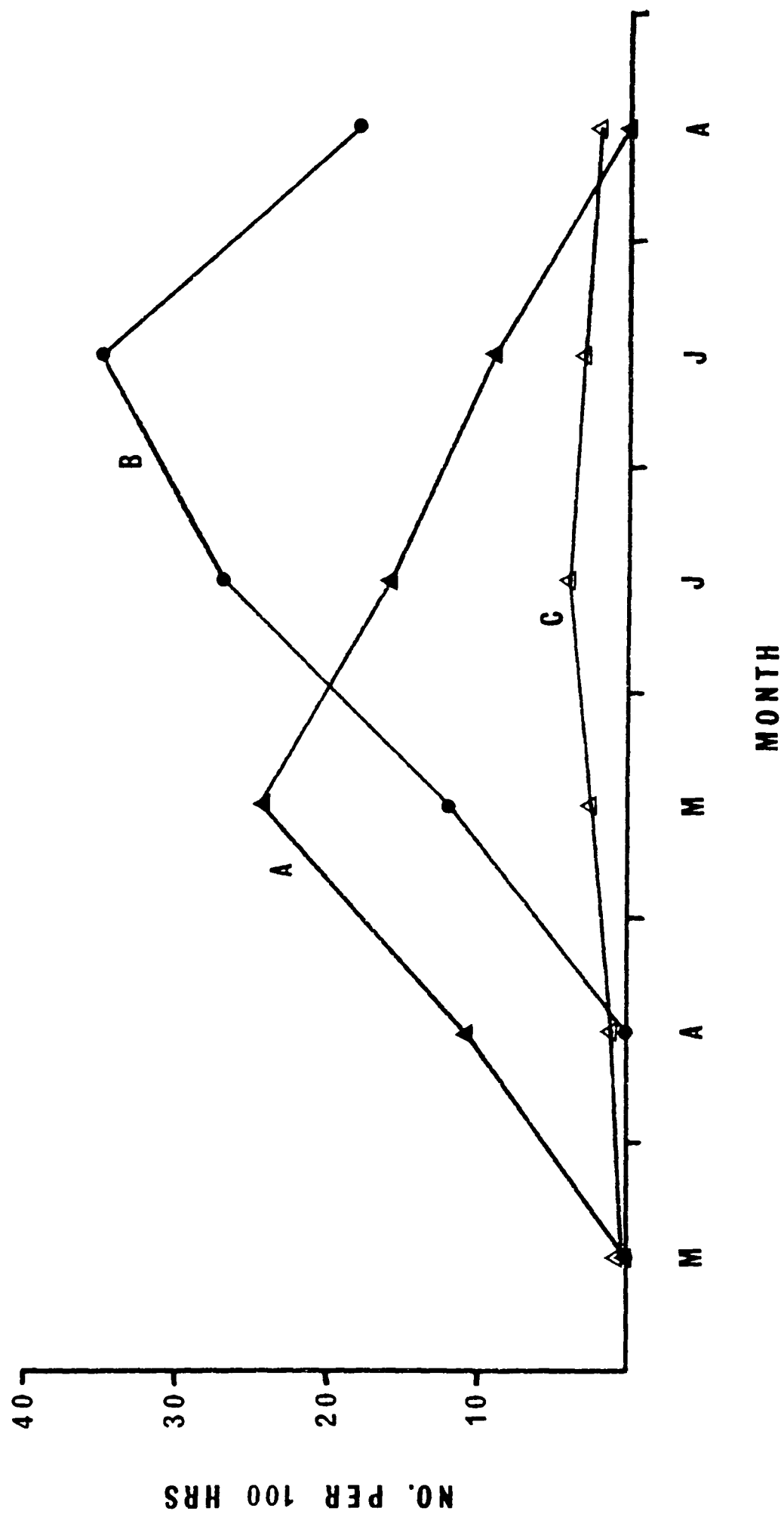
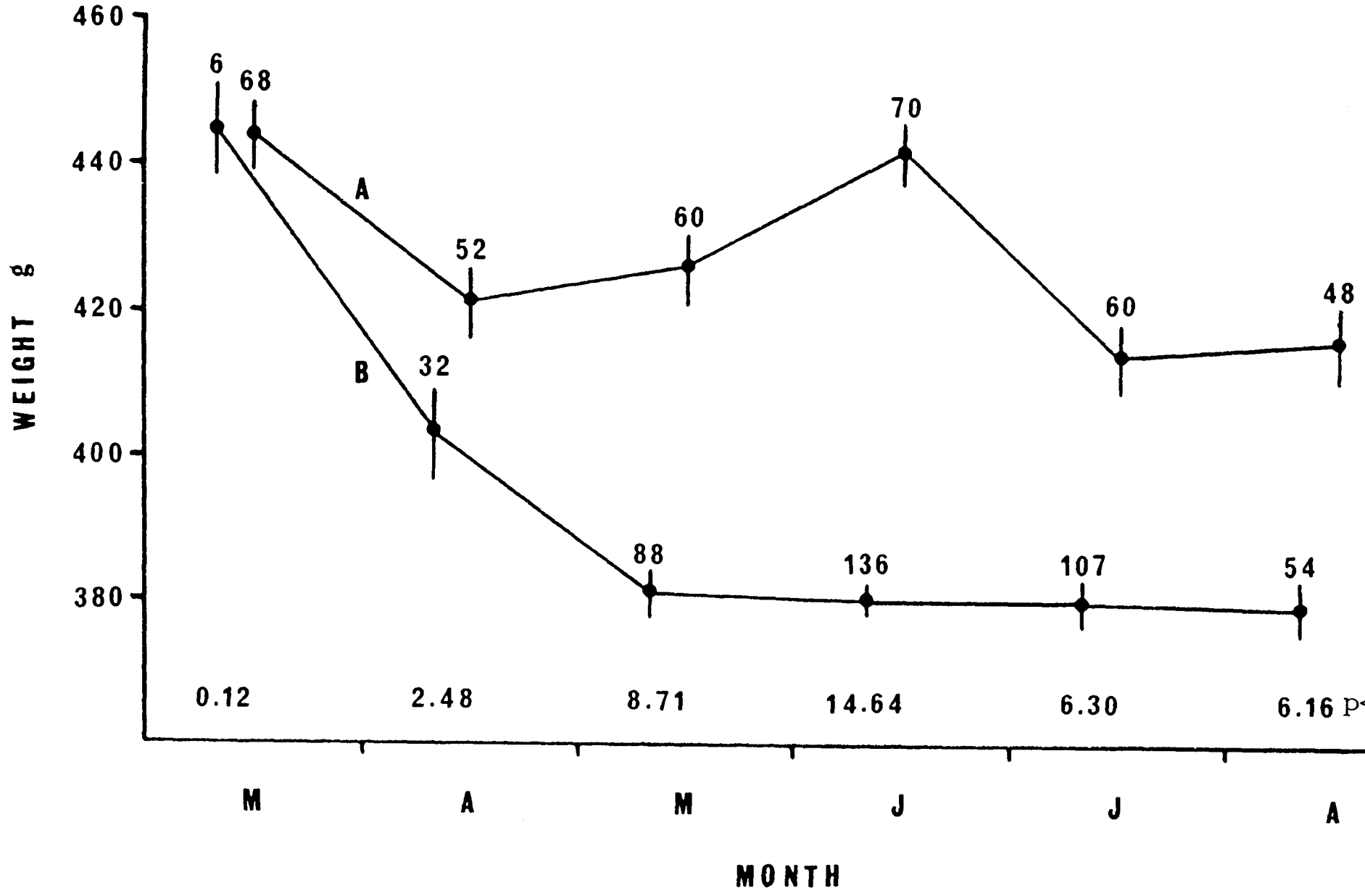

NO. PER 100 HRS
40
30
20
10
M
A
M
J
J
A
MONTH
A
B
C

Figure 2.6

The mean $\pm$ s.e. weights of (A) breeding shearwaters and (B) shearwaters caught in all trap types each month. Numbers along the ordinate are calculated t values; all except March are significant. Sample sizes are shown at each point.



$p<0.001$ except April ($p<0.02$)

Table 2.5

The sex of Manx Shearwaters
caught in different trap types

	Male	Female	X^2	P
Male calling trap	24	42	16.4	< 0.001
Female calling trap	47	8	14.8	< 0.001
Silent trap	213	96	10.5	< 0.001

Expected values based on 0.60
chance of catching a male(Figure 2.7)

traps than females entered female calling traps (X^2 = 4.74, d.f. = 1, $p < 0.05$).

Seasonally, the proportion of males caught in both silent and female calling traps was significantly higher than that found on the surface (Figure 2.7). In contrast, the proportion of males caught in male calling traps was significantly lower. The proportion of males caught in female calling traps was significantly higher than that caught in silent traps. Seasonally, the proportion of males caught in both silent and female calling traps showed no trends (Figure 2.7). However, male calling traps showed a marked increase in the proportion of males caught from May to August.

The proportion of males that were caught on the surface through the season was significantly lower than that heard at ground level (Figures 2.8 and 2.4). This probably reflected the higher likelihood that males go underground (Table 2.5), and their increased vocal activity once there.

Discussion

Significantly more shearwaters were attracted to both male and female calling traps than to silent traps (Figure 2.5). This suggests that in the natural situation, burrow calling is a powerful signal. That the peaks of shearwaters caught coincided with the influx of immatures into the colony also suggests that these signals are particularly important to unpaired birds. A possible explanation for the fact that the peak catches of female and silent traps (which catch males, Table 2.5) occurs before the peak of male calling traps is that immature males arrive earlier in the season than immature females. This effect has been demonstrated for breeding adults in a number of Procellariiformes (Davis 1957, Harris 1966a, Pinder 1966, Harris 1969, Beck & Brown 1971, 1972) so it is possible that this occurs in the immature populations too.

Figure 2.7

The proportion of shearwaters trapped each month that were male in (A) female calling traps (B) silent traps and (C) male calling traps. The dashed line shows the proportion in samples caught on the surface by hand. The proportions in all three trap types are significantly different from that on the surface: G (Multiway Independence Tests) = 15.90, 5.71 and 13.63 respectively. $p<0.001, 0.05, 0.001$ The proportion in female calling traps is significantly higher than that in silent traps: G = 7.24. $p<0.01$ All d.f. = 1. Sample sizes are shown at each point.

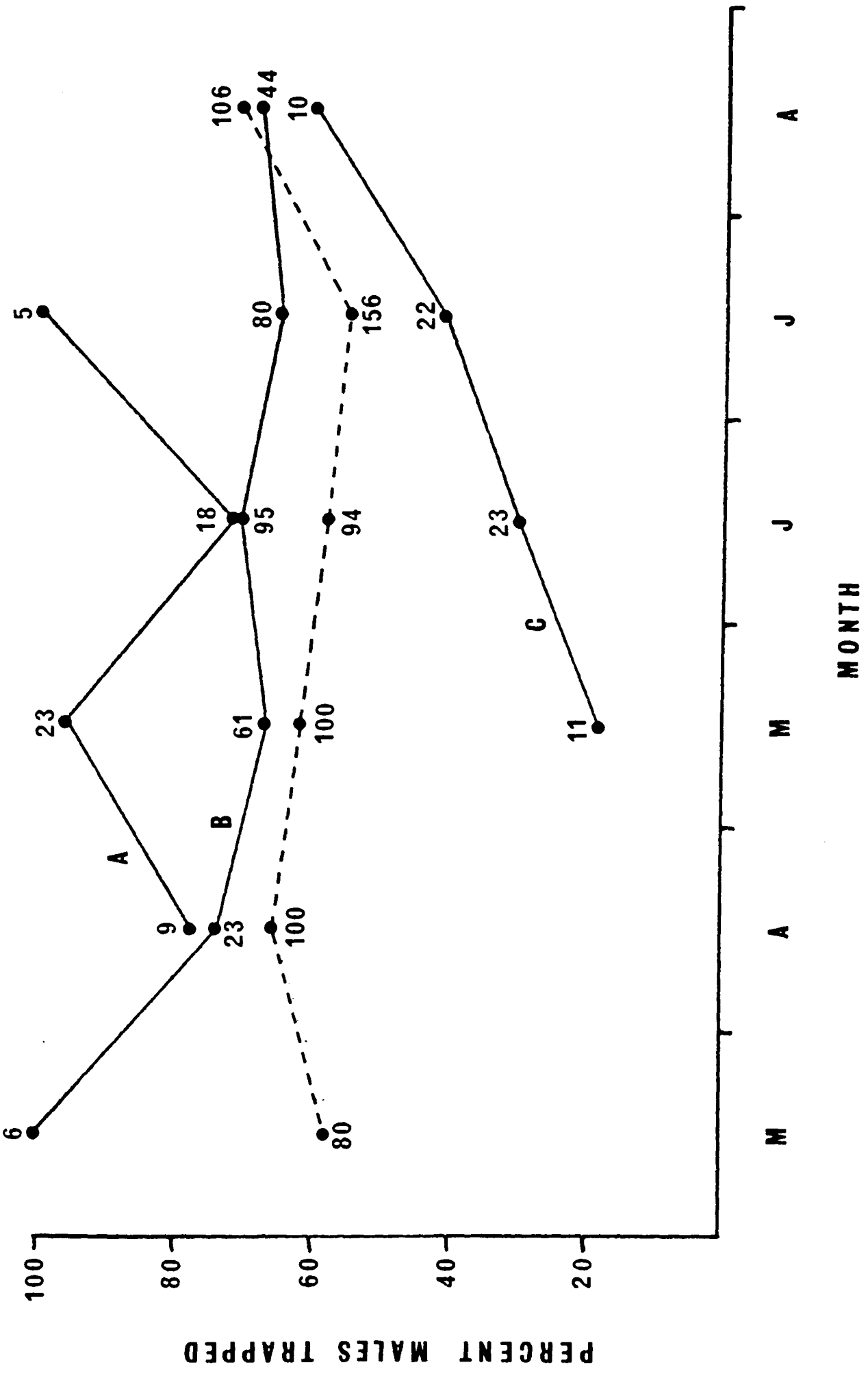
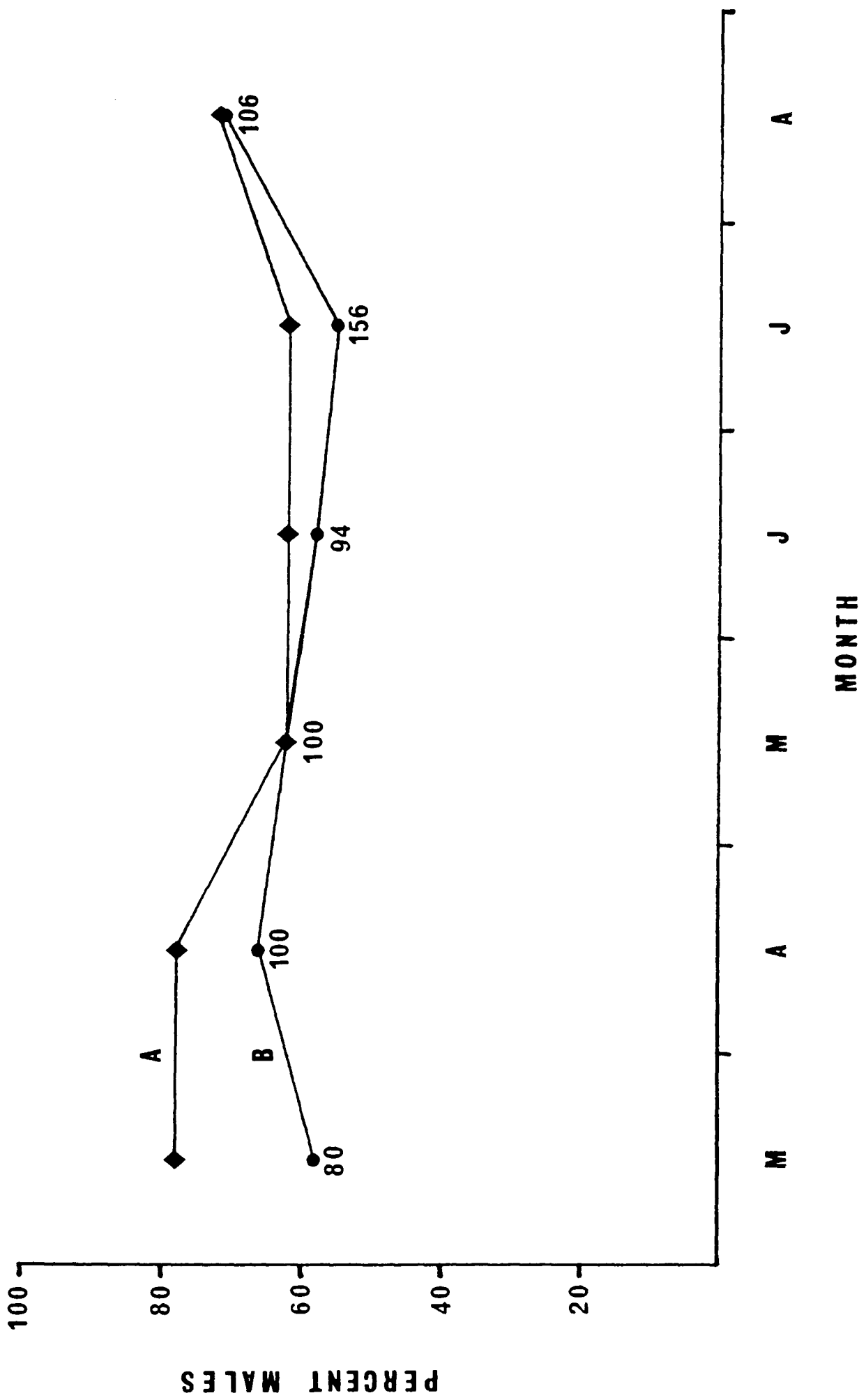

PERCENT MALES TRAPPED
100
80
60
40
20
M
A
M
J
J
A
MONTH
A
B
C
6
23
9
23
100
80
61
100
18
95
94
23
11
5
80
156
22
106
44
10

Figure 2.8

The proportion of (A) calls heard at ground level that were male (see Figure 2.4) and (B) the proportion of surface birds caught that were male (see Figure 2.7) each month. A significant difference exists between the two proportions: G (Multiway Independence Test) = 11.69, d.f. = 1. $p<0.001$


PERCENT MALES
100
80
60
40
20
A
B
106
156
94
100
100
80
M
A
M
J
J
A
MONTH

from April onwards

The mean monthly weights of shearwaters trapped were significantly lower than those of breeding shearwaters (Figure 2.6). This result confirms the suspicion that as the season progresses, the majority of birds engaged in vocal behaviour at ground level were immatures, and not birds of breeding age (Table 2.3). Other studies on nocturnal Procellariiformes have suggested that the immatures are responsible for the majority of calling at the colonies (Richdale 1944, Warham 1956, Tickell 1962, Harper 1976), although this has never been verified.

It is perhaps not surprising that males were significantly more attracted to female calling traps and vice versa for females (Table 2.5), but does support the hypotheses that burrow calling serves both a sexual and a territorial function in immatures. This suggestion is further supported in Figure 2.7 where the proportion of males caught in male calling traps was significantly lower than that found on the surface, suggesting a repelling effect. The same was true for females caught in female calling traps. That males entered silent traps significantly more than females (Table 2.5) supports the idea that males are primarily concerned with burrow establishment and defence.

Significantly more males entered male calling traps than females entered female calling traps (Table 2.5) and this requires explanation. Figure 2.7 shows that the incidence of males caught in male calling traps increased through the season. This suggests that as the season progresses, and the availability of burrows decreases with the arrival of an increasing number of immatures (Brooke 1978b), prospecting males are forced more and more to attempt evictions of males already occupying burrows.

The high proportion of males caught in female calling traps (Table 2.5, Figure 2.7) suggests the possibility that some females may, in the natural situation, be responsible for establishing burrows and then advertising the fact to males. On two occasions, I have discovered immature

females alone in burrows who responded vocally to the playback of a male call. Breeding females never respond to a call of a strange male (Brooke 1978d, pers. obs.), and so it was possible that these females were establishing burrows. An alternative interpretation is that the presence of a female calling in a burrow attracts males because they know she is alone. When mated or immature pairs are together in a burrow, they always duet, as one responds to the calls of the other. A female calling with no male calling almost certainly means she is alone. The male can then enter the burrow knowing he is safe from immediate attack. With a lone female present, a male has the chance of acquiring not only a mate, but also a burrow. If, for some reason, he does not pair with her, it is easier to evict her rather than a larger male in order to control the burrow. This may explain the very low incidence of immature females found alone in burrows compared with the many males encountered alone.

Calling in flight

Methods

The study consisted of three parts: The seasonal mistnetting of flying shearwaters in order to reveal their sex and age composition; the use of vocal playback on flying shearwaters to note vocal responses, and finally, direct observation with the aid of an image intensifier of flying shearwaters marked with small luminescent lights.

Shearwaters were caught throughout the season in a 20 m mistnet erected in the colony one hour after the start of vocal activity. All birds caught were ringed, weighed and measured (bill and tarsus) as before. Calls of male and female shearwaters were alternately played for ten minute periods through an amplified system interspersed with equal periods of silence. The numbers of male and female flight calls heard in the immediate vicinity (about a

30 m radius) were counted for each period. The loudspeaker was placed in one of two positions, (1) on the ground facing the sky and (2) at the top of a 10 m pole erected in the colony. For the latter situation, the calls used for playback were of birds recorded in flight, hence they took account of the Doppler Shift in flight calls heard naturally.

Lastly, 10 immature males and 10 immature females all associated with burrows, had a small 'Starlit' luminescent light glued to a central tail feather. They were followed at the colony with the aid of a Modulux 130 image intensifier fitted with a biocular viewing lens and a Nikon 50 mm objective lens. Only two birds were followed in any one night, and only on moonless nights. The life of a luminescent light was about two days. Time budget data was collected on the birds with regard to the time spent on the surface, below ground and in flight. The approximate total areas enclosed by flying birds were determined by reference to familiar landmarks and a large scale map of the area. The calling activity of flying birds was monitored with respect to their rate of calling and the proportion of flight time spent calling. Following the attachment of lights all birds were allowed to settle for half an hour before observations began.

Results

Weights of flying shearwaters

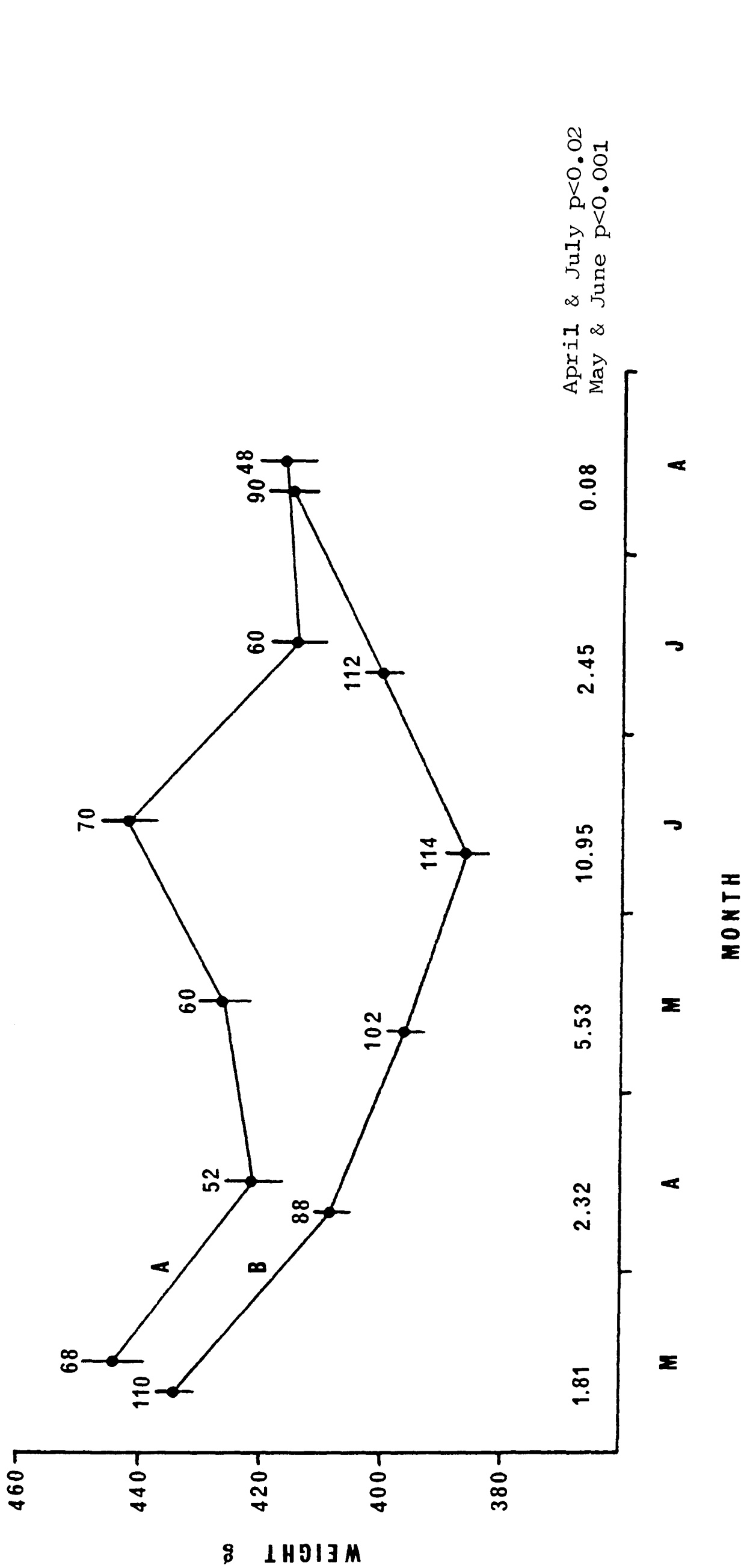
The mean monthly weights of netted shearwaters were significantly lower than those of breeding birds from April to July inclusively, but not for March and August, when there were no significant differences (Figure 2.9).

Sex of flying shearwaters

Expressed as the proportion of males, the sex ratio of birds netted

Figure 2.9

The mean $\pm$ s.e. weights of (A) breeding shearwaters and (B) shearwaters netted in flight each month. The numbers along the ordinate are calculated t values; all except March and August are significant. Sample sizes are shown at each point.


April & July p<0.02
May & June p<0.001
WEIGHT g
MONTH
460
440
420
400
380
10.95
2.45
0.08
1.81
2.32
5.53
J
J
A
M
A
M
A
B
70
60
112
114
90
48
60
52
102
88
68
110

was significantly different from that heard in flight (Figures 2.10 and 2.4), with the proportion of male calls heard being much lower than the proportion of males actually present in flight. This difference was much greater than the corresponding one at ground level (Figures 2.8 and 2.10).

Vocal responses to playback

In both loudspeaker positions (ground and pole), the playback of male calls resulted in a significant change in the sex of calls heard (Table 2.6). More female and fewer male calls were heard compared with the periods of no playback. The playback of female calls resulted in no such significant changes.

Observations of marked immatures

All marked immature shearwaters called either from within burrows or from the surface around burrows. In addition, whether 'paired' or not, on leaving the burrows, they investigated other neighbouring burrows or took flight and engaged in calling displays in the vicinity. There were no significant differences between male and female time budgets (Table 2.7), although this may reflect low sample sizes and high variances. Overall in fact, females spent about 2.2 times more time in flight than males. This was possibly due to females making longer rather than more flights, despite there being no significant difference between males and females with respect to the length of time per flight (Table 2.8). The ratio of the time spent by each sex in flight (29% by males) corresponds closely to the sex ratio of calls heard in flight (24% male, Figure 2.4).

There was also no significant difference between the areas enclosed by males and females during their flighting activity (Table 2.8). In addition, there was no significant difference between male and female calling rates (Table 2.8). The marked shearwaters spent on average 8-11% of their flight time calling, with a lower, but only just not significant,

Figure 2.10

The proportion of (A) shearwaters netted in flight that were male and (B) calls heard in flight that were male (see Figure 2.4). There is a highly significant difference: G (Multiway Independence Test) $p<0.001$ = 1899.30. Sample sizes are shown at each point.

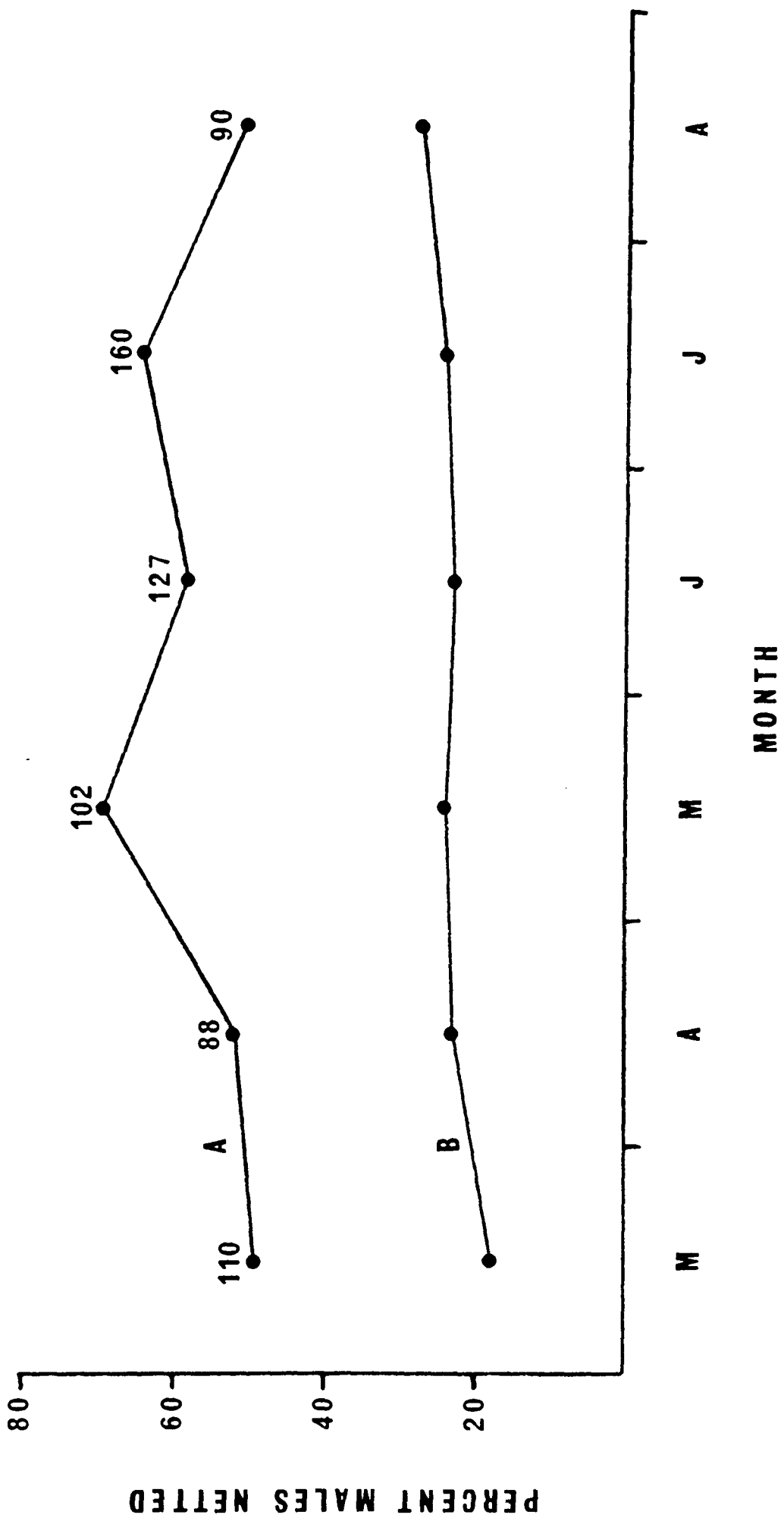

PERCENT MALES NETTED
80
60
40
20
M
A
M
J
J
A
MONTH
102
88
110
A
127
160
90
B

Table 2.6

The number of flight calls heard of each sex in response to the playback of male and female calls on the ground and at the top of a 10 m pole

	Ground				Pole			
	Male	Female	X^2	P	Male	Female	X^2	P
Male played	10	67	7.28	< 0.01	4	104	7.88	< 0.005
Silent	15	30	0.34	N.S.	12	66	0.16	N.S.
Female played	10	15			3	22		

Table 2.7

Mean ± s.d. percent time budgets of 10 male and 10 female immature Manx Shearwaters marked with luminescent lights

Activity	Males (10)	Females (14)	U*	P
Above surface	51.2 ± 33.0	51.7 ± 33.4	74	N.S.
Flying	7.5 ± 8.8	16.4 ± 22.4	79.5	N.S.
Below surface	41.3 ± 37.6	31.9 ± 35.1	72.5	N.S.
Total time (min)	1324	1330		

* Mann-Whitney U Tests

Table 2.8

Mean characteristics (± s.d.) of flighting activity of 10 male and 10 female immature Manx Shearwaters marked with luminescent lights

	Males (N)	Females (N)	U*	P
Time per flight (min)	3.6 ± 3.74 (18)	6.5 ± 7.92 (24)	269[1]	N.S.
Area covered (m^2)	74800 ± 55700 (14)	65500 ± 62600 (10)	94	N.S.
Number of call bouts per min	1.1 ± 0.38 (12)	0.9 ± 0.27 (12)	92	N.S.
% flight time calling	10.7 ± 4.00 (12)	8.4 ± 2.65 (12)	104	N.S.

* Mann-Whitney U-tests

1 t = 1.39, Wilcoxon Test

proportion spent calling by females (Table 2.8). This is probably due to the fact that a male call is longer than a female call (see Chapter 4).

Discussion

The fact that birds caught in mistnets weighed significantly less than breeding birds (Figure 2.9) strongly supports the suggestion that these birds were immature, and that it was these who were largely responsible for the aerial calling. Again, this idea has been forwarded for other species (Richdale 1944) but not formally demonstrated. The result supports those obtained for birds caught in the experimental traps while immatures also predominated (Figure 2.6). The large discrepancy between the sex ratio of calls heard in flight and the actual sex ratio of flying birds (Figure 2.10) is somewhat unexpected. The observations on shearwaters marked with luminescent lights showed no obvious differences between the sexes both in the area covered (Table 2.8) or in their relative flying heights. In addition, there was no difference in the recapture rates of netted males and females. The mistnet samples are probably therefore not biased toward one sex or the other. Instead, the difference in the sex ratios (Figure 2.10) may arise if males and females have different calling rates, or if a proportion of males are comparatively silent in flight. The results from birds marked with lights (Table 2.8) show no such differences in calling rates, so it seems most likely that some proportion of the males engaged in the flighting activity are more silent than others. In addition, that proportion apparently increased from April to July inclusive, as the proportion of males netted also increased, but the proportion of male calls heard in flight remained fairly constant (Figure 2.10). This increase coincided with the influx of immatures into the colony (Perrins et al. 1973, Brooke 1978b).

Why should this apparent vocal dichotomy in flying males exist? It

is clear from the playback results that birds engaged in flighting behaviour were listening, as well as calling, as their vocal responses were significantly altered (Table 2.6). This suggests two functions to aerial activity:

(1) Calling to advertise oneself to the opposite sex and possibly repel the same sex, although the latter is less likely, and

(2) Listening for responses to one's calling or to those elicited by other calling shearwaters.

Indeed, only about 8-11% of flight time was spent calling (Table 2.8), suggesting a large proportion of flight time spent listening.

If it is assumed that pair formation takes place in a burrow, then males should be primarily concerned with first acquiring a burrow, and females should be primarily concerned with acquiring a mate with a burrow. This is supported by the trapping results (Table 2.5). If aerial calling is a sexual display, there is no obvious selective advantage for a male without a burrow to call in flight. It is therefore possible that the more silent males are those as yet without burrows. Aerial calling by males may serve as an unambiguous signal to potential mates that a burrow-owner is calling, and would therefore be selectively advantageous. There can be no cheating by males without burrows, as in the present context, females are less likely to remain with them once both return to ground level as the male will not guide her to a burrow.

Why then do not males without burrows call in flight for other reasons, such as giving other males the impression that the area is full? This might increase their chances of acquiring a burrow, and eventually a mate. In the present study, it was not shown that burrowless males never called at all (all birds marked with lights had burrows). However, if they do, they certainly call less frequently. Presumably the advantages to a male without a burrow calling in flight are outweighed by the advantages of remaining silent. By doing so, they give themselves more time for listening,

possibly allowing a more effective way of assessing potential breeding areas. The Manx Shearwater, in common with other nocturnal Procellariiformes, is extremely awkward on land. Assessing a breeding area in flight, rather than on foot alone, may well prove to be a better strategy, despite the extra energy output, as much time is saved, and the risk of predation is possibly lowered. This is supported by the flighting activity of species without aerial calls, in which males form a large proportion (James 1983, Chapter 3).

There also exists the possibility that the more silent males in flight are composed mainly of the younger immature age classes. The studies of Perrins et al. (1973) and Brooke (1978b) have shown that younger immatures arrive latest in the season, and that immatures returned progressively earlier each year as they grow older. However, these results were based on surface-caught birds, and it is consistent with their findings that the younger immatures are present at the colony but engage more in aerial activity, and are therefore less available for capture on the surface. Scott (1970) demonstrated with mistnets that younger immature British Storm Petrels are more mobile than older immatures, and even suggested that they did not alight on the surface. This supports the possibility that immature Manx Shearwaters also engage less in aerial activity as they approach breeding age. The youngest birds are also going to be the least likely to have acquired burrows, which also agrees with the hypothesis that silent males are those as yet without them.

It is clear from the preceding discussion that the time budgets shown in Table 2.7 are only representative for immatures associated with burrows. After inclusion of the flying activity of silent males, there may be less differences between the sexes. Presumably, males with burrows spend less time airborne than females due to burrow competition from other males. Females do not have this extra limitation, so perhaps can afford to display in flight for a greater amount of time. Once a pair have settled on each

other, flight displays probably cease. Until that decision is reached (shearwaters first breed at six or seven years of age), there is no reason why a pair occupying the same burrow should not seek to improve their mate or burrow choice. By including aerial displays in this process, they probably increase the effectiveness of their signalling in much the same way as other birds do in open habitats (Marten & Marler 1977), as well as increase the likelihood of noting a favourable response or of acquiring a nest site.

CHAPTER THREE

Studies on the vocal behaviour of other nocturnal Procellariiformes

Studies on the vocal behaviour of other nocturnal Procellariiformes

Introduction

The present chapter reports the results of research conducted on the vocal behaviour of six species of Procellariiform other than the Manx Shearwater.

General Methods

The field work on the British Storm Petrel was conducted on Skomer Island, whereas the other five species were studied on Great Salvage Island. All tape recordings were made on a Uher 4000 Report IC tape recorder, and sonagrams were produced on a Kay 6061-B Sound Spectrograph using the wide band filter. Recordings were usually made of either spontaneously-calling birds or of birds responding to the playback of the relevant calls on a Sony M9 microcassette recorder.

Birds were sexed either by cloacal inspection (Serventy 1956) or by using comparative measurements of body size. Bills and tarsi were measured with Vernier calipers to the nearest 0.1 mm; wings and tails were measured with a stopped rule to the nearest mm and weights were usually recorded to the nearest g using a Pesola balance.

British Storm Petrel

The British Storm Petrel breeds on islands in the northeastern Atlantic and Mediterranean (Cramp & Simmons 1977). Although its calls have been described (Davis 1957), their functional significance remains obscure. I report here the results of playing back the calls of this species to breeding males and females incubating eggs, and also to birds engaged in flighting activity over the colony.

Methods

Test recordings of the two main calls (Figure 3.1) were obtained from spontaneously-calling males and females. These were used to perform a total of 177 playback tests on 43 male and 39 female Storm Petrels incubating alone in their nesting burrows. All birds had been ringed and sexed by cloacal inspection, and their bill, tarsus, wing and tail lengths measured. In each playback test, the test recording of either the Purr-Call or the Flight-Call was played, and the response of the incubating bird noted. Brooke (1978d) used similar methods in his investigation of Manx Shearwater vocalizations. No bird was tested twice on the same day, or with the same playback test.

The fact that the Flight-Call is labelled as such is unfortunate. The species rarely calls in flight and the call itself is often given in burrows along with the Purr-Call. However, to prevent further confusion, the original name will be used.

In order to investigate what effect the ground calling activity had on the flighting activity of Storm Petrels, the following experiment was also performed. A 20 m mist net was erected for six nights in the proximity of the breeding colonies. Half-hourly intervals of silence were alternated with half-hourly periods when a tape recording of the Purr-Call was played at the centre of the net. All birds caught were ringed and their tarsi, wings and tails measured as for the breeding birds.

Results

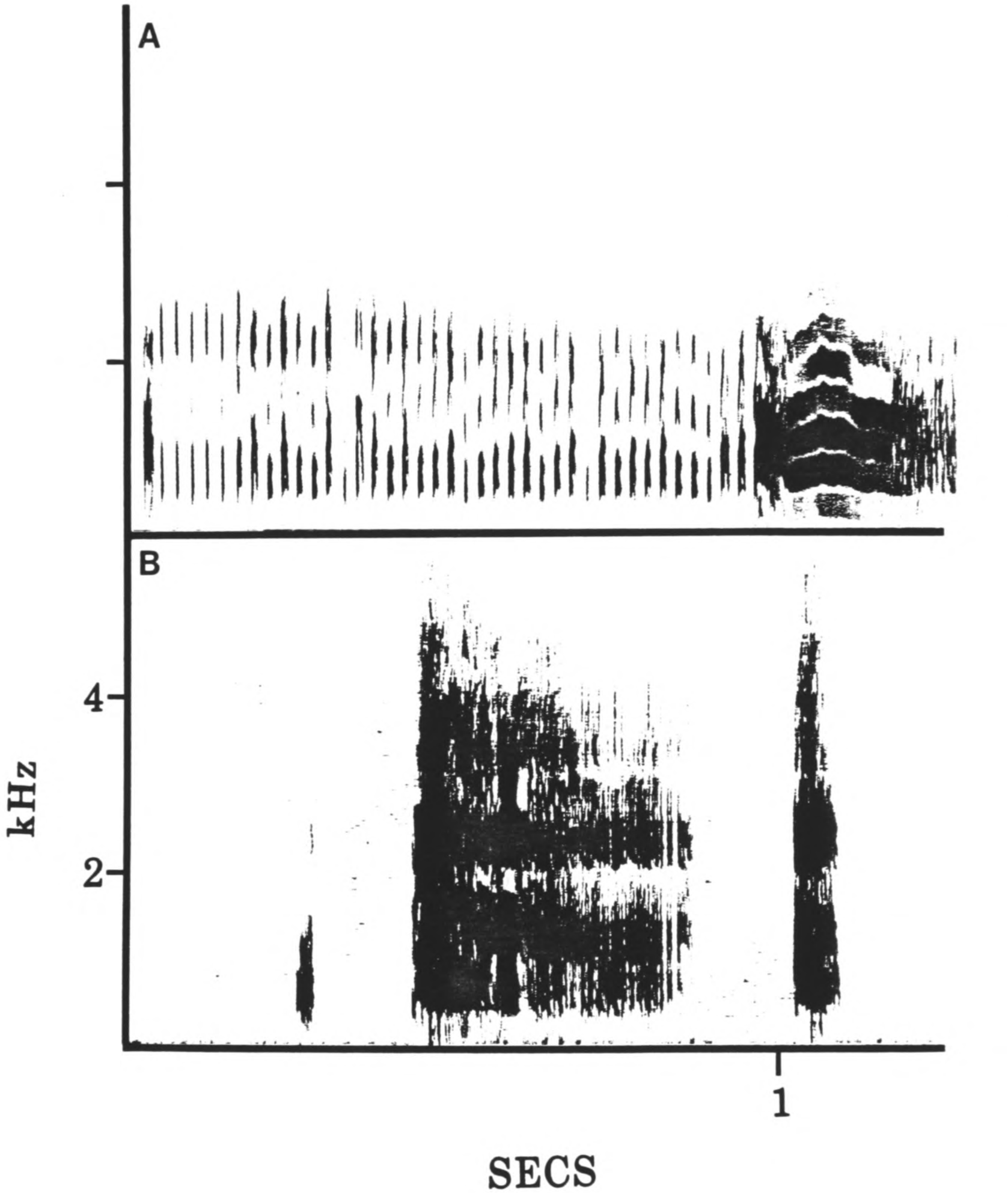
The playback results are presented in terms of response type (Purr- and/or Flight-Call given) and response frequency (Response or No response given).

Response type

Male Storm Petrels responded either with a Purr- and Flight-Call or

Figure 3.1

Sonagrams of typical (A) British Storm Petrel Purr-call and (B) Flight-call.


A
B
4
2
kHz
1
SECS

only a Flight-Call to the playback of Purr-, male Flight- or female Flight-Calls (Table 3.1). Female Storm Petrels responded only with a Flight-Call. The difference in response types between the sexes is significant for each call type played (Table 3.1). Further analysis of the male response type shows that it is independent of which call is played (X^2 = 2.30, d.f. = 2).

Response frequency

Male Storm Petrels were significantly more likely to respond with a call than females regardless of the call type played (Table 3.2). In addition, males were significantly more likely to respond to a Purr-Call than they were to Flight-Calls of either sex (X^2 = 11.20, d.f. = 2, $p < 0.005$) Females, on the other hand, were equally likely to respond to any of the calls played (X^2 = 1.4, d.f. = 2).

Table 3.3 shows statistically significant differences in the tail and wing lengths between male and female breeding Storm Petrels. The difference in tarsus is not quite significant, and mean bill lengths are almost identical. These differences allow the sexing of birds caught in the mist net during the playback experiment. To do so more effectively, discriminant function analyses were performed on the breeder biometrics. The results (Table 3.4) suggest that it is possible to sex Storm Petrels morphometrically with a reasonable degree of accuracy. The best separation is achieved by using the wing and tail discriminant function. The use of all three variables together does not increase the separation provided by wing and tail alone.

A total of 100 birds were caught during the netting experiment, 57 with the Purr-Call playing (capture rate 9.5/h) and 43 without (capture rate 4.3/h). The capture rates are significantly different (Mann-Whitney, U = 153.5, n = 15,14, $p < 0.025$). There was no significant change in the sex ratio of birds caught when the Purr-Call was played compared with when

Table 3.1

The response type of male and female British Storm Petrels to the playback of Purr-, male Flight- and female Flight-Calls

	Male response type		Female response type			
Call played	Purr- with Flight-Call N(%)	Flight-Call only N(%)	Purr-with Flight-Call N(%)	Flight-Call only N(%)	X^2	p
Purr-call	19(51.4)	18(48.6)	0(0.0)	13(100.0)	10.6[1]	<0.01
Male Flight-Call	20(62.5)	12(37.5)	0(0.0)	17(100.0)	17.8	<0.001
Female Flight-Call	9(75.0)	3(25.0)	0(0.0)	4(100.0)	-	0.019[2]

1 For each call played, X^2 (d.f. = 1) compares the male and female response types.

2 Fisher Exact Test.

Table 3.2

The response frequency of male and female British Storm Petrels to the playback of Purr-, male Flight- and female Flight-Calls

	Male response frequency		Female response frequency			
	Responded	Did not respond	Responded	Did not respond		
Call played	N(%)	N(%)	N(%)	N(%)	X^2	p
Purr-Call	37(100.0)	0(0.0)	13(46.4)	15(53.6)	25.5[1]	< 0.001
Male Flight-Call	32(74.4)	11(25.6)	17(43.6)	22(56.4)	8.1	< 0.01
Female Flight-Call	12(75.0)	4(25.0)	4(28.6)	10(71.4)	6.6	< 0.02

1 For each call played, X^2 (d.f. = 1) compares the male and female response frequencies.

Table 3.3

The mean ± s.d. bill, tarsus, wing and tail lengths (mm) of 26 male and 20 female British Storm Petrels

	Male	Female	t	P
Bill	12.0 ± 0.4	12.1 ± 0.4	0.84	N.S.
Tarsus	22.6 ± 0.8	22.9 ± 0.7	1.44	N.S.
Wing	120.4 ± 2.5	123.7 ± 2.7	4.29	<0.001
Tail	54.2 ± 1.6	56.5 ± 1.8	4.58	< 0.001

Table 3.4

The accuracy of sexing British Storm Petrels using four different discriminant functions

Variables used	% Males correct	% Females correct	% Overall
Tarsus, Wing	80.8	80.0	80.4
Tarsus, Tail	80.8	70.0	76.1
Wing, Tail	88.5	80.0	84.8
Tarsus, Wing, Tail	88.5	80.0	84.8

it was not (Table 3.5). However, there was a slight excess of males caught both with or without the call playing.

Discussion

The results show that the two sexes of the British Storm Petrel tend to give different calls (Table 3.1). Males and females share the Flight-Call, but the male has the additional Purr-Call. This is also the form of the vocal dimorphism found in another hydrobatid, the Fork-tailed Storm Petrel Oceanodroma furcata (Simons 1981).

British Storm Petrels usually give the Purr-Call when alone in a burrow (Davis 1957), and occasional reports of birds purring simultaneously (Hall-Craggs & Sellar 1976) are probably of two males contesting a burrow, or occupying two nest sites of close proximity (Cramp & Simmons 1977). The Purr-Call has been attributed the dual function of announcing ownership of a burrow and of advertising to other birds (Davis 1957). Table 3.1 suggests its territorial role is less important, as males responded with either call type to playback. The Purr-Call is extremely attractive to other Storm Petrels and is used extensively by ringers to lure birds into mist nets and increase catches severalfold (Scott 1970, Furness & Baillie 1981, Fowler et al. 1982). Such was the case here with significantly more birds captured in the net with the call playing than when it was not. The function of the Flight-Call is unknown but, as it is common to both sexes, it may serve as a contact or recognition call between members of a pair. Examination of numerous sonagrams of Flight-Calls suggests this possibility, as considerable individual variation exists, a prerequisite for individual recognition.

In general, males were more likely to give a vocal response to playback than females (Table 3.2). This is probably related to the roles of the sexes in the breeding cycle. As with the male Manx Shearwater (Harris

Table 3.5

The classification of British Storm Petrels netted with and without playback of the Purr-Call using three different discriminant functions

	No Purr-Call (N=43)		Purr-Call (N=57)			
Variables used	Male	Female	Male	Female	X^2	P
Tarsus, Wing	26	17	32	25	0.17	N.S.
Tarsus, Tail	26	17	39	18	0.72	N.S.
Wing, Tail	23	20	31	26	0.60	N.S.

1966a, Chapter 2), the male Storm Petrel is largely responsible for establishing and defending the nest site (Davis 1957). This is further shown by the fact that males were more likely to respond with a call to the exclusively-male Purr-Call than to the Flight-Calls of either sex (Table 3.2), something that females do not do. That both sexes failed to discriminate between male and female Flight-Calls suggests the call is very similar in both sexes. To my ear at least, the two are not separable, and casual and quantitative inspection of sonagrams confirms this.

Considering that only male Storm Petrels give the Purr-Call, it is perhaps surprising that the sex ratios caught with and without the call playing are not different (Table 3.5). However, males may be attracted to this call for different reasons than females. For example, the presence of males purring may signify suitable nesting habitat, and so prospecting males may be attracted to the area, either to investigate unoccupied burrows or to attempt an eviction of a calling occupant. Scott (1970) showed that immatures in their first year at the colony were not site-faithful, and even suggested that they did not alight on the surface. Such wandering may serve as an effective method of assessing potential breeding areas. Purr-Calls attract a greater proportion of immatures (Furness & Baillie 1981). It is therefore possible that such assessment involves flying over potential breeding areas, and listening for calling occupants. This would be of benefit to both sexes, as males could establish potential rival density, and females potential mate density. The fact that immatures do not engage in aerial displays (Scott 1970) supports this interpretation of their flighting behaviour.

Madeiran Storm Petrel

The Madeiran Storm Petrel Oceanodroma castro is a species inhabiting both Atlantic and Pacific Oceans (Cramp & Simmons 1977). Unlike the British

Storm Petrel, this species produces a considerable amount of calling in flight at the colony (Allan 1962, Harris 1969).

Methods

At the time of the visit, the Madeiran Storm Petrels were laying eggs. It was thus possible to sex birds cloacally and ring them. Nesting pairs were located at night from their vocal activity, and 22 incubating birds (15 male, 7 female) were recorded using playback of their Purr-Call.

Results

Both male and female Madeiran Storm Petrels produced three types of calls in response to the playback of their Purr-Calls (Figure 3.2). Two of the calls (Purr- and Flight-Call) have been previously described (Cramp & Simmons 1977), but the third (the High-Call) appears not to fit closely any of the descriptions in the literature, although it could be the 'Pre-copulation-Call' (Cramp & Simmons 1977). Sexual dimorphism exists for two of the call types, the Purr-Call and most notably, the Flight-Call (Figure 3.2). Both Flight-Calls consist of an irregular repetition of short notes. However, in the male, these notes are markedly clearer, producing a more melodious call. The female, by comparison, produces only harsh-sounding notes. The sexual difference in the Purr-Call is seen in the end flourish of the call. Again, the males' notes at the end of a Purr-Call have a clearer quality than those of the females.

There was no significant difference between the sexes in the number of times each call type was used in response to playback (Table 3.6). As it was possible to distinguish male and female Flight-Calls, it was decided to investigate the sex ratio of these calls heard at the colony. For three nights, 9 to 11 July, male and female Flight-Calls were counted for a five minute period at the same time and site. The results, 81, 83, 86 (total

Figure 3.2

Sonagrams of typical (A) male Flight-Call (B) female Flight-Call (C) male Purr-Call (D) female Purr-Call (E) male High-Call and (F) female High-Call of Madeiran Storm Petrel.

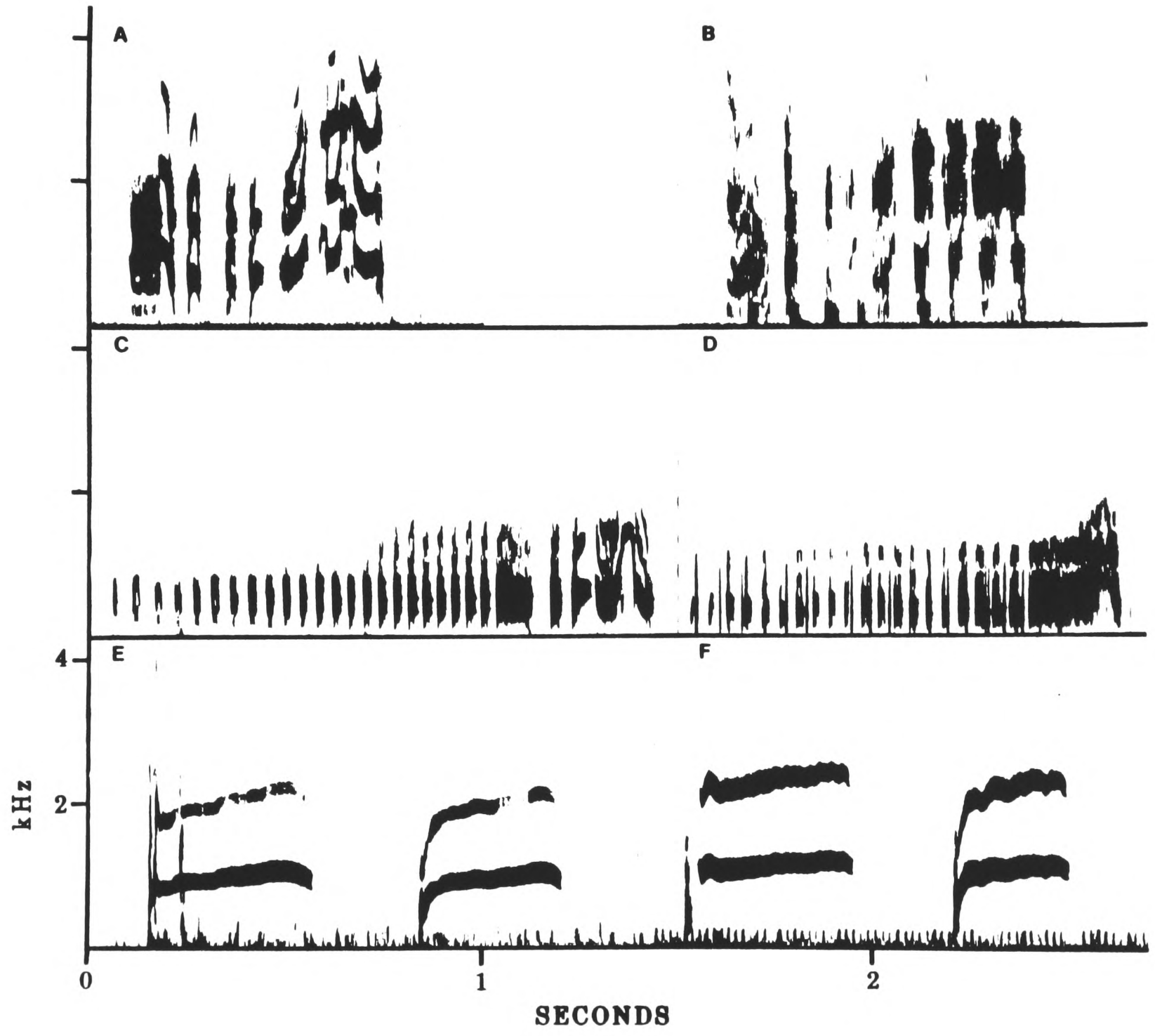

A
B
C
D
E
F
4
2
kHz
0
1
2
SECONDS

Table 3.6

The frequency that male and female Madeiran Storm Petrels used the three call types in response to playback

	Call type response		
	Purr	Flight	High
Males	14	15	6
Females	8	6	4

X^2 = 0.47, d.f. = 2, N.S.

It was believed that the number of birds counted more than once was small in relation to the total.

250) male calls and 71, 73, 78 (total 222) female calls are not significantly different from parity (X^2 = 1.66, d.f. = 1).

Discussion

It is clear that sexual dimorphism exists in the Purr-Call and Flight-Call of the Madeiran Storm Petrel. As the last few notes in the Purr-Call are very similar to those used in the Flight-Call (Figure 3.2), the sexual difference in the Purr-Call could be attributed to the inclusion of Flight-Call-like notes in the call.

Most, if not all of the Oceanodroma storm petrels exhibit aerial calling at their colonies. Based on the results above, it is very likely that similar voice differences exist throughout the genus. Ainley (1980) proposed a new subspecies of Leach's Storm Petrel O. leucorhoa based on, among other things, vocal characters. The sample sizes used for the vocal comparisons are small, but more importantly, the sonagram of the Flight-Call of the new subspecies is clearly that of a female. He compares this with the sonagrams of Flight-Calls of other subspecies that are clearly males. Bourne & Jehl (1982) caution against the use of vocal characters with such small sample sizes, but it is now apparent that the real danger lies not in ignoring the inherent population variance, but in ignoring the sexual dimorphism in voice that may exist in such populations. Despite being a party to the above caution, Jehl (1982) compares the calls of Manx Shearwater subspecies with samples of one, and also ignores the sexual dimorphism that had already been demonstrated in the voice of this species (Brooke 1978d). Clearly, it is premature to use vocal characters in support of a taxonomic classification until those characters can be analysed as rigorously as traditional mensural characters (Bourne & Jehl 1982).

Compared with the Manx Shearwater (Brooke 1978d, Chapter 2), the sex

ratio of calls heard in flight is markedly different in the Madeiran Storm Petrel, with proportionately more male calls being heard. Further discussion will be given at the end of the chapter.

Cory's Shearwater

Cory's Shearwater Calonectris diomedea breeds in the Mediterranean and sub-tropical eastern Atlantic (Cramp & Simmons 1977). Research on the nominate race in Greece has shown that sexual dimorphism in voice exists (Ristow & Wink 1980). Research was conducted on the vocalizations of the significantly larger race borealis.

Methods

Egg-laying had been completed some weeks earlier (Zino 1971) so sexing cloacally was not possible. However, males are significantly larger than females (Wink & Ristow 1979). The nest sites of 19 pairs were visited and the sitting birds stimulated to call by either playback of Cory's Shearwater calls or by being prodded with a stick. Different birds were prodded or subjected to playback.

All birds were individually marked on the forehead with black felt pen, and their bill lengths, depths, tarsus and wing lengths measured. The birds' weights were also recorded to the nearest 5 g.

Results and Discussion

There was a consistent difference between the calls produced by the members of each pair (Figure 3.3). Again, the dimorphism was not one of temporal patterning, but one of frequency distribution, with a higher-sounding call in one partner, and a much deeper call in the other. As cloacal sexing was not possible, the two call groups were compared biometrically (Table 3.7). In all five parameters measured, the birds with a higher call were significantly larger

Figure 3.3

Sonagrams of typical (A) male Cory's Shearwater and (B) female Cory's Shearwater.

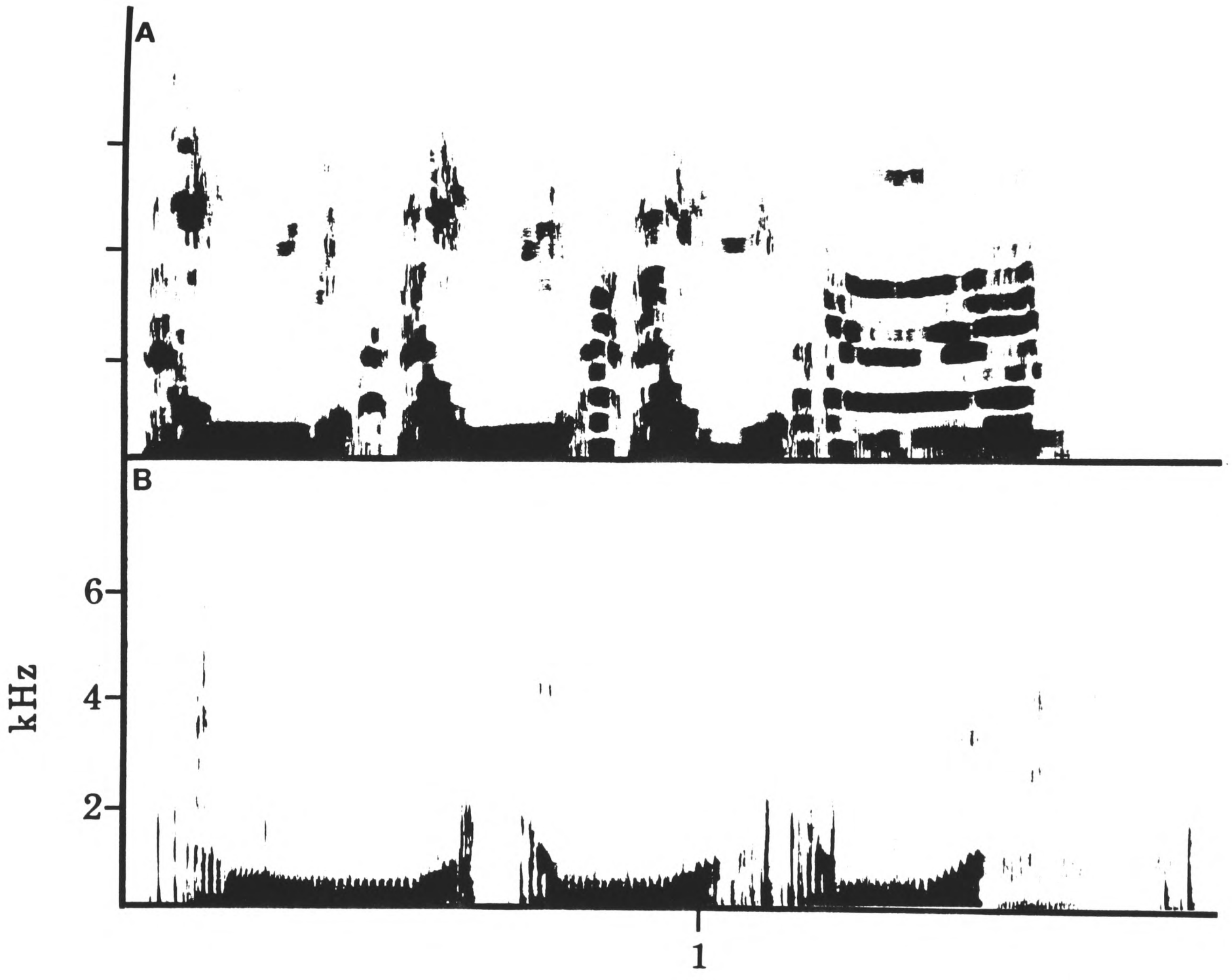

A
B
6
4
2
kHz
1
SECS

Table 3.7

The mean ± s.d. measurements (mm) and weights (g) of 19 Cory's Shearwater pairs producing two call types

	Call type			
	High	Deep	t^1	P
Bill length	58.5 ± 1.6	55.8 ± 1.9	5.06	<0.001
Bill depth	22.5 ± 0.6	20.2 ± 0.6	9.27	<0.001
Tarsus	59.9 ± 1.1	58.0 ± 1.3	4.27	<0.001
Wing	369.9 ± 6.5	361.1 ± 6.9	3.63	<0.01
Weight	962.4 ± 48.4	810.8 ± 69.1	9.54	<0.001

1 Paired t-tests

than those with a deeper call. As male Cory's Shearwaters are significantly larger than females (Zino 1971, Cramp & Simmons 1977, Wink & Ristow 1979), it is concluded that the males produced the higher call and the females the deeper one. This agrees with the form of the vocal dimorphism found in the sexes of the nominate race in Greece (Ristow & Wink 1980).

As the calls of males and females could be distinguished easily, it was decided to investigate the sex ratio of flight calls heard at the colony. For four evenings between 30 June and 8 July, male and female calls given in flight were counted at the same time and site. The counts were 29, 28, 31 and 28 female calls and 79, 89, 86 and 84 male calls respectively. The totals (116 female and 338 male) are significantly different from parity (X^2 = 454.0, d.f. = 1, $p < 0.005$). This is completely the opposite result observed in the Manx Shearwater (Brooke 1978d, Chapter 2) and different from that observed in the Madeiran Storm Petrel (this chapter). Further discussion will be given later.

It was believed that the number of birds counted more than once was small in relation to the total.

Little Shearwater

The biology of the Little Shearwater Puffinus assimilis is poorly understood, probably because it is mostly a winter breeder throughout its range in the Atlantic and Pacific Oceans (Serventy et al. 1971, Cramp & Simmons 1977). As a result, few ornithologists have visited its breeding colonies.

Methods

The Little Shearwaters were visiting the colony following their breeding season (Jouanin 1964). The burrows of 14 pairs were located at night from their vocal activity, and the occupants within stimulated to call by the playback of Little Shearwater calls.

Temporary removal of individuals from pairs and subsequent playback to

the remaining birds established the exact identity of the callers recorded. All birds were ringed, and their bill lengths, depths and tarsus lengths measured. Bill length was taken at the dorsal edge of the feathering, and the birds were weighed.

Results and Discussion

In all 14 pairs, there was a consistent difference between the calls produced by the members of each pair (Figure 3.4). The calls did not differ so much in their temporal pattern, but did so in the distribution of their fundamental frequencies. The one call sounded higher-pitched and had a more clear, strident quality than that of the other call, which sounded harsher or rasping. The difference was such that all birds heard at the colony could be assigned to one group or the other.

The most obvious interpretation of this vocal dimorphism among the pairs is that the Little Shearwater has sex-specific calls, similar to those described in the Manx Shearwater (Brooke 1978d) and Cory's Shearwater (Ristow & Wink 1980). The sexes of the individuals in the present case were not known. Egg-laying had long been completed, so it was not possible to sex birds cloacally. However, if the biometric data for the birds in the two call groups are compared (Table 3.8), it is clear that they are distinct morphometrically. In three out of the four characters measured, the birds with a clear call were significantly larger. As it is usual in Little Shearwaters for males to be larger than females (Witherby et al. 1940, Palmer 1962, Cramp & Simmons 1977), it is concluded that the males produced the clearer call, and the females the harsher one. This is also the form of the vocal dimorphism found in the Manx Shearwater (Brooke 1978d) and Cory's Shearwater (Ristow & Wink 1980).

Figure 3.4

Sonagrams of typical (A) male Little Shearwater and (B) female Little Shearwater.

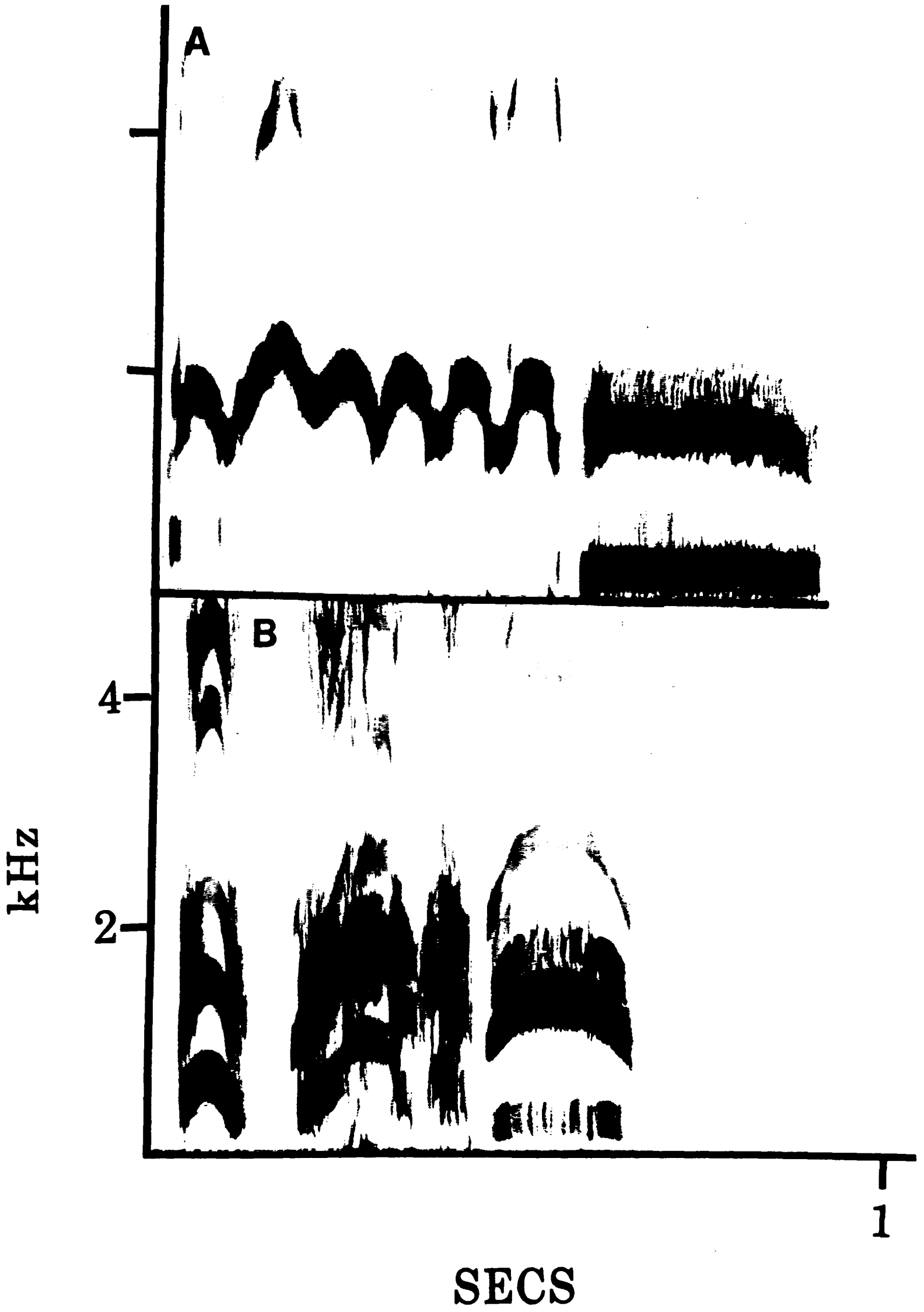

A
B
4
2
kHz
1
SECS

Table 3.8

The mean ± s.d. measurements (mm) and weights (g) of 14 Little Shearwater pairs producing two call types

	Call type			
	Clear	Harsh	t^1	P
Bill length	25.3 ± 0.9	25.0 ± 0.6	1.49	N.S.
Bill depth	9.4 ± 0.3	8.8 ± 0.2	8.54	<0.001
Tarsus	37.3 ± 0.8	36.1 ± 0.7	3.42	<0.01
Weight	161.4 ± 11.4	152.1 ± 7.6	2.85	<0.02

1 Paired t-tests

Bulwer's Petrel

Bulwer's Petrel *Bulweria bulwerii* occurs in the sub-tropical sectors of both the Pacific and Atlantic Oceans (Cramp & Simmons 1977). Its very distinctive call is apparently common to both sexes (Cramp & Simmons 1977).

Methods

Breeding pairs of Bulwer's Petrels were located at night from their vocal activity. At the time, they were commencing egg-laying. It was thus possible to sex birds cloacally before ringing them. Incubating males and females were stimulated to call mostly by giving a vocal imitation of their call. Conflicting reports (Cramp & Simmons 1977, Thibault & Holyoak 1978) of whether or not the species calls in flight were also investigated.

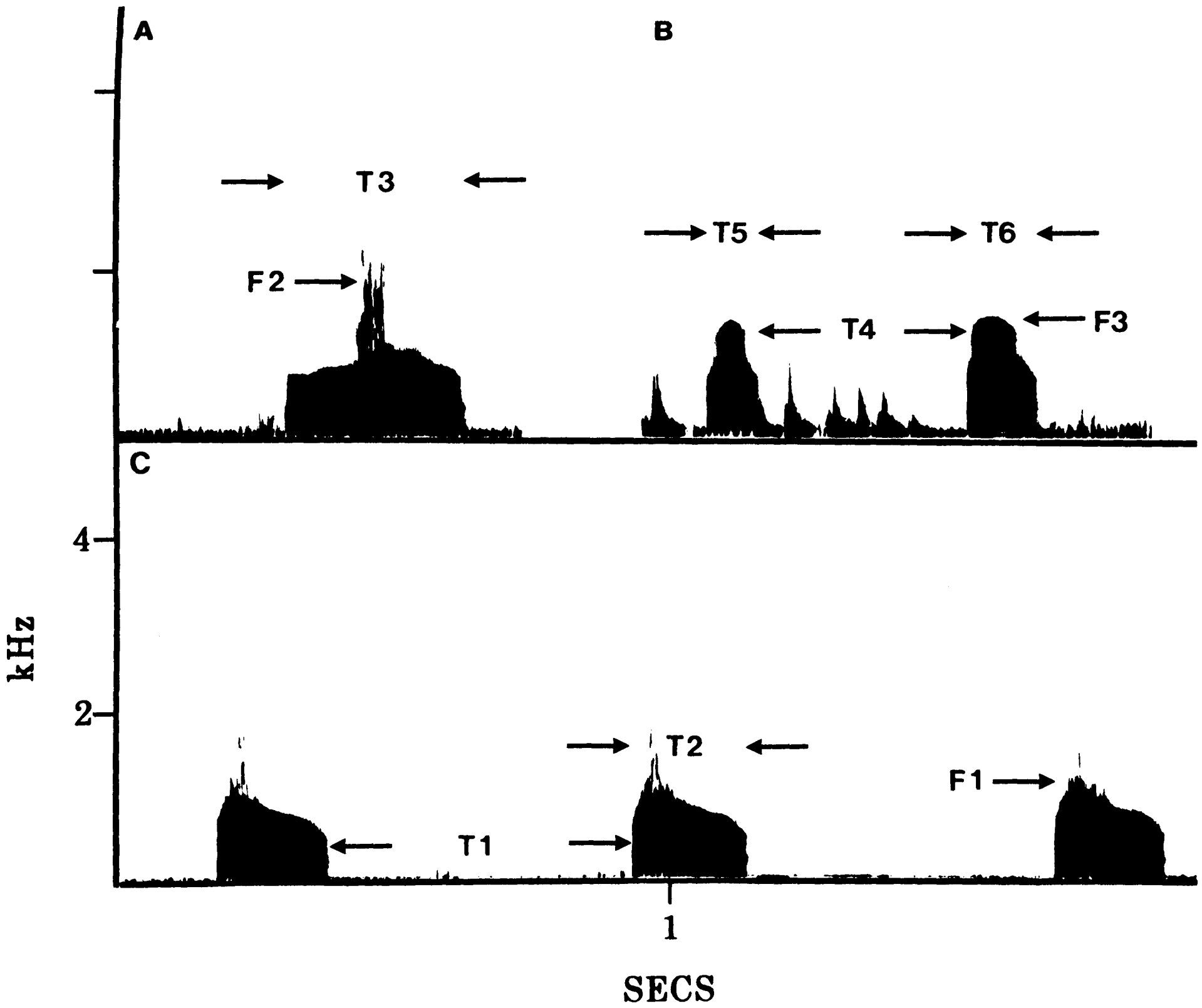
Results

To the ear, the calls of male and female Bulwer's Petrels were indistinguishable. A more quantitative analysis of their vocalizations was therefore performed to look for more subtle differences.

Figure 3.5 shows that Bulwer's Petrel gives three basic call "types", separable by their temporal patterning. Both males and females produced all three. They were labelled the Repeat-Call, Single-Call and Double-Call. The Repeat-Call was by far the commonest call heard at the colony, where birds would give it continuously for several minutes at a time. The Single-Call was given in two contexts; at the end of a long series of Repeat-Calls or by itself. The Double-Call was always given by itself and not in conjunction with the other call types. Figure 3.5 shows the temporal and frequency characteristics measured for each call type from sonagrams. Only one of the nine parameters measured was significantly different between males and females, that of the time interval between

Figure 3.5

Sonagrams of typical Bulwer's Petrel (A) Single-Call (B) Double-Call (C) Repeat-Call. Also shown are the frequency (F) and time (T) variables measured on each call type. The maximum frequencies in each call type were measured (F1, F2 and F3).


A
B
T3
T5
T6
F2
T4
F3
C
4
kHz
2
T2
F1
T1
1
SECS

successive repetitions in the Repeat-Call (Tables 3.9 and 3.10). In other words, females called at a faster rate than males. The difference in the maximum frequencies of male and female Double-Calls was almost significant (Table 3.10).

The number of times that each call was used by males and females in response to my vocal imitation was also compared (Table 3.11). Again, there was no significant difference between the sexes. In agreement with Thibault & Holyoak (1978) and Jouanin et al. (1979), observations on birds performing flighting activity confirmed that Bulwer's Petrel does not call in flight. This is in opposition to that stated in Cramp & Simmons (1977).

Discussion

Clearly, Bulwer's Petrel does not show the marked sexual dimorphism in voice that other species of nocturnal Procellariiform possess (Brooke 1978d, Ristow & Wink 1980, Simons 1981, James 1984). While it is possible that males and females distinguish between each other on the basis of their Repeat-Call rates (Table 3.9), further experimentation will be necessary to demonstrate it. Even if they do, the degree of vocal sexual dimorphism is still much reduced over that of other species. As it has been suggested that such dimorphism is an adaptation to a nocturnal life style (Brooke 1978d) this result requires further explanation, which is deferred to the General Discussion.

White-faced Storm Petrel

The White-faced Storm Petrel Pelagodroma marina is another species found in both the Pacific and Atlantic Oceans (Cramp & Simmons 1977). As with Bulwer's Petrel, there is confusion as to whether it gives flight calls at the colony (Cramp & Simmons 1977).

Table 3.9

Male and female Bulwer's Petrel mean ± s.d.

temporal call characteristics (sec)

Call type and measurement	Male (N)	Female (N)	t	P
Repeat, T1	0.82 ± 0.17 (18)	0.68 ± 0.19 (24)	2.47	< 0.02
Repeat, T2	0.15 ± 0.04 (18)	0.14 ± 0.04 (24)	0.84	N.S.
Single, T3	0.28 ± 0.07 (7)	0.29 ± 0.07 (10)	0.29	N.S.
Double, T4	0.39 ± 0.11 (12)	0.37 ± 0.08 (11)	0.48	N.S.
Double, T5	0.10 ± 0.02 (12)	0.09 ± 0.03 (11)	1.09	N.S.
Double, T6	0.15 ± 0.04 (12)	0.14 ± 0.05 (11)	0.67	N.S.

Table 3.10

Male and female Bulwer's Petrel mean ± s.d.

frequency call characteristics (Hz)

Call type and measurement	Male (N)	Female (N)	t	P
Repeat, F1	2147.5 ± 752 (18)	2086.4 ± 743 (24)	0.26	N.S.
Single, F2	2144.3 ± 557 (7)	2566.5 ± 689 (10)	1.34	N.S.
Double, F3	3386.7 ± 1065 (12)	2737.3 ± 839 (11)	2.01	N.S.

Table 3.11

The frequency that male and female Bulwer's Petrels used the three call types in response to playback

	Call type response		
	Repeat	Double	Single
Males	18	19	11
Females	24	17	23

$X^2 = 3.03$, d.f. = 2, N.S.

Methods, Results and Discussion

During the visit, the White-faced Storm Petrels had chicks at various stages of development, so again, sexing adults by cloacal inspection was not possible. Breeding burrows were visited at night, when parents were feeding chicks, and calls played of White-faced Storm Petrels in order to try and elicit vocal responses. However, the species was extremely unresponsive, and the net result was a single recording of a pair calling together (Figure 3.6). The identity of the callers was determined, and each bird had its bill, tarsus, wing and tail length measured, and in addition, they were weighed.

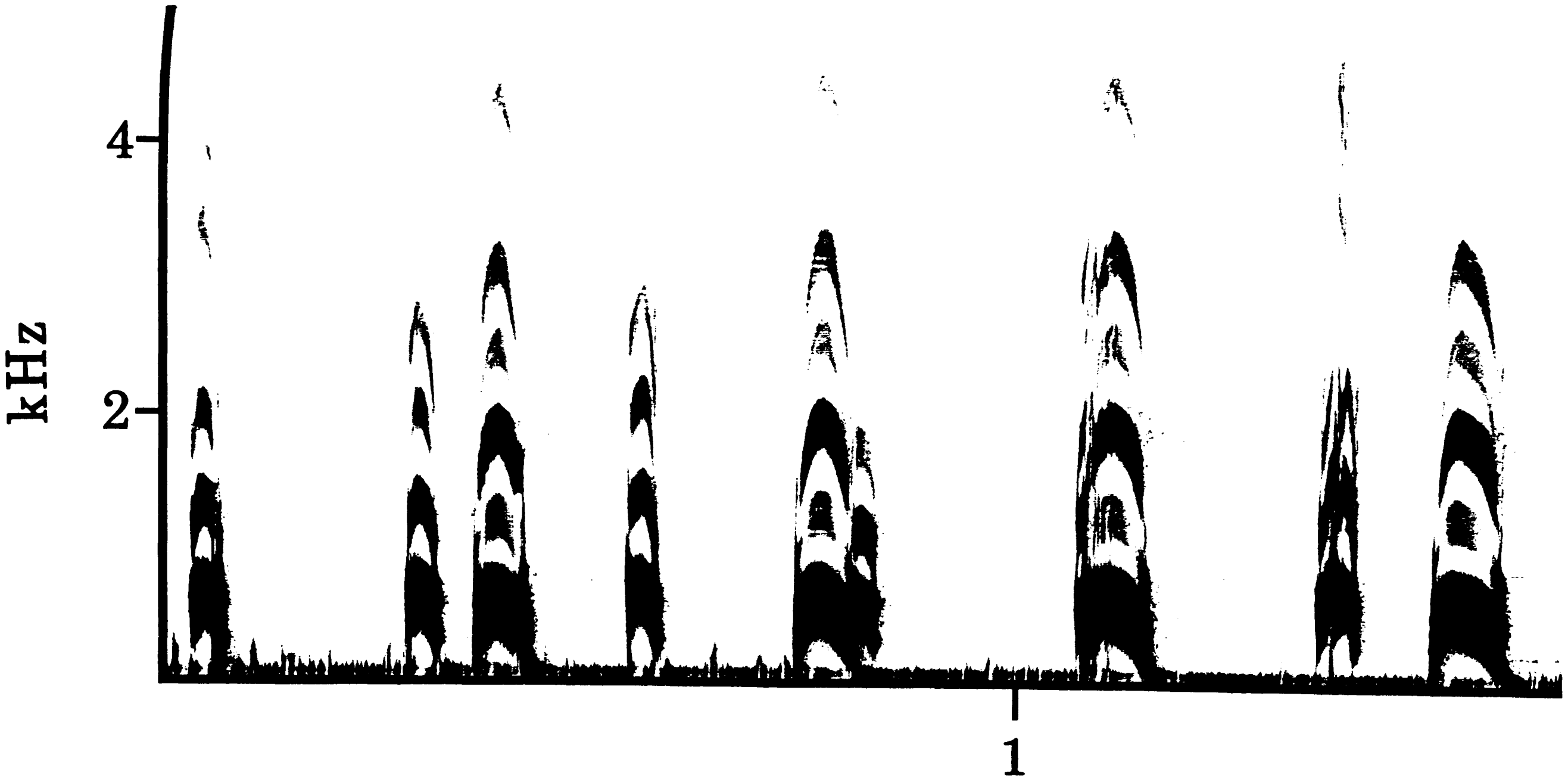
As it is usual for females to be larger than males in this species (Murphy & Irving 1951, Jouanin & Roux 1965), it was possible to tentatively sex the pair. The male's measurements (mm) were: Bill 18.2, Tarsus 44.1, Wing 155, Tail 68 and Weight 48 g. The female's were: Bill 18.2, Tarsus 45.3, Wing 160, Tail 71 and Weight 47 g.

As with Bulwer's Petrel, there is no obvious sexual dimorphism to the ear between the male and the female (Figure 3.6). However, there are again differences in the temporal spacing of the calls. The time interval between successive calls is about 0.2 sec in the male and 0.3 sec in the female. In addition, the time length of the call in the female was approximately double that in the male. A sonagram of a pair calling in Cramp & Simmons (1977) also shows these differences, and it is concluded that they are consistent. Again, it cannot be assumed that these subtle differences act as markers for sexual recognition, but it can be concluded that sexual dimorphism in voice, if it exists, is much reduced in this species too.

In agreement with Murphy (1936), Witherby et al. (1940) and Warham (1958a), no flight calls were given by this species. References quoted in

Figure 3.6

Sonagram of White-faced Storm Petrel pair calling.


kHz
4
2
1
SECS

Cramp & Simmons (1977) that this species does call in flight (Lockley 1942, Richdale 1965) are inconclusive. Lockley (1942) is speaking of birds taking flight in the beam of his torch, and Richdale's (1965) statement is ambiguous and could be interpreted either way.

Other species

The results show that sexual dimorphism exists in some but not all of the nocturnal Procellariiformes. In an attempt to identify further species exhibiting the phenomenon, copies of all nocturnal Procellariiform recordings held at the British Library of Wildlife Sounds were requested. These were examined on a Princeton 4512 FFT Real Time Spectrum Analyser to look for possible sexual differences within the same call types.

Clear differences within call types were detected in the Fluttering Shearwater Puffinus gavia (Figure 3.7), Hutton's Shearwater Puffinus huttoni (Figure 3.8), Mottled Petrel Pterodroma inexpectata (Figure 3.9) and Fairy Prion Pachyptila turtur (Figure 3.10). Differences could also be heard in several other species, but the recordings were of such poor quality that good sonagrams could not be made. These included the Sooty Shearwater Puffinus griseus, Short-tailed Shearwater Puffinus tenuirostris, Flesh-footed Shearwater Puffinus carneipes, Streaked Shearwater Calonectris leucomelas, Greater Shearwater Puffinus gravis and Black Storm Petrel Oceanodroma melania.

General Discussion

The results show that some, but not all of the nocturnal Procellariiformes examined have sexual dimorphism in voice. The Little Shearwater, Cory's Shearwater, British Storm Petrel and Madeiran Storm

Figure 3.7

Sonagrams showing possible sexual dimorphism in the voice of Fluttering Shearwater Puffinus gavia, Long Island, N.Z. G. Wragg.

Male? above; Female? below.

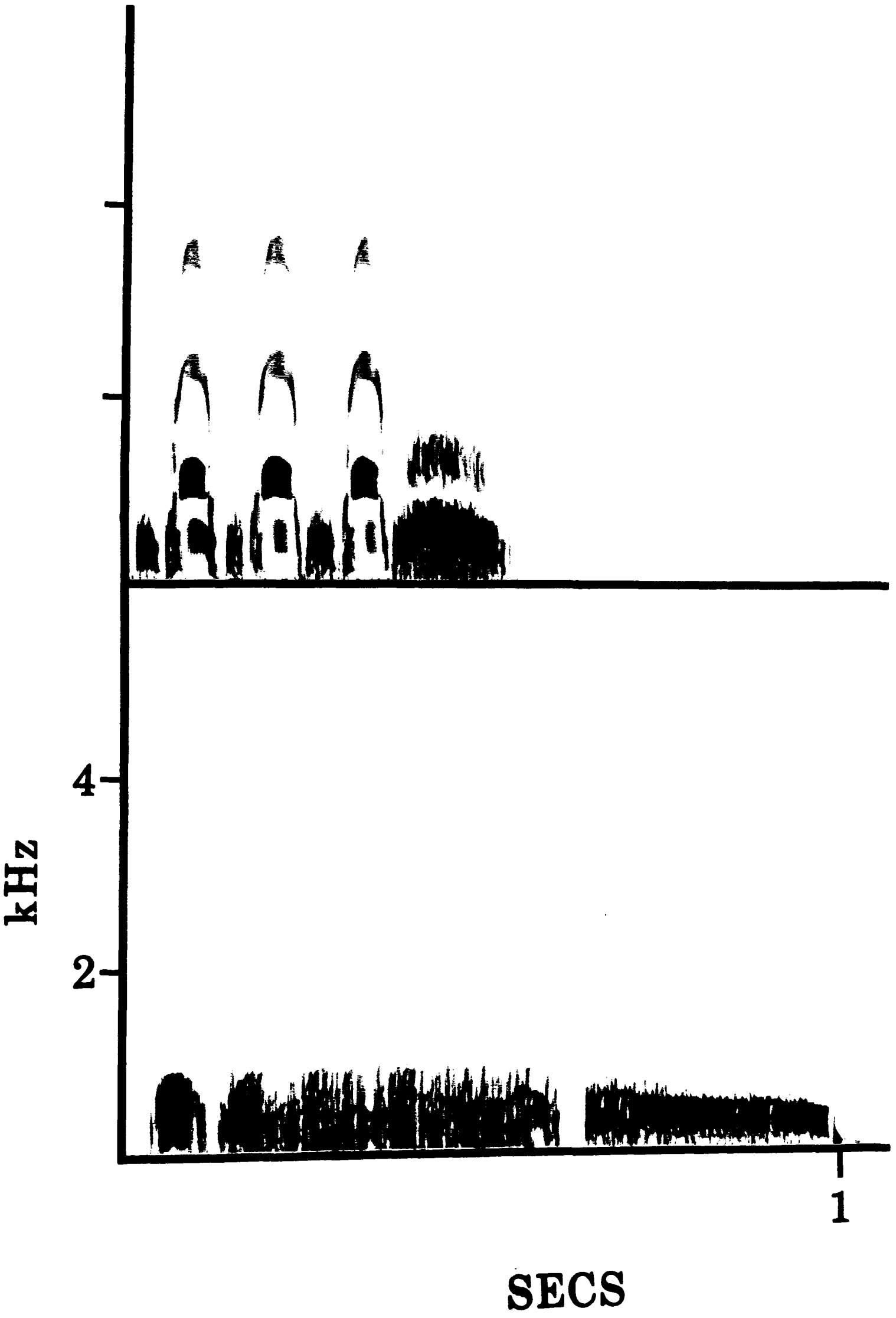

4
2
kHz
1
SECS

Figure 3.8

Sonagrams showing possible sexual dimorphism in the voice of Hutton's Shearwater Puffinus huttoni, Kaikoura Mountains, N.Z. L. McPherson.

Male? above; Female? below.

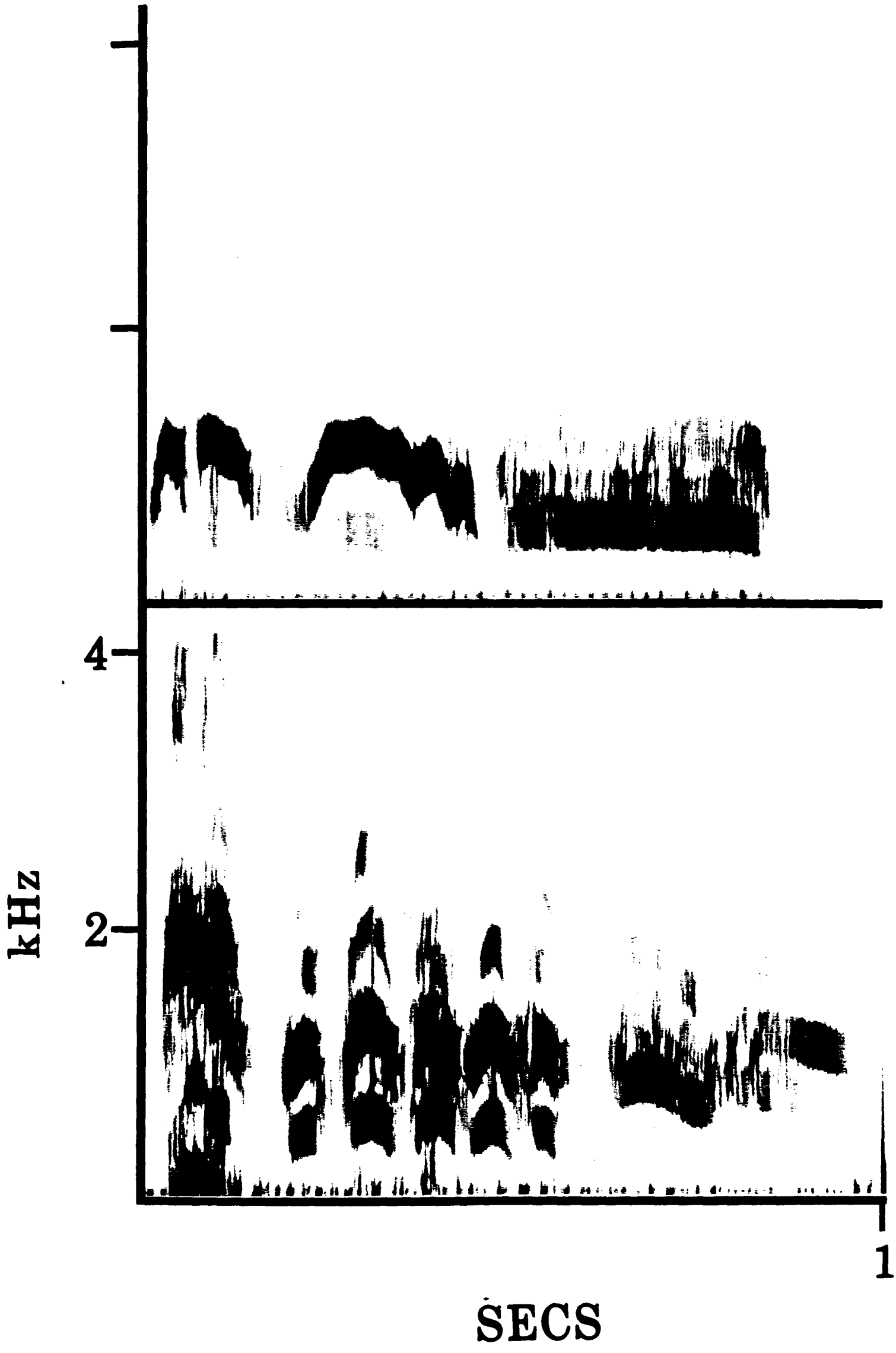

4
2
kHz
1
SECS

Figure 3.9

Sonagrams showing possible sexual dimorphism in the voice of Mottled Petrel Pterodroma inexpectata, Snares Islands, N.Z.

H. Best.

Male? above; Female? below.

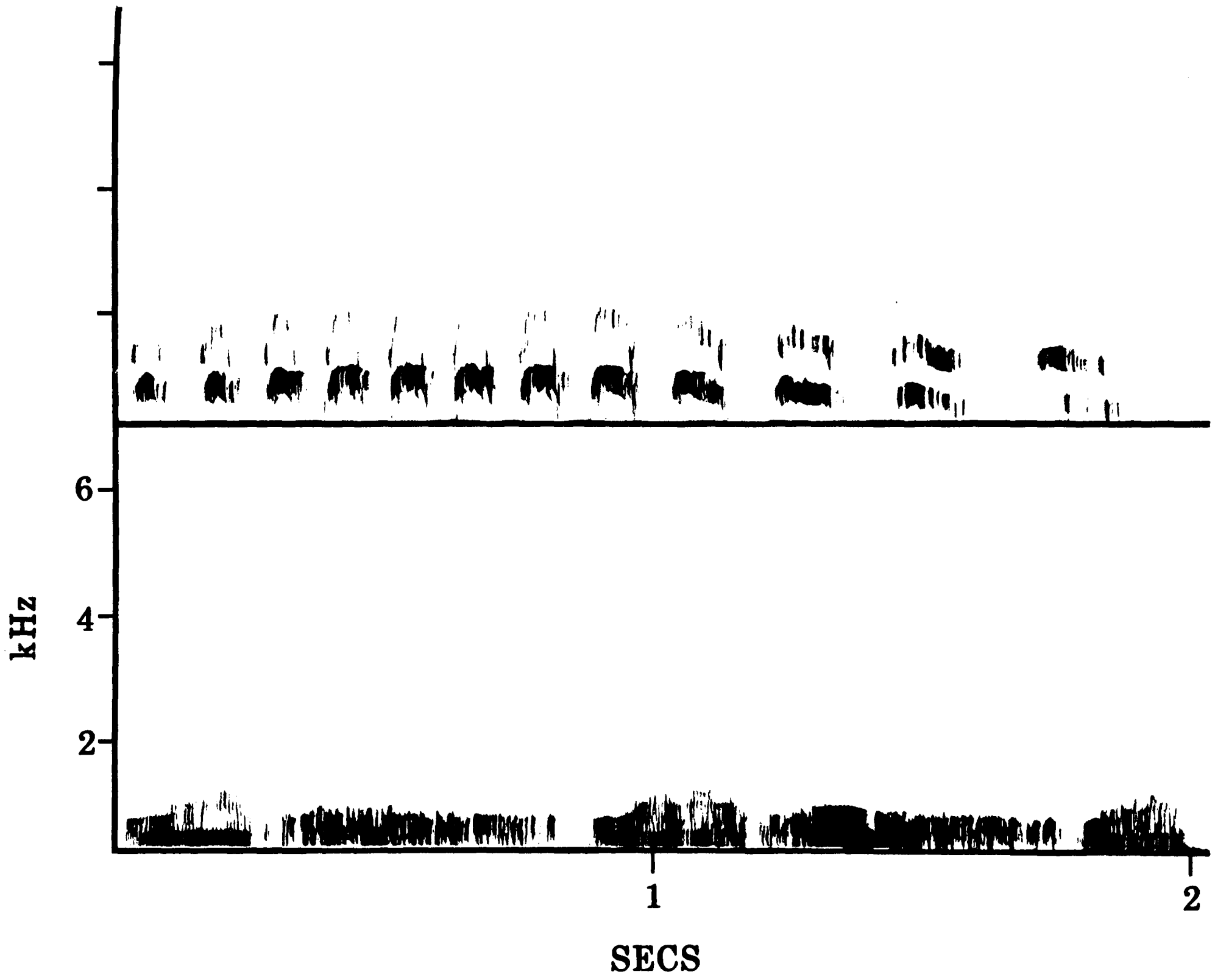
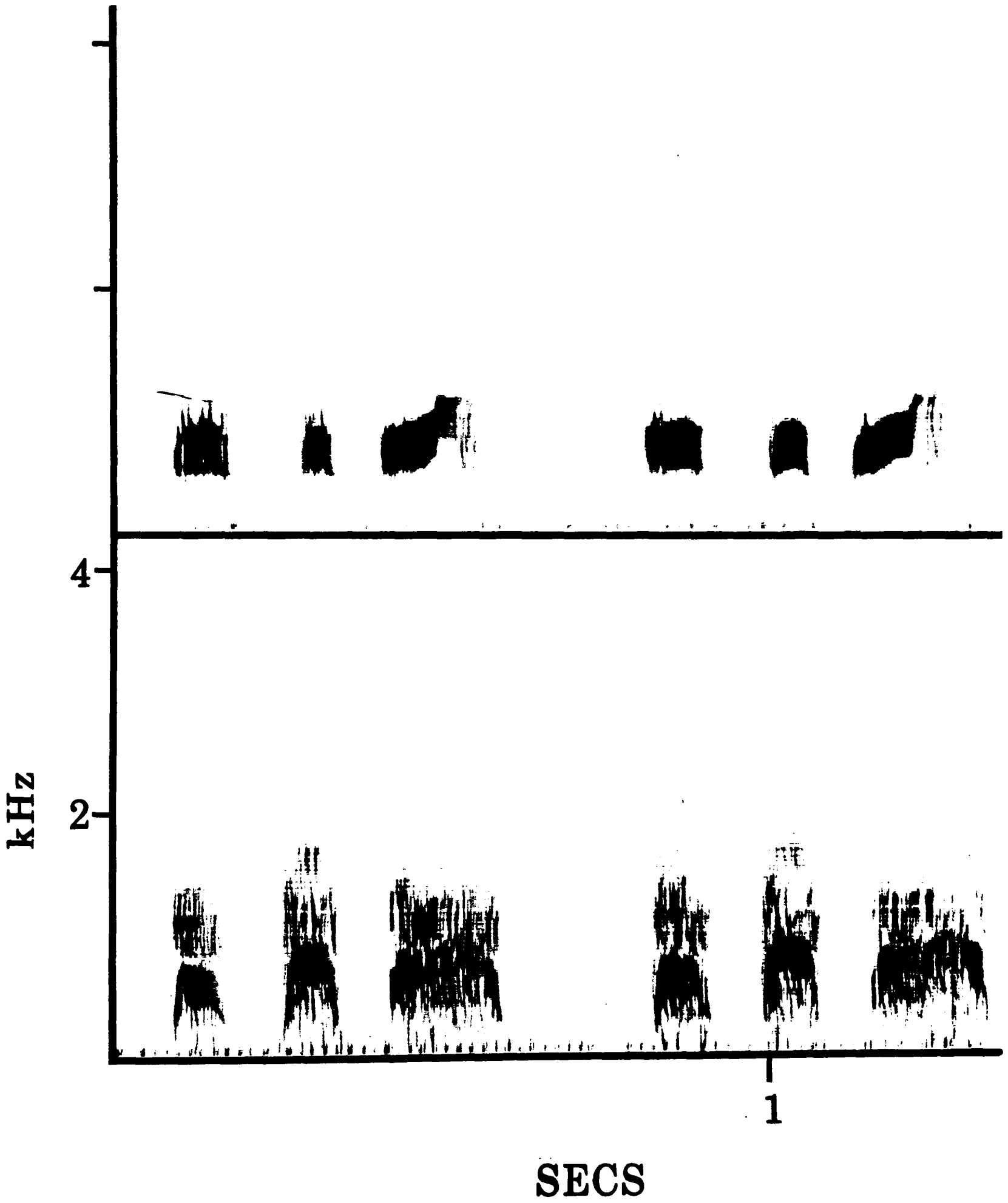

6
4
2
kHz
1
2
SECS

Figure 3.10

Sonagrams showing possible sexual dimorphism in the voice of Fairy Prion Pachyptila turtur, Stephens Island, N.Z.

J. Kendrick.

Male? above; Female? below.


4
2
kHz
1
SECS

Petrel all have strong vocal dimorphism, whereas Bulwer's Petrel and the White-faced Storm Petrel do not. To the first list can be added the Manx Shearwater (Brooke 1978d), Fork-tailed Storm Petrel (Simons 1981) and Snow Petrel Pagodroma nivea (Guillotin & Jouventin 1980). To the latter list can be added the Wedge-tailed Shearwater Puffinus pacificus (Shallenberger 1973, M. de L. Brooke, pers. comm.).

The inclusion of the Snow Petrel is perhaps exceptional. Nesting at such high latitudes, it cannot be described as being truly nocturnal. It is though, apparently crepuscular at the breeding colonies (J. - L. Mougin, pers. comm.). In addition, there is an inverse correlation between body weight and the fundamental frequency of their calls with males being much larger and having lower frequencies (Guillotin & Jouventin 1980). The vocal dimorphism then could just be a result of body size. Croxall (1982) suggested that perhaps selection favoured sexual dimorphism in size in order to promote voice differences in this species which is entirely devoid of plumage markings. However, based on the results of all other species, where the smaller females produce the lower sound frequencies, it seems possible that the vocal difference between male and female Snow Petrels has been derived independently from their body size differences.

Sexual differences in call have also been suggested, but not demonstrated, for a number of other nocturnal Procellariiformes including the Black-capped Petrel Pterodroma hasitata (Wingate 1964), Mottled Petrel Pterodroma inexpectata (Warham et al. 1977), White-headed Petrel Pterodroma lessoni (Warham 1967), Pycroft's Petrel Pterodroma pycrofti (Fleming 1941), Great-winged Petrel Pterodroma macroptera (Warham 1956), Soft-plumaged Petrel Pterodroma mollis (Warham 1979), Barau's Petrel Pterodroma baraui (Jouanin & Gill 1967), Bonin Petrel Pterodroma hypoleuca (Grant et al. 1983) and Thin-billed Prion Pachyptila belcheri (Strange 1980).

As with most biological phenomena, the situation is complex and not

simply a function of taxonomy. Table 3.12 summarizes some of the vocal characteristics for nocturnal species in relation to whether sexual dimorphism in voice is proven or not. Some species have aerial calling, and some do not. If we are to assume that such behaviour is adaptive, then examination of these characters for trends may help to understand the evolution of vocal behaviour in the group.

One relationship that is apparent is that between vocal dimorphism and aerial calling (Table 3.12). Those species with aerial calls show sexual dimorphism within them. The reverse is also true in those species without aerial calls where vocal dimorphism does not exist, apart from the British Storm Petrel in which the "dimorphism" is a call given by one sex only. This is also the form of the vocal dimorphism in the Fork-tailed Storm Petrel which does have aerial calling (Simons 1981). If it is assumed that aerial calling is concerned with, among other things, sexual advertisement, then why are some species silent in their flighting activity, particularly as calling would seem to confer considerable signalling advantages? For example, the ground is a major cause of sound attenuation, and studies have shown that it diminishes significantly by just moving a few feet above the ground (Marten & Marler 1977). Thibault & Holyoak (1978) speculated that aerial vocal displays in Bulwer's Petrel have been replaced by vocal and olfactory displays in the burrow. However, the species still engages in flighting activity, albeit silently.

One possible disadvantage to aerial calling is that it may attract predators, but this is difficult to reconcile when both species with and without aerial calls breed in close proximity to one another. If we extend the argument applied to Manx Shearwaters that males who indulge in aerial calling are those with burrows trying to attract potential mates, it may be disadvantageous to leave the burrow to call in flight as another male may claim the burrow. That burrow competition exists in these species is beyond

Table 3.12

Summary of vocal behaviour in some nocturnal Procellariiformes

Species	Aerial calls?	Dimorphic in aerial calls?	Dimorphic in ground calls?	Sex ratio of aerial calls	Authors
Manx Shearwater	Yes	Yes	Yes	F > M	Brooke 1978d
Cory's Shearwater	Yes	Yes	Yes	M > F	This study
Little Shearwater	Yes	Yes	Yes	?	"
Madeiran Storm Petrel	Yes	Yes	Yes	M=F	"
Fork-tailed Storm Petrel	Yes	?	Yes	?	Simons 1981
Bulwer's Petrel	No	-	No	-	This study
White-faced Storm Petrel	No	-	No	-	"
British Storm Petrel	No	-	Yes	-	"
Wedge-tailed Shearwater	No	-	No	-	Shallenberger 1973

doubt (Nelson 1980), and it could influence to what degree males call in flight. Those males in species with acute nest site competition may forego aerial calling entirely, compared with the males of species with less nest site competition. Such competition may arise either through an excess of males prospecting for burrows or through a shortage of burrows. The former could be affected by breeding season synchrony and interspecific competition for burrows, although it has been suggested that such competition has promoted breeding asynchrony (see Buckley & Buckley 1980). In species with extended breeding seasons, such as those in the tropics, it is possible that nest site competition is relatively relaxed compared with more synchronous breeding populations. Interspecific competition for burrows will only be important when species are similar in size which rarely happens. Shortages of nest sites could result from habitat differences. For example, species nesting in soil substrates are likely to have relatively less burrow competition (Nelson 1980), as prospecting birds have a choice of looking for existing burrows or digging their own. Species nesting in rock substrates do not have such a choice, and the number of potential nest sites is relatively more limited. A review of the literature looking at the incidence of aerial calling, breeding season synchrony and nest site habitat shows that aerial calling is unaffected by breeding season synchrony but significantly affected by nest site habitat (Table 3.13). As predicted, those species nesting in soil substrates tend to produce aerial calls, whereas those nesting in rock substrates tend not to.

In evolutionary terms then, it would appear as if nest site habitat has influenced the vocal behaviour of these species. Males of species nesting in rock substrates are probably less able to leave burrows in order to display. Without males calling in flight, sexual dimorphism in voice is not selected for, as there is no need to promote sexual identity among a mixture of calling males and females. Males are sufficiently

HABITAT

Calling/Rocks

Pterodroma leucoptera, *Pachyptila desolata*, *P. turtur*, *Calonectris diomedea*, *Puffinus assimilis*, *Oceanodroma castro*, *Puffinus lherminieri*.

Calling/Soil

Pterodroma macroptera, *P. lessoni*, *P. hasitata*, *P. cahow*, *P. rostrata*, *P. inexpectata*, *P. mollis*, *P. phaeopygia*, *P. cooki*, *P. hypoleuca*, *P. pycrofti*, *Pachyptila vittata*, *P. belcheri*, *Puffinus carneipes*, *P. gravis*, *P.griseus*, *P. tenuirostris*, *P. puffinus*, *P. gavia*, *Oceanodroma leucorhoa*, *O. furcata*, *Pelecanoides urinatrix*.

Silent/Rocks

Pachyptila crassirostris, *Bulweria bulwerii*, *Oceanites oceanicus*, *Fregetta tropica*, *Hydrobates pelagicus*.

Silent/Soil

Procellaria westlandica, *Puffinus pacificus*, *Pelagodroma marina*.

BREEDING SEASON

Calling/Distinct

All *Pterodroma* spp., rest of *Puffinus*, *Calonectris diomedea*, all *Pachyptila*, *Oceanodroma leucorhoa*, *O. furcata*, all *Pelecanoides*.

Calling/Indistinct

Puffinus lherminieri, *Oceanodroma castro*.

Silent/Distinct

As for Silent/Rocks including *Procellaria westlandica*.

Silent/Indistinct

Puffinus pacificus.

Table 3.13

The number of nocturnal Procellariiformes who do or do not produce aerial calls in relation to their breeding season and nest site habitat[4]

	Breeding Season[1]			Habitat[3]			
	Distinct	Indistinct	p[2]	Rocks	Soil	X^2	p
Species with aerial calls	21	2	N.S.	7	22	4.2	<0.05
Species without aerial calls	6	1		5	3		

1 Distinct = egg-laying over about one month; Indistinct = egg-laying over several months.

2 Fisher Exact Test.

3 Rocks = Substrate manipulation not possible.
Soil = Substrate manipulation possible.

4 See opposite page for details

identified by occupying nest sites and calling from within them. But why do females not call in flight in these species without aerial calls, if only to promote calling from males below or to repel other females? This seems to be linked to the fact that females vocally respond in flight to males calling in flight. For example, male and female Manx Shearwater calling intensities in flight were significantly correlated, and female calling in flight increased in response to male playback, but male calling in flight did not in response to female playback (Chapter 2). This suggests that aerial calling in females is concerned with response to males already calling, and not in promoting calling from males below. Without males calling in flight, females apparently do better to remain silent and spend their flight time listening for calling males below.

The sex ratio of calls heard in flight varies from species to species (Table 3.12). Enough data do not exist on this point, but these ratios may reflect the level of nest site competition that exists. For example, if female calling predominates (Manx Shearwater), this may mean that nest site competition is keener than when male calling predominates as in Cory's Shearwater. Presumably, the situation for the Madeiran Storm Petrel lies somewhere between these two extremes.

It is clear that in the Procellariiformes at least, sexual differences in voice do not necessarily follow if one is nocturnal. However, the suggestion that such dimorphism, when it occurs, is an adaptation to low light levels (Brooke 1978d) is supported by the fact that no examples of vocal dimorphism could be found in diurnal species. Observations on several pairs of Fulmars Fulmarus glacialis on Skomer revealed no obvious vocal differences within pairs, and a detailed study of two albatross species has also showed no sexual differences in voice (Sparling 1977).

While no such dimorphism is apparent in the diurnal Procellariiformes, it does exist in other diurnal seabird groups. For example, the two species

of Aptenodytes penguins have sex-specific calls in contrast to the other penguin species (Jouventin 1982), as do several of the Sulidae (Nelson 1978), Phalacrocoracidae, Pelecanidae, Fregatidae and Laridae (Cramp & Simmons 1977, 1983).

For the penguins at least, there appears to be an inverse relationship between vocal and physical dimorphism (Jouventin 1982), suggesting that voice differences have been selected for when visual cues to sexual identity are reduced. In a sense, this is analogous to the situation existing in the nocturnal Procellariiformes. For the sulids, no such relationship is evident as vocal dimorphism exists in species with considerable physical dimorphism (Nelson 1978). The smaller males produce calls with higher frequencies, so perhaps in this group body size is more important in shaping voice differences, which may secondarily result from selection favouring physical dimorphism.

In conclusion, it would appear as if no single adaptive explanation will account for the phenomenon of sexual dimorphism in the voices of various seabird groups. This difficulty is further compounded by the fact that detailed knowledge concerning the calls of many species is unavailable.

CHAPTER FOUR

Geographical and temporal variation in the calls of the Manx Shearwater and British Storm Petrel

Geographical and temporal variation in the calls of the Manx Shearwater and British Storm Petrel

Introduction

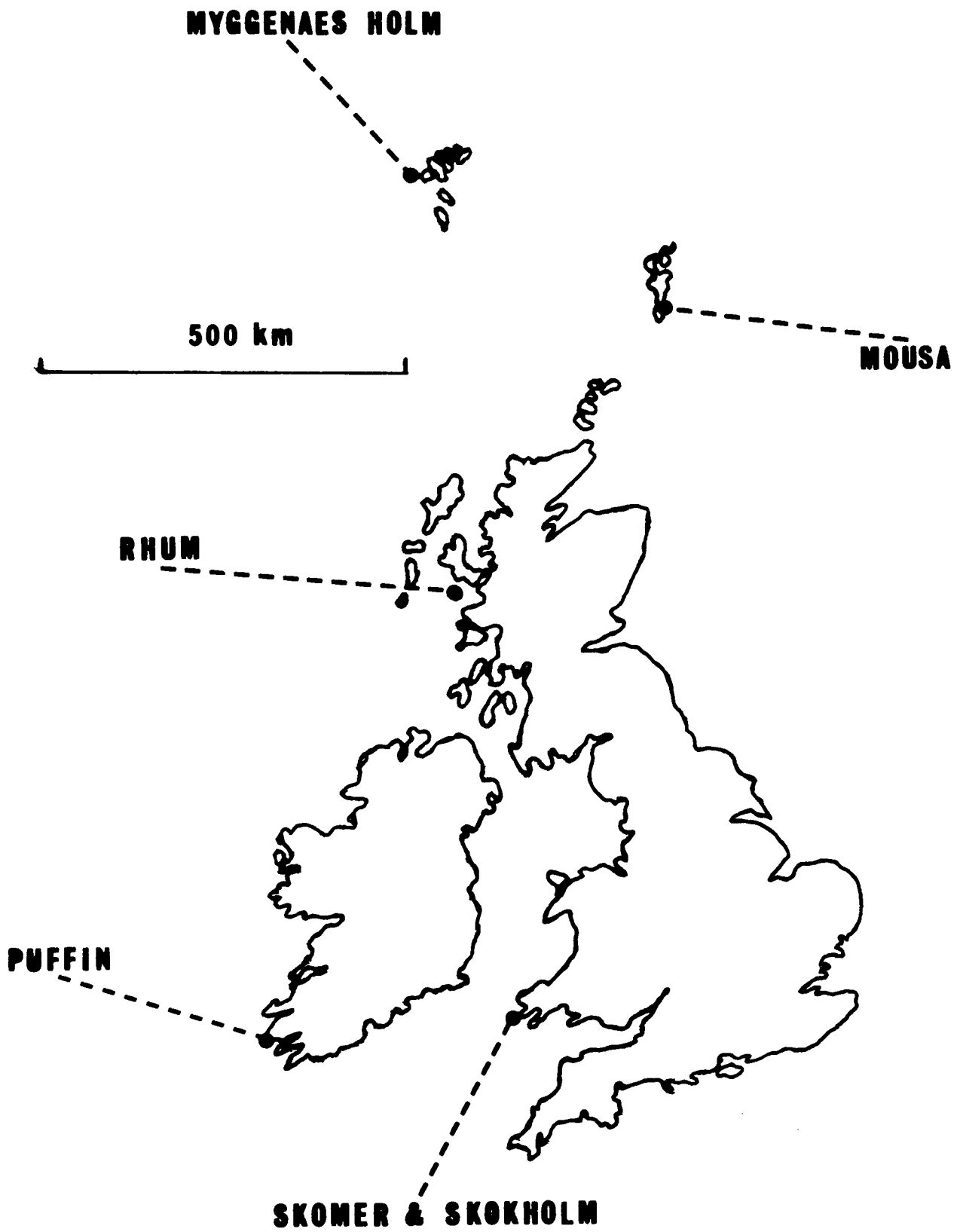
Much attention has been focused recently on how and why bird song varies geographically at both local and regional levels (for reviews, see Krebs & Kroodsma (1980) and Mundinger (1982). However, the vast majority of this research has concentrated on the sounds produced by passerines (Mundinger 1982) and few studies have considered non-passerine vocalizations (Snow 1968, Wiley 1971, Van der Weyden 1973, Mirsky 1976, Goldstein 1978), especially seabirds (Hand 1981, Jouventin 1982). In this regard I report here on the geographical variation in the calls of two seabird species, the Manx Shearwater and British Storm Petrel. In addition, the related issue of the temporal stability of such variation is considered for the Manx Shearwater.

Methods

Five Manx Shearwater colonies (Skomer and Skokholm, Wales; Puffin, Eire; Rhum, Scotland and Myggenaes Holm, Faeroes) and four Storm Petrel colonies (Skomer, Skokholm, Puffin and Mousa, Scotland) covering a latitudinal range of about 1500 km were visited (Figure 4.1). Tape recordings were made of birds calling in burrows in response to the playback of the relevant species' calls. All recordings were made on a Uher 4000 Report IC tape recorder except those of the Faeroes shearwaters (Phillips cassette recorder) and Mousa petrels (Phillips microcassette recorder). Recordings were made between April and June 1981 (Skomer), during April 1982 (Skokholm), May 1982 (Rhum), July 1982 (Faeroes), May 1983 (Skokholm), and June 1983 (Puffin and Mousa).

Figure 4.1

Map showing the positions of the six Manx Shearwater and British Storm Petrel colonies visited for the purposes of investigating geographical variation in voice.


MYGGENAES HOLM
500 km
MOUSA
RHUM
PUFFIN
SKOMER & SKOKHOLM

In order to investigate whether Manx Shearwater calls varied on a microgeographic scale, three separate colonies were sampled on Skomer (Figure 4.2). The three, North Haven, Farm and the Spit colonies were on the east side, in the middle and on the west side of the island respectively. The distance between North Haven and the Spit was about 2000 m.

Finally, in order to see whether the calls of a Manx Shearwater population changed with time, the tape recordings made on Skokholm in 1982/83 were compared with those made by Brooke (1978d) in the same area on Skokholm in 1976.

For all calls recorded, sonagrams were produced on a Kay 6061-B Sound Spectograph using the wide band filter. These were used to measure temporal characteristics. Frequency characteristics were measured by playing the tapes through a Princeton 4512 Spectrum Analyser coupled to a Unigon SC-1 Scan Converter. For the Manx Shearwater calls, four temporal and four frequency variables were measured for males, and four temporal and one frequency variable were measured for females (Figure 4.3). The difference was due to the lack of frequency structure in female calls. The British Storm Petrel produces two distinct calls. For both of them, the Purr-Call and the Flight-Call, four temporal and one frequency variable were measured (Figure 4.4). Only male Storm Petrels produce the Purr-Call (James 1984), and as no detectable differences exist between male and female Flight-Calls (James 1984), they were combined for the analyses.

Results

Microgeographical variation

Univariate analyses of variance on the 13 male and female call variables of Skomer Manx Shearwaters show that only one has significant differences between the North Haven, Farm and Spit colonies (Tables 4.1 and 4.2); this

Figure 4.2

Map of Skomer Island showing the locations of the three shearwater colonies sampled for voice differences at a local level.

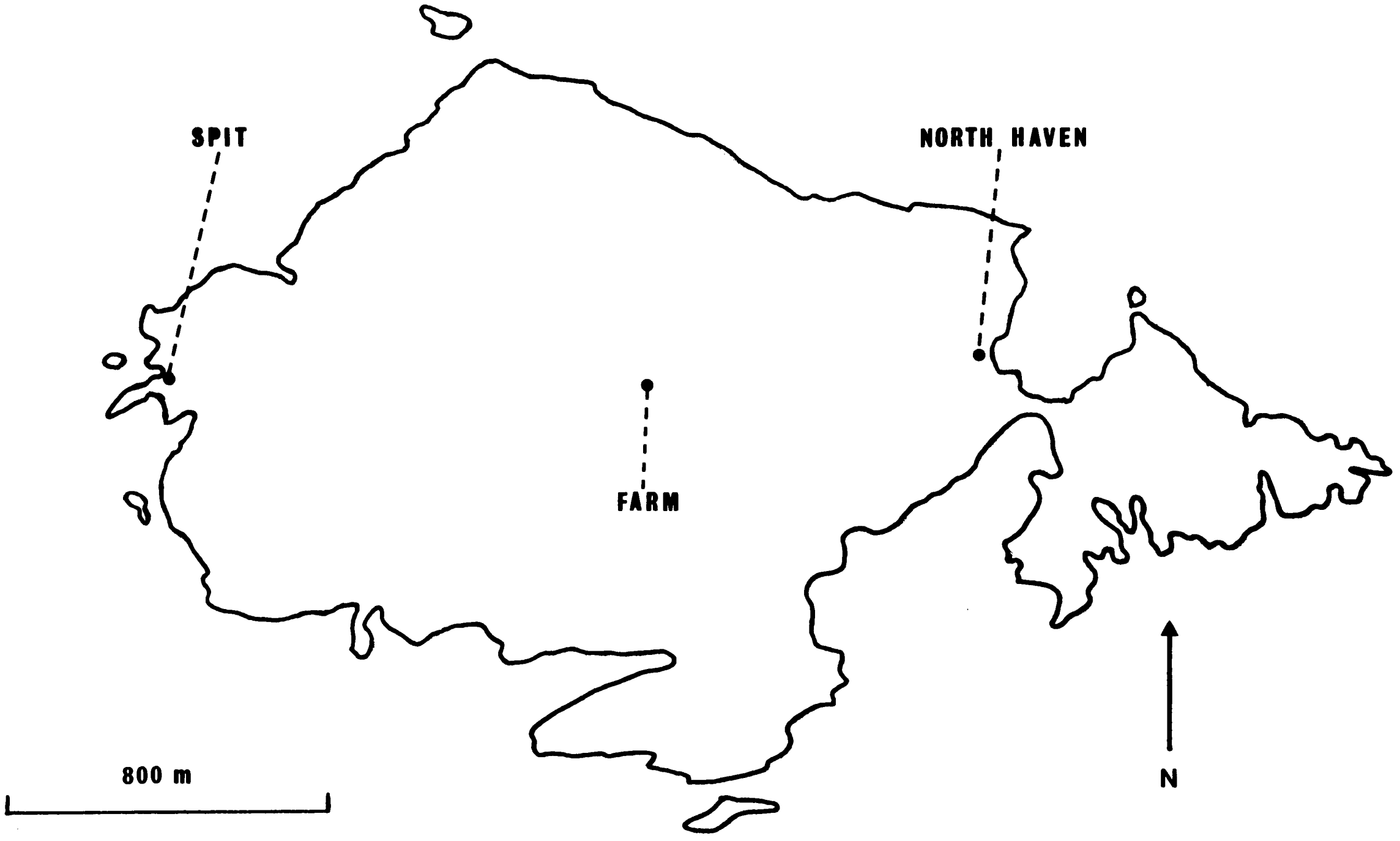

SPIT
NORTH HAVEN
FARM
800 m
N

Figure 4.3

Sonagrams of (A) female Manx Shearwater and (B) male Manx Shearwater call

variables measured:

F1 (female) = main freq. breath note

F1 (male) = max. freq. introductory note

F2 = max freq. whole call

F3 = min. freq. whole call

F4 = main freq. breath note

T1 = call length

T2 = breath note length

T3 = gap between breath note and rest of call

T4 = gap between successive calls

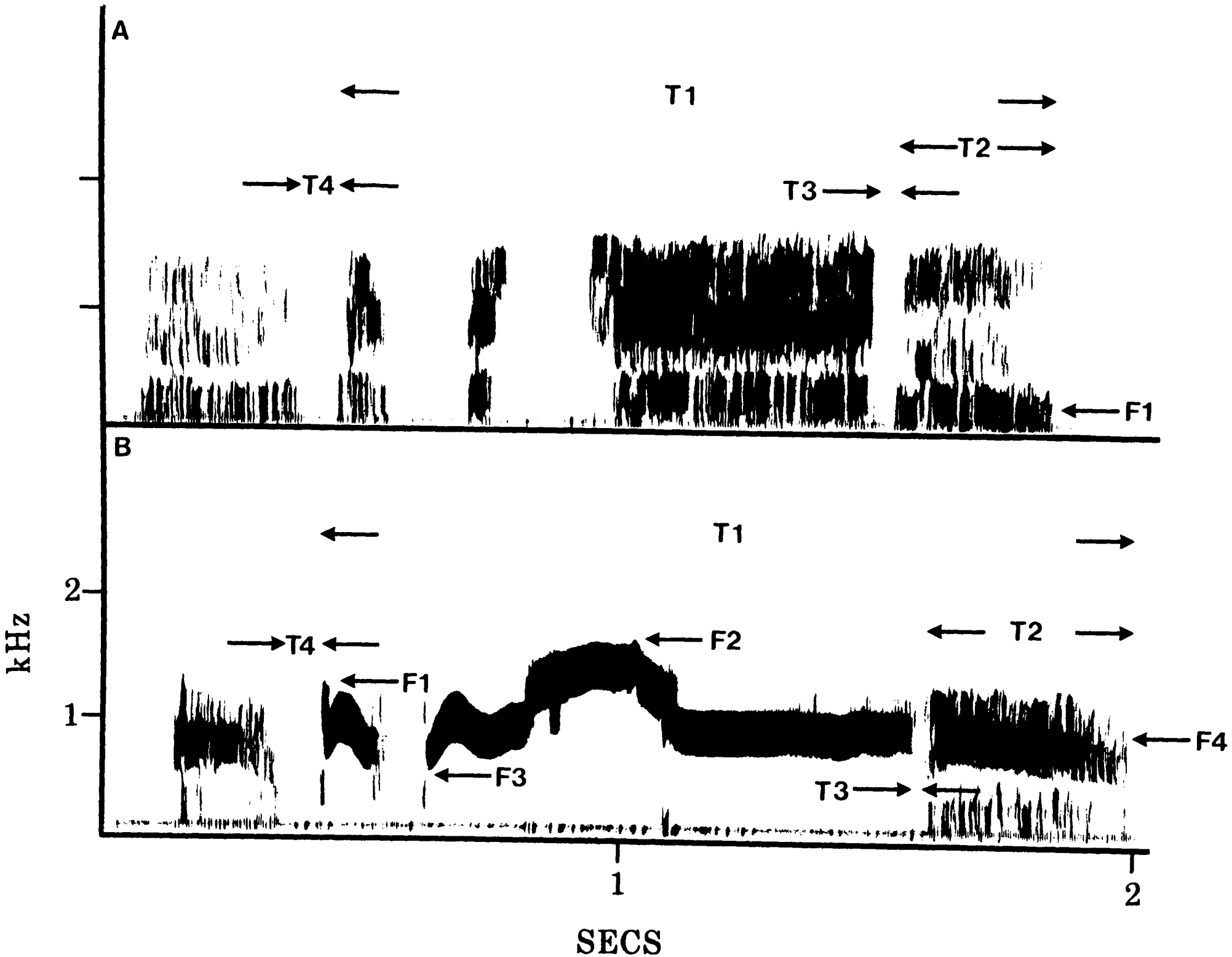

A
T1
T2
T3
T4
F1
B
T1
T2
T4
F1
F2
F3
F4
T3
kHz
2
1
1
2
SECS

Figure 4.4

Sonagrams of British Storm Petrel

(A) Flight-Call and (B) Purr-Call

variables measured:

F1 (Flight) = max. freq. middle note

F1 (Purr) = max. freq. breath note

T1 (both) = call lengths

T2, T3, T4 (Flight) = 1st, 2nd, 3rd note lengths

T2 (Purr) = breath note length

T3 (Purr) = gap between successive calls

T4 (Purr) = notes per second

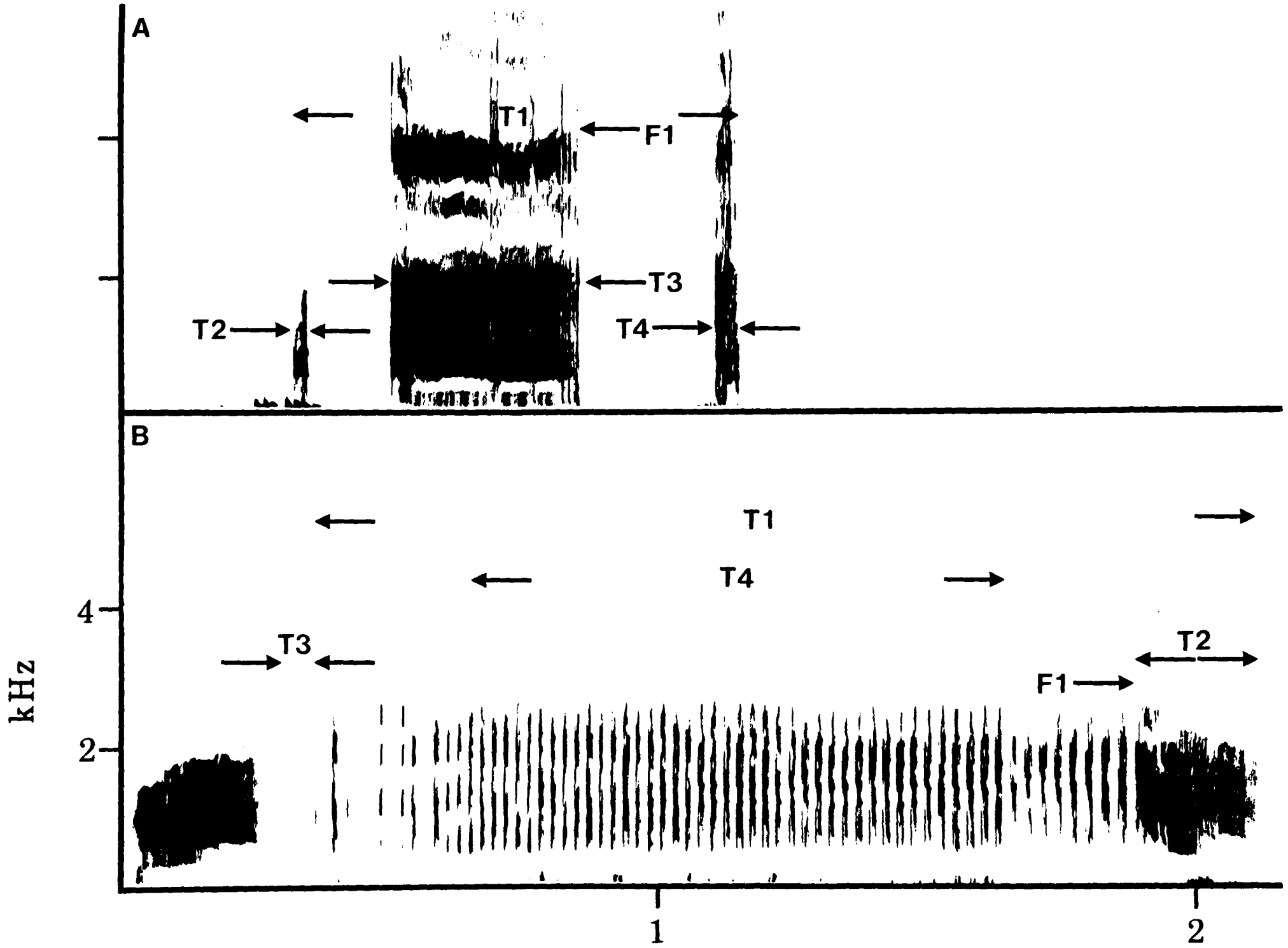

A
T1
F1
T3
T2
T4
B
T1
T4
T3
T2
F1
4
2
kHz
1
2
SECS

Table 4.1

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of male Manx Shearwaters in three colonies on Skomer Island. Sample sizes in parentheses.

Colony	T1	T2	T3	T4	F1	F2	F3	F4
Farm	1.40 ± 0.16 (55)	0.41 ± 0.08 (55)	0.03 ± 0.02 (55)	0.11 ± 0.03 (46)	1215 ± 130 (97)	1189 ± 157 (97)	753 ± 82 (97)	830 ± 94 (97)
North Haven	1.40 ± 0.21 (30)	0.42 ± 0.08 (30)	0.03 ± 0.02 (30)	0.09 ± 0.02 (20)	1270 ± 135 (26)	1215 ± 160 (26)	720 ± 82 (26)	857 ± 91 (26)
Spit	1.41 ± 0.19 (31)	0.43 ± 0.06 (31)	0.03 ± 0.02 (31)	0.09 ± 0.04 (27)	1252 ± 125 (30)	1164 ± 151 (30)	721 ± 68 (30)	845 ± 107 (30)
F(ANOVA)	0.01	0.24	0.12	3.23	2.20	0.73	2.87	0.92
P	N.S.	N.S.	N.S.	<0.05	N.S.	N.S.	N.S.	N.S.

Table 4.2

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of female Manx Shearwaters in three colonies on Skomer Island. Sample sizes in parentheses.

Colony	T1	T2	T3	T4	F1
Farm	1.11 ± 0.14 (27)	0.29 ± 0.05 (27)	0.02 ± 0.01 (27)	0.07 ± 0.04 (27)	750 ± 171 (27)
North Haven	1.09 ± 0.12 (31)	0.30 ± 0.05 (31)	0.03 ± 0.02 (31)	0.07 ± 0.03 (31)	793 ± 203 (31)
Spit	1.11 ± 0.15 (17)	0.31 ± 0.07 (17)	0.03 ± 0.01 (17)	0.07 ± 0.04 (17)	774 ± 172 (17)
F(ANOVA)	0.11	1.30	0.94	0.35	0.40
P	N.S.	N.S.	N.S.	N.S.	N.S.

is the time between successive male calls. Multivariate stepwise discriminant analyses were performed on the male and female call variables. For males overall, 42% (North Haven 59%; Farm 43%; Spit 28%) of individuals were classified into their correct colony (Figure 4.5). This is not significantly better than chance classification (Z = 1.46) (Titus et al. 1984). For females overall, only 31% (North Haven 23%; Farm 44%; Spit 24%) of individuals were classified into their correct colony (Figure 4.6). Again, this represents no significant improvement over classification by chance (Z = -0.60). In conclusion, it appears that both male and female calls are not differentiated at a local level, and visual inspection of sonagrams also confirmed this as no dialects were apparent.

Macrogeographical variation

Univariate analyses of variance on the 8 male and 5 female Manx Shearwater call variables gives significant differences between islands for 6 male and 3 female variables (Tables 4.3 and 4.4). Again, multivariate stepwise discriminant analyses were performed on the male and female call variables. For males overall, 44% (Skomer 40%; Skokholm 50%; Puffin 15%; Rhum 58%; Myggenaes Holm 42%) of individuals were correctly classified (Figure 4.7). This represents a significant improvement over chance classification ($Z = 8.35$, $p < 0.001$). For females overall, 40% (Skomer 41%; Skokholm 24%; Puffin 50%; Rhum 47%) of individuals were correctly placed into their island group (Figure 4.8). Again, this is significantly better than classifying them by chance ($Z = 3.22$, $p < 0.01$).

Univariate analyses of variance show significant between-island differences for 3 of the 5 Purr-Call variables measured for British Storm Petrels (Table 4.5). Multivariate stepwise discriminant analysis (Figure 4.9) on these call variables was successful overall in placing 47% of the individuals in the correct island category (Skomer 43%; Skokholm 27%;

Figure 4.5

Discriminant analysis of male Manx Shearwater calls within Skomer, (A) Farm (B) North Haven (C) Spit. Points indicate the position of group means.

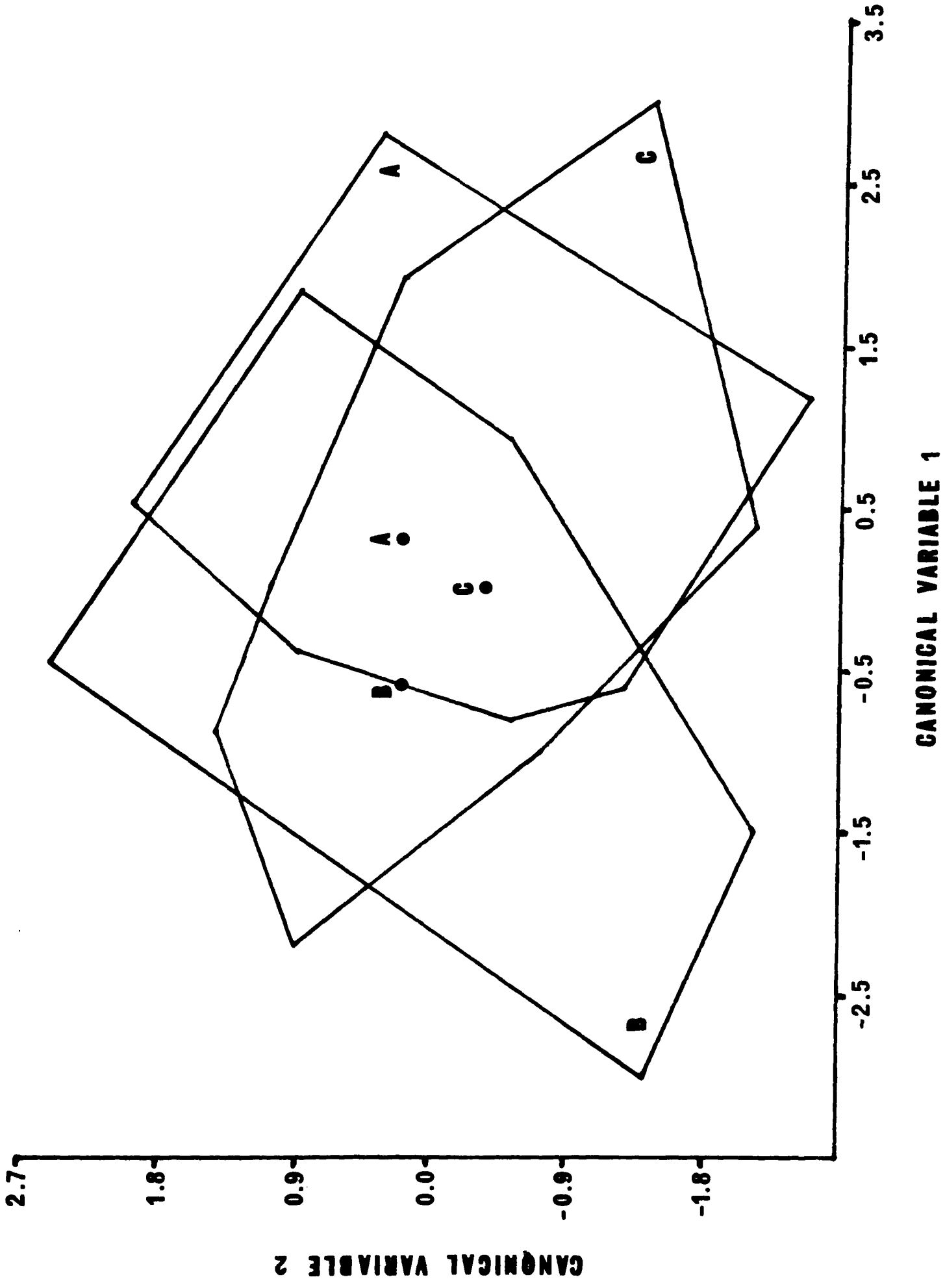

A
C
B
A
C
B
2.7
1.8
0.9
0.0
-0.9
-1.8
CANONICAL VARIABLE 2
-2.5
-1.5
-0.5
0.5
1.5
2.5
3.5
CANONICAL VARIABLE 1

Figure 4.6

Discriminant analysis of female Manx Shearwater calls within Skomer, (A) Farm (B) North Haven (C) Spit. Points indicate the positions of group means.

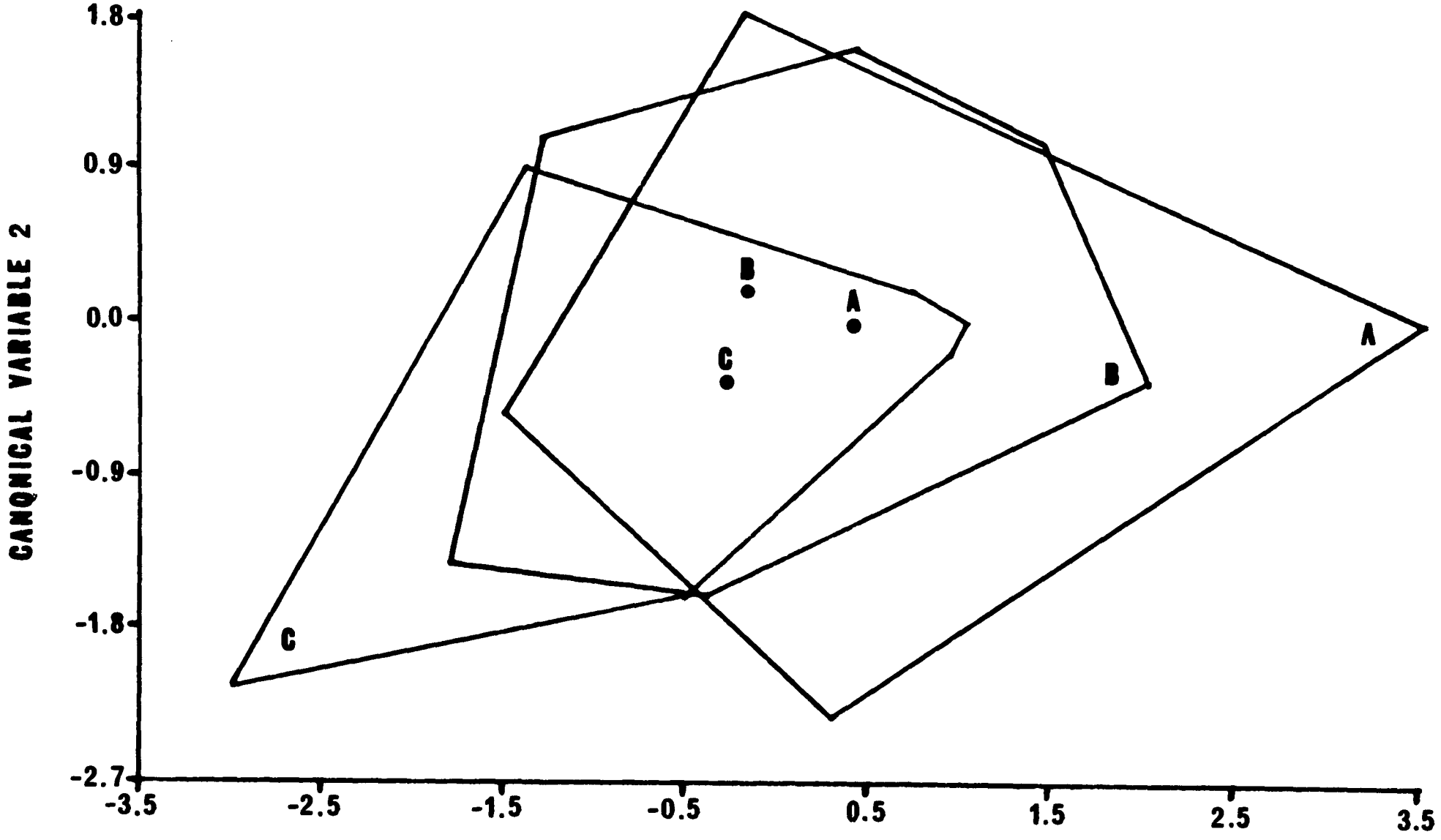

1.8
0.9
0.0
-0.9
-1.8
-2.7
-3.5
-2.5
-1.5
-0.5
0.5
1.5
2.5
3.5
CANONICAL VARIABLE 2
CANONICAL VARIABLE 1
A
B
C
A
B
C

Table 4.3

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of male Manx Shearwaters on five islands. Sample sizes in parentheses.

Island	T1	T2	T3	T4	F1	F2	F3	F4
Skomer	1.41 ± 0.18 (116)	0.42 ± 0.08 (116)	0.03 ± 0.02 (116)	0.10 ± 0.03 (93)	1232 ± 130 (153)	1189 ± 156 (153)	741 ± 79 (153)	838 ± 96 (153)
Skokholm	1.40 ± 0.19 (65)	0.43 ± 0.08 (65)	0.04 ± 0.03 (65)	0.11 ± 0.03 (63)	1259 ± 160 (61)	1301 ± 140 (61)	746 ± 92 (61)	847 ± 76 (61)
Rhum	1.55 ± 0.19 (65)	0.47 ± 0.09 (65)	0.02 ± 0.01 (65)	0.10 ± 0.04 (64)	1164 ± 155 (63)	1226 ± 144 (63)	722 ± 87 (63)	838 ± 92 (63)
Puffin	1.42 ± 0.16 (34)	0.44 ± 0.07 (34)	0.03 ± 0.01 (34)	0.09 ± 0.04 (34)	1201 ± 124 (35)	1250 ± 108 (35)	709 ± 67 (35)	818 ± 46 (35)
Myggenaes	1.38 ± 0.14 (14)	0.46 ± 0.05 (14)	0.03 ± 0.01 (14)	0.07 ± 0.02 (12)	1249 ± 120 (14)	1269 ± 85 (14)	731 ± 46 (14)	829 ± 59 (14)
F(ANOVA)	7.69	5.09	10.24	3.24	4.22	7.13	1.75	0.61
P	<0.001	<0.001	<0.001	<0.025	<0.005	<0.001	N.S.	N.S.

Table 4.4

The mean ± s.d. temporal T, and frequency (Hz) F call variables of female Manx Shearwaters on four islands. Sample sizes in parentheses.

Island	T1	T2	T3	T4	F1
Skomer	1.10 ± 0.14 (75)	0.30 ± 0.06 (75)	0.03 ± 0.02 (75)	0.07 ± 0.03 (75)	773 ± 183 (75)
Skokholm	1.13 ± 0.14 (21)	0.32 ± 0.08 (21)	0.02 ± 0.01 (21)	0.08 ± 0.03 (21)	630 ± 83 (21)
Rhum	1.21 ± 0.14 (17)	0.33 ± 0.04 (17)	0.02 ± 0.01 (17)	0.08 ± 0.03 (17)	674 ± 83 (17)
Puffin	1.08 ± 0.14 (10)	0.34 ± 0.05 (10)	0.02 ± 0.01 (10)	0.05 ± 0.02 (10)	676 ± 74 (10)
F(ANOVA)	3.15	2.68	2.16	1.75	6.08
P	<0.05	=0.05	N.S.	N.S.	<0.001

Figure 4.7

Discriminant analysis of male Manx Shearwater calls between islands, (A) Skomer (B) Skokholm (C) Puffin (D) Rhum (E) Myggenaes. Points indicate the positions of group means.

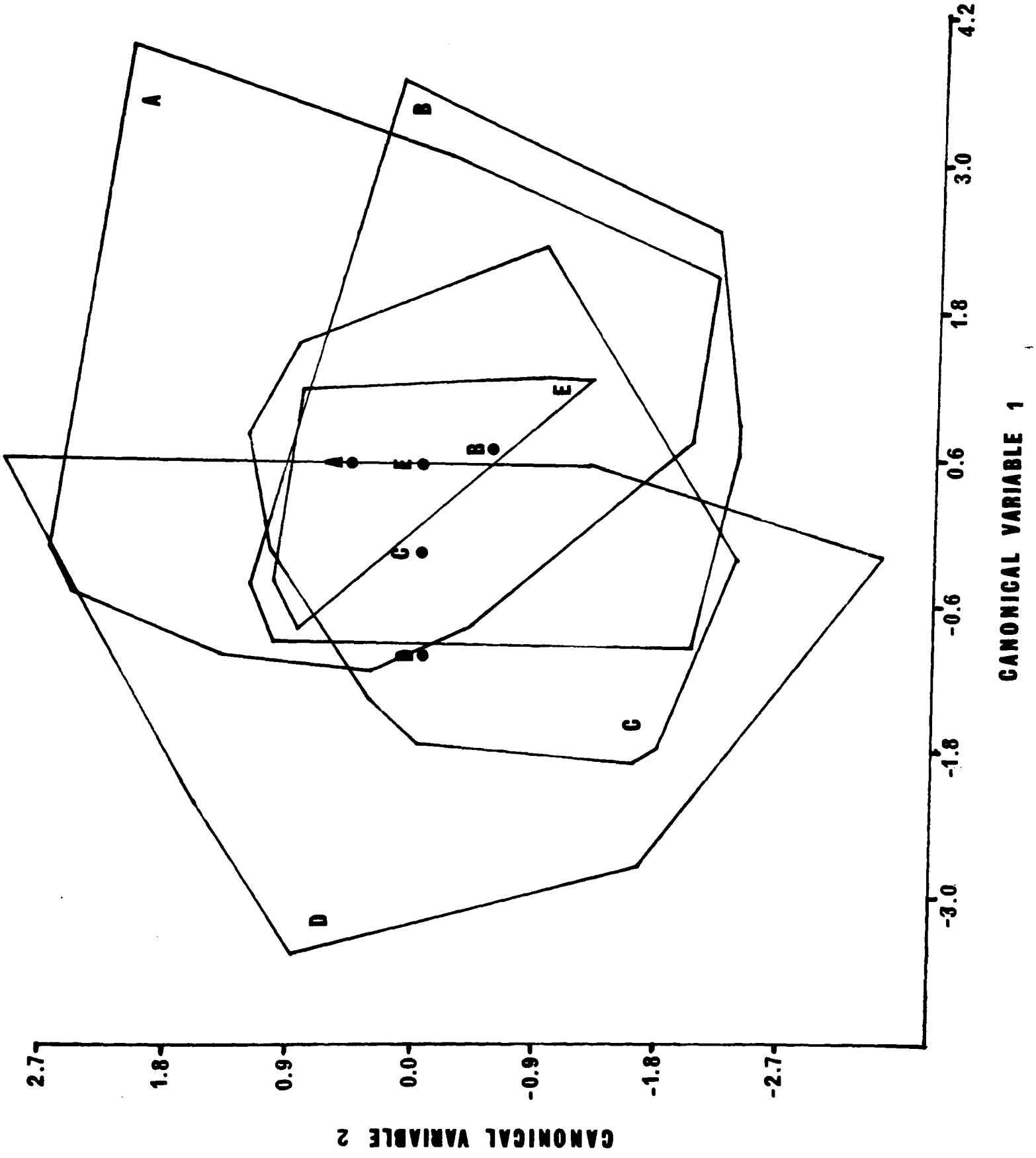

A
B
E
B
E
C
C
D
2.7
1.8
0.9
0.0
-0.9
-1.8
-2.7
CANONICAL VARIABLE 2
4.2
3.0
1.8
0.6
-0.6
-1.8
-3.0
CANONICAL VARIABLE 1

Figure 4.8

Discriminant analysis of female
Manx Shearwater calls between islands,
(A) Skomer (B) Skokholm (C) Rhum (D) Puffin.
Points indicate the positions of
the group means.

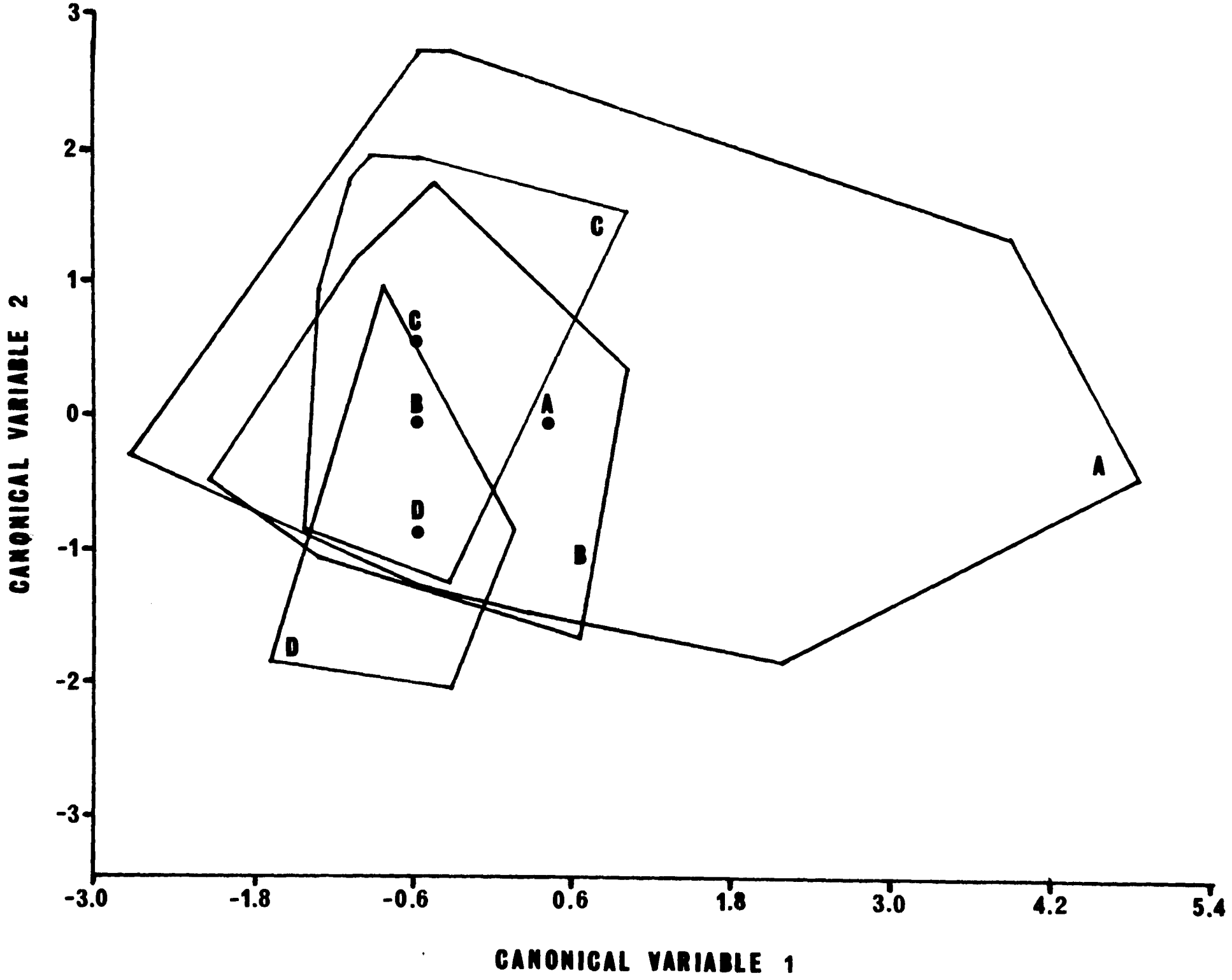

3
2
1
0
-1
-2
-3
CANONICAL VARIABLE 2
C
C
B
A
D
D
B
A
-3.0
-1.8
-0.6
0.6
1.8
3.0
4.2
5.4
CANONICAL VARIABLE 1

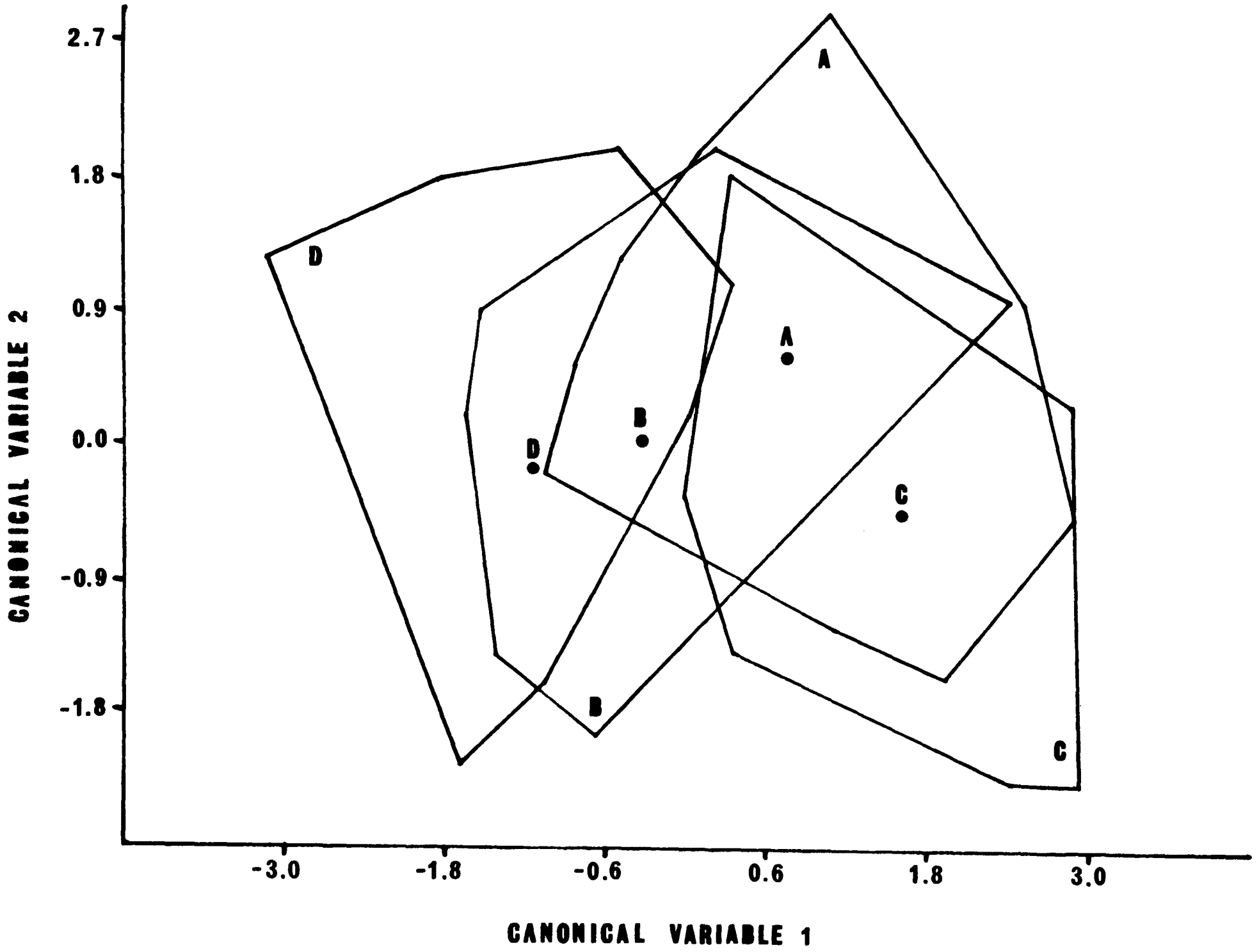
Table 4.5

The mean ± s.d. temporal (sec) T, and frequency (Hz) F variables of British Storm Petrel Purr-Calls on four islands. Sample sizes in parentheses.

Island	T1	T2	T3	T4	F1
Skomer	1.42 ± 0.22 (30)	0.29 ± 0.05 (30)	0.02 ± 0.01 (30)	38.3 ± 4.4 (30)	2170 ± 320 (30)
Skokholm	1.40 ± 0.22 (34)	0.24 ± 0.05 (34)	0.02 ± 0.01 (34)	39.2 ± 2.1 (34)	2270 ± 370 (34)
Puffin	1.41 ± 0.19 (20)	0.30 ± 0.05 (20)	0.03 ± 0.02 (20)	34.7 ± 5.7 (20)	2490 ± 340 (20)
Mousa	1.31 ± 0.18 (33)	0.20 ± 0.04 (33)	0.01 ± 0.01 (33)	41.3 ± 2.1 (33)	2330 ± 560 (33)
F(ANOVA)	1.97	24.53	4.61	13.64	2.48
P	N.S.	<0.001	<0.005	<0.001	N.S.

Figure 4.9

Discriminant analysis of British Storm Petrel Purr-Calls between islands, (A) Skomer (B) Skokholm (C) Puffin (D) Mousa. Points indicate the positions of group means.


2.7
1.8
0.9
0.0
-0.9
-1.8
CANONICAL VARIABLE 2
-3.0
-1.8
-0.6
0.6
1.8
3.0
CANONICAL VARIABLE 1
A
A
B
B
C
C
D
D

Puffin 50%; Mousa 70%). This classification is significantly better than one by chance ($Z = 6.09$, $p < 0.001$). In addition, Mousa Purr-Calls are distinct from those on Puffin Island (Figure 4.9).

Univariate analyses of variance on the 5 Flight-Call variables measured show no significant differences between Skomer and Puffin Island, the only islands where sufficient numbers of Flight-Calls were recorded (Table 4.6). A multivariate stepwise discriminant analysis placed 51% (Skomer 53%; Puffin 46%) of the individuals into the correct island category. This was not significantly better than chance ($Z = 0.05$). As a comparison, the Purr-Calls of Skomer and Puffin Island only were examined. In contrast to the Flight-Call analysis, univariate analysis of variance identified 2 out of 5 call variables that were significantly different between the islands, F1 ($F = 11.30$, $p < 0.005$) and T4 ($F = 6.12$, $p < 0.025$). A multivariate stepwise discriminant analysis placed 68% (Skomer 60%; Puffin 80%) of the individuals in their correct island category. This is significantly better than by chance alone ($Z = 2.72$, $p < 0.01$). There was no tendency for misclassified cases to be placed into the geographically-nearest island category, suggesting that inter-island distances are not related to call divergence.

Temporal variation

For male Manx Shearwaters, 3 out of the 8 call variables measured showed significant changes between 1976 and 1982 (Table 4.7), and for female Manx Shearwaters, one of the 5 call variables measured changed significantly between 1976 and 1983 (Table 4.8).

Of the males tape recorded in 1982, three were wearing rings and had also been recorded in 1976. On comparing their 8 call variables between these years, 5 out of the 24 comparisons are significantly different (Table 4.9). However, only two of these were the same call variables

Table 4.6

The mean ± s.d. temporal (sec) T, and frequency (Hz) F variables of British Storm Petrel Flight-Calls on Skomer and Puffin Island. Sample sizes in parentheses.

Island	T1	T2	T3	T4	F1
Skomer	0.82 ± 0.12 (36)	0.05 ± 0.03 (36)	0.33 ± 0.06 (36)	0.08 ± 0.07 (36)	4130 ± 470 (36)
Puffin	0.81 ± 0.12 (13)	0.04 ± 0.03 (13)	0.34 ± 0.06 (13)	0.07 ± 0.02 (13)	4380 ± 519 (13)
F(ANOVA)	0.10	2.87	0.11	0.37	2.47
P	N.S.	N.S.	N.S.	N.S.	N.S.

Table 4.7

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of male Manx Shearwaters on Skokholm in 1976 and 1982. Sample sizes in parentheses.

Year	T1	T2	T3	T4	F1	F2	F3	F4
1976	1.43 ± 0.18 (23)	0.43 ± 0.07 (23)	0.03 ± 0.02 (23)	0.09 ± 0.03 (22)	1178 ± 141 (25)	1309 ± 92 (25)	741 ± 76 (25)	802 ± 83 (25)
1982	1.40 ± 0.19 (65)	0.43 ± 0.08 (65)	0.04 ± 0.03 (65)	0.11 ± 0.03 (63)	1259 ± 160 (61)	1301 ± 140 (61)	746 ± 92 (61)	847 ± 76 (61)
t	0.72	0.20	1.34	1.98	2.20	0.26	0.24	2.43
P	N.S.	N.S.	N.S.	=0.05	<0.05	N.S.	N.S.	<0.02

Table 4.8

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of female Manx Shearwaters on Skokholm in 1976 and 1983. Sample sizes in parentheses.

Year	T1	T2	T3	T4	F1
1976	1.26 ± 0.29 (20)	0.32 ± 0.07 (20)	0.03 ± 0.01 (20)	0.09 ± 0.03 (20)	737 ± 182 (20)
1983	1.13 ± 0.14 (21)	0.32 ± 0.08 (21)	0.02 ± 0.01 (21)	0.08 ± 0.03 (21)	630 ± 81 (21)
t	1.85	0.00	0.32	1.34	2.45
P	N.S.	N.S.	N.S.	N.S.	< 0.02

Table 4.9

The mean ± s.d. temporal (sec) T, and frequency (Hz) F call variables of three male Manx Shearwaters on Skokholm recorded both in 1976 and 1982. Sample sizes in parentheses.

Bird	T1	T2	T3	T4	F1	F2	F3	F4
FS 77105 (76)	1.55 ± 0.07 (4)	0.46 ± 0.01 (4)	0.06 ± 0.01 (4)	0.08 ± 0.01 (4)	1060 ± 20 (4)	1290 ± 33 (4)	790 ± 17 (4)	800 ± 28 (4)
t	1.28	0.41	4.08*	2.09	3.93*	1.10	0.14	3.54*
(82)	1.50 ± 0.03 (4)	0.47 ± 0.06 (4)	0.04 ± 0.01 (4)	0.09 ± 0.01 (4)	1120 ± 20 (3)	1227 ± 94 (3)	787 ± 38 (3)	867 ± 19 (3)
EC 84421 (76)	1.36 ± 0.05 (4)	0.47 ± 0.03 (4)	0.02 ± 0.01 (4)	0.05 ± 0.02 (3)	1020 ± 140 (4)	1360 ± 98 (4)	720 ± 102 (4)	800 ± 40 (4)
t	0.33	1.49	0.74	1.74	0.66	2.21	0.84	1.31
(82)	1.35 ± 0.03 (3)	0.50 ± 0.02 (3)	0.02 ± 0.01 (3)	0.02 ± 0.01 (3)	1067 ± 19 (3)	1213 ± 68 (3)	667 ± 38 (3)	760 ± 40 (3)
EF 36545 (76)	1.75 ± 0.03 (4)	0.50 ± 0.01 (4)	0.02 ± 0.01 (4)	0.13 ± 0.01 (3)	1210 ± 91 (4)	1470 ± 114 (4)	690 ± 33 (4)	810 ± 17 (4)
t	0.83	4.78*	1.48	1.73	1.24	2.04	1.02	4.16*
(82)	1.81 ± 0.08 (3)	0.54 ± 0.01 (3)	0.02 ± 0.01 (3)	0.11 ± 0.01 (3)	1270 ± 33 (4)	1330 ± 77 (4)	730 ± 71 (4)	760 ± 17 (4)

* $p < 0.05$

differing in the same direction as the general population (Table 4.7), suggesting that call changes within individuals were not sufficient to account for the changes seen in the population.

Discussion

Microgeographical variation

The univariate analyses of the call variables (Tables 4.1 and 4.2) clearly indicate that geographical variation in voice is not well-developed at a local level in either Manx Shearwater males or females. This was confirmed by multivariate analyses (Figures 4.5 and 4.6) and the visual inspection of sonagrams. The shearwaters therefore do not exhibit dialects in the sense that neighbouring birds have calls which are more similar to one another than to the calls of more distant but potentially interbreeding birds (Catchpole 1979, Krebs & Kroodsma 1980). The result parallels that of a blood protein study (Whitehouse 1979), which showed that there was no genetic structuring of the Manx Shearwater population within Skokholm Island.

The discriminant separation for Skomer males (42%) is higher (though not significantly, X^2 = 1.89, d.f. = 1) than that for females (31%) suggesting that male calls are relatively more distinct locally. The Manx Shearwater shows differential dispersal of the sexes with 85% of males subsequently breeding within 100 m of where they were hatched, but with only 49% of females doing so (Brooke 1978c). Coupled with the relative difference in the calls already described, this suggests that Manx Shearwaters produce a call more related to their natal area than to the areas they settle in. This would be accomplished either through the genetic transmission of calls through parents or culturally by copying parents or neighbours in the natal vicinity, rather than copying the calls of birds in the area they eventually breed in. There is no information on how the

calls of Manx Shearwaters are transmitted from one generation to the next, so it is not possible to differentiate between the relative contribution of genes and culture to the observed pattern. However, it is possible to say that genes alone cannot be responsible, as the temporal changes observed in the Skokholm population were probably too rapid for genetic evolution (Tables 4.7 and 4.8). In addition males' calls changed more rapidly than females', the opposite of what one would predict if call was transmitted genetically with the observed dispersal patterns. Cultural transmission of calls therefore appears to take place in the Manx Shearwater. Research on the vast majority of birds so far investigated has shown that there is a large learned component in the acquisition of their songs (Kroodsma & Baylis 1982).

Macrogeographical variation

In contrast to the local situation, univariate analyses of variance of the call variables between islands shows more developed geographical variation in both male and female Manx Shearwaters (Tables 4.3 and 4.4). While the multivariate analyses appear to show little improvement over the within-Skomer discrimination (Figures 4.7 and 4.8), both male and female island classifications were significantly better than chance alone, a result not obtained from the within-Skomer analyses. Macrogeographical variation therefore exists between islands, but it is not sufficient to assign any one individual with certainty to any one island. The variation in calls therefore may be thought of as being continuous rather than as existing in discrete units. Furthermore, overall classification into the correct island categories was more similar for males (44% and females 40%).

The fact that an increase in inter-island distance did not result in an increase in call divergence is perhaps not surprising if one takes into account the potential effect of coastlines and possibly oceanographic

features. These could act to limit the dispersal opportunities available to the shearwaters at any one island. Even in seabirds with apparently unobstructed dispersal opportunities, such as the sub-Antarctic penguins, it has been found that population divergence is related more to sea temperatures than to inter-island distances (Jouventin 1982). That Manx Shearwater dispersion is constrained around Britain by factors in addition to inter-island distances is suggested by ringing studies (Harris 1972, Swann & Ramsey 1976), and more convincingly, by blood protein studies (Whitehouse 1979). Both show that the Irish Sea shearwaters are distinct from those in the Scottish colonies. Such divergence could have arisen if the Scottish shearwaters reach their colonies via the west coast of Britain (the shortest route) and not via the Irish Sea (Whitehouse 1979). In addition, while substantial gene flow can occur from a colony, it is likely to be rather localized (Brooke 1978c). Examination of misclassified cases in the discriminant analyses could detect no effect of Irish Sea shearwaters being placed with other Irish Sea colonies rather than west coast colonies, and vice versa suggesting that call divergence has not reached the same level as the genetic divergence of the respective populations (Whitehouse 1979).

As with the Manx Shearwater, univariate analyses of variance on call variables between islands showed significant differences in the British Storm Petrel. However, such differences existed only for the Purr-Call (Table 4.5) and not the Flight-Call (Table 4.6). As with the Manx Shearwater, these differences in the Purr-Call are not sufficient for a multivariate discriminant analysis to correctly classify a large proportion of the birds (Figure 4.9), but again, the classification is significantly better than chance alone. In addition, Mousa Purr-Calls are distinct from Puffin Island Purr-Calls (Figure 4.9), a situation not encountered in the Manx Shearwater analyses (Figures 4.7 and 4.8). Macrogeographical

variation in voice therefore exists for the British Storm Petrel.

The fact that Purr-Calls were more differentiated than Flight-Calls is possibly related to males alone producing the Purr-Call, and both sexes producing the Flight-Call (James 1984). If females disperse more than males, as in the Manx Shearwater (Brooke 1978c), then the Purr-Calls will be less mixed than the Flight-Calls. The multivariate discriminant analyses of Skomer and Puffin Purr-Calls versus Skomer and Puffin Flight-Calls supports this with 68% of Purr-Calls correctly placed (significantly better than chance alone) but only 51% of Flight-Calls (not significantly better).

The divergence of Manx Shearwater and British Storm Petrel calls between islands is probably more related to cultural evolution and relative isolation rather than being adaptations to local conditions such as habitat (Wiley & Richards 1982) or the total sound environment of the avifauna (Miller 1982). Manx Shearwaters and British Storm Petrels nest in the same types of habitat throughout their respective ranges in northwestern Europe. In addition, there are no differences in the species composition contributing to the sounds heard at night on the islands examined. Leach's Storm Petrel does overlap its range with that of the British Storm Petrel on other islands. It would be interesting to see if British Storm Petrels have diverged their Purr-Calls in response to competition with Leach's Storm Petrel Purr-Calls compared to those found on islands without Leach's Storm Petrels.

The macrogeographical variation in calls is also not likely to be a result of differences in body size (Shy 1983). If body size is important, it is usual for larger birds to produce lower frequencies in their songs or calls (Bergmann 1976, Schubert 1976, Bowman 1979, Guillotin & Jouventin 1980). This is directly opposite to what is observed in the nocturnal Procellariiformes, where the smaller females produce the lower frequency

calls (Brooke 1978d, Ristow & Wink 1980, Chapter 3). In addition, no significant correlations were detected between either the tarsus or bill lengths (indices of body size) of 20 female and 22 male Manx Shearwaters and the 5 frequency variables measured in their respective calls (Table 4.10).

Temporal variation

The results (Tables 4.7 and 4.8) show that over a period of 6 or 7 years, some call variables became significantly altered in both male and female Manx Shearwaters on Skokholm. The males had 3 call variables change out of 8 measured, and the females 1 out of 5. As already mentioned, this result appears to support the idea that transmission of calls in the Manx Shearwater involves a cultural component, as more change occurred in the relatively static male population, and the changes were too rapid for genetic evolution.

The extent to which song will change in a population over a period of time depends on such things as the mortality rate, the exactitude of copying and the dispersion of young birds (Ince et al. 1980, Payne et al. 1981). Unlike the songbirds, the Manx Shearwater has a low annual adult mortality of about 10% (Perrins et al. 1973). Over a period of 6 to 7 years then, 53 and 48% of the birds recorded in 1976 will still be alive in 1982 and 1983 respectively. The majority of new males appearing in the local population will be hatched there, whereas only half the new females will be, the rest being immigrants from elsewhere (Brooke 1978c). Changes in the calls of surviving shearwaters were not likely to have contributed to the observed vocal 'drift' (Table 4.9). Therefore, the changes that did occur did so through the appearance of new shearwaters in the population. The fact that changes in the male population were more pronounced than those in the female population suggests that cultural evolution (through errors in learning) was more important in promoting the vocal 'drift' than dispersion was.

Table 4.10

Correlation coefficients of 22 male and 20 female Manx Shearwater bill and tarsus lengths (mm) versus the birds' respective call frequency measures (Hz)

Call measure	Bill length	Tarsus length
Male F1	0.078	0.134
Male F2	0.007	0.236
Male F3	0.103	0.195
Male F4	0.064	0.245
Female F1	0.043	0.004

CHAPTER FIVE

The calls of the nocturnal Procellariiformes: a review, with an evaluation of their use in systematics

The calls of the nocturnal Procellariiformes: a review, with an evaluation of their use in systematics

Description of the calls

Introduction

The research reported so far has concentrated on aspects of vocal behaviour in relation to individual species, such as call variation (both sexual and geographical) and function. In this section, I review the full range and diversity of calls that exist in the nocturnal Procellariiformes.

Methods

Copies of all tape recordings of nocturnal Procellariiformes held at the British Library, London and the Laboratory of Ornithology, Cornell University were requested. In order to obtain approximate indices of range and diversity, these were played through a Princeton 4512 FFT Real Time Spectrum Analyser coupled with a Unigon SC-1 Scan Converter, and the maximum and minimum frequencies of each call type were measured. Sonagrams of the calls were also produced on a Kay 6061-B Sound Spectrograph using the wide band filter. These were used to measure the duration of each call type, and to count the number of notes each was composed of. A complete review of the literature was conducted to look for published sonagrams of these birds.

These methods of investigation limited the types of analyses undertaken, as the number of individuals sampled per species was very small. Calls are therefore compared only in a qualitative sense. In addition, the sex of calling individuals was usually unknown, and as previously demonstrated, calls can vary between sexes. However, this was considered

unimportant for the present comparisons, as even when sexual dimorphism in voice exists, it is in the distribution of frequencies within a particular frequency range, not in the maximum or minimum frequencies. In addition, calls between males and females do not usually differ considerably in their temporal patterning.

Results

The calls of the Procellariidae

Sonagrams were examined for 10 species of gadfly petrel *Pterodroma*, 11 species of shearwater *Puffinus* and *Calonectris*, 3 species of shearwater-like petrel *Procellaria*, 3 species of prion *Pachyptila*, the Blue Petrel *Halobaena* and Bulwer's Petrel *Bulweria bulwerii*.

Pterodroma

The calls of the gadfly petrels are very diverse both in their frequency and temporal characteristics (Table 5.1). With regard to general structure, they can be placed into three groups, possibly corresponding to three or more call types within each species.

The first group consists of the "ti-ti-ti" calls (Figure 5.1, Warham *et al*. 1977, Grant *et al*. 1983), and are composed of a rapidly repeated series of notes (up to 15) at fairly high frequencies. Some evidence is emerging that they are produced by males only (Grant *et al*. 1983).

The second grouping is that consisting of calls with a long single note (Figure 5.2, Cramp & Simmons 1977, Warham 1979, Grant *et al*. 1983). They may be very low in pitch or somewhat higher as in *Pterodroma mollis*. Again, there is some evidence that only males produce the call (Grant *et al*. 1983).

The last group is composed of calls with notes intermediate in length between the other two call groups (Figure 5.3, Warham *et al*. 1977, Grant

Table 5.1

Some general call characteristics* of nocturnal Procellariiformes

Genus (species)	Call types examined	Max. Freq.	Min. Freq.	Range	Notes	Length	Notes/sec
Pterodroma (10)	16	4.8 ± 1.3	1.1 ± 0.9	3.8 ± 1.7	5.8 ± 4.7	1.4 ± 0.6	4.1 ± 2.7
Puffinus (9)	14	2.4 ± 1.3	0.1 ± 0.1	2.3 ± 1.3	3.9 ± 1.8	1.1 ± 0.5	4.3 ± 3.3
Calonectris (2)	4	4.2 ± 2.1	0.6 ± 0.8	3.6 ± 2.0	3.5 ± 0.9	1.4 ± 0.4	2.8 ± 1.3
Procellaria (3)	5	4.4 ± 0.7	0.6 ± 0.4	3.8 ± 0.4	66.6 ± 51.4	11.2 ± 4.7	6.8 ± 2.4
Pachyptila (3)	3	1.7 ± 0.3	0.3 ± 0.2	1.4 ± 0.3	4.3 ± 1.9	0.9 ± 0.7	5.7 ± 1.6
Bulweria (1)	1	1.2	0.0	1.2	1.0	0.1	3.8
Halobaena (1)	1	2.2	0.2	2.0	7.0	2.3	3.0
Oceanodroma (6)	11	3.5 ± 1.0	0.6 ± 0.8	2.9 ± 1.1	18.9 ± 21.3	1.7 ± 1.0	9.3 ± 6.1
Oceanites (1)	1	6.5	0.7	5.8	1.0	0.2	3.1
Halocyptena (1)	2	4.1 ± 0.3	0.2 ± 0.1	3.9 ± 0.4	47.5 ± 41.5	1.8 ± 0.6	21.3 ± 16.3
Fregetta (1)	1	3.1	1.1	2.0	1.0	0.05	6.9
Hydrobates (1)	2	3.7 ± 0.8	0.6 ± 0.1	3.1 ± 0.9	22.5 ± 19.5	1.2 ± 0.4	15.0 ± 11.3
Pelagodroma (1)	1	2.3	0.0	2.3	1.0	0.2	1.3
Pelecanoides (2)	2	2.1 ± 0.7	0.2 ± 0.0	1.9 ± 0.7	2.0 ± 0.0	1.1 ± 0.3	2.0 ± 0.6

* figures given are mean ± s.d. Frequencies in kHz; Times in secs.

Figure 5.1

Sonagrams of (A) Grey-faced Petrel *Pterodroma macroptera*, Eclipse Island, Australia P. Fullagar (B) Mottled Petrel *P. inexpectata*, Big South Cape Island, J. Kendrick (C) Cook's Petrel *P. cooki*, Little Barrier Island, J. Kendrick. Both N.Z.

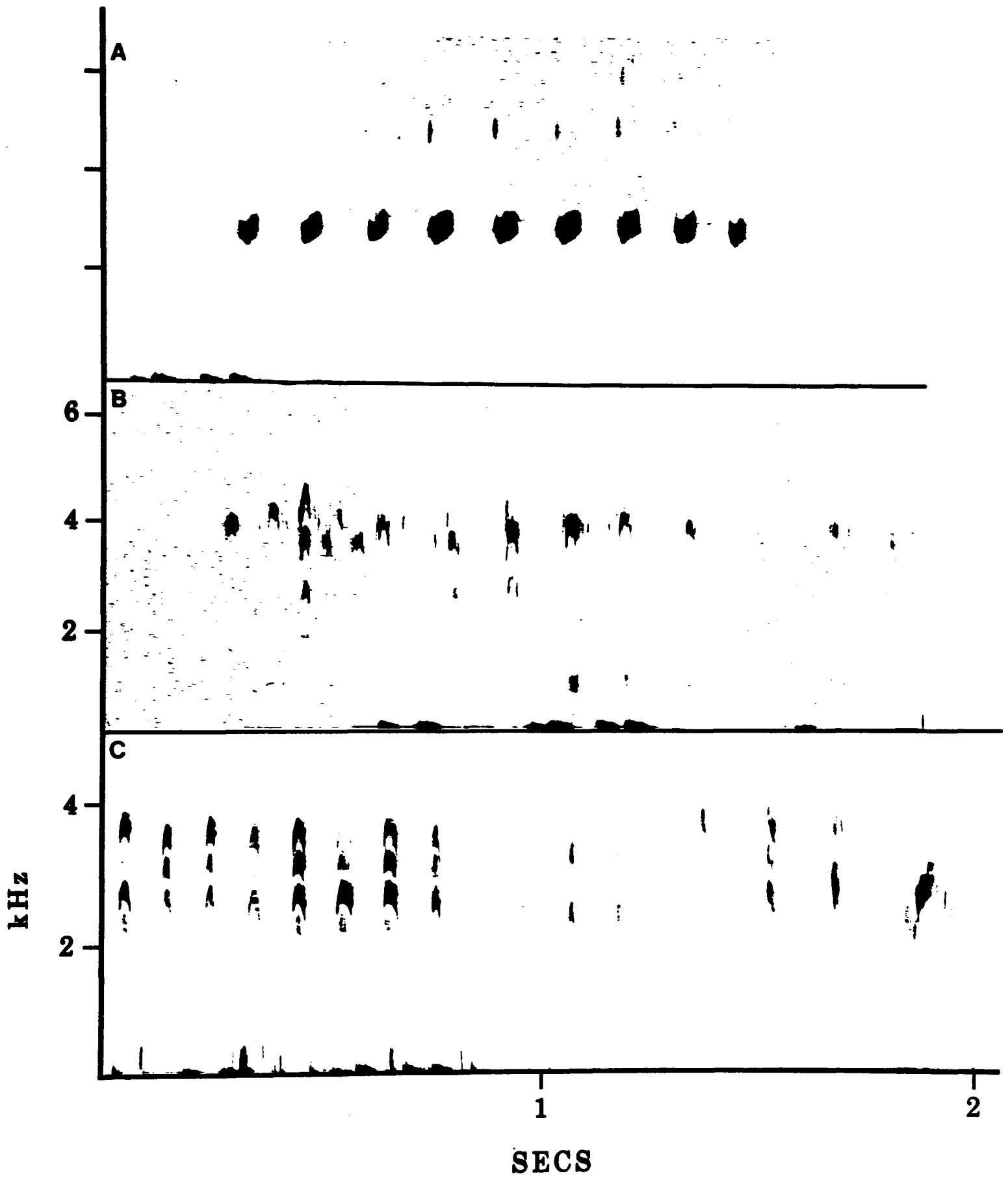

A
B
C
6
4
2
4
2
kHz
1
2
SECS

Figure 5.2

Sonagrams of (A) Soft-plumaged Petrel *Pterodroma mollis*, Gough Island, M. Swales (B) Bermuda Petrel *P. cahow*, Bermuda, D. Wingate (C) Dark-rumped Petrel *P. phaeopygia*, James Island, Galapagos R. Perry (D) Grey-faced Petrel *P. macroptera*, Gough Island, M. Swales.

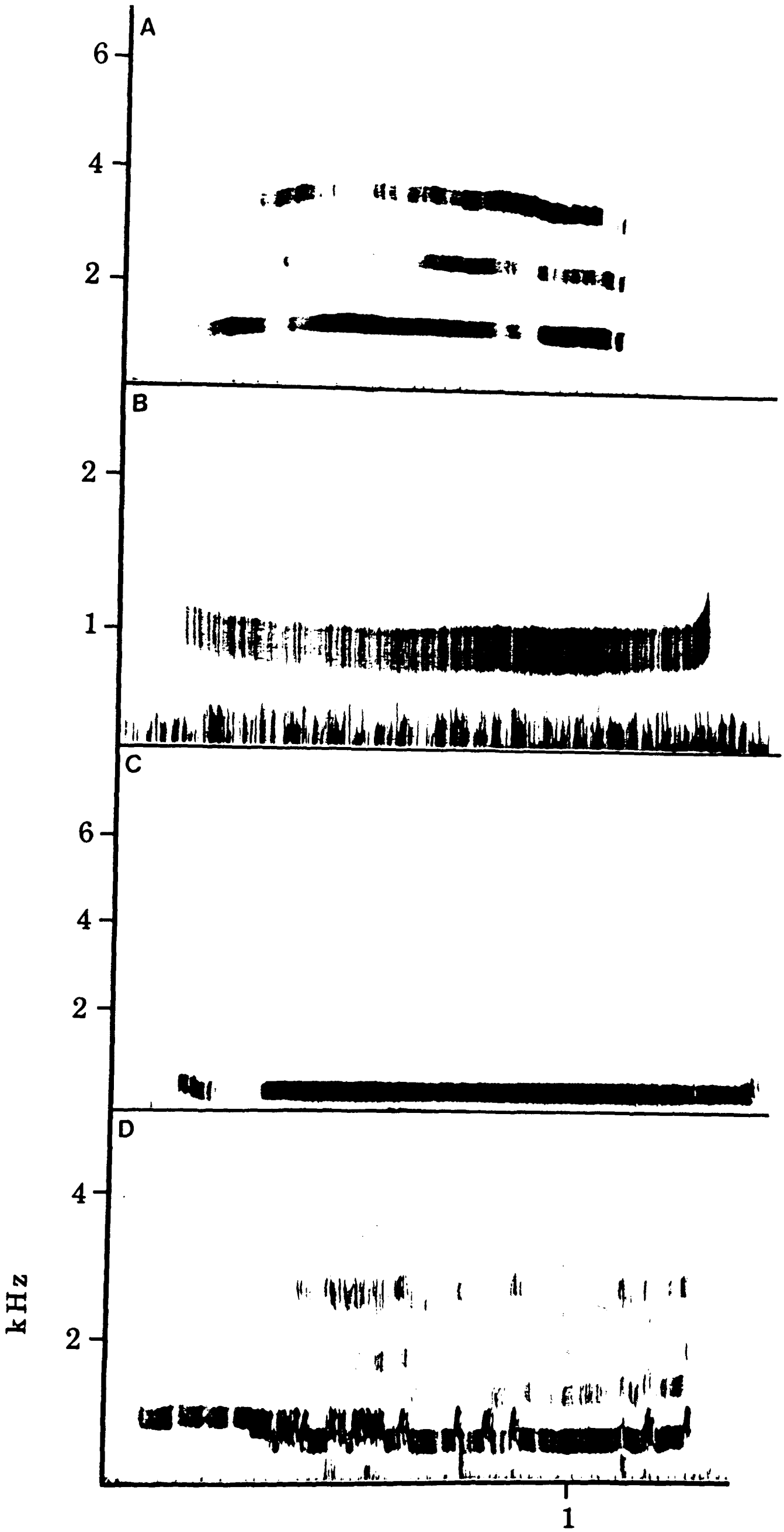
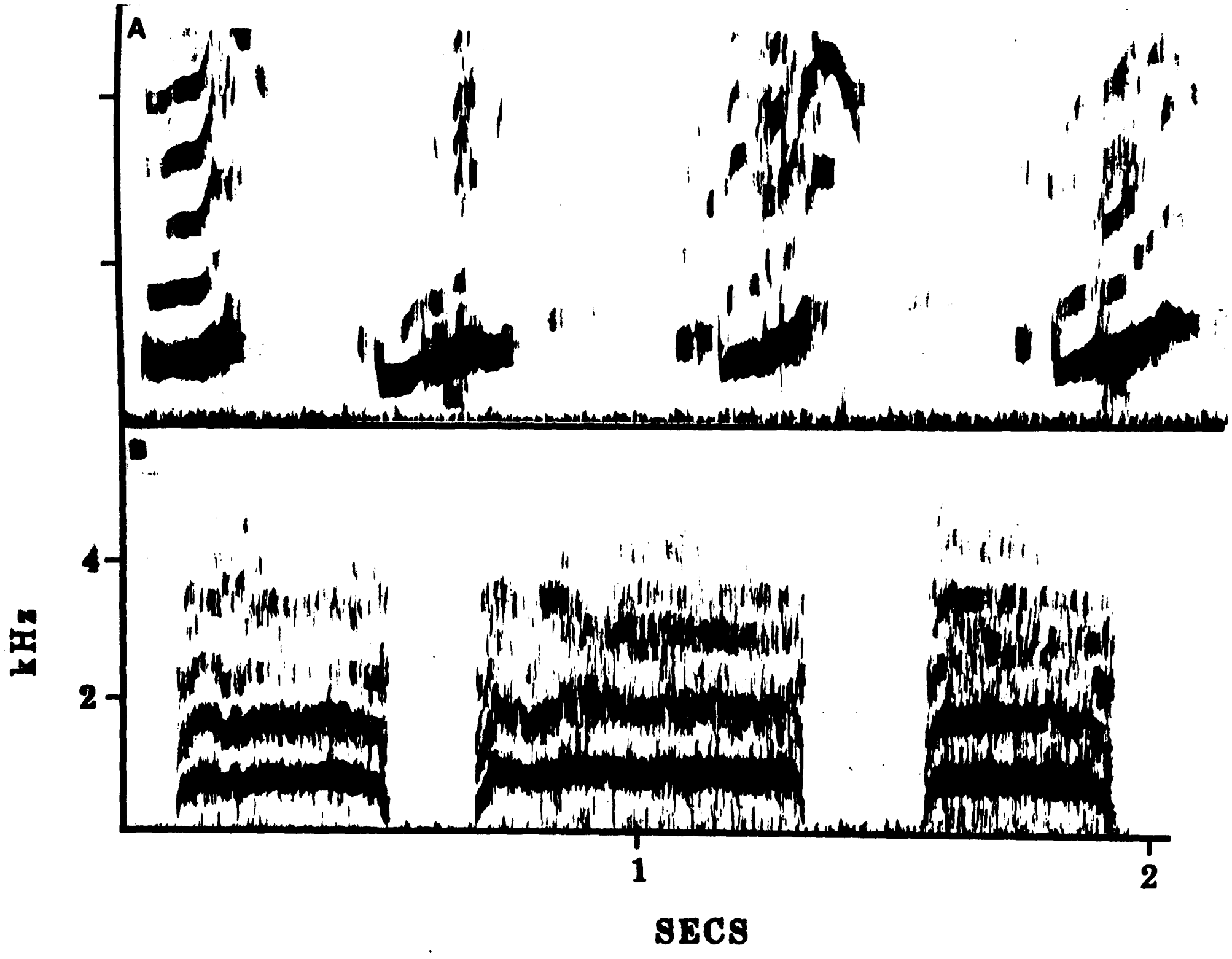

A
6
4
2
B
2
1
C
6
4
2
D
4
2
kHz
1
SECS

Figure 5.3

Sonagrams of (A) Atlantic Petrel *Pterodroma incerta*, Gough Island, M. Swales (B) Kerguelen Petrel *P. brevirostris*, Gough Island, M. Swales.


A
B
4
2
kHz
1
2
SECS

et al. 1983). They also tend to be rather less structured than those in the other two groups. It seems likely that, at least for some species, only females produce them (Grant et al. 1983).

Puffinus and Calonectris

The calls of the shearwaters are rather less diverse than those of the gadfly petrels, particularly with regard to the ranges of all frequency measures, and the number of notes incorporated per call (Table 5.1). In addition, apart from sexual differences, there appears to be only one call type per species (Brooke 1978d). However, regarding their general structure, they can be divided into two groups. The first comprises calls with more notes, given at a faster rate and at a higher pitch (Figure 5.4). These calls are typical of the smaller shearwaters such as Puffinus assimilis, P. huttoni and P. gavia. The second group is composed of calls with fewer notes at somewhat lower frequencies (Figure 5.5) and comprises the rest of the shearwater species examined.

Procellaria

The calls of these shearwater-like petrels stand apart from both the gadfly petrels and shearwaters (Table 5.1). They consist of a long repetition of notes lasting for up to 20 seconds, and given at a rapid rate (Figure 5.6). The number of call types per species is probably two with possible sexual differences.

Pachyptila

Prion calls are typified by having low frequencies and a rapid delivery of notes (Table 5.1). The number of call types per species is probably one or two, again, with possible sexual differences. The Dove Prion Pachyptila desolata call seems to be distinct with seven notes, versus

Figure 5.4

Sonagrams of (A) Hutton's Shearwater *Puffinus huttoni*, Kaikoura Mountains, L. McPherson (B) Fluttering Shearwater *P. gavia*, Hen Island, N.Z., J. Kendrick (C) Little Shearwater *P. assimilis*, Eclipse Island, P. Fullagar.

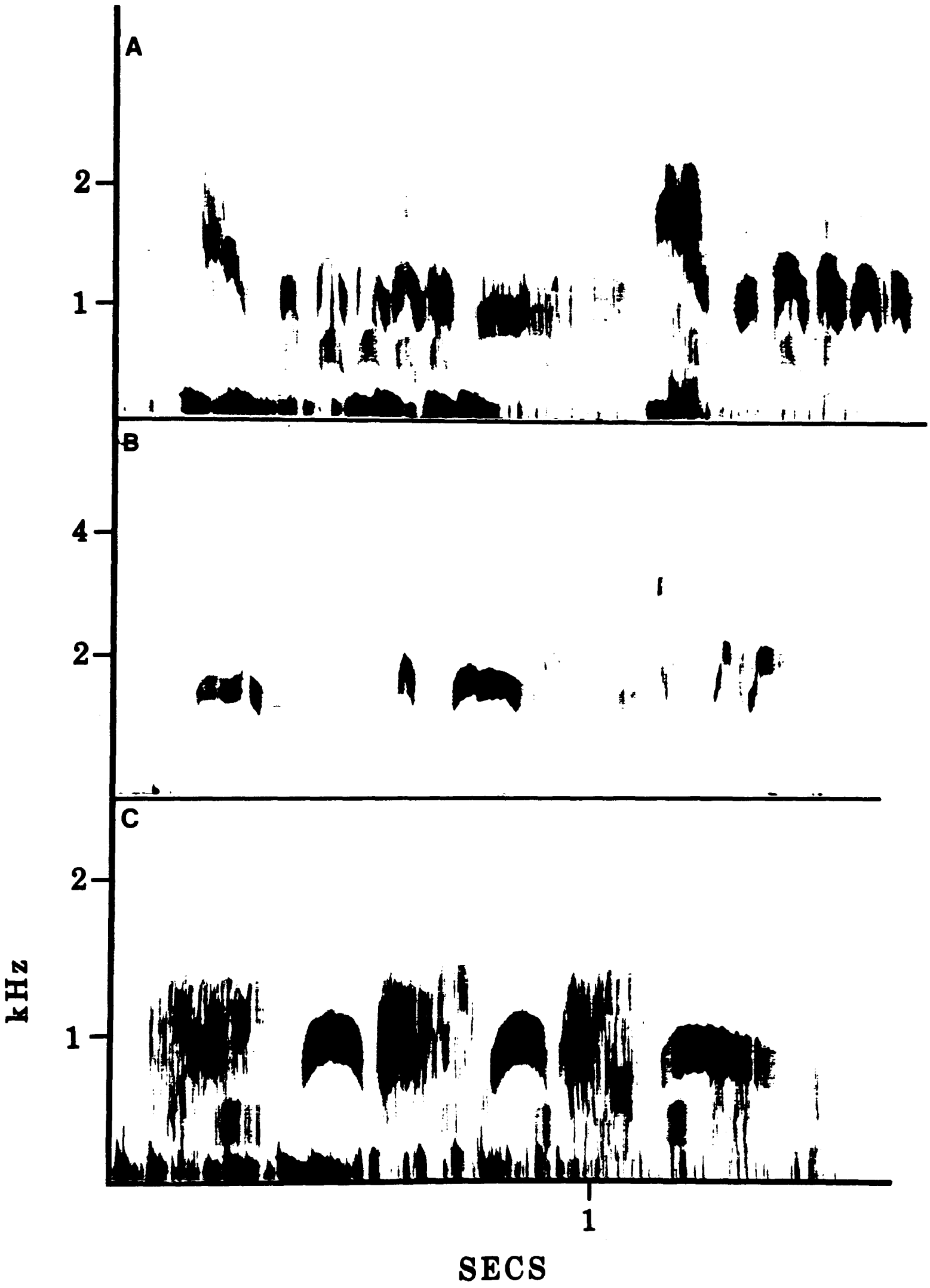

A
2
1
B
4
2
C
2
1
kHz
1
SECS

Figure 5.5

Sonagrams of (A) Sooty Shearwater *Puffinus griseus*, Montague Island, Australia P. Fullagar (B) Flesh-footed Shearwater *P. carneipes*, Eclipse Island, E. Lindgren (C) Greater Shearwater *P. gravis*, Gough Island, M. Swales (D) Wedge-tailed Shearwater *P. pacificus*, Montague Island, N. Robinson.

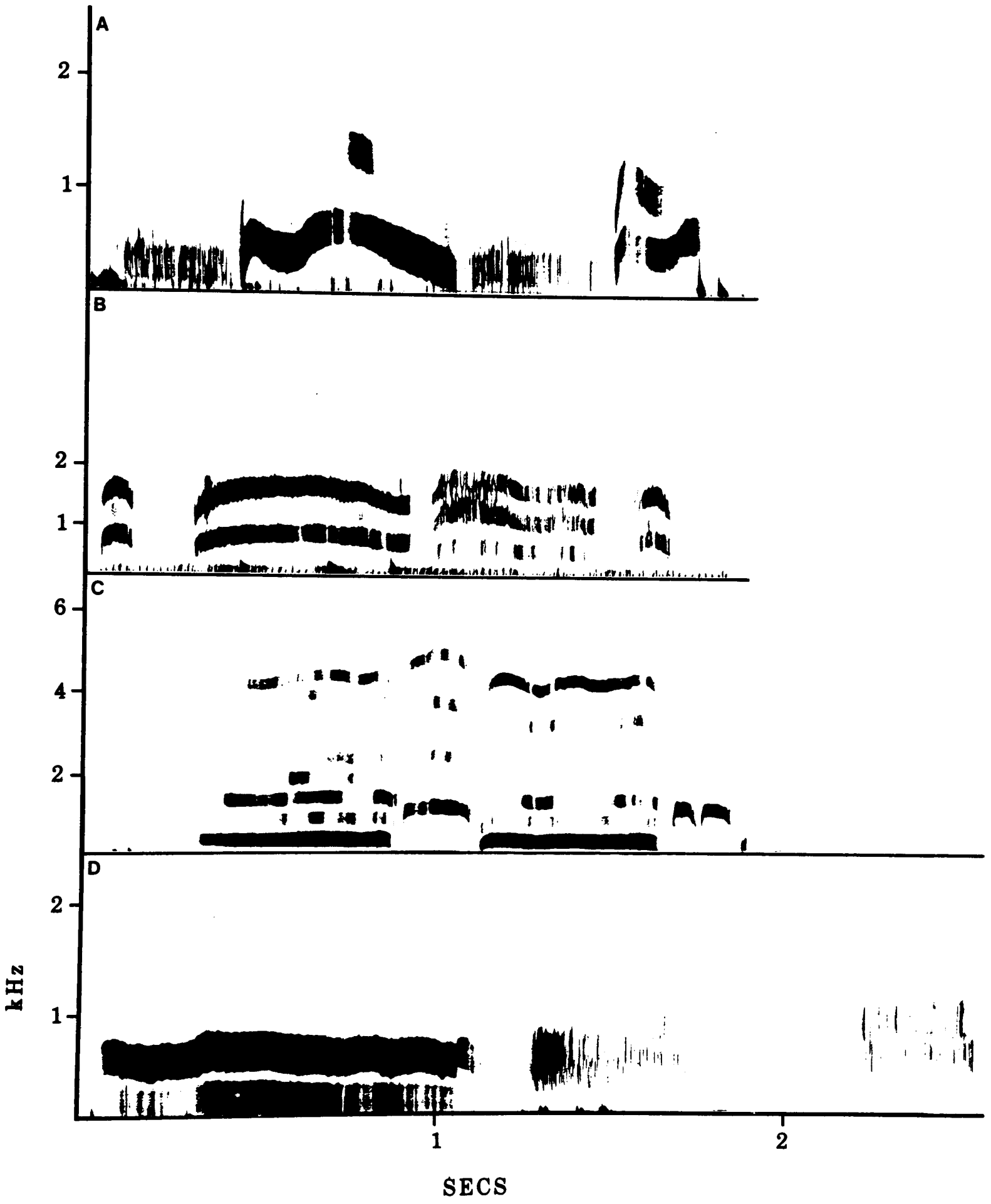
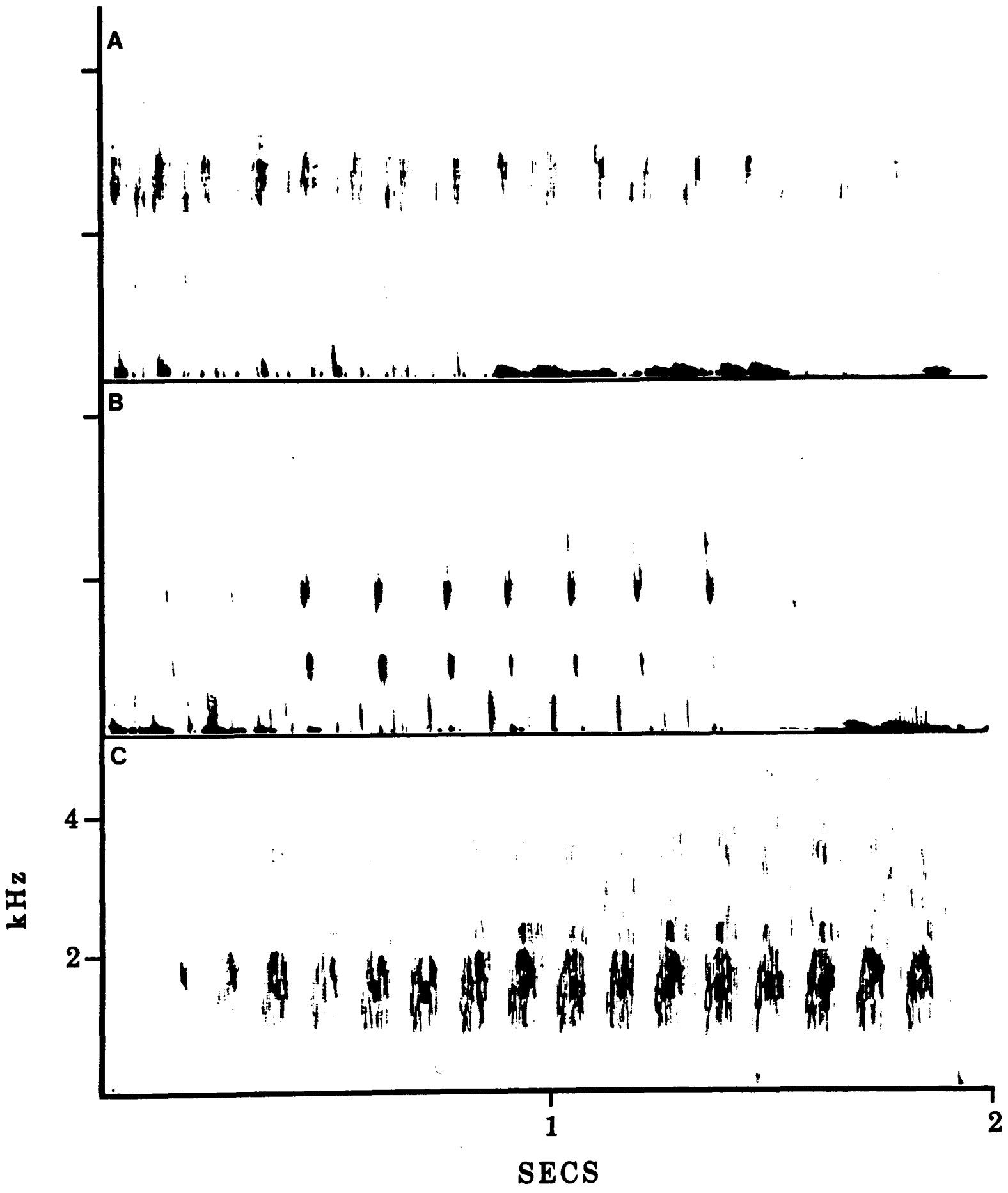

A
2
1
B
2
1
C
6
4
2
D
2
1
kHz
1
2
SECS

Figure 5.6

Sonagrams of (A) Black Petrel Procellaria parkinsoni, Great Barrier Island, L. McPherson (B) White-chinned Petrel P. aequinoctialis, Auckland Islands, G. Williams (C) Westland Black Petrel P. westlandica, Barrytown, L. McPherson. All sites in N.Z.


A
B
C
4
2
kHz
1
2
SECS

three in P. turtur and P. vittata (Figure 5.7), although the latter species does produce a call with more.

Bulweria and Halobaena

The one and only call of Bulwer's Petrel has already been examined in detail. A repeated, single note call with a low frequency (Figure 5.8, Cramp & Simmons 1977), it is very distinctive. It, and the fact that the species lacks aerial calls have been proposed as reasons why the genus should remain distinct from that of Pterodroma (Thibault & Holyoak 1978), despite opinions to the contrary based on their considerable anatomical overlap (Mathews 1948, Olson 1975).

The call of the Blue Petrel consists of about seven notes (Figure 5.8), and has been described as being indistinguishable from that of the Dove Prion (Watson 1975). Indeed, both species respond to the playback of each other's calls (Hunter et al. 1982). Inspection of Figures 5.7 and 5.8 suggests that the frequency distribution of both calls are very different, although it is possible that the recordings represent sexual differences. Curiously, the bird itself also resembles a prion (see Tuck & Heinzel 1978), but it is clearly more related to the gadfly petrels (Harper 1978). It has been suggested that such convergence is the result of diurnal predators, such as skuas Catharacta (= Stercorarius) promoting the disruptive patterning and cryptic colouration that both taxa exhibit (Harper 1978).

The calls of the Hydrobatidae

Sonagrams were examined for 11 species of storm petrel, six of which were Oceanodroma. Also examined were single species of Oceanites, Halocyptena, Fregetta, Hydrobates and Pelagodroma.

Figure 5.7

Sonagrams of (A) Broad-billed Prion *Pachyptila vittata*, Gough Island, M. Swales (B) Fairy Prion *P. turtur*, Stephens Island, J. Kendrick (C) Dove Prion *P. desolata*, South Georgia Bird Island, D. Turner.

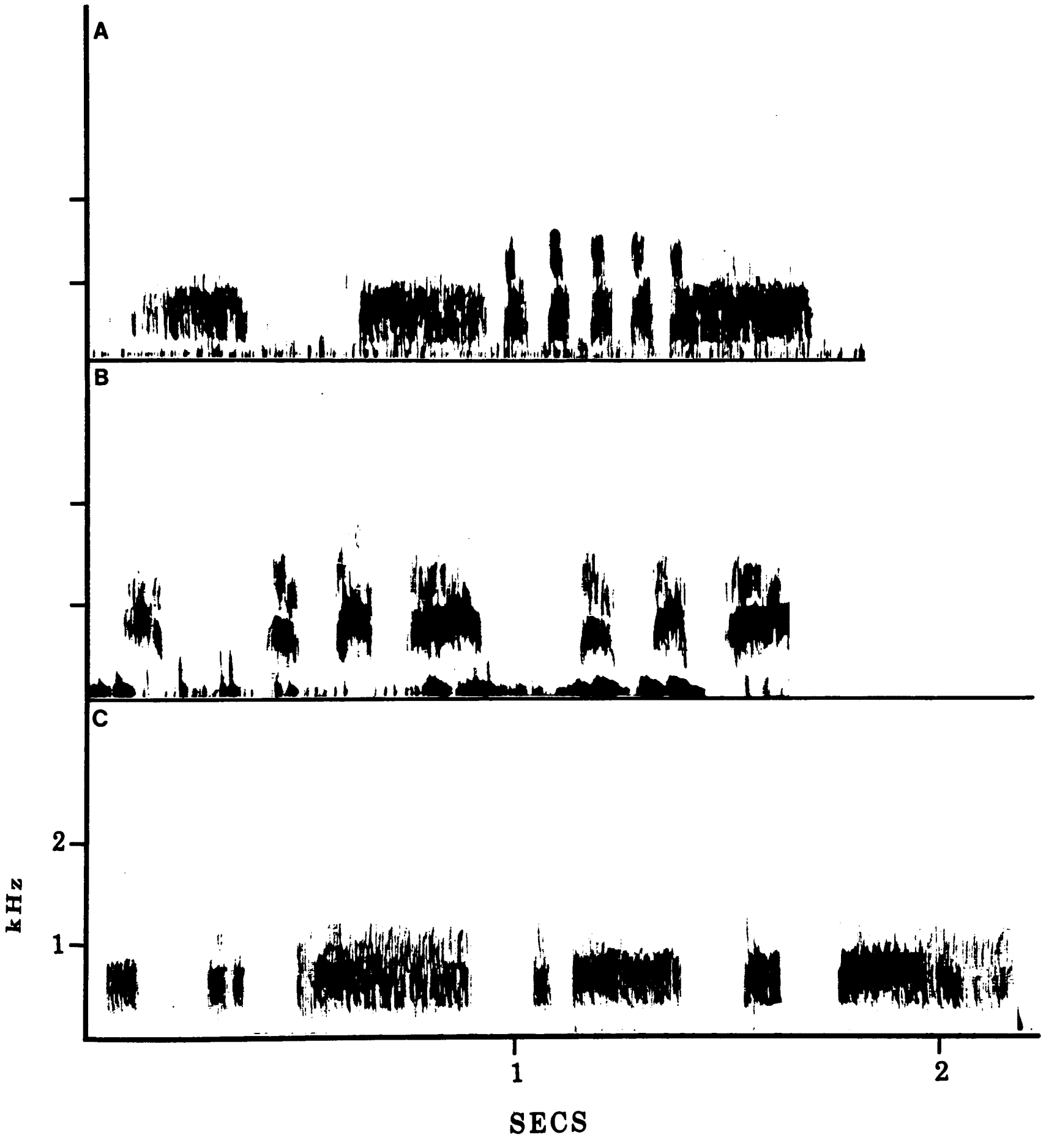
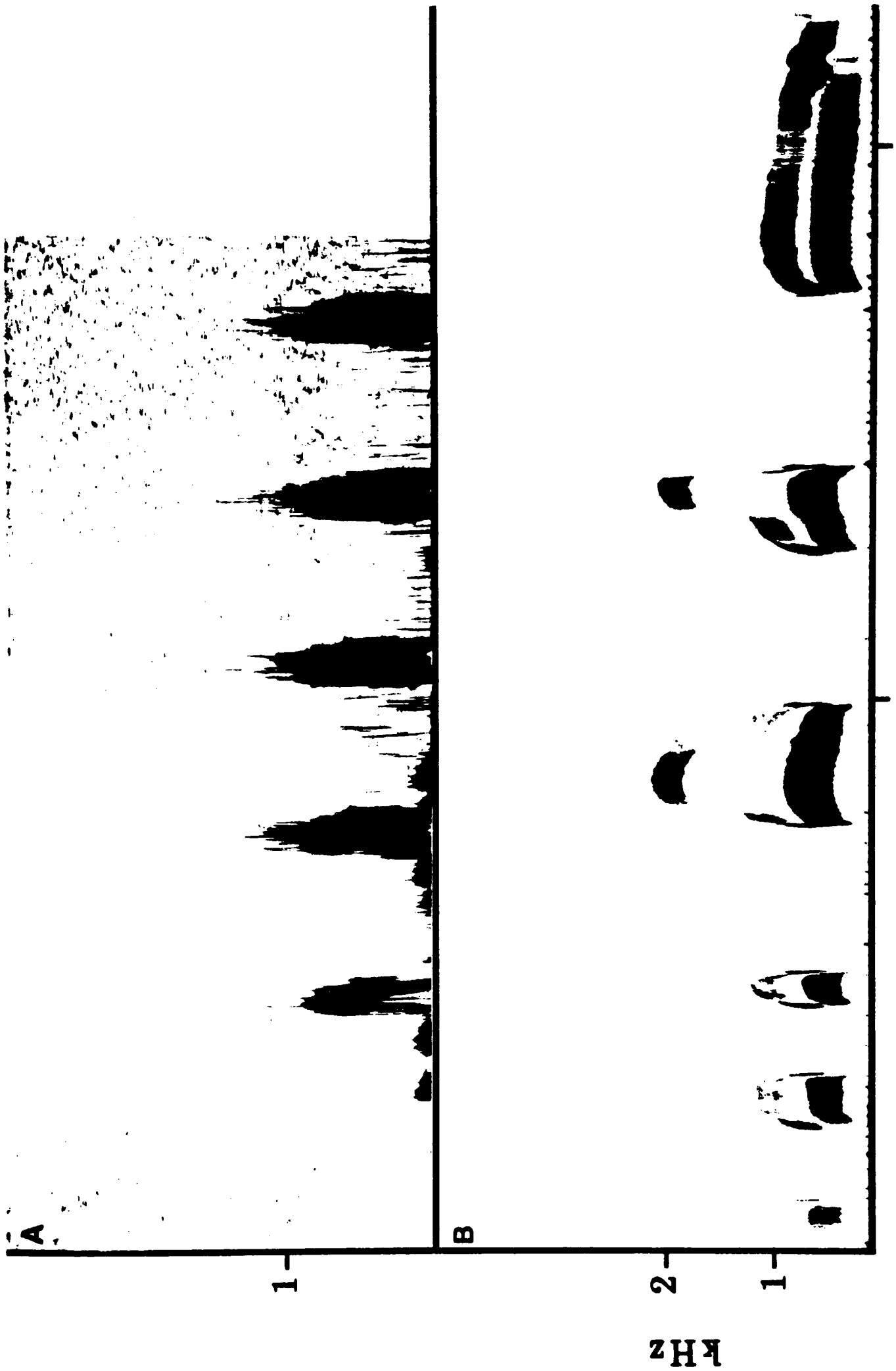

A
B
C
2
1
kHz
1
2
SECS

Figure 5.8

Sonagrams of (A) Bulwer's Petrel Bulweria bulwerii Hawaii
Popoia Island, J. Ward (B) Blue

Petrel Halobaena caerulea Bird Island, D. Turner.


A
B
1
2
1
2
1
kHz
SECS

Oceanodroma

The calls of the Oceanodroma storm petrels can be placed into two main groups, probably corresponding to two call types within each species. The first group is composed of rather short, stacatto flight-calls of 4 up to 20 notes given in 1-2 seconds (Figure 5.9, Cramp & Simmons 1977, Ainley 1980, Simons 1981).

The second group of calls are usually referred to as purr, churr- or chattering-calls. They are rather more prolonged and consist of a rapid repetition of notes interspersed with single breath notes, used mainly in the burrow (Figure 5.9, Hall-Craggs & Sellar 1976, Cramp & Simmons 1977, Ainley 1980). Mention should be made of the fact that O. furcata appears not to possess a purr-call (Simons 1981).

Hydrobates and Halocyptena

These single-species genera also possess two call types analogous to those described for the Oceanodroma, the flight-call and the purr-call. As mentioned before, the term flight call for Hydrobates is rather misleading as the species rarely calls in flight. The call itself usually consists of three harsh notes (Hall-Craggs & Sellar 1976, Cramp & Simmons 1977). The Hydrobates purr-call is much the same as Oceanodroma purr-calls, except the rate of note production is higher (Hall-Craggs & Sellar 1976).

The flight-call of Halocyptena appears to be more related to those of the Oceanodroma (Figure 5.10). Its purr-call has the highest rate of note production in the storm petrels, or probably for that matter, in the entire Procellariiformes (Figure 5.10).

Oceanites, Fregetta and Pelagodroma

These southern-breeding species have vocal repertoires entirely different from those found in the northern Oceanodroma, Hydrobates and

Figure 5.9

Sonagrams of (A) Tristram's Storm Petrel Oceanodroma tristrami Flight-Call, Torishima, Japan Broadcasting Corp. (B) Black Storm Petrel O. melania Flight-Call and (C) Purr-Call, Partida Island, Mexico R. Templeton.

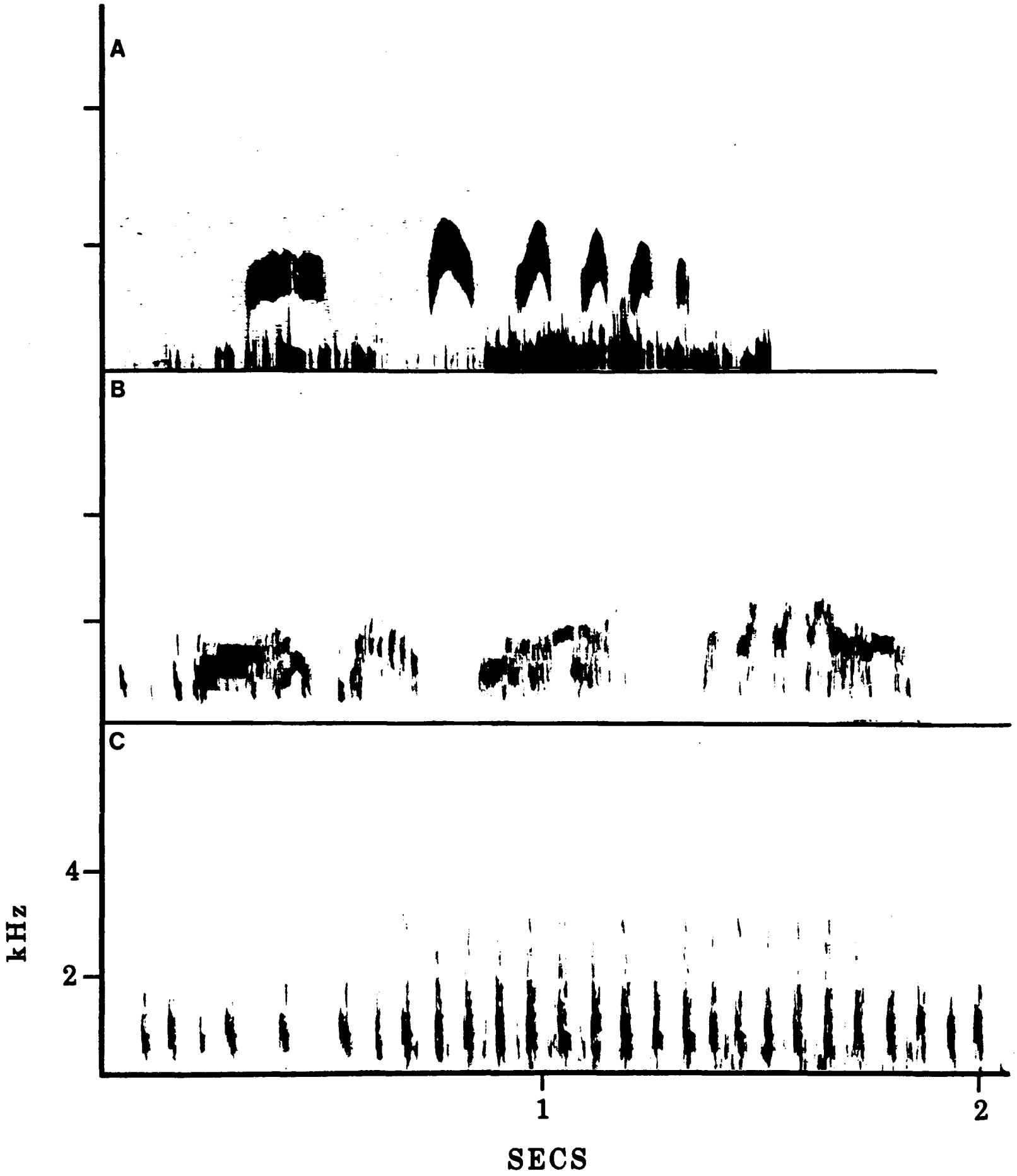
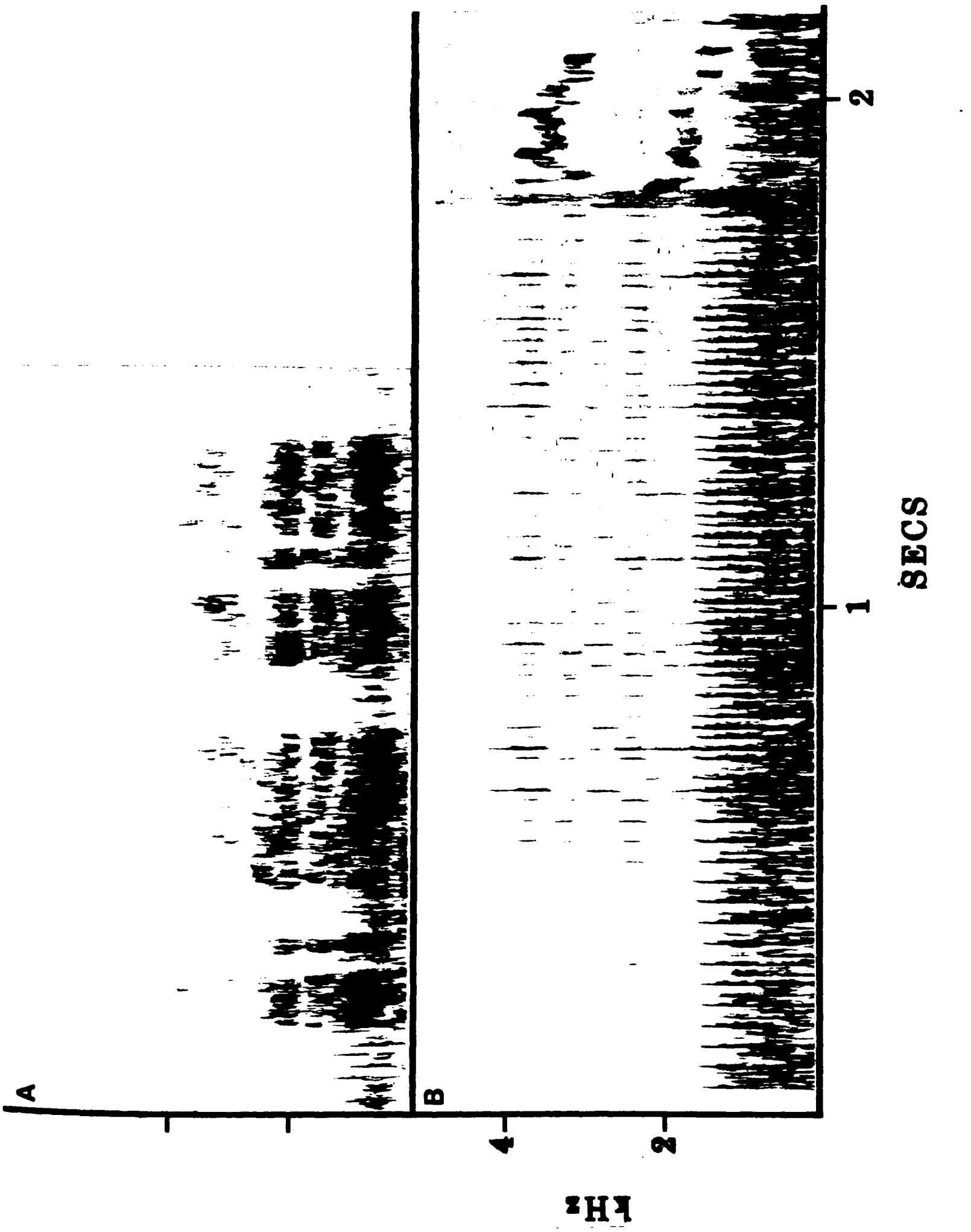

A
B
C
4
2
kHz
1
2
SECS

Figure 5.10

Sonagrams of Least Storm Petrel *Halocyptena microsoma* (A) Flight-Call and (B) Purr-Call, Partida Island, R. Templeton.


A
B
4
2
kHz
1
2
SECS

Halocyptena (Bourne 1977). Their calls consist of repeated whistles and chirps (Figure 5.11) rather than the sustained purring and twittering flight calls found in the former species. The reasons for this are unclear, though possibly suggest two main areas of storm petrel evolution in the respective hemispheres. Their morphologies also seem distinct with the northern species possessing short legs and long wings, and the southern species possessing long legs and short wings (Bourne 1977).

The calls of the Pelecanoididae

Sonagrams were examined for two species of diving petrel (Figure 5.12, Payne & Prince 1979). The calls of these species are very simple and usually consist of two notes given at a low pitch. For each species, there only appears to be one call, with possible sexual variation.

Discussion

The results show that the calls of the nocturnal Procellariiformes are diverse, both in their frequency structure and temporal patterning (Table 5.1). In general though, it can be seen that the calls of a particular genus resemble each other more than they do the calls of other genera. Given that the calls were not originally used systematically, such a situation would exist if the evolution of calls parallelled the evolution of the group.

Unfortunately, the calls of each genera are so distinct that the construction of phylogenetic relationships is difficult, at least with the material available. However, a few qualitative systematic points will be considered.

The genus Pterodroma is a diverse assortment of species, whose taxonomic classification is complex, with polymorphism being common, further compounded with the occurrence of sibling species (Serventy et al. 1971).

Figure 5.11

Sonagrams of (A) White-bellied Storm Petrel Fregetta grallaria, Lord Howe Island, P. Fullagar (B) Wilson's Storm Petrel Oceanites oceanicus, Bird Island, W. Tickell.

Australia

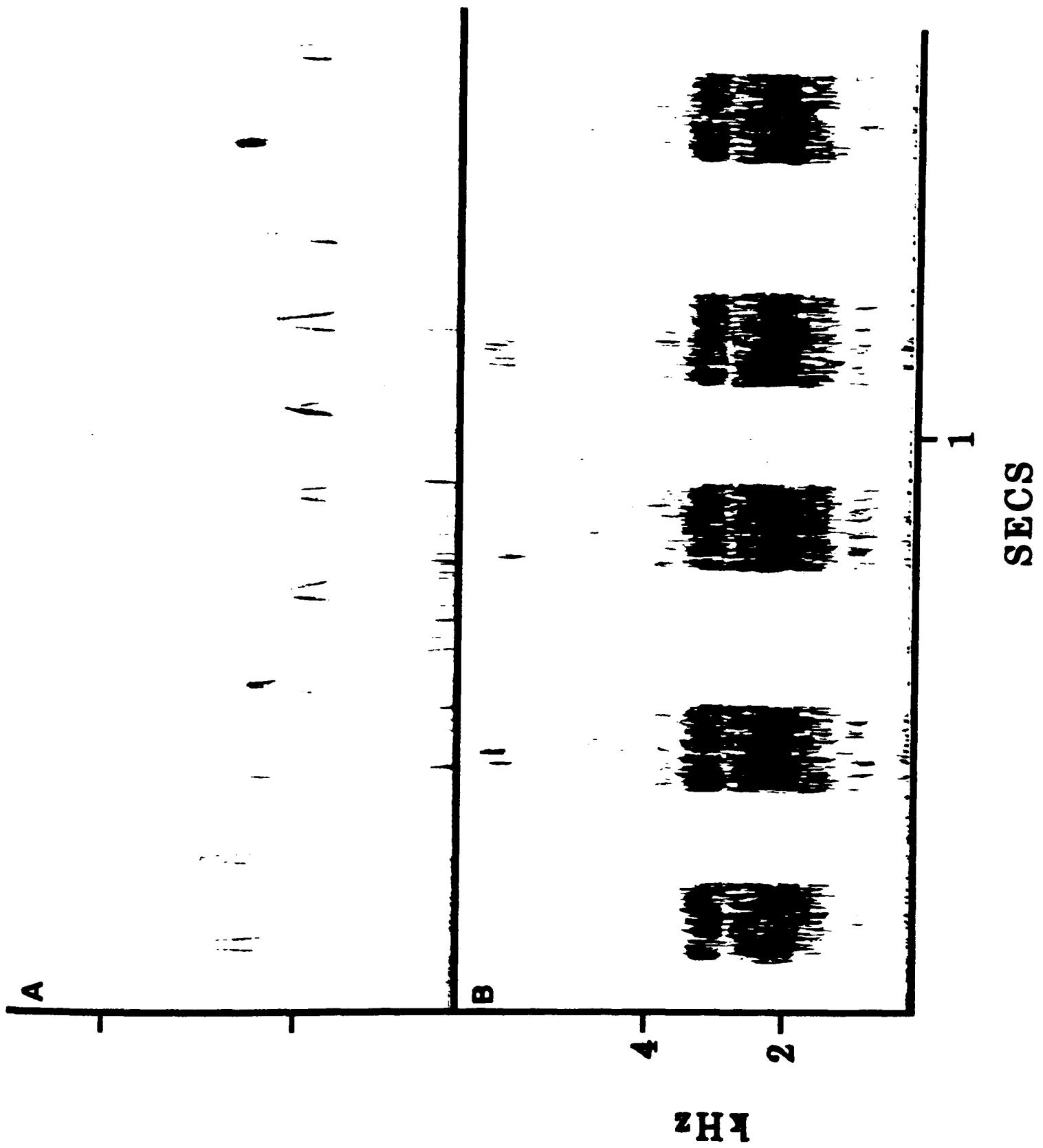
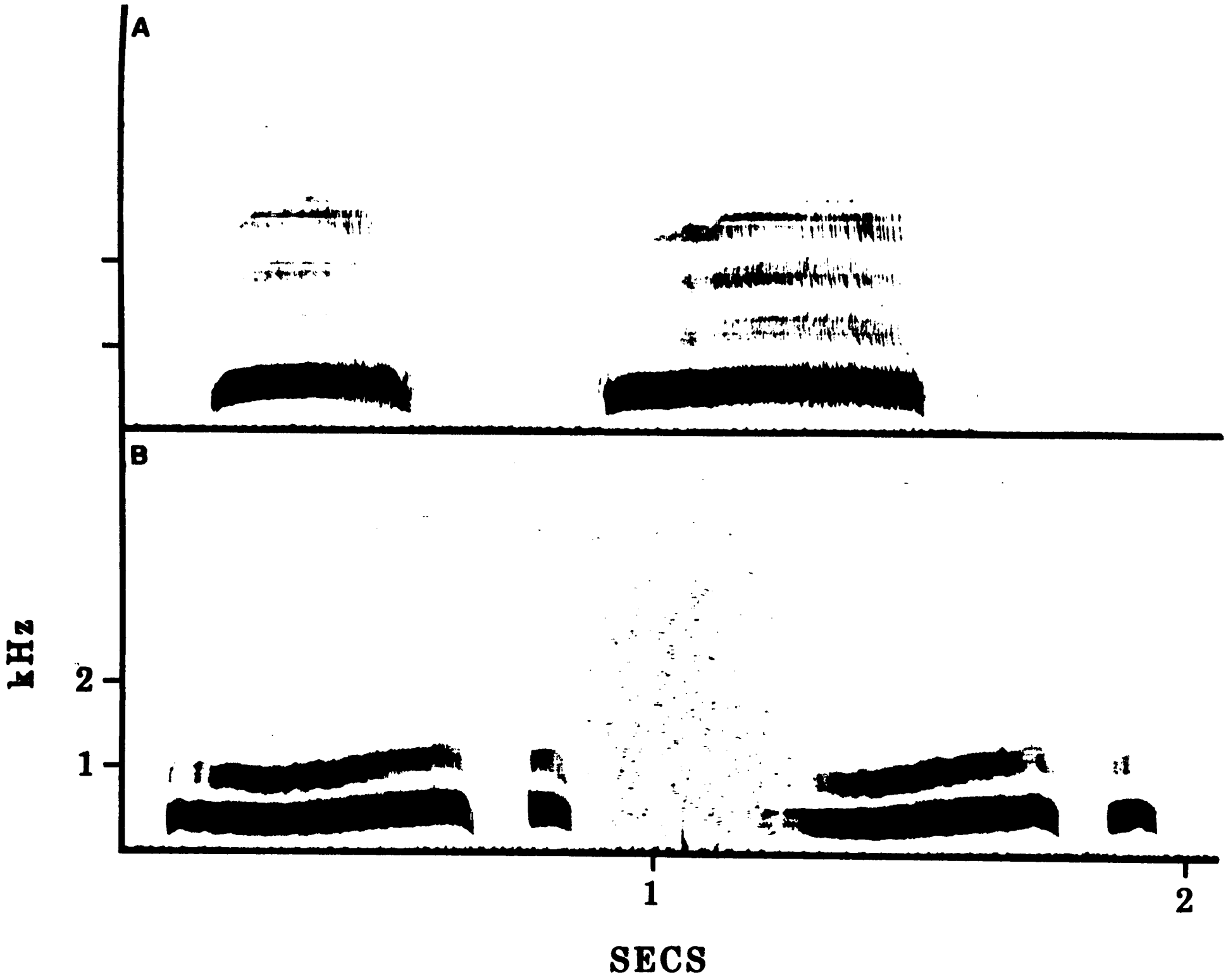

A
B
4
2
kHz
1
SECS

Figure 5.12

Sonagrams of (A) Georgian Diving Petrel *Pelecanoides georgicus* and (B) Common Diving Petrel *P. urinatrix*, Bird Island, D. Turner.


A
B
kHz
2
1
1
2
SECS

Morphologically, they fall into two groups, with the smaller species having short wings and long wedge-shaped tails, and the larger species possessing long wings and rounded tails. Their calls, however, do not seem to diverge in a similar way. The majority of species possess the "ti-ti-ti" call (Figure 5.1, Serventy et al. 1971, Watson 1975), but at least one, the smaller Pterodroma mollis does not (Figure 5.2, Jouanin et al. 1969, Cramp & Simmons 1977, Warham 1979) suggesting a divergence of some sort within the genus. The close association between Bulweria, Halobaena and the Pterodroma petrels is well established (Olson 1975, Harper 1978), yet their calls are quite distinct (Figure 5.8), supporting their separation from Pterodroma. Furthermore, Bulweria bulwerii does not call in flight, a feature not described for any Pterodroma species (Thibault & Holyoak 1978). Halobaena does possess a flight call (Murphy 1936), so one might suggest that it is more closely related to Pterodroma than Bulweria is.

As with the genus Pterodroma, the shearwater group Puffinus is taxonomically difficult (Harrison 1983). Its closely allied genus Calonectris is usually considered intermediate between Puffinus and Procellaria (Serventy et al. 1971). Again, two types of adaptive morphology exist in the two shearwater groups (Harper 1978). The larger sub-tropical species have broad wings and wedge-shaped tails, while the rest are adapted to a more aquatic lifestyle, with narrower wings and shorter tails (Kuroda 1954). Their calls, however, show divergence unrelated to these morphological differences, with the smaller species producing shorter, higher-pitched sounds (Figures 5.4 and 5.5). A recent suggestion that Puffinus assimilis be removed from the genus (Harper 1978) is not supported by their calls. The calls of Calonectris and Puffinus are not as distinct as those of Procellaria, suggesting it is more distantly related.

All four species of Procellaria produce a series of penetrating tapping

sounds (Figure 5.6), supporting their separation as a distinct genus (Harper 1978), although Procellaria westlandica apparently has a more varied vocal repertoire, which includes a shearwater-like braying and howling (Harper 1978).

Mention has already been made of the vocal and morphological divergence of the northern and southern storm petrels (Bourne 1977). However, within the northern genera, it would appear as if Halocyptena is more closely related to Oceanodroma than Hydrobates is. The flight-calls of Halocyptena and Oceanodroma are similar (Figures 5.9 and 5.10, Hall-Craggs & Sellar 1976, Cramp & Simmons 1977, Ainley 1980), whereas the 'flight-call' of Hydrobates (which rarely calls in flight) is quite distinct (Figure 3.1, Hall-Craggs & Sellar 1976, Cramp & Simmons 1977). Oceanodroma furcata does not possess a purr-call (Simons 1981), casting some doubt on its present taxonomic position, although it does possess an Oceanodroma-like flight-call. As far as the southern species are concerned, Fregetta grallaria and Pelagodroma appear to be more closely related to each other than to Oceanites oceanicus based on their calls (Figures 5.11 and 3.6). Their separation as distinct genera, however, is apparently correct (Harper 1978).

While the primary reason behind call divergence has probably been their function as isolating mechanisms, other factors could potentially act to shape or constrain them, such as species morphology and the ecology of their island breeding places.

Body size has been shown to be important in some birds, in that those species which are larger tend to produce lower frequencies in their songs or calls (Chapter 4). In order to see whether body size influenced call frequencies in the nocturnal Procellariiformes, body weights (thought to be reliable measures of body size) of the species examined were extracted from the literature (Jouanin & Roux 1965, Swales 1965, Serventy et al. 1971, Zino 1971, Harris 1974, Cramp & Simmons 1977, Warham 1977, Brooke 1978b,

Payne & Prince 1979) and correlated with the maximum and minimum frequencies and the frequency ranges of their calls. No significant correlations could be detected within genera, families or overall, suggesting that body size is not important in explaining the diversity of calls found in the group.

Another factor promoting call divergence may have been the habitats in which these species nest. Most do so on islands, which may be forested or open, in microhabitats ranging from rocks to soil. In general, it has been shown that species nesting in open habitats produce sounds with higher frequencies and larger frequency ranges than those in closed habitats (Morton 1975, Hunter & Krebs 1978). In the case of the nocturnal Procellariiformes, it is not unusual for several taxa to breed in the same place, with calls correspondingly covering a wide range of frequencies etc.. It is therefore difficult to pinpoint habitat differences as promoting call divergence. Some species nest in both open and closed habitats, and a close inspection of their calls may reveal differences in the predicted fashion, although account might then have to be taken of relative isolation.

A further ecological factor possibly acting to promote call divergence is the problem of acoustic interference in multi-species communities (Cody & Brown 1969, Morton 1975). In song birds, it has been suggested that this is overcome to some extent by different species occupying different time niches for singing (Krebs & Davies 1981). This idea could be applied to the nocturnal Procellariiformes, as studies have shown differences between species in nightly arrival times in mixed colonies (Ainley et al. 1974, Harris 1974, Warham et al. 1977, Furness & Baillie 1981, pers. obs.). As acoustic interference is only going to occur when call frequencies and temporal patterning are similar, it is also possible that each species has adapted its call to particular frequency and time niches in the general acoustic environment. Each species' call is certainly distinctive with

respect to its frequency and time characteristics. Again, though, it is difficult to say with certainty that such potential competition has promoted call divergence. As with habitat, it would be interesting to compare a species' call in a mixed community and when alone, or in a different community. If acoustic competition was important, one might expect a type of 'character release' to occur in such situations. As with habitat comparisons though, account might have to be taken of the effects of relative isolation on call. Brémond (1978) showed that a rich acoustical environment did affect communication, but concluded that such hinderance is seldom complete, as the decrease in the received information is compensated by the song's inherent redundancy. It is perhaps worth noting in this respect that the calls of many nocturnal Procellariiformes are repeated many, many times over several hours. Such redundancy may have been partly selected for via acoustical competition with other species.

The potential use of calls in petrel systematics

Introduction

The preceding review raises the possibility that calls could be a useful systematic tool in petrel taxonomy. The taxonomic history of the group has been one of conflicting and diverse opinion (Alexander et al. 1965, Sibley & Ahlquist 1972, Harper 1978), and problems remain such as the relationships within the Pachyptila, Pterodroma, Puffinus and Pelecanoides groups (Serventy et al. 1971, Nelson 1980, Harrison 1983). Yet the calls of these species could potentially be very powerful systematic indicators. As many are nocturnal, the use of visual displays in courtship behaviour is reduced, and it is likely that voice has risen to prominence in differentiating one species from another in the darkness. As such, the calls of these species are good examples of prezygotic isolating mechanisms (Dobzhansky et al.1977). Other authors have appreciated

this point with respect to other species groups (Lanyon 1969, Marshall 1978).

Avian taxonomy is still largely based on morphological features, but increasing attention is being paid to behavioural characters, especially vocal ones (Lanyon 1969, Selander 1971). Attempts have been made to compare the calls of Procellariiformes (Hall-Craggs & Sellar 1976, Sparling 1977, Sparling & Williams 1978, Thibault & Holyoak 1978, Ainley 1980, Jehl 1982), but most of these have been inadequate. Problems include low sample sizes and the neglect of potential sexual dimorphism in voice. It has been suggested that such comparisons should not be made until the vocal characters concerned can be analysed as rigorously as more traditional mensural characters (Bourne & Jehl 1982). As a result, there is a danger that such a technique will lose its validity before its full potential has been evaluated. With this in mind, the calls and biometrics of two species pairs of Procellariiformes were compared using multivariate discriminant analyses, in order to see whether the calls were as useful as traditional morphometrics in separating species. Stepwise discriminant analysis was chosen as the statistical procedure as it is commonly used in systematics (Sokal & Rohlf 1969).

Methods

The calls and measurements of male Manx and Little Shearwaters, and those of male British and Madeiran Storm Petrels were used for the comparisons. The Manx Shearwater and British Storm Petrel calls and measurements were taken at Skomer Island, and those of the Little Shearwater and Madeiran Storm Petrel were taken at Great Salvage Island.

For the shearwater pair, four morphological variables were compared, those of tarsus length, bill length, wing length and body weight. These measurements were taken in the usual way. The calls were also recorded and sonagrams produced in the usual way. Six call variables were compared

for each species (Figure 5.13).

For the storm petrel pair, four morphological variables were also compared (bill, tarsus, wing and tail lengths), and five variables compared from their respective purr-calls (Figure 5.14).

Results

As might be expected, highly significant differences existed between the Manx and Little Shearwater with regard to their respective body size measures (Table 5.2). However, the differences between their respective call variables were also significant (Table 5.2). The multivariate discriminant analyses of the body size and call variables produced highly significant separations for both types of measure (Figure 5.15). However, the body size variables produced a stronger discrimination between the two species than the call variables did.

A parallel situation was found in the storm petrel pair. Both body size and call variables were significantly different between British and Madeiran Storm Petrels (Table 5.3). In addition, multivariate discriminant analyses of their respective body size and call variables produced highly significant separations (Figure 5.16). However, as with the shearwater pair, the discrimination between the two species was greater using the body size measures.

Discussion

The results (Figures 5.15 and 5.16) suggest that the quantitative use of call variables is useful in separating petrel taxa. Despite this, and the fact that vocalizations have been extensively employed in avian systematics (Löhrl 1963, Lanyon 1969, Selander 1971, Hand 1981, Jouventin 1982, Lemon et al. 1983, Sparling 1983), most studies of the Procellariiformes have used more traditional morphological comparisons (Murphy 1952, Murphy

Figure 5.13

Sonagrams of male (A) Little Shearwater and (B) Manx Shearwater call variables measured:

F1 = max. freq. introductory note

F2 = max. freq. whole call

T1 = call length

T2 = breath note length

T3 = gap between breath note and rest of call

T4 = gap between successive calls

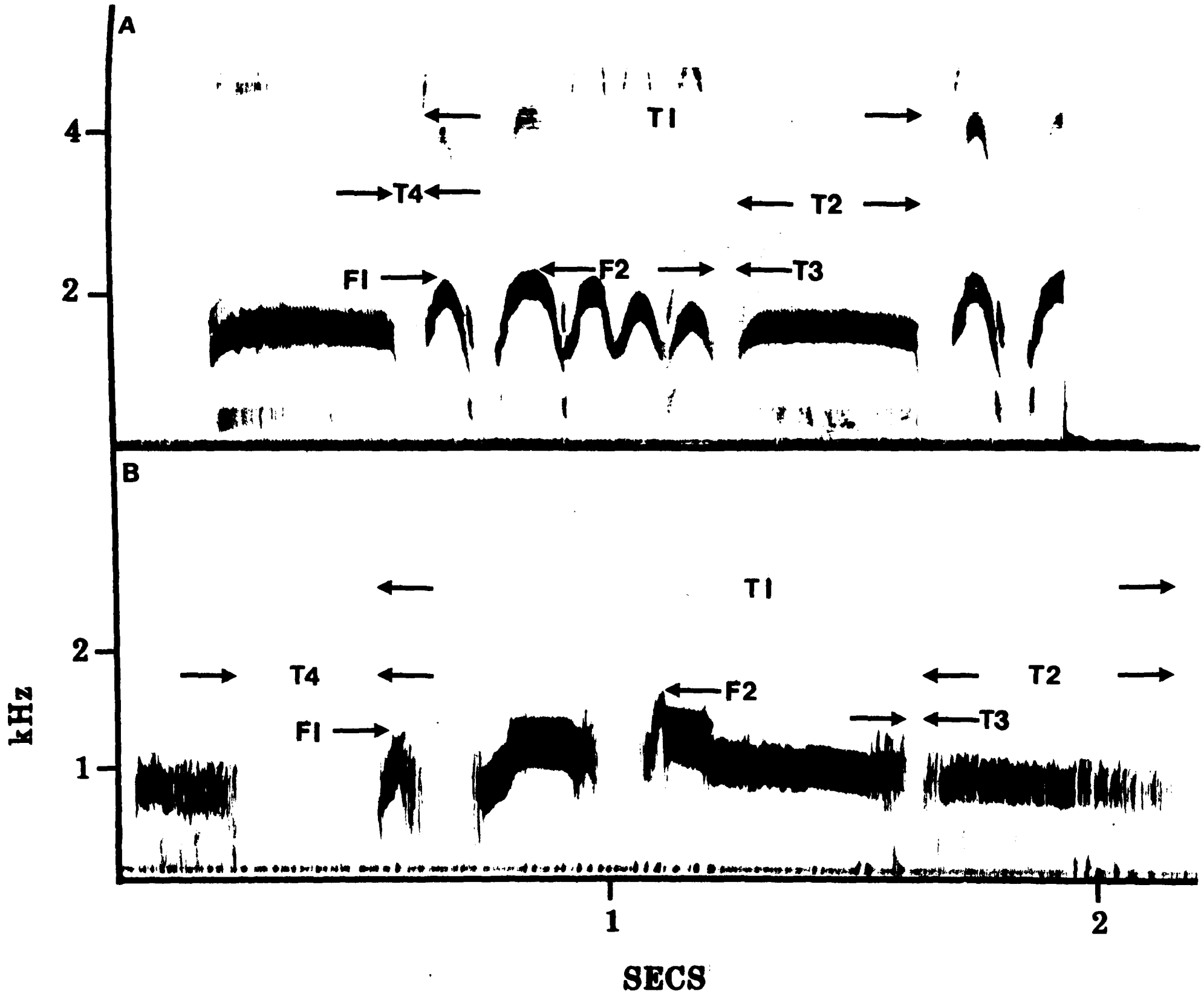

A
4
2
T1
T4
T2
F1
F2
T3
B
2
1
kHz
T1
T4
T2
F2
F1
T3
1
2
SECS

Figure 5.14

Sonagrams of male (A) Madeiran Storm Petrel and (B) British Storm Petrel purr-call variables measured:

F1 = max. freq. breath note

T1 = call length

T2 = breath note length

T3 = gap between successive calls

T4 = notes per second

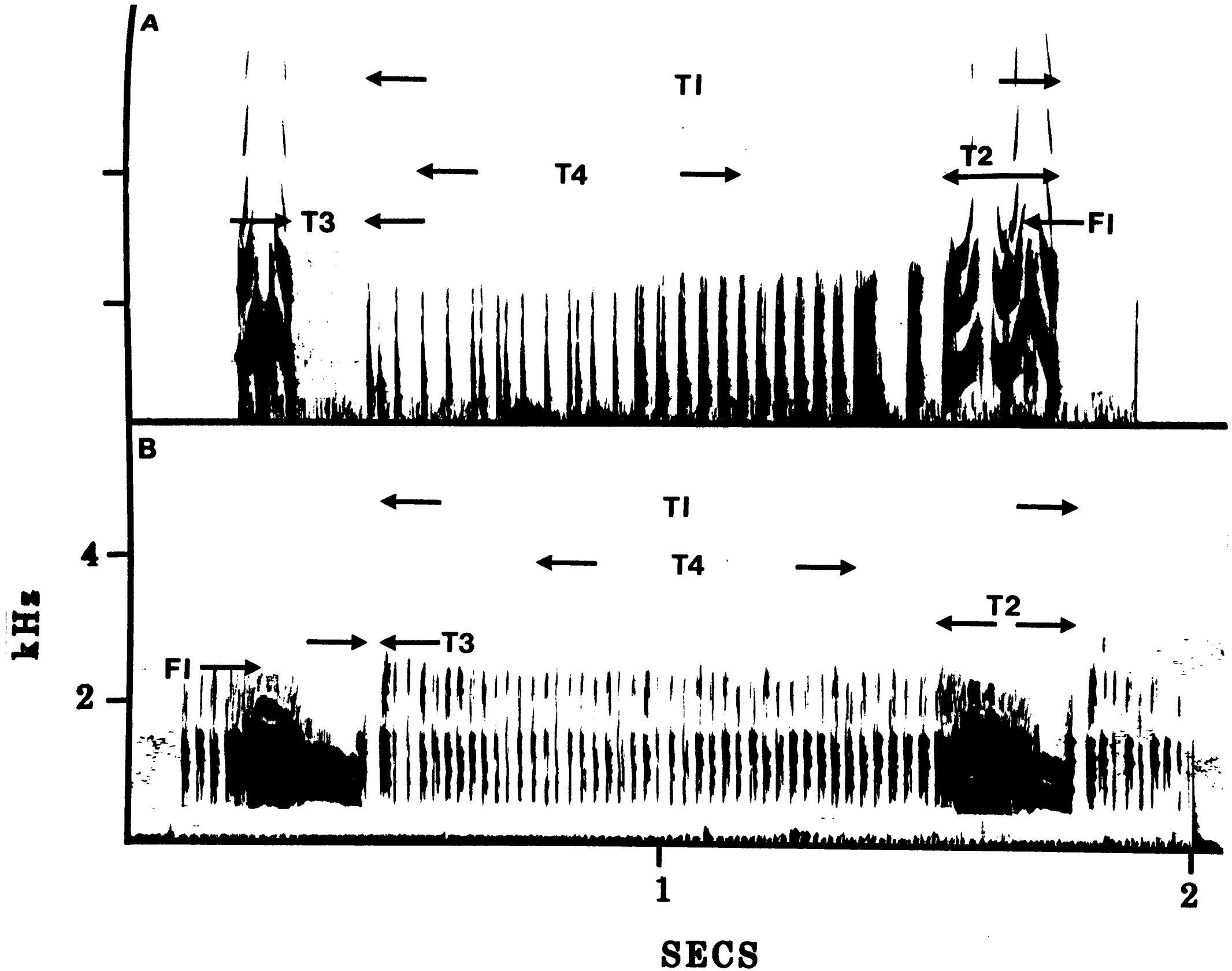

A
T1
T2
T4
T3
F1
B
T1
T4
T2
T3
F1
4
2
kHz
1
2
SECS

Table 5.2

Mean ± s.d.* body size and call variables of male Manx and Little Shearwaters

Variable	Manx	Little	F(ANOVA)	P
Tarsus (mm)	46.5 ± 0.9	36.8 ± 1.1	1398.5	< 0.001
Bill (mm)	35.5 ± 1.2	25.4 ± 0.9	1189.6	< 0.001
Wing (mm)	240.7 ± 4.0	171.2 ± 8.5	1823.7	< 0.001
Weight (g)	418.2 ± 34.8	160.1 ± 12.0	1218.6	< 0.001
T1 (sec)	1.4 ± 0.2	1.0 ± 0.1	117.1	< 0.001
T2 (sec)	0.4 ± 0.07	0.3 ± 0.06	28.1	< 0.001
T3 (sec)	0.03 ± 0.02	0.02 ± 0.01	5.1	< 0.05
T4 (sec)	0.1 ± 0.03	0.07 ± 0.03	15.1	< 0.001
F1 (kHz)	1.3 ± 0.1	2.1 ± 0.2	591.6	< 0.001
F2 (kHz)	1.2 ± 0.1	2.3 ± 0.2	891.3	< 0.001

* body size N = 36 Manx, 24 Little

call N = 72 Manx, 25 Little

Figure 5.15

Discriminant analyses of male Little (L) and Manx (M) Shearwater call and body size measures.

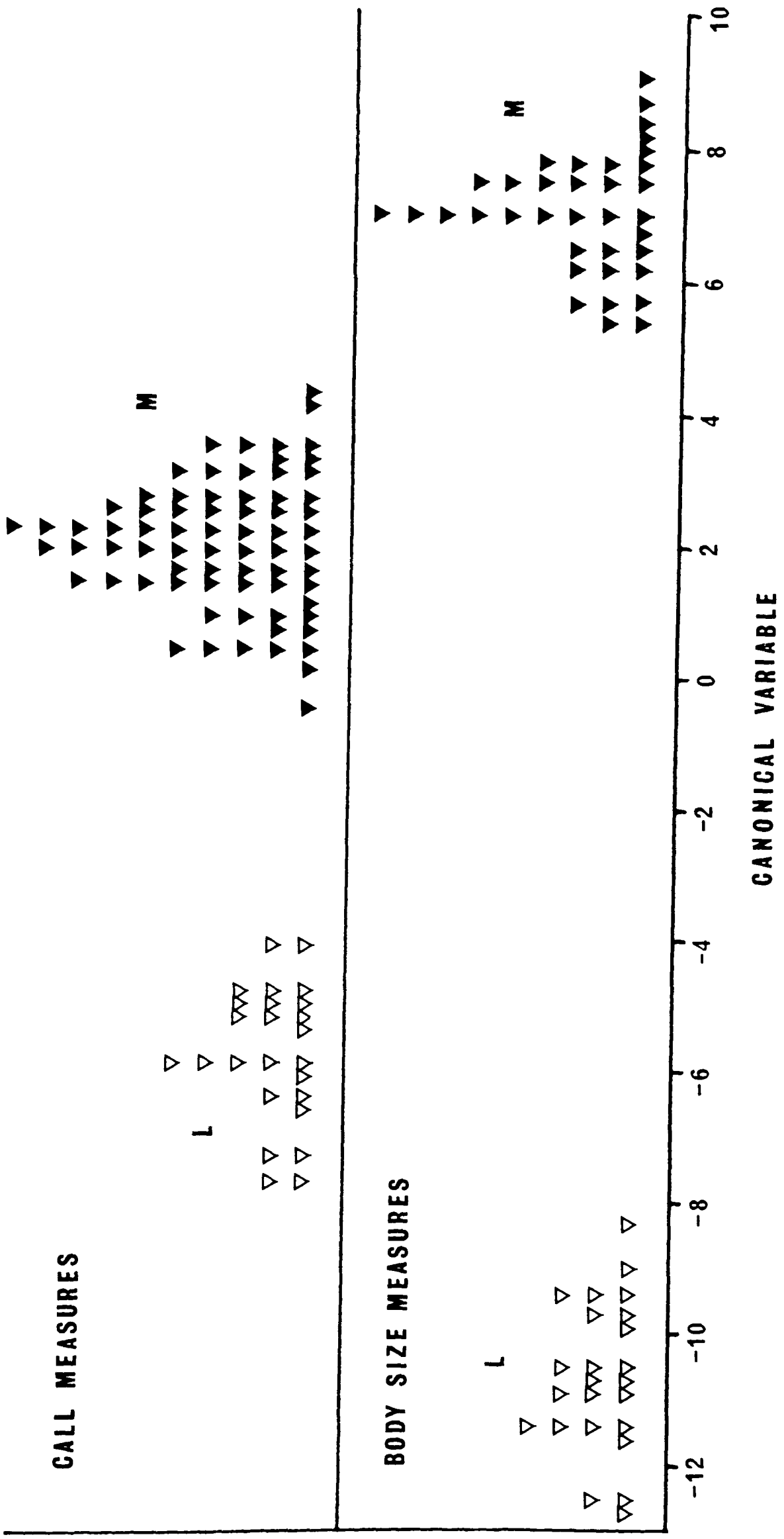

CALL MEASURES
BODY SIZE MEASURES
M
L
M
L
NUMBER OF CASES
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
CANONICAL VARIABLE

Table 5.3

Mean ± s.d.* body size and call variables

of male British and Madeiran Storm Petrels

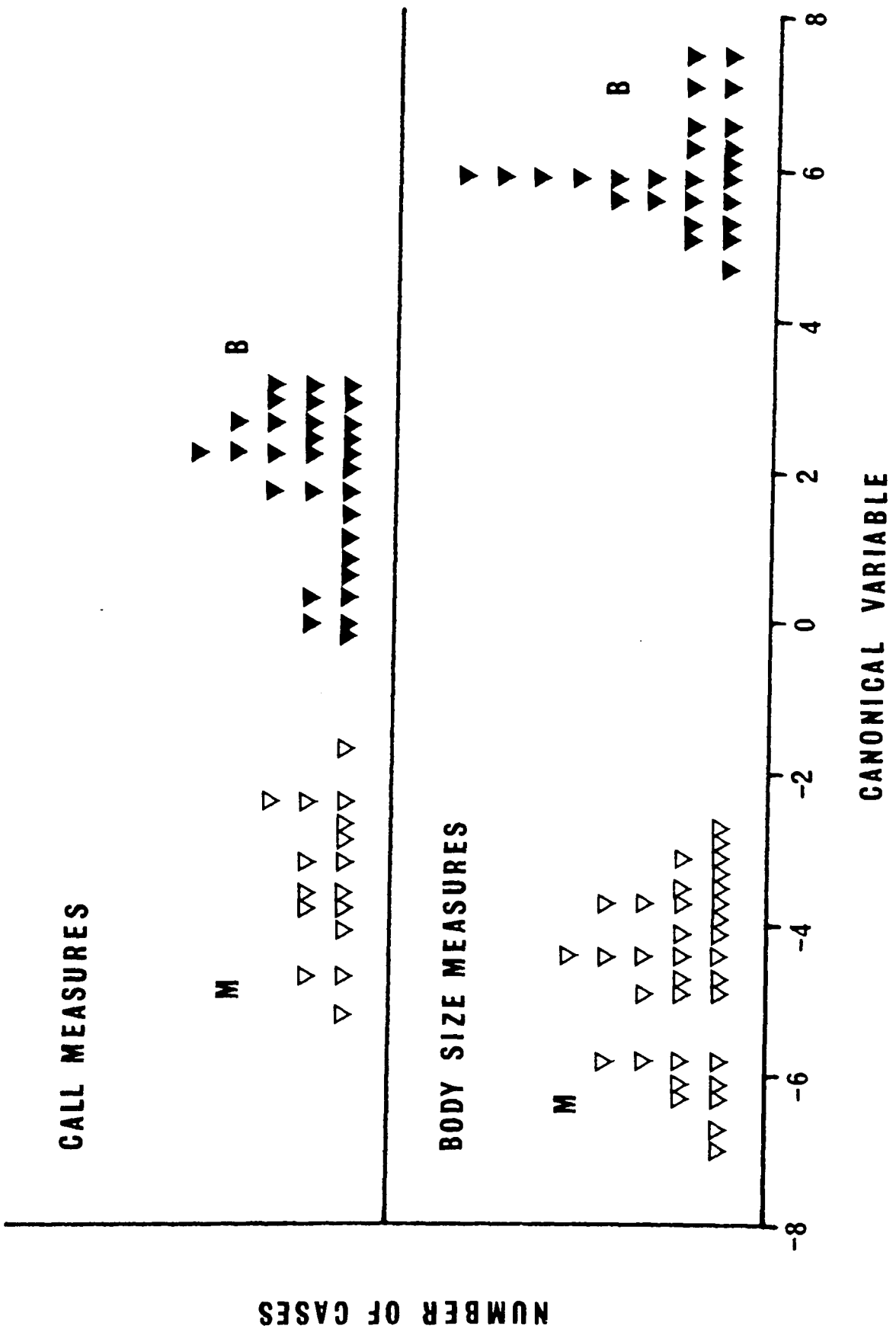
Variable	British	Madeiran	F(ANOVA)	P
Bill (mm)	12.0 ± 0.4	14.7 ± 0.7	343.1	< 0.001
Tarsus (mm)	22.6 ± 0.8	23.1 ± 0.7	5.5	< 0.05
Wing (mm)	120.4 ± 2.5	149.4 ± 4.0	1038.7	< 0.001
Tail (mm)	54.2 ± 1.6	65.8 ± 1.6	739.2	< 0.001
T1 (sec)	1.4 ± 0.2	1.8 ± 0.8	6.1	< 0.05
T2 (sec)	0.3 ± 0.05	0.4 ± 0.09	18.6	< 0.001
T3 (sec)	0.02 ± 0.02	0.5 ± 0.4	41.9	< 0.001
T4 (N/sec)	38.3 ± 4.4	22.3 ± 3.2	163.3	< 0.001
F1 (kHz)	2.2 ± 0.3	3.4 ± 0.3	144.5	< 0.001

* body size N = 26 British, 34 Madeiran

call N = 30 British, 16 Madeiran

Figure 5.16

Discriminant analyses of male Madeiran (M) and British (B) Storm Petrel call and body size measures.


CALL MEASURES
M
B
B
BODY SIZE MEASURES
M
NUMBER OF CASES
-8
-6
-4
-2
0
2
4
6
8
CANONICAL VARIABLE

& Pennoyer 1952, Bourne 1968, Sibley & Ahlquist 1972, Harper 1980) or newer biochemical ones (Sibley & Ahlquist 1972, Harper 1978, Barrowclough et al. 1981, Sibley & Ahlquist 1983).

Most comparisons concerning the calls of Procellariiformes have been insufficient (Hall-Craggs & Sellar 1976, Thibault & Holyoak 1978, Ainley 1980, Jehl 1982), with very few demonstrating the thorough analyses required (Sparling 1977, Sparling & Williams 1978).

The comparisons made here were somewhat artificial in that there are no systematic problems concerning the two species pairs examined. However, the analyses were undertaken in order to demonstrate that significant separations could be achieved using call variables between already-existing valid species. The separations so obtained were not as good as those obtained using morphological variables (Figures 5.15 and 5.16), yet this does not detract from this potentially useful approach, as the vocal separation was distinct enough. In the present examples, the interspecific variation in calls more or less parallelled that of morphology. However, in petrel taxa in which morphological characters are relatively conservative, studies of calls could be important in establishing species limits, as has been done for other groups (Selander 1971). It is also possible that hitherto undetected sibling species may be uncovered. An alternative approach to that of comparing calls directly might be to use call playbacks to test group or taxa discriminations (Lanyon 1969, Selander 1971, Nuechterlein 1981). However, this was not attempted in the present study.

It has been suggested that vocalizations have little value for discerning relationships above the generic level, because the very attributes of vocal characters that tell us most about avian relationships is their specific distinctiveness (Lanyon 1969). As far as petrel taxa are concerned, this seems a reasonable assertion. The presently-accepted familial groupings of the Procellariiformes are not in dispute (Harper

1978). It is the distinctions at generic level and downwards which need to be examined more closely.

The same author (Lanyon 1969) also concludes that vocal characters will not gain wide usage in avian systematics simply because they are not needed. Morphological characters are usually adequate in demonstrating specific limits. It was acknowledged, however, that in certain groups, vocal characters may permit discrimination between taxa. Among the non-passerines, these groups were indicated as those with birds whose courtship is performed under conditions of low light intensity or in habitats that restrict visibility. Systematic studies using voice have been performed on owls (Marshall 1978), and the nocturnal Procellariiformes would also seem to be good candidates for similar analyses.

CHAPTER SIX

The burrow homing behaviour of the Manx Shearwater

The burrow homing behaviour of the Manx Shearwater

Introduction

Many species of Procellariiformes locate their individual nest burrows at night, often in light intensities further reduced by cloud, and often out of many other such burrows. How they do so has been a matter of great speculation, but very little experimentation. Vision, audition, olfaction or some combination of these may function in guiding birds back to their burrows (Grubb 1974). Burrow location by visual means would rely on recognition of learned characteristics in the vicinity of the burrow. Burrow location by auditory means could be achieved either by incoming birds echolocating their way home, or by them homing to sounds emanating from the burrow. Olfactory homing would require the recognition of odours specific to one's own burrow or route taken back to the burrow.

Whatever sense or senses is employed, all three hypotheses predict different behaviours for shearwaters moving to their burrows. If following airborne odours, they should fly in, land and walk upwind to their burrows. If using visual or auditory cues, they should not be so directionally restricted. Navigation by auditory means would require vocalizations by the incoming bird and/or by its mate in the burrow. In order to evaluate these alternatives, the approaches of Manx Shearwaters to their nesting burrows were monitored on Skomer Island.

Observations on returning shearwaters

Methods

A small area (c. 7 x 7m) of a Manx Shearwater colony was selected with a good viewing position on a rock outcrop nearby. This position was

about 4 m above ground level and 10 m from the area under observation. All breeding burrows (15) in the area were fitted with an inspection cover and the pairs nesting in each burrow ringed.

The area was watched at night during the incubation periods in 1981 and 1982 with the aid of a Modulux 130 image intensifier fitted with a biocular viewing lens and a Nikon 50mm objective lens. All shearwaters returning to their burrows for incubation change-overs were watched, and the direction that they took on their final approach to the burrow was noted with respect to the wind direction, as determined with a small wind vane. The general direction that birds flew from just prior to landing was also noted. In addition, a note was kept of whether birds called just after landing or from within burrows prior to entry.

Results

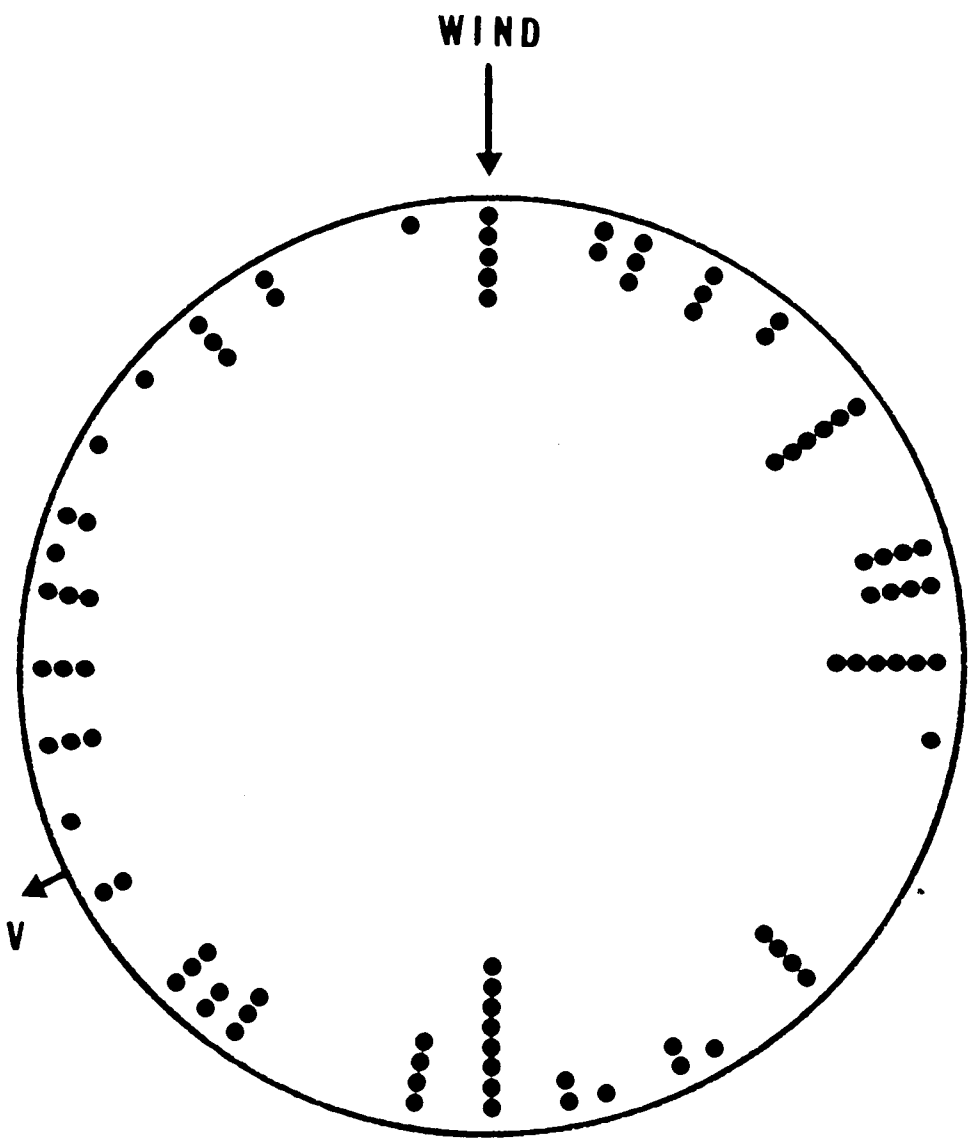
All shearwaters approaching the area to land did so into the wind. Once on the ground, they generally waited for a short period before setting off for their burrows. In going to their burrows, the distribution of their approach headings was not significantly different from random (Figure 6.1), indicating that they did not walk upwind. No birds called after landing, and no birds called from inside burrows prior to the partner's entry. Once inside, the re-united pairs always called together, and, after several minutes the incubating bird left the burrow and flew out to sea. Checks on burrows after such apparent change-overs confirmed that the partner had indeed returned home. Owing to the numbers of birds calling in flight, it was not possible to determine if individual birds returning to burrows called in flight before landing.

Discussion

The returning shearwaters did approach the nesting area into the wind,

Figure 6.1

Final approaches to nesting burrows with respect to wind direction for Manx Shearwaters. The mean vector (v) is (244°, 0.048), and the distribution of approaches is random: Z (Rayleigh's Test) = 0.205, N.S.


WIND
V

consistent with the idea that olfactory cues may be guiding them. However, the fact that these birds always land into the wind, whether on land or ocean, raises the possibility that this behaviour may just facilitate the mechanics of landing by increasing lift and thus reducing stalling speed. The habit of waiting for a short period before setting off to the burrow has been noted before in the Manx Shearwater (Lockley 1942) and other species (Warham 1960, Bartle 1968, Shallenberger 1973). It presumably may give the bird the chance to re-orient itself after touchdown. That the shearwaters did not walk upwind to their burrows (Figure 6.1) strongly suggests that olfactory cues are not important for locating burrows. Neither are pathway odourants likely to be used, as the same individuals used different approaches to their burrows on different nights.

Similar results have been obtained for the Wedge-tailed Shearwater (Shallenberger 1973), but significant upwind movements to burrows have been described for Leach's Storm Petrel (Grubb 1974). This latter species nests under a forest canopy, whereas the two shearwater species nest in open habitats. It is possible that under the lower illuminations of a forest, the storm petrel has evolved an olfactory guidance system.

The total lack of calls, both from incoming birds on the ground and from partners inside burrows also dismisses the use of auditory cues to facilitate homing in the Manx Shearwater. Similar conclusions have been made for other species (Warham 1955, 1958b, Grubb 1974). This is reasonable as there are many occasions when birds return to empty therefore silent burrows. Burrow homing using chick calls is not considered to be likely, as chicks normally sit quietly until the adult arrives in the nest chamber, and adults do not recognize their own chicks (Harris 1966a, Perrins et al. 1973).

Echolocation by vocalization of flying birds is also not considered to be occurring. The species of birds which do employ echolocation, the

swiftlets Aerodramus (Medway & Pye 1977) and Oilbird Steatornis (Griffin 1953) produce very brief pulses of audible sound of a frequency range different from that of the Manx Shearwater, whose call in no way resembles these other species. The possibility that ultrasonic frequencies (inaudible to humans) as used by bats (Chiroptera) exist in Manx Shearwater calls is also very unlikely. The echolocating swiftlets do not possess them (Cranbrook & Medway 1965) and neither do Leach's Storm Petrels (Grubb 1974).

Both olfactory and auditory hypotheses then fail to explain burrow location in the Manx Shearwater. The last possibility is that they can see well enough in the dark in order to find their burrows. Brooke (1978e) has already demonstrated experimentally that displacing a visually prominent cue impaired the ability of Manx Shearwaters to locate their own burrows. From this, it was suggested that vision may play a role in burrow location. The results presented here support this suggestion. That vision is an important homing mechanism has also been proposed for other species (Warham 1955, 1958b, 1960, 1964, Shallenberger 1973).

In his investigation of burrow homing in Leach's Storm Petrel, Grubb (1974) dismissed the importance of visual cues by reference to a limited investigation of the retinae of the Manx Shearwater and Fulmar Fulmarus glacialis (Lockie 1952). It is generally accepted that two main types of visual cells occur in most retinae, and that these cells, the cones and rods, are concerned with daylight and night vision respectively (Walls 1942). Lockie's (1952) data show that the Fulmar possesses a significantly higher density of cones in its retina overall than does the Manx Shearwater. There was no such difference between the two species with regard to their overall rod densities. However, the shearwater possesses almost double the ratio of total number of visual cells to that of ganglion nuclei compared with the Fulmar. A high ratio is considered to be an adaptation to a nocturnal

lifestyle (Lockie 1952). The similarity in rod densities between the diurnal Fulmar and Manx Shearwater may reflect the hitherto underestimated nocturnal activities of the former species (Moss 1965, Coulson & Horobin 1972, Dott 1975), particularly as Lockie's (1952) data show both seabirds with significantly more rods than the strongly diurnal House Sparrow Passer domesticus.

Lockie (1952) also states that no eyeshine was observed in any of the shearwaters handled at night by torchlight. This is clearly an oversight as Manx Shearwaters do possess a pale red or orange eyeshine, seen in many hundreds of individuals. In addition, a similar eyeshine was observed in the British Storm Petrel, Cory's Shearwater, Little Shearwater and Bulwer's Petrel, and it has been recorded in the Wedge-tailed Shearwater (Berger 1972). Its presence in birds is usually associated with nocturnal species (Van Rossem 1927).

In summary, Lockie's (1952) paper is incomplete evidence with which to dismiss the possibility that the Manx Shearwater and other related species have eyes sufficiently adapted for a nocturnal lifestyle (Grubb 1974, Wenzel 1980). Clearly, further investigation is needed on this point.

As a matter of interest, the rod and cone densities of the Manx Shearwater (Lockie 1952) were compared with those of humans (Østerberg 1935). Comparison between species is only valid if care is taken to define the retinal loci being sampled, as variation exists in rod and cone densities with retinal eccentricities (J.D. Pettigrew, pers. comm.). The human fovea corresponds to the avian area centralis. The range of cone densities (per $500u^2$) in the human fovea is 7-74 and of rod densities 5-45 (Østerberg 1935). The respective ranges for the Manx Shearwater area centralis are cones 24-28 and rods 11-13 (Lockie 1952). So as far as visual cell densities are concerned, the Manx Shearwater retina overlaps

that of the human retina. While other factors (f ratio, pecten size, eyeshine) may have to be taken into account (J.D. Pettigrew, pers. comm.), it appears as if shearwater visual acuity is comparable to our own, which is certainly adequate for getting about in the reduced light levels that they encounter. Even on the darkest nights, when the image intensifier was barely sufficient to watch them with, they never appeared to have difficulty locating their burrows.

Experiment on auditory homing

The previous observations suggest that auditory cues are not involved in the process by which Manx Shearwaters locate their burrows at night. However, would shearwaters use a vocal cue if offered one? Individual recognition by voice does exist (Brooke 1978d) so this option is potentially open to them. With this in mind, the following experiment was conducted.

Methods

The experiment was performed during the incubation periods in 1981 and 1982 using ringed birds sexed by cloacal inspection (Serventy 1956) or voice (Brooke 1978d). The average incubation stint of a Manx Shearwater is about six days (Harris 1966a). When the time approached for an incubation change-over in a pair, the following was performed. The incubating bird was stimulated to call by the playback of a Manx Shearwater call. Its vocal response was recorded onto a tape loop on a Uher 4000 Report IC tape recorder. The bird was then removed from the burrow and placed in a box some distance away. An artificial burrow was dug one metre from the burrow entrance with its entrance orientated in a similar fashion to the true burrow. The artificial burrow was made to look like the actual burrow as much as possible. At the far end of the artificial burrow, a loudspeaker was placed, and a simple walk-in trap put into the burrow. The recorded loop was played at a volume to match that of calls

heard naturally. Both burrows were checked until the returning bird arrived. The experiment was repeated 16 times for 8 males and 8 females.

To control for the possibility that birds were wary of artificial burrows, and hence would not enter them, ten such burrows with traps were dug into already existing nest sites. In all cases, the nesting pairs were caught, suggesting that the artificial burrows were acceptable to returning birds. In addition, to control for the possibility that the tape loops did not represent the calls accurately, the male loops were played back to all the females. Each female responded vocally to the playback of its mate's voice only, suggesting the recorded calls were representative. Female calls could not be similarly tested as male shearwaters respond vocally to both stranger and partner playback (Brooke 1978d).

Results and Discussion

In all 16 trials, the returning birds did not enter the loop burrows, but returned to their own burrows and began incubation. The result is highly significant for both males and females (Binomial Tests, $p = 0.004$), and suggests that visual and/or olfactory cues were overriding the obvious auditory cue. This supports the conclusion that auditory cues are not important for burrow location in Manx Shearwaters. The evolution of individual recognition by voice in this species (Brooke 1978d) has probably therefore been promoted by other factors, such as the re-establishment of pairs each season in a species with extended pair bonds, and the need for such individual recognition at incubation change-overs.

Experiments on olfactory homing

The previous observations suggest that Manx Shearwaters do not use olfactory cues for locating their burrows, as birds walking to burrows moved at random with respect to the wind direction. As a check, however,

two experiments were performed.

Burrow odourant experiment

Methods

The area used previously for night observations was again watched for four nights during the chick periods in 1981 and 1982 with the aid of the image intensifier. Returning birds were scored for the following:

(1) The time (sec) taken from landing to entering the burrow as measured with a stopwatch.

(2) The distance (m) between the point of landing and the burrow as estimated to the nearest 0.25m by reference to a standard distance.

(3) The number of times the returning shearwater stopped once it had left the point of landing.

(4) The number of times the returning shearwater changed direction after it had left the point of landing.

Household odour wicks were now placed into all of the burrows during the day when the birds were at sea. These were very odourous and easily replaced the usual burrow smell. The area was again watched for four nights, and the returning shearwaters scored again for the same measures. Once in the burrows, all shearwaters were checked in order to determine that they had entered the correct burrow.

Results and Discussion

There were no significant differences in any of the behavioural measures between shearwaters returning to burrows before and after the introduction of wicks (Table 6.1). Again, it was not likely that the shearwaters used odourant pathways as individuals used different approaches on different nights. With the lack of any auditory cues (the chicks

Table 6.1

The mean ± s.d. time (sec) taken from landing to burrow entry, distance (m) between landing and burrow, number of stops and direction changes made en route to the burrow for nesting shearwaters before and after the introduction of odour wicks.

	Before (N = 49)	After (N = 58)	t	P
Time	191.0 ± 216.8	212.8 ± 184.7	0.55	N.S.
Distance	1.3 ± 0.8	1.3 ± 0.9	0.24	N.S.
Stops	1.1 ± 1.3	1.3 ± 1.0	0.76	N.S.
Directions	1.2 ± 1.3	0.9 ± 1.0	1.02	N.S.

remained silent until fed) it is concluded that burrow odour cues are not important for the successful location of burrows.

Burrow displacement experiment

Methods

Ten plywood nest boxes were buried early in 1982 in places where previous nesting burrows had existed. Most of the boxes were adopted by the previous burrow owners and were subsequently nested in. In both 1982 and 1983, four pairs in boxes produced chicks. Each year, once the chicks were several weeks old, and the nest boxes had the characteristic smell associated with normal burrows, they were dug up and re-buried in similar orientations one metre away. In their place, simple walk-in traps were buried and made to look as much as possible like the original nest box burrows. That night and during subsequent nights, the traps and nest boxes were checked for shearwaters returning to feed chicks.

Results and Discussion

All 16 shearwaters arriving to feed chicks entered the traps and not their nest boxes one metre away. The result is highly significant (Binomial Test, $p = 0.00001$). Again, the result suggests that burrow odours are not important cues by which shearwaters locate their burrows. Coupled with the results of the burrow odourant experiment, it seems likely that vision is the most important sense employed by returning birds.

Experiment on visual homing

As the observations and experiments so far suggested that the use of vision was of primary importance in burrow location, the following experiment was performed.

Methods

During the chick period in 1983, the area described before was again watched at night with the image intensifier. The same behavioural measures as scored before were again taken for each shearwater arriving to feed its chick i.e.

(1) The time taken between landing and entering burrow.

(2) The distance between landing point and burrow.

(3) The number of stops en route to burrow.

(4) The number of direction changes en route to burrow.

During the day, the area was now altered visually. All plants (mostly Pteridium) above the turf were removed, and twelve rocks (approximately rugby ball size) were placed on the turf in a regularly-spaced fashion so that they covered the area. The area was again watched for the next three nights and the same behavioural parameters scored for incoming birds.

Results and Discussion

Two of the four behavioural parameters changed significantly following visual alteration of the area (Table 6.2), that of the number of stops and direction changes made en route to burrows. The shearwaters also took on average half a minute longer to reach their burrows following visual alteration. The result is consistent with the idea that they use visual cues to locate their burrows, as the presentation of novel visual cues slowed their burrow homing. While it may be argued that this does not constitute proof of visual homing, as birds may have just been wary of the changes, it does demonstrate that the shearwaters can see objects which could be potentially useful to them if using vision. The rocks used had no detectable odour and the shearwaters did not bump into them while moving about, suggesting that if they were wary, it was because they could see them.

If the shearwaters do use visual cues following landing, the result

Table 6.2

The mean ± s.d. time (sec)taken from landing to burrow entry, distance (m) between landing and burrow, number of stops and direction changes made en route to the burrow for nesting shearwaters before and after the visual alteration of the nesting area.

	Before (N = 24)	After (N = 23)	t	P
Time	228.9 ± 194.2	295.4 ± 247.8	0.47	N.S.
Distance	1.4 ± 1.1	1.6 ± 0.8	0.57	N.S.
Stops	1.0 ± 1.0	2.0 ± 1.7	2.65	< 0.05
Directions	0.7 ± 1.0	1.6 ± 1.6	2.21	< 0.05

suggests that at least some of the cues are within a short distance of the burrow, say within 5m. The result supports Brooke's (1978e) conclusion that displacement of a visually prominent cue impaired the ability of homing shearwaters.

General Discussion

The observations and experiments on Manx Shearwaters returning to their burrows indicate that visual cues are probably the most important in the burrow location process. A similar conclusion was reached following a series of observations and experiments on the Wedge-tailed Shearwater (Shallenberger 1973). In the only other detailed study, Grubb (1974) concluded that olfactory cues were the most important for Leach's Storm Petrel. Mention has already been made of the possible divergence of homing mechanisms under different illuminations. Yet despite being quoted as such (Brooke 1978e, Wenzel 1980), Grubb (1974) did not demonstrate olfactory navigation to individual burrows, or a discrimination between different burrow odours, a prerequisite for successful homing. He demonstrated an upwind movement of returning birds, the ability to discriminate nest material from control material, and the failure of surgically-operated birds to return home with their olfactory nerves severed. All of this points to a developed sense of smell, but not necessarily to its use in burrow homing.

That the Procellariiformes possess a useful sense of smell is almost beyond doubt (Wenzel 1980). The anatomical, physiological and behavioural observations support its existence. Yet the evidence to date indicates that such facility is concerned mainly with food-finding at sea (Grubb 1972, Jouventin 1977, Hutchison & Wenzel 1980). No conclusive evidence exists as yet to demonstrate burrow homing by olfactory means. The only positive evidence for any of the senses potentially used for burrow homing is

Brooke's (1978e) work showing the importance of vision to Manx Shearwaters. Clearly, further research is necessary to determine the type and extent of sensory usage by homing Procellariiformes. In a review of the echolocatory ability of swiftlets, Medway & Pye (1977) showed that closely-related species differed in such ability, according to whether or not the species used the total darkness of cave interiors for nesting and roosting. Similar divergence may have evolved in the homing methods of nocturnal Procellariiformes, which nest in a variety of habitats and latitudes, and consquently in a range of nocturnal illuminations.

CHAPTER SEVEN

Concluding Remarks

Concluding Remarks

I would like to think that the research presented in the previous chapters has gone some way in answering questions concerning the diversity, adaptive value and evolution of calling behaviour in the nocturnal Procellariiformes. Despite this, the opportunities for further research are virtually limitless.

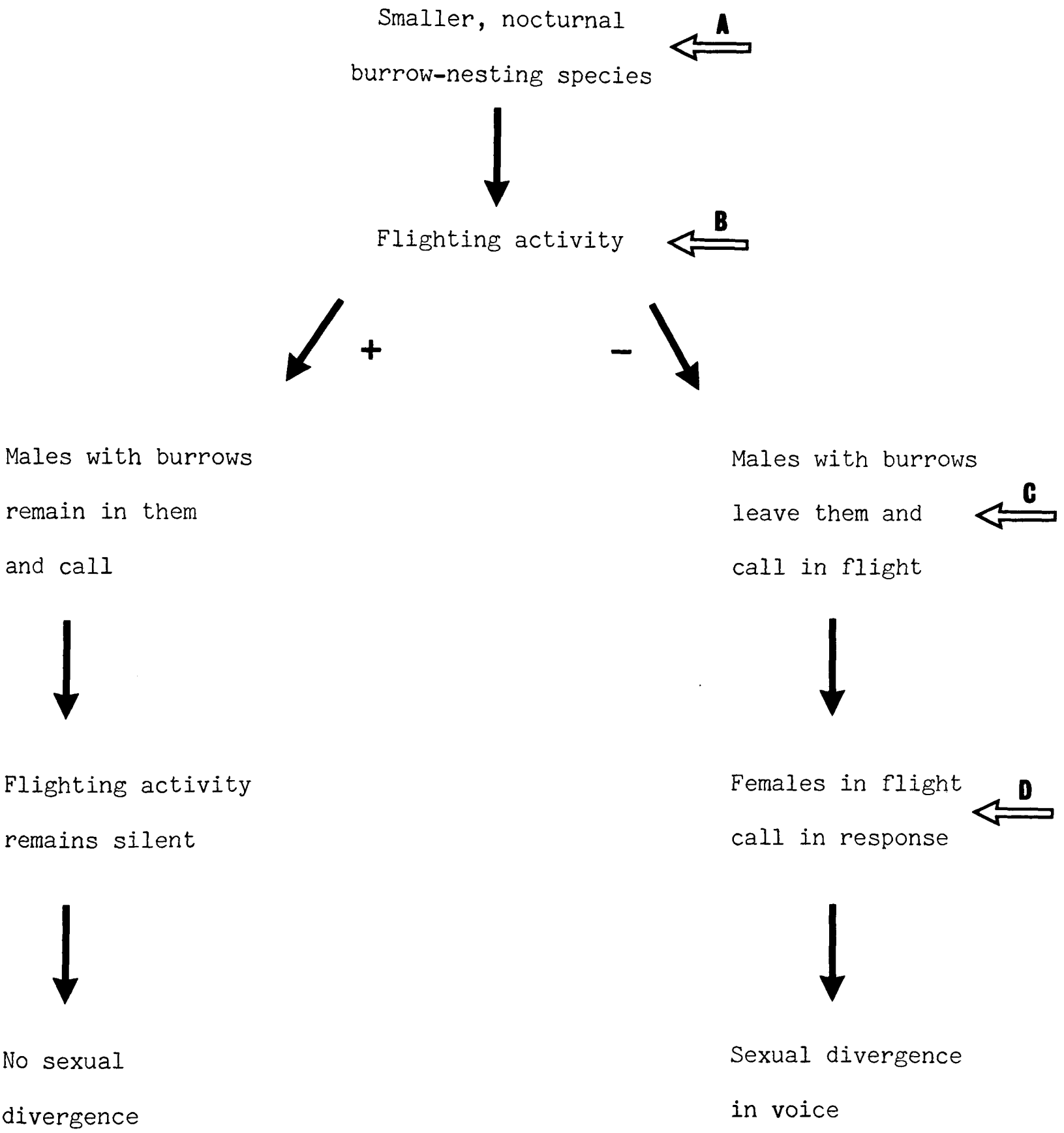
I demonstrated that immature, rather than adult Manx Shearwaters are responsible for the majority of calling heard at the breeding colony, both at ground level and in flight. This may well apply to the other nocturnal Procellariiformes and in addition those species that are nocturnal in other seabird groups, such as the penguins and auks (Nelson 1980). However, further research is clearly needed to confirm this suggestion. The fact that calling at ground level serves as both a sexual and a territorial signal was also shown in the Manx Shearwater, and again, this may well be true in other species. The possibility that aerial calling also has a dual function is perhaps less convincing. The idea that territorial defence extends into the airspace above the burrow is difficult to reconcile.

A proportion of immature male shearwaters were found to be relatively silent in their flighting activity. At first, this seemed to be an unexpected result, but when one considers that in species without aerial calling, males participate in the flighting activity (British Storm Petrels, Chapter 3), it is perhaps less surprising. Why then do some species call in flight, and others not? The ideas generated from this research on several species are tentatively summarized as a model, shown in Figure 7.1.

To begin with, the evolution of morphological adaptations to the marine environment has resulted in these birds being very awkward on land. If the diurnal and nocturnal Procellariiformes are compared, it is apparent that, in general, the diurnal forms are large surface-nesters, and the nocturnal forms are smaller and burrow-nesting. The nesting behaviour of the latter

Figure 7.1

Hypothetical model to describe the evolution of calling behaviour in the nocturnal Procellariiformes. Open arrows indicate selection pressures due to (A) Morphology (B) Burrow Competition, + = intense, - = less intense (C) Signalling (D) Pairing. See text for full description and discussion.


Smaller, nocturnal
burrow-nesting species
A
Flighting activity
B
+
−
Males with burrows
remain in them
and call
Flighting activity
remains silent
No sexual
divergence
Males with burrows
leave them and
call in flight
C
Females in flight
call in response
D
Sexual divergence
in voice

has presumably resulted through the selection pressures of avian predators acting on smaller forms at the breeding colonies. To overcome the problem of poor terrestrial locomotion when it was time to prospect for nest-sites or for mates, selection favoured the flighting activity of immatures over breeding colonies. Although such a behaviour is an energetically demanding activity, the benefits in terms of areas covered are very great and flying birds may further benefit from a reduced risk of predation. I have suggested that for some species, burrow competition among immatures was relatively relaxed when compared with other species. I further suggested (Chapter 3) tentatively that such competition could be mediated through microhabitat selection, where rock substrates resulted in more intense competition for burrows than in soil substrates. The net effect of relaxed burrow competition was that the immature males who had acquired burrows (and only males do so) could leave them for short periods and call in flight to attract females, with a reduced risk of losing the burrows to other males. They could also return to their burrows, and call from there. The selective advantages of aerial calling over burrow calling are reduced sound attenuation (Marten & Marler 1977), allowing signals to travel further, and a moving signaller, again allowing signals to be transmitted over a wider area. However, with males now calling in flight, selection favoured females who responded to them. By doing so, they indicated to calling males that a potential mate was available. The males could now return to ground level and guide the females down to their burrows. That females in flight respond to males in flight was demonstrated in playback experiments (Chapter 2). However, with both males and females calling in flight, selection now favoured vocal divergence between the sexes, as it was in the interest of both sexes to know which sex was calling. The voice of the Wedge-tailed Shearwater, which does not call in flight or show vocal dimorphism, is more similar to the calls of other male shearwater species than to the calls of

the females (Shallenberger 1973) suggesting that selection has acted on the female calls of species with aerial calling in order to promote the divergence.

The model, although hypothetical, does at least lead to several testable predictions:

(1) All nocturnal Procellariiformes should indulge in flighting activity, silent or otherwise. Such appears to be the case.

(2) Burrow competition should be more intense in species without aerial calls than in species with them. Burrow competition *per se* would be difficult to quantify, but various indirect measures can be used, such as fighting, interference, the presence of two-egg clutches (it is generally agreed that these species cannot lay two eggs in the same season) indicating that two females are competing for the burrow and the relative size of males to females (increased competition might promote larger males). During the course of the present study, the level of two-egg 'clutches' was determined for four species, including one (Bulwer's Petrel) without flight calls. For each species, the proportion of nests with two eggs (with sample size) were Bulwer's Petrel (51) 9.8%, Cory's Shearwater (52) 0.0%, Manx Shearwater (100) 1.0% and Madeiran Storm Petrel (32) 0.0%. Although the data are limited, they do tentatively support the hypothesis that burrow competition is more intense in species without flight calls.

(3) The calls of species with aerial calling should attenuate less above ground level than from below it. This would confirm the work of Marten & Marler (1977).

(4) In species with aerial calling, immature males should leave their burrows and call in flight. The research on the Manx Shearwater showed that this did happen.

(5) In species without aerial calling, immature males with burrows should remain in them and only call from there. As with the Manx Shearwater, this could be investigated using luminescent lights.

(6) The proportion of males engaged in flighting activity should be higher in species with aerial calling than in those without, because males with burrows could leave them and call in flight. The mistnetting and sexing of birds caught would allow this to be tested.

(7) In species with aerial calling, male and female calling intensities in flight should be correlated both in time and space, since flying females should respond to males calling in flight. This was the case for the Manx Shearwater for timing (Chapter 2); spacing was too difficult to quantify, but seemed to be true.

(8) Sexual dimorphism in flight calls should exist in species with aerial calling. I know of only one exception to this relationship, that of the Fork-tailed Storm Petrel (Simons 1981). The vocal dimorphism is expressed as a call common to males only. However, as with other Oceanodroma up until this point, it is possible that dimorphism within flight calls has been overlooked.

(9) No such vocal dimorphism should exist in species without aerial calling. Again, there is only one exception, the British Storm Petrel, where males uniquely possess a call (James 1984). It is possible that the males of some species without aerial calls have evolved distinct calls in order to overcome the problem of sound transmission through nesting substrates. If this is so, the model will have to be modified.

That macrogeographical differences in the calls of the Manx Shearwater and British Storm Petrel were more pronounced than microgeographical differences is perhaps not surprising, particularly if the origin of such differences is determined by things such as relative isolation. That the

differences were not greater probably means that no selective forces have operated to diverge calls further than that caused by vocal 'drift', (i.e. an essentially random process). Clearly, much more work could be performed in this area in parallel with that carried out on song birds, particularly in connection with the use of calls in petrel systematics. That calls could be used as such was demonstrated, and their application may go some way in resolving long-standing taxonomic problems.

The reader may be asking at this stage whether the investment involved in sending people off to remote islands to study petrel vocalizations would be justified? The simple answer is no. However, these places are visited for other reasons, and the collecting of sound recordings could be performed by people primarily engaged in other work. It is not necessary to engage experts in bird vocalizations to produce useful collections of tape recordings, and neither is it necessary to use expensive equipment. The burrow-nesting species usually respond strongly to playback, and are therefore easy to record. However, the sexing of birds would be almost a necessity, requiring some ornithological skill. The problem of wind noise is overcome by placing microphones into burrow entrances, resulting in first class recordings. The recording of birds calling in flight is of limited value owing to the Doppler Shift of call frequencies. Of course, some people have already started this process. Swales (1965) not only stands as an inspiring piece of fieldwork, but he also had the imagination to make tape recordings too, the quality of which is impressive, even by today's standards. However, these contributions allow only the simplest comparisons to be made. The sound libraries of the world are filled with single recordings of one species, when, with a little extra work to collect 20 or so individuals, they could be transformed into important data depositories in much the same way skin collections have been. Of course, sound libraries too have to be prepared to accept more than one recording of a species from

the same locality.

In conclusion, much remains to be done. It is the author's hope that the present research will provide some impetus to other people elsewhere, so that petrel vocalizations can take their rightful place in relation to central issues concerning marine ornithologists.

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APPENDIX A

The use of playback recordings to detect and census nocturnal burrowing seabirds

The Use of Playback Recordings to Detect and Census Nocturnal Burrowing Seabirds

Introduction

The nocturnal, burrow-nesting seabirds, of which examples are found in the Spheniscidae, Procellariidae, Hydrobatidae, Pelecanoididae and Alcidae are notoriously difficult to census (Cramp et al. 1974). Indeed, small colonies may easily be overlooked. Previous attempts to census these species have employed one of three basic techniques: direct burrow counts (Lockley 1930, Van Gessel 1978), direct burrow counts with an estimate of occupancy (Nettleship 1976, Wormell 1976, Harris & Bode 1981, Hunter et al. 1982, Warham & Wilson 1982) and mark-release-recapture (Harris 1966a, Perrins 1967, Corkhill 1973, Alexander & Perrins 1980).

The main problem in estimating population sizes by direct burrow counts lies in the difficulty of relating the number of burrow entrances to the number of breeding pairs present. Occupancy estimates can be made indirectly, by using characteristics such as flattened soil and vegetation, droppings, feathers and odour at the burrow entrance, or disturbance of barricades at the burrow entrance; or directly by reaching into, or opening, a sample of burrows to record chicks or eggs. Mark-release-recapture involves extensive ringing of near-fledged chicks in burrows, and their subsequent recapture on the surface. By applying the Lincoln Index and knowing breeding success, a calculation of population size can be made. Although some of the methods produce satisfactory results, they can involve disturbance to nesting birds and also involve considerable time and effort. A technique is presented here which as well as enabling a census of colonies to be made, gives workers a valuable tool for the rapid detection of breeding birds in small colonies, rock screes, and multi-species communities.

Methods

The proposed technique involves the use of a playback recording of a species' call in order to elicit responses from incubating individuals of the same species, therefore enabling counts of breeders to be made within a sample quadrat or from a small colony. The general use of playback recordings as an avian censusing technique has been advocated by Johnson et al. (1981), but in their discussion they do not consider nocturnal seabirds. Some workers have used this technique to establish the presence of birds in burrows (Hunter et al. 1982), but this has not been done quantitatively.

The best period for the census is just following the completion of egg-laying. In addition, if the census is conducted during the day, few prospecting immatures will be present in the burrows. At census time, it is necessary to know the approximate sex ratio of birds present, and the proportions of each sex that respond vocally to the playback of a call. These two factors will have the most influence on the number of responses produced to the playback of that particular call.

If we call the proportion of males present M, and the proportion of females F, i.e. $M + F = 1$, and if we call the probability that a male, or a female will respond to playback x, or y respectively, then the correction factor, C, needed to calculate the number of breeding pairs from the number of responses heard is given by: $C = 1/(M(x) + F(y))$. This correction factor makes allowance for the birds present underground which do not respond to playback.

The sex ratio present may differ from 1:1 because in species where egg-laying is synchronous, the sex ratio of birds underground will tend to alternate between mostly male and mostly female. In addition, if one sex has longer incubation stints, this will also tend to skew the sex ratio.

In order to evaluate the technique in the field, a census trial was

carried out of Manx Shearwaters using playback, and compared with the burrow count with occupancy estimate method. The work was performed on 9 and 10 June 1983 on Skomer Island. All burrows were counted in two quadrats (25 x 50 m and 6 x 7 m), and occupancy estimates were derived by opening 20% of the burrows in each. These quadrats were selected to give very different breeding densities. The playback technique was then used by playing male calls of the Manx Shearwater within 0.3 m of each burrow entrance for several seconds, using a Sony M9 microcassette recorder at full volume. The total number of responses was noted for each quadrat. The correction factor was calculated as:

$C = 1/ (0.55(0.92) + 0.45(0.00)) = 1.98$, where the sex ratio was generated from incubation stints in Brooke (1978a) and the probability of response to a male call from Brooke (1978d). A different correction factor would have to be calculated if female calls had been used instead, as the frequency of responses is different (Brooke 1978d). The possible effect of laying synchrony on sex ratio was considered unimportant as this species lays over a period of about one month (Brooke 1978a, Harris 1966a).

Results

In the larger quadrat (total 153 burrows), 53% were occupied by an incubating adult, leading to an estimate of 81 pairs. In the smaller quadrat (40 burrows) 62% were occupied leading to an estimate of 25 pairs. The total time required to complete the census for both quadrats was 180 minutes.

Using playback, 35 responses were heard in the larger quadrat and 11 in the smaller. Applying the correction factor (1.98) gave estimates of 69 pairs, and 22 pairs respectively. The total time taken was 35 minutes. The estimates are within 15% of one another, but playback took only 19% of the time.

Discussion

Clearly, the playback technique's main potential is its saving of time in producing comparable estimates of the population size of burrow-nesting seabirds. It is obvious that as yet the information required to use this method is not available for many of these species. However, the aim of this note is to highlight its potential value. As the vocal behaviour of more species is understood, the method will become generally applicable. The technique as described produces absolute population estimates. If the information is not available to calculate a correction factor, responses to playback may still be used as a relative population estimate. In addition, it is possible to empirically generate a correction factor on the spot by opening a sample of burrows where no response occurs.

Two sources of potential error (apart from the estimates used in producing the correction factor) should be borne in mind. These are unattended eggs (either deserted, or briefly left between incubation shifts), and eggs attended by both adults. From experience neither of these is likely to be numerically significant. Whether the correction factor calculated here will suffice for all Manx Shearwater colonies is not known. However, the probability of Manx Shearwaters responding to pl yback on Skomer, Skokholm, Rhum and Puffin Island show no obvious quantitative differences, and the sex ratios of incubating birds handled was similar. Amongst seabirds, it appears that the incubation stint of the male is generally slightly longer than of the female and so a figure of M = 0.55 may suffice in many cases.

The role of the playback technique in establishing if breeding is occurring at all is also very important as this method allows rapid location of occupied nest sites. This is particularly useful if, as often happens, a limited amount of time is available to workers landed on islands. Fowler & Butler (1982) have recently used call playback to prove breeding

in a newly-discovered colony of Leach's Storm Petrel.

The use of this technique for censusing scree- or wall-nesting species, and multi-species communities is particularly attractive. In these cases, it is often difficult to decide what constitutes a nest entrance of the particular study species, and so the usual censusing methods are not easy to apply. From studies in these situations on Skomer and Great Salvage Islands, it has been found that using the playback technique with the relevant calls overcomes this problem, and this could enable badly-needed counts of these species to be carried out with a considerable saving of time and without disturbance to nesting birds.

APPENDIX B

The number of British Storm Petrels on Skomer Island

The number of British Storm Petrels on Skomer Island

History and Introduction

The Storm Petrel colony on Skomer Island was first mentioned by Mathew (1894) who noted 'nests in the chinks of an old wall on the top of the cliff'. Drane (1898), who made a substantial visit described the species as 'numerous' and 'abundant' on the island. However, half a century later, Buxton & Lockley (1950) stated that the species was 'scarce' and only managed to locate about 30 nest sites. The first attempt at any sort of a census was that of Scott (1970) who mist-netted birds, and using a mark-release-recapture calculation, estimated the breeding population at between 500 and 1000 pairs. Based on this, 'Operation Seafarer' classified the colony as Order 3 (100-999 pairs) (Cramp et al. 1974). During 1981 and 1982, a thorough survey was carried out of the island's Storm Petrel colonies, and what seems to be a major decline was detected.

Methods

Suitable Storm Petrel breeding habitat (rockfalls, walls, boulder slopes etc.) was slowly and systematically traversed during the day and a tape recording of a bird giving the purr-call was played aloud. Birds which were present in the burrows responded to this by giving the second call "terr-chick" and thus could be detected. Research had shown that males always responded to this call, but that only half the females did so (James 1984). For this reason, and the fact that the species has a protracted laying period, it was necessary to visit each colony several times. The census was carried out during the egg-laying period to avoid the bias of prospecting immatures occupying burrows, as these birds do not arrive until after egg-laying is completed. Nest sites were marked with a small cane to avoid confusion. Nests were sometimes also detected by

their characteristic musky odour, but occupation was always confirmed by voice. The census was repeated over two years (1981-82) so pairs which may have missed a breeding season were detected the following year. The majority of breeders found in 1981 were again found in 1982, suggesting the method was reliable.

Results and Discussion

Table 1 shows the distribution and total of Storm Petrel nests found. These values have been rounded up to the nearest 5 to allow for odd nests missed. Also in Table 1 is Scott's (1970) estimates for three areas on the island: Mew Stone, Wick Basin and Tom's House (including Amos). Scott (1970) also performed his survey early in the breeding season so there is little effect of immatures, although his figure is likely to be an over-estimate, especially if a lure was used.

The total breeding population of Skomer was estimated to be about 100 pairs, considerably fewer than Scott's (1970) estimate of perhaps 1000 pairs. No petrels were found breeding in walls, and other suitable places were completely devoid of petrels, such as the very large rockfall area between Littlewill Bench and the Spit.

Although it is difficult to compare Scott's (1970) results with the present result, owing to the different methods involved, it does seem as if a decline has occurred. For example, differences between the two counts were not uniform. The Mew Stone has 80.0% of Scott's estimate, but Tom's House and Amos has only 9.5% of his figure. If the two methods were producing different results, then the difference should be more or less consistent. As they are not, it suggests the two surveys are comparable to some extent.

What has caused the decline? Assuming that factors such as winter mortality and fecundity have not altered, it is likely that mortality at the colony is excessive. Species that are known predators of Storm Petrels

Appendix B, Table 1

Number of Pairs of Storm Petrels

on Skomer in 1981-82 and 1969

Place	81/82	Scott (1970)
N. Haven	5	?
Mew Stone	40	50
Wick Basin	10	50
Basin	10	?
Tom's House (inc. Amos)	20	210
Spit	10	?
Table	5	?
Total	100	500-1000

that are present on Skomer are the Larus gulls, particularly Larus marinus, the Short-eared Owl Asio flammeus and the Little Owl Athene noctua. The Greater Black-backed Gull has been controlled on Skomer for a number of years now, and several nests visited had no evidence of Storm Petrel predation. The Short-eared Owls by virtue of their protected status may be excused taking odd petrels, although they were never observed near the petrel colonies. On Skomer, they appear to feed mainly on rodents. The Little Owl however, is a well-documented, efficient predator of Storm Petrels (Lockley 1934, 1938, Hibbert-Ware 1938a and b, Cowdy 1963). During 1982, the following evidence of Little Owl predation on Skomer Storm Petrels was obtained:

(1) Direct observations (with an image intensifier) of a Little Owl hawking petrels at the Mew Stone. An owl was present there on most nights the observer was.

(2) On one occasion, a Little Owl homed in on the tape recorder which at the time was playing the purr-call aloud. It was clearly attracted to the vocalization, and only swerved off when a few feet away.

(3) Collection of feather piles and pellets in 1982. A total of 16 piles of feathers were found distributed as follows: Mew Stone 7, Basin 4, Wick Basin 2, Table 1, Payne's Ledge 2. About half of these were found in June, indicating that breeders were being taken too. Several pellets were found with petrel remains in them. No systematic search was carried out to find pellets or feather piles, so these represent minimum figures.

It is probable that the Storm Petrel colony on Skomer has declined drastically since the turn of the century. A visitor to the island now would be lucky to see one at all, in contrast to Robert Drane's time. This decline has been described before (Lockley 1938), but not heeded. The

present survey shows a total population of only 100 pairs, and this is apparently suffering excessive predation pressure. While only 16 feather piles were found, this almost accounts for the year's annual recruitment to the breeding population (20 birds) if a 10% mortality is assumed (Scott 1970). As this represents a minimum estimate, the population is probably still declining, particularly if other predators are taking petrels. All available evidence points to the Little Owl's depredations as being responsible. In Robert Drane's time, the island held both Larus marinus and Asio flammeus and the petrels were abundant. The Little Owl probably became established on Skomer and Skokholm during the mid-1920's (Buxton & Lockley 1950) and petrels were scarce by 1940. Its destruction of Storm Petrels on Skokholm (Lockley 1934) led to its complete removal in 1954 (Scott 1970). The question that must be asked is why it was allowed to remain on Skomer for so long?

Recommendations

(1) The complete removal of Little Owls and subsequent management of further immigration.

(2) A standard census of Storm Petrels to be performed at regular intervals to monitor future changes. A mark-release-recapture method would allow a comparison with Scott (1970), but the method described here could also be repeated.

APPENDIX C

Madeiran Little Shearwater prospecting on Skomer Island

Madeiran Little Shearwater prospecting on Skomer Island

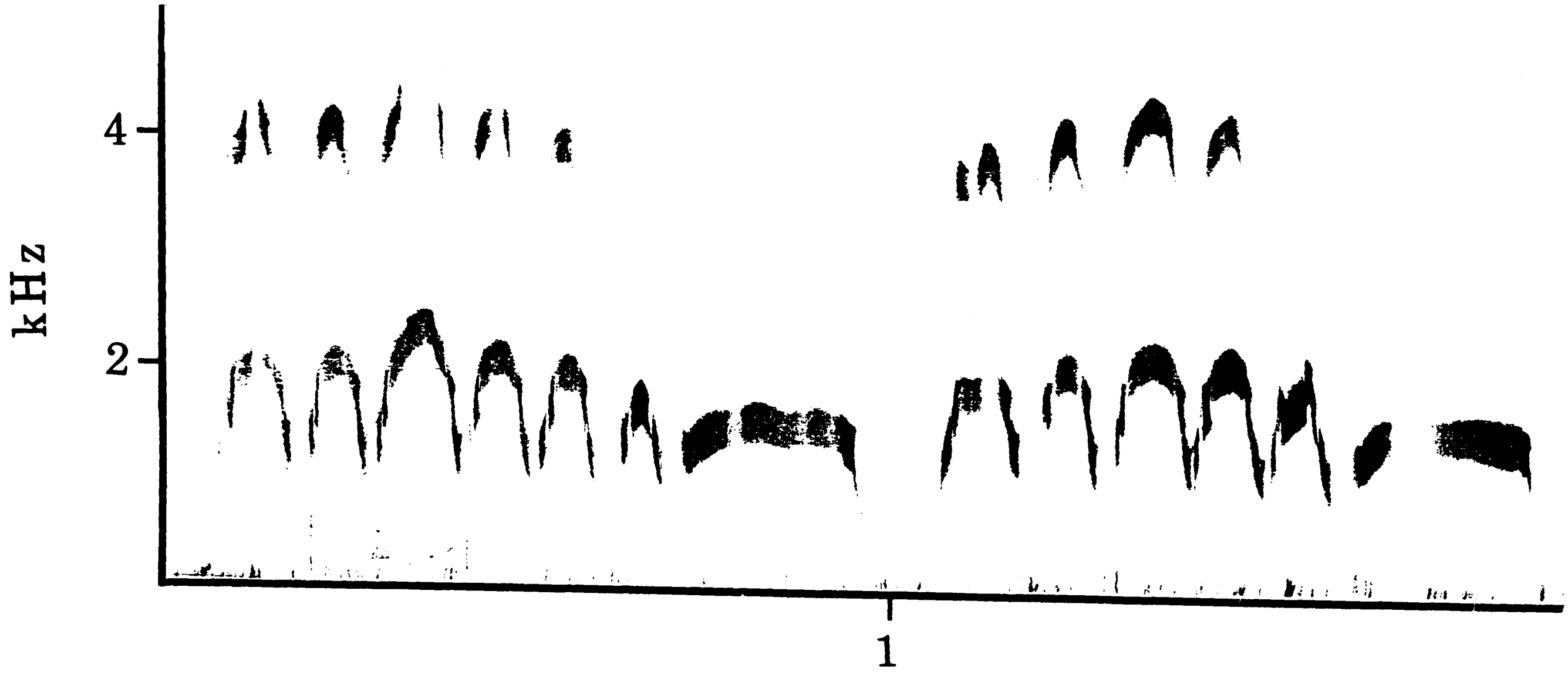
On June 29, 1981 a small shearwater was captured ashore at the large Manx Shearwater colony of Skomer Island. It had first been noticed in a burrow on June 26 from its calling, distinct from that of the surrounding Manx Shearwaters. The bird was measured, ringed, photographed, tape-recorded (Figure 1) and a full field description taken. It was clearly a Madeiran Little Shearwater Puffinus assimilis baroli owing to its small size, blue legs and feet, and white underwing and undertail coverts (Cramp & Simmons 1977). Some measurements are: wing 175 mm; tail 67 mm; bill length 25.2 mm and tarsus 36.5 mm.

The bird remained at the island, visiting on most dark nights throughout July, but it did not reappear during or following the August new moon. Its behaviour at the colony was similar to that of the prospecting immature Manx Shearwaters on the island. It arrived each night with them, first calling in flight, and then from its burrow located under large boulders, habitat also chosen at its known breeding colonies (Cramp & Simmons 1977). It would periodically leave the burrow and call in flight for several minutes at a time, when its rather rapid wing beats were clearly visible. The bird responded strongly to the playback of its own voice, both in flight and in the burrow. Inspection of the burrow revealed that some nesting material had been brought in. Similar habitat on the remainder of the island was searched but no others found.

The same individual returned to Skomer in 1982, being first noted on June 21. It had moved to another burrow some 5 m away, again under some rocks. As before, it attended the colony on most nights during the new moon period in July, and did not reappear in August. The bird did not return in 1983, although a second individual with a different voice was heard calling in flight in another location on May 3.

Appendix C, Figure 1

Sonagram of call of male
Little Shearwater prospecting
on Skomer Island in 1981 and 1982.


4
2
kHz
1
SECS

Subsequent research (Chapter 3) on Great Salvage Island has shown that, like the Manx Shearwater (Brooke 1978d), this species is sexually dimorphic in voice. It was thus established that the bird prospecting on Skomer was a male, and that the second individual heard in flight on May 3 was a female.

The nearest known breeding place of the Little Shearwater is in the Azores (Cramp & Simmons 1977). In spite of the short distance, the species is recorded rarely though regularly in British waters (Sharrock & Sharrock 1976). The seasonal timing of the visits to Skomer coincided with the post-breeding arrival of Little Shearwaters at their colonies in the North Atlantic (Jouanin 1964), when most birds are moulting. However, no moult was observed on the Skomer bird. It is possible of course that Little Shearwaters are prospecting elsewhere, and workers at seabird colonies in northwestern Europe should be alert to this possibility.

APPENDIX D

First record of Swinhoe's Storm Petrel in the Atlantic Ocean

First record of Swinhoe's Storm Petrel in the Atlantic Ocean

On 29 June 1983, while conducting research on the vocalizations of the petrels and shearwaters breeding on Great Salvage Island the calls of a storm petrel were heard that were very different from those of the two resident species Oceanodroma castro and Pelagodroma marina.

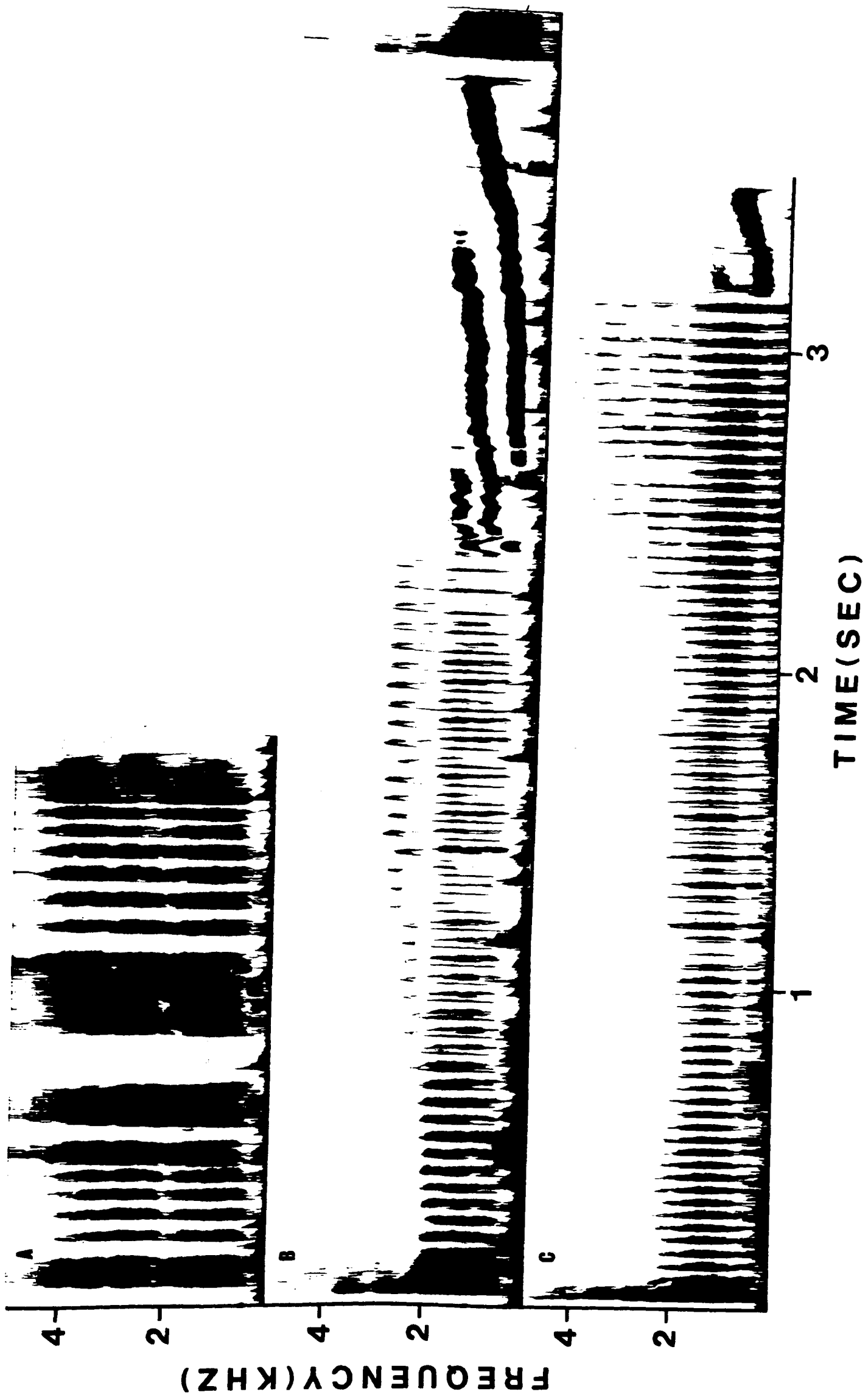
The calls were again heard on subsequent nights after about 2300 hrs from the same site in a delapidated rock wall. The purr-call, and a short burst of flight-call were recorded on a Uher 4000 Report IC tape recorder (Figure 1). On 8 July the wall was excavated during daylight, and later an all-dark storm petrel was caught at 2320 hrs in a small nest chamber containing twigs and plant fragments. The site and nesting material were similar to that being used by O. castro elsewhere in the same wall at that time, and the pattern of calling behaviour of the bird was similar to that of O. castro prospecting for nest sites in the study area.

The bird was measured (wing 154 mm, tail (outer) 81 mm, tail (inner) 64 mm, bill length 14.0 mm, tarsus 22.9 mm, weight 41 g), photographed, ringed, and released. The bird was compared with several O. castro in the field which ruled out the possibility that the bird was a melanistic form of that species as the bird had a more deeply forked tail, was larger, and had a different bill shape. The bird also had distinct whitish bases to the primary shafts which O. castro does not possess. The bird was identified as a Swinhoe's Storm Petrel Oceanodroma monorhis after comparing the descriptions and photographs with the collection of Leach's Storm Petrels and other all-dark storm petrels (seven species) in the British Museum of Natural History (Tring).

Swinhoe's Storm Petrel breeds in the northwestern Pacific Ocean on islands off eastern Russia, Korea, Japan, northeastern China, and northeastern Taiwan (Vaurie 1965, Dement'ev & Gladkov 1969), with egg-

Appendix D, Figure 1

Sonagrams of Swinhoe's Storm Petrel (A) Flight-Call (B) Purr-Call compared with (C) Leach's Storm Petrel Purr-Call.


A
B
C
4
2
4
2
4
2
FREQUENCY(KHZ)
1
2
3
TIME(SEC)

laying between May and August (Netschajew 1969). It migrates southwards to the west tropical Pacific and the Sunda Sea, and is frequently found in the vicinity of Singapore (Gibson-Hill 1948). Some regularly pass through the Straits of Malacca westward into the Indian Ocean and the Arabian Sea (Bailey et al. 1968). In the Indian Ocean, Swinhoe's Storm Petrels have been recorded widely, including some to more than 10° S - to the northeast of Madagascar (Bailey 1965, Gill 1967, Bailey et al. 1968) and may possibly reach at least 20° S (Bailey et al. 1968). A beach-washed specimen at Eilat in the Gulf of Aqaba at the head of the Red Sea in January 1958 (Merom 1960) was the only previous western Palearctic record. The occurrence of Swinhoe's Storm Petrel in the Atlantic Ocean would require the bird to pass either around the Cape of Good Hope or through the Red Sea, and then the Mediterranean.

Swinhoe's Storm Petrel is sometimes considered to be a subspecies of Leach's Storm Petrel. Following Ainley's (1980) review of geographic variation in O. leucorhoa, Bourne & Jehl (1982) called for an investigation of the vocalizations of O. monorhis of the western Pacific. The record now gives that opportunity, as it appears that the calls of O. monorhis have not previously been recorded. Its calls and those of O. leucorhoa (Ainley 1980, Cramp & Simmons 1977) are quite distinct (Figure 1) and do not fit on the clinal range shown by Ainley (1980), and so it probably should still be treated as a distinct species pending further research.

APPENDIX E

Cassette tape of species studied

Cassette tape of species studied

There is no doubt that the advent of the sound spectrograph revolutionized the study of bird vocalizations (Catchpole 1979). By allowing a pictorial representation of the sound to be made, it has completely removed the need for far less objective phonetic descriptions. However, it is still not easy to relate a sonagram to the actual sounds that it represents, particularly for people unfamiliar with its use. For this reason, a cassette tape was produced containing examples of the calls produced by the main study species in this thesis. These can be listened to, and compared with the relevant sonagrams. Table 1 gives the details for each call presented. All recordings are by the author.

Appendix E, Table 1

Cut	Species	Sex	Call	Time & Place
1	Manx Shearwater	Male	-	May 81, Skomer
2	"	Female	-	"
3	British Storm Petrel	Male	Purr	June 81, Skomer
4	"	-	Flight	"
5	Madeiran Storm Petrel	Male	Flight	June 83, Great Salvage
6	"	Female	"	"
7	"	Male	Purr	"
8	"	Female	"	"
9	"	-	High	"
10	Cory's Shearwater	Male	-	July 83, Great Salvage
11	"	Female	-	"
12	Little Shearwater	Male	-	"
13	"	Female	-	"
14	Bulwer's Petrel	-	Repeat	June 83, Great Salvage
15	White-faced Storm Petrel	Pair	-	July 83, Great Salvage
16	Swinhoe's Storm Petrel	Female?	Purr/Flight	June 83, Great Salvage