THE BIOLOGY OF SPECIES OF THE GENUS

PSEUDOPHRYNE (ANURA : LEPTODACTYLIDAE)

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This thesis is my original work, except where specifically acknowledged.

R. K. Pengilley

Frontispiece

Pseudophryne corroboree, Coree Flats, Brindabella Range, N.S.W.

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Chapter 1 INTRODUCTION

Most of the recent studies on Australian amphibia have been on species occurring in south-western Australia. These studies include work on speciation within various genera, principally Crinia (Main, 1957; Main et al., 1958; Littlejohn, 1959), the behavioural and physiological adaptations of desert-inhabiting species (Bentley et al., 1958; Main et al., 1959; Main and Bentley, 1964; Packer, 1963) and general biology (Calaby, 1956, 1960; Main, 1965; Main and Calaby, 1957).

In contrast, the eastern Australian species have been little studied since the early work of Fletcher (1889, 1890, and subsequent papers) and of Harrison (1922). Recently, Moore (1961) and Jacobson (1962, 1963) have dealt with certain aspects of the biology, specially embryological development, of eastern New South Wales species. Littlejohn and Martin have reported on the natural history of a number of species found in Victoria (Littlejohn, 1963; Martin, 1965) in addition to their studies on speciation (Littlejohn, 1964, 1965; Littlejohn and Martin, 1964, 1965).

Despite all these studies, much remains to be known about the ecology of any one species or a group of species.

It was for this reason that a study was undertaken of three species of the genus Pseudophryne occurring in the southern highlands of New South Wales. Pseudophryne corroboree was the principal species investigated, because preliminary surveys indicated that it was abundant at certain localities in the Brindabella Range west of Canberra, A.C.T. Initially, an attempt was made to investigate the population dynamics of this species at Coree Flats near the northernmost limit of its distribution in the Brindabella Range. Because of the difficulties involved in sampling and the limited time available for field work this project was abandoned. Instead, the emphasis changed to a comparative study of the biology of the three species of Pseudophryne - P. corroboree, P. dendyi and P. bibroni - occurring in the southern highlands of New South Wales.

One of the principal requirements of any field study, or for that matter, any biological problem, is to know the taxonomy of the species selected for study. Colour pattern has been one of the major characters used so far to separate species of the genus Pseudophryne. Jacobson (1962), however, suggested that this could possibly be replaced by characters based on the type of embryological

development. While there are undoubtedly characteristics in the development of any species that are of taxonomic utility the impracticability of utilizing these would preclude them from ready acceptance. In the present study, morphology and behaviour have been utilized to delineate the three species. However, the specific status of certain populations of P. dendyi are still unresolved despite the many-sided approach, and their correct taxonomic status must therefore await further intensive study.

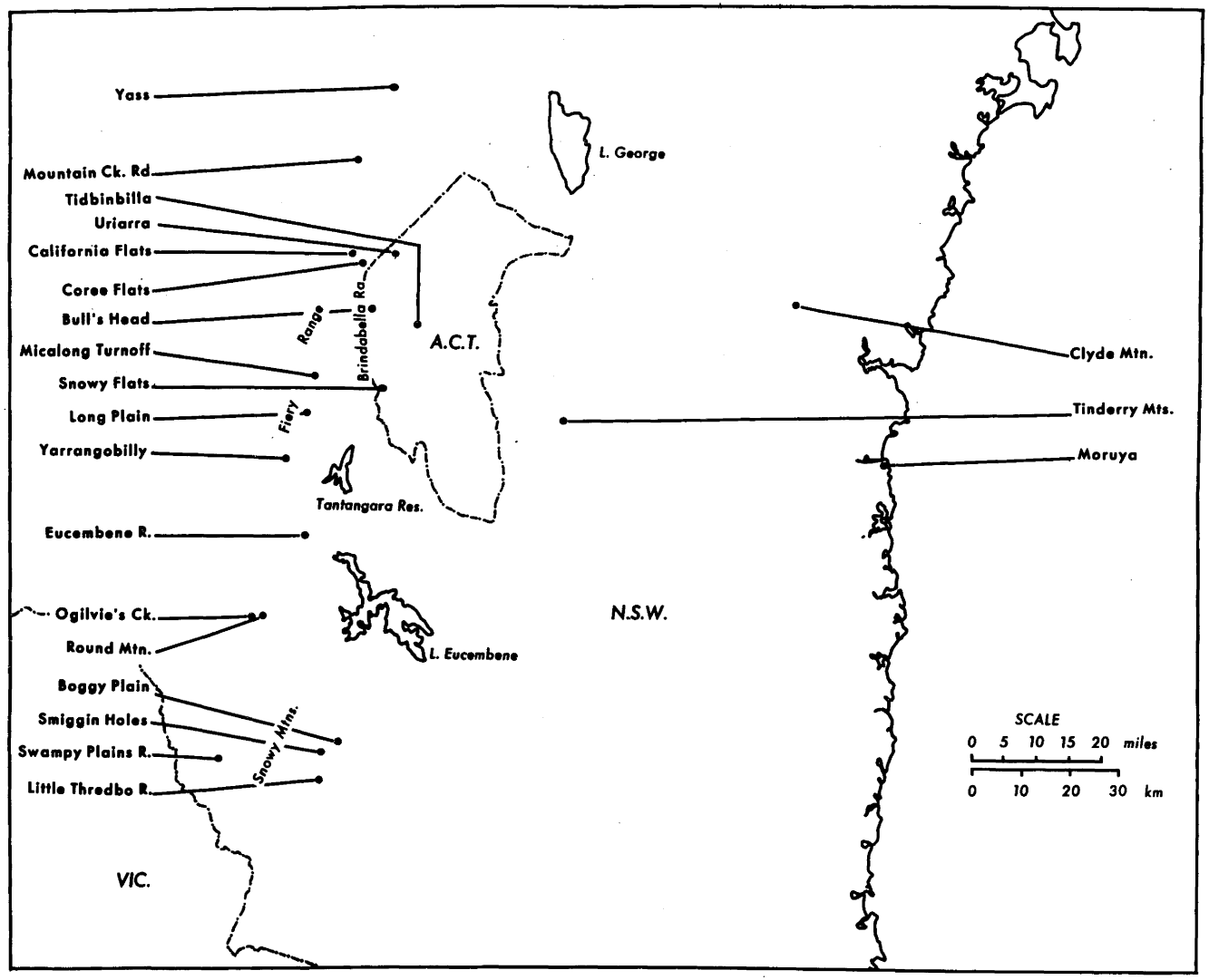
Certain aspects of the breeding biology of the three species were examined in detail, in particular, breeding seasons and calling behaviour. Information on the breeding seasons of Australian frogs, and the possible factors inducing and inhibiting breeding, is meagre and, for the most part, extremely vague. Apart from the early work of Fletcher (1889) and to a certain extent, of Harrison (1922), the only comprehensive account of the natural history of reproduction of a number of species is that of Main (1965).

The importance of vocality and especially mating call as a pre-mating isolating mechanism in some frogs has been fairly well established by workers in Australia

(Littlejohn, 1959; Littlejohn and Main, 1959; Main et al., 1958) and in the United States (Blair, 1955, 1958; Michaud, 1964). However, very few attempts have been made to describe and define the various calls made by frogs, so that the impression may be gained that the mating call is their only vocalization. This is definitely not the case, as the recent review by Bogert (1960) has clearly demonstrated. Most species that vocalize make two or more calls during different behavioural states. Because of the absence of any field studies describing the calls of frogs, attempts were made to record and analyse all the types of calls produced by the three species of Pseudophryne, though this objective was not wholly realized because more time was spent observing P. corroboree than either of the other two species. From the data obtained however, it emerged that calling behaviour of these frogs was even more complex than had been thought initially.

Fig. 2.1

A map of south-eastern N.S.W. showing the principal localities mentioned in the text. The approximate position of this area is shown as a broken rectangle in Fig. 3.1.


Yass
Mountain Ck. Rd
Tidbinbilla
Uriarra
California Flats
Coree Flats
Bull's Head
Micalong Turnoff
Snowy Flats
Long Plain
Yarrangobilly
Eucumbene R.
Ogilvie's Ck.
Round Mtn.
Boggy Plain
Smiggin Holes
Swampy Plains R.
Little Thredbo R.
VIC.
Range
Brindabella Ra.
Fiery
A.C.T.
L. George
Tantangara Res.
L. Eucumbene
N.S.W.
Snowy Mtns.
Clyde Mtn.
Tinderry Mts.
Moruya
SCALE
0 5 10 15 20 miles
0 10 20 30 km

Chapter 2 STUDY AREAS

2.1 Introduction

Most of the places which were visited fairly frequently are in the southern highlands of New South Wales (Fig. 2.1) and occur within the subalpine, montane and tableland zones of Costin (1954). Localities above the tree line, i.e. in the alpine zone, were not visited as preliminary surveys in the more accessible parts of this region revealed that Pseudophryne were not found in this zone. Crinia signifera and Hyla verreauxi are the only species found in the alpine zone in south-eastern Australia.

The characteristics of the three zones and the major study areas from each of these zones are given in Table 2.1.

2.2 Subalpine Localities

The area here called 'Smiggin Holes' is about 3.2 km north of the village of Smiggin Holes on the Smiggin Holes-Guthega Road at an elevation of about 1,650 m. It is a small sphagnum bog surrounded by disclimax heath (Costin, et al., 1959), which was originally subalpine woodland

Fig. 2.2

Upper photograph: Subalpine woodland, disclimax heath and portion of the sphagnum bog, Smiggin Holes, N.S.W.

Lower photograph: Small part of the sphagnum bog Smiggin Holes, N.S.W. The dark, oblique area is a small hollow in the bog which becomes a temporary pool in the winter and spring. The breeding sites of P. corroboree are generally distributed around the edges of these hollows.

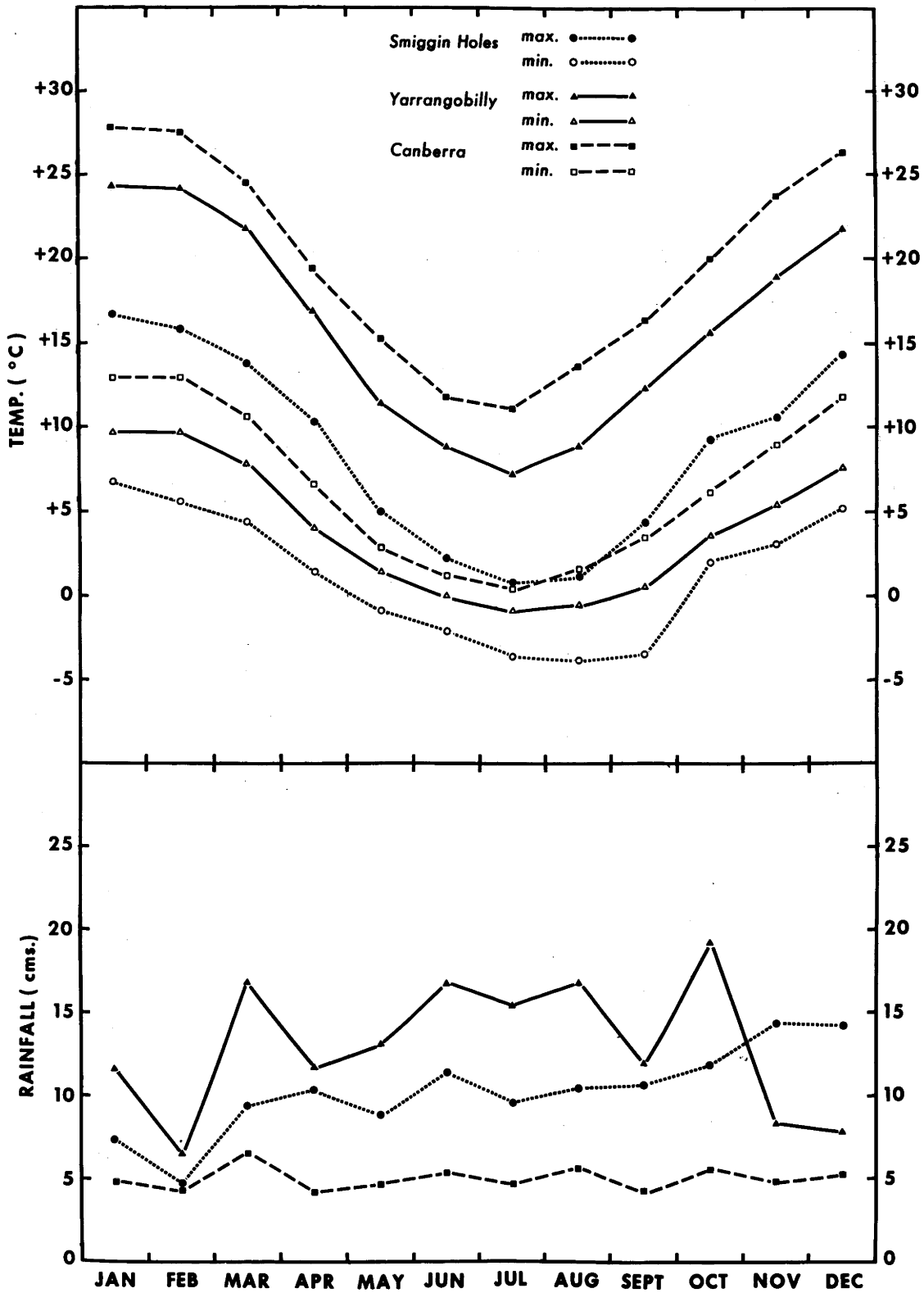
Table 2.1 Vegetational and climatic characteristics of the subalpine, montane and tableland zones of south-eastern Australia. Data mainly after Costin (1954, 1959).

Zone	Vegetation and Climate	Localities
Subalpine (1,524-1,829 m)	Subalpine woodland mainly of snow gum (Eucalyptus pauciflora). Raised and valley bogs in poorly drained valleys. Mean mid-summer temperatures range from 16-24°C. Mean monthly temperatures below 0°C from 1-4 months. Normally snow covered for 1-4 months. Average annual precipitation ranges from 100-240 cm. Winds of Antarctic origin cause precipitation (mainly snow) to be maximal during winter.	Smiggin Holes, Boggy Plain, Round Mtn. (Snowy Mtns. area). Snowy Flats (Brindabella Ra.).
Montane (914-1,524 m)	Wet and dry sclerophyll forests. Some savannah woodland. Heaths in poorly drained areas. Mean monthly minimum temperatures below 0°C from 0-6 months. Average annual precipitation ranges from 76-100 cm with winter maximum.	Little Thredbo River Flats (Snowy Mtns. area). Yarrangobilly (Fiery Ra.). Coree Flats (Brindabella Ra.)
Tableland (610-914 m)	Dry sclerophyll forest and savannah woodland. Mean monthly minimum temperatures below 0°C from 0-4 months. Average annual precipitation 50-76 cm. Generally uniform rainfall distribution.	Uriarra (foothills of Brindabella Ra.).

Fig. 2.3

Upper graph: The mean maximum and minimum monthly screen temperatures of three selected stations in the southern highlands and tablelands of N.S.W.

Lower graph: The average monthly rainfall in centimeters for the same three stations. Smiggin Holes ●·····● Yarrangobilly ▲——▲ and Canberra ■— — —■. The temperature and rainfall records for Smiggin Holes and Yarrangobilly were supplied by the Meteorological Branch, Snowy Mountains Hydroelectric Authority, Cooma, N.S.W.


Smiggin Holes
max.
min.
Yarrangobilly
max.
min.
Canberra
max.
min.
TEMP. (°C)
+30
+25
+20
+15
+10
+5
0
-5
RAINFALL (cms.)
25
20
15
10
5
0
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC

(Fig. 2.2). Screen temperatures at Smiggin Holes revealed that generally temperatures are fairly low with relatively small differences of 5-10°C between mean monthly maxima and minima (Fig. 2.3). During the summer the differences between day and night temperatures may even be greater than the range of the mean monthly temperatures as is indicated in Table 2.2.

Table 2.2 Selected temperature readings obtained at Smiggin Holes, 31 January, 1965 (the air temperatures are those recorded at moss level and the moss temperatures refer to readings obtained from a depth of 10-15 cm in the moss).

Time (hrs)	Air Temp. (°C)	Moss Temp. (°C)
1620	21.0	20.0
1700	17.0	19.0
1800	13.0	18.0
2130	2.5	12.0
2200	7.0	13.0

Fig. 2.4

Upper photograph: Sphagnum bog (foreground) and subalpine woodland (background), Snowy Flats, A.C.T.

Lower photograph: A hollow (pool) surrounded by hummocks of Sphagnum cristatum and other vegetation, Snowy Flats, A.C.T. Photograph taken in the late autumn, 1965. The burrows of P. corroboree are situated around the edges of the hummocks below water level.

At Smiggin Holes rainfall is fairly evenly distributed throughout the year except for January and February which are relatively dry (Fig. 2.3). Monthly total precipitation shows a winter maximum due mainly to snow.

Boggy Plain (alt. 1,585 m) is located about 5 km south-east of Smiggin Holes on the same mountain range. As the name suggests this was once a very wet sphagnum bog but due to repeated burning off and grazing of sheep, it is now very dry and there is little actively growing sphagnum. The most common species of frog, other than P. dendyi, found at Boggy Plain were Crinia signifera and Hyla verreauxi.

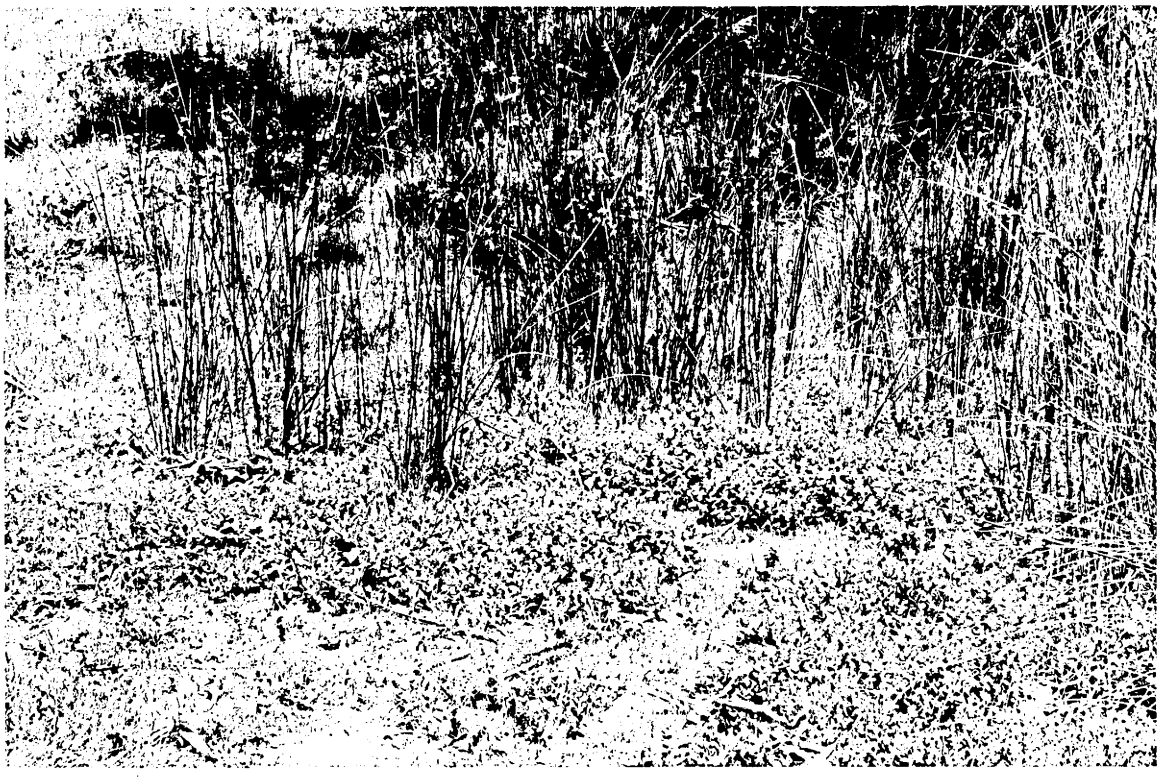
Round Mountain is 39 km N.N.W. of Smiggin Holes at an elevation of 1,585 m. It is a small bog surrounded by subalpine woodland.

Snowy Flats is situated on the Brindabella Range approximately 33 km south of Coree Flats at an elevation of 1,646 m. It is essentially a valley bog surrounded on the slopes by a subalpine woodland (E. pauciflora) underlain by a well developed and virtually continuous herbaceous layer of the snow grass Poa caespitosa (Fig. 2.4 upper photograph). The bog is an example of the

Fig. 2.5

Upper photograph: An open portion of wet sclerophyll forest, near Yarrangobilly, N.S.W.

Lower photograph: Part of the breeding area of *P. corroboree* and *P. dendyi* near Yarrangobilly, N.S.W. The small plant covering most of the foreground is the monkey musk *Mimulus moschatus*.



Carex gaudichaudiana - Sphagnum cristatum bog alliance (Costin et al., 1959) of which a large part consists of active sphagnum moss showing hollow-hummock development (Fig. 2.4 lower photograph).

Frog species found in this area include P. corroboree, P. dendyi, Crinia signifera and Hyla verreauxi.

2.3 Montane Localities

Little Thredbo River Flats (alt. 1,280 m) is located near the junction of the Little Thredbo and Thredbo Rivers in the Thredbo Valley approximately 7 km south of Smiggin Holes. The area consists of a disturbed sphagnum bog surrounded by wet sclerophyll forest. Frog species found in the area include P. dendyi, Crinia signifera, Hyla verreauxi, Limnodynastes dorsalis and L. tasmaniensis.

The area here called 'Yarrangobilly' is actually 2 km south-east of the village of Yarrangobilly on Highway 18 at an elevation of approximately 1,260 m. It is part of the western montane zone of Costin (1954) and consists mainly of wet sclerophyll forest (Fig. 2.5). The vegetation in, and surrounding, small, temporary streams is similar to the wet heath at Coree Flats.

Most of the work was carried out at Coree Flats

(alt. 1,036 m) situated about 4 km north of the north-western corner of the N.S.W. - A.C.T. border in N.S.W. Coree Flats, which is near the lower limit of the montane zone, consists of a wet heath surrounded by wet sclerophyll forest. The forest formation occupies the slopes of the surrounding ridges and consists of the mountain gum (Eucalyptus dalrympleana) - narrow-leaved peppermint (E. robertsoni) alliance with the broad-leaved peppermint (E. dives) and the snow gum (E. pauciflora) as sub-dominants. This is underlain by a well developed shrub layer comprising the bitter pea, Daveisia mimosoides, and juveniles of the broad-leaved peppermint and snow gum (Fig. 2.6 upper photograph). Throughout most of the forested area except for the stony ridges and slopes there is a dense sward of the snow grass Poa caespitosa. Where there are dense stands of trees, leaf litter, logs and branches cover most of the ground providing ample cover for Pseudophryne corroboree and other species of frog.

The wet heath is demarcated from the surrounding forest by a fairly well developed ecotone zone of Leptospermum myrtifolium, Epacris breviflora and Baechea utilis underlain by a herbaceous layer predominantly of

Fig. 2.6

Upper photograph: Wet sclerophyll forest underlain by the bitter pea Daveisia mimosoides (shrub) and snow grass Poa caespitosa at Coree Flats, N.S.W.

Lower photograph: Ecotonal zone demarcating the wet heath (foreground) and wet sclerophyll forest (background).

Juncus sarophorus and snow grass (Fig. 2.6 lower photograph). Within the heath proper, the vegetation consists of tussocks of snow grass and Restio australis. At the northern and southern ends of the heath the vegetation has been partly modified by man such that it now contains a very diverse assemblage consisting of snow grass, species of Agrostis, various herbs and an unidentified moss (Fig. 2.7 upper photograph). Apparently these modified areas are more favourable as breeding sites for P. corroboree than the intervening area mentioned above. It seems that the bases of grass tussocks and clumps of Restio australis are too compact for male Pseudophryne to construct burrows. In addition evaporation from the soil tends to be greater in these areas than in those which are carpeted by various herbs and short grasses. In the areas more favourable for breeding the plant species which develop after the temporary pools have dried up are important in the life of the frog species occurring in the locality. They not only provide cover for the newly metamorphosed frogs, but by aiding water retention in the soil, provide a moist breeding site for P. corroboree and P. dendyi. The most important plant is the monkey musk Mimulus moschatus. The vegetation in the

Fig. 2.7

Upper photograph: Southern portion of the wet heath, Coree Flats, N.S.W. The most favourable breeding sites were located in the area in the middle of the photograph.

Lower photograph: Disturbance of the breeding area at the northern end of Coree Flats, N.S.W., caused by the feral pig, Sus domestica.

breeding areas, particularly in those places where the monkey musk is common, is often uprooted by the feral pig Sus domestica when scratching for food. In some areas this is of an advantage to Pseudophryne spp. as these clods of soil and vegetation increase the number of breeding sites available (Fig. 2.7 lower photograph). Sometimes, however, pigs uproot the vegetation after eggs have been laid resulting, in some cases, in the death of the eggs.

Air temperatures recorded at Coree Flats at ground level under vegetation in the heath showed marked seasonal and annual differences (Fig. 2.8 upper graph). During the period August to January temperatures increased at the mean rate of 0.09°C per day in 1963, and at the rate of 0.08°C per day in 1964. The rate of decrease from mid-summer to late autumn (January to May) was much greater in 1964 than in 1965, the mean rate being 0.12°C and 0.09°C per day respectively. Water temperatures of one pool in the heath (shown as dotted lines on the graph) followed air temperatures rather closely. Pools never became completely frozen even though they ranged from 2-15 cm deep.

Fig. 2.8

Upper graph: Mean monthly maximum and minimum air and water temperatures recorded at Coree Flats over a 30 month period. Air temperatures are of readings taken at ground level beneath the cover of vegetation in the wet heath. Water temperatures are recordings of temperatures taken in the shaded part of a small pool at a depth of approximately 10 cm within the wet heath.

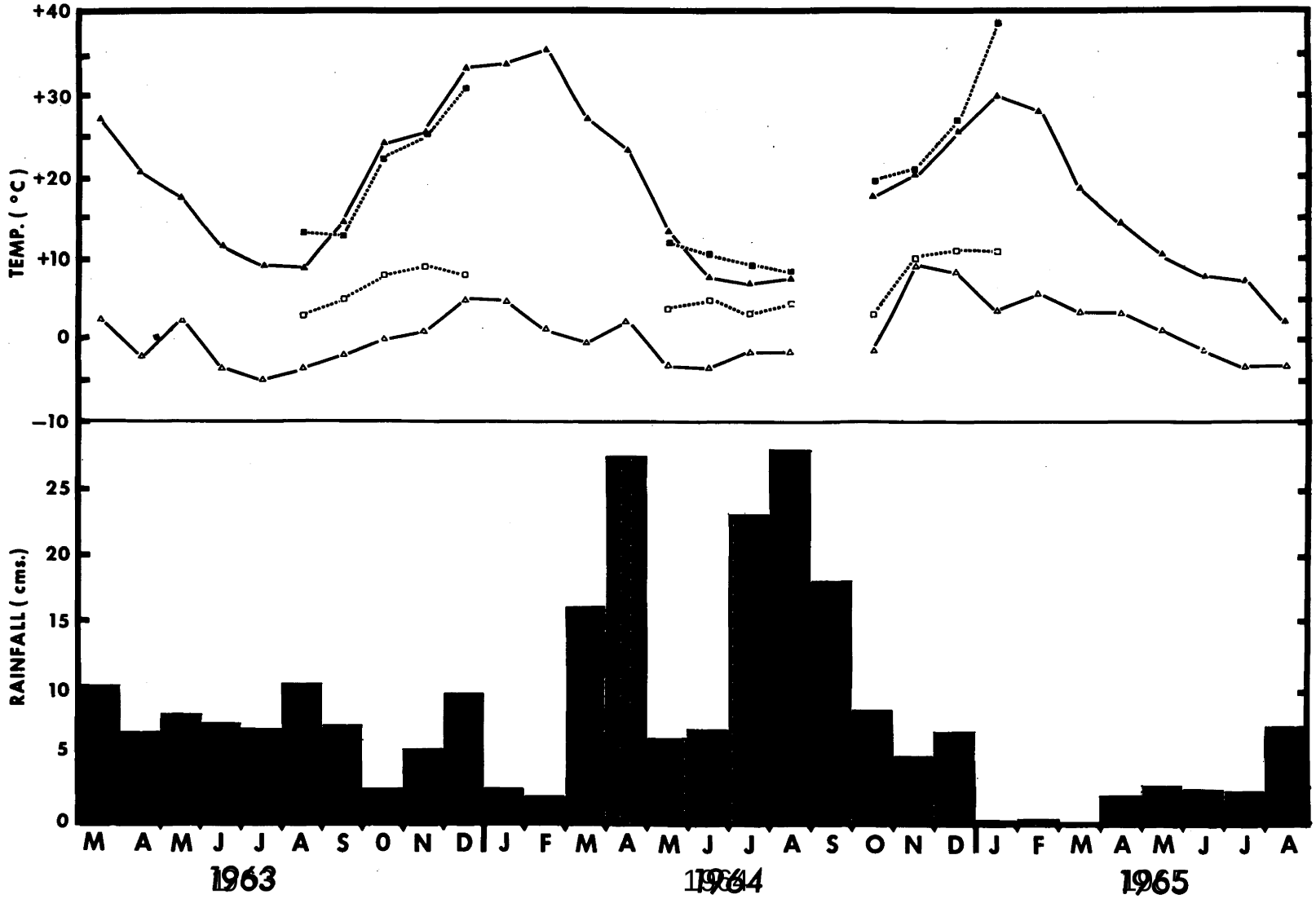
Air temperature maximum ▲——▲

" " minimum △——△

Water " maximum ■·····■

" " minimum □·····□

Lower graph: Mean monthly rainfall recorded from a station 1.5 miles south of Coree Flats. These records were supplied by the Forest and Timber Bureau, Department of Interior, Commonwealth of Australia, Canberra, A.C.T.


+40
+30
+20
+10
0
−10
TEMP. (°C)
25
20
15
10
5
0
RAINFALL (cms.)
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1963
1964
1965

Most of the precipitation is in the form of rain. Snow may contribute to the total precipitation in some years. No snow fell in 1963, but some falls were recorded in July and August, 1964, and June and July, 1965.

Rainfall is generally maximal in winter but (during the years of this study) 1964 was a very wet year and 1965 was a drought year (Fig. 2.8 lower graph). In 1963 most pools in the breeding area were dry by mid-December but because of the unusually heavy rains during the winter and spring of 1964 pools still contained water which remained until January, 1965. Little rain was recorded during the winter of 1965 and was insufficient to form pools for more than a few weeks. Generally, pools begin to form in late May at the onset of the winter rains. The pH of four pools recorded in June, 1963, ranged from 6.0 to 6.4.

2.4 Tableland Locality

The locality here called 'Uriarra' (alt. approximately 600 m) is a small roadside seepage area located between a pine plantation of Pinus radiata and dry sclerophyll forest about 22.5 km west of Canberra, A.C.T. at the foothills of the Brindabella Range.

As an example of the tablelands area, temperature and rainfall records for Canberra are shown in Fig. 2.3. In this area there is marked seasonal variation in the mean monthly maximum and minimum temperatures. Rainfall is distributed fairly evenly throughout the year. No snow falls were recorded in 1963. Some light falls were recorded in August, 1964, and June, 1965, and heavy falls of snow were reported in August, 1965.

Chapter 3 SYSTEMATICS AND DISTRIBUTION

3.1 Introduction

The genus Pseudophryne has been placed in various families since Fitzinger (1843) introduced the name. Cope (1865) considered them to be bufonids and Noble (1922) did likewise. Later, Noble (1931) subdivided the bufonids into a number of subfamilies, to one of which, the Crininae, Pseudophryne was referred. Parker (1940), however, considered all bufonid-like Australian frogs to be members of two subfamilies of the family Leptodactylidae; the genus Pseudophryne being placed into the subfamily Myobatrachinae. Although these species have been referred to the family Leptodactylidae, the relationships between them and the South American forms still have not been satisfactorily determined (Hetch, 1963).

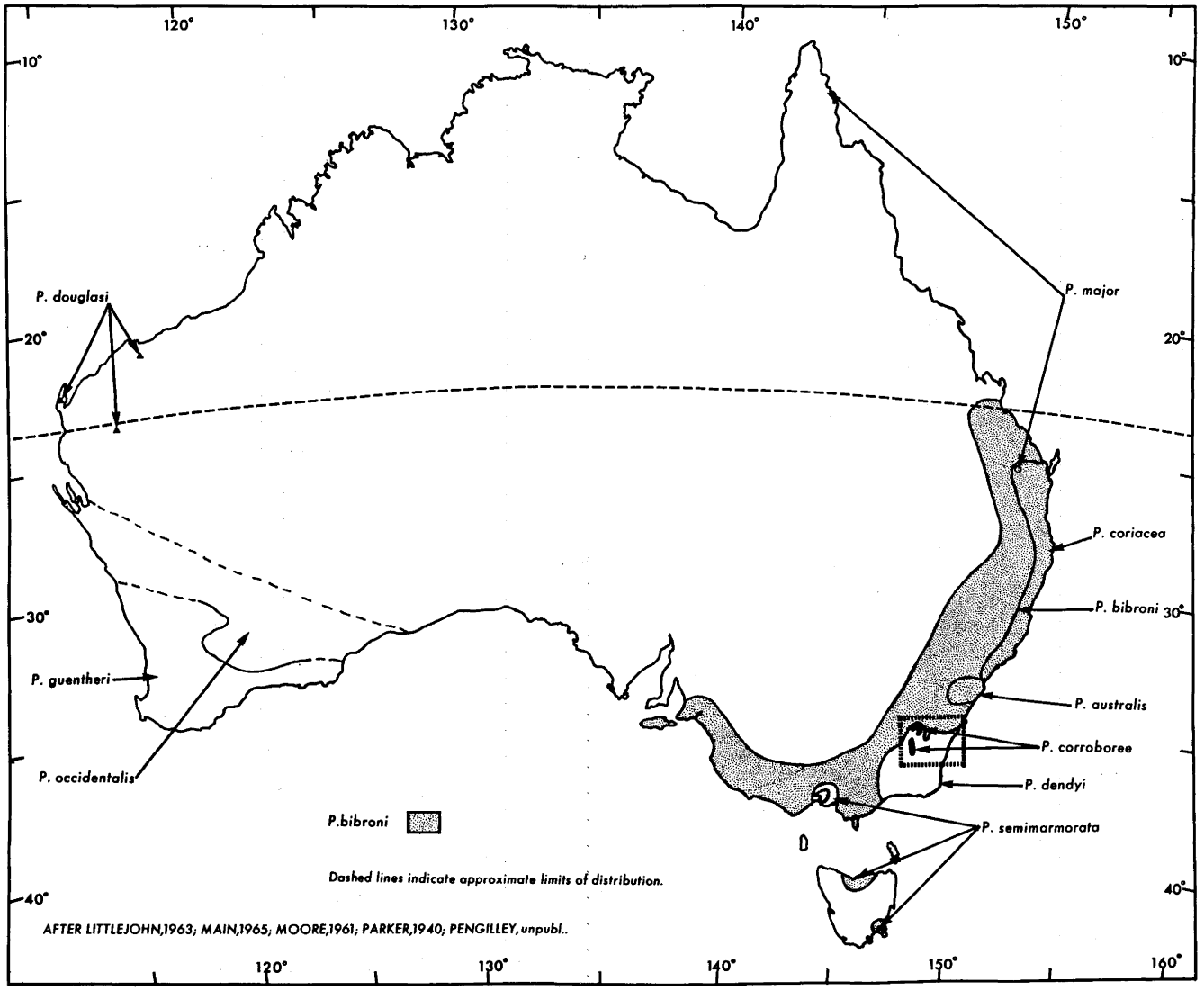
3.2 The genus Pseudophryne

The genus Pseudophryne includes ten species, three of which are confined to Western Australia, the remainder being found in eastern and southern Australia including Tasmania.

The relationships of the various species are not very well known. Parker (1940), in referring to the eastern Australian species, considered Pseudophryne bibroni, P. semimarmorata and P. coriacea to be members of one group.

Fig. 3.1

The geographical distribution of species of the genus Pseudophryne compiled from various sources. The rectangular area outlined on the map refers approximately to the area shown in Fig. 3.2.


120°
130°
140°
150°
10°
20°
30°
40°
160°
P. douglasi
P. major
P. coriacea
P. bibroni
P. australis
P. corroboree
P. dendyi
P. semimarmorata
P. guentheri
P. occidentalis
P.bibroni
Dashed lines indicate approximate limits of distribution.
AFTER LITTLEJOHN,1963; MAIN,1965; MOORE,1961; PARKER,1940; PENGILLEY, unpubl..

He gave no criteria for the affinities of these species but presumably they were morphological. P. coriacea, however, is so different in colour and pattern from the other species that it is difficult to see why they were grouped together. On morphological grounds, P. bibroni, P. dendyi, P. semimarmorata and P. australis, and possibly P. corroboree, could be placed in one group. From the photographs published by Main (1965) both P. occidentalis and P. douglasi are similar morphologically to P. bibroni while the third species, P. guentheri, is similar to P. semimarmorata.

The distribution of members of the genus Pseudophryne conforms to the peripheral pattern as described by Keast (1959 a). Except for two species, the majority occur in regions of reliable, generally uniform rainfall in the temperate zone of the continent (Fig. 3.1). P. occidentalis is the only species which has been recorded from localities receiving less than 25.4 cm of rain per year.

In eastern Australia, the species range in altitude from near sea-level at the coast to over 1,524 m in the Great Dividing Range. The habitats occupied are very diverse, ranging from tropical woodland through sclerophyll forest and savannah woodland to subalpine woodland. No species has been recorded from subtropical or tropical rainforest

although P. major, which is recorded from southern Queensland and the Cape York Peninsular, may occur in tropical rainforest at the latter locality.

3.3 The Species Studied

i) P. corroboree Moore 1953

P. corroboree was first described by Moore (1953) from a specimen collected at Round Mountain in the Snowy Mountains region of N.S.W. Later, (1961) after examining specimens collected from the Snowy Mountains region and the Brindabella Range, A.C.T., he concluded that this species showed very little morphological variation. Jacobson (1963), however, stated that this was not so and that specimens from the Brindabella Range could be distinguished because of the disrupted yellow dorsal stripes. This observation has been confirmed and amplified by the present study.

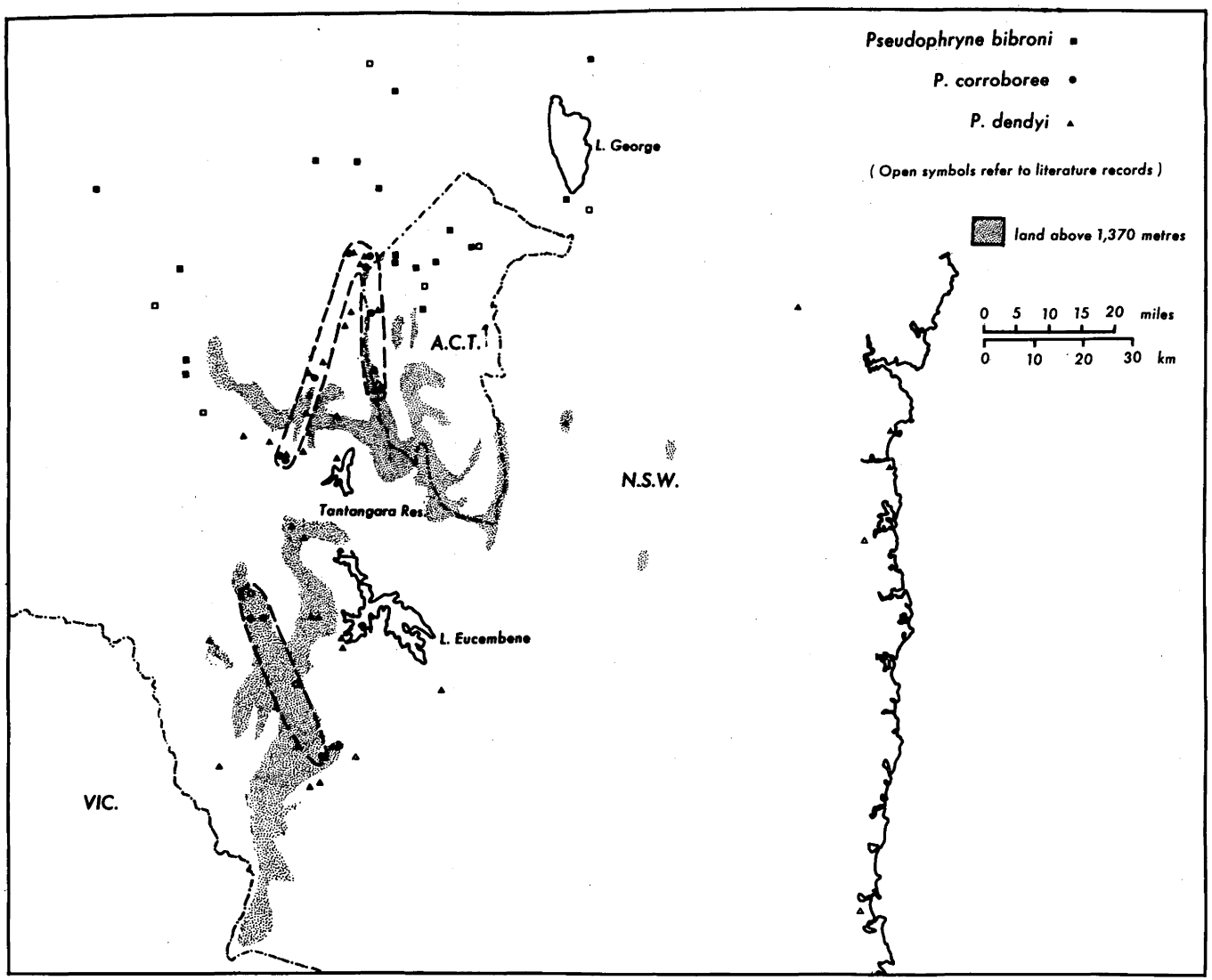
Because of the absence of any information on potential, or actual, barriers to interbreeding in the populations from these two areas, the two forms of P. corroboree discussed here are considered as one species.

Distribution

The distribution of the two forms of P. corroboree are shown enclosed by dashed lines in Fig. 3.2. Both forms

Fig. 3.2

Distribution of *P. corroboree*, *P. dendyi* and *P. bibroni* in the southern highlands of N.S.W. The two areas enclosed by dashed lines represent the distributional range of the two forms of *P. corroboree*.


Pseudophryne bibroni
P. corroboree
P. dendyi
(Open symbols refer to literature records)
land above 1,370 metres
0 5 10 15 20 miles
0 10 20 30 km
L. George
A.C.T.
N.S.W.
Tantangara Res.
L. Eucumbene
VIC.

are confined to the montane and subalpine zones of the southern highlands of New South Wales including the Australian Capital Territory.

In the Snowy Mountains region P. corroboree occurs from 8 km north of Round Mountain, near Cabramurra, (Colefax, 1956) southwards to near Smiggin Holes. The altitudinal range of the species in this area is not very great, ranging from 1,220 m at Ogilvie's Ck. about 4 km west of Round Mountain, to approximately 1,770 m at Alpine Hut. The usual habitats appear to be areas surrounding sphagnum bogs. Moore (1961) gives Mt. Kosciusko as a locality but two trips to this area failed to locate the species. It is possible that this locality has been given in error for Smiggin Holes. The only species known to occur above 1,828 m in south-eastern Australia are Hyla verreauxi and Crinia signifera.

The other form of P. corroboree is confined to the Brindabella and Fiery Ranges. In Fig. 3.2 the limits of its distribution are shown as an inverted 'V' where the longer, south-westerly directed arm represents the Fiery Range and the shorter, southerly directed arm, the Brindabella Range. Within this region, P. corroboree occurs from about 5 km south-west of Yarrangobilly on

the Fiery Range to as far north as 6 km north of the north-western corner of the A.C.T. - N.S.W. border on the Brindabella Range (California Flats). The southern-most locality for this species in the Brindabella Range is Snowy Flats.

The altitudinal range and hence the diversity of habitat which P. corroboree occupies is much greater in these areas than in the Snowy Mountains. The highest known altitudinal limit is at Snowy Flats, A.C.T., (alt. 1,650 m), while the lowest is for California Flats, N.S.W., (alt. 975 m). Above 1,220 m P. corroboree is generally associated with sphagnum bogs but below this altitude it occurs in and around wet heaths and other ground-water communities.

Colour and Pattern

There is no obvious sexual dimorphism in colour or pattern in P. corroboree adults.

The two forms of P. corroboree differ in colour and pattern (Table 3.1) with the differences being associated with the amount and distribution of yellow on the dorsal and ventral surfaces of the body. Specimens from the Snowy Mountains (Round Mountain and Smiggin Holes) have the dorsal yellow stripes unbroken (Fig. 3.3 A) and the ventral

Table 3.1 Morphological features of the two forms of *P. corroboree*

	Snowy Mountains	Brindabella and Fiery Range
Colour of light pigment	bright yellow	dull yellow to greenish yellow
Dorsal stripes	unbroken	broken
Ventral pattern	more than 50% of ventral surface covered by yellow blotches	less than 50% of ventral surface covered by blotches. Amount of yellow varies from 0-50%

Fig. 3.3

A. Dorsal pattern of P. corroboree, Smiggin Holes, N.S.W.

B. Ventral pattern of specimen shown in A.

C. Dorsal pattern of P. corroboree, Coree Flats, N.S.W.

D. Ventral pattern of specimen shown in C.

E. Dorsal pattern of P. corroboree, Yarrangobilly, N.S.W.

F. Ventral pattern of specimen shown in E.

In A, C and E the white areas are yellow. In B, D and F the white areas are mainly yellow on the Smiggin Holes specimen but are both yellow and white or light blue on the Coree Flats and Yarrangobilly specimens.

G. Dorsal pattern of P. dendyi, Swampy Plains River, N.S.W.

H. Ventral pattern of specimen shown in G.

In G the white areas are yellow, and in H they are white, on the specimen.

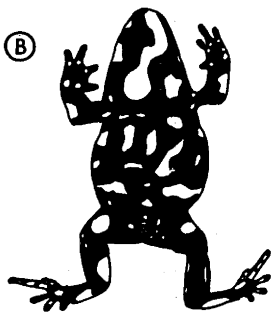
I. Dorsal pattern of P. dendyi, Long Plain, N.S.W.

J. Ventral pattern of a female P. dendyi, Long Plain, N.S.W.

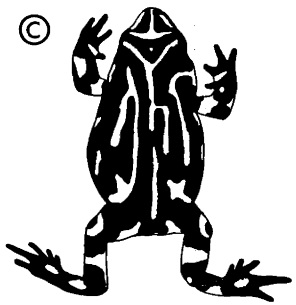
K. Ventral pattern of a male P. dendyi, Long Plain, N.S.W.

In I the white areas on the upper forearm and in the cloacal region are yellow and on the hands and feet they are white, on the specimen. In J and K the white areas are white on the specimen.

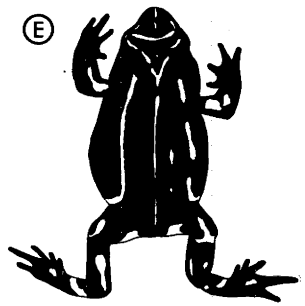
Smiggin Holes

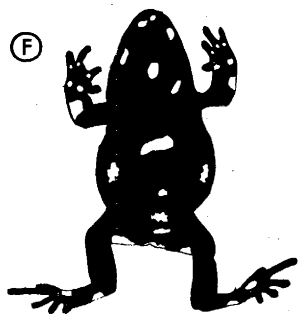


Coree Flats

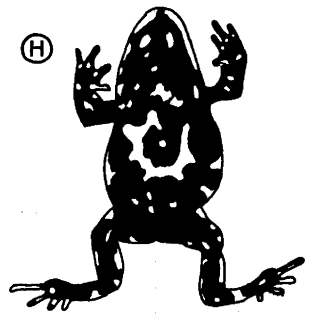


Yarrangobilly

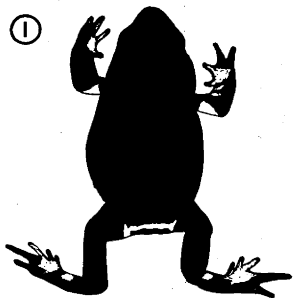




Swampy Plains R.



Long Plain



surface marked by yellow blotches (Fig. 3.3 B). There is very little variation in the dorsal pattern. Of 120 adults examined, only 3 differed greatly in pattern from the one shown in Fig. 3.3 A. In these individuals there was some disruption of the typical pattern near the urostyle, but this was in no way similar to the pattern exhibited by P. corroboree from the Brindabella and Fiery Ranges.

Individuals from the Brindabella (Snowy Flats and Coree Flats) are distinguished by the broken stripes on the back (Fig. 3.3 C), and the reduction in the amount of yellow on the ventral surface (Fig. 3.3 D). In most specimens, the blotches have only small amounts of yellow, the rest being white or light blue. Specimens from Yarrangobilly (Fiery Range) exhibit the greatest reduction of the amount of yellow dorsally (Fig. 3.3 E) and ventrally (Fig. 3.3 F).

Size

Samples of sexually mature males and females were obtained from a number of localities differing greatly in altitude. All measurements of snout-urostyle length, including those of P. dendyi and P. bibroni, are measurements of preserved specimens.

In P. corroboree adults, as in most anuran species, the females are larger than the males. However, because of

the small difference between the mean size of males and females (less than 3 mm) in most of the samples examined, the sexes cannot be distinguished on size in the field.

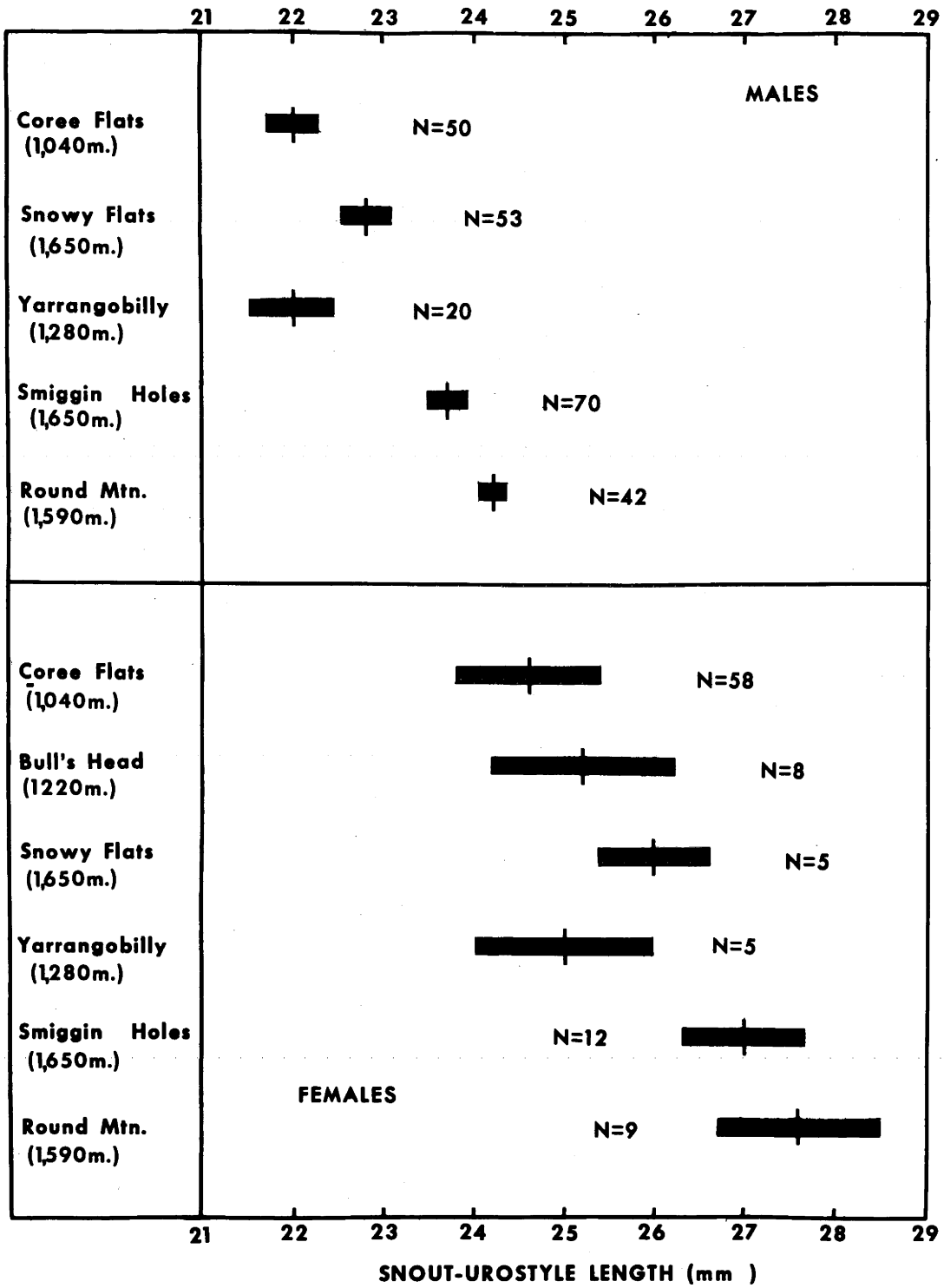
Males from the Snowy Mountains (Round Mountain and Smiggin Holes) are significantly larger than those from the Brindabella (Snowy Flats and Coree Flats) and Fiery Ranges (Yarrangobilly) (Fig. 3.4). Samples obtained from the two localities in the Brindabella Range suggest that the mean body size is directly related to altitude with the larger individual being found at high altitudes and the smaller at low altitudes.

Female body lengths also showed a similar trend (Fig. 3.4) but in this case it was not so clearly defined.

Decrease in body size with decrease in altitude has been recorded in other species of frog (Rensch, 1961) and also in a salamander, Desmognathus ochrophaeus carolinensis (Hairston, 1949). These are considered to be direct applications of Bergmann's Rule where the larger animals are found in colder regions and the smaller in warmer regions. Although generally applied to homeotherms, it has been demonstrated that this rule relating size and temperature is also applicable to poikilotherms (Ray, 1960).

Fig. 3.4

Snout-urostyle lengths of adult males and females of *P. corroboree* from a number of localities in the southern highlands of N.S.W. The thin vertical line represents the mean and the solid dark rectangle represents twice the standard error (S.E.) on either side of the mean. The sample sizes are shown to the left or right of the diagrams.


21
22
23
24
25
26
27
28
29
MALES
Coree Flats
(1,040m.)
N=50
Snowy Flats
(1,650m.)
N=53
Yarrangobilly
(1,280m.)
N=20
Smiggin Holes
(1,650m.)
N=70
Round Mtn.
(1,590m.)
N=42
Coree Flats
(1,040m.)
N=58
Bull's Head
(1220m.)
N=8
Snowy Flats
(1,650m.)
N=5
Yarrangobilly
(1,280m.)
N=5
Smiggin Holes
(1,650m.)
N=12
FEMALES
Round Mtn.
(1,590m.)
N=9
21
22
23
24
25
26
27
28
29
SNOUT-UROSTYLE LENGTH (mm)

ii) P. dendyi Lucas 1892

There has been some doubt about the status of this species which was originally described by Lucas (1892) from a specimen collected near Wellington River, north Gippsland, Victoria. Some workers have considered P. dendyi to be but a form of P. bibroni (Fry, 1912) while others have regarded it as being a distinct species (Loveridge, 1935; Moore, 1961; Parker, 1940).

Both Loveridge (1935) and Parker (1940) described populations from near Sydney as being P. dendyi. Moore (1961) considered these to be P. bibroni and recognized as P. dendyi only those populations occurring in the south-eastern corner of eastern Australia (see Fig. 3.1). This is essentially the view that has been accepted here.

Distribution

Within south-eastern N.S.W. P. dendyi occurs on the Kosciusko Plateau, Tinderry Mountains, the coastal range and coastal plain south of Jervis Bay (Fig. 3.2). On the Kosciusko Plateau within the Snowy Mountains region P. dendyi is allopatric with P. corroboree. A population of P. corroboree at Smiggin Holes occurs within 5 km of P. dendyi at Daner's Gap, near the Kosciusko Chalet. In the Fiery and Brindabella Ranges, the two species are

sympatric. P. dendyi has not been recorded from the south-eastern tableland area but this is probably due to the lack of collecting in this area by herpetologists.

P. dendyi is found in a variety of habitats. At high altitudes, above 1,220 m, it occurs in subalpine woodland and wet sclerophyll forest surrounding sphagnum bogs or wet heaths, and at low altitudes it is frequently found in dry sclerophyll forest and savannah woodland adjacent to wet heaths, temporary streams and other places subject to slight seasonal flooding.

In the Snowy Mountains area P. dendyi ranges in altitude from 427 m at Swampy Plains River to 1,585 m at Boggy Plain. Further north in the Brindabella Range it occurs from 975 m at California Flats to 1,640 m at Snowy Flats.

Colour and Pattern

Both P. dendyi and P. bibroni are very similar in colouration and patterning of the body. Moore (1961) distinguished P. dendyi from P. bibroni on the basis that in "Pseudophryne dendyi the yellow patch on the arm is conspicuous, whereas in Pseudophryne bibroni it is inconspicuous. Pseudophryne dendyi always has a

conspicuous yellow spot restricted to the cloacal region and the proximal portion of the thighs. The post femoral glands are not included. Pseudophryne bibroni may have some yellow on the posterior surface."

These characters, however, are very variable in both species. In most specimens of P. dendyi examined from the southern tablelands of N.S.W., the yellow patch on the upper forearm was conspicuous (Figs. 3.3 G and 3.5 A) but in some it was inconspicuous and represented by only a very small spot. Individuals displaying such a feature have been found at Little Thredbo River Flats in the Snowy Mountains region, Clyde Mountain and Moruya on the coast, and at California Flats in the Brindabella Range.

The yellow cloacal patch, as Moore (1961) noted, tends to be more variable in shape than the patch on the upper forearm. Moore's observation that it does not include the post femoral glands only applies when the patch is very well developed i.e. when it is in the form of a dumb-bell (Fig. 3.3 G) or a square. In most individuals of P. dendyi the cloacal patch reaches the proximal extremity of the post femoral glands and in some it runs across this gland to the distal extremity. The shape of this patch varied from the forms already noted above to

those where it was represented by only a very thin, slightly curved line. In some individuals the cloacal region was marked by three or four spots rather than a composite patch. All or most of these variations were found in one population, e.g. at Little Thredbo River Flats, Coree Flats, Clyde Mountain and a few kilometres west of the northern extremity of Lake Eucembene.

Some populations appeared to be fairly consistent in regard to the amount of yellow on the body. In a small sample of 8 males from Kiandra Ck., a few kilometres north of Kiandra, the yellow patch on the upper arm was prominent and covered three-quarters of the upper surface; the cloacal patch was well developed and in addition there were yellow spots on the lateral sides of the head. Only one other population (Swampy Plains River) showed a greater development of yellow. Specimens from this locality were characterized by having yellow on the snout, above the eyes and on and near the urostyle (Fig. 3.3 G).

Patterns on the ventral surface of the body of P. dendyi varied within and between populations and there appeared to be no obvious geographical trends. Most individuals had belly patterns which were similar to

Fig. 3.5

A. Dorsal view of P. bibroni, Uriarra, A.C.T.

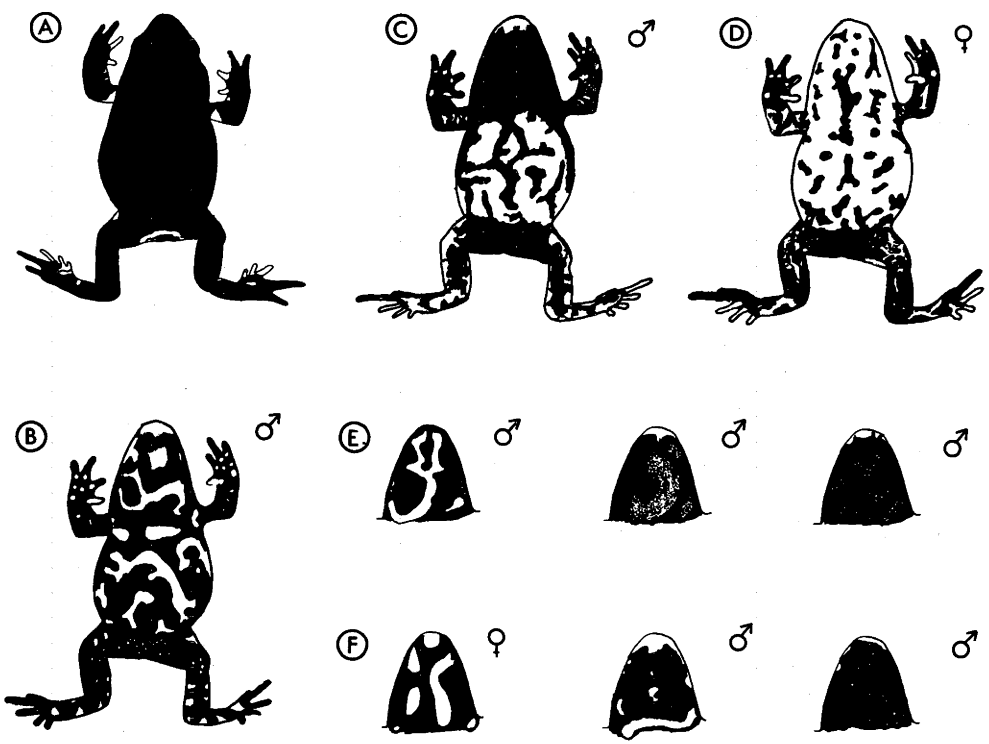
B. Ventral view of same individual.

C. Ventral view of male P. bibroni, near Yass, N.S.W.

D. Ventral view of female P. bibroni, near Yass, N.S.W.

E. Throat patterns of breeding males of P. bibroni, Uriarra, A.C.T.

F. Throat patterns of one female and two males of P. dendyi, Clyde Mountain, N.S.W.


A
C
♂
D
♀
B
♂
E
♂
♂
♂
F
♀
♂
♂

the ones shown in Figs. 3.3 J and H. Throat patterns differed between individuals but this seemed to be associated with sex. The lighter throat patterns tended to be more characteristic of females (Figs. 3.3 J,K and 3.5 F) and the darker patterns of males (Figs. 3.3 H,K and 3.5 F). This difference was more apparent in mature individuals obtained during the breeding season. In some samples of breeding individuals, the sexes could not be distinguished solely on throat pattern as in some males the pattern was similar to that of the females (Fig. 3.5 F). Specimens from Long Plain (Figs. 3.3 I,J,K) and Yarrangobilly displayed considerably more variation in colour and pattern than those from any other locality. In some individuals the morphological features were similar to those characterizing P. dendyi (yellow on the upper forearm and around the cloaca) whereas in others they were similar to P. bibroni (yellowish-orange to orange on the upper forearm and around the cloaca). Generally, the patch on the upper forearm and near the cloaca was not as conspicuous nor as well developed as in most individuals of P. dendyi. The belly patterns ranged from those that were marbled (Fig. 3.3 J) to those that were speckled (Fig. 3.3 K). Although the populations

at Long Plain and Yarrangobilly have been called P. dendyi they may include individuals of P. bibroni as well as hybrids of these two species.

Size

No clearly defined trends in size were evident in the samples of males and females of P. dendyi. There were, however, some differences between localities differing greatly in altitude over a short distance which may indicate clinal variation. For example, males from Boggy Plain are significantly larger than those from Little Thredbo River Flats which is lower than Boggy Plain and only three miles south (Fig. 3.6). Similarly, males from Clyde Mountain were larger than those from Moruya near sea level.

iii) P. bibroni Günther 1858

The history of the taxonomic status of P. bibroni has been discussed by Parker (1940) and more recently by Moore (1961). Moore's conclusions regarding the status and distribution of this species have been accepted in the present study.

Distribution

P. bibroni is the most widely distributed of the three species. It occurs from Rockhampton in Queensland,

south along the Great Divide and the eastern and western slopes to Victoria and then north-westwards to Adelaide. It is also found in Tasmania (Fig. 3.1).

P. bibroni is not found throughout this whole region for it is absent from certain areas, notably on the Hawkesbury sandstone areas in the County of Cumberland, in south-eastern Australia and in the vicinity of Melbourne. In the three areas it is replaced by other members of this genus.

Because of the morphological similarity with P. dendyi, a number of populations have been described as being P. bibroni but are probably P. dendyi. Jacobson (1963) recorded P. bibroni from the Brindabella Range at an elevation of approximately 1,158 m but as this is out of the normal range of P. bibroni it is most likely that this population is P. dendyi. Similarly, in Victoria, Brazenor (1947) reported P. bibroni from near Gelantipy in the north-east corner of the state. If these are P. bibroni they represent an inlier within the distributional range of P. dendyi.

The distribution of P. bibroni in south-eastern N.S.W. is shown in Fig. 3.2 where it occurs over most of the northern part of this region. P. bibroni may extend

south from Canberra along the Murrumbidgee Valley to near Cooma but as yet there are no records of its occurrence in this area. Generally, P. bibroni is found below 610 m. Above this altitude it is replaced by its cogener P. dendyi.

Colour and Pattern

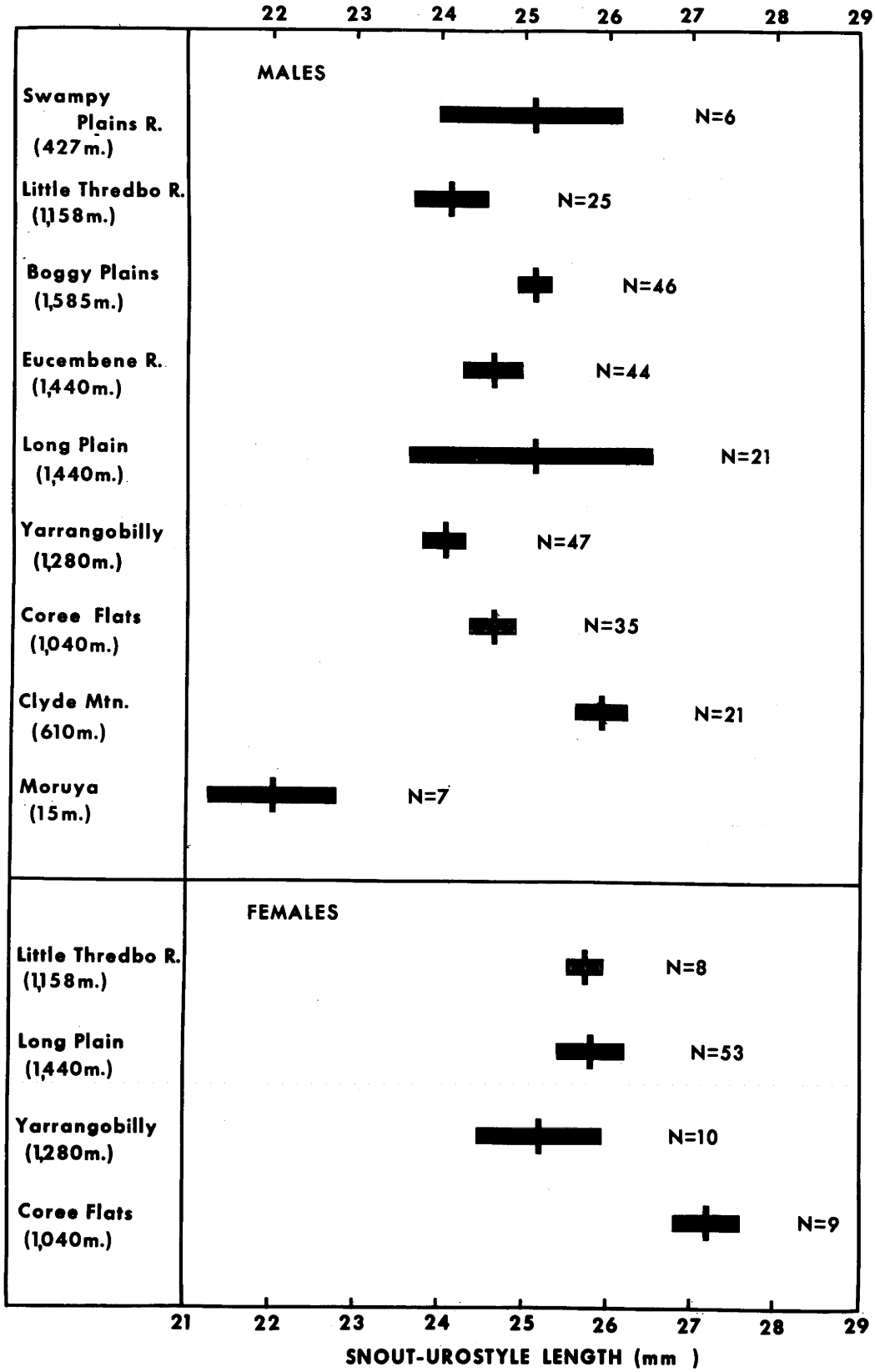
Morphologically, P. bibroni is similar to P. dendyi but differs from that species principally in the colour and conspicuousness of the patch on the upper forearm and in the cloacal region. In P. bibroni the upper forearm and cloacal patches are dull yellow to cream and are generally less well developed and inconspicuous.

These two species also differ in body colour. Specimens of P. bibroni from the north-eastern foothills of the Brindabella Range, near Yass, and from Canberra tend to have a very light body colour which is dark grey rather than dark brown. This light body colour tends to make the pale yellow or cream patch on the upper forearm less conspicuous even though it may cover more than half the upper surface of the forearm.

Some morphological variation was noticed between specimens of P. bibroni from within the region extending west from Lake George to Yass and Uriarra. Specimens from the north-east foothills of the Brindabella Range

Fig. 3.6

The snout-urostyle length of adult males and females of *P. dendyi*.


22
23
24
25
26
27
28
29
MALES
Swampy Plains R. (427m.)
N=6
Little Thredbo R. (1,158m.)
N=25
Boggy Plains (1,585m.)
N=46
Eucembene R. (1,440m.)
N=44
Long Plain (1,440m.)
N=21
Yarrangobilly (1,280m.)
N=47
Coree Flats (1,040m.)
N=35
Clyde Mtn. (610m.)
N=21
Moruya (15m.)
N=7
FEMALES
Little Thredbo R. (1,158m.)
N=8
Long Plain (1,440m.)
N=53
Yarrangobilly (1,280m.)
N=10
Coree Flats (1,040m.)
N=9
21
22
23
24
25
26
27
28
29
SNOUT-UROSTYLE LENGTH (mm)

(Uriarra and Mountain Ck. Rd.) tend to have less of the ventral body surface covered with white marking than do specimens from Yass or Lake George. In addition, it was noticed that one specimen from Uriarra could have been classed as P. dendyi on the basis of the dark body colour, the nature of the ventral pattern and the development of the yellow patch on the upper forearm. Whether this specimen is P. dendyi is not certain but as P. dendyi is known to occur within three miles of this locality it is quite possible that it is. Some males collected from burrows near Yass, N.S.W. had very dark throats (Fig. 3.5 C) in contrast to the very white marbling pattern exhibited by the gravid females (Fig. 3.5 D). A sample of males collected in the breeding area at Uriarra, A.C.T., showed a progressive gradation in throat patterns from light to dark (Fig. 3.5 E). The throat patterns of males obtained during the non-breeding season are similar to the one shown as the first illustration in Fig. 3.5 E.

P. bibroni, therefore, exhibits the same kind of sexual dimorphism in throat patterns as was noted in P. dendyi.

Size

The snout-urostyle lengths of adult males and females found in the breeding areas are shown on Table 3.2.

Because of the small numbers of females collected it is not certain whether there is any sexual dimorphism in size. The Uriarra population appears to be the only one where sexual differences in size are apparent.

Male P. bibroni from these three localities are about the same size as male P. dendyi from Coree Flats but female P. bibroni are much smaller than female P. dendyi from the same locality. However, they are about the same size as females from Long Plain and Yarrangobilly, two localities which are probably at the northern limit of the range of P. dendyi.

Table 3.2 Snout-urostyle lengths* of adult P. bibroni

Locality		Males	Females
7 mls south Yass, N.S.W.	No.	25	5
	Mean	24.8	25.6
	S.D.	1.26	1.47
	S.E.	0.25	0.62
Mountain Ck. Rd., N.S.W.	No.	11	2
	Mean	23.8	24.2
	S.D.	1.25	4.84
	S.E.	0.38	3.42
Uriarra, A.C.T.	No.	19	2
	Mean	24.4	25.4
	S.D.	1.14	0.08
	S.E.	0.26	0.06

* all measurements are in mm

Chapter 4 GENERAL BIOLOGY

4.1 Outline of the Life History of *Pseudophryne corroboree*

Much of the information given in this chapter concerns the populations of *P. corroboree* at Coree Flats. In order that the facts may be viewed in perspective, an outline of the life history of *P. corroboree* is given below.

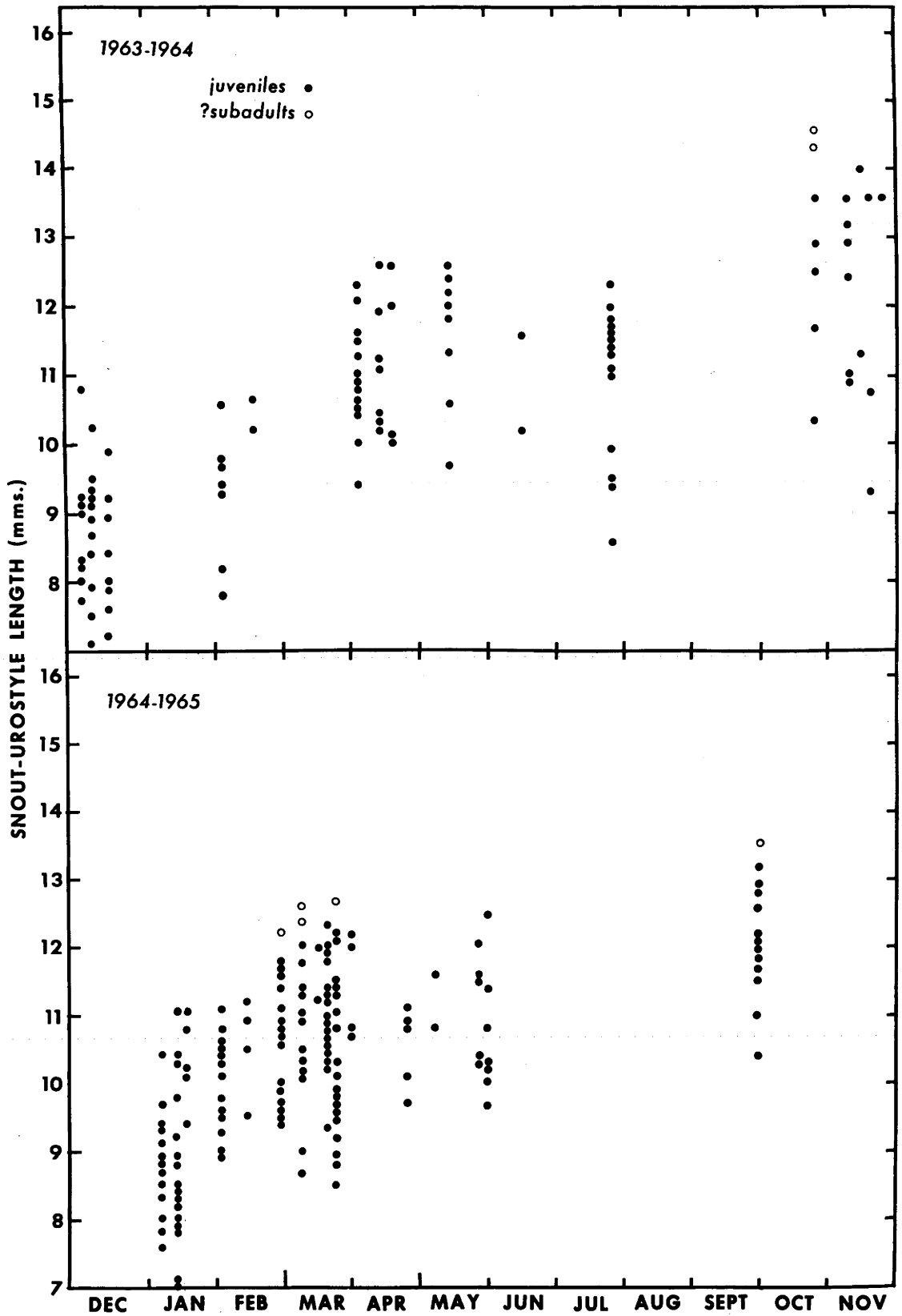
At Coree Flats *P. corroboree* breeds during the early autumn (March to April) and lays large, heavily yolked eggs in burrows on land. These burrows are constructed by males and are generally situated in moss, other vegetation, and soil, around the edges of slight depressions which will become pools during the winter. In places where there is permanent water the burrows are from 5 to 10 cm above the early autumn water level.

The eggs develop until a fairly advanced tadpole stage is reached which usually takes from two to three weeks. Further morphological changes in the tadpoles are not apparent until hatching occurs (May to June) when the burrows are flooded as a result of the increased rainfall at the onset of winter. Very little growth takes place in the tadpole during the winter, presumably because of the low water temperatures experienced in the pools (Fig. 2.8). Metamorphosis occurs during spring

and early summer. After metamorphosis for about 3 to 10 weeks, the juvenile frogs remain around the edges of the pools, which are by then beginning to dry up. The length of time spent in these micro-habitats depends upon the evaporation rate of ground moisture which is governed partly by the type of vegetation cover. The monkey musk, Mimulus moschatus, tends to retain moisture in the soil for a greater length of time than do grass species, including the various species of Agrostis, and is therefore utilized as cover by the majority of recently metamorphosed juvenile frogs. When these areas begin to dry up, the juvenile frogs move to moister areas usually found in the ecotone zone bordering the wet heath. By the beginning of the breeding season (March) the majority of juveniles have dispersed to these areas, though a few are sometimes found in the central portion of the heath. The juveniles apparently remain in the ecotonal zone until they are about subadult size (14 to 20 mm in snout-urostyle length). This means that they spend two or more winters in this area. Dispersal up into the wet sclerophyll forest probably occurs when they are reaching adulthood. Of more than 600 individuals marked by toe-clipping in the forest at Coree Flats, only one subadult

Fig. 4.1

The snout-urostyle length of P. corroboree juveniles collected over a two-year period at Coree Flats, N.S.W. Juveniles are those individuals which are below 14 mm in snout-urostyle length; subadults are those which are between 14 and 20 mm in snout-urostyle length.


1963-1964
juveniles
?subadults
1964-1965
SNOUT-UROSTYLE LENGTH (mms.)
16
15
14
13
12
11
10
9
8
7
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV

was found more than 30 yards from the edge of the ecotone zone of Leptospermum sp. Although most of the adults are found under logs, leaf litter and vegetation in the forest, some occur in the peripheral areas of the ecotone zone. Adults remain under cover for most of the year and are only seen out in the open during the period December to April.

4.2 Growth of Juveniles

The only information on growth in P. corroboree has been derived from snout-urostyle measurements of preserved juveniles which were collected at infrequent intervals throughout the year over a two-year period. Because of the small samples involved, and the lack of data on individual growth rates, growth during the first year of the life of juveniles can only be approximated.

The size at, and time of, metamorphosis are probably two of the major factors affecting growth during the few months following metamorphosis. Unfortunately, the estimate of the size at which this species metamorphoses is based on only a few individuals because it was difficult to find specimens which showed signs of having recently metamorphosed. Two such specimens collected at Coree Flats measured 7.0 and 8.3 mm in body length and four

specimens collected at Snowy Flats ranged from 7.3 to 9.4 mm.

An indication of when this begins is obtainable by noting the upper size limit at metamorphosis and the size distribution of specimens in the first sample collected. Thus estimated , metamorphosis would have begun during 1963 in November, and during 1964 in December. Metamorphosis was later in 1964 probably because of the relatively lower temperatures recorded for the period September to December, 1964 (Fig. 2.5).

In the beginning of winter most of the individuals were between 9 and 12 mm in body length (Fig. 4.1). Very little growth occurs during the winter probably because of the low temperatures experienced in the micro-habitat. By the time these individuals are about one year old, most of them have attained a size of between 10 and 14 mm.

4.3 Sex Ratio

In P. corroboree there are no external secondary sex characters and normally the sexes can only be differentiated on dissection, though adult females can be distinguished from males during their brief periods of gravidity and immediately following egg laying.

The results shown in Table 4.1 have been derived from samples collected at Coree Flats from March, 1963 to May, 1965. All adults and some subadults were collected from under logs and leaf litter in the wet sclerophyll forest surrounding the breeding area. Juveniles and the remainder of the subadults were obtained from the breeding area. The samples have been divided into two periods, March to August ('winter') and September to February ('summer') to determine whether there were any differences in sex ratio, principally in the adults, between the colder and warmer months of the year.

The sex ratio in the juveniles as revealed by these samples was approximately 1:1 for both periods of the year and in each period except for the period March to August, 1964, when there were twice as many females as males represented in the sample. In the subadults the male to female ratio was approximately the same during the 'winter' period but varied from 1:1 to approximately 2:1 in those obtained during the 'summer' periods of 1963-64 and 1964-65, respectively. A similar picture was also obtained in the adults except that in this age group there was an even greater disparity between the sexes. In the two 'winter' samples the ratio of males to females ranged from 5:1 to 6:1

Table 4.1 Male:Female ratio of juveniles, subadults and adults of *P. corroboree* at Coree Flats

Period	Year	Juveniles		Subadults		Adults	
		Males	Females	Males	Females	Males	Females
March-August ('winter')	1963	13	19	7	3	45	7
	1964	8	17	9	4	50	10
March-May (autumn)	1965	39	32	12	6	27	2
September-February ('summer')	1963-64	6	6	12	12	52	43
	1964-65	38	40	28	16	89	26

but in both 'summer' samples there was a proportional increase in the females with the greatest increase occurring in the 'summer' period of 1963-64.

The changes which occurred in the sex ratio of the adults between the 'winter' and 'summer' periods are most probably due to the migration of sexually mature males from the forest or non-breeding area to the breeding area. The effect which emigration has on the sex ratio can be seen by comparing the ratios obtained during the two 'summer' periods. Towards the end of the summer 1964-65, the majority of males moved into the breeding area and this resulted in a large increase in the proportion of females in the forest population. During January and February, 1965, conditions were generally unfavourable for breeding and relatively few males were found in the breeding area. The proportion of females collected in the forest area was much less than in the corresponding period of 1964, the sex ratio being approximately 3:1.

These results therefore, suggest that the number of males greatly exceeds the females, for if the ratio was 1:1, an even greater increase in the proportion of females could be expected during the period following the emigration of the males. It also appears that the

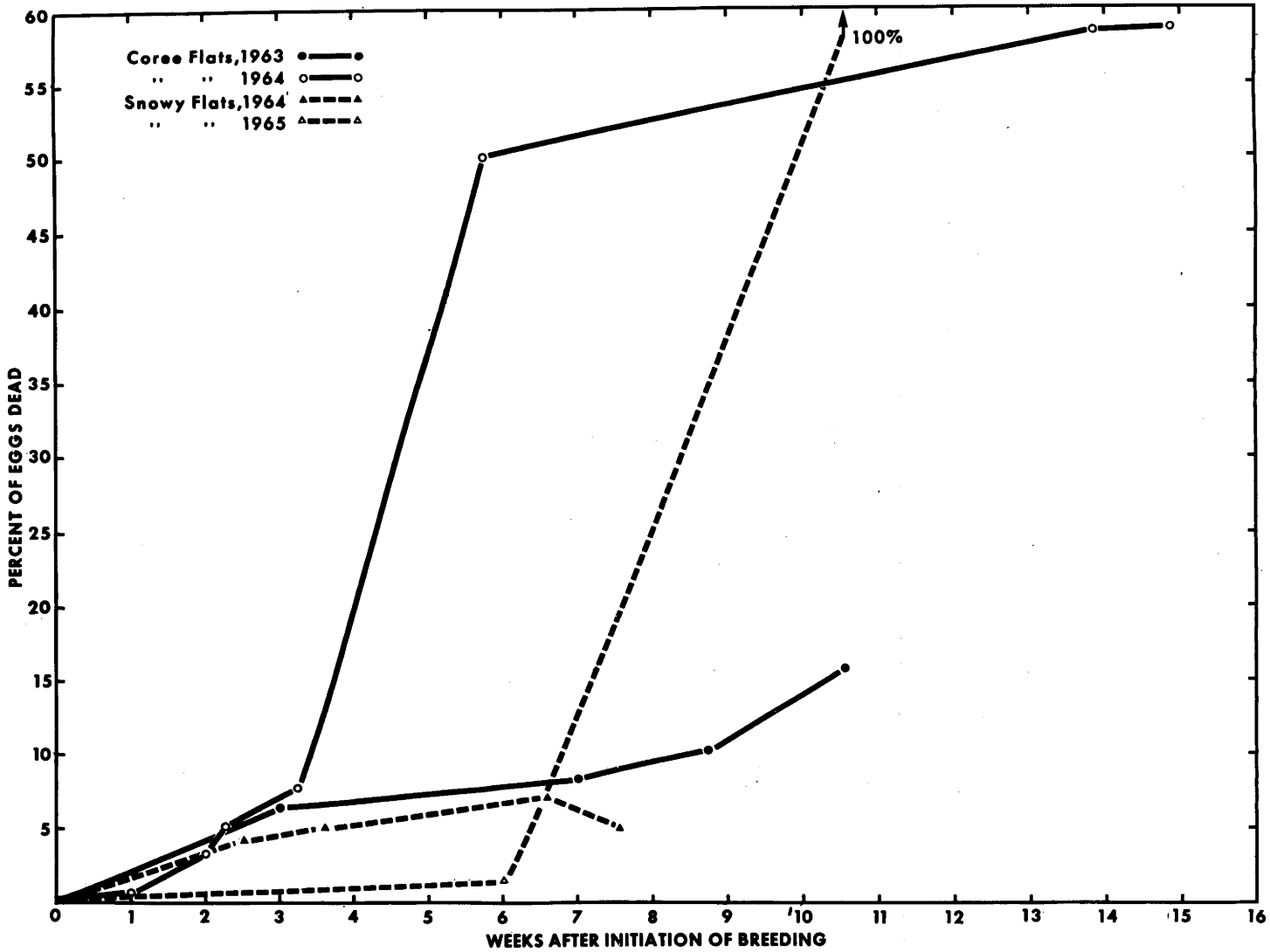
proportion of females in the population decreases with age. This decrease is possibly due to differential mortality of the females in the subadult and adult phases of the life history. In the adult phase, females may be more vulnerable to predators, especially during the breeding season. Gravid females probably spend 2 to 4 days in the breeding area and, except for a brief period when the eggs are being deposited, they are not in burrows but are under cover of vegetation, or out in the open. Predators could attack them when they were searching for calling mates.

4.4 Mortality and Predation

Although there have been many studies on the population dynamics of amphibians, very few workers have examined the population consequences of the larval stages of the life history of a species. This has been partly due to the difficulties experienced in sampling eggs or tadpoles, as most of the species selected for population studies are aquatic during this phase of their life history. Species of Pseudophryne are more amenable to studies of this sort because they lay relatively small numbers of eggs in burrows on land which enables them to

Fig. 4.2

The percentage of eggs of P. corroboree found dead in nests at various times following breeding.


Coree Flats,1963
" " 1964
Snowy Flats,1964
" " 1965
100%
PERCENT OF EGGS DEAD
WEEKS AFTER INITIATION OF BREEDING
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
5
10
15
20
25
30
35
40
45
50
55
60

be sampled fairly easily. Because there is an aquatic tadpole stage in these species, the same sampling difficulties are encountered as in other species where the early life history is wholly aquatic. For this reason most of the data obtained on mortality refer to the eggs.

To obtain some data on the mortality of eggs in P. corroboree, a random sample of nests was examined at infrequent intervals during 1963 and 1964 at Coree Flats, and during 1964 and 1965 at Snowy Flats. The number of nests examined and eggs counted on various dates during 1963, 1964 and 1965 have been tabulated in Table 4.2. Figure 4.2 shows the percent of eggs found dead at the two localities during these years.

Within a month after breeding had begun the mortality was fairly low ranging from 1.4% to nearly 8.0% (Fig. 4.2). Most of this mortality can be attributed to deaths from desiccation and those arising from abnormal development, with subsequent infection of the eggs by fungi. At Snowy Flats during 1964 most of the eggs which died did so as a result of disruption of early development or as a result of subsequent infection by fungus in the egg cluster. Desiccation was a negligible mortality factor. However,

Table 4.2 Deaths in eggs of *P. corroboree* at two localities in the Brindabella Range

Date	Snowy Flats		Coree Flats	
	No. of Eggs in Nests*	% Dead	No. of Eggs in Nests	% Dead
17.3.63	-	-	953 (19)	6.4
15.4.63	-	-	713 (14)	8.3
27.4.63	-	-	859 (16)	10.4
9.5.63	-	-	1,305 (30)	15.9
8.2.64	427 (10)	4.0	-	-
16.2.64	1,276 (24)	5.0	-	-
7.3.64	1,007 (18)	7.0	854 (31)	0.7
14.3.64	464 (10)	5.8	369 (8)	3.3
16.3.64	-	-	419 (16)	5.0
22.3.64	-	-	874 (27)	7.6
10.4.64	-	-	466 (18)	50.0
6.6.64	-	-	207 (7)	57.0
14.6.64	-	-	407 (12)	58.7
16.3.65	212 (7)	1.4	-	-
8.5.65	212 (7)	100.0	-	-

* number of nests examined are shown in parentheses

during 1965, all eggs died from desiccation. Normally, the sphagnum moss in which these eggs had been laid would have contained a great deal of water but during this period it became very dry and brittle and all eggs were dead by the beginning of May (Table 4.2).

At lower altitudes (about 1,050 m) mortality through desiccation is probably much greater due to the relatively low rainfall and the near absence of hydrophilous plants such as sphagnum moss. From February until about June when the winter rains begin, the moisture levels in the breeding areas were fairly low except for places near permanent pools and beside streams.

Harrison (1922) suggested that the adults of P. australis, by remaining in the nest after the eggs had been laid, kept the eggs moist. Although male P. corroboree tend to remain with the eggs for some weeks after they are laid, no relationship was found between the presence or absence of a male and the percent mortality in eggs at Coree Flats during 1963 and 1964. By remaining in a nest a male, whether of P. corroboree, P. dendyi or P. bibroni, may affect the survival of the eggs in other ways. It was observed repeatedly that in breeding areas which were dry, recently-laid eggs quickly

became coated with a layer of soil through the movement of the male in the nest. This layer of soil around the egg could act as a barrier to desiccation, thereby reducing the amount of water lost by the egg.

When fully hydrated the eggs of P. corroboree are about 7-8 mm in diameter but on dehydration they shrink to about 3.5 mm in diameter. Although the tolerance to water loss of the eggs of this species is not known it would seem that they can withstand a great deal of water loss before death ensues.

As nests at Coree Flats were only examined just before hatching in 1964 no comparisons can be made between different years or between the two localities. Approximately 40% of the eggs laid in 1964 survived to hatching. The mortality of tadpoles in the pools was not followed as closely as was that of the eggs, but three pools in the middle of the breeding area were sampled a few weeks before the tadpoles metamorphosed. The mortality in the three pools was 50%, 86.5% and 93.6%, and was probably caused by predation by the nymphs of two species of dragonfly (Acanthaescha sp. and Synthemis sp.) present in all pools. Predation by these nymphs would probably be moderated by the presence of

cover (leaves, sticks and aquatic vegetation) and by the behaviour of Pseudophryne tadpoles in burrowing in the soft bottom if no cover is available. At two areas near Coree Flats in 1963 some pools dried up before the tadpoles metamorphosed but this was never observed at Coree Flats during 1963 or 1964.

Data on mortality of frogs are very difficult to obtain since dead animals are only very rarely found in the field, and even then it is nearly impossible to determine the cause of death. During the two and a half years of this study only 9 juveniles and 7 adults were found dead at Coree Flats. All of the juveniles were seen or collected during the drought of 1965 in areas which were extremely dry. Apparently, these individuals had died from the lack of moisture. Of the adults found dead, one had probably been crushed by a motor vehicle, another by a log. Two of the remaining five adults were marked males, found dead in burrows during the breeding season of 1964; these individuals appeared as if they had only recently died. The remaining three adults were found dead beneath logs during the 1965 drought, and as the soil beneath the logs was very dry it was assumed that they had died from desiccation. Large numbers of emaciated and

dehydrated juvenile and adult frogs were seen from February to April, 1965. The extremely poor condition of these frogs probably was a result of lack of moisture under logs as well as lack of food. Predation probably causes most mortalities in drought-free years although parasitism may have some effect (see pages 49-62).

Although predation has not been observed in the field, snakes and birds are possibly the major predators of these and other frogs. The only report on predation is by Colefax (1956) who observed predation by a black snake, presumably Pseudechis porphyriacus Shaw, on P. corroboree adults at Alpine Hut, Snowy Mountains. The black snake is found throughout the southern tablelands of N.S.W. and occurs at various localities on the Brindabella Range including Coree Flats. The white-lipped snake, Denisonia coronoides Günther, is the only other species seen or collected at Coree Flats, where it is more abundant than the black snake. According to Worrell (1963) this species feeds on small skinks and immature frogs. The examination of the stomachs of three adult specimens collected at Coree Flats revealed only the remains of a skink, Siaphos maccoyi. Since this skink occurs in the same micro-habitat as juvenile

and subadult P. corroboree frogs it seems feasible that they are also preyed upon.

Very few predaceous birds were seen at Coree Flats. An unidentified owl, which could have been either the Boobook (Ninox boobook Latham) or Powerful Owl (Ninox strenua Gould), was seen periodically during the 1964 breeding season, though Cayley (1931) makes no mention of these two species preying on frogs.

Predation of adult frogs probably occurs during migration of both sexes to the breeding areas and during the actual breeding season. Gravid females would be more liable to predation during the latter period as they, unlike the males, spend very little time in burrows concealed from large predators. The actual time that a female spends in the breeding area is very short, and probably does not exceed 3 or 4 days, though this would be ample time for her to fall prey to snakes or owls.

4.5 Parasitism

Much of the work on parasitism in frogs has been done by investigators primarily interested in the morphology, physiology or pathology of parasites. As a result, the ecological aspects of parasites, such as their

distribution and abundance in a host has received very little attention.

While examining specimens of five species of frog, including P. corroboree, P. dendyi and P. bibroni, for food contents, some information was also obtained on the natural history of three macroscopic parasites infecting these species. Two of these parasites, a protocephalid cestode and an oxyuroid nematode, are confined to the alimentary canal, while the third, the larvae of the fly Batrachomyia sp., is generally found under the skin of the host. Although this myiasid-producing parasite was recorded in all five species, only the results of its occurrence in the three species of Pseudophryne are reported here.

i) Parasitism by Batrachomyia spp.

Ten species of the exclusively Australian dipteran genus, Batrachomyia or frog flies, have been described but only four of these have been positively related to anuran host species. Batrachomyia quadralineata is reported to parasitize Pseudophryne bibroni (Skuse, 1889) and an undescribed species parasitizes P. corroboree (MacAlpine, 1966, pers. comm.). Apart from the species infecting P. corroboree, these parasites were not reared

to adulthood so their identification must remain tentative at this stage.

Information on the life cycles of Batrachomyia spp. is virtually non-existent. Both Elkan (1965) and Zumpt (1965) have recently summarized the biology of these species which is largely known from the study by MacAlpine (1955). According to Zumpt "the eggs are deposited on the substrate and not on the frog's skin. They are very sensitive and require a high humidity..... It is not known how the young larvae reach the frog..... The last larval instar is located in the subcutaneous lymph spaces, and is almost invariably in contact with the exterior by a small hole in the skin through which the posterior spiracles project slightly. The swellings measure about 1 cm and are found mainly on the trunk. The larvae feed on blood by piercing the vessels. When mature the larvae leave the swellings actively in the daytime, move to a dark shelter and normally pupate within the next 24 hours."

Results

Table 4.3 shows the percentage of parasitized individuals of the various species of Pseudophryne from a number of localities. The number of specimens examined represents the total of all samples collected during two

Table 4.3 The incidence of the fly parasite *Batrachomyia* sp. (Diptera: Chloropidae) in *Pseudophryne* spp.

Species	Locality	Age Group	No. Examined	% Parasitized
Pseudophryne corroboree	Smiggin Holes	A	76	0.0
"	Round Mtn.	A	44	0.0
"	" "	J	4	25.0
"	Snowy Flats	A	54	0.0
"	" "	J	1	0.0
"	Coree Flats	A	255	12.6
"	" "	SA	85	58.8
"	" "	J	214	63.6
P. dendyi	Boggy Plain	A	46	19.6
"	Little Thredbo R. Flats	A	34	5.9
"	Yarrangobilly	A	57	5.3
"	"	SA	9	77.8
"	Coree Flats	A	43	32.6
P. bibroni	near Yass	A	40	5.0
"	Mountain Ck. Rd.	A	13	15.4
"	Uriarra	A	25	0.0

A = adults; SA = subadults; J = juveniles

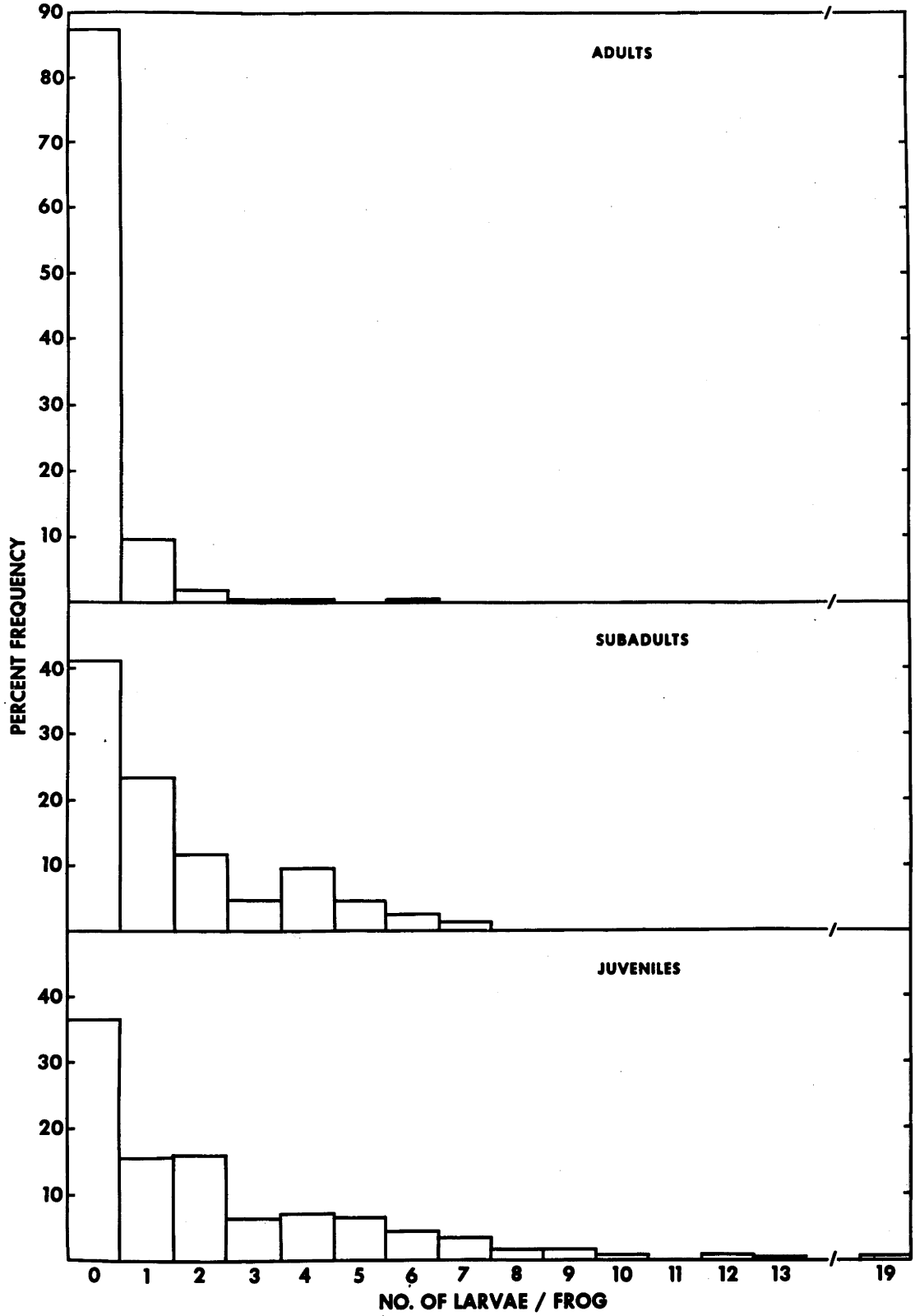
breeding seasons or at various times throughout the year.

In P. corroboree the incidence of parasitism, as revealed by the percentage of individuals parasitized, varied with age and with altitude (Table 4.3). Of the 214 juveniles examined from Coree Flats, approximately 64% were infected with Batrachomyia larvae. Approximately the same percentage of subadults from the same locality were also infected but in the sample of adults only 12.6% were parasitized. Comparison of the samples of adults from four localities (three from the subalpine zone and one from Coree Flats) revealed that no adults from the subalpine areas were infected (Table 4.3).

The incidence of parasitism in P. dendyi and P. bibroni varied considerably between localities without exhibiting any obvious geographical or altitudinal trends (Table 4.3). The greatest percentage of adult individuals of P. dendyi parasitized occurred in the sample from Coree Flats (32.6%) and the least in a sample of 57 adults from Yarrangobilly (5.3%). In the Snowy Mountains region the incidence of parasitism was greater in the sample from Boggy Plain (19.6%) than in the one from Little Thredbo River Flats (5.9%). The percentage of adult P. bibroni parasitized varied from nil in the Uriarra sample to 15.4%

Fig. 4.3

The number of larvae of *Batrachomyia* sp. per individual of *P. corroboree*. Samples were obtained from Coree Flats, N.S.W.


ADULTS
SUBADULTS
JUVENILES
PERCENT FREQUENCY
90
80
70
60
50
40
30
20
10
40
30
20
10
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
19
NO. OF LARVAE / FROG

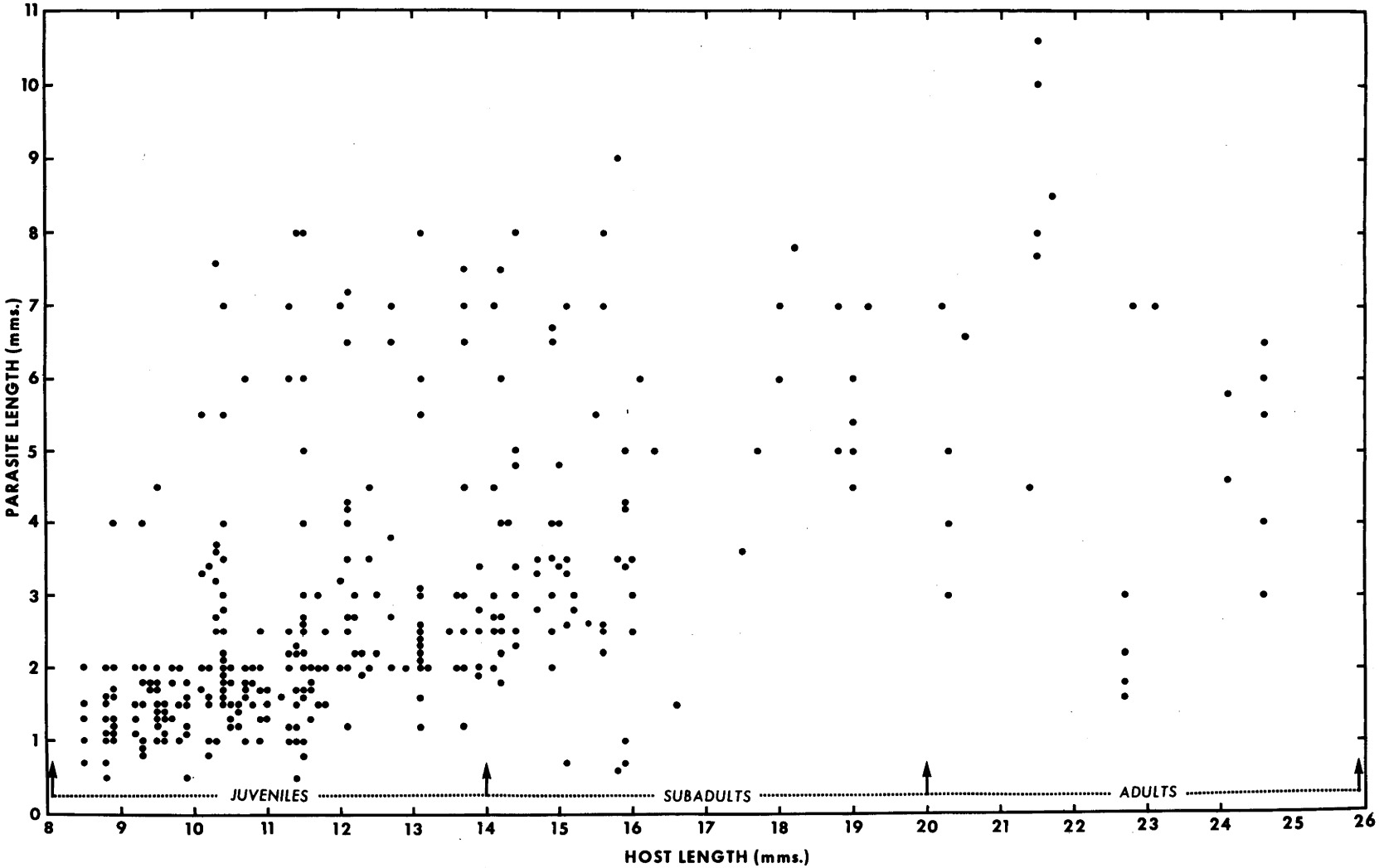
in the Mountain Creek Road sample (Table 4.3).

Data on the level of infection - as defined by the number of parasites per individual - the size of the parasite in relation to the host size, and the distribution of parasites on the host are available for P. corroboree from Coree Flats. Juvenile frogs were more heavily infected than either the subadults or the adults (Fig. 4.3). The greatest numbers of larvae found in juveniles, subadults and adults were 19, 7 and 6 respectively. Except for the juveniles, the majority of parasitized individuals contained only one parasite.

Although most juveniles were infected with more than one larvae, approximately 60% of these parasites were less than 2 mm in body length, 32.7% were 2 to 6 mm in length and the remainder were greater than 6 mm in length (Fig. 4.4). In the larger frogs most of the parasites were greater than 2 mm in body length. The parasites obtained from adult frogs were the largest and in this age group more than 41.7% of the parasites were greater than 6 mm. From Fig. 4.4 it seems that there is some relationship between the size of the parasite and the size of the host, in the juvenile and to a certain extent in the subadult age groups. The dissociation

Fig. 4.4

A scatter diagram of the length of *Batrachomyia* sp. larvae against the body-length of the host, *P. corroboree*.

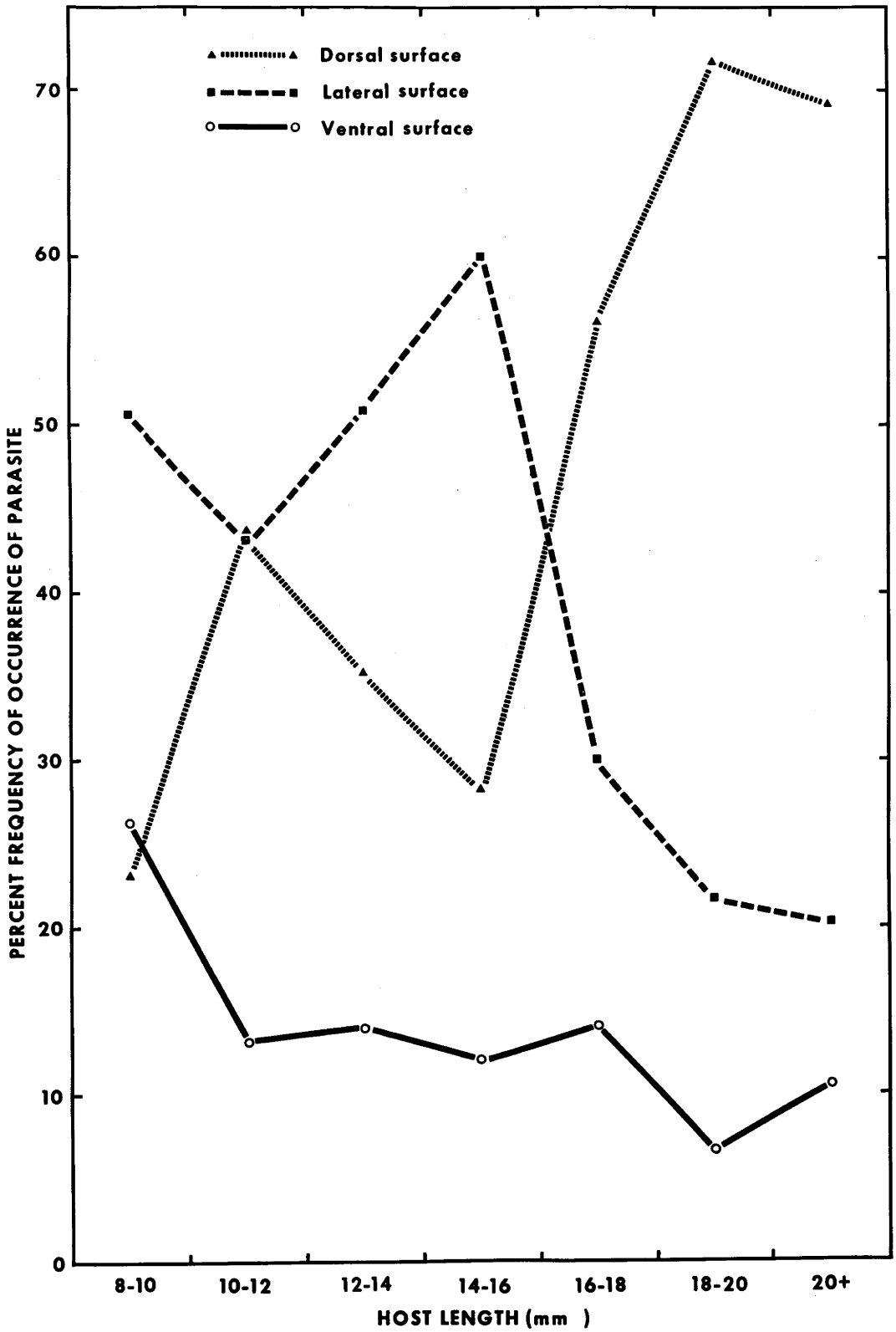

PARASITE LENGTH (mms.)
HOST LENGTH (mms.)
JUVENILES
SUBADULTS
ADULTS
0
1
2
3
4
5
6
7
8
9
10
11
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

between size of the parasite and the host size in frogs greater than 16 mm in body length could be due to differential growth of parasite and host or to some frogs being infected when they were subadults or adults and not juveniles. The differences in the growth rates of parasite and host may also explain why some of the frogs less than 16 mm contained large parasites. From the data obtained on the growth of juvenile frogs (Fig. 4.1) it is likely that individuals 10 mm or so in body length could differ in age by 6 to 12 months.

From Fig. 4.5 it seems that the distribution of parasites under the skin of P. corroboree changes with the size of the host. In the juveniles and subadults between 12 to 16 mm in body length, most parasites were found on the ventral and lateral surfaces of the body, and in the remainder of the subadult age group and the adults, on the dorsal surface. The reciprocity between the occurrence of the parasites on the dorsal and the lateral surfaces suggests that the parasites migrate from the lateral to the dorsal surface of the body. The large percentage of subadults 12 to 14 mm in length with parasites on the lateral surface indicates that these frogs were only recently infected. It is possible that

Fig. 4.5

The distribution of *Batrachomyia* sp. larvae under the skin of *P. corroboree*.


Dorsal surface
Lateral surface
Ventral surface
PERCENT FREQUENCY OF OCCURRENCE OF PARASITE
0
10
20
30
40
50
60
70
8-10
10-12
12-14
14-16
16-18
18-20
20+
HOST LENGTH (mm)

the breeding of the flies is related to the time of metamorphosis of the frogs, and any frogs present in these wet areas are liable to infection about this time of the year.

Of those parasites found on the ventral surface of the juveniles, 19.6% were under the throat, 41.2% on the belly and 39.6% on the ventral surface of the legs. In the subadults, rather more parasites were found under the throat (34.0%). Three of the four adults parasitized on the ventral surface had parasites on the belly.

Although parasites were distributed unevenly over the dorsal surface of the body, they appeared to show some predilection for certain areas. In juveniles, approximately equal numbers of parasites were found on the head and near the urostyle, but in the subadults and adults more were located near the urostyle than in any other region.

ii) Other Parasites

Table 4.4 shows the percentage of individuals of five species of frog infected with a proteocephalid cestode. P. corroboree from Coree Flats and Snowy Flats and Crinia signifera from Coree Flats were the only populations found parasitized. Apart from the sample of P. corroboree subadults from Coree Flats all populations that were

Table 4.4 The numbers of proteocephalid cestodes and the incidence of parasitism in various species of frog including *Pseudophryne* spp.

Species	Locality	Age Group	No. Examined	No. of Cestodes/Frog		% Parasitized
				Mean	Range	
Pseudophryne corroboree	Coree Flats	adults	229	2.5	1-6	7.5
"	" "	subadults	27	3.4	1-8	37.0
"	" "	juveniles	48	1.3	1-2	6.3
"	Snowy Flats	adults	21	2.0	-	4.8
"	Snowy Mtns.	"	25	0.0	-	0.0
P. dendyi	Coree Flats	"	52	0.0	-	0.0
" "	Boggy Plain	"	16	0.0	-	0.0
P. bibroni	near Yass	"	29	0.0	-	0.0
Crinia signifera	Coree Flats	"	37	4.0	2-6	10.8
Hyla verreauxi	" "	"	11	0.0	-	0.0

Table 4.5 Numbers of oxyuroid nematodes and the incidence of parasitism in various species of frog including *Pseudophryne* spp.

Species	Locality	Age Group	No. Examined	No. of Nematodes/Frog		% Parasitized
				Mean	Range	
Pseudophryne corroboree	Coree Flats	adults	229	2.1	1-8	21.8
"	" "	subadults	27	1.3	1-2	11.1
"	" "	juveniles	48	1.0	-	4.2
"	Snowy Flats	adults	21	2.0	1-4	28.6
"	Snowy Mtns.	"	25	2.2	1-6	56.0
P. dendyi	Coree Flats	"	52	2.4	1-7	42.3
" "	Boggy Plain	"	16	4.3	1-9	75.0
P. bibroni	near Yass	"	29	4.3	2-8	10.3
Crinia signifera	Coree Flats	"	37	1.6	1-4	16.2
Hyla verreauxi	" "	"	11	7.0	6-8	18.2

parasitized contained approximately the same percentage of infected individuals. The level of infection was generally very low and no frog contained more than 8 cestodes.

The incidence of oxyuroid nematodes in the rectum varied considerably between species and between populations of the same species (Table 4.5). The highest percentage of parasitized individuals occurred in the sample of P. dendyi adults from Boggy Plain, Snowy Mountains (75%), and the lowest in 48 juveniles of P. corroboree collected at Coree Flats (4.2%). Samples of the three age groups, juveniles, subadults and adults of P. corroboree collected at Coree Flats showed that the incidence of parasitism increased with age. The level of infection in the various populations was low and the majority of infected individuals contained less than 4 nematodes.

iii) Discussion of Parasitism

From these results it seems that juvenile frogs are the most likely age group to be infected with Batrachomyia larvae. They probably become infected 3 to 8 weeks after they have metamorphosed as no frogs less than 8.5 mm in snout-urostyle length were ever found parasitized (Fig. 4.4).

From the size (Fig.4.4) and the distribution

(Fig. 4.5) of the parasite in the juvenile host it could be inferred that larval parasites gain entry to the host by boring through the skin on the ventral and lateral surfaces of the body. Elkan (1965) has suggested that they may enter the host by way of the alimentary canal and eventually come to lie under the skin. Examination of the stomach contents of 41 juveniles showed that only in two cases were fly-larvae present and in both the parasites were partly digested. If the mode of infection is via the alimentary canal one would expect to find larvae in the body cavity unless of course, the transition from the alimentary canal to the skin is accomplished in a very short period. Of the 136 juveniles parasitized, only 2.9% had larvae in the body cavity. It would seem, therefore, from these results and from the fact that partly digested larvae have been found in the alimentary canal, that the usual mode of entry into the host is through the skin. Corroborative evidence for this view comes from the observations made on the distribution of the parasite in Crinia signifera. In the juveniles of this species the larval parasites are found under the skin but in the adults the parasites are invariably found in the body cavity. Although this is probably not the same species of parasite

that infects P. corroboree, it is unlikely that its mode of entering the host would be radically different.

The decrease in the incidence of parasitism, and the level of infection with age, in P. corroboree from Coree Flats is probably due to a number of factors, among which could be the death of heavily infected juveniles and subadults. This would explain part of the decrease noted, provided the individuals that were not parasitized as juveniles did not become infected in the later phases of their life cycle. Although the duration of the larval period is not known it seems that the parasite may take from 1 to 2 years to complete this stage of its life history. This is based on the data shown in Fig. 4.4 which shows that most frogs greater than 16 mm in body length (one year old or more) were infected with larvae greater than 6 mm in body length. Pupation probably occurs in larvae which are within this size range. If this is the case, then it is quite likely that some of the 'mature' larvae found in juvenile and subadult frogs would pupate before the host reached maturity. It was thought that the differences in the habitat of the two age groups - juveniles and adults - may influence the differences in the incidence of parasitism. However, this can be discounted for several

reasons. First, both juvenile and adult male frogs are found in the same micro-habitat about the same time that the parasites are first seen in the juveniles, i.e. from late December to the beginning of February. Second, the very few, small larvae found in infected adult frogs suggests that these frogs have been parasitized at a much earlier age. Third, the low percentage of adults infected with small larvae probably indicates that adults are less susceptible to infection either because of immunity to the parasite or for other physiological reasons.

Another interesting observation which arises from these results is the difference in the incidence of parasitism between P. corroboree and P. dendyi adults from Coree Flats. There does not appear to be any difference in the habitat distribution of the juveniles of both species which might explain these results. However, it is possible that each of the two Pseudophryne species are infected with a different species of parasite. If this is so then some difference in the incidence of parasitism between them is possible. Until the parasites are reared to maturity, however, this question must remain open.

At higher altitudes no P. corroboree adults were

found infected, in contrast to the results obtained from a sample of P. dendyi from Boggy Plain (alt. 1,585 m), Snowy Mountains. Although difficult to explain, these results probably indicate that: a) the parasite is very patchy in its distribution, or b) the two species of Pseudophryne differ in their susceptibility to infection, with P. dendyi adults being more susceptible than P. corroboree. The results of samples of P. dendyi from various localities seem to indicate that the parasite does vary in its distribution and abundance. That the two species differ in their susceptibility to parasitism is also suggested from the data obtained from Coree Flats. However, on the rather limited data at present available there is very little certainty in any of these suggestions.

Chapter 5 BREEDING BIOLOGY

5.1 Introduction

Most species of the genus Pseudophryne are terrestrial breeders, laying their eggs in burrows in soil, under leaf litter, or in moss in areas which are subject to seasonal inundation. The number of relatively large, heavily yolked eggs laid varies from 20 in P. australis, to well over 100 in P. bibroni. From the information available (Table 5.1), it appears that most species breed during the late summer to late autumn or early winter. Both P. australis and P. occidentalis are atypical in this respect as the former species is reported to breed throughout the year after rain (Harrison, 1922) and the latter "breeds after summer rains and when these fail....breeds after the first warm rains of winter" (Main, 1965).

In P. corroboree, P. dendyi and P. bibroni the male constructs the burrow which also serves as a calling site. Colefax (1956) reported that in P. corroboree the female performs this task as he observed in the laboratory, females making burrows in moss after injection with Bufo marinus pituitaries. In nature no female has been observed to make a burrow.

Table 5.1

Summary of breeding biology of

Pseudophryne species.

Summary of breeding biology of *Pseudophryne* species

Species	Calling season	Breeding season	Clutch size	Egg Diam. (mms.)	Length of larval life (days)	Locality	Reference
Pseudophryne bibroni		Apr. - June					Fletcher, 1889
		Apr. - June	130	2.0	150-180	Sydney, N.S.W.	Harrison, 1922
		Apr. - May		2.1			Moore, 1961
			260	2.0			Jacobson, 1962
		Mar. - May				Melbourne, Vic.	Littlejohn, 1963
		Feb.				New England, N.S.W.	Pengilley, unpubl.
	Mar. - Jun.	Apr. - May	80-99[b]		120 - 150	Southern Highlands, N.S.W.	" "
					180 - 210	Melbourne, Vic.	Martin, 1965.
P. dendyi		Feb.	85	2.2		Jindabyne, N.S.W.	Moore, 1961
	Jan.	Jan. - Feb.	80-89[a]		180 - 210	Snowy Mts., N.S.W.	
		Feb.				Clyde Mtn., N.S.W.	Pengilley, unpubl.
		March			180 - 210	Coree Flats, N.S.W.	
P. corroboree		Dec. - Jan.	12	3.5	180 - 210	Snowy Mts., N.S.W.	Colefax, 1956
	Dec. - Feb.	Jan. - Feb.	20 - 30[b]		180 - 210	Snowy Mts., N.S.W.	
	Dec. - Feb.	Jan. - Feb.	20 - 30[b]		180 - 210	Snowy Flats, A.C.T.	Pengilley, unpubl.
	Jan. - Apr.	Feb. - Mar.	20 - 30[b]		180 - 210	Coree Flats, N.S.W.	
P. semimarmorata		Mar. - May				Melbourne, Vic.	Littlejohn, 1963
		Mar. - May				Tasmania	Parker, 1940
					180 - 210	Melbourne, Vic.	Martin, 1965
P. australis		Nov.,Jan.,May					Fletcher, 1889
		Sept.					
		All year?	20	2.8	28	Sydney, N.S.W.	Harrison, 1922
	Aug. - Mar.	Aug., Jan.,	15		30 - 40		Moore, 1961
			10 - 20	3.0 - 3.5			Jacobson, 1962
	Aug.					near Mittagong, N.S.W.	Pengilley, unpubl.
	Jan.					Sydney, N.S.W.	Pengilley, unpubl.
P. coriacea		March	110 - 180			North Coast, N.S.W.	Straughan, 1963 (pers. comm.)
	Feb.					North Coast, N.S.W.	Pengilley, unpubl.
P. guentheri	Mar. - Jun.	Winter			40 - 50		Main et al, 1959
	Apr. - May	Apr. - May			90 - 120		Main, 1965
P. occidentalis	Jan. - June	summer - early winter			40 - 50		Main et al, 1959
	Dec. - Mar.	summer - early winter			40 - 50		Main, 1965
P. douglasi		May	89		90 - 120		Main, 1964.

a based on 1964 data

b modal class size

From the literature species appear to differ in their behaviour after egg laying. Males of P. douglasi (Main, 1964), P. coriacea (Straughan, 1963, pers. comm.), P. dendyi (Moore, 1961), P. corroboree (Jacobson, 1963) and females of P. australis (Harrison, 1922) have been found in burrows containing eggs. Jacobson (1963) reported that both sexes of P. bibroni remain with the eggs. This is contrary to my observations on this species, where only males have been found in nests containing eggs.

Because of the paucity of information available on the breeding biology of species of this genus a number of populations of P. corroboree, P. dendyi and P. bibroni were examined as frequently as possible during the breeding seasons. During the examination of these areas particular attention was placed on obtaining fairly accurate information on the duration of the calling and breeding seasons of the three species. In the case of the calling season it was thought that the time when the males were first heard calling probably indicated that males were beginning to move into the breeding areas. Known burrows in the breeding areas were periodically checked to see whether there were any males present. The examination of burrows during these visits also provided information on the date of commencement of breeding,

the number of eggs laid, the mortality of the eggs and the time males spent in a burrow.

By knowing the dates when males were first and last seen, or heard calling, in the breeding area, and by noting when breeding began and finished, it was hoped to be able to relate the duration and timing of these processes to corresponding changes in the climate.

The calling season is defined as that period when males have been heard calling. As mentioned above the beginning and end of this period is probably a reasonable indication of the time when males are migrating to and from the breeding areas. The breeding season is considered to be that period when mating occurs as determined by when recently deposited eggs were first and last seen. The dates given for the commencement of breeding are reasonably accurate for P. corroboree but are probably less accurate for the other two species as these populations were not visited frequently

5.2 Calling Season

i) P. corroboree

Table 5.2 gives the dates from a number of localities for the period December, 1963, to April, 1964, when males have been observed in the breeding area. At all localities

the males moved down into the breeding area some four to six weeks before breeding commenced.

During 1963-64 Smiggin Holes was probably the earliest locality when migration commenced as large numbers of males were heard calling on 27 December, 1963, and if they follow the same pattern as those elsewhere it is most probable that some males were present in early December. At the same altitude in the Brindabella Range, at Snowy Flats, males were first seen on 14 December, 1963, when only a few were heard calling.

During the 1964-65 season the Snowy Mountains localities and Snowy Flats were not visited until late in January after breeding had begun ... therefore the commencement of the migratory period could not be determined. At Coree Flats a few males were present on 5 January, 1965, which was five days earlier than the previous year. At Bull's Head, 183 m higher on the same mountain range, males were not present until towards the end of January.

In 1964 males were last observed in the breeding area at Smiggin Holes on 14 January, and at Snowy and Coree Flats on 7 March and 10 April respectively. Conditions during the summer and autumn, 1965, were such that a rather extended calling season resulted, and the males in most

Table 5.2 Calling and breeding seasons of *P. corroboree*, 1964

Locality	Males in breeding area, not calling or one or two calling	Large numbers of males calling	Females in breeding area	Breeding Season	Last male seen in breeding area
Smiggin Holes (1,650 m)	-	27 Dec.	-	17 Jan.-?	14 Feb.
Snowy Flats (1,650 m)	14 Dec.	3 Jan.	-	19 Jan.-20 Feb. (approximately)	7 Mar.
Bull's Head (1,220 m)	4 Jan.	-	8 Feb.	16 Feb.-7 Mar.	Males still present 14 Mar.
Coree Flats (1,040 m)	10 Jan.	16 Feb.	-	1 Mar.-18 Mar.	10 Apr.

areas did not complete the return migration until later in the year. A few males were still present at Smiggin Holes on 2 April. At Snowy Flats most males had departed by the end of March, but at Coree Flats it was not until the end of April that this movement had been virtually completed.

ii) P. dendyi and P. bibroni

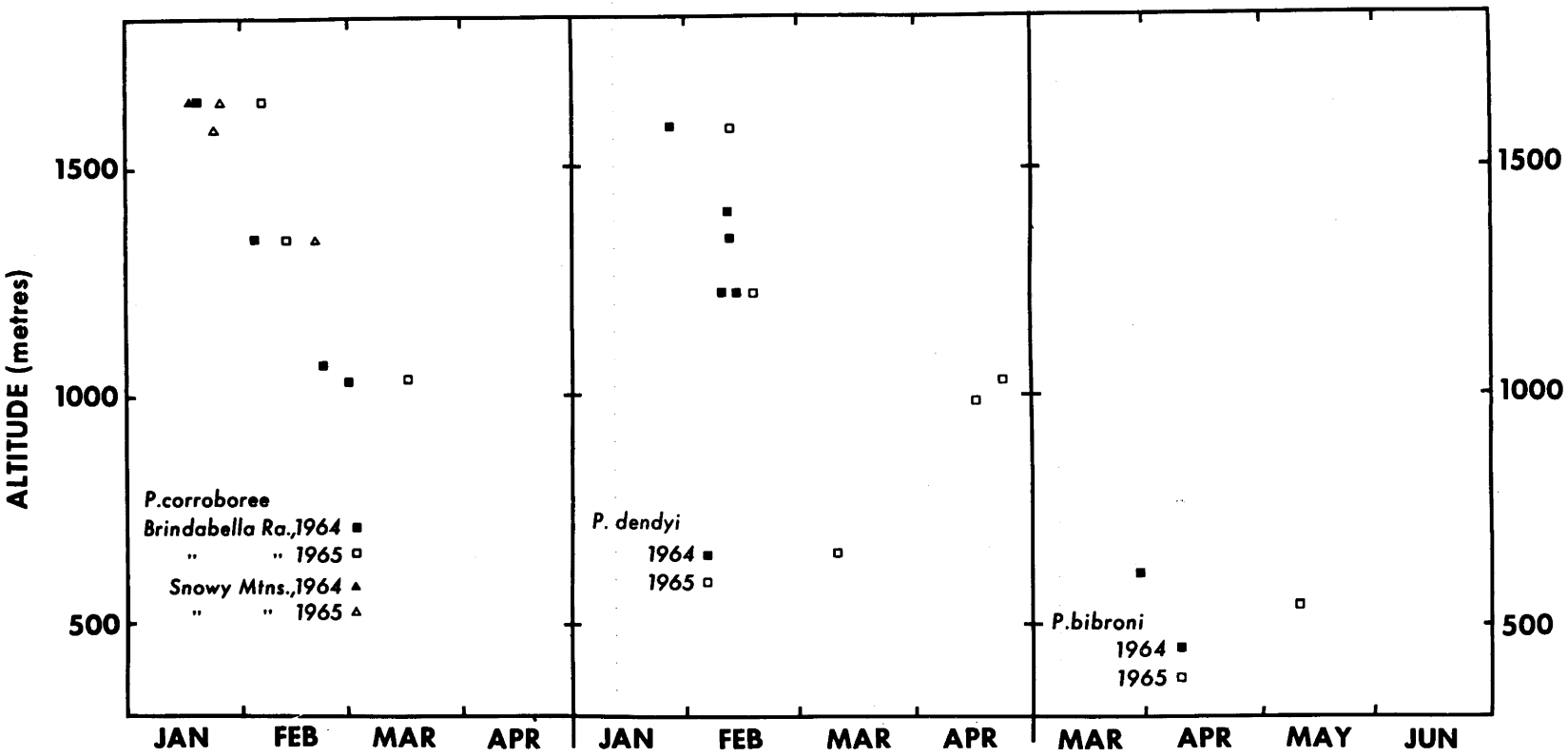
The breeding of P. dendyi and P. bibroni tends to follow the same pattern as of P. corroboree in that the males migrate into the breeding areas some weeks before breeding commences.

During 1965 males of P. dendyi were observed in the breeding areas towards the end of January at both Boggy Plain and Little Thredbo River Flats but were not heard calling until early March at Coree Flats. By the second week of April the majority of males had moved out of the breeding area at Boggy Plain but this did not take place until at least early May at Coree Flats as males were still present on 26 April.

Male P. bibroni were first heard calling at 610 m on 13 April, 1964, but as these populations were not visited before this date calling possibly could have begun much earlier. Males were last heard calling towards the end of May of the same year.

Fig. 5.1

The time of commencement of breeding in P. corroboree, P. dendyi and P. bibroni at various altitudes in the southern highlands and southern tablelands of N.S.W. and the A.C.T.


ALTITUDE (metres)
1500
1000
500
P.corroboree
Brindabella Ra.,1964
" " 1965
Snowy Mtns.,1964
" " 1965
P. dendyi
1964
1965
P.bibroni
1964
1965
JAN
FEB
MAR
APR
JAN
FEB
MAR
APR
MAR
APR
MAY
JUN

5.3 Breeding Season

The data on the commencement of breeding of the three species at various altitudes are shown in Fig. 5.1

i) P. corroboree

Colefax (1956) recorded P. corroboree breeding in the latter half of December at Alpine Hut (alt. approx. 1,768 m) but no populations were found breeding before mid-January during the course of this study.

Populations of P. corroboree in the subalpine zone (1,524 m) begin breeding some weeks before those at lower altitudes and for every 304 m decrease in altitude breeding begins approximately three weeks later. In 1964 breeding began at Snowy Flats on 19 January, and at approximately the same time at Smiggin Holes. At Coree Flats, however, breeding did not commence until 1 March.

In 1965 breeding was much later at all localities except for Round Mountain and Smiggin Holes in the Snowy Mountains when recently laid eggs were found on 24 and 25 January. If allowances are made for errors in estimating the date of commencement of breeding, the dates given do not differ greatly from those of the previous year. At both Snowy and Coree Flats, however, breeding was two to three weeks later than the previous year.

Very little information was obtained on the time of the day when breeding occurred. From the few clasping pairs found it seems that breeding occurs most commonly at night. A spent female was found in a nest containing a male and 13 recently laid eggs at 2215 hrs. Two pairs were seen in amplexus between 0900 and 1000 hrs but egg laying must have begun much earlier since both nests contained recently laid eggs. A third pair was in amplexus at 2030 hrs, but there were no recently laid eggs in the burrow.

ii) P. dendyi

The close correspondence seen in breeding schedule and altitude of P. corroboree was not so apparent in P. dendyi during 1964 and 1965. In 1964 at 1,219 m breeding began towards the end of January and at 1,585 m eggs were first noticed towards the end of the second week in February. Delayed breeding was also observed in 1965 when most populations bred approximately two weeks later than in the previous year.

iii) P. bibroni

The data available for P. bibroni are too limited to indicate whether breeding schedule is related to altitude. However, some observations made in 1963 suggest that breeding in this species is partially dependent on latitude.

P. bibroni was found breeding near Pt. Lookout (alt. approximately 1,220 m), New England tablelands, N.S.W. on 16 January, 1963. Three days later in the Blue Mountains, males were found calling in burrows but no eggs were present. At Canberra, however, males were not heard calling until towards the end of March.

5.4 Comparison of the Breeding Seasons of P. corroboree and P. dendyi

Where P. corroboree and P. dendyi are sympatric there is some overlap in breeding seasons but with P. corroboree tending to breed much earlier than P. dendyi. At Coree Flats P. dendyi males begin to move into the breeding area at the time when P. corroboree is just beginning to breed. There is always the possibility then that P. dendyi males could mate with P. corroboree females but as will be explained more fully in the chapter on calling behaviour (Chapter 6) the courtship calls of the two species are quite different and this undoubtedly plays some part in enhancing reproductive isolation between the two species. Where P. corroboree and P. dendyi are allopatric there is some evidence which suggests that there is greater overlap in breeding seasons. During 1964 in the Snowy Mountains, P. dendyi began breeding about one week later than

P. corroboree and if a correction is made for the difference in altitude between the two localities there is very little difference between the times at which they breed. In 1965, however, the overlap was not as great as the breeding of populations of both species at the same altitude, but at different localities, differed by three weeks. It is not known whether this difference was partially a result of topographical effects influencing climate or the result of the unusual climatic conditions which prevailed during this period.

5.5 The Effect of Drought on Breeding

The drought of 1965 affected the breeding of all populations below 1,560 m in one of two ways: breeding was either restricted to very wet places in the breeding areas or it was totally inhibited. No breeding of P. corroboree occurred in the main study area at the southern end of Coree Flats. A total of seven nests containing eggs were found however in two small areas bordering a small stream in the northern and western edges of the wet heath.

In this area male frogs were largely confined to the relatively moist, peripheral, ecotonal zone of

Leptospermum myrtifolium and Epacris breviflora. Only a few males were located in the central part which, in 1963 and 1964, had provided the most favourable breeding sites. It was estimated that the area suitable for breeding in this small part of the flat had been reduced to about 1 to 10% of the 1964 value.

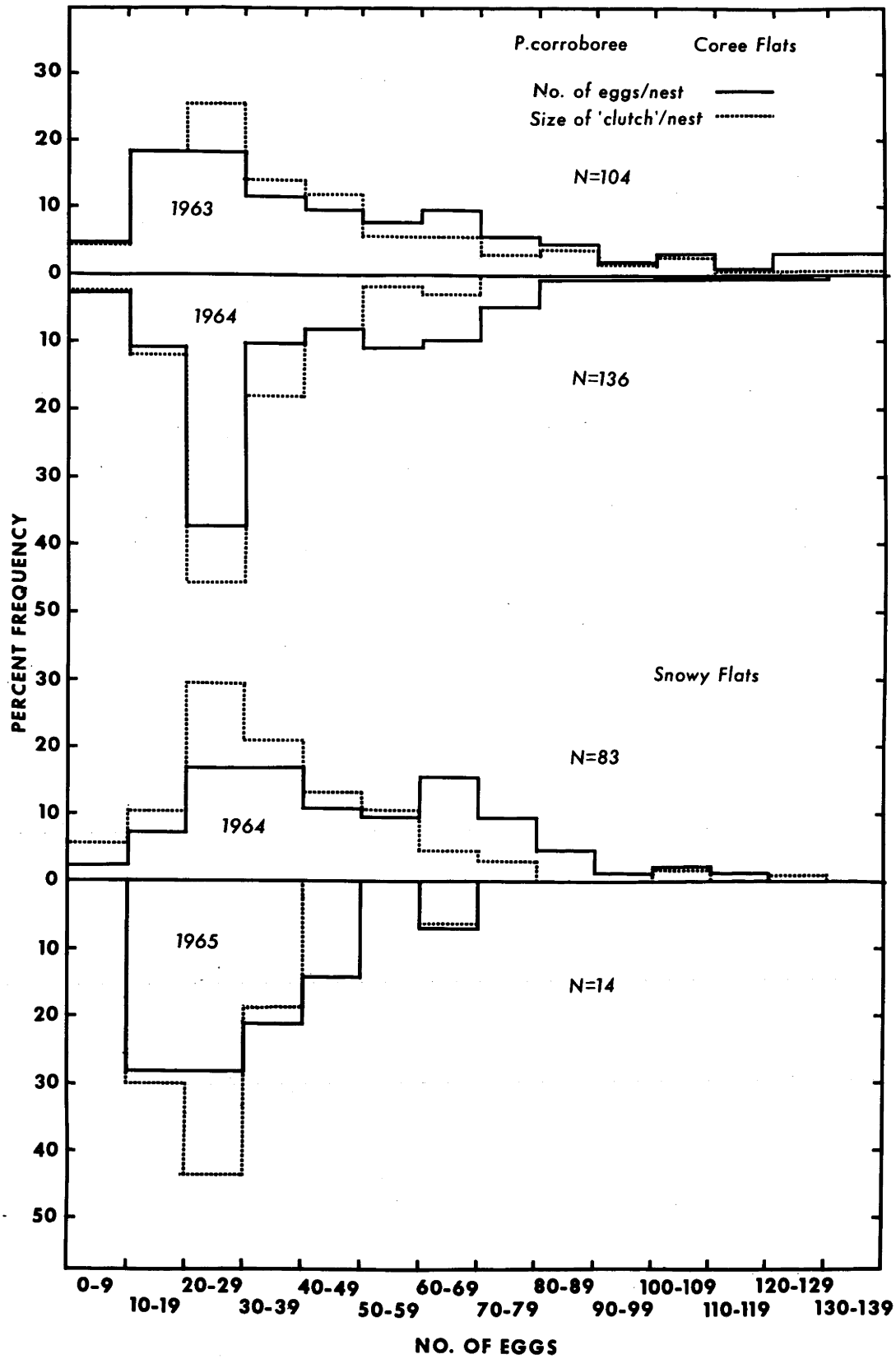
At Coree Flats, P. dendyi was not as greatly affected by the drought as P. corroboree because it bred much later in the year when climatic conditions were less severe. In other areas on the southern highlands where the date of vegetation of the breeding areas of a few populations between Kiandra and Yarrangobilly was denuded by the bushfire which swept through this area in February, 1965.

Populations of P. bibroni on the tablelands were also greatly affected by the drought. Males migrated to the breeding areas at 5 localities but eggs were found at only one of these.

At localities above 1,500 m on the Brindabella Range and the Snowy Mountains all populations of P. corroboree and P. dendyi bred. However, the breeding was not entirely successful as large numbers of eggs became desiccated and died as a result of the sphagnum drying up.

Fig. 5.2

Frequency distribution of the number of eggs found in nests and the 'clutch' size per nest in P. corroboree at two localities on the Brindabella Range. The number of nests and the year during which they were examined are shown on the diagram.


P.corroboree
Coree Flats
No. of eggs/nest
Size of 'clutch'/nest
N=104
1963
1964
N=136
Snowy Flats
N=83
1964
1965
N=14
PERCENT FREQUENCY
30
20
10
0
10
20
30
40
50
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
NO. OF EGGS

5.6 Number of Eggs laid

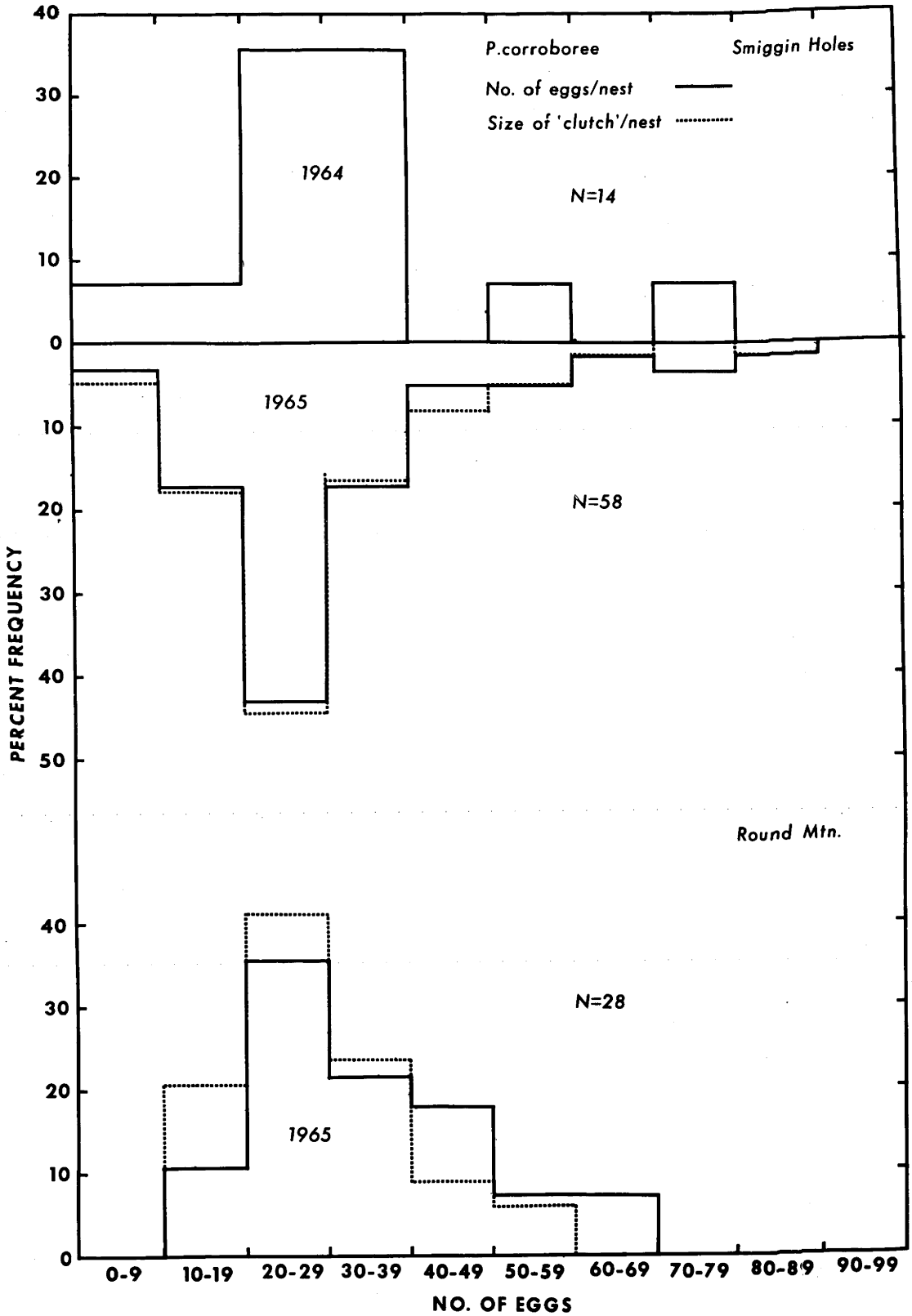
Two methods were employed in estimating the number of eggs laid by three species of Pseudophryne. Gravid females were dissected and the mature eggs in the ovaries were counted. In the second method eggs in nests were counted and their stage of development was noted. If one or more groups of eggs were at different stages of development, these groups were referred to as 'clutches'. Since this method relied on being able to separate the eggs into groups based on differences in the stage of embryological development it would have been ideal to examine nests soon after deposition of the eggs. As this was not practicable in most cases, beacuse matings occurred over an extended period and considerable distances were involved in travelling to these localities, errors were introduced into the calculations especially of the mean 'clutch' size. This is shown clearly in the data for P. corroboree at Coree Flats obtained during the 1963 and 1964 breeding seasons. Nests were examined later in the breeding season 1963 than in 1964, which resulted in the estimate of the mean 'clutch' size being much higher in 1963 than in 1964 (Table 5.3), because 'clutches' could not be separated on the basis of embryological development.

Table 5.3 'Clutch' size and the number of eggs per nest in P. corroboree

Locality	Year	Mean No. of Eggs Laid/'Clutch'	Mean No. of Eggs Laid/Nest
Coree Flats	1963	39.6	44.4
	1964	31.7	38.7
Snowy Flats	1964	38.8	49.0
	1965	25.3	28.9
Smiggin Holes	1964	30.6	30.6
	1965	28.7	30.2
Round Mountain	1965	25.2	31.1

Fig. 5.3

Frequency distribution of the number of eggs found in a nest and the 'clutch' size per nest in P. corroboree at two localities in the Snowy Mountains region. The number of nests and the year during which they were examined are shown on the diagram.


P.corroboree
Smiggin Holes
No. of eggs/nest
Size of 'clutch'/nest
1964
N=14
1965
N=58
Round Mtn.
N=28
1965
PERCENT FREQUENCY
NO. OF EGGS
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99

i) P. corroboree

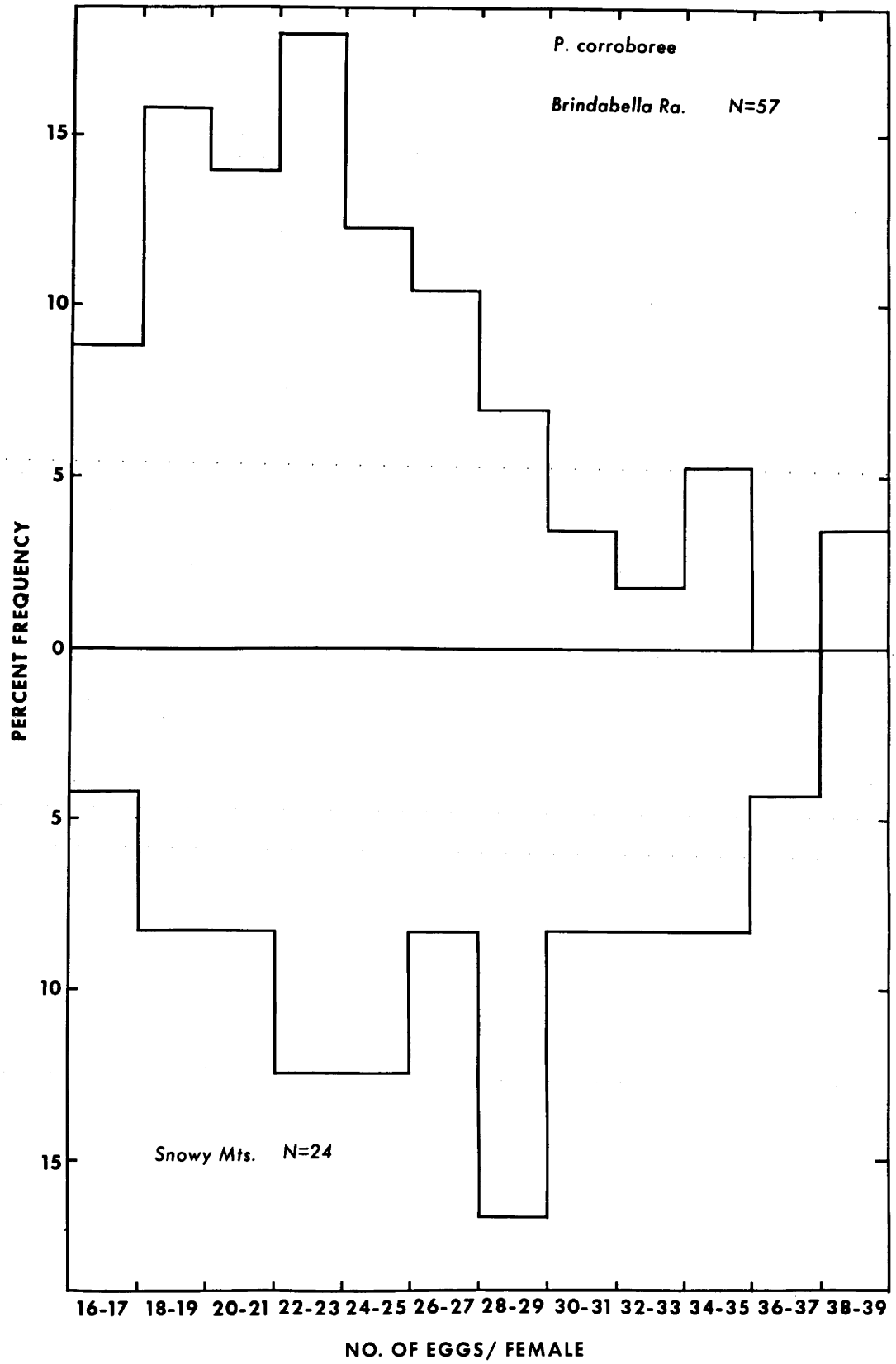
Colefax (1956) reported that P. corroboree lays 12 eggs. This is much lower than any mean or modal value recorded in this study where the modal 'clutch' size based on counts of eggs in nests was between 20-29 for most populations (Figs. 5.2 and 5.3). No geographical or annual variations in the mean 'clutch' size could be detected that were meaningful because of the errors involved in estimating the 'clutch' size.

The results (Fig. 5.4) obtained from dissecting gravid females revealed that there was a statistically significant difference in the number of eggs found per female between the Brindabella and Snowy Mountains samples, the mean number of eggs per female being 24.0 and 26.4 respectively. As the Snowy Mountains females are significantly larger than those from the Brindabella Range (Fig. 3.4), this may account for the differences in the mean number of eggs. Within each population, however, there was no relationship between size and the number of eggs (Fig. 5.5). The correlation coefficient for the Brindabella sample was +0.037 and for the Snowy Mountains sample, -0.007.

Although a greater percentage of females had more eggs in the right than in the left ovary (Table 5.4) in both

Fig. 5.4

Frequency distribution of the number of eggs found per female in a sample from the Brindabella Range and the Snowy Mountains. Fifty-three of the 57 specimens from the Brindabella Range were collected at Coree Flats. The Snowy Mountains sample comprises specimens from Smiggin Holes and Round Mountain.


P. corroboree
Brindabella Ra. N=57
Snowy Mts. N=24
PERCENT FREQUENCY
15
10
5
0
5
10
15
16-17 18-19 20-21 22-23 24-25 26-27 28-29 30-31 32-33 34-35 36-37 38-39
NO. OF EGGS/ FEMALE

samples, the Snowy Mountains sample had a considerable percentage which had more eggs in the left ovary. The significance of the imbalance in egg distribution is not known.

Table 5.4 Distribution of Mature Eggs in the Ovaries of *P. corroboree*

Locality	Sample Size	More in Right Ovary (%)	More in Left Ovary (%)	Equal Numbers in Both (%)
Brindabella Ra.	21	57.1	14.3	28.6
Snowy Mountains	20	55.0	40.0	5.0

In Table 5.5 are shown the percentage of males that mated with one or more females. These data have been derived from those shown in Figs. 5.2 and 5.3 in which the 'clutch' size of a female was taken as being 29 eggs. This figure was chosen because it was the upper limit of the modal class of the 'clutch' size for most populations and was near the mean number of eggs found per female.

Fig. 5.5

A plot of the number of eggs found per female against snout-urostyle length. The specimens used in plotting these data are the same as those used in plotting Fig. 5.4. The open squares represent specimens obtained from Snowy Flats, Brindabella Range.

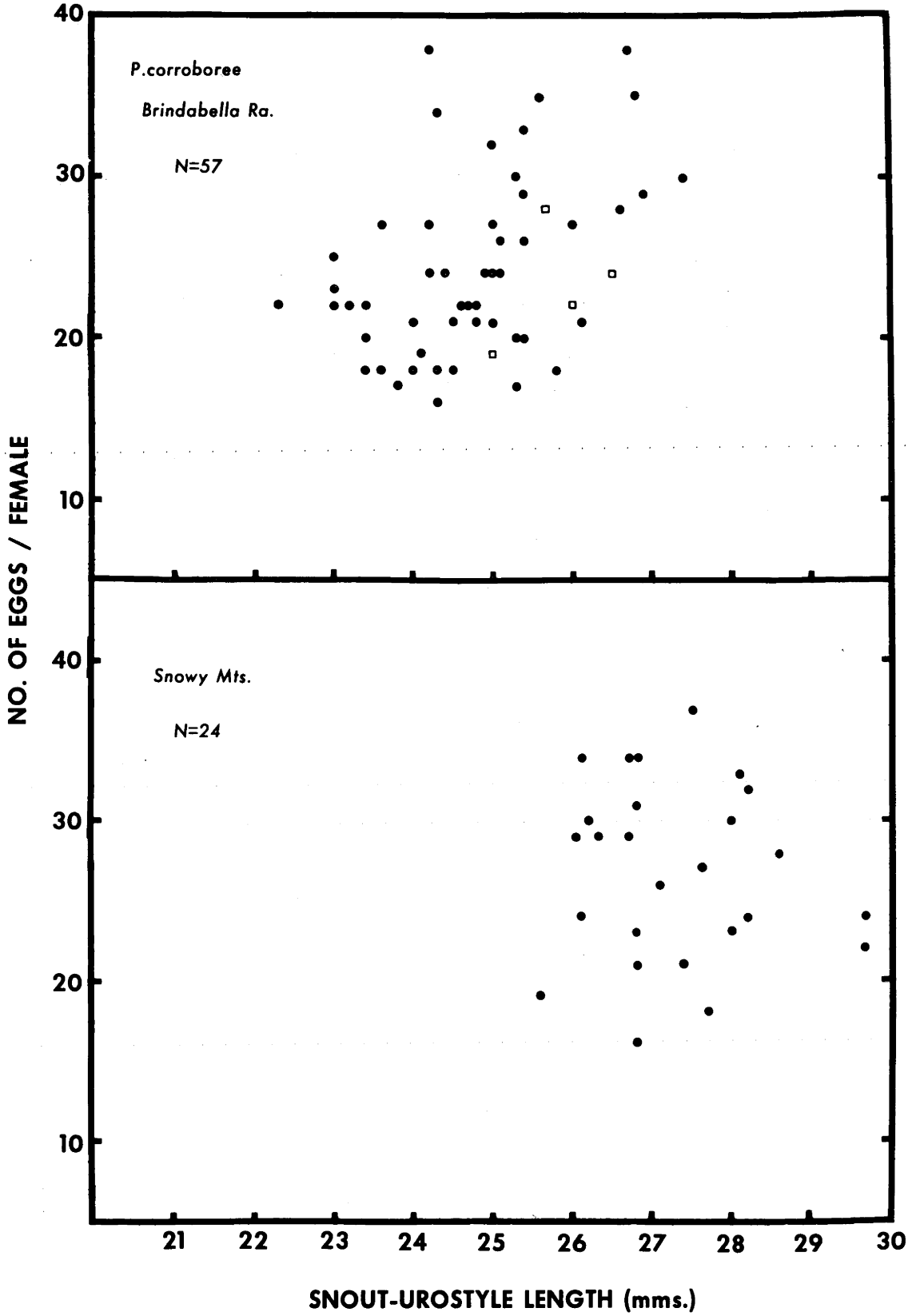

P.corroboree
Brindabella Ra.
N=57
Snowy Mts.
N=24
40
30
20
10
NO. OF EGGS / FEMALE
21
22
23
24
25
26
27
28
29
30
SNOUT-UROSTYLE LENGTH (mms.)

Table 5.5 The percentage of male P. corroboree that mated with one or more females. These data have been calculated from the 'clutch' size/nest where the upper limit of the 'clutch' size was taken as 29.

Locality	Year	No. of Nests Examined	No. of Females with which the % of Males shown below mated				
			1	2	3	4	5
Coree Flats	1963	104	48.3	31.7	13.3	5.0	1.6
	1964	136	60.0	34.3	5.0	0.6	0.0
	1965	7	77.8	22.2	0.0	0.0	0.0
Snowy Flats	1964	83	45.7	43.8	7.7	1.9	1.0
	1965	14	75.1	18.8	6.3	0.0	0.0
Smiggin Holes	1964	14	49.9	42.8	7.1	0.0	0.0
	1965	58	67.2	29.5	3.2	0.0	0.0
Round Mtn.	1965	28	61.8	38.2	0.0	0.0	0.0

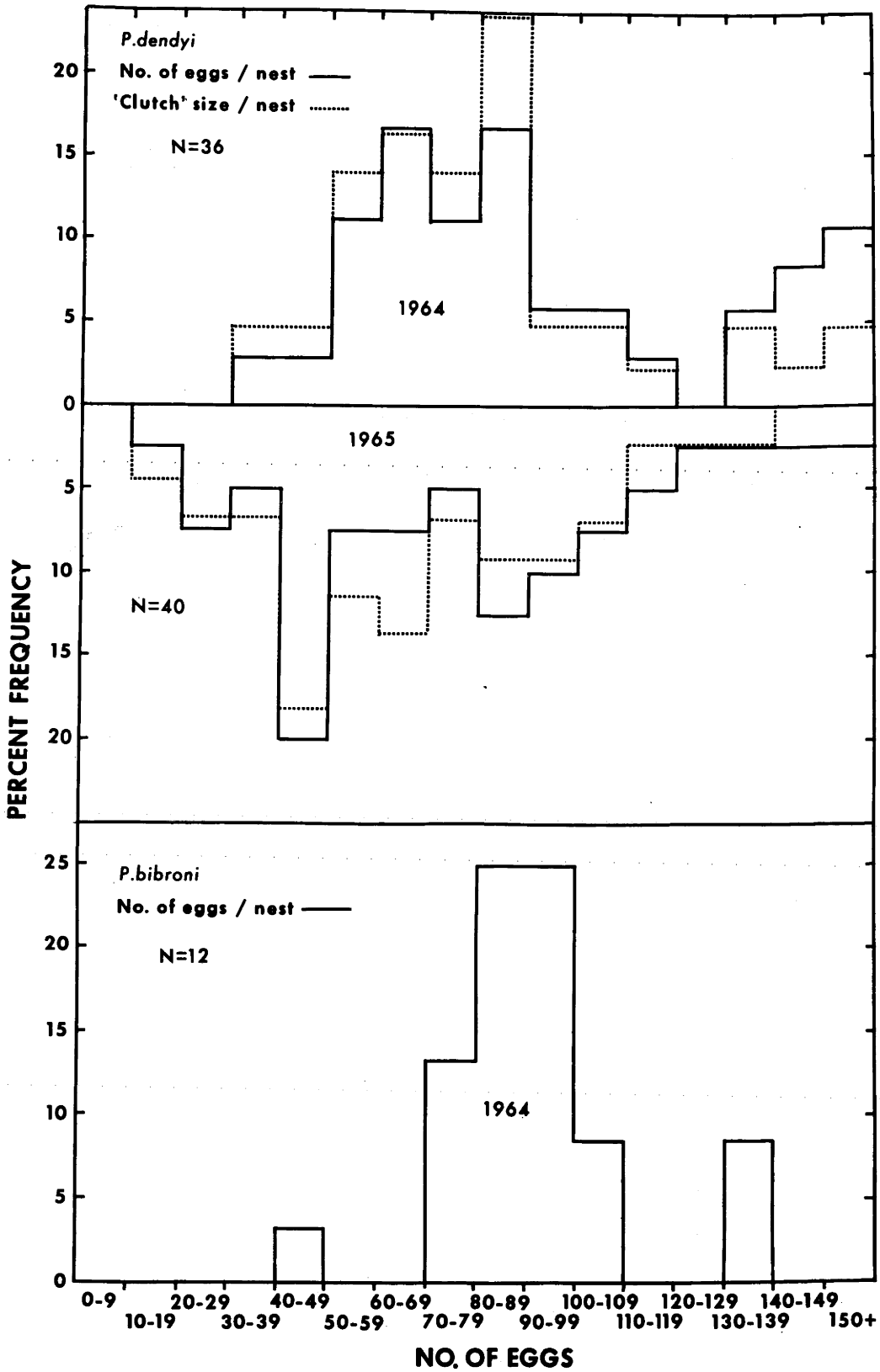
In calculating the percentage of males that mated with one or more females it has been assumed that once eggs are laid in a nest the male either remains in the nest until breeding has finished or if he does desert the nest he does not seek out another burrow or nest and mate with another female. Observations on marked males at Coree Flats, Snowy Flats and Smiggin Holes indicate that this assumption is generally valid. It has also been assumed that a female lays only once during a season. Although more difficult to substantiate it does seem that because of the very short breeding season females breed only once a year.

Where 50 or more nests were examined, approximately 33 to 50% of males that had mated, apparently did so with more than one female. At Coree Flats, for example, the percentage of males that mated with more than one female varied from about 40 to 50% (Table 5.5). Since males greatly outnumber females in the adult population at this locality (see Chapter 4) these data indicate that a large percentage of sexually mature males do not contribute to the gene pool. It is not known whether there is any competition between males for gravid females.

Fig. 5.6

Upper graph: Frequency distribution of the number of eggs found in nests and the 'clutch' size per nest in P. dendyi. Note the shift in the mode and the mean of the 'clutch' size in the 1965 data.

Lower graph: Frequency distribution of the number of eggs found in 12 nests of P. bibroni at Uriarra, A.C.T. during the 1964 breeding season.


P.dendyi
No. of eggs / nest
'Clutch' size / nest
N=36
1964
1965
N=40
P.bibroni
No. of eggs / nest
N=12
1964
PERCENT FREQUENCY
NO. OF EGGS
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150+

ii) P. dendyi

The only report in the literature on the number of eggs laid by P. dendyi is that of Moore (1961) who found 85 eggs in a nest of P. dendyi near Jindabyne, N.S.W.

In 9 nests of P. dendyi at Coree Flats examined in 1963, the number of eggs ranged from 45 to 154, the mean being 101.1. Examination of 36 nests during the 1964 breeding season showed that the modal 'clutch' size was within the range 80-89 (Fig. 5.5), and the mean was 81.8. In 1965 there was a reduction in the modal (40-49) and mean (65.0) 'clutch' size. The difference between the two means was statistically significant at the 5% level.

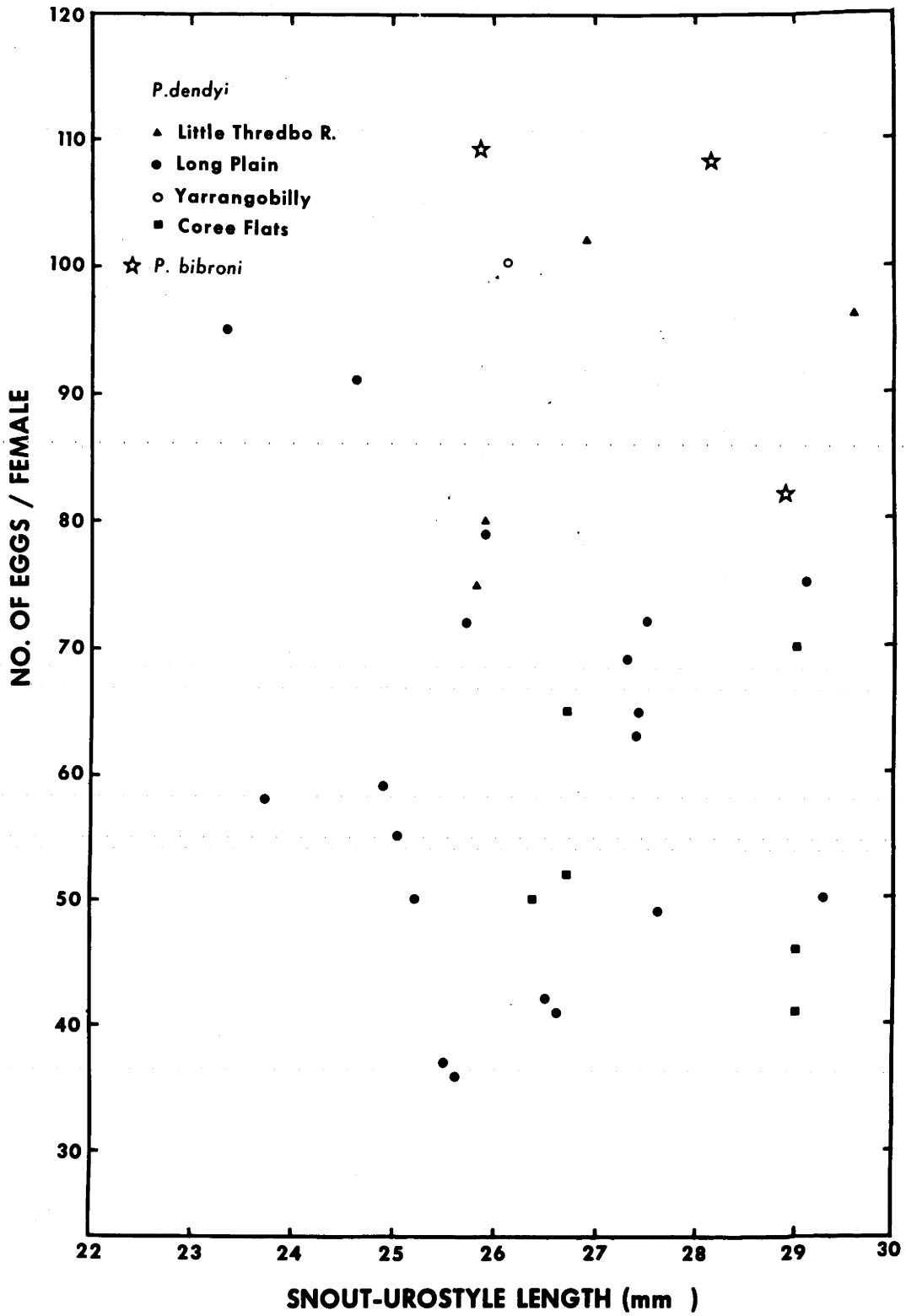
The smaller mean 'clutch' size recorded in 1965 was most probably due to the drought of that year. Keast (1958) reported that similar effects are often seen in certain birds breeding during drought years.

The percentage of males that mated with more than one female was 22.2% in 1964, and 41.8% in 1965. These data are based on the upper limit of the 'clutch' size as being 89 in 1964, and 69 in 1965.

In general, there was no correlation between the size of females and the number of mature eggs contained in the ovaries. The correlation coefficient for the largest

Fig. 5.7

The number of eggs found per female in *P. dendyi* and *P. bibroni* plotted against snout-urostyle length.


P.dendyi
Little Thredbo R.
Long Plain
Yarrangobilly
Coree Flats
P. bibroni
NO. OF EGGS / FEMALE
SNOUT-UROSTYLE LENGTH (mm)
120
110
100
90
80
70
60
50
40
30
22
23
24
25
26
27
28
29
30

sample showed the best correlation (r = +0.64) but this was based on only four specimens.

iii) P. bibroni

This species is recorded as laying 130 (Harrison, 1922) and 260 eggs (Jacobson, 1962). From 12 nests at Uriarra, A.C.T., the modal 'clutch' size was between 80-99, the mean 85.3.

Since only three gravid females were dissected it is not known whether there is any relationship between body length and egg complement.

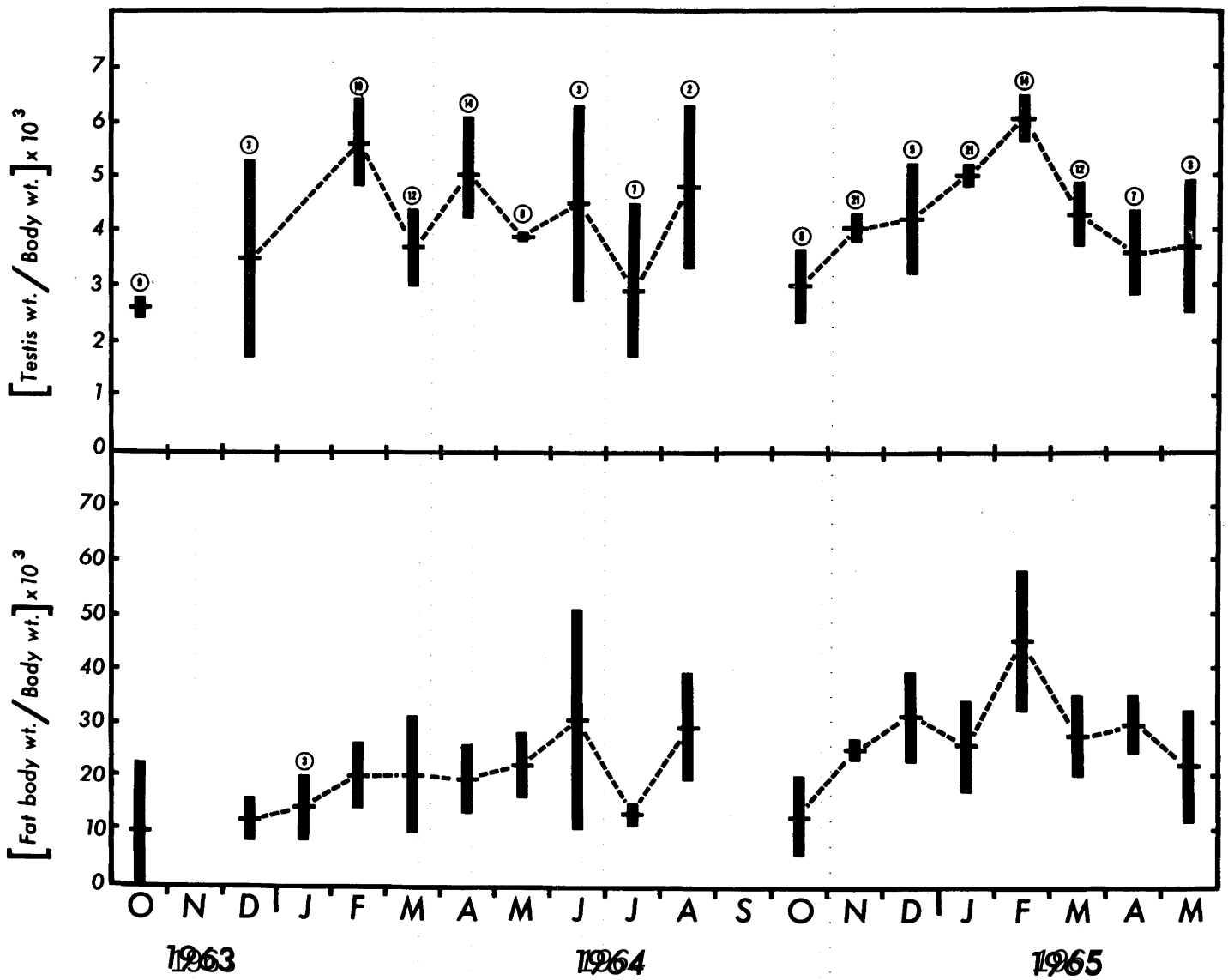
5.7 Reproductive Cycle of P. corroboree

Monthly samples of males and females were collected at Coree Flats from October, 1963 to May, 1965, except for the months of November, 1963, and September, 1964. Generally, more than five individuals of each sex were collected every month. Very few females were obtained during the winter despite intensive searching.

The individuals were killed within 24 hours of capture and were initially preserved in Bouin and later transferred and stored in 70% alcohol. Later the animals were blotted and weighed; the reproductive organs and associated fat bodies were then dissected out, blotted and weighed. The weights of these organs were expressed as a ratio of the preserved body weight.

Fig. 5.8

Seasonal changes in the weights of testes (upper graph) and fat bodies (lower graph) of male *P. corroboree*, Coree Flats, N.S.W. over a 20 month period. The means are shown as short horizontal bars joined by dashed lines. The solid vertical bar represents twice the standard error (S.E.) on either side of the mean and the sample size is shown encircled above this bar.


[Testis wt. / Body wt.] x 10³
[Fat body wt. / Body wt.] x 10³
O N D J F M A M J J A S O N D J F M A M
1963
1964
1965

i) The Male

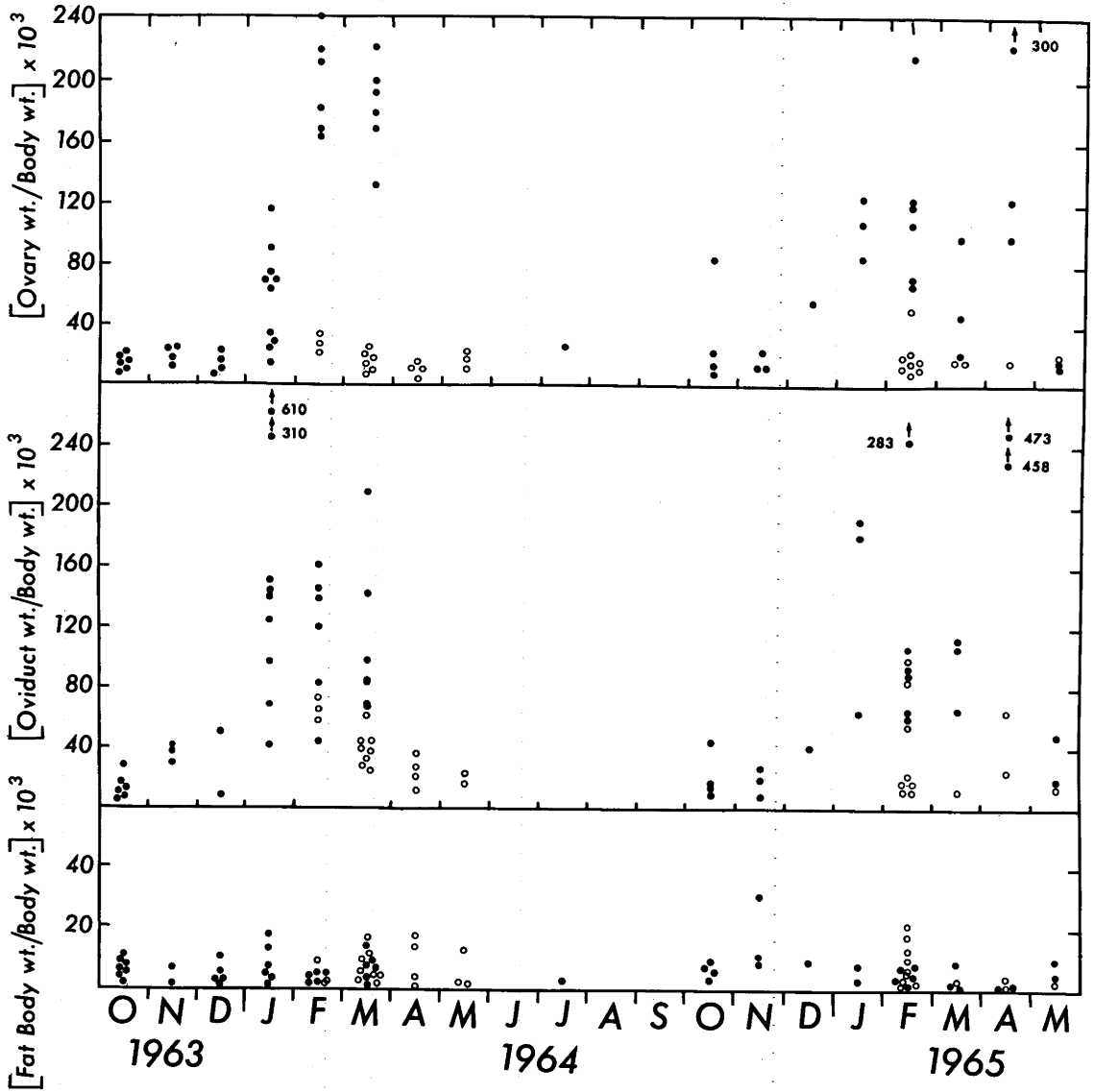
The seasonal weight changes of the testes and the fat bodies are shown in Fig. 5.8.

Significant monthly changes in the weights of the testes and fat bodies were only evident during the 1964-1965 season. The reason for the absence of any change during the previous season was most probably due to the time in which the organs had been preserved as some of the earlier samples were not weighed until about two years after they had been collected. During the 1964-1965 season both the testes and fat bodies exhibited a gradual increase in weight and reached their maximum weight in February just before breeding and thereafter decreased in weight. Both the testes and fat bodies appear to have been at their minimal weight during the winter.

P. corroboree seems to differ from most other species especially in the relationship between the development of the fat bodies and the testes. In Xenopus laevis (Gitlin, 1941) and Bufo regularis (Chapman and Chapman, 1958) there is a reciprocal relationship between the development of the fat bodies and the gonads. Smith (1950) showed that in Rana temporaria the fat bodies

Fig. 5.9

Seasonal changes in the weights of the ovaries (upper (graph), oviducts (middle graph) and fat bodies (lower graph) of female P. corroboree collected at Coree Flats, N.S.W. The closed circles refer to females collected during the non-breeding season and to gravid, but unovulated females obtained during the breeding season. The open circles refer to ovulated females.


[Ovary wt./Body wt.] x 10³
240
200
160
120
80
40
300
[Oviduct wt./Body wt.] x 10³
610
310
283
473
458
[Fat Body wt./Body wt.] x 10³
40
20
O N D J F M A M J J A S O N D J F M A M
1963
1964
1965

were at their maximum development approximately 2 to 3 months before the gonads. These workers have suggested that the fat bodies provide a food reserve for the animal during periods of climatic stress as well as being a source of nourishment for the gonads. Since both the fat bodies and testes of male P. corroboree are at their maximum development in February, the fat bodies probably do not provide nourishment for the growth of the testes. The fat bodies may be utilized, however, as a somatic reserve during the breeding season. It is during this period that breeding males take little or no food. Another fact which suggests that this may be the case is that the fat bodies of males at this time of the year are much greater than those of the female (Fig. 5.9).

ii) The Female

Figure 5.9 shows the weights of ovaries, oviducts and fat bodies plotted against the month of collection. The closed circles refer to females collected during the non-breeding season and to gravid but unovulated females obtained during the breeding season. The open circles refer to ovulated females.

Only the ovaries and oviducts show any marked seasonal weight change: the fat bodies show little, or no

change in weight throughout the 20 month period.

During 1964, the ovaries began to increase in weight in January and reached their greatest weight in February. As one would expect there was a significant decrease in weight of the ovaries in ovulated females. No gravid females were found after March. During the second breeding season (1965) when only a few females bred there was no clearly marked weight change and gravid females were found as late as May. As the ovarian weights of these individuals were similar to those of ovulated females this suggests that the unovulated eggs were fairly quickly resorbed when breeding did not occur. One female was found in October, 1964, with eggs still in the body cavity. This individual had apparently ovulated 6 months previously but had not mated.

The changes in the weights of the oviducts were similar to those of the ovaries during both breeding seasons.

5.8 Discussion of Breeding Biology

The demonstration of well defined seasonal breeding in these species of Pseudophryne suggests that their reproductive activities are controlled by climatic conditions. Temperature and rainfall are considered as being the two most important climatic factors affecting reproduction in

amphibia (Gallien, 1959; Noble and Noble, 1923; Smith, 1955). Although experimental evidence is available only for the effects of temperature (van Oordt, 1960) there is much field evidence which suggests that one or both factors are influential in determining the time of breeding.

The most thorough and long term analysis of external factors inducing breeding in frogs has been by Savage (1961) on Rana temporaria in England. Savage found that rainfall and temperature during the few months before breeding were the most important factors affecting the date of breeding.

In P. corroboree and to a lesser extent in P. dendyi it appears that the breeding schedule is determined by temperature, since in the southern highlands of N.S.W. temperature depends on altitude (Costin, 1954). The precise temperature conditions necessary to induce breeding are not known. However, the rate of decline of temperatures during the period January to May may be of some importance. At Coree Flats, for example, breeding was much later in 1965 than in 1964. In 1965 temperatures declined at the mean daily rate of 0.09°C, whereas in 1964 the rate was 0.12°C. Robinson (1965, pers. comm.) suggested that the slower rate observed in 1965 may have been responsible for delayed breeding in the winter breeding lyre-bird

Menura novae-hollandiae at a locality about 17 km south of Coree Flats.

In P. corroboree, and also in P. dendyi populations above 1,524 m, males migrate to the breeding areas when temperatures are decreasing whereas at lower altitudes males are not in the breeding areas until much later in the year when temperatures are decreasing. From these observations and those on breeding it seems that whether temperatures are increasing or decreasing at a fast or slow rate may not be crucial in eliciting these responses. Instead it is probable that certain ranges of temperatures are needed before migration and breeding will occur. Although rainfall has been implicated as a stimulus for breeding in some species of Pseudophryne (Fletcher, 1889; Jacobson, 1963; Main, 1965) it seems from the data obtained on P. corroboree and P. dendyi that there is very little relationship between the two. Both species breed from late summer to mid-autumn (Fig. 5.1), a period during which rainfall is generally minimal (Figs. 2.3 and 2.8). The absence of rain, however, can affect reproduction by making the breeding sites too dry for egg deposition. In moist areas at the same localities breeding will occur.

P. corroboree, P. dendyi and P. bibroni like most

species of this genus breed on land. A number of ideas have been advanced to explain the development of this feature of the life cycle of some amphibia. Lutz (1948), Poyton (1964) and Tihen (1960) consider it as a device to reduce predation of the eggs and very young larvae and not as a means of avoiding desiccation as implied by Romer (1957). Goin and Goin (1962) noted that the majority of species with terrestrial development were found in montane habitats and suggested that terrestrial breeding was a means of avoiding the regions of swift flowing streams. Since only one species of Pseudophryne, P. occidentalis, occurs in arid or semi-arid habitats (Main et al., 1959), terrestrial breeding in this genus may not have evolved through selection by climate. However, the time of breeding (autumn) of most of these species may possibly reduce the effect of desiccation of the eggs.

Whether the mortality rate in eggs and tadpoles of species of Pseudophryne is less than in those of aquatic breeders such as Crinia signifera and Hyla verreauxi is not known. The data available on mortality in P. corroboree (Chapter 4) indicates that it is variable and fluctuates from year to year.

Chapter 6 CALLING AND ASSOCIATED BEHAVIOUR

6.1 Introduction

Studies on vocality in frogs have been mainly concerned with the analysis of the mating call and its importance as a premating isolating mechanism (Blair, 1958, 1964; Littlejohn, 1959, 1961; Mecham, 1961). That the mating call serves as a means whereby a gravid female can locate a conspecific male seems to be fairly well established in some species on the basis of field observations (Blair, 1958; Bragg, 1959; Jameson, 1955; Littlejohn, 1958; Noble and Noble, 1923; Mecham, 1961) and discrimination tests performed in the laboratory (Littlejohn and Michaud, 1959).

The mating call has also been suggested as being responsible for increasing the level of sexual excitement, presumably of both males and females; location of the breeding site and formation of breeding aggregations (Mecham, 1961); inducing ovulation in females (Bogert, 1960; Gosner and Rossman, 1959) and the assertion of territorial rights (Bogert, 1960; Rabb and Rabb, 1963).

In contrast to the studies on bird song by Thorpe and his colleagues (Thorpe, 1961; Marler, 1956; Armstrong, 1963), behavioural studies on frog calls apart from the mating call have been very little studied. Rabb and Rabb (1963)

described the various calls of a pipid frog, Hymenochirus boettgeri and more recently Capranica (1965) analysed the calls of both sexes of the bullfrog Rana catesbeiana. Both of these studies indicate that before calling is fully understood as a means of communication, an analysis of all calls of a species needs to be undertaken.

Attempts were made in the study described here to analyse the calling and associated behaviour of Pseudophryne corroboree, P. dendyi and P. bibroni as an evaluation of vocal communication in these species. Various factors, however, hindered a detailed examination of their breeding behaviour. All three species breed in burrows in moss, vegetation or in moist soil and, therefore, they are very difficult to observe without undue disturbance of their activities. Behaviour immediately prior to amplexus has not been observed either in the field or in the laboratory, so it is not known what other channels of communication are utilized for mating. Certain aspects of aggressive behaviour are the only facets of their behaviour which have been observed both in the field and in the laboratory.

6.2 Materials and Methods

The calls produced by P. corroboree, P. dendyi and P. bibroni were classed as mating, courtship or threat calls

on their association with the patterns of behaviour exhibited in mating, courtship and aggression. All calls recorded were those made by males during the calling season.

Calling activity of P. corroboree at Coree Flats, Brindabella Range, was measured using an omnidirectional sound level meter over seven 24-hour periods from 1 March to 25 March, 1964. For each run of recordings the sound level meter was placed at the same location in the middle of the breeding area. The sound pressure reading was taken as the mean of the sound pressure registered during one minute.

Sounds produced by wind and other animals such as blowflies, crickets and birds often interfered with readings of sound pressure levels. Blowflies tended to be most active during the late afternoon and crickets began calling for a short period at sunset. These were silenced before a reading was taken. Birds were only a serious interference before and during sunrise. Readings of frogs calling were taken only when there was a lull in the calling of the birds. Noise caused by wind was only important during the day and this was circumvented partly by enclosing the microphone of the sound pressure meter in a plastic bag. In most cases readings were taken half hourly to hourly except 30 to 60

minutes before, and during, sunrise and sunset when they were taken at least every 15 minutes. The temperature of the air above ground and within a burrow site were recorded in conjunction with the sound pressure on every occasion, and light readings, using a 'Weston' light meter, were obtained over two 24-hour periods.

Calls were recorded in the field using a Fi-Chord 202 A model tape recorder at a tape speed of $7\frac{1}{2}$ inches per second. The time of day and the temperature of the burrow and the outside air were noted after the call had been recorded. As far as possible all calls were related to the behaviour of the animals. After a call had been recorded, the burrow which contained the calling male was carefully opened up to observe what behaviour was being displayed.

In order to test the signalling function of certain calls a number of simple experiments were performed in the field.

All recordings were analysed for call duration and pulse repetition rate on a Tektronix 564 storage oscilloscope and a selected number were further analysed for fundamental and dominant frequency on a sound spectrograph (Kay Model 662 A sonagraph) within the frequency range 80 cycles to 6 kilocycles. This range was selected after it was found

that it was greater than the frequency range of all calls produced by the three species.

6.3 Terminology

Various workers have evolved their own terms for describing the physical parameters of anuran calls and as yet there has not been any agreement on their usage. Ideally, the terms should be defined on the basis of the physical nature of the sound produced (Broughton, 1963) and not, as it often happens, on the type of sound-producing organ or how it sounds to man. The terms used here are defined below and some of these are also shown in Fig. 6.2 B.

A call or call sequence is a vocalization which is usually composed of discrete units of sound or components (note, according to Littlejohn (1965) and Fouquette (1960)) given in an ordered sequence. When more than one component is present in a call, the components are separated from each other by a period of silence which is generally greater than half the length of the component. Each component is composed of one or more syllables. In poly-syllabic components the syllables are units of sound consisting of one or more pulses which are frequently separated from similar units by a period of silence (an interphase) or by an abrupt change in pulse repetition

rate. Components in which these conditions do not occur are considered to be composed of one syllable only.

A pulse is a burst of sound which corresponds to a single vibration of the vocal chords. The rate at which pulses are produced is the pulse repetition rate and is equivalent to the fundamental frequency of the sound made (McAlister, 1961). Littlejohn (1959, 1965) refers to this as the pulse repetition frequency.

6.4 Calling Activity of P. corroboree

Very little information is available on diel changes in calling activity of frogs apart from isolated observations which indicate that most frogs are vociferous at night.

Calling activity of a population of P. corroboree was therefore studied to determine the periodicity of this activity and also to obtain some information on the environmental factors which might be instrumental in inhibiting or stimulating calling.

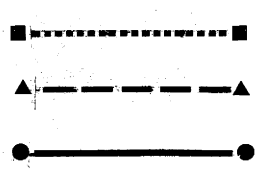
Results

From Fig. 6.1 it seems that calling activity of P. corroboree exhibits diel fluctuations which are more pronounced at the beginning of the breeding season (upper graph) than towards the end (lower graph).

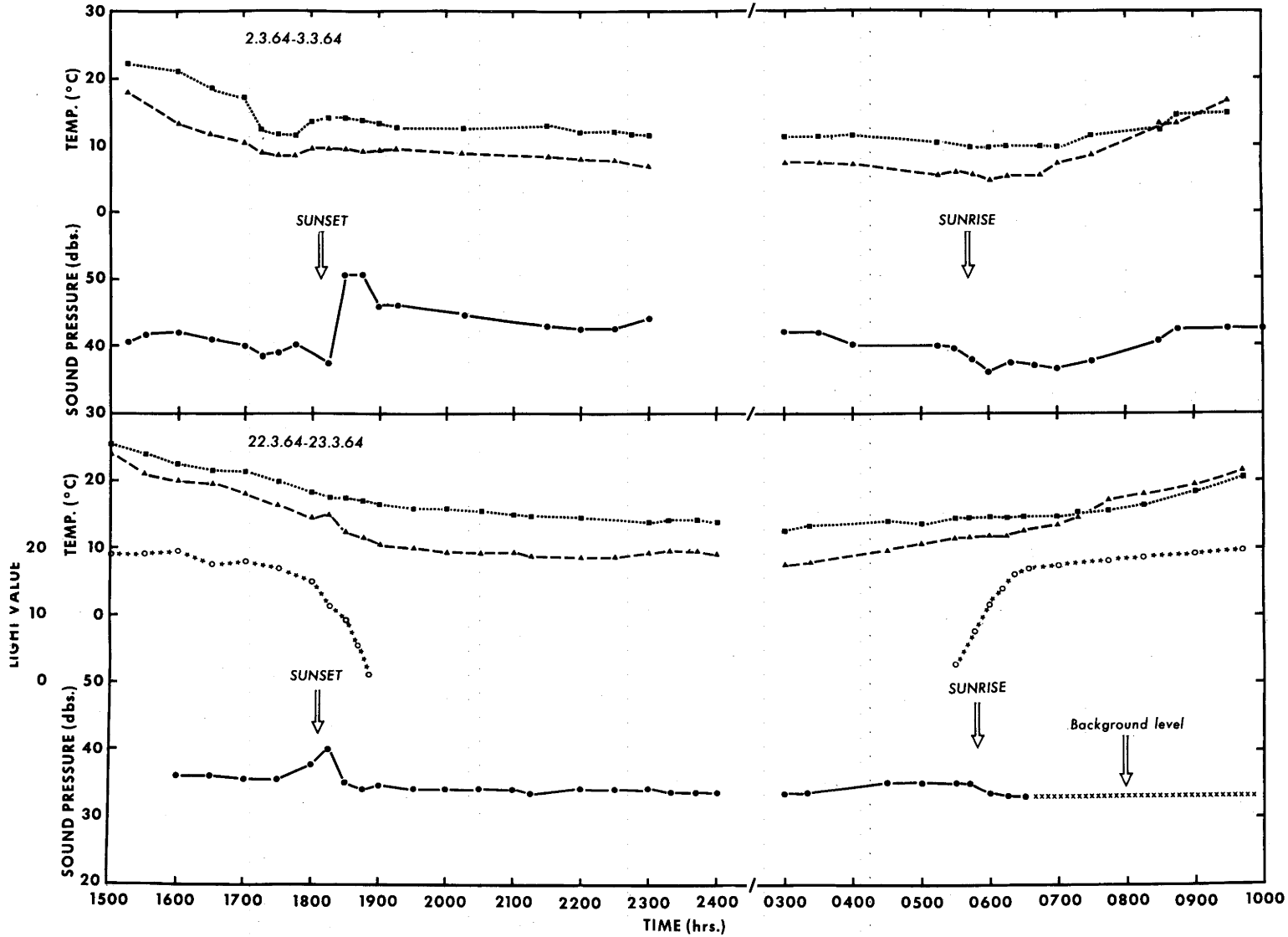
At the beginning of the breeding season there are three

Fig. 6.1

Calling activity in P. corroboree at Coree Flats at the beginning of the 1964 breeding season (upper graph) and towards the end of the breeding season (lower graph).



- Mean burrow temp. (^{o}C)
- Mean air temp. (^{o}C)
- Mean sound pressure level (dbs)


2.3.64-3.3.64
TEMP. (°C)
SOUND PRESSURE (dbs.)
SUNSET
SUNRISE
22.3.64-23.3.64
TEMP. (°C)
LIGHT VALUE
SOUND PRESSURE (dbs.)
SUNSET
SUNRISE
Background level
1500 1600 1700 1800 1900 2000 2100 2200 2300 2400 0300 0400 0500 0600 0700 0800 0900 1000
TIME (hrs.)

well defined changes in calling activity: one immediately following sunset, another at sunrise and a third in the early afternoon between 1300 to 1500 hours (not shown on the Fig.). The variations in activity following sunset and sunrise, as shown by fluctuations in sound pressure levels, appeared to be associated with the changes in light intensity. Decreasing light intensities are associated with an increase in calling activity whereas increasing light intensities are associated with a reduction in activity. The probable action of these two aspects of this factor is also indicated by the minor, momentary fluctuations in calling activity prior to sunset. During this period it was observed that when shadows were cast on the breeding area by the tree canopy there was a slight increase in the number of males calling. But as the sun sank lower on the horizon to the level of the tree boles the breeding area was illuminated by sunlight and the number of males calling decreased. Since not all parts of the breeding area were in shade or sunlight simultaneously, the resultant changes in activity were barely detectable by the sound pressure meter.

The greatest activity in calling occurred during the short period following sunset, and generally lasted for

about 15 minutes. This burst of sound did not appear to result in movements of females into or within the breeding area. Most of the gravid females seen in the breeding area were observed between 2100 to 0100 hrs.

The decrease in sound pressure noticed in the early afternoon between 1300 and 1500 hrs was most probably due to the high temperatures experienced in the burrows. As the temperatures began to decrease following this period there was an increase in the number of males calling but only a slight change in the sound pressure level.

Calling activity of males towards the end of the breeding season (lower graph) was very much reduced and only exhibited two minor fluctuations associated with changes in light intensity. Although no recordings of sound pressure were obtained before breeding commenced it was observed, however, that calling activity was similar to that recorded towards the end of the breeding season.

6.5 Description of Mating and Courtship Calls

From Table 6.1 it appears that the mating calls of 8 of the 10 species of the genus are very similar with the possible exception of P. guentheri. It is possible that the 'squelch' call of this species is a threat call, judging by its similarity in sound to the threat calls of three

Table 6.1 Onomatopoeic descriptions of the mating calls of 8 species of *Pseudophryne*

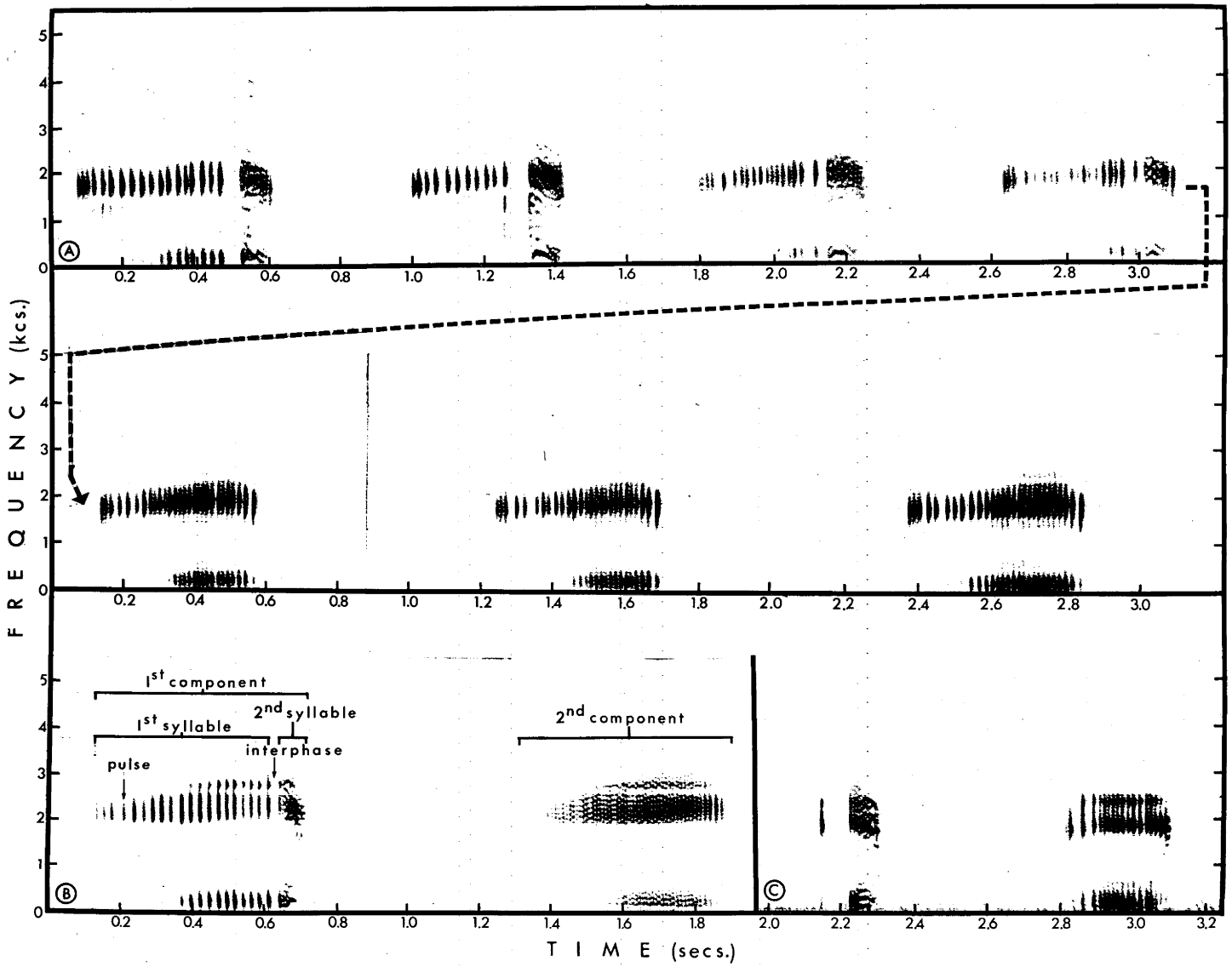
Species	Call	Reference
Pseudophryne bibroni	usual call is a nasal 'ank-ank' or 'ank' repeatedly slowly Sometimes the call is a short 'erk'	Moore, 1961
	a short, harsh 'creek'	Littlejohn, 1963
P. dendyi	a nasal 'erk' like that of *P. bibroni*	Moore, 1961
P. corroboree	a nasal 'wrank' of about 1 sec. duration	Moore, 1961
P. semimarmorata	same as *P. bibroni*	Littlejohn, 1963
P. australis	a short grating 'creek' sometimes repeated two or three times	Harrison, 1922
	same as *P. bibroni*	Moore, 1961
P. guentheri	a short grating 'ka-a-k' repeated slowly	Main, 1965
P. occidentalis	rather variable: long 'squelch' to short 'chick'	Main, 1965
P. douglasi	typical harsh grating *Pseudophryne* call	Main, 1965

Fig. 6.2

A. The courtship call of P. corroboree. This call is composed of seven components of which four are disyllabic and three are monosyllabic.

B. The mating call of P. corroboree. The first disyllabic component of the mating call is similar to that shown in A. The second component of this call is similar to the monosyllabic components of the courtship call and is also similar to the threat calls in Fig. 6.3 A and B.

C. The mating call of P. dendyi. The first component of this call is similar to that of P. corroboree except that this call has fewer pulses in the first syllable.


FREQUENCY (kcs.)
TIME (secs.)
A
B
C
1st component
1st syllable
2nd syllable
interphase
pulse
2nd component

Pseudophryne species analysed. If so, then all the mating calls are characterized as harsh sounds, the endings of which are similar in sound to the harsh terminal consonant 'k'.

i) P. corroboree

In the mating call of P. corroboree there are a number of discrete components, often more than two, of which the first is generally disyllabic and the second and all subsequent components are monosyllabic. The first and second components of a typical call are shown in Fig. 6.2 B.

All the components of the call are pulsate but the pulses are generally only discernible in the first syllable of the first component. In this component there is a tendency for the pulse repetition rate to increase throughout the length of the component. The pulse repetition rate of the first syllable varies from 20 to 100 pulses per second and in the second syllable from 98 to 555 pulses per second (Table 6.2). The first syllable is frequently clearly distinguished from the second by a well marked period or interphase. In some calls, however, there is no interphase and the two syllables are only recognizable by the abrupt change in pulse repetition rate (Fig. 6.3 C). The durations of the two syllables differ with the first syllable being much greater than the second.

Table 6.2

Some of the physical characteristics of the mating call of *P. corroboree*.

Physical Characteristics of the Mating Call of *P. corroboree*

LOCALITY		No. of Pulses			Pulse Repetition Rate (pulses/sec.)			Duration (secs.)		
		1st. Syll.	2nd Syll.	2nd Comp.	1st Syll.	2nd Syll.	2nd Comp.	1st Syll.	2nd Syll.	2nd Comp.
Coree Flats	No.	21	20	13	21	20	13	21	20	13
	Mean	18.4	9.7	37.7	43.3	213.3	77.8	0.47	0.050	0.460
	Range	11-30.7	4.0-16.5	24.0-61.4	21-75	98-555	37-121	0.24-0.85	0.018-0.076	0.06-0.65
Smiggin Holes	No.	18	16	14	18	16	14	18	15	14
	Mean	16.6	14.4	34.3	54.1	144.6	80.4	0.34	0.087	0.386
	Range	7.5-28.5	6.5-33.0	22.0-40.5	31-93	120-339	39-152	0.12-0.65	0.047-0.200	0.086-0.61
Round Mtn.	No.	14	14	8	14	13	8	13	13	8
	Mean	17.8	17.1	42.9	45.7	221.1	87.4	0.435	0.078	0.548
	Range	6.0-31.0	9.0-44.0	14.0-60.0	20-100	138-394	24.0-150	0.17-0.64	0.048-0.171	0.400-0.870

In a few calls there is a third syllable barely distinguishable from, and immediately following, the second syllable. This syllable has the appearance of the 'tock' call (see p.112) being very short in duration (less than 0.05 secs) and having a very high pulse repetition rate.

The dominant frequency of the first and second components of the mating call is a broad emphasised band occurring between 1,500 to 3,200 cycles per second. In some calls the dominant frequency rises slightly throughout the length of the first syllable and then declines rather rapidly during phonation of the second syllable. Some other calls exhibit no change in dominant frequency and yet others show an undulating pattern suggesting marked frequency modulation. The fundamental frequency of most calls is within a band of 80 to 500 cycles per second and displays the same pattern as the dominant frequency. In most calls harmonics are not well expressed in the first syllable of the first component but they are, however, very prominant in the second syllable.

The courtship call of P. corroboree (Fig. 6.2 A) is essentially a modified mating call. It generally has three to four disyllabic components instead of one as is the case of the mating call (Fig. 6.2 B), followed by three

Fig. 6.3

Sonagrams of some calls of P. corroboree, P. dendyi and P. bibroni.

A. Courtship call of P. dendyi recorded at Little Thredbo River Flats, N.S.W.

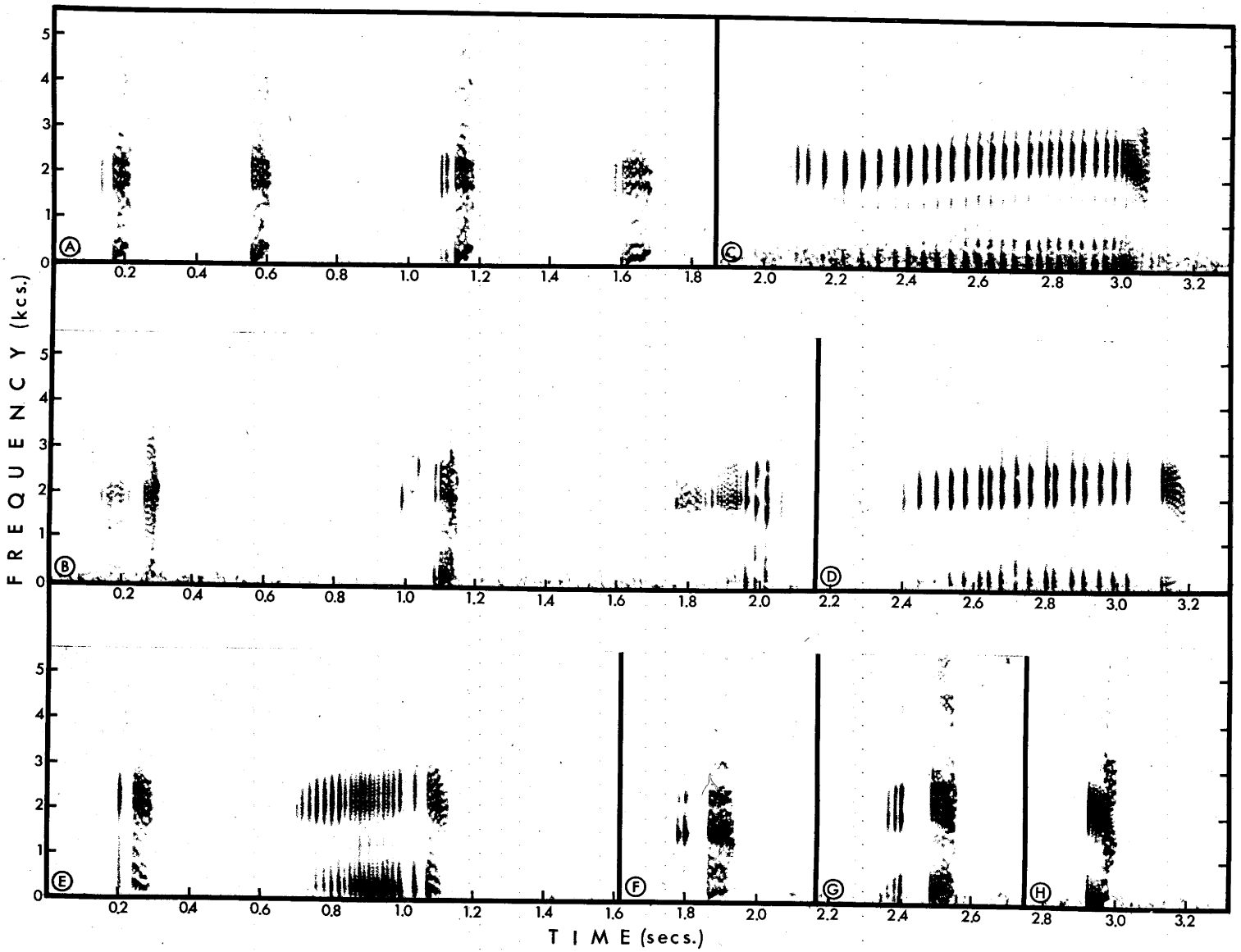
B. Probable courtship call of P. bibroni recorded at Uriarra, N.S.W.

C. A variation in the first component of the mating call of P. corroboree. Note that this call is composed of three syllables.

D. A variation of the mating call of P. bibroni. Note the similarity of this call to that shown in C.

E. Portion of the courtship call of P. corroboree. The first component of this call resembles the components in the mating call of P. dendyi (F) and P. bibroni.

F. Mating call of P. dendyi, N.S.W. The first syllable of this call consists of two pulses and is separated from the second syllable by a period of silence or interphase.


FREQUENCY (kcs.)
TIME (secs.)
A
B
C
D
E
F
G
H

to four monosyllabic components. All these components are similar in structure to those described for the mating call.

A variant of the courtship call recorded at Snowy Flats (Fig. 6.3 E) is of interest, as it shows one feature which is also possessed by the mating calls of P. dendyi and P. bibroni, and that is the small number of pulses in the first syllable of the first component. All other components of this call were normal.

ii) P. dendyi and P. bibroni

The mating calls of both P. dendyi (Figs. 6.2 C and 6.3 F) and P. bibroni (Figs. 6.3 G and H) are essentially the same and are similar to the mating call of P. corroboree (Fig. 6.2 B). The only difference found between the mating calls of P. dendyi and P. bibroni was in the second monosyllabic component. This component was present in only six of the thirty-seven calls of P. dendyi but not in any of the twenty-one calls recorded of P. bibroni.

The structure of the mating calls of P. dendyi and P. bibroni corresponds to that described for P. corroboree.

In Tables 6.3 and 6.4 are shown the physical characteristics of the mating calls of P. dendyi and P. bibroni, respectively.

The most significant feature of the first component

Table 6.3

Some of the physical characteristics of the mating call of *P. dendyi*.

Physical characteristics of the Mating call of *P. dendyi*

LOCALITY		No. of Pulses				Pulse Repetition Rate (pulses/sec.)				Duration (secs.)				
		1st Syll.	2nd Syll.	3rd Syll.	2nd Comp.	1st Syll.	2nd Syll.	3rd Syll.	2nd Comp.	1st Syll.	Inter-phase	2nd Syll.	3rd Syll.	2nd Comp.
Snowy Mtns	No.	13	17	16	6	9	10	16	6	13	13	17	16	6
	Mean	2.9	7.3	6.2	23.8	125.6	164.7	388	159	0.028	0.048	0.044	0.018	0.206
	Range	1.0-7.3	3.5-13.0	3.0-11.0	13.0-32.0	64-272	121-285	280-600	97-234	0.004-0.088	0.006-0.076	0.024-0.086	0.006-0.035	0.056-0.325
Coree Flats	No.	2	3	4	-	1	3	4	-	2	2	3	4	-
	Mean	16.9	3.9	7.9	-	107	143.3	339.3	-	0.018	0.056	0.028	0.025	-
	Range	1.0-32.9	3.6-4.0	4.0-12.7	-	-	111-173	250-433	-	0.002-0.035	0.053-0.058	0.023-0.036	0.009-0.041	-
Yarrangobilly	No.	10	10	10	1	6	10	10	1	10	10	10	10	1
	Mean	6.4	7.8	7.4	33.5	48.1	132.1	252.3	65.0	0.149	0.089	0.057	0.031	0.52
	Range	1.0-24.0	3.3-12.0	3.7-14.0	-	33 - 67	84-181	221-292	-	0.004-0.380	0.020-0.300	0.012-0.101	0.012-0.058	-
Clyde Mtn.	No.	3	6	5	1	1	6	5	1	3	3	6	5	1
	Mean	1.7	5.4	6.7	25.0	52	152.7	348.7	124	0.041	0.054	0.034	0.015	0.210
	Range	1.0-2.0	3.6-7.6	4.5-9.6	-	-	113-187	266-386	-	0.002-0.081	0.040-0.069	0.023-0.055	0.002 - 0.025	-

of the calls of both species was that there was an increase in pulse repetition rate, with concomitant decrease in duration, from the first to the third syllable. There was an increase in the number of pulses per syllable from the first to the third syllable in P. bibroni and in calls of P. dendyi recorded at Clyde Mountain. In the other samples of P. dendyi the number of pulses per syllable varied inconsistently with duration of the first component of the call. Although there is some overlap in the pulse repetition rate between the first and third syllable in both species (Table 6.3 and 6.4) there is a tendency for the pulse repetition rate to increase with the duration of the call.

In the mating calls of both species the number of pulses in the first syllable is generally less than 10 although some calls have more than 20. Despite the variability in the number of pulses in the first syllable of the first component of the mating call of P. dendyi and P. bibroni it appears that the calls of these species can be distinguished from those of P. corroboree on the basis of the number of pulses present in this syllable. The mating call of P. corroboree generally has a greater number of pulses in the first syllable (Table 6.2).

Table 6.4

Some of the physical characteristics of the mating call of *P. bibroni*.

Physical Characteristics of the Mating Call of P. bibroni

LOCALITY	Burrow Temp. (°C)		No. of Pulses			Pulse Repetition Rate (pulses/sec.)			Duration (secs.)			
			1st Syll.	2nd Syll.	3rd Syll.	1st Syll.	2nd Syll.	3rd Syll.	1st Syll.	Inter phase	2nd Syll.	3rd Syll.
Uriarra	12-18.5	No.	12	12	11	12	12	11	12	12	12	11
		Mean	2.8	5.4	7.7	49.8	155.3	301.5	0.044	0.045	0.040	0.026
		Range	1.0-5.0	3.0-10.3	4.0-13.0	41.7-134	92-266	184-409	0.004-0.105	0.009-0.078	0.025-0.078	0.010-0.049
Tidbinbilla	12.0	No.	1	1	1	1	1	1	1	1	1	1
		Mean	3	3	7.2	57	114	252	0.054	0.026	0.026	0.028
		Range	-	-	-	-	-	-	-	-	-	-
Mountain Ck.Rd.	11.5-15.0	No.	7	8	8	7	8	8	7	7	8	8
		Mean	6.2	6.4	7.3	65.3	130.7	249.1	0.168	0.057	0.053	0.045
		Range	1.5-20.3	5.3-9.0	4.8-10.0	24.7-143.0	86.8-159.7	100-398.9	0.009-0.820	0.024-0.102	0.030-0.090	0.017-0.100

The fundamental frequency of the mating calls of P. dendyi and P. bibroni varied from 80 to 700 cycles per second but in most calls that were analysed the emphasized band occurred between 250 and 500 cycles per second. The dominant frequency occurred from 1,700 to 2,600 cycles per second.

The duration of the first component of the mating calls varied quite considerably, being largely dependent upon the length of the first syllable. In P. dendyi this component, including the interphase, varied from 0.048 to 1.112 secs.

The calls of P. dendyi and P. bibroni which have been called courtship calls are not so clearly defined as those described for P. corroboree. These calls have been so designated because they were uttered in comparable situations to the courtship calls of P. corroboree and also because of their structural similarity to these calls.

The only courtship call of P. dendyi which was recorded (Fig. 6.3 A) shows that the call is approximately 1.5 secs in duration and is composed of four similar components. Each of these components is similar to the polysyllabic first component of the mating call, and if there were not so many of these in one call sequence the call could be regarded as being a mating call.

In one of two courtship calls recorded of P. bibroni (Fig. 6.3 B) the call differs from that of P. dendyi, particularly in the variability in pulse repetition rate. In the last component of the call the pulse repetition rate is initially high but decreases during phonation of the component. This was observed in some mating calls and threat calls of all three species. The significance of the variability in pulse repetition rate is not known.

The mating call is the most frequently heard call during the calling season although in P. corroboree threat calls are also fairly frequently produced during the early part of the calling and breeding seasons.

It has been generally assumed that the mating call attracts gravid females to the calling conspecific male, but evidence for this assumption has been produced for only a few species. During this study a gravid P. corroboree female was the only one seen to orientate towards, and locate, a calling male. It was evident from her behavioural pattern that she was endeavouring to locate a particular male that had been calling persistently for some hours. From the time when she was first observed it took her 25 minutes to locate the male who was in a well hidden burrow only three feet from her. Although the female remained in

the burrow with the male for approximately 2 hours no eggs were laid. Throughout this period the male continued to call, but the call produced was similar to the one shown in Fig. 6.2 C which is a variant of the typical disyllabic component of the mating call. In all other cases where a gravid female has been found in or near a burrow the male has been heard to utter the courtship call. It is possible that the courtship call plays some part in ensuring that mating does occur by signifying that the male is ready to mate.

It has been suggested that the mating call may also serve to attract both other males and females to the breeding area (Mecham, 1961). Savage (1961) has definitely shown that calling does not have such an effect in Rana temporaria and Cummins (1920) also came to the same conclusion with regard to a number of North American species of frog. In P. corroboree most males probably move into the breeding areas under the influence of external factors, probably temperature, without the stimulus from calling (see Chapter 4 Breeding Biology).

Some males, however, could be attracted to the breeding area by the calls of other males especially during the few weeks prior to the commencement of the breeding season

when calling activity is beginning to increase. It is more likely that calling plays a greater part in attracting females to the breeding area. But even in this case the factors of the physical environment are probably influential at least during the initial stages of the migratory phase. Climatic factors possibly stimulate the growth of the reproductive organs which in turn cause an increase in sexual activity which usually results in the tendency for the animals to wander (Gorbman and Bern, 1962). The resultant movement is probably orientated towards the breeding areas either through past 'experience' or some innate mechanism. Once the females have reached a point where they are able to hear males calling, the calls could act as the stimulus for further movement.

The initial movement of the females as a result of the action of climatic factors may partly explain why females are attracted to areas where there are only a few males calling. The sound produced by a few males is barely audible (to the human ear) at a distance of about 30 to 50 metres even on a still night. If sound were the only means whereby females could find the breeding areas, females either must live within a short distance of them or they must have acute hearing. Information on both of these facets of their biology is sorely lacking.

As with the mating call, the precise function of the courtship call is not known. It does appear, however, that the increase in number of polysyllabic components in the calls of the three species may be indicative of the increase in the level of sexual excitement of the male. In the eastern wood peewee an increase in the rate of calling indicates an increase in the intensity of the level of activity (Sebeok, 1965). I have observed similar behaviour in Crinia signifera and Hyla verreauxi where the number of components (or notes) in the mating call is a reliable guide to whether or not there is any breeding activity. Calls which contain a large number of notes generally signify that breeding will occur.

A gravid P. corroboree was introduced into the burrow of a calling male on three separate occasions in the field to clarify the question of the function of the courtship call. No results were obtained on two of these occasions and on the third the only reaction by the male was the utterance of threat calls. These aggressive tendencies may have been elicited as a result of the artificial situations caused by pushing a gravid female into the burrow or as a result of disturbing the calling male. Since the results were inconclusive the question of the function of the courtship call must remain open.

Table 6.5 Physical characteristics of threat calls of *P. corroboree*

Type		No. of Pulses	Pulse Repetition Rate (pulses/sec.)	Call Duration (secs)
'Short' threat	No.	7	7	7
(Burrow temp.	Mean	44.7	122.0	0.441
13.0-17.5°C)	Range	33.0-53.5	79.0-159.7	0.333-0.595
'Long' threat	No.	36	36	36
(Burrow temp.	Mean	44.5	107.8	0.520
9.5-22.3°C)	Range	21.3-75.9	23.0-229.0	0.240-1.270
'Tock' call	No.	3	3	3
(Burrow temp.	Mean	18.5	330.0	0.057
14-17.5°C)	Range	15.0-22.0	244.0-379.0	0.050-0.063

6.6 Description of Threat Calls

i) P. corroboree

P. corroboree produces three or four different threat calls and at least two of these signify different states of aggressive behaviour.

Both of these calls have similar physical characteristics (Table 6.2) but differ in the number of components produced in one call sequence. In the first type, or 'short' threat call, the call is composed of two or three similar monosyllabic components whereas in the second, or 'long' threat call, there is only one monosyllabic component present. Generally, the 'short' threat call is given by the male occupant of a burrow when another male intrudes. If the intruding male is not chased out of the burrow the occupant of the burrow or both males will utter the 'long' threat call. From this behaviour it could be inferred that the 'short' threat call is the initial challenge to intrusion and its repetitive nature is probably indicative of the level of aggression. When this fails to prevent a foreign male entering a burrow that is already occupied, the level of aggressive behaviour of the occupant is probably lowered as shown by the production of only one component per call and by the fact that the intruder will also call. Both threat calls are harsh sounds to the human

Fig. 6.4

A. 'Short' threat calls of P. corroboree.

B. 'Long' threat call of P. corroboree.

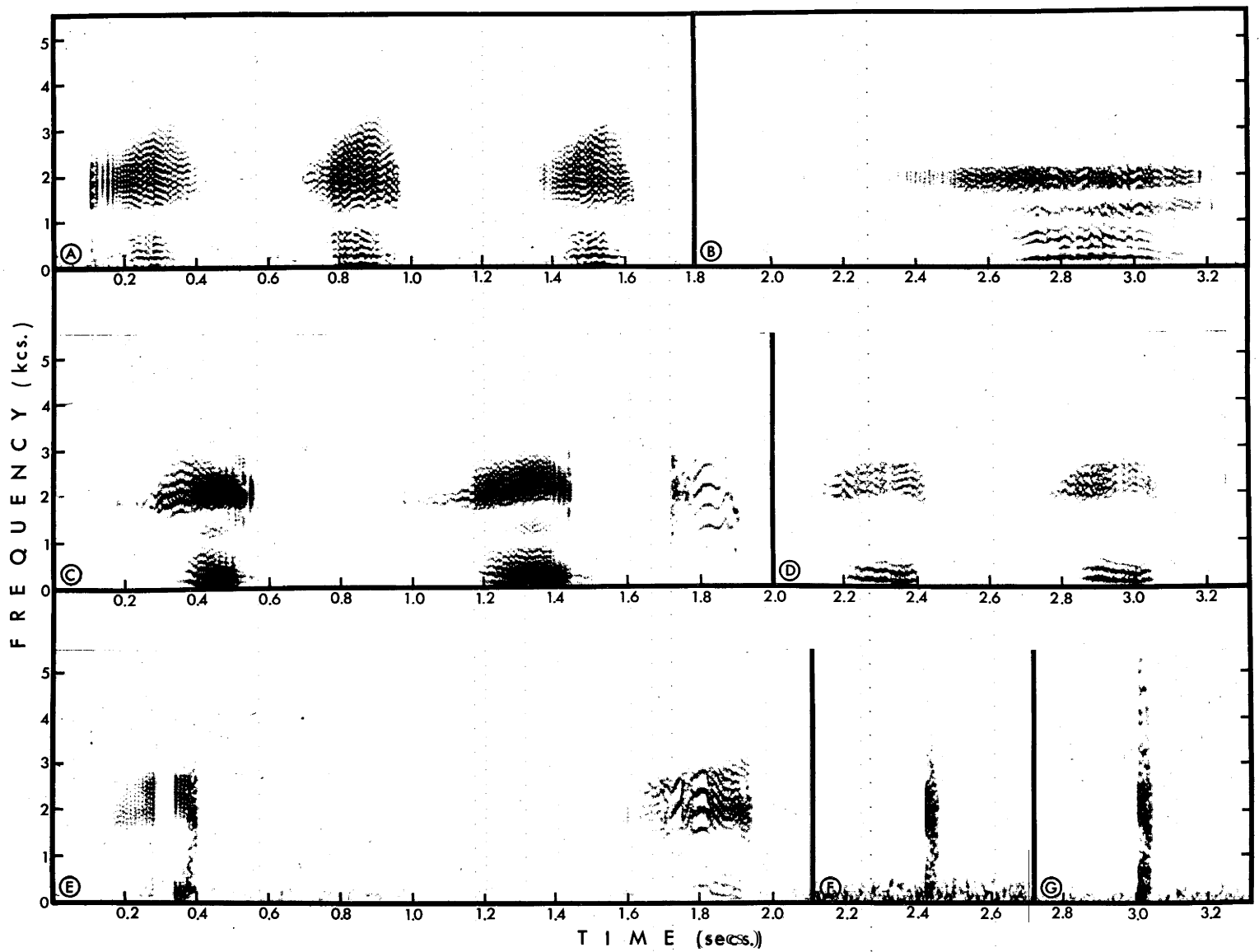
C. Two 'short' threat calls of P. corroboree followed by a non-pulsate threat call of another individual. Note the well defined harmonics of this call.

D. Two 'short' threat calls of P. dendyi.

E. A mating call of P. bibroni followed by a call which is probably a threat call. This call shows some similarities to the non-pulsate threat call of P. corroboree shown in C.

F. A disturbance or 'tock' call of P. dendyi.

G. A disturbance or 'tock' call of P. bibroni.


FREQUENCY (kcs.)
TIME (secs.)
A
B
C
D
E
F
G

ear. The 'short' threat call (Fig. 6.4 A) is generally shorter in duration (0.333 to 0.595 secs) than the 'long' threat call (Fig. 6.4 B) (0.240 to 1.270 secs) but there is a good deal of overlap between these two calls in this character as well as in pulse repetition rate. The dominant frequency of both calls is approximately the same occurring within 1,500 to 2,700 cycles per second. The fundamental frequency lies between 80 to 225 cycles per second.

The third type of threat call (Fig. 6.4 C) is a short (less than 0.2 secs in duration), non-pulsate call which is characterized by six or seven well defined harmonics showing marked frequency modulation.

The 'tock' or disturbance call could be classified as a threat call as it is uttered whenever more than one male are found in a burrow. The call is extremely short in duration (0.050-0.063 secs), generally has few pulses per call but has a very high pulse repetition rate (244.0-370.0 pulses per second). There is very little difference between this call and those of the same name recorded for P. dendyi and P. bibroni (Figs. 6.4 F, G).

ii) P. dendyi and P. bibroni

In P. dendyi and P. bibroni, 'short' threat, 'long' threat and the 'tock' calls have been recorded and the

Table 6.6 Physical characteristics of threat calls of *P. dendyi*

Type		No. of Pulses	Pulse Repetition Rate (pulses/sec.)	Call Duration (secs)
'Short' threat	No.	2	2	2
(Burrow temp.	Mean	53.0	196.0	0.242
17.5-20.0°C)	Range	37.0-69.0	187.0-206.0	0.206-0.520
'Long' threat	No.	5	5	5
(Burrow temp.	Mean	43.1	108.5	0.442
15.5-17.5°C)	Range	35.0-60.8	66.0-152.0	0.230-0.652
'Tock' call	No.	7	7	7
(Burrow temp.	Mean	17.0	200.0	0.046
15.5-20.0°C)	Range	3.5-64.0	102.0-265.0	0.026-0.075

Table 6.7 Physical characteristics of threat calls of *P. bibroni*

Type		No. of Pulses	Pulse Repetition Rate (pulses/sec.)	Call Duration (secs)
'Short' threat	No.	2	2	2
(Burrow temp.	Mean	29.5	193.0	0.18
16.0°C)	Range	23.0-36.0	174.0-212.0	0.17-0.19
'Long' threat	No.	4	4	4
(Burrow temp.	Mean	81.2	48.1	0.58
15.0-17.0°C)	Range	34.0-188.6	79.0-270.2	0.24-0.86
'Tock' call	No.	4	4	4
(Burrow temp.	Mean	10.9	285.9	0.054
16.0-17.0°C)	Range	8.0-16.0	240.0-342.0	0.031-0.092

characteristics exhibited by these do not differ greatly from those of P. corroboree (Table 6.6 and 6.7). What is probably a non-pulsate threat call has been recorded only once in P. bibroni and not at all in P. dendyi.

As in P. corroboree, the 'short' threat call of P. dendyi and P. bibroni is a call consisting of two or more similar monosyllabic components repeated rapidly (Fig. 6.4 D) whereas in the 'long' threat call there is only one component present in each call sequence. The non-pulsate call of P. bibroni, which is probably a threat call, shows the characteristic frequency modulated harmonics (Fig. 6.4 E). On the same sonagram is shown what is probably a variation of the mating call. On the occasion when these calls were recorded two males were found in the same burrow.

The 'tock' or disturbance call is similar in both species (Figs. 6.4 F, G). It is extremely short in duration (less than 0.1 secs) with a pulse repetition rate ranging from 102.0 to 265.0 in P. dendyi, and from 240 to 342 pulses per second in P. bibroni.

At least two of the threat calls made by all three species are definitely known to be associated with aggressive behaviour. The 'short' threat call is evoked by a male whenever another male attempts to enter its burrow. The usual sequence of events in P. corroboree is that the

occupant of the burrow will lunge forward at the intruder and give out the 'short' threat call. The subsequent behavioural display, however, differs between males from the two major areas, the Snowy Mountains and the Brindabella and Fiery Ranges. Males from the Snowy Mountains are definitely more aggressive and they will not only give the threat call but will also butt the intruder vigorously. Similar behaviour associated with territorialism has also been observed in a pipid frog, Hymenochirus boettgeri (Rabb and Rabb, 1963). If the intruder persists in staying within the burrow then the occupant will crawl under the trespasser and attempt to throw the latter up and out of the burrow by flexing its fore and hind limbs. This element of behaviour called 'tossing' is also displayed by males from the Brindabella and Fiery Ranges but in a languid manner. Generally, this aggression results in the intruder being chased out of the burrow with the accompaniment of 'short' threat calls. If this does not result in the intruder being deterred from staying within the burrow, and this appears to be a frequent feature of the Brindabella and Fiery Range populations, then both occupant and intruder will begin to produce the 'long' threat calls. On a few occasions it has been observed that the intruding male,

will, without displaying any apparent aggression, displace the occupant from the burrow. However, on the occasions when this was seen the burrow had been opened up in order to observe their behaviour. It may well be that this interference has caused the displacement of the male occupying the burrow.

Aggressive behaviour by the males is not only elicited by the conspecific male entering the burrow; on one occasion, a male was heard to utter threat calls at a female which had just recently deposited eggs in the burrow. Apparently the male had been in amplexus with this female prior to this display of aggression. Male P. corroboree will also direct threat calls at adult Crinia signifera, juvenile P. corroboree and adult male P. dendyi. Towards the end of the breeding season of P. corroboree at Coree Flats, male P. dendyi begin to move into the same area as is used by P. corroboree and may even be found in the same burrow. In these situations aggressive behaviour is always displayed by male P. corroboree and often this can last for three or four hours before the male P. dendyi moves out of the burrow.

The 'short' threat call of P. corroboree also appears to have the same function as the 'male release' call observed

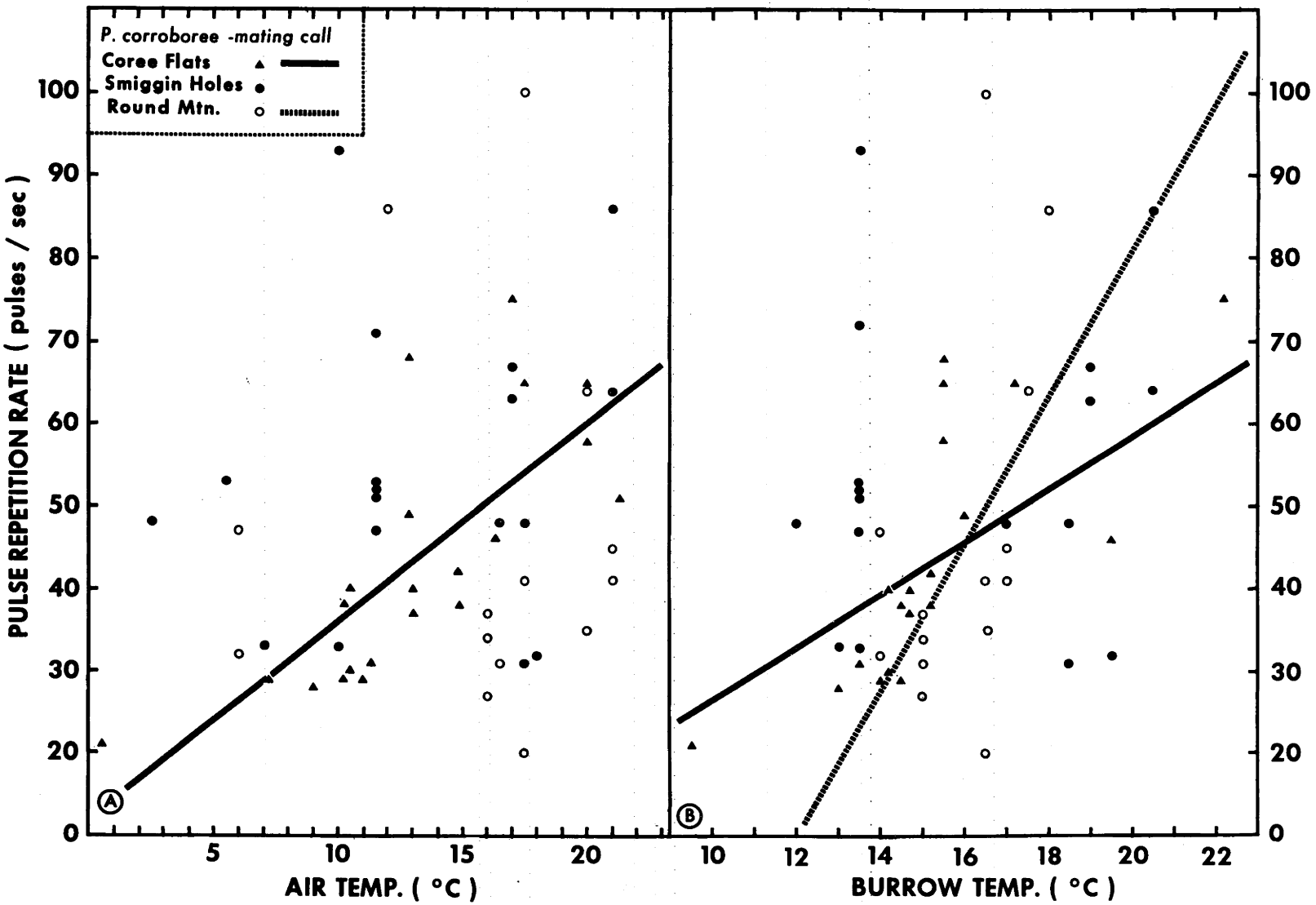
in other species. One male was observed to utter this call when clasped by another male. This was the only case of homosexual behaviour noted in all the encounters recorded between males.

Other stimuli such as human coughing, the slamming of a car door and the crude human imitations of the 'short' or 'long' threat calls can induce male P. corroboree to utter the 'short' threat calls. The calls are most readily elicited in response to these stimuli before and during the early part of the breeding season. Once breeding is well under way, the responses are not as vigorous and generally only one or two males will call. Little or no response was obtained from P. dendyi and P. bibroni males when they were presented with these stimuli during the breeding season. Interference with a burrow by a human observer will also result in the production of threat calls by males but only by those from the Snowy Mountains region. On two separate occasions whilst I was removing eggs from a burrow which also contained a male, the male lunged forward at my hand and gave out the 'short' threat call.

There is further evidence that these calls are associated with aggressive behaviour. Two burrows of P. corroboree were found in each of which there were a male and gravid

Fig. 6.5

The relationship between the pulse repetition rate of the first syllable of the mating call of P. corroboree and temperature.

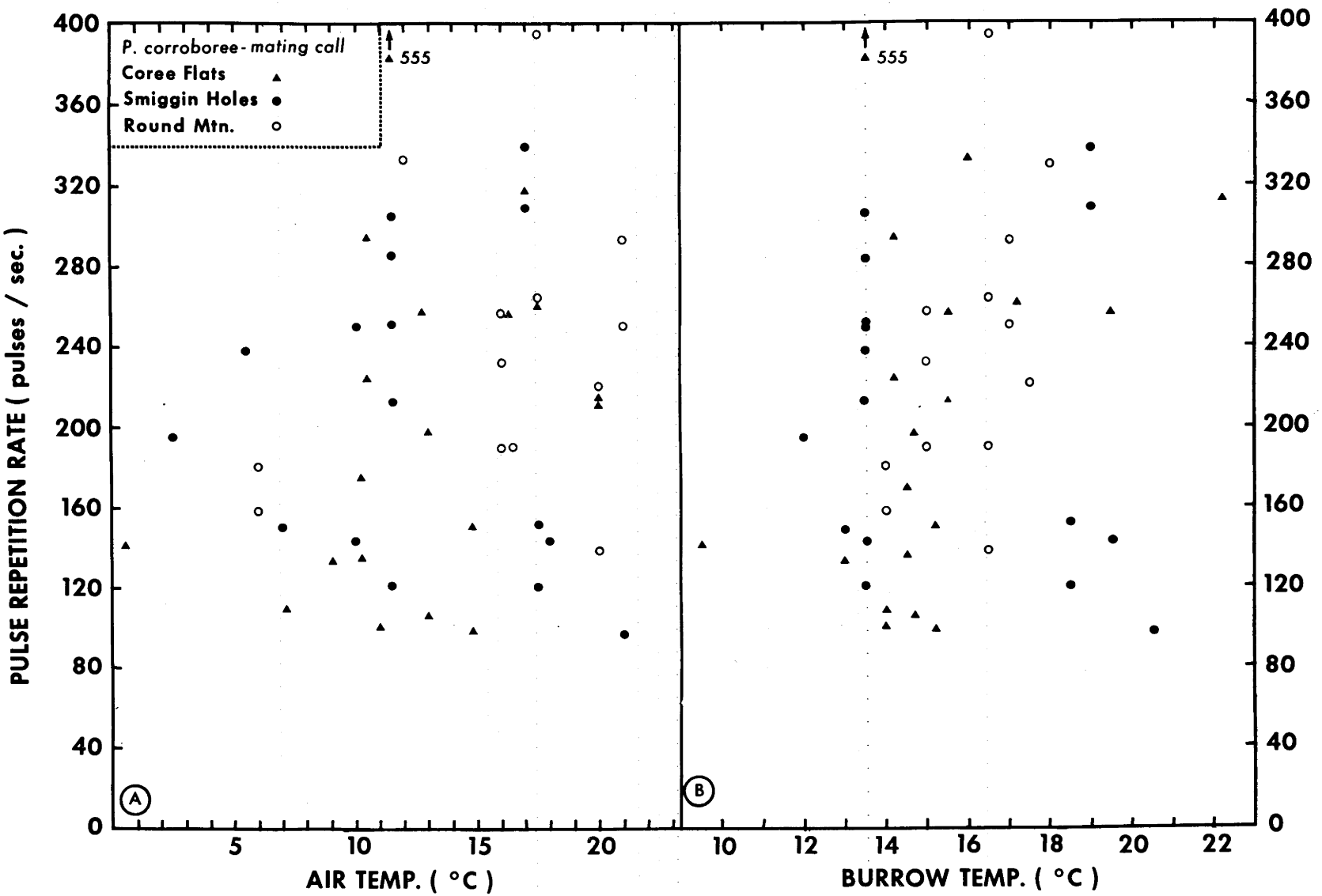

P. corroboree -mating call
Coree Flats
Smiggin Holes
Round Mtn.
PULSE REPETITION RATE (pulses / sec)
AIR TEMP. (°C)
BURROW TEMP. (°C)
A
B
0
20
30
40
50
60
70
80
90
100
5
10
15
20
10
12
14
16
18
20
22

female, but not in amplexus. In both cases the male had been giving the courtship call. The females were removed and replaced by males. Immediately following this the occupant of the burrow started uttering threat calls. Similar results were obtained in three other cases where another male had been placed in a burrow containing a calling male.

The two other calls which have been designated threat calls are not so clearly defined as the 'short' and 'long' threat calls described above. The non-pulsate call is probably associated with aggressive behaviour for it is uttered where this behaviour is likely to be displayed and that is whenever two males are found in the same burrow. On the two occasions during which these have been recorded in P. corroboree it is not certain from the sonagrams whether these calls were made by the occupant or the intruder. The sonagram of one of these recordings shows the non-pulsate call preceded by two 'short' threat calls (Fig. 6.4 C). It is possible that the 'short' threat calls were made by the occupant of the burrow and the non-pulsate call was produced by the intruder as an answering challenge to this display of aggression.

Fig. 6.6

The relationship between the pulse repetition rate of the second syllable of the mating call of P. corroboree and temperature.


P. corroboree - mating call
Coree Flats
Smiggin Holes
Round Mtn.
555
555
PULSE REPETITION RATE (pulses / sec.)
AIR TEMP. (°C)
BURROW TEMP. (°C)
A
B
0
40
80
120
160
200
240
280
320
360
400
5
10
15
20
10
12
14
16
18
20
22

6.7 Effects of Temperature on Call Parameters

i) Introduction

A number of studies have shown that call parameters are dependent upon temperature (Bellis, 1957; Blair, 1958; Zweifel, 1959). In general, pulse repetition rate, number of pulses and frequency increase with temperature, while call duration decreases with temperature.

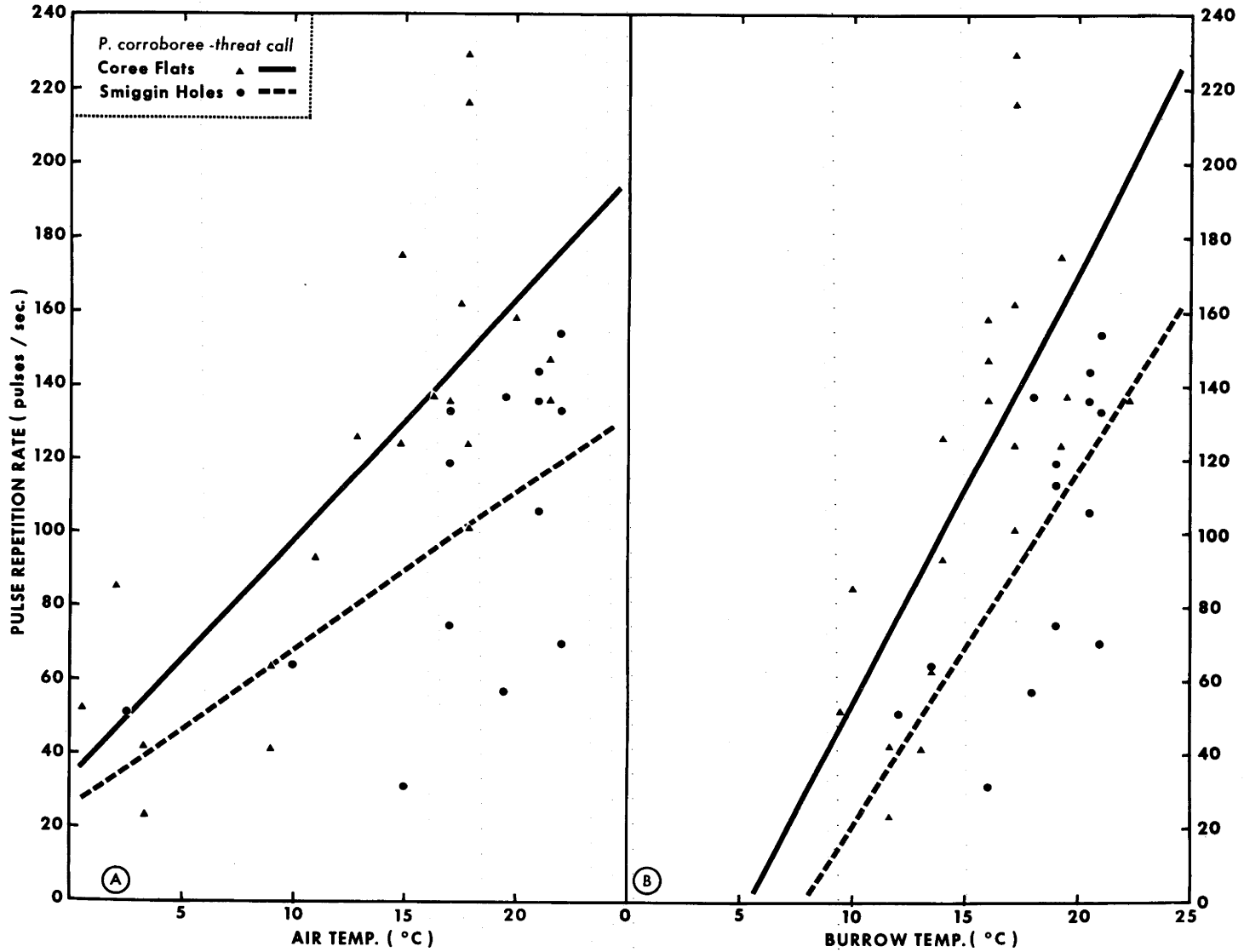
The mating and threat calls of P. corroboree and the mating calls of P. dendyi were analysed in relation to temperature, firstly, to determine the effects of temperature, on pulse repetition rate and duration of the syllables and secondly, to compare calls of populations of the two species. Pulse repetition rates of the matings and threat calls were analysed in relation to both air and burrow temperature. However, after it was found that better correlations were generally obtained with burrow temperature, this temperature was used in all subsequent calculations.

The relation of frequency and temperature was not calculated because of the great variability of this characteristic in the calls of P. corroboree and P. dendyi. The call parameters of P. bibroni were not analysed with respect to temperature because of the small samples obtained.

Regression equations were not plotted if the correlation

Fig. 6.7

The relationship between the pulse repetition rate of threat calls of P. corroboree and temperature.


P. corroboree -threat call
Coree Flats
Smiggin Holes
PULSE REPETITION RATE (pulses / sec.)
AIR TEMP. (°C)
BURROW TEMP. (°C)
A
B
0
20
40
60
80
100
120
140
160
180
200
220
240
5
10
15
20
25

coefficients were less than +0.5 or greater than -0.5.

All correlation coefficients are given in the appendix.

ii) Results

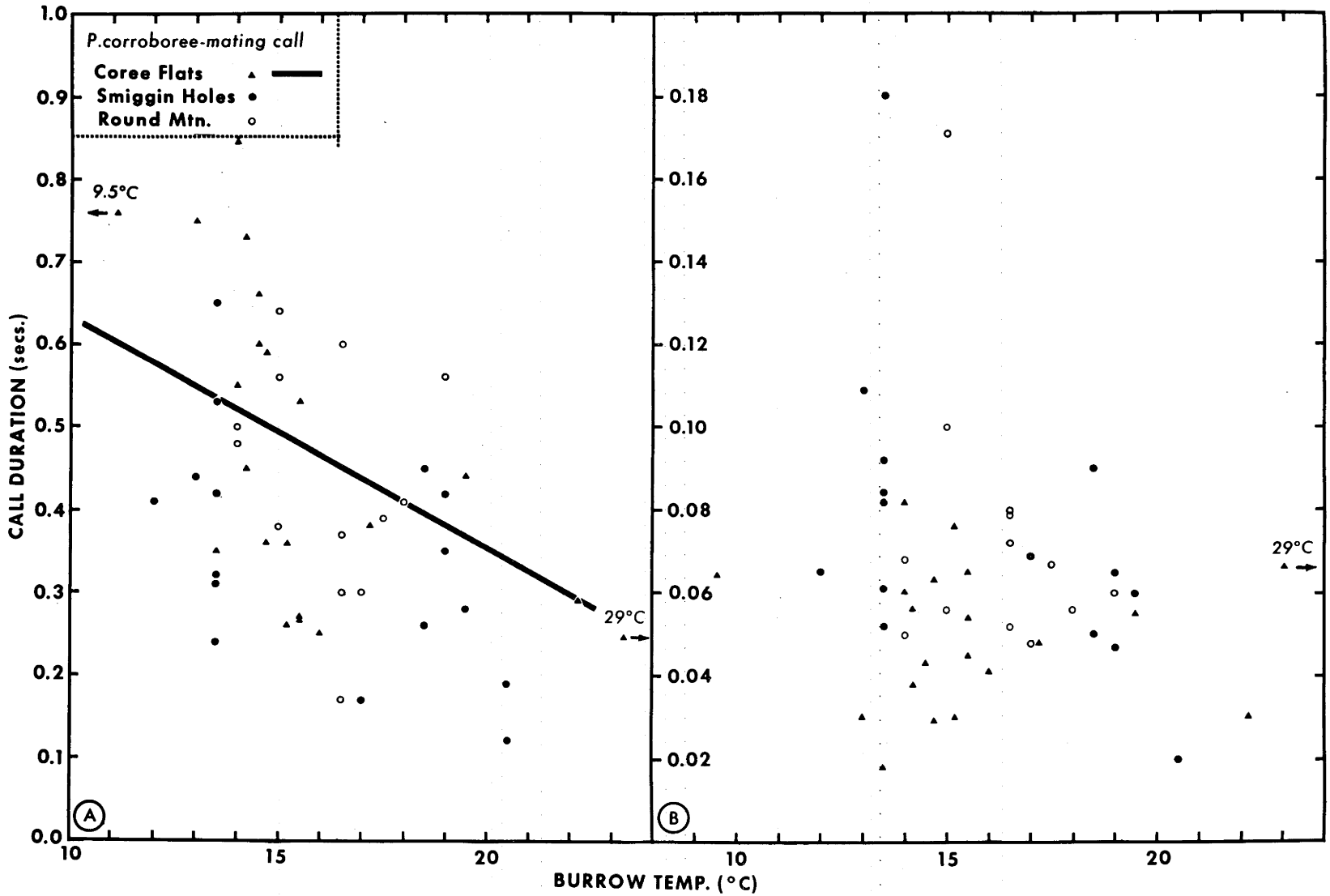
P. corroboree

Fairly consistent results were obtained only for the Coree Flats population. The pulse repetition rate of the first syllable of the first component of the mating call was positively correlated with air (Fig. 6.5 A) and burrow temperature (Fig. 6.5 B). The correlation coefficients were approximately the same in both cases (r = +0.75 and +0.74 respectively). There was a moderate correlation with the pulse repetition rate of the first syllable and burrow temperature (r = +0.5) in the sample from Round Mountain but there was only weak or no correlation of the Smiggin Holes sample (Fig. 6.5 B).

All populations exhibited only weak correlation of pulse repetition rate of the second syllable and temperature except in the case of the Round Mountain sample (Fig. 6.6) which showed moderate correlation with burrow temperature (r = +0.49). With the threat call, however, there was a definite relationship between pulse repetition rate and air and burrow temperature (Fig. 6.7 B). There was a greater correlation with air temperature than with burrow temperature

Fig. 6.8

The relationship between duration of the first (A) and second (B) syllable of the mating call of P. corroboree and temperature.


P.corroboree-mating call
Coree Flats
Smiggin Holes
Round Mtn.
9.5°C
29°C
29°C
CALL DURATION (secs.)
BURROW TEMP. (°C)
A
B
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
10
15
20

in the Coree Flats sample whereas the reverse held for the Smiggin Holes sample.

There was very little relationship between call duration and burrow temperature except for the Coree Flats sample which showed a negative correlation with temperature for the first syllable of the mating call and the threat call (Figs. 6.8 and 6.9) ($r = +0.54$ and -0.80 respectively).

P. dendyi

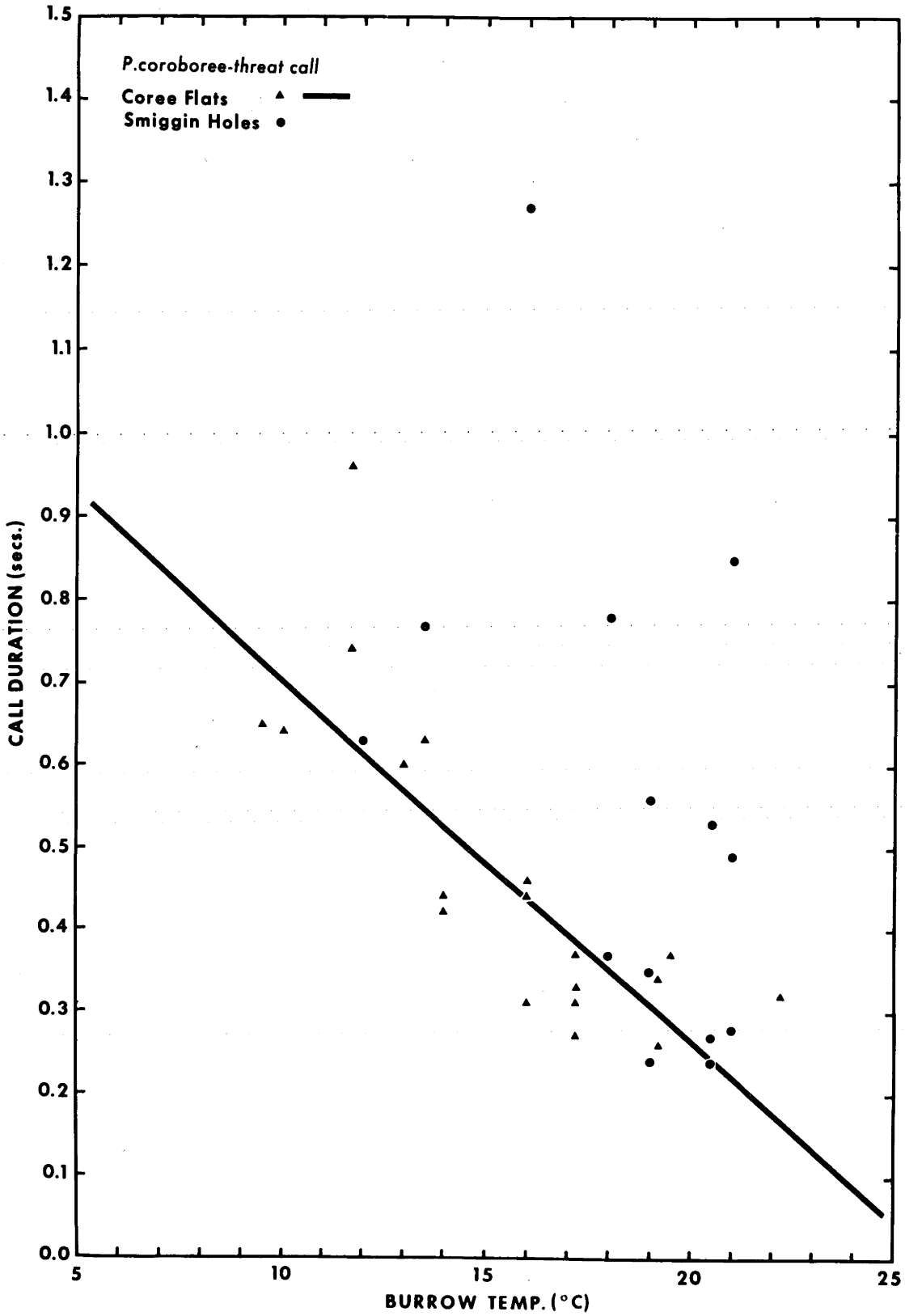
Only the second and third syllables of the mating call of this species have been plotted against temperature; the data on threat calls were too limited to warrant graphical representation. The sample sizes of the mating call from the four localities - Snowy Mountains, Coree Flats, Yarrangobilly and Clyde Mountain - were too small to allow the calculation of correlation coefficients and the plotting of regression equations.

Scatter plots of the pulse repetition rate of the second and third syllables of the mating call against burrow temperature are shown in Figs. 6.10 and 6.11 respectively.

Apart from the Coree Flats and Snowy Mountains samples there is some suggestion of a relationship between pulse repetition rate of the second syllable and burrow temperature. It appears that in most cases the pulse repetition rate increases rapidly with temperature.

Fig. 6.9

The relationship between call duration of the threat calls of P. corroboree and burrow temperature.

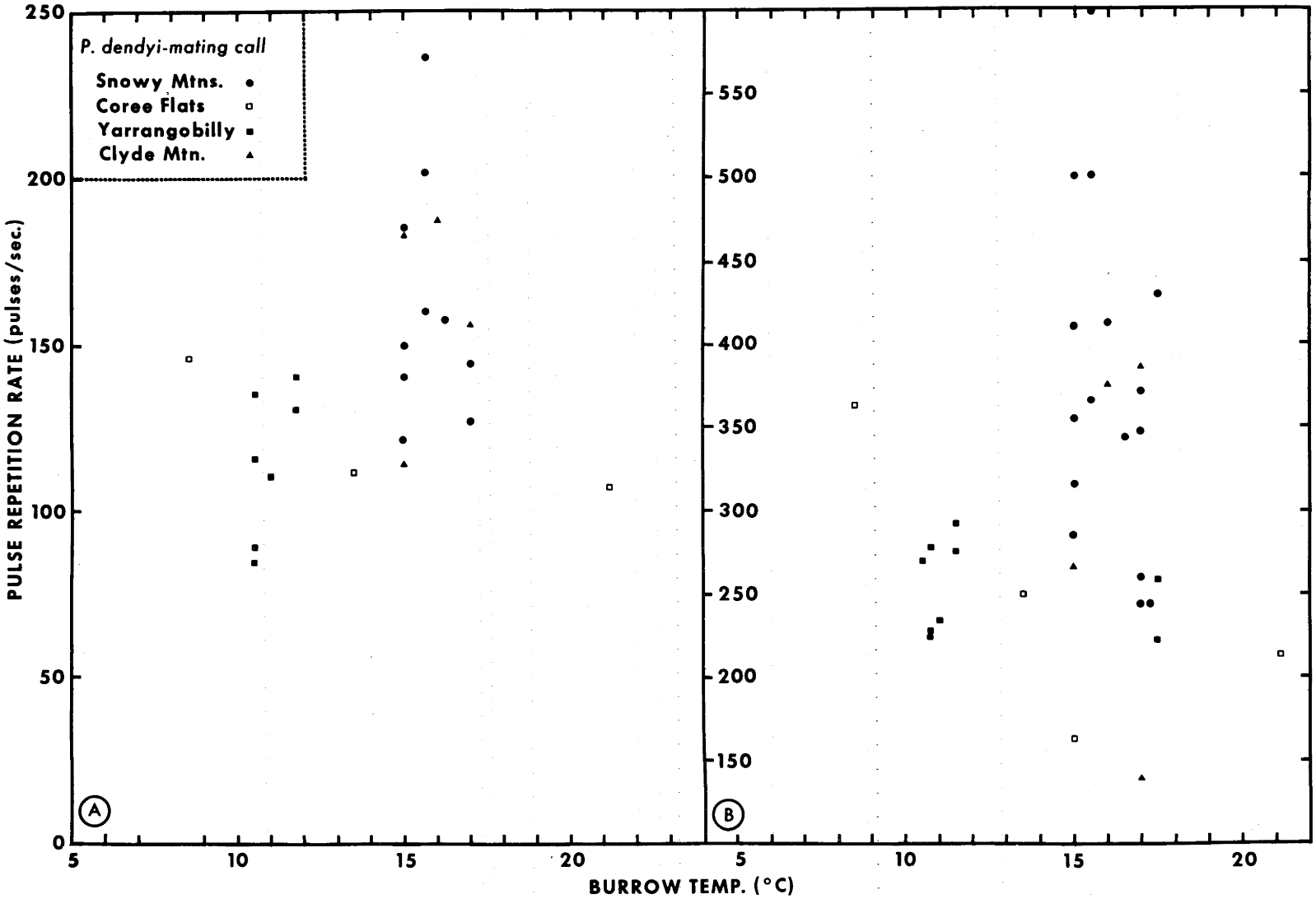

P.coroboree-threat call
Coree Flats
Smiggin Holes
CALL DURATION (secs.)
BURROW TEMP. (°C)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
5
10
15
20
25

6.8 Discussion of Calling and Associated Behaviour

The results obtained from the analyses of the mating calls of P. corroboree, P. dendyi and P. bibroni indicate that very little divergence in structure of the calls has occurred either between species or between populations of the same species. The calls of P. dendyi and P. bibroni cannot be distinguished by the methods of analysis used and there is some overlap in call characteristics of both species and P. corroboree. The mating call of P. corroboree does tend to differ, however, from those of the other species in the number of pulses in the first syllable of the first component and in the number of components in one call sequence. Other studies on the analysis of mating calls of sympatric species have shown that there are usually well defined differences in one or more call characteristics between species. It is thought that these differences enable a female to locate a conspecific male (Blair, 1958; Littlejohn, 1959, 1965). However, a female may respond to the whole pattern of sound and not to these differences alone (Martof and Thompson, 1964). This is probably what happens in the three species of Pseudophryne. In areas where P. corroboree and P. dendyi are sympatric there are probably other factors such as differences in the courtship

Fig. 6.10

The relationship between the pulse repetition rate of the second (A) and third (B) syllables of the mating call of P. dendyi and burrow temperature.


P. dendyi-mating call
Snowy Mtns.
Coree Flats
Yarrangobilly
Clyde Mtn.
PULSE REPETITION RATE (pulses/sec.)
BURROW TEMP. (°C)
A
B
0
50
100
150
200
250
300
350
400
450
500
550
5
10
15
20

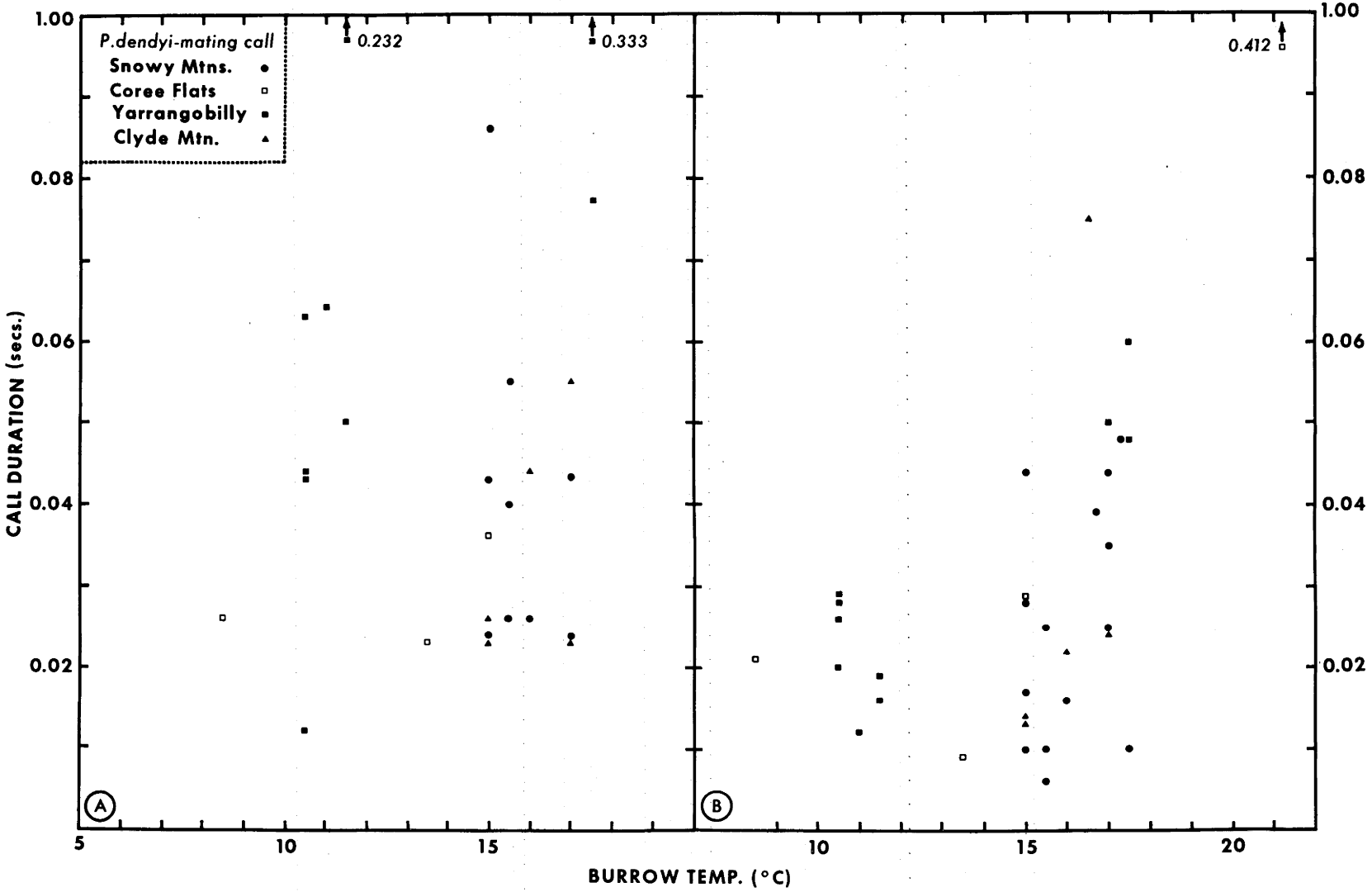
calls, in time of breeding and in colour and pattern, which may operate to enhance specific distinctiveness. But in the case of P. dendyi and P. bibroni where both species have similar calls and are similar morphologically, discrimination on the part of the female would be difficult and this could perhaps lead to hybridization.

Some workers consider the main function of the mating call as an attractant for conspecific receptive females (Blair, 1965; Littlejohn, 1959, 1963; Mecham, 1961). Bogert (1960) suggested that it may be analogous in function to the ('territorial') song of many passerine birds and therefore may act as an attractant to receptive females as well as a repellent to other males. Rabb and Rabb (1963) consider the mating call of Hymenochirus boettgeri as subserving both functions.

The mating call of the species studied here may also have these functions in addition to the function of advertising the presence of the male. Evidence is available, however, for only the attractant function of the call. Nevertheless, it is possible that the mating call is associated with territorial behaviour as it is uttered long before the breeding season has begun when only males are present in the breeding area. By advertising the presence

Fig. 6.11

The relationship between call duration of the second (A) and third (B) syllables of the mating call of P. dendyi and burrow temperature.


P.dendyi-mating call
Snowy Mtns.
Coree Flats
Yarrangobilly
Clyde Mtn.
0.232
0.333
0.412
1.00
0.08
0.06
0.04
0.02
CALL DURATION (secs.)
A
B
5
10
15
20
BURROW TEMP. (°C)

of a male and therefore signifying that a burrow is already occupied it may help to reduce the number of conflicts between males which would occur if no call was uttered. This would be particularly important during the breeding season when aggressive conflicts between males could disrupt mating or could result in males engaging in such conflict failing to obtain mates. It is not known whether it serves to space males out in the breeding area but it is more likely that actual contact between males and subsequent aggressive behaviour is more important here.

The similarity in threat calls of P. corroboree, P. dendyi and P. bibroni support the idea that "aggressive calls are often very similar in different species and appear to be mutually understood" (Koenig, 1951, cited in Marler, 1957). Vocalizations denoting aggression are generally associated with territorial behaviour and this appears to be the case in the three species studied. The males of these species appear to be territorial as defined by Nice (1941) as they: a) advertise their presence by uttering the mating call, b) are intolerant of trespassers, c) are isolated from other conspecific males, and d) generally remain in the same burrow for a portion of the time spent in the breeding area.

Territorial behaviour appears to vary in intensity between the three species of Pseudophryne. If the three species are arranged in a series with regard to increasing aggressiveness, as shown by the frequency of production of threat calls and the intensity of the displays, the series would be, P. bibroni, P. dendyi, P. corroboree (Brindabella and Fiery Ranges), P. corroboree (Snowy Mountains). Although the expression of aggressiveness may be partly dependent upon the density of the breeding male populations it seems that as far as P. dendyi and the two forms of P. corroboree are concerned the series does denote innate differences in aggressiveness. The densities of breeding populations of both these species are high and very similar. In contrast P. bibroni tends to occur in much lower densities and in most populations there are never more than 50 males present.

Chapter 7 FOOD

7.1 Introduction

There has been very little information published on the food of Australian amphibia. Main (1957) examined the faecal contents of a number of Crinia spp. occurring in south-western Australia and both Main and Calaby (Main and Calaby, 1957; Calaby, 1956, 1960) reported the stomach contents of a few desert inhabiting species.

In the study described here the stomach contents of five species of frog occurring in the southern highlands of N.S.W. were examined. These are Pseudophryne corroboree, P. dendyi, P. bibroni, Crinia signifera and Hyla verreauxi. The objectives of this study were to determine: a) the food of the three species of Pseudophryne, b) the changes in the diet of P. corroboree with size, season and habitat, and c) the food of a number of species coexisting in the same habitat.

7.2 Materials and Methods

Most specimens were collected during the day, normally between 1200-1700 hours, from under logs and leaf litter. They were then anaesthetized by chloroform and injected with 7% formalin generally within twelve hours of capture.

P. corroboree adults (greater than 20 mm in snout-

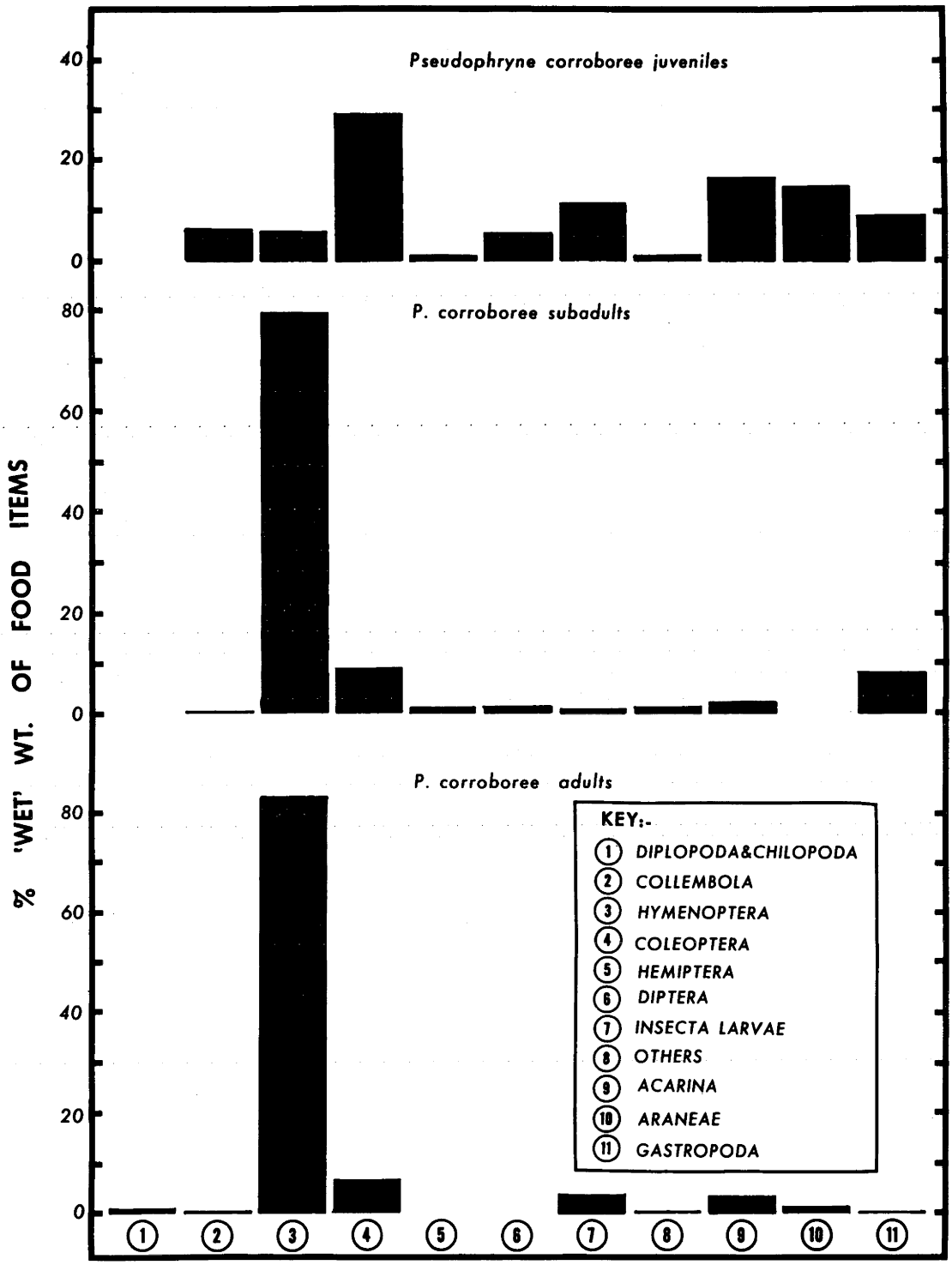
urostyle length) from Coree Flats were collected monthly from May, 1963 to May, 1964 inclusive. Additional samples of sexually mature males were taken from burrows during the breeding season of 1964 (February-April). Most juveniles (7-14 mm in body length) and subadults (14-20 mm in body length) were collected during the period January to May, 1965, from beneath vegetation and logs. Small collections of P. corroboree from higher altitudes were also examined, including 16 adult specimens from Snowy Flats, Brindabella Range (alt. 1,646 m) and 32, all adults, from the Snowy Mountains (alt. 1,590 m to 1,650 m).

P. dendyi, Crinia signifera and Hyla verreauxi from Coree Flats were collected throughout the year but mainly during the spring and summer months. Additional specimens of P. dendyi from Boggy Plain, Snowy Mountains, were taken from burrows in a sphagnum bog. All specimens of P. bibroni were collected in one area 8 miles south of Yass, N.S.W.

The food contents of the stomachs of most samples have been expressed as percentages of the total food by weight. The exceptions are P. corroboree adults from Snowy Flats and Hyla verreauxi from the Snowy Mountains region. In these, as in all other samples, the analyses of the stomach contents are shown as the percent occurrence

Fig. 7.1

The percentage 'wet' weight of food items in the stomachs of juveniles, subadults and adults of P. corroboree from Coree Flats, N.S.W. The age groups have been delimited on the basis of size; thus, juveniles are 7-14 mm in snout-urostyle length; subadults are 14-20 mm and adults are 20 mm and longer.


Pseudophryne corroboree juveniles
P. corroboree subadults
P. corroboree adults
% 'WET' WT. OF FOOD ITEMS
0
20
40
60
80
KEY:-
1 DIPLOPODA&CHILOPODA
2 COLLEMBOLA
3 HYMENOPTERA
4 COLEOPTERA
5 HEMIPTERA
6 DIPTERA
7 INSECTA LARVAE
8 OTHERS
9 ACARINA
10 ARANEAE
11 GASTROPODA

of the food items and the total number of items.

For examination the whole gut was dissected out and the stomach removed. The stomach contents were placed in a small petri dish and then examined and counted under a binocular microscope. One or more of each major food item, depending on its size, was blotted to remove excess preservative and then weighed. The resultant weight was designated the 'wet' weight. Because of the variation in weight due to the kind of prey item and the length of time in preservative, the estimations of 'wet' weight of food consumed can only serve as approximations to the actual live weight of the food items.

7.3 Results

i) P. corroboree

Fig. 7.1 shows the percentage 'wet' weight of the various food items found in the stomachs of juvenile, subadult and adult Corroboree frogs. In Tables 7.1 to 7.3 are shown the percent frequency of occurrence of the food items and the total number of each item recorded.

Stomach content analyses revealed that the juvenile frogs differed from the two older age groups in the absence of any obvious preference for a particular taxonomic category (Fig. 7.1, Table 7.1). The most important items

Table 7.1 Analysis of the stomach contents of *P. corroboree* juveniles, Coree Flats (41 specimens)

Empty stomachs - 4 (9.8%)

Food Items	Percent Occurrence of Items	Total Number of Items
Insecta		
Collembola	44.4	86
Coleoptera	45.9	23
Hymenoptera	10.8	6
Formicidae	16.2	54
Hemiptera	54.0	32
Diptera	24.3	9
Insect larvae	37.8	56
Arachnida		
Acarina	100.0	234
Araneae	10.8	10
Gastropoda		
Pulmonata	16.2	14
Others	3.3	2

Table 7.2 Analysis of the stomach contents of *P. corroboree* subadults, Coree Flats (27 specimens)

Empty stomachs - 3 (11.1%)

Food Items	Percent Occurrence of Items	Total Number of Items
Insecta		
Collembola	12.5	5
Coleoptera	50.0	15
Hymenoptera	8.3	2
Formicidae	70.8	255
Hemiptera	12.5	4
Diptera	8.3	2
Insect larvae	12.5	4
Arachnida		
Acarina	100.0	97
Gastropoda		
Pulmonata	16.7	7

Table 7.3 Analysis of the stomach contents of *P. corroboree* adults, Coree Flats (207 specimens)

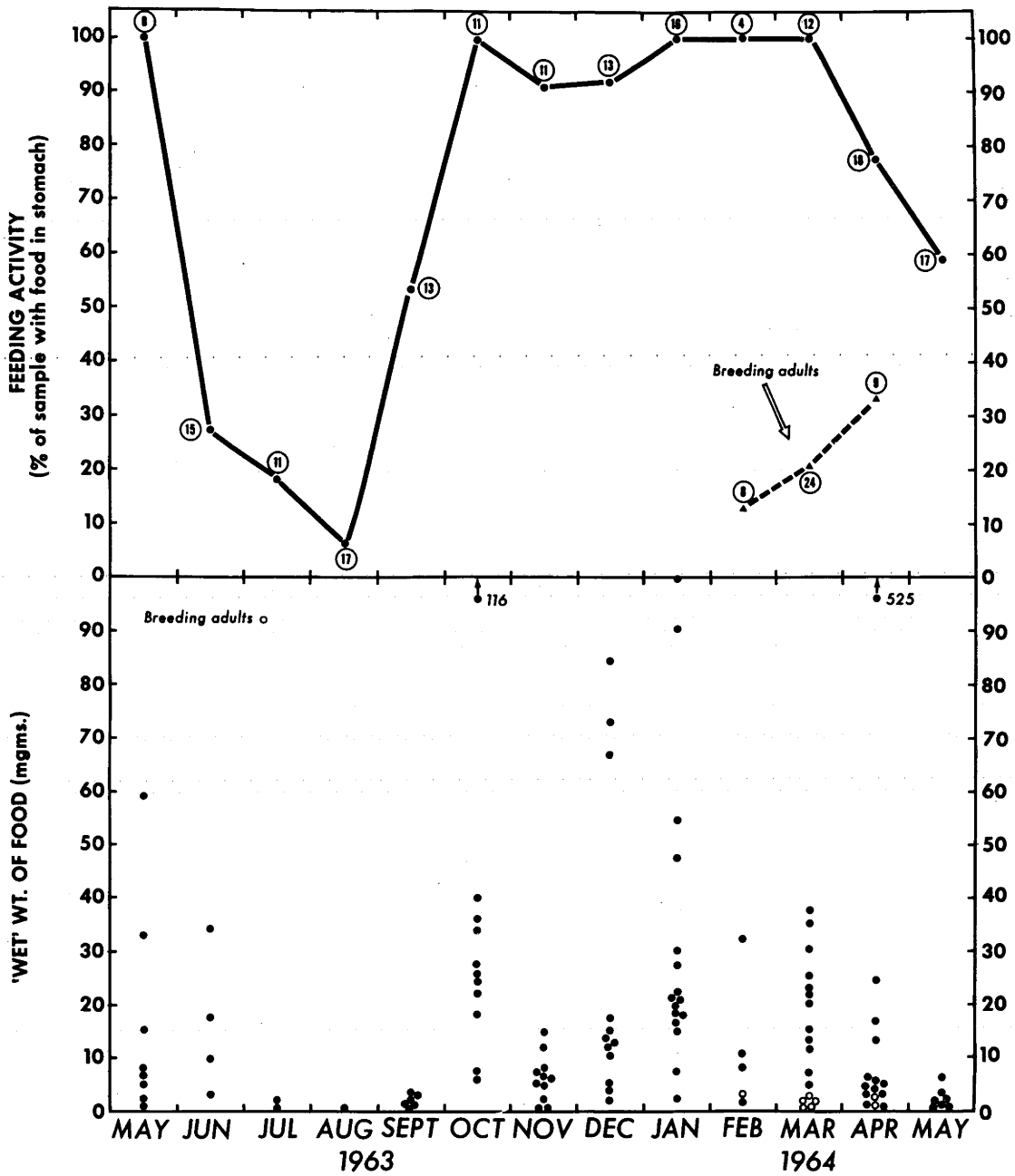
Empty stomachs - 75 (36.2%)

Food Items	Percent Occurrence of Items	Total Number of Items
Diplopoda	6.1	41
Crustacea	1.5	2
Insecta		
Collembola	7.6	46
Coleoptera	37.5	99
Hymenoptera	2.3	3
Formicidae	77.3	1,808
Diptera	2.3	5
Hemiptera	3.8	8
Insect larvae	16.7	29
Other Insects	2.3	4
Arachnida		
Acarina	53.8	418
Araneae	6.8	9
Other Arachnida	3.0	4
Gastropoda		
Pulmonata	5.3	12

Fig. 7.2

Upper graph: Seasonal variation in feeding activity of *P. corroboree* adults. 'Breeding adults' refers to adult males found in burrows in the breeding area. The sizes of the monthly samples are encircled.

Lower graph: Seasonal variation in the amount of food found in the stomachs of individuals from the same samples as shown in the upper graph. Each point represents one individual. Note that both diagrams give a similar pattern.


FEEDING ACTIVITY
(% of sample with food in stomach)
Breeding adults
'WET' WT. OF FOOD (mgms.)
Breeding adults o
116
525
MAY JUN JUL AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY
1963
1964

preyed upon by juveniles were Coleoptera, which comprised approximately 30% by weight of the total food, and Acarina (17.8%) and Araneae (15.3%). Acarina were numerically the most abundant prey item recorded, occurring in every stomach which contained food.

The food items contained in the stomachs of subadults did not differ appreciably from those found in adults. In both age groups Hymenoptera, which were mainly ants, were the most prominent category in the food either numerically (Tables 7.2, 7.3) or by weight (Fig. 7.1).

Both juveniles and subadults tend to feed on smaller items than do the adults (Table 7.4). All three age groups fed on very small prey (mites) but only the adults took prey larger than 5.0 mm in body length.

Examination of monthly samples of P. corroboree adults showed that there was significant seasonal variation in feeding activity (Fig. 7.2 upper graph) and in the amount of food found in the stomach (Fig. 7.2 lower graph). In the samples of July and August, 1963, very few animals had food in the stomach and what food was present consisted of only a few ants or mites. Feeding at this time of the year was probably inhibited by low temperatures (Fig. 2.8). In the spring and summer samples the stomachs of most individuals contained food.

Table 7.4 The size of prey items eaten by juvenile, subadult and adult *P. corroboree*

Age Group	Mean Size of Prey (mm)	Size Range of Prey (mm)
Juveniles (7-14 mm)	1.4	0.2-4.5
Subadults (14-20 mm)	1.7	0.3-4.5
Adults (20+ mm)	2.1	0.3-11.0

The amount of food present in stomachs of breeding adults, particularly males, was very low compared with adults collected outside the breeding area. Of the 38 stomachs of breeding males examined, 21 (55.3%) were empty, 10 (26.3%) had soil and plant material and only 7 (18.4%) had animal food present. In 5 of these 7 stomachs there was only one item represented. Two of the 3 females collected in the breeding area had food in the stomach. Only 5.9% of adults collected under logs outside the breeding area had empty stomachs.

Differences in habitat did not appear to have an appreciable effect on the diet of adult Corroboree frogs.

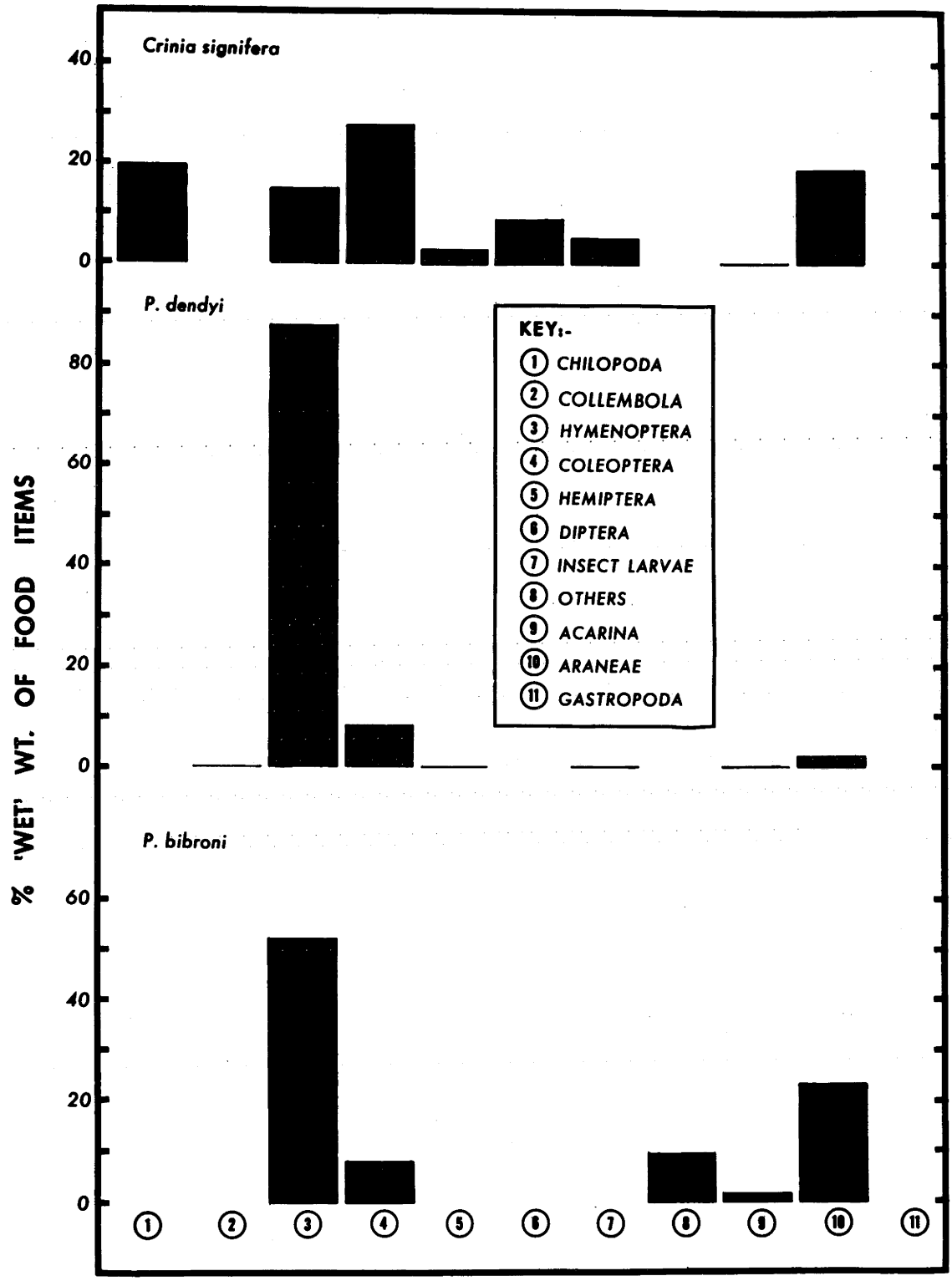
Table 7.5 Analysis of stomach contents of *P. corroboree* adults, Snowy Flats (16 specimens)

Empty stomachs - 6 (37.5%)

Food Items	Percent Occurrence of Items	Total Number of Items
Diplopoda	10.0	1
Crustacea		
Isopoda	10.0	2
Insecta		
Collembola	10.0	1
Coleoptera	20.0	2
Hymenoptera	10.0	1
Formicidae	80.0	102
Insect larvae	10.0	1
Arachnida		
Acarina	30.0	17
Opiliones	10.0	1
Araneae	10.0	1

Fig. 7.3

The percentage 'wet' weight of food items in the stomachs of adults of *Crinia signifera*, *Pseudophryne dendyi* and *P. bibroni*. Samples of *C. signifera* and *P. dendyi* were obtained from Coree Flats, N.S.W. and *P. bibroni* from near Yass, N.S.W.


Crinia signifera
P. dendyi
P. bibroni
% 'WET' WT. OF FOOD ITEMS
KEY:-
1 CHILOPODA
2 COLLEMBOLA
3 HYMENOPTERA
4 COLEOPTERA
5 HEMIPTERA
6 DIPTERA
7 INSECT LARVAE
8 OTHERS
9 ACARINA
10 ARANEAE
11 GASTROPODA
0
20
40
60
80
1
2
3
4
5
6
7
8
9
10
11

The stomach contents of 16 adults collected from under logs in subalpine woodland at Snowy Flats (Table 7.5) were similar to those obtained from adults in wet sclerophyll forest at Coree Flats (Table 7.4).

Examination of the stomachs of 31 breeding males collected in the Snowy Mountains showed that 13 (41.9%) were empty, 9 (12.9%) had large amounts of sphagnum and other plant material, 4 (12.9%) had animal material only. Of the 11 stomachs which contained food, 8 (72.7%) contained ants (Table 7.6).

ii) P. dendyi

The feeding habits of P. dendyi appear to be very similar to P. corroboree. In the sample of adults obtained from Coree Flats, ants were the most prominent item by weight (Fig. 7.3) and in terms of numbers (Table 7.7). Apart from Coleoptera the other prey species were only sparingly represented. The size of items found in the stomachs of this species ranged from 0.5 to 7.0 mm ($\bar{x}$ = 2.8 mm).

A large percentage of males collected in the breeding area during the breeding season at Coree Flats and Boggy Plain had no food in the stomach (69.3% and 68.7% respectively). In addition both samples contained a large

Table 7.6 Analysis of the stomach contents of *P. corroboree*, Snowy Mountains region (31 specimens)

Empty stomachs - 20 (64.5%)

Food Items	Percent Occurrence of Items	Total Number of Items
Insecta		
Coleoptera	9.1	2
Diptera	9.1	1
Hymenoptera	9.1	1
Formicidae	72.7	28
Hemiptera	9.1	1
Other Insects	9.1	1

Table 7.7 Analysis of the stomach contents of *P. dendyi*, Coree Flats (54 specimens)

Empty stomachs - 22 (41.5%)

Food Items	Percent Occurrence of Items	Total Number of Items
Diplopoda	3.2	1
Insecta		
Collembola	12.9	17
Coleoptera	41.9	28
Diptera	3.2	1
Hymenoptera		
Formicidae	87.1	1,134
Hemiptera	6.4	2
Insect larvae	9.7	3
Arachnida		
Acarina	38.7	29
Araneae	12.9	5

Table 7.8 Analysis of the stomach contents of *P. bibroni* adults near Yass, N.S.W. (29 specimens)

Empty stomachs - 9 (31.0%)

Food Items	Percent Occurrence of Items	Total Number of Items
Insecta		
Collembola	35.0	269
Coleoptera	40.0	13
Hymenoptera		
Formicidae	90.0	865
Diptera	5.0	1
Others (Isoptera)	20.0	117
Arachnida		
Acarina	15.0	72
Pseudoscorpionidea	10.0	2
Araneae	25.0	5

number of males with soil and plant material in the stomach. These represented 75% of the Boggy Plain sample and 42.3% of the Coree Flats sample.

iii) P. bibroni

The stomach contents of P. bibroni (Fig. 7.3, Table 7.8) were similar to those of P. corroboree and P. dendyi, even though these specimens were collected from a different habitat. Ants comprised 50% of the total food by weight and spiders and termites comprised the greater bulk of the remainder (22% and 10% respectively). The high percentage of termites found in the stomachs of these animals undoubtedly reflects their availability in this type of habitat (savannah woodland).

P. bibroni resembled P. dendyi in preying on organisms of similar size (range: 0.5-6.5 mm; $\bar{x}$ = 3.3 mm).

Analysis of the stomach contents of Crinia signifera revealed a diet similar in some respects to that of P. corroboree juveniles. A relatively diverse array of items was preyed upon (Table 7.9) and no item accounted for more than 30% by weight of the total food eaten (Fig. 7.3). The most important categories were Coleoptera (26%), Araneae (21%) and Chilopoda (19%). Collembola did not appear in any of the stomachs examined and mites comprised

Table 7.9 Analysis of the stomach contents of *Crinia signifera*, Coree Flats (46 specimens)

Empty stomachs - 21 (45.7%)

Food Items	Percent Occurrence of Items	Total Number of Items
Chilopoda	4.0	1
Insecta		
Coleoptera	52.0	18
Hymenoptera	8.0	2
Formicidae	40.0	15
Hemiptera	25.0	9
Diptera	28.0	15
Insect larvae	4.0	2
Arachnida		
Acarina	4.0	5
Araneae	12.0	3
Others	16.0	6

Table 7.10 Analysis of the stomach contents of *Hyla verreauxi* adults, Coree Flats (11 specimens)

Empty stomachs - 6 (54.5%)

Food Items	Percent Occurrence of Items	Total Number of Items	Percentage 'Wet' Weight of Items
Insecta			
Coleoptera	20.0	3	2.7
Diptera	20.0	1	0.4
Hemiptera	20.0	1	-
Orthoptera	20.0	1	95.0
Insect larvae	40.0	2	1.3
Gastropoda			
Pulmonata	20.0	1	0.4

Table 7.11 Analysis of the stomach contents of *Hyla verreauxi* adults, Snowy Flats and Snowy Mountains (10 specimens)

Empty stomachs - 0

Food Items	Percent Occurrence of Items	Total Number of Items
Insecta		
Coleoptera	60.0	11
Diptera	20.0	7
Dermaptera	10.0	1
Hymenoptera		
Formicidae	10.0	3
Lepidoptera		
(larvae)	20.0	3
Odonata	10.0	1
Orthoptera	10.0	1
Arachnida		
Araneae	20.0	2

a very minor portion of the total food. The size of food items eaten by Crinia signifera ranged from 0.9 to 7.0 mm ($\bar{x}$ = 3.1 mm).

Five of the 11 Hyla verreauxi adults collected at Coree Flats contained food in the stomach. One grasshopper found in one stomach formed 95% by weight of the total food. Coleoptera and insect larvae comprised the bulk of the remaining weight (Table 7.10). In the 10 specimens from the Snowy Mountains and Snowy Flats there were more items represented (Table 7.11). Coleoptera occurred in 60% of the stomachs and Diptera, Lepidoptera larvae and spiders were each found in 20% of the stomachs. The size of items found in the stomachs of this species ranged from 0.8 mm to 27.5 mm ($\bar{x}$ = 8.7 mm).

7.4 Discussion

The similarity in the food eaten by adults of three species of Pseudophryne suggests that they are exploiting the same or similar food niche. The predominance of ants in their diet probably indicates the relative abundance of ants in the habitat and the feeding habits of the predators. From superficial observations it seemed that ants were the most common prey item found under logs in subalpine woodland, wet sclerophyll forest and savannah woodland. Termites

appeared to be more common under logs in savannah woodland than either of the other two habitats.

The feeding behaviour of Pseudophryne spp. tends to restrict them to feeding under logs, leaf litter and grass on prey which are relatively slow moving and ground dwelling. These species of frog are slow moving, and toad-like in their mode of locomotion, and they do not actively pursue their prey but tend to remain stationary waiting for the prey to come within their range of vision. A gravid female was observed to stop and begin feeding on a group of ants (Iridomyrmex sp. probably nitidiceps) at 0900 hours on 29 December, 1963. After a few minutes the ants moved a few inches away. They were not pursued. Feeding then ceased and the female continued on her way. Similar behaviour has also been observed in animals fed in the laboratory.

The stomach contents of P. corroboree and P. dendyi obtained from Coree Flats were extremely similar even to the species of ants preyed on. It is not known whether there is any competition for food but from observations it appears that ants suitable as prey are abundant. The only time when ants were scarce was during the drought of 1965.

The habit of feeding predominantly on ants may be a

characteristic of members of this genus. Hickman (1966, pers. comm.) records that ants are the most abundant food item eaten by P. semimarmorata in Tasmania.

The differences in diet between juveniles and older frogs of P. corroboree may be related to the size of the gape of the mouth. Smith and Bragg (1949) found that juveniles (10-29 mm in body length) of four Bufo species tended to feed on small organisms such as ants and beetles. In Rana esculenta the juveniles feed on similar categories as listed for P. corroboree juveniles and the stomachs of adults were found to contain the same items in addition to juvenile R. esculenta and fish (Tyler, 1959). R. esculenta differs from P. corroboree and possibly P. dendyi and P. bibroni in that the food of the adults is more diversified than the juveniles.

Seasonal differences in the amount of food consumed by adult P. corroboree are presumably related to changes in climatic conditions. Lower temperatures experienced during the winter months probably immobilized both predator and prey resulting in a cessation of feeding activity.

Differences in feeding habits between the sexes of P. corroboree are clearly associated with breeding behaviour. While males are in the breeding area very little feeding

occurs. It seems that if no food is available males will ingest soil or plant material. If females of this species construct burrows as Colefax (1956) has suggested it would mean that they could be without food for 6 to 12 weeks. This may have quite an appreciable effect on the reproductive potential of the female as most of the energy would be going into maintenance of body condition rather than in the formation of the eggs.

Investigations of the food of species coexisting in the same habitat indicate that the diet is determined largely by the availability of the prey although there is a tendency for some species to concentrate on one or a few taxonomic categories. Inger and Marx (1961) showed that species of Bufo, Artholeptis and Phrynobatrachus they examined from the Congo fed primarily on one taxonomic item. Berry (1965) also found that of 7 species examined from Singapore Island, 4 fed on one or two items. At Coree Flats, P. corroboree and P. dendyi concentrate on ants, Crinia signifera feed on a wide range of small items and Hyla verreauxi eat mainly the larger, more active forms such as grasshoppers.

Chapter 8 GENERAL DISCUSSION AND CONCLUSIONS

The history of biology has demonstrated, I believe, the heuristic value of the comparative approach to biological problems, whether they be on the biochemical or whole organism level and especially if the mode of thinking is from an evolutionary viewpoint. As ecology is essentially a study in the processes of evolution, comparative studies may be of some value in supplying or suggesting answers to problems that now exist in this field, particularly with reference to the niche, the competitive exclusion principle (Hardin, 1960) and allied problems.

Because of the small number of species investigated in this report and the main emphasis on one species, the discussion and conclusions about their ecology are rather tentative and general.

Comparative studies on the three species of Pseudophryne reveal that they are similar in morphology, behaviour and ecology and from the information available on other species of the genus it appears that members of this genus occupy distinct ecological niches. They can be characterized as cryptozoic species which are rarely seen out in the open except during breeding. In four Pseudophryne species (P. corroboree, P. dendyi, P. bibroni

and P. semimarmorata) the diet of adults consists mainly of ants with other arthropods, particularly beetles or termites as minor constituents. Breeding occurs generally during the autumn. Most species lay less than 100 eggs, in burrows on land which are constructed by the male frog. The tadpoles are benthonic and are frequently found in pools formed as a result of seasonal inundation. It seems that since this group is ecologically distinct and is morphologically separable from other members of the family it comprises a natural group or genus as defined by Inger (1958) and Mayr (1963).

The distribution of members of this genus also suggests that the species have similar ecological requirements. P. bibroni and, to some extent, P. dendyi, are the only known species which coexist with other members of the genus. Harper et al. (1961) have indicated that three conditions must be met for the continued coexistence of closely related species: reproductive isolation, ability to tolerate the physical and biological hazards which are preserved by the mutually occupied environment, and sufficient biological differences such that one species does not succeed at the expense of the other.

In south-eastern Australia P. corroboree and P. dendyi

are the only two species of the genus which coexist without interbreeding. In the region of sympatry the diets of both species are extremely similar (Chapter 7) even to the species preyed on. Both use the same sites for breeding and infrequently both species may be found under the same log. Generally, however, they appear to differ in the habitats selected. At Coree Flats, P. dendyi is most frequently found in the drier micro-habitats such as exist on the rocky ridges and slopes surrounding part of the flat, whereas P. corroboree is abundant on the moister, more heavily wooded slopes. The relative abundance of both species also differs markedly. In the Brindabella Range P. corroboree is the more abundant species, being common at all localities from 1,646 to 1,036 m. P. dendyi on the other hand, is relatively rare at high altitudes (1,646 m) but appears to be more common at lower altitudes (1,036 m) and is more abundant than P. corroboree at two localities in the Fiery Range. It is possible that the differences in these two aspects of the species' biology plus the heterogeneity of the habitat may allow them to cohabit without one species supplanting the other. Displacement of P. corroboree by P. dendyi could perhaps occur in these areas if the environmental conditions became much drier than at present.

Probably the most important factors affecting the distribution and abundance of the three species in south-eastern Australia are primarily, the physical conditions of the environment, and secondarily, the biological factors such as parasitism, predation and territorial behaviour.

The shelter available in a habitat is likely to be one of the major physical factors which limit the distribution of the species, and may also provide the limits of the upper and lower levels of the population.

The kind and amount of cover, which is principally in the form of vegetation, occurring in the southern highlands and tablelands of N.S.W., is the result of the combined effects of physiography, soils and climate and, since European settlement, has been modified by activities associated with the pastoral industry, and more recently forestry, hydroelectric schemes and tourism. Throughout much of the region the original vegetation has been either removed by man or affected indirectly through his activities especially in the tableland, lower montane and parts of the subalpine zones, apart from the Brindabella Range. In these denuded areas the population densities of species of Pseudophryne are very low, presumably because of the alteration of suitable areas for breeding and the removal of fallen logs, leaf

litter and herbaceous vegetation which provide cover during the terrestrial phase of the life cycle of the species.

The cover necessary for breeding must be such that it can be easily burrowed into by the males, provide protection for eggs and males from desiccation and extremes in temperature; and provide males with protection from likely predators. In addition, the cover must be located in areas which are subject to seasonal flooding. It is possible that P. corroboree, especially the form occurring in the Snowy Mountains region, has been the species most severely affected by the modification of wet areas. Although this species occurs in high densities in a few 'pockets', some contraction of its range may have occurred as a result of the drainage of sphagnum bogs and their conversion to grazing land. The habitats of P. corroboree in the Brindabella Range have largely been left in a near natural condition. Modification of the breeding habitat by man has occurred at Coree Flats but in this instance has apparently resulted in an improvement rather than a deterioration of the habitat because of the change from a rather simple plant community consisting largely of coarse, tussocky grasses and sedges to a very complex community of small herbs, grasses and mosses (Chapter 2).

Large scale diminution of the area covered by fallen logs, leaf litter and snow grass on the lower montane and tableland areas has not only removed the frogs' protective cover but also the micro-habitats of their principal food source: ants and termites.

Fluctuations in the population densities of the species are most probably the result of adverse conditions, such as drought, combined with the biological effects of fungal infection and predation causing large yearly variations in mortality in the egg and larval stages. Unfortunately this statement is based on incomplete data from one population of P. corroboree (Chapter 4) but observations of other populations seem to indicate that this is the case. Savage (1952) suggested that larval mortality is the primary regulator of British anuran populations. In the absence of data on survival in the terrestrial stage of the life cycle of species of Pseudophryne it is impossible to evaluate the influence of parasitism, predation and territorial behaviour on the population dynamics of the species.

The calls of P. corroboree, P. dendyi and P. bibroni are structurally similar and do not provide any indication of relationship that is not already shown by morphology. However, they do appear to have some features in common

with the mating calls of Crinia species figured by Littlejohn (1959). The mating calls of the Crinia parinsignifera superspecies are, apart from differences in dominant frequencies, similar to the threat calls of Pseudophryne, while the pulsate calls of the Crinia signifera superspecies are similar to the first syllable of the first component of the mating call of P. corroboree and P. dendyi. In addition there are similarities between the second syllable of the first component of the mating call of the three species of Pseudophryne and the mating call of Crinia sloanei. This is not to imply that the mating call of e.g. P. corroboree, has resulted from an amalgamation of the calls of the three groups of Crinia but it does perhaps suggest that the two genera may have been derived from a common stock. It could be postulated that the call of this ancestral group may have been a long call of approximately one second in duration which increased in pulse repetition rate from beginning to end. Fragmentation and simplification of this call may have given rise to the mating calls of Crinia; fragmentation plus modification of these components, most probably associated with the development of terrestrial breeding, could have produced the calls of Pseudophryne. In the absence of any data on the structure of calls other than the mating

call of species of Crinia and the lack of information on the calls of other species of Pseudophryne these ideas are at present very speculative. Information is needed especially on the calls of those species of Crinia which have similar breeding habits to Pseudophryne. Some support for this view of the relationship of the two genera comes from the suggestion by Noble (1922) that the Crinia and Pseudophryne are similar in morphology.

The relationship between the various species of Pseudophryne cannot be determined until a revision of the genus is undertaken, but some comments may be offered on the possible relationship of the three species investigated. Two possible hypotheses on their relationship may be given of which the first is probably the more plausible. In this hypothesis it is postulated that the centre of speciation of P. corroboree, P. dendyi and P. bibroni has been located in the southern highland region of south-eastern Australia and, furthermore, it is suggested that P. corroboree (Snowy Mountains) represents the ancestral stock of this group. Both P. dendyi and P. bibroni and the other form of P. corroboree may have evolved through being isolated as a result of fluctuations in climate during Pleistocene and post-Pleistocene times. The possible course of speciation

may have occurred as follows. During one of four pluvial phases of the Pleistocene P. corroboree (Snowy Mountains) may have been distributed over much of the highland region including the valleys. In an interpluvial period the range of this species may have contracted such that it left isolates on the mountain tops, probably in Victoria, which could have given rise to P. dendyi. Through a similar process as a result of climatic oscillations during post-Pleistocene times, P. dendyi may have given rise to P. bibroni. This species is probably a recent derivative of P. dendyi since the biology of both species is extremely similar. Although the time when P. bibroni evolved from P. dendyi is conjecture it probably occurred at least 12,000 years ago. This is based on the fact that P. bibroni is found in Tasmania and may have migrated there before this island became separated from the mainland about 12,000 years ago. Since the form of P. corroboree found in the Brindabella and Fiery Ranges is morphologically and ecologically similar to the Snowy Mountains' form, it probably represents a fairly recent separation and may be about the same age as P. bibroni.

If this has been the possible course of speciation then this series represents: a) a reduction in the amount

of yellow colouration, b) an increase in 'clutch' size, and c) a decrease in call structure with attendant decrease in the aggressiveness of males and the decrease of the density of breeding populations.

The alternative hypothesis to account for the relationship of these species is that P. bibroni represents the ancestral stock which has given rise to P. dendyi which in turn produced P. corroboree (Snowy Mountains). The other form of P. corroboree could be a recent derivative of P. corroboree (Snowy Mountains). These species most probably evolved through being isolated during interpluvial or warm and arid periods in much the same way as was postulated in the first hypothesis.

The reason for favouring the first hypothesis is extremely tenuous and is based on the assumption that the ancestral or most primitive species is usually found in the centre of the distribution of the genus or group (Mayr, 1963). This idea has some foundation in certain theories on population dynamics.

SUMMARY

Certain aspects of the biology of Pseudophryne corroboree, P. dendyi and P. bibroni occurring in the southern highlands and tablelands of N.S.W. were studied. The most intensively studied species, P. corroboree, is confined to areas above 914 m. This species comprises two forms, one of which is restricted to the Brindabella and Fiery Ranges, and the other to the Snowy Mountains region. P. dendyi is found throughout this area except in localities in the Snowy Mountains where P. corroboree also occurs. P. bibroni is the lowland species.

All three species breed on land during the late summer to early autumn in areas subject to seasonal inundation. P. corroboree lays the smallest complement of eggs (20-29) and P. dendyi and P. bibroni the largest complement of eggs (80-89). The tadpoles hatch out at the onset of the winter rains and over winter in pools formed by these rains. Metamorphosis occurs from late spring to early summer. Adverse conditions such as drought have a pronounced effect on breeding by inhibiting it or restricting it to moist areas or by reducing the 'clutch' size (P. dendyi). The mortality of eggs and tadpoles varies from year to year. Most mortality in the tadpole stage is probably attributable

to predation by dragonfly nymphs.

Calls made by adult males of the three species were analysed by a sound spectrograph and an oscillograph. Six calls are uttered by P. corroboree during the period of seasonal sexual activity. Two are sexual and comprise the mating and courtship calls; three are threat calls, and the function of one is unknown but may be allied to the threat calls. The calls of the other two species are structurally similar to, but less complex than, the calls of P. corroboree. The greatest difference between the calls of the species is in the courtship call. Because of this it is suggested that as far as auditory isolation is concerned the differences in the courtship call constitute the prime isolating mechanism. No character displacement in call characteristics was observed in P. dendyi in areas of sympatry and allopatry with P. corroboree. There were slight differences in pulse repetition rate and call duration in the mating calls of the two forms of P. corroboree. The call parameters of P. corroboree and P. dendyi showed inconsistent dependence upon temperature. In areas of sympatry between P. corroboree and P. dendyi there seems to be some temporal isolation in time of breeding which may reinforce already existing isolating mechanisms.

Males are territorial during the breeding season, the burrow being the territory. There are differences between the species and between the two forms of P. corroboree in the degree of aggressiveness shown between males in the breeding season. Male P. corroboree (Snowy Mountains) are the most aggressive and P. bibroni males the least aggressive.

The three species consume essentially the same food items which consist mainly of ants. In P. corroboree the diet changes with age, being diverse in the juveniles and becoming more selective in the adults and subadults. No feeding occurs during the winter. Breeding males of the three species do not feed during the breeding season if they occupy burrows.

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* Not seen

Appendix

Table 1

		Correlation Coefficients		
		Coree Flats	Smiggin Holes	Round Mtn.
1st Syllable	P.R.R.* and Air Temp.	+0.75	+0.19	-0.003
	P.R.R. and Burrow Temp.	+0.74	+0.16	+0.05
	Duration and Burrow Temp.	-0.54	-0.44	-0.21
2nd Syllable	P.R.R. and Air Temp.	+0.21	-0.14	+0.26
	P.R.R. and Burrow Temp.	+0.28	-0.15	+0.49
	Duration and Burrow Temp.	+0.045	+0.076	-0.28
Threat Call	P.R.R. and Air Temp.	+0.77	+0.58	-
	P.R.R. and Burrow Temp.	+0.68	+0.66	-
	Duration and Burrow Temp.	-0.80	-0.29	-

* P.R.R. = Pulse Repetition Rate (pulses/sec.)