SOME ASPECTS OF THE BIOLOGY OF THE SPURWINGED PLOVER

- VANELLUS MILES NOVAEHOLLANDIAE (STEPHENS,1819)

By

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THE SPURWINGED PLOVER

VANELLUS MILES NOVAEHOLLANDIAE (STEPHENS)

SUMMARY

Research was made into aspects of the biology of the Australian Spurwinged Plover, Vanellus miles novae - hollandiae, a member of the family Charadriidae.

The distribution, status and habitats of the Spurwinged Plover and the related Banded Plover, Vanellus tricolor, were studied in Tasmania. The methods used in this study were a road survey of selected areas of Tasmania and a set of survey questionnaires sent to 230 Tasmanian schools. The survey demonstrated marked contrasts between the two species with regard to their general ecological requirements.

An analysis of morphological characteristics and their function was made in Spurwinged Plovers with special reference to wing spurs and wattles and their use in behaviour.

Field studies of behaviour in Spurwinged Plovers were made during the breeding and non-breeding seasons.

Observations and descriptions were made of the behavioural sequences and postures of Spurwinged Plovers and the social structure of a flock on the campus of the University of Tasmania was briefly studied. Indications of a flock social hierarchy were apparent.

Stomach analyses of 28 plovers shot on cultivated land and tidal flats were compared. Differences in stomach contents occurred and it was found that birds on tidal flats fed on small marine molluscs and polychaete worms.

Breeding biology studies were made in relation to; territories, nest construction, laying, incubation, hatching and chick development. The study area was Kingston Beach Golf Course.

A preliminary sonograph analysis was carried out on some common flock calls of the Spurwinged Plover.

GENERAL INTRODUCTION:

The Australian Spurwinged (Vanellus miles novae - hollandiae) is a member of the family Charadriidae in the order Charadriiformes. The family Charadriidae has a world - wide distribution and includes lapwings, dotterels, turnstones and other similar birds. Most species are totally or partially shorebirds and all charadriids are ground - nesters.

Taxonomic History of the Charadriidae.

Prior to the generic review of the Charadriidae by Bock (1958), the classification of charadriid species varied many times between monotypic generic concepts and polytypic generic concepts.

Before 1800 the species of plovers were placed in one of two large inclusive genera, Charadrius or Vanellus. In the next century taxonomists proposed many new genera, almost to the extreme of having only one species to each genus (Bock, 1958).

Seebohm (1888), in his classification of the shorebirds, considered the trend toward a monotypic generic concept to be impractical and subsequently, in his classification, placed the plovers in three genera, Charadrius (= the Charadriinae of Peters, 1934), Vanellus and Lobivanellus (= the Vanellinae of Peters, and Bock loc. cit.) considered this classification more acceptable then the classification used prior to his generic review, even though in this classification the genera Vanellus & Lobivanellus were considered artificial.

Sharpe (1896) once again divided the plovers into many genera which, according to Bock (loc. cit.) were so unnaturally arranged that no clear indications of generic relationships could be gained from the classification.

Lowe (1922) investigated the anatomy, relationships and classification of shore birds, including the plovers, and his subsequent papers provided a basis for much of the classifications of the Charadriidae, prior to Bock (1958). Unfortunately, as discussed by Bock (loc.cit), most of Lowe's interpretations concerning plover classification are questionable and have led to an unacceptable taxonomic arrangement.

Peters (1934) corrected some of the errors in Lowe's classification and proposed a revised classification of the Charadriidae into two monophyletic sub-families, the Charadriinae and the Vanellinae. However, Bock (loc. cit.) maintains that these sub families are divided into too many genera and that the classification still contains most of Lowe's misinterpretations.

Bock (loc. cit.) studied the relationships of the Charadriidae and proposed a reclassification of the plovers based on a new interpretation of the studies of Lowe. Bock's classification concerns mainly a study of external characters, habits, habitat; and internal anatomy (especially osteology). Bock was unable to use behaviour as a taxonomic criterion in his classification because the behaviour of most plover species was unknown.

However, he stated that a comparative ethological study could provide the key to clarification of phylogeny within the large genera that he proposed. The lack of behavioural studies of many species makes a large-scale, comparative ethological study impossible, even now.

Bock proposed that the 56 recognised species be placed in 6 genera as compared with 61 species and 32 genera in Peters' classification.

The genera are as follows:

Genus	Vanellus - comprising	25 species
"	Charadrius - "	24 species
"	Pluvialis - "	4 species
"	Anarhynchus - "	1 species
"	Eudromias - "	2 species
"	Pluvianellus - "	1 species.

Bock's classification has been widely accepted and will be adopted for the present study.

Australian Vanelline Plovers

Three vanelline plovers occur in the Australian region; the Banded Plover, Vanellus (= Zonifer) tricolor (Vieillot) 1818, the Masked Plover, Vanellus (= Lobibyx) miles miles (Boddaert) 1783, and the Spurwinged Plover, Vanellus (= Lobibyx) miles novae - hollandiae (Stephens) 1819.

Nomenclature:

Peters (1934) in his classification of the Charadriidae regarded the Spurwinged Plover and the Masked Plover as distinct.

species, Lobibyx novae - hollandiae and Lobibyx miles respectively.

Book (1958), however, assumed that they were conspecific because their distribution were apparently allopatric and, they appeared similar in most features; the major differences being in body size, wattle size and the black neck and shoulder colouration. Book could not determine whether the distributions of these two forms overlapped in Queensland; but if so, he considered that they must be regarded as distinct species and would constitute a super-species. However, in his generic review, he gave them subspecific status as Vanellus miles miles and Vanellus miles novae - hollandiae.

Cooper (1966) observed an overlap in the distributions of the Masked and Spurwinged Plovers in South Australia and south-western New South Wales but found no evidence of hybridisation between them. He, therefore, acknowledged specific status for each bird and used the terminology of Peters (1934).

Thomas (in press) regarded the Spurwinged and Masked Plovers as members of a super species. He suggested that the merging of the genera Lobibyx and Zonifer into the genus Vanellus, by Book (1958), had much to recommend it on "ecological and ethological grounds", even though Book had stated that both the ecology and ethology of vanelline plovers required much more detailed studies before they could be used as taxonomic criteria.

Van Tets *et al* (1967) found that the nesting distribution of the Masked Plover was allopatric with that of the Banded and Spurwinged Plovers, which nest sympatrically in south-east Australia. It was also observed that at the meeting of the nesting ranges of the Masked and Spurwinged Plovers in Townsville there occurred plovers intermediate in the extent of black on the neck and shoulders and the size and shape of wattles. Van Tets *et al* (*loc. cit.*) concluded from this apparent hybridization that Bock was correct in regarding the Spurwinged Plover as a subspecies of the Masked Plover, *Vanellus miles*. They also considered Bock's grouping of the vanelline plovers in the genus *Vanellus* as preferable to the monotypic genera classifications and recommended that the *Official Checklist of Australian Birds* be ammended to conform with Bock's suggested nomenclature for the Banded, Masked and Spurwinged Plovers.

The nomenclature proposed by Bock for the Australian vanelline plovers will be used throughout this thesis.

Distribution:

Each of the species of Australian vanelline plover has a wide distribution within Australia.

The Banded Plover is confined to Australia but both the Masked and Spurwinged Plovers have been observed outside the continent; the Masked Plover occurring in New Guinea and some adjacent islands (Cooper, 1966) and the Spurwinged Plover recorded as a breeding species in New Zealand in 1932 (Oliver, 1955) and now regarded as a common species in that country.

During the past decade in Australia there have been considerable changes in the extent of the ranges of each species.

The Banded Plover, which originally occurred across the southern regions of the continent, has extended its range into northern Queensland.

The Spurwinged Plover, which was confined to south-eastern Australia has extended its range into northern Queensland and has also moved large distances across inhospitable country to the south-western corner of the continent. Similarly, the Masked Plover which was originally confined to the northern regions of Australia, has extended its range to the south-western courner of Australia and become a resident bird of this region.

Van Tets *et al* (1967) consider that the northward extension of the range of Spurwinged and Banded Plovers may have been facilitated by the clearing of large areas of rain forest along the Queensland coast.

THE SPURWINGED PLOVER - Previous Research.

General observations and discussions have been made of the distribution, external morphology and habits of Spurwinged Plovers in Australia (Legge, 1901; Littler, 1910; Sharland, 1958; Ford, 1960; Warham, 1960; Serventy & Whittell, 1962; Cayley, 1966; Cooper, 1966; Van Tets *et al*, 1967; Thomas, 1968).

The Victorian Ornithological Research Group (Allen, 1963) is conducting a long-termed project of colour - banding Spurwinged Plovers in the Phillip Island area to determine the extent of local and long-distance movements of the birds but no results have been published.

DISTRIBUTIONS, STATUS AND HABITAT REQUIREMENTS OF VANELLINE PLOVERS IN TASMANIA.

Introduction

It has been previously stated that of the three Australian vanelline plovers only two, the Spurwinged (Vanellus miles novae - hollandiae) and Banded (V. tricolor) Plovers, occur in Tasmania. The present status of the two species in Tasmania shows a marked contrast with their status in the 1880's.

Legge (1901) stated that in the 1880's the Banded Plover (= Black-breasted Plover) was the commonest plover in Tasmania and sightings of the Spurwinged Plover were considered a rare occurrence. The number of Spurwinged Plover in Tasmania increased after the drought in 1888, presumably because of the movements of individuals from the drier mainland habitats across Bass Strait to the comparatively wetter conditions of Tasmania. From then the numbers continued to increase, especially in the lower midlands, until by 1901 flocks of up to 50 birds were sighted after the breeding season (Legge, 1901). The numbers of V. tricolor appeared to be fairly static in the 1900's.

As mentioned by Thomas (in press), Littler (1901) gives a similar appraisal of the status of the two species during the early 1900's.

Lord and Scott (1924) considered the Banded Plover to be a well-known bird in Tasmania with flocks occuring along the sea-shore or in the inland districts. They claimed the Spurwinged Plover was

evenly distributed throughout Tasmania, but not as numerous as the Banded species, which occurred in drier country than the Spurwing. The term "evenly distributed" as used by Lord and Scott in describing the distribution of the Spurwing is misleading since even today the Spurwing is confined to relatively open country such as grazed native grassland, agricultured land, marshes, tidal flats and beaches and it is inferred that they were indicating an even distribution in these particular habitats.

During the next thirty years the Spurwinged Plover population in Tasmania greatly increased while at the same time there was an apparent decline in the numbers of the Banded Plover. Unfortunately there is no way of assessing whether this was a genuine decline in the population numbers of the Banded Plover or whether the considerable increase in the numbers of Spurwinged Plover associated with increase in land clearing and productivity during this period focussed the attention of ornithologists on the Spurwinged Plover rather than the Banded Plover. If so, biased observation in favour of the Spurwinged Plover could have occurred.

Sharland (1958) considered the increase in the size of the Spurwinged Plover population in Tasmania to be of such proportion that he called Tasmania "the strong-hold of the Spurwinged Plover". Although this claim was not substantiated quantitatively, it was apparent that the density/of Spurwinged Plover populations had increased throughout Tasmania in

suitable habitats. The Banded Plover, which had apparently shown irregular fluctuations in population size during the preceding years, was then diminishing appreciably in numbers.

Thomas (in press) correlated the increase in Spurwinged Plovers with an increase in the development of agricultural lands:

> "the increase in the Spurwinged Plover has coincided with the increase in the acreage of improved pasture brought about by the use of super-phosphate and trace element fertilizers and sowing of northern hemisphere temperate grasses. This acreage has increased from 289,000 in 1900 to 733,000 in 1930 and 1,500,000 in 1964... The Banded Plover is more common on the poorer, drier areas of improved native pasture. The changed pattern of grassland management has probably caused the change in status of the two plovers".

The main objective of this part of the present study was to obtain a quantitative analysis of the present distribution, status and habitat preferences of both the Spurwinged and Banded Plovers in Tasmania.

METHODS

The investigation consisted of a survey which involved sending questionnaires to 230 schools throughout Tasmania and secondly, a road count of plover in selected regions of Tasmania.

The results of the road survey were to be used to check the accuracy of the school survey results.

SCHOOL SURVEY

The form of the school survey was adapted from a similar census carried out by Readshaw (1968), in which he determined the distribution of pied currawong (Strepera graculina) flocks in regions of South-eastern Australia.

The survey, consisted of two questionnaires accompanied by an explanatory letter and a plover identification chart which were sent out to all country schools and many urban schools throughout Tasmania and the Bass Strait islands. The schools were selected from a list consisting of State and private schools compiled by the Tasmanian Department of Education. Wherever possible, survey papers were sent to two or more schools in each area to provide a basis for within-area comparison. The two questionnaires (Appendix I, Table...) were identical in content, one being for Spurwinged and the other for Banded Plovers. The questionnaires were constructed to obtain information on occurrence, flocks sizes, population sizes and habitats of each species.

Distribution of the questionnaires commenced in early July and was completed within two weeks. July was selected for distribution because it was expected, and subsequently observed, that at this time the large autumn-winter flocks of both species would be dispersed more evenly over their habitats in

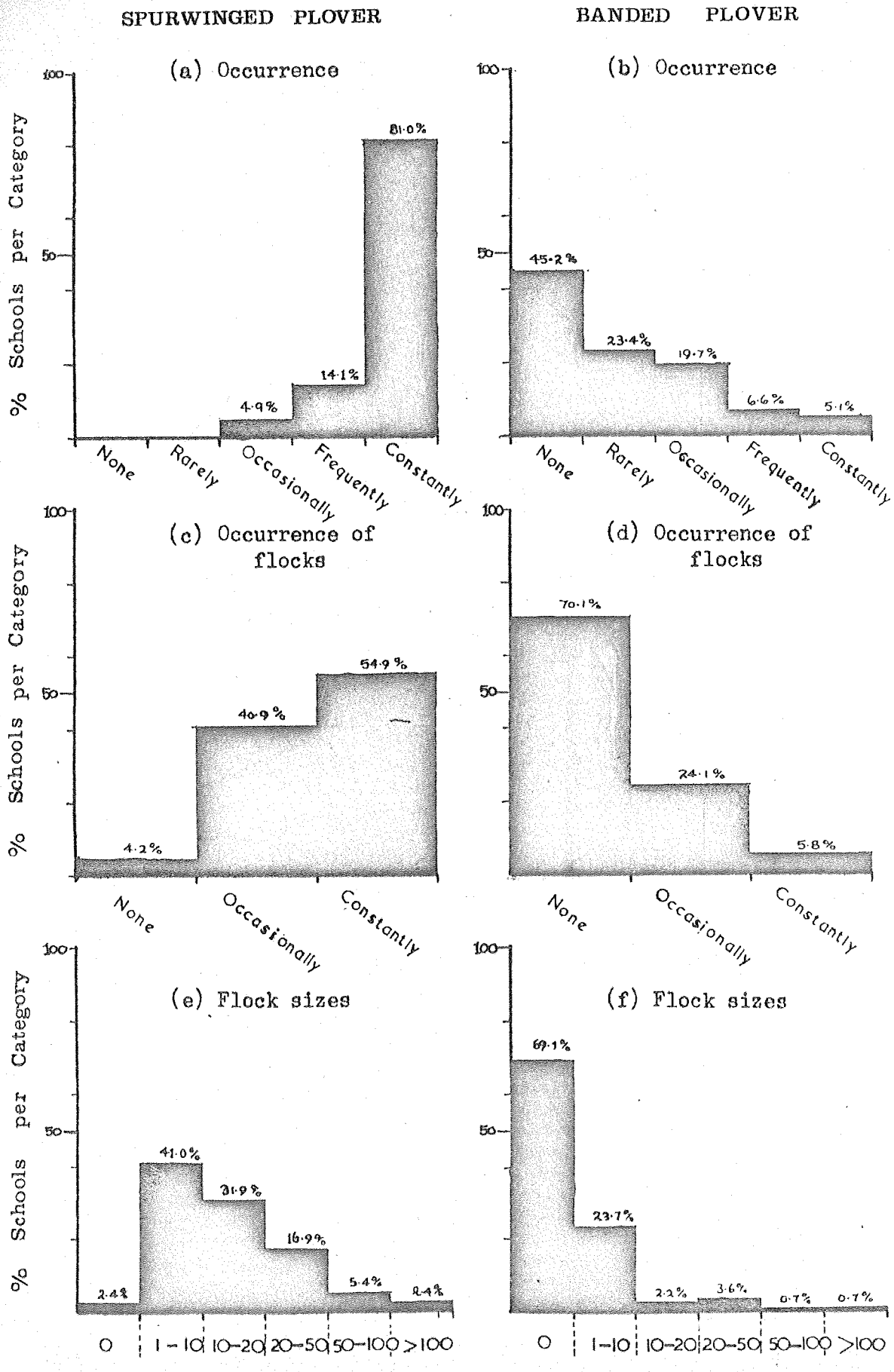
preparation for the breeding season (Sharland, 1958; Thomas, in press). This factor would reduce considerably any census errors which could arise from movements of large numbers of birds into different areas during the survey. It has been shown that although movements of Spurwinged Plover flocks are usually short-ranged (Allen, 1963; Thomas, in press), Banded Plovers are much more mobile during the non-breeding season, the reason for which is not clear. These nomadic tendencies of Banded Plover flocks are substantiated by Thomas (1968).

Returns from the survey were received until mid-September and as most of the birds had not associated into flocks until November, it was assumed that a relatively similar set of sampling conditions were prevalent through-out the period of the survey. The returned data was analysed and tabulated as shown in Figs. 1 and 2. The occurrence and abundance of both plover species throughout Tasmania are shown in Figs. 21-24 in Appendix I .

Road Survey

The road survey was conducted in five areas; Kingston, Ulverstone, Deloraine, Riana and Triabunna. The Kingston observations were made at various times throughout the year but, due to the lack of time and the distance from Hobart, observations were only made twice in the four remaining areas. In these areas observations were made once in late July and in

FIG. 1


SPURWINGED PLOVER
BANDED PLOVER
(a) Occurrence
(b) Occurrence
(c) Occurrence of flocks
(d) Occurrence of flocks
(e) Flock sizes
(f) Flock sizes
% Schools per Category
100
50
81·0%
14·1%
4·9%
45·2%
23·4%
19·7%
6·6%
5·1%
54·9%
40·9%
4·2%
70·1%
24·1%
5·8%
41·0%
31·9%
16·9%
5·4%
2·4%
69·1%
23·7%
2·2%
3·6%
0·7%
0·7%
None
Rarely
Occasionally
Frequently
Constantly
0
1–10
10–20
20–50
50–100
>100

late August and the results were averaged.

The road survey areas were chosen to include; a southern area (Kingston), an eastern area, (Triabunna) a northern area, (Deloraine) and two north-west areas (Ulverstone & Riana) of Tasmania.

The survey consisted of counting the number of plovers of both species seen from roads traversed within a five mile radius of the selected areas. An average of approximately thirty-five miles of road was traversed in each area and the numbers of each species seen and type of habitat in which they occurred were recorded. A comparison was made of the road survey results with the school survey results in these areas.

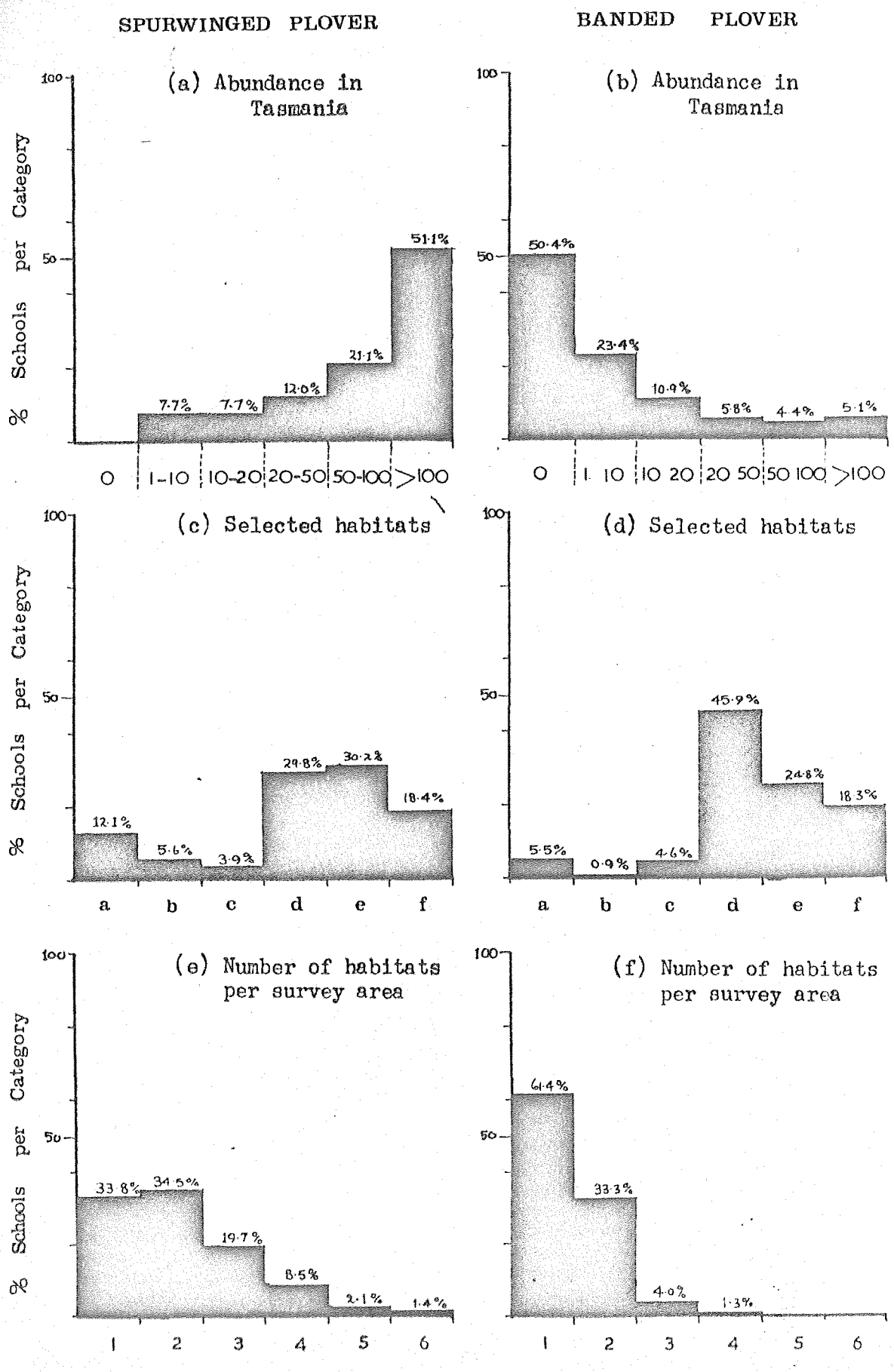
Results

(a) School Survey

A total of 57% of the schools replied and, although this percentage return was much lower than the 75% return obtained in the survey by Readshaw (1968), the survey yielded much useful information.

The only doubtful returns concerned the Banded Plover. One questionnaire was rejected because it described the Banded Plover as a "tree-nesting" species (probably confusing it with the Golden Whistler, Pachycephala pectoralis, which, although much smaller, has a similar colour pattern, except for a bright yellow breast). Two returns were considered doubtful (see Appendix I , Fig. 24) because they described the Banded Plover as

FIG.2


SPURWINGED PLOVER
BANDED PLOVER
(a) Abundance in Tasmania
(b) Abundance in Tasmania
(c) Selected habitats
(d) Selected habitats
(e) Number of habitats per survey area
(f) Number of habitats per survey area
% Schools per Category
100
50
51·1%
7·7%
7·7%
12·0%
21·1%
50·4%
23·4%
10·9%
5·8%
4·4%
5·1%
0
1-10
10-20
20-50
50-100
>100
1 10
10 20
20 50
50 100
12·1%
5·6%
3·9%
29·8%
30·2%
18·4%
5·5%
0·9%
4·6%
45·9%
24·8%
18·3%
a
b
c
d
e
f
33·8%
34·5%
19·7%
8·5%
2·1%
1·4%
61·4%
33·3%
4·0%
1·3%
1
2
3
4
5
6

frequenting seashore habitats. It seems likely here that the Banded Plover was being confused with the related Hooded Dotterel (Charadrius cucullatus) or Black-fronted Dotterel (Charadrius melanops) which are quite common shore birds in Tasmania.

The results of the survey are summarised in Table 1 and also in ~~Appendix~~ , Figs. 1 and 2

Table 1 shows a comparative analysis of the percentages of categories indicated per question by the participating schools. A further comparison was made of the number of habitats occupied by each species in each area (Table 1 (f)).

Figs. 21 & 22 show the comparative occurrence of Spurwinged Plovers and Banded Plovers in the areas of Tasmania covered by the survey.

Figs. 23 & 24 demonstrates the relative abundance of the Spurwinged and Banded Plovers in each survey area throughout Tasmania. The wide distribution and high relative abundance of the Spurwinged Plover throughout surveyed parts of the state is markedly contrasted with the localised distribution of Banded Plover populations.

It should be noted that in sending the survey questionnaires to schools throughout Tasmania, only the populated areas were sampled. However, previous correlations of plover distributions with land productivity (Thomas, in press) indicate that these areas are, in general, the selected habitats of both plovers.

TABLE

(a) Occurrence (Qu.1)	Percentage of school reporting					No. of Schools.
	None	Rarely	Occasionally	Frequently	constantly	
Spurwinged Plover	0	0	4.9	14.1	81.0	142
Banded Plover	45.2	23.4	19.7	6.6	5.1	137

(b) Winter Flocks (Qu.2a)	None	Occasionally	Constantly	
Spurwinged Plover	4.2	40.9	54.9	142
Banded Plover	70.1	24.1	5.8	137

(c) Flock Size (Qu.2b)	0	1-10	10-20	20-50	50-100	>100	
Spurwinged Plover	2.4	41.0	31.9	16.9	5.4	2.4	166
Banded Plover	69.1	23.7	2.2	3.6	0.7	0.7	139

(d) Estimated Abundance (Qu.3)	0	1-10	10-20	20-50	50-100	>100	
Spurwinged Plover	0	7.7	7.7	12.0	21.1	51.5	142
Banded Plover	50.4	23.4	10.9	5.8	4.4	5.1	137

(e) Habitat Selection (Qu.4)	(a)	(b)	(c)	(d)	(e)	(f)	
Spurwinged Plover	12.1	5.6	3.9	29.8	30.2	18.4	305
Banded Plover	5.5	0.9	4.6	45.9	24.8	18.3	109

(a) margins of lakes, swamps and rivers
(b) seashore
(c) lightly timbered areas
(d) dry paddock
(e) wet paddock
(f) cultivated land

(f) No. Habitats Recorded Questionnairs	1	2	3	4	5	6	
Spurwinged Plover	33.8	34.5	19.7	8.5	2.1	1.4	142
Banded Plover	61.4	33.3	4.0	1.3	0	0	

(b) Road Survey.

The averaged results of the five road survey areas were compared with the school survey results of the same areas (Table 2). Comparison of the road and school survey results for the Spurwinged Plover indicates an acceptable accuracy in the school survey results. This also applies for the Banded Plover results although here, in general, the road count was slightly less than the school survey results. This seems explained by the timidity of Banded Plovers and their distribution in habitats which are drier and often more remote than the Spurwinged Plover. It is possible, from the previously stated fact, that in some of the school surveys, the Banded Plover results may be an underestimation of the true population characteristics.

As shown by the results, it was only possible to estimate the abundance, occurrence and habitats of the two species in the road survey (except in the Kingston area). Flock size and flock occurrence were not included because of the short duration of the road surveys.

DISCUSSION.

The results confirm the observations made by Sharland (1958) and Thomas (in press.) that the Spurwinged Plover is much more widely distributed and abundant than the Banded Plover.

Although some areas, especially in western Tasmania, indicated an occasional occurrence of Spurwinged Plovers, no survey

TABLE 2

COMPARISON OF ROAD & SCHOOL SURVEY

SPURWINGED PLOVER Answers to Questions*

Area	1.	2(a)	2(b)	3.	4.
Kingston (school)	e	c	(1-10) (10-20) (50-100)	100	a, b, c, d, e, f
" (road)	e	c	(10-20) (20-50) (50-100)	100	a, b, d, e, f
Ulverstone (school)	e	c	(10-20) (20-50 (50-100)	100	c, d, e, f
" (road)	e	?	?	100	b, d, e, f
Deloraine (school)	e	c	(1-10)	100	d, e
" (road)	e	?	?	100	b, d, e
Riana (school)	e	c	(10-20) (20-50)	100	d, e
" (road)	e	?	?	100	d, e
Triabunna (school)	e	b	10-20	100	f
" (road)	e	?	?	50-100	d, e, f

BANDED PLOVER

Kingston (school)	c	b	1-10 100	10-20	c, d
" (road)	c	b	1-10	10-20	d, e
Ulverstone (school)	c	b	1-10	10-20	d, e, f
" (road)	b	?	?	1-10	d,
Deloraine (school)	d	b	1-10	20-50	d, e
" (road)	b	?	?	1-10	d, e
Riana (school)	c	b	1-10	1-10	d, e
" (road)	a	?	?	0	0
Triabunna (school)	b	a	0	1-10	d
" (road)	a	?	?	0	0

* See Table 4

areas showed Spurwinged Plover occurrences as "none" or "rarely". This contrasted markedly with the occurrence of Banded Plovers which was reported as "none" or "rarely", by 45.2% and 23.4% of schools, respectively.

The results (see Fig. 21 & 23) show that Spurwinged Plovers are ubiquitous throughout the state, occurring in numerous habitats, both natural and "man-made". In fact, it is not uncommon for Spurwinged Plovers to breed in parks and gardens of densely populated urban areas. The Spurwinged Plover, unlike the Banded Plover, are able to closely co-exist with man and appear to have benefitted from the development of land and the associated increased primary productivity. The maintenance, throughout the year, of large populations of Spurwings in some drier midland areas appears to have been facilitated by the construction of numerous artificial dams which subsequently provide the necessary water requirements of the Spurwinged Plover. Drought greatly affects these plovers and many survey returns indicated decreases in Spurwinged plover populations in the preceding five years, which they attributed to the semi-drought conditions prevalent in these areas during this period. Sharland (1958) states that many birds were reported to have died during times of drought but it is not known whether the population decreases previously discussed were due to mortality or population movements away from drought areas.

The survey results seem to confirm the localised distribution of Banded Plovers. In fact, many schools indicated that these plovers occurred in very localized groups usually associated with native grasslands and poor soil conditions.

The main concentrations of Banded Plovers in Tasmania appeared to be in three areas (see Fig.24).

(i) the far north-western region; e.g. Smithton, Edith Ck., and Montague areas. This region is close to King Is., which has a medium density Banded Plover population, and it is possible that there is an interchange of these birds between the King Is. and far north-west regions. If so, this could explain the comparatively high concentration of Banded Plovers in the Smithton Montague area.

(ii) the central region; this extends approximately from Port Sorell east to the Tamar River (e.g. Riverside and Exeter) and southwards, through Deloraine, to the Lower Midlands. Although few surveys were received from the Central Midlands (e.g. Longford to Ross), personal observations indicate localised populations in this area. The central region also extends westward in the south encompassing the Ouse-Hamilton areas.

(iii) the far northeastern region; e.g. Scottsdale, Ringarooma and Cape Portland(Guiler, pers. comm.). Although no Banded Plover Survey was received from Flinders Is., two surveys reported large concentrations there.

If so, there may be population interchanges of Banded Plovers between Flinders Is. and north-eastern Tasmania, especially Cape Portland.

Personal observations indicated that, in all the above regions, Banded Plovers mostly occurred on unimproved grasslands. There were, however, many exceptions.

Many schools reported that Banded Plovers were more timid than Spurwinged Plovers. This was, to some extent, substantiated by personal observations and it was also noticed that Banded Plovers were less visible in the field than Spurwings. It was concluded from these facts that, in some surveys, the population size of Banded Plovers could have been underestimated, but confirmation of this would only be possible by a larger scale road survey than was attempted in the present study.

The information pertaining to flock sizes indicated that Spurwinged Plover flock size varied from approximately ten birds to aggregations of more than one hundred. In most areas varying flock sizes were recorded, the more common being 1-10 (41.0%), 10-20(31.9%) and 20-50(16.9%) birds. Observations of Banded Plover flocks were much less common and, in fact, 70% of the schools reported that no flocks had been seen. The most commonly reported flock size for the Banded Plover was approximately 10 birds (23.7%) but a few flocks of more than one hundred birds were observed. Thomas (1968) recorded a mobile flock of approx. 200 birds in southeastern Tasmania.

A comparison of the habitats occupied by the Spurwinged and Banded Plovers is given in Figs. 2(c) & 2(d). The Spurwinged Plover occurs in the six habitats although it is more common on cultivated land (18.4%) and in "dry" (29.8%) and "wet" (30.2%) paddocks. The Banded Plover was shown to be most common in "dry paddocks" (45.9%). This shows a good correlation with the habitat descriptions of Sharland (1958) and Thomas (in press.). However, the Banded Plover was also commonly observed on; "wet" paddocks (24.8%), cultivated land (18.3%), lakes, swamps and rivers (5.5%) and occasionally in lightly timbered country (4.6%). The seashore observations of Banded Plovers (0.9%) appeared to be erroneous and are indicated by a "?" in Fig.24.

Fig.2(e) indicates the diversity of habitats occupied by the Spurwinged and Banded Plover in the survey areas and demonstrates the flexibility of the Spurwinged Plover in occupying a much wider variety of habitats than the Banded Plover.

The success of the Spurwinged Plover in Tasmania seems related to its ability to occupy and breed in a wide variety of habitats. Spurwings are excluded only from areas of rainforest, wet sclerophyll and dense, dry sclerophyll. It is interesting that throughout Tasmania there are numerous suitable areas which are not inhabited by the Spurwinged Plover. The reason for its absence in these areas is not clear but it could be relate to unsuitable food or water sources.

The present study, although demonstrating the present distribution and status of the two plover species, is incomplete because more information is required on the factors limiting their distribution, especially in the Banded Plover. Clearly, an extensive comparative study of the physiological and ecological characteristics of both species is required to elucidate the reasons for the selection of particular habitats and to determine the extent of competition between the Spurwinged and Banded Plovers.

MORPHOLOGY

Introduction.

It was necessary to gain some knowledge of morphological characteristics and their variation between the sexes in Spurwinged Plovers in order to determine to what extent sexual dimorphism occurs in the species and also to assess, by observing the use of morphological features in behavioural sequences, the possible functional significance of particular characters in relation to behaviour.

Methods.

Examination and measurements were made on 28 birds shot during the year under a permit issued by the Animals and Birds Protection Board. These observations were augmented by field observations and three birds caught during the breeding season in a nest trap (as described in the section on Breeding Biology).

Specimens were shot throughout the year and the low yield of 28 birds can be attributed to the timidity of the birds, which usually moved out of the range of the .410 shotgun.

The birds were sexed and the following measurements recorded for each:

(1) weight

(2) bill length and width

(3) wing length

(4) tarsus length

(5) tail length

(6) Spur length

(7) wattle length and width.

Measurements (1), (2), (3), (4) and (5) were made in accordance with the standards laid down by Disney (1963). The measurement of spur length was made from the most distal extremity to the middle of the basal line (i.e. the line at which the keratin sheath finishes).

The wattle measurements were taken as follows:

(1) length - from the most anterio-dorsal part of the upper lobe to the most ventral part of the lower lobe.

(2) width - from the centre of the upper part of the orbital ring to the most anterio-dorsal part of the upper lobe.

The width of the wattles was measured in this manner because the growth of dorsal and anterior edges of the upper lobe was noticably different between birds and was likely to be dependent upon age.

All linear measurements were made with vernier calipers except for wing length which was determined with a wooden rule using method as described by Disney (1963).

Specimens were weighed in a light plastic bag hooked to a 500 gm. spring balance. No weight correction was required for the plastic bag. Weighing was usually carried out in the field and the birds were then injected with approximately 15 cc of 10% neutral formalin so that gut content and body organs

could be preserved for laboratory examination.

Results and Discussion

Fig. gives details of the number of birds of each sex taken per month. The high ratio of males shot (20 males: 8 females) seems to be indicative of the more aggressive behaviour of males towards potential predators and intruders.

The means and standard errors of the measurements recorded from male and female plovers shot during the year are presented in Table .3.. In addition, Figs.6a-f show graphically the relationship between weight and the other measurements recorded. It can be seen from the table and figures that there is no significant difference in body measurements between male and female Spurwinged Plovers. However, males show a tendency to be slightly larger than the females.

Plumage.

The Spurwinged Plover shows no apparent variation in summer and winter plumage as shown to occur in the Lapwing (Vanellus vanellus) by Spencer (1953). A relatively large plover, Vanellus miles novae-hollandiae has a light olive-brown mantle and pure white underparts, which extend up the ventral region of the neck to the bill and face.

The crown is black and extends backwards forming a nuchal crest which joins a black patch on the sides of the breast which form the prominent shoulders. It is interesting

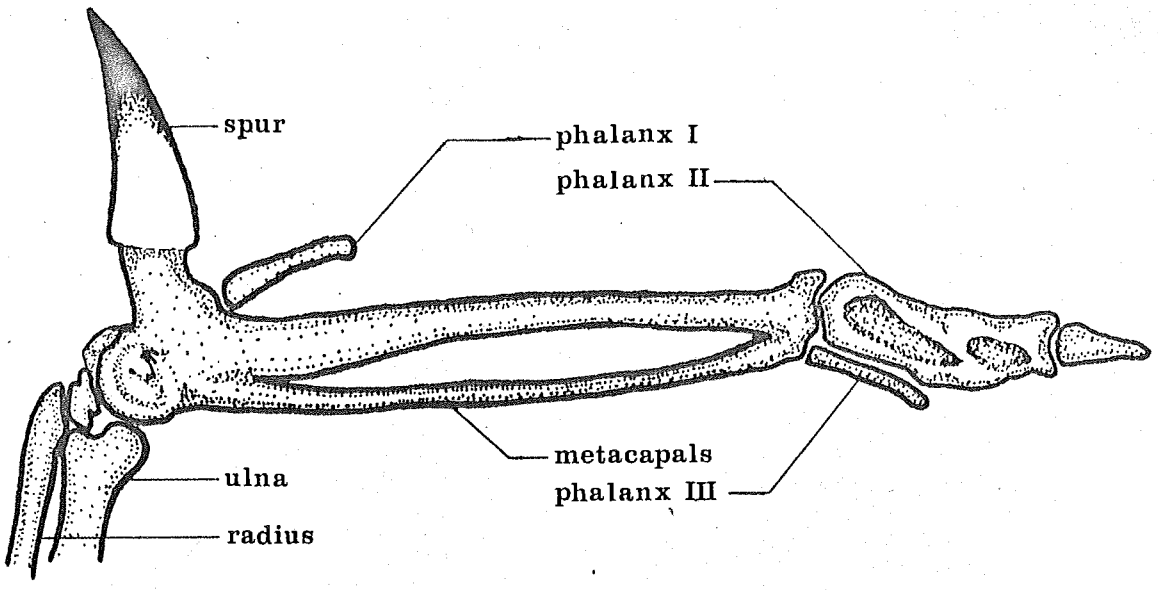


Fig. 3 WING SPUR STRUCTURE

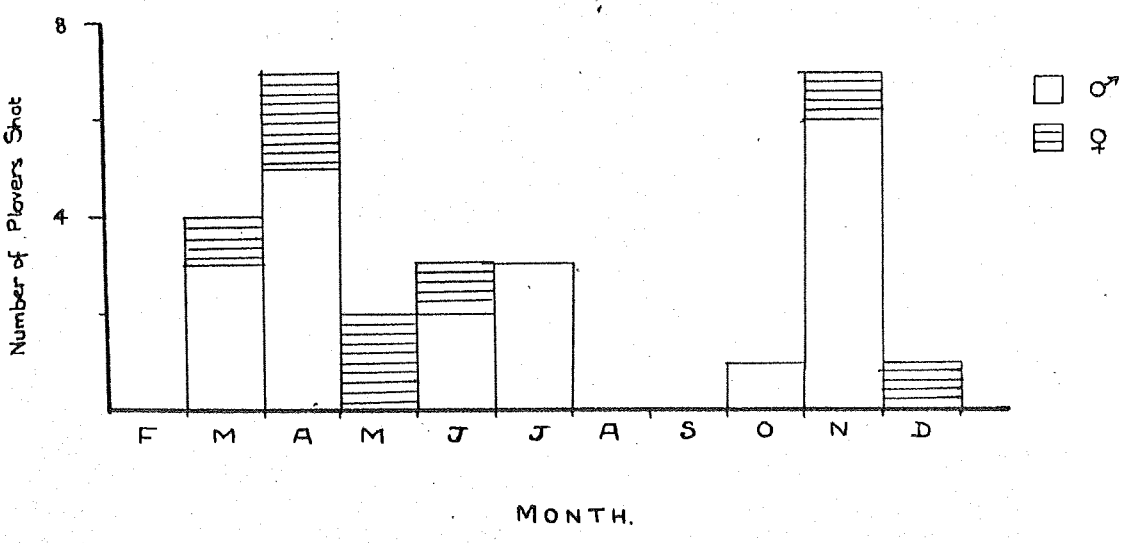


FIG.4 Number of plovers shot/ month

that the conspecific Masked Plover (V. miles) differs morphologically from the Spurwinged Plover only in the absence of black on the shoulders; the reduced amount of black on the neck and differences in size and shape of the wattles.

The primaries and their coverts are black; the greater coverts have a narrowed edging of white and secondaries are black with white on the inner webs. The Lapwing, Spurwinged and Masked Plovers are the only species of the genus Vanellus which lack a broad wing stripe. In the other species it begins on the greater coverts of the primaries and extends diagonally across the 2^{0} coverts and the secondaries (Bock, 1958). It seems, from observations, on the Banded Plover (V. tricolor) that these wing stripes signal intentions of flight. Spencer (1953) observed in Lapwings a sexual dimorphism in wing shape.

"When they are taking-off or in flight, most males, can be told fairly easily by their broad and rounded wings as compared to the female's more tapered ones".

Dimorphism in wing shape does not seem to occur in Spurwinged Plovers and it is difficult to visualize the functional significance of this character.

The upper tail coverts are white and the tail is white with a broad subterminal black band and white or greyish tips to the outer feathers. The colour and pattern of the tail

in the Spurwinged Plover is a common feature of all vanelline plovers except for Vanellus leucurus which has an all white tail (Beck, 1958).

From the observations made, there appears to be no sexual dimorphism in plumage of the adult birds.

The juvenile plumage of fledglings has been described by Oliver (1955, p.271) and is easily distinguished from the adult plumage. The crown is black lightly barred with brown and the remainder of the upper surface is barred black, brown and buff. The nuchal crest is present but ill-defined especially in newly fledged birds and this probably results from remanants of the white nestling down on the outer extremities of the black neck feathers. The black shoulder patches are clearly visible and well defined.

Leg colouration

The leg colouration of nestling and juvenile birds is a dark slaty blue but in adult birds becomes a dark crimson colour. This red colouration is especially apparent on the cruz, the knee joint and the feet.

The intensity of the adult colouration varies but it was observed that birds in breeding condition developed a significantly more vivid carmine appearance. It seems likely that this phenomenon indicates attainment of breeding conditions, thus aiding in pair selection of unmated birds and also signifying attainment of breeding condition in paired birds. As will be

discussed later in the section on behaviour, leg colour may function as a releaser during the "courtship run".

The Wing Spur (Fig. 3)

The structure and function of wing spurs in birds has been discussed by Rand (1954). The spur is situated at the proximal end of the metacarpal and consists of a bony core, which is an extension of the metacarpal bone, and an outer layer of horny keratin. Between the bone core and horny sheath is a layer of germinative tissue which produces new keratin material. The bright yellow colour of the spurs in the adult birds is due to a pigmentation of the germinative layer and is not incorporated into the outer horny sheath. The horny covering of the spur is transparent, except for the distal end which is heavily pigmented with melanin. It seems that this pigmentation is functional during some agonistic displays in outlining the spurs against the white flanks.

In resting or fleeing postures, the carpals are held close to the body concealing the spurs beneath the black shoulder feathers. If the spurs are accidentally bared in non-aggressive postures (e.g. during preening) the melanic tips are indistinguishable against the black shoulder feathers.

In aggressive postures the spurs are bared by the interaction of two movements. Firstly, the carpals are flexed away from the body and lowered slightly to expose the spurs.

Secondly, the head and neck are raised causing an upward displacement of the black shoulder feathers. The spurs, especially the melanic tips, then become prominently featured against the white flanks.

It would be interesting to have information on comparative positions of the spurs in the conspecific Masked Plover, which has no black shoulder feathers.

In fledglings and most first - year birds the spurs are short, rounded at the tip and bone - coloured. This indicates a lack of yellow pigment in the germinative layer and as no juveniles were observed to adopt the full aggressive postures which involved the spurs, it seems there is a close relationship between sexual maturity, attainment of maturity in spur shape, size and colour, and the development of high intensity aggression postures in the behavioural repertoire.

Spur Moult:

Spur moult in vanelline plovers has been recorded by Chapin (cited in lit. Rand, 1954) in Vanellus (= Xiphidiopterus) albiceps. Chapin observed that in V. albiceps, an African Spurwinged Plover, spur moult was associated with the moult of rectrices and remiges.

Rand (1954) found evidence of spur moult in Vanellus (=Hoplopterus) Armatus and inferred that correlation of this spur cover moult with wing moult indicated the former to be a

regular part of the annual wing moult.

Since then no literature has been published which refers to spur moult in vanelline plovers.

In specimens of the Spurwinged Plover which were examined during this study, three birds, (two adults and one juvenile) were in the process of spur moult. In the adults, as described by Rand (1954) for V. armatus, spur moult caused no change in the shape or colour of the spurs but left them approx. 2 mm. shorter. Further examination showed that both adults were in wing moult and were collected in late January and early February respectively.

The spurs of the juvenile birds were bone - coloured and rounded with only a small amount of melanin deposited at the tip. However, the spurs were in the process of moult and it was possible to remove the horny sheath revealing underneath a small but fully developed spur of the adult form, in both shape and colour. It is interesting that this specimen was examined in July (i.e. at the beginning of the breeding season) and was not in the process of wing moult. This transition from juvenile to adult spur morphology prior to the breeding season may be interpreted as a "pre-nuptual" spur moult in preparation for the first breeding season.

The spur is well developed in both sexes although generally in birds of similar size and weight, and therefore presumably of similar age, the spurs of the males are approximately 1-2 mm. longer than the females. (see Fig.6(a)).

TABLE 3

PLOVER DIMENSIONAL STATISTICS

	MALE			FEMALE		
	MEAN, $\bar{x}$	STANDARD DEVIATION, S_x	STANDARD ERROR,	MEAN, $\bar{x}$	STANDARD DEVIATION, S_x	STANDARD ERROR
WEIGHT (gms)	390	± 30	± 14	360	± 39	± 32
TARSUS (mm.)	67.9	± 5.2	± 2.5	67.1	± 1.7	± 1.4
SPUR LENGTH (mm.)	16.2	± 2.4	± 1.16	13.1	± 3.4	± 2.84
WING LENGTH (mm.)	243	± 8.0	± 3.8	238	± 7.0	± 5.8
TAIL LENGTH (mm.)	101.5	± 3.6	± 1.7	95.5	± 5.0	± 4.2
WATTLE LENGTH (mm.)	30.0	± 3.50	± 1.73	23.7	± 4.34	± 4.02

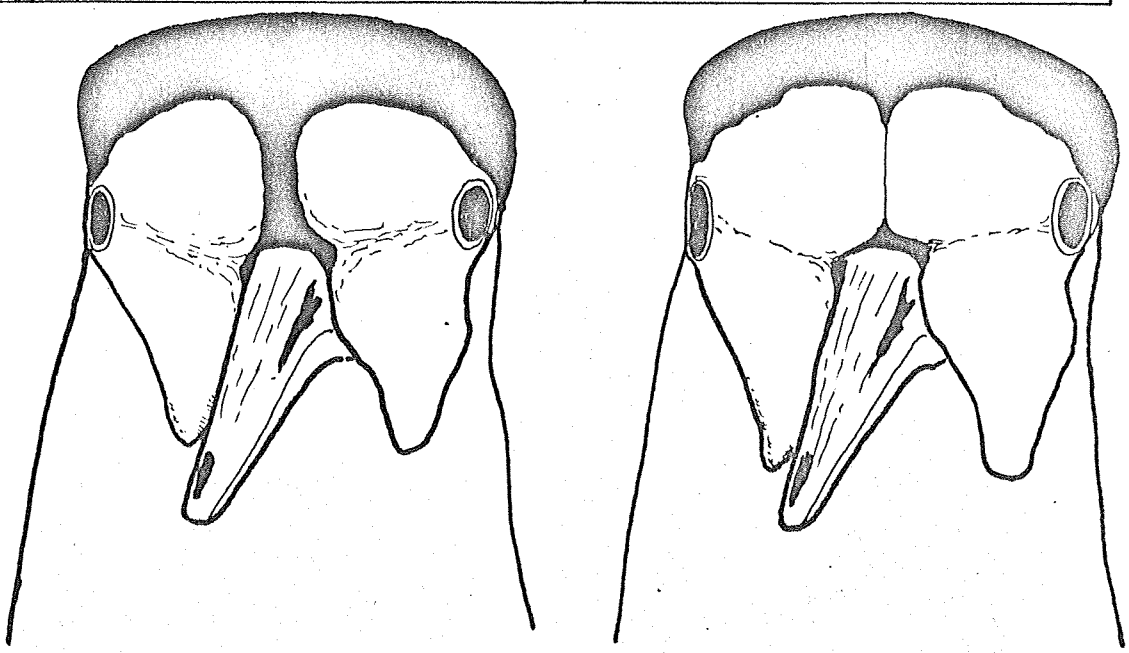


FIG.5 Diagram illustrating wattle inflation

The Wattles

The wattles in the Spurwinged Plover are large, bilobed structures which are derived from the epidermal region between the bill and the eye.

In chicks the wattles are small and colourless but as adulthood is approached a marked increase in size occurs which is associated with the development of a bright yellow cololuration. The colourless wattles in the chicks appear to have survival value during concealment crouching in the presence of predators because they blend in with the background colouration more effectively than would the bright, yellow wattles of adult birds.

The wattles are highly vascularized and capable of inflation (Fig. 5) and there appears to be a direct correlation between body size, wattle size and increase in wattle size after inflation, although this has not been demonstrated statistically.

It was observed that during periods of "above-normal" temperatures, especially in the summer, the wattles became so distended with blood that their inner, vascularized surfaces developed a reddish colouration. In colder temperatures the blood supply to the wattles was noticably restricted and the wattles were held close against the head. From these observations it was considered that the wattles may function in regulation of body temperature in Spurwinged Plovers and other related species which possess wattles.

Evidence for this hypothesis would require a series of detailed physiological experiments but, if confirmed, it could possibly explain, in terms of heat regulation, the following two phenomena:

(i) the apparent correlation between wattle size and body size in Spurwinged Plovers.

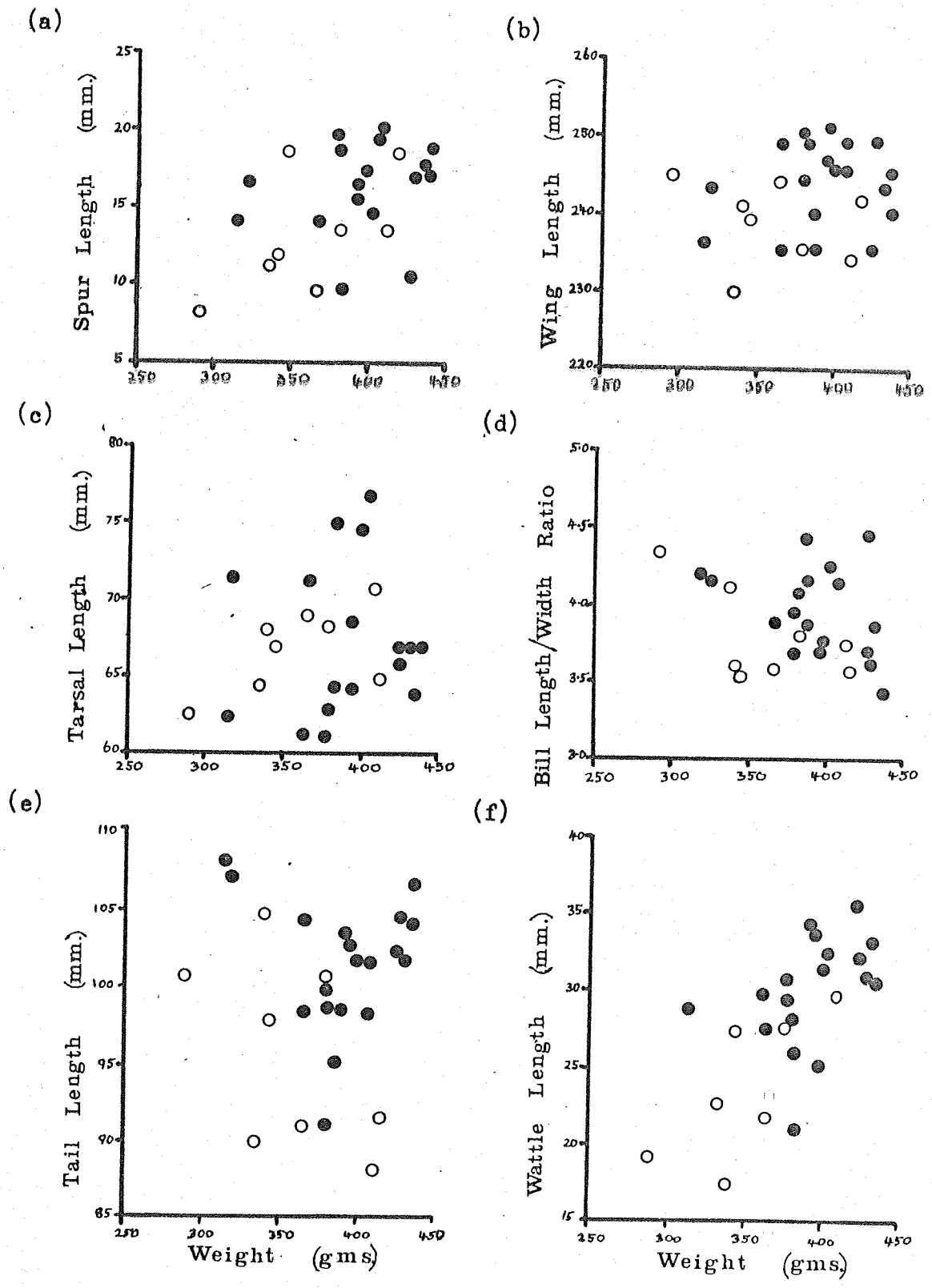
(ii) the development of larger wattles in the conspecific Masked Plover which is confined to higher temperature areas of Eastern Australia, above the Tropic of Capricorn (Van Tets, 1968)

Bock (1958) briefly discussed the occurrence and variation of wattles in the genus Vanellus and concluded that their possible functions were in relation to threat, "courtship" display and species - specific recognition.

Observations of mating in the Spurwinged Plover indicate that wattles have no functional significance in "courtship" displays (see Behaviour:Copulation) but there is evidence that they are utilised during some threat displays, where the visual stimulus of size and the amount of the black forehead covered by the wattles appears to be significant (see Behaviour. Agonistic Behaviour).

No attempt was made to determine whether the wattles were functional in species - specific recognition. However, this could possibly be determined by testing the behavioural reactions of Spurwinged Plovers to familiar individuals which have

FIG.6



Comparative dimensions of male and female Spurwinged Plovers shot during 1968

had their wattles painted or dyed in various colours (e.g. red, blue, black etc.). Similarly, by dyeing parts of the wattles black, and thus reducing the area of yellow in a dominant flock bird it may be possible to determine whether or not wattle size is utilized in determining social status in Spurwinged Plover flocks.

BEHAVIOUR

INTRODUCTION

The literature pertaining to bird behaviour is extensive, especially in the Laridae (Tinbergen, 1959; Moynihan, 1962;) Fringillidae (Hinde 1955, 1956) Emberizines (Andrew, 1957) Anatidae (Johnsgarde, 1965), but few attempts have been made at comparative behavioural analyses of plovers (family Charadriidae).

Prior to the work by Simmons (1952, 1953 & 1955) only a few studies on the behaviour of charadriid species had been documented. These studies were mainly concerned with aspects of reproductive behaviour and usually were confined to observations of distraction - displays, courtship, mating and nidification in single species of European plovers (Nethersole - Thompson, 1940; Rintel, 1940; Laven, 1940; Laven, 1941; Deane, 1944 and Williamson, 1948).

Simmons (1952, 1953 & 1955) comprehensively discussed the comparative behavioural reactions of waders (Charadriiformes) towards predators, especially man, in relation to escape, displacement - activities, demonstration, distraction display, threat behaviour and attack but made reference to the Lapwing only in discussing behavioural reactions of vanelline plovers.

There has been only one comparative ethological study, published on species of the genus Vanellus (Steifel, 1964). In fact, because of the lack of behavioural studies of Vanellus species, Bock (1958) in his generic review of the plovers was unable to use ethology as a taxonomic criterion for demonstrating relationships between the vanelline plovers. Only the Lapwing (Vanellus vanellus) has been studied sufficiently to be of use in a comparative sense and Bock states that the lack of study of the other species is probably a result of their being distributed in areas remote from civilization.

Apart from some observations on breeding behaviour of lapwings by Brock (1911) and Brown (1926) no detailed discussions on the behaviour of Vanellus species were published until Rinkel (1940).

Rinkel (loc. cit.) made an extensive investigation of the lapwing and recorded observations of its behaviour during the breeding season, including discussion of possible behavioural releasers in this species, such as the chestnut coloured tail coverts which appeared to be exposed by the male during the "scrape ceremony" to attract the female to the nest scrapes.

Nethersole - Thompson (1940) discussed the threat and distraction - displays of the Lapwing as did Laven (1941)

who also observed and described courtship and mating behaviour.

Spencer (1953) studied the lapwing and gave detailed descriptions of its behaviour in relation to the breeding season as well as the period during which the birds were associated in flocks. Spencer also interpreted phonetically the vocalisations of lapwings and correlated particular calls with the corresponding behavioural postures or sequences.

A limited study of territorial behaviour in lapwings in autumn (i.e. the end of the breeding season) was published by Lind (1957) who described a series of postures associated with agonistic behaviour. In addition to aggressive postures Lind also recorded a form of appeasement behaviour.

Steifel (1964) compared the breeding behaviour of two vanelline plovers, the lapwing and an African spurwinged plover Hoplopterus (= Vanellus) Spinosus. From this study, despite the findings of Von Helversen (1963), Steifel demonstrated a marked similarity between these two plovers in most aspects of their reproductive behaviour.

Very little behavioural work has been carried out on Australian vanelline plovers. In fact the only research seems to be that of Van Tets (pers. comm.) who has made a study of the social signals of the three vanelline plovers Vanellus miles, V. m. novae - hollandiae and V. tricolor and their importance in relation to behaviour. This work, however, is as yet unpublished.

The purpose of the present behavioural study of the Spurwinged Plover was threefold:

1. to observe, describe and interpret; where possible, its postures and displays during flocking and the breeding season.
2. to assess the functional significance of certain morphological characteristics of Spurwinged Plovers which are incorporated into behavioural sequences.
3. to determine whether or not there exists any social organization within the flocks and if so in what form it occurs.

It was hoped that from this study enough information could be collected on the behaviour of Vanellus miles novae hollandiae to enable an ethological comparison of its behaviour with the behaviour of the Lapwing.

STUDY AREAS.

All behavioural observations were carried out in the field. Most of the breeding behaviour was observed on the main study area at Kingston Beach golf course where a total of 15 pairs maintained territories. Flock behaviour was observed at three locations: Kingston Beach golf course, Ralph's Bay and on the campus of the University of Tasmania.

TERMINOLOGY

There is virtually no published work on plover behaviour but as many of the behavioural patterns of the Spurwinged Plover

can be directly compared with patterns observed by Tinbergen (1953, 1960), Moynihan (1962) and Nelson (1968) in Laridae, another family in the order Charadriiformes, it was decided, where possible, to adopt the behavioural terminology of these authors.

AGONISTIC BEHAVIOUR

Fighting:

Spurwinged Plovers, like many other charadrids, are strongly territorial, defending a large and relatively constant area against intrusion during the breeding season. Overt aggression only occasionally evokes actual fighting which is most commonly seen in the flocks, especially in May - July when birds begin to select breeding territories. It was observed that contact fighting was an uncommon occurrence during the breeding season and most territorial intrusions were repelled by postural behaviour rather than actual fighting.

When fighting does occur it is either in the form of an aerial attack or a ground charge. This depends mainly, it seems, on the proximity and behaviour of the rival.

Aerial attacks usually occur if the rival bird is some distance from the attacker. The attacker flies swiftly at the rival delivering a wing-blow to the head or body. This is followed quickly by a stalled landing with wings outspread, tail partially fanned and body held in an upright

aggressive position. When faced with an aerial attack the rival may avoid the attacker by crouching to the ground with wings slightly open or if already in an upright aggressive posture it may retract the head and perform a quick side-step.

Ground charges occur less often than aerial attacks. Charges are initiated at close quarters and usually during upright aggressive displays between two (or more) birds in which a "dead-lock" occurs and neither bird assumes the submissive posture. In this situation, which has been observed on several occasions, the birds charge at each other with wings outspread and held "defiantly" rigid. The fighting consists of charging and side-stepping and may, if wing buffeting or pecking is severe, result in loss of feathers.

No fighting was observed in which birds mounted and attacked rival birds as has been observed in species of gull (Tinbergen 1960, Moynihan 1962) and it seems from this; the brevity of the mount during copulation, and the absence of any allopreening or contact between pairs of birds that contact, even between paired birds, is maintained at a minimum level.

Upright postures

The only documentation of threat postures in Vanelline Plovers was by Lind (1957), who described three threat postures used by Lapwings; they closely resemble postures observed in Spurwing.

Tinbergen (1960) distinguishes three forms of the upright posture in the herring gull, Larus argentatus, (aggressive, intimidated and anxiety).

Nelson (1968) was able to observed only the aggressive and anxiety upright postures in the Swallow-tailed Gull Creagrus furcatus).

In the Spurwinged Plover the upright posture is rather variable. Within the normal range of variation it is possible to distinguish two extreme types: the "aggressive" upright and the "anxiety" upright.

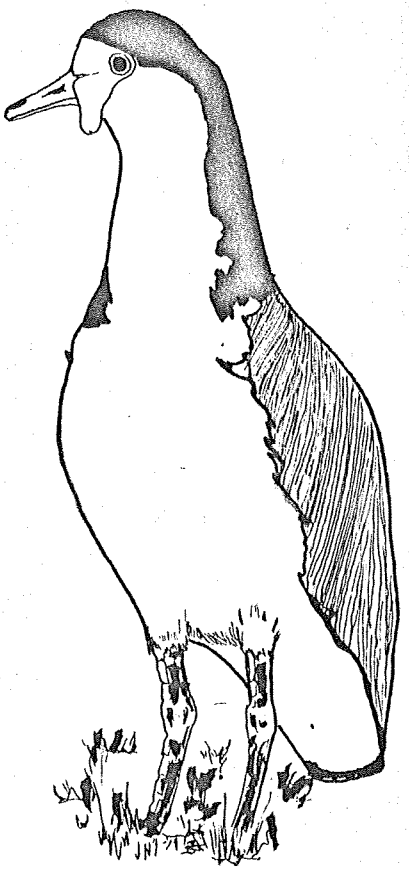
(1) Aggressive upright (Fig. 7)

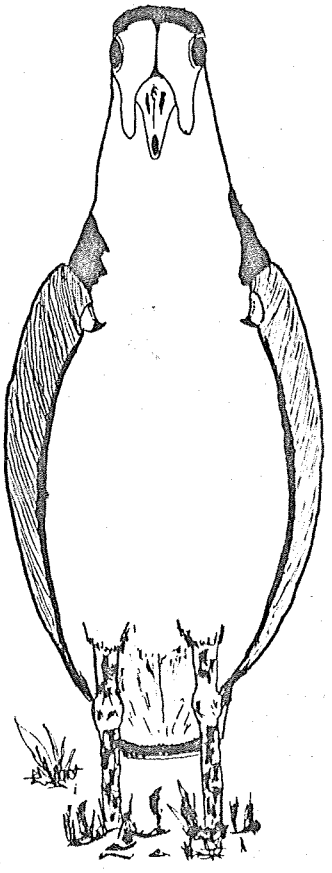
This is one of the commonest threat postures of the Spurwinged Plover and is very similar to the posture described for the Lapwing by Lind (1957) as a "strong activation" aggression posture.

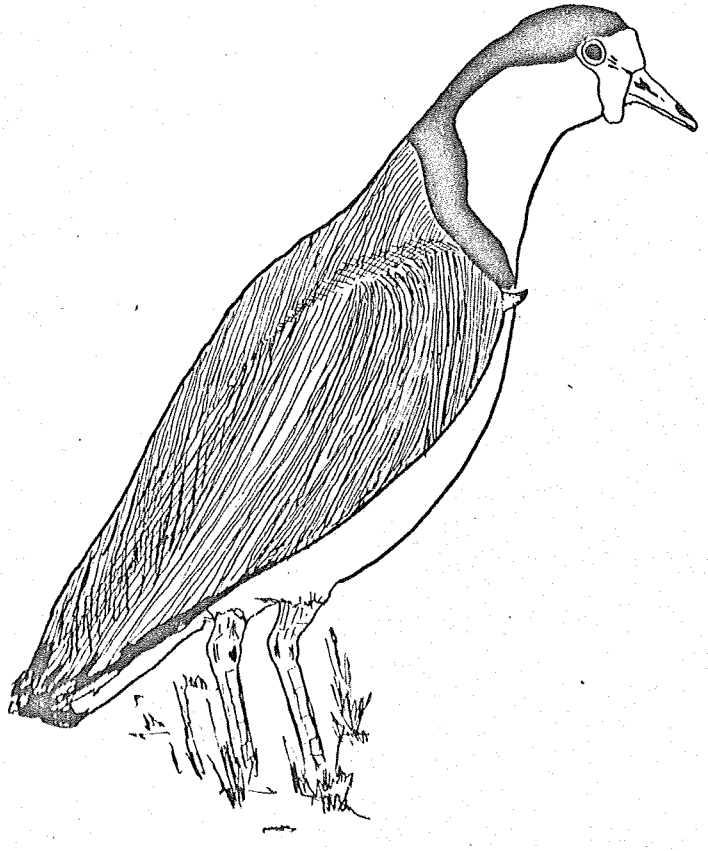
In this posture, the neck is stretched either vertically upward or upward and slightly forward, while the head and bill are pointed obliquely downward. The neck, as in gulls (Tinbergen 1953), is greatly thickened, apparently due to muscular contraction of neck muscles, and the carpal joints are held away from the body in a position slightly lower than normal.

The spurs, which in non-aggressive situations are covered by the black shoulder feathers, are bared by the flexure of the wings, and the stretching of the neck elevates the black shoulder

FIG.7 Various forms of the UPRIGHT AGGRESSIVE POSTURE







feathers so that the spurs and especially the melanic tips become outlined against the white flank feathers.

The body is held diagonally (although in high intensity aggression it may be almost vertical) with the breast raised and the hinder parts of the body lowered. The tail feathers are not spread. The head "crest" is raised and the wattles, which are highly vascularized, become inflated, especially the upper lobes which, in the larger Spurwings, form an uninterrupted plate across the forehead. In smaller individuals when the wattles are inflated there remains a conspicuous region of black feathers between the upper lobes.

Plovers in this particular posture usually face, or advance toward, opponents and the duration of this posture depends directly on the behaviour of the rival bird(s).

The orientation of any particular bird seems to be determined primarily by the strength of its attack and escape drives. A plover with a relatively strong attack drive usually directly faces its opponent, while a plover with a relatively weak attack drive usually faces away slightly.

In territorial encounters the duration of the aggressive upright posture is usually short because of the high fleeing tendency of the intruding bird(s). However, in flocks where

the threshold for escape is apparently much higher, birds may remain facing each other in the upright posture until either the attacking drive becomes so great that contact fighting, usually in the form of a charge, occurs or one of the birds (or more if three or more are involved) gradually assumes the "upright submissive" posture (see Plate I) or the hunched submissive posture, which also occurs in gulls. As will be discussed later these postures are considered to be submissive postures and are usually associated with turning of the body away from the aggressor.

Often when a bird with a strong attack drive is faced with a rival in a submissive posture it shows highly aggressive displacement pecking which is usually directed towards plant material. Similar behaviour has also been observed in many species of Laridae (Tinbergen, 1953, Moynihan, 1962).

A low intensity form of the upright aggressive posture is quite often observed. This differs from the high intensity form in that the neck is not fully extended, the spurs remain sheathed, the wattles are not inflated and the crest remains in a normal position. This posture usually precedes the high intensity form but if the attack stimulus is low the transition from the low to the high intensity form may not occur.

It was observed in paired birds that the intensity of the upright aggressive posture of the male bird was invariably higher than the female and in many cases of territorial intrusion only the male assumed the aggressive posture.

PLATE I.

(a) Dominant male (right) in a high intensity upright aggressive posture. Subdominant male (left) in lower intensity aggressive posture (transition between aggression and submission).

(b) Subdo minant male (left) has assumed a submissive posture - note the withdrawl of the neck and wings. Dominant male still maintains a high intensity upright aggressive posture with spurs bared and wattles inflated.

It is interesting that although the disruptive colouration of Spurwinged Plovers in the normal relaxed postures renders them not easily visible even at close quarters, the white under parts of a bird assuming the upright aggressive posture is conspicuous even at a distance of two hundred yards and has obvious value as a threat signal.

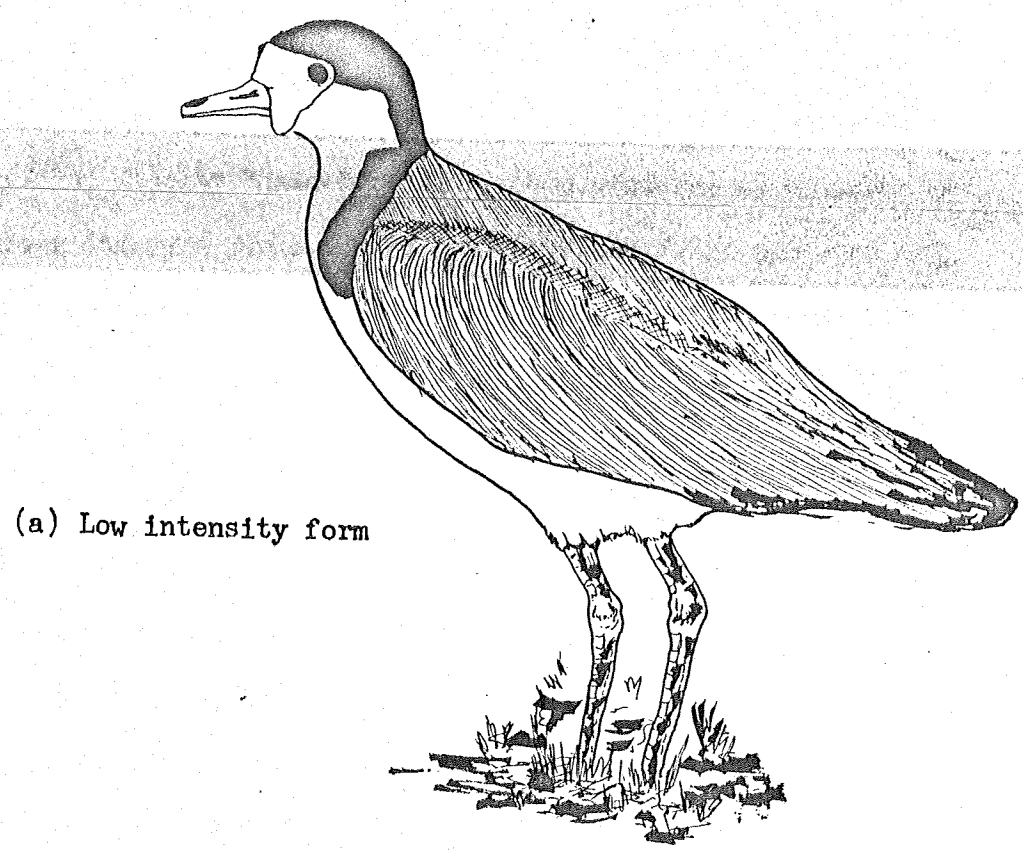
ii. Anxiety posture (Fig. 8)

This posture differs slightly, but significantly, from the aggressive upright and is most usually performed by alarmed birds.

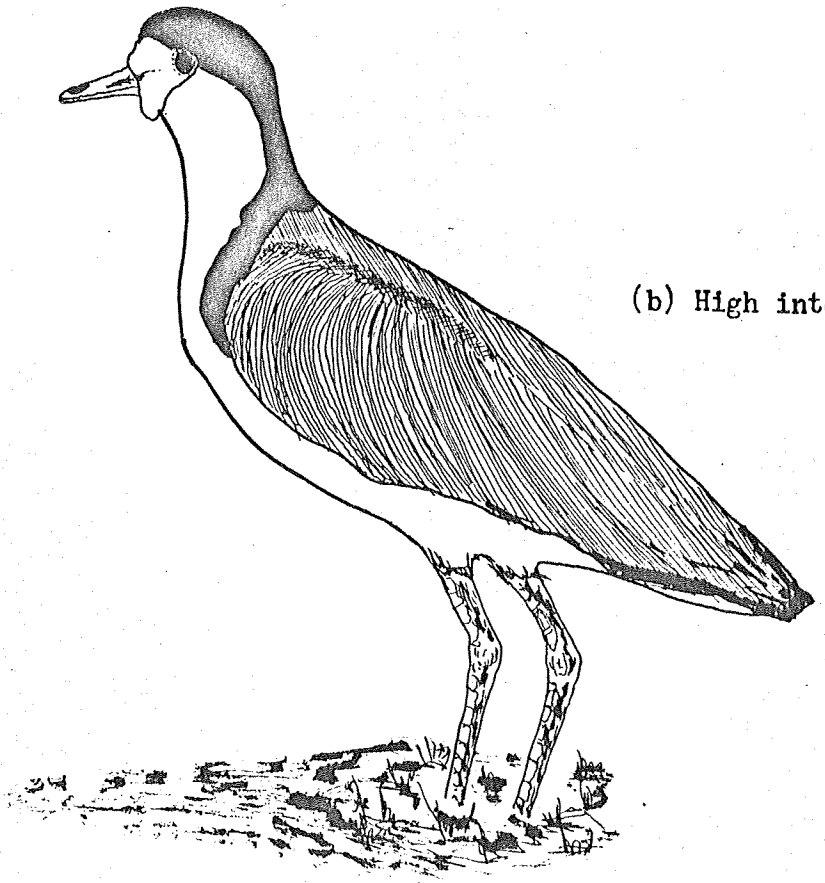
The most apparent differences are associated with the bill, neck and body positions. In the anxiety posture the neck is almost fully lengthened but shows no muscular contraction as seen in the aggressive upright. The body and the bill were held more horizontally than in the aggressive posture, the eyes are open with pupils dilated and the whole plumage is flattened.

The body orientation in this posture is usually away from the opponent and the wings are positioned ready for flight. The anxiety posture is explicable in terms of a combination of intention movements; the same movements as occur in the aggressive upright but the components of advance and pecking being small in comparison with the escape tendency, (Moynihan, 1955).

FIG.8 ANXIETY POSTURES



(a) Low intensity form



(b) High intensity form

Birds which assume the high intensity anxiety posture may also display "head-bobbing". This consists of a number of abrupt downward jerks of the head from the fully extended neck position to the retracted position and is considered an intention movement of flight since it almost invariably precedes flight in alarmed birds.

Choking Posture (Fig. 9)

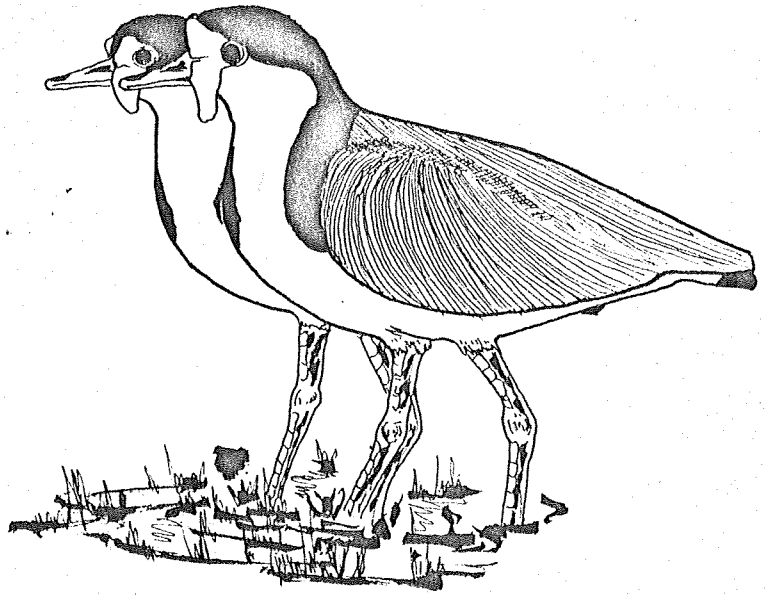
The agonistic postures described above are usually individual reactions but choking is almost invariably a pair reaction. The frequent occurrence of choking with in flocks indicates that the pair bond is probably maintained throughout the year both in and out of the breeding season.

Choking in the Spurwinged Plover is very similar in form to choking in gulls as described by Tinbergen (1953, 1960) and Moynihan (1955, 1962).

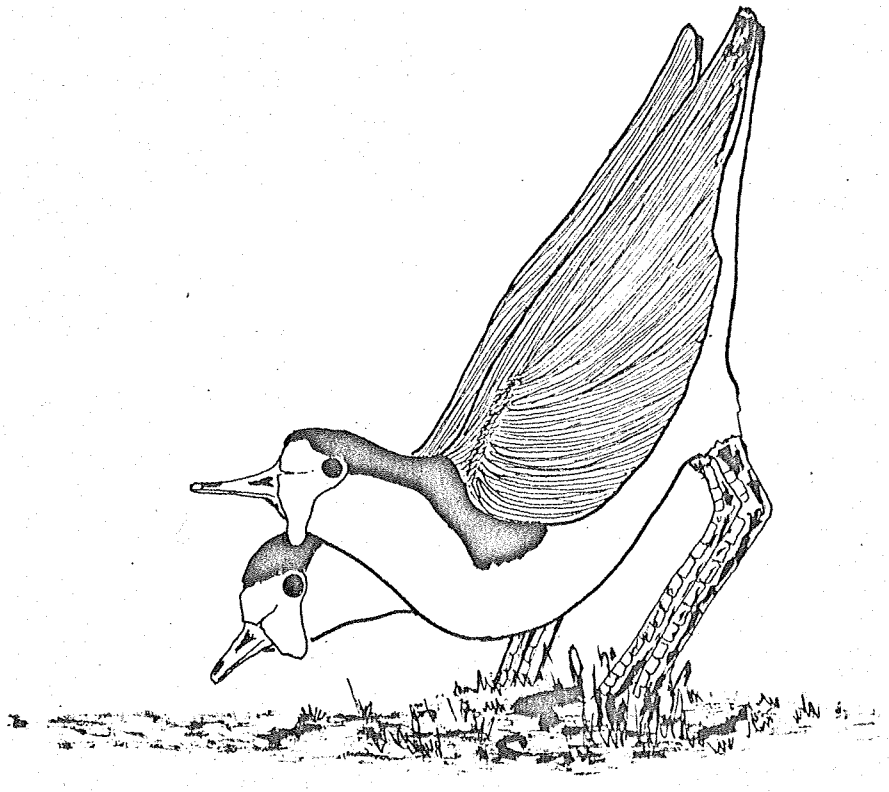
In the aggressive form choking is preceded by the pair, running abreast towards an intruder or intruding pair in an almost horizontal position with the head not fully retracted. This can evoke a variety of actions and the sequence which ensues is dependent entirely upon the behaviour of the threatened bird.

Choking in its complete form usually occurs when a pair succeed in driving off the intruding bird, after a "run-up" chase. When this occurs they lower the breast and raise the hind quarters until, in high intensity choking, the body is angled almost vertically

FIG.9 CHOKING BEHAVIOUR



(a) Running posture of a pair towards an intruder



(b) Choking posture

downward and the head and bill are pointed downwards or, if the rival is fleeing, up towards the rival. The head - jerking which is associated with choking in gulls (Tinbergen, 1953) is rarely performed but,"flicking" behaviour, (see section on nest scrape) associated with nesting in Spurwinged Plovers, is not uncommon. During confrontation in the choking posture a peculiar, gutteral call is uttered which is characteristically associated with choking in a hostile situation.

If the intruder assumes an upright aggressive posture, then it is usual for the pair to adopt similar postures. Choking results only occasionally from this situation, usually occurring if the challenged bird suddenly flees. If the challenged bird flies off before being confronted,the birds may resume previous activities without choking.

Choking may occur when two, or more, pairs confront each other at their territorial boundaries or during territorial intrusion but is more commonly seen in flocks, where contact between bird is more frequent.

If choking is performed so that the tail is toward the opponent it seems to have an inhibitory effect on aggression in the attacker and could be termed a submissive posture. Lind (1957) observed this behaviour in lapwings and described it as a submissive posture.

A form of apparently non-aggressive choking is performed by the male towards the female at selected nest sites in territory. Here choking is often followed by the "scrape - ceremony" (see Pair Interactions) and also "flicking" behaviour.

Aggressive choking is considered by Tinbergen (1959) to be a displacement activity which is derived from nest - building behaviour. A full discussion of the origin of choking and the drives involved is given by Tinbergen (1953, 1960) and Moynihan (1955, 1962).

From my observations, I consider choking to be a low intensity form of threat in Spurwinged Plovers because the spurs are not usually bared nor the wattles fully inflated in this posture.

Lind (1957) has observed lapwings retreating after a "sham" flight in a position similar to the choking posture but I have never observed this in Spurwinged Plovers.

Display flight

The display flight is considered an integral part of the territorial behaviour of lapwings (Spencer, 1953) and an African Spurwinged Plover Hoplopterus (= Vanellus) spinosus (Steifel, 1964).

In the Spurwinged Plover display flights occur infrequently and are usually associated with advertisement of the territory after intrusion. I have observed display flights on several occassions after displays of territorial aggression against territorial intruders. These flights were of short duration and consisted of an aerial patrol of the territorial boundary during which the bird incessantly gave the threat call and often chased the intruder.

The spontaneous occurrence of display flights in lapwings, especially at dusk, is not replicated by the Spurwinged Plover although the noisy return of pairs to territory at dusk during the breeding season seem to be functionally similar to display flights.

PAIR INTERACTIONS

In Spurwinged Plovers, very little time is spent engaged in courtship activities. The absence of courtship feeding and allopreening, which is prevalent in larids during courtship (Moynihan, 1962; Nelson, 1968), means that contact between paired birds is limited to the brief period in which the male mounts the female during copulation.

Despite the lack of elaborate courtship and pre-coition behaviour in Spurwinged plovers the pair interactions which do occur are extremely stereotyped and very interesting when compared with similar behaviour patterns in other vanelline species which have been studied.

The following behavioural patterns may not be in chronological order because I was unable to determine exactly whether or not copulation preceded the "scrape-ceremony" and nest site selection. However, as copulation was sometimes observed in the flocks before they had completely dispersed for the breeding season it seems likely that nest-site selection is preceded by copulation. In fact, I consider that copulation prior to nest - building activities may effect a more rapid development of breeding condition in female and render her more receptive towards nest - building activities.

Copulation:

Spurwinged Plovers copulate prolifically during the early part of the breeding season but copulatory behaviour wanes rapidly when egg laying ceases and the incubation drive becomes dominant.

There appears to be no specific time of day at which copulation occurs and copulation was inferred during night observations from the characteristic pre-copulatory calls uttered by male plovers.

Mating appears always to be initiated by the male and although I have observed copulatory behaviour on numerous occasions I am still uncertain of the stimulus which initiates the copulatory drive in male birds.

Mating behaviour is extremely stereotyped and the following behavioural sequence is alway observed in association with mating:

1. the male approaches the female in a stiff horizontal posture uttering a low, staccato call which is characteristic of the male and only given during mating behaviour.

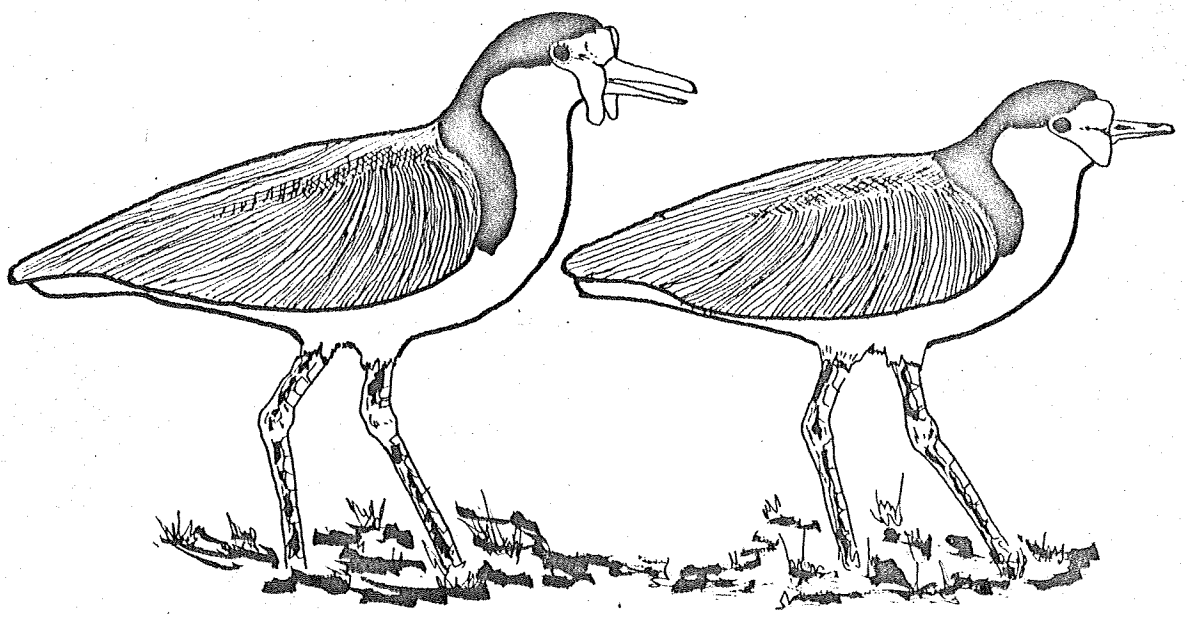
2. the female commences to run in front of the male in a similar horizontal posture but with the head slightly more retracted (Fig.10(a)).

3. the intensity of the male's precopulatory call is increased during the "courtship run" until the female becomes receptive and assumes the soliciting position for copulation.

4. the male then abruptly ceases the pre-copulatory call and mounts the female (Fig.10(b)). Cloacal contact occurs for approximately five seconds and then the male dismounts.

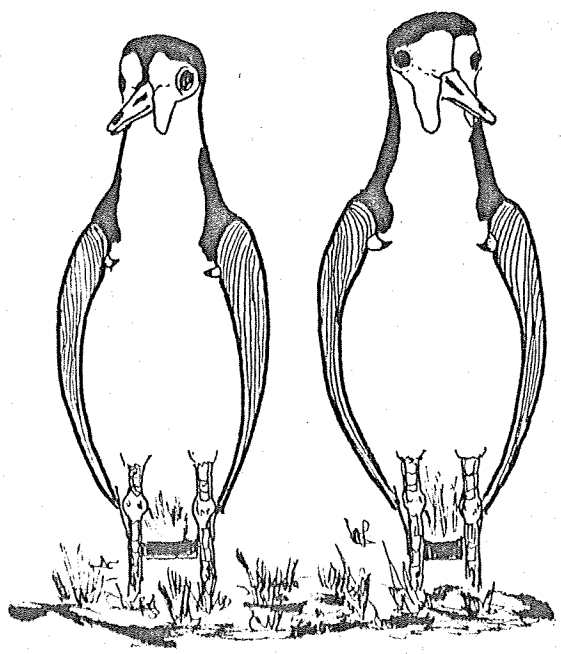
5. both birds adopt the post-copulatory posture (Fig.10(c)) which consists of the high intensity aggressive posture with the head angle away from the mate. This posture resembles closely the larid behaviour of "head flagging" Moynihan (1955,1962) in both form and function.

FIG.10



(a)"Courtship run"

(b) Copulation



(c) Post-copulatory posture

The posture assumed by the female during the "courtship run" is very similar to the posture adopted by a plover fleeing after an aggressive encounter and I consider from this that the male during the "courtship run" is showing mild threat behaviour toward the female.

The "courtship run" has been described in the Lapwing (Spencer, 1953) and the Golden Plover (Williamson, 1948) and in both was considered a mutual stimulant for copulation. In Spurwinged Plovers it also seems to be a form of mutual pre-copulatory stimulation and, as all coition observed was preceded by the "courtship run", it appears to be a fundamental and necessary element of mating behaviour.

Aborted attempts at copulation were observed during the breeding season, due to the female not assuming the soliciting position during the "courtship run". The male was never observed to attempt mounting in these circumstances and both birds resumed normal activities.

Sock (1958) considered that wattles may be utilised in courtship displays of vanelline plovers. In the Spurwinged Plover this is not so, in fact, the form of mating behaviour is such that on no occasion do the mating pair face each other or adopt any posture in which the wattles could serve as behavioural releasers. The only morphological character which may function as a releaser during courtship are the bright

carmine - coloured legs and feet. It was observed during the "courtship - run" that the leg movements were accentuated and by these movements the female may stimulate the sexual drive of the male.

Nest-site Selection and the Scrape - Ceremony

Nest - site selection in Spurwinged Plovers is always performed by the male. This has also been observed in Lapwings (Spencer 1953, Stiefel 1964) and many larids (Tinbergen, 1953; Moynihan, 1955; Nelson, 1968).

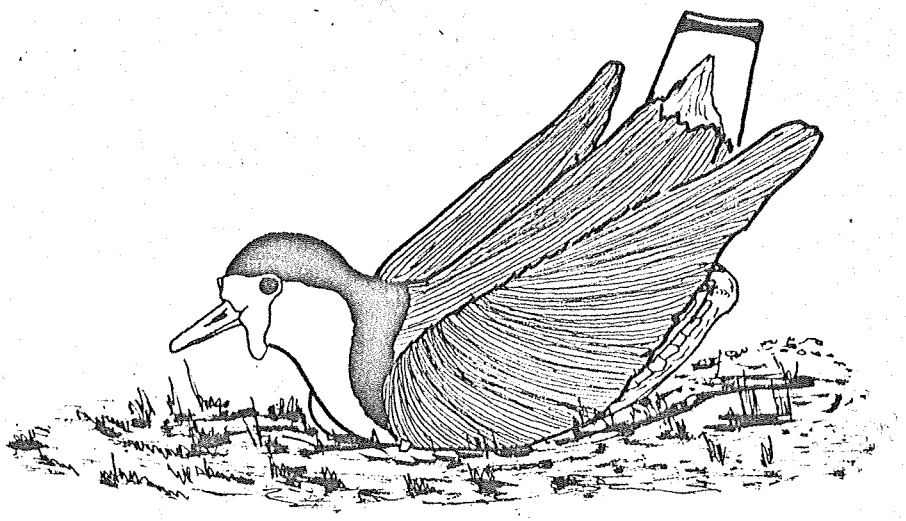
In Spurwings the advertisement of selected nest - sites, is, as in Lapwings (Spencer, loc. cit.; Steifel, loc. cit;) and Hoplopterus (= Vanellus) spinosus (Stiefel, loc. cit.), by means of the "scrape - ceremony".

SCRAPE CEREMONY:

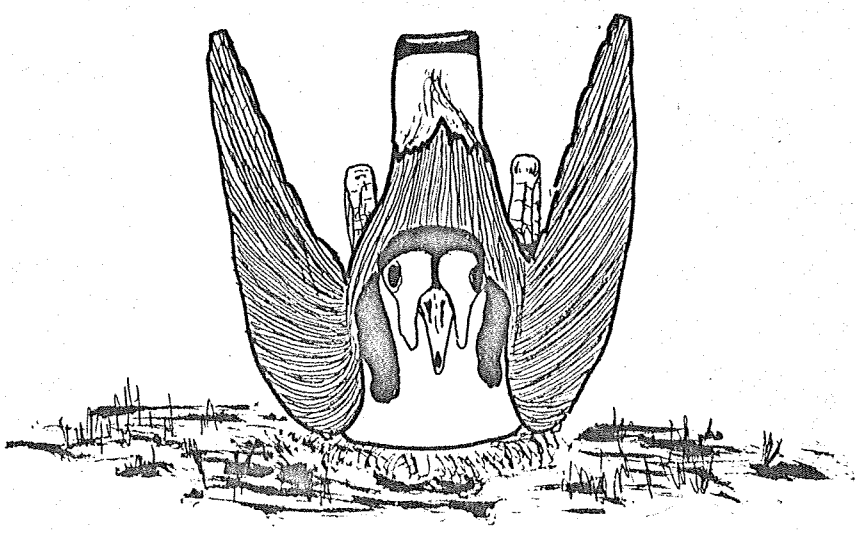
The following sequence is the normal form of the scrape ceremony but variations are not uncommon.

1. the male approaches the selected nest - site with the female and performs "flicking" behaviour interspersed with choking. "Flicking" is the term I have used to describe the particular behaviour in which small stones and herbage are picked up in the bill and flicked backwards over the bird's shoulder.
2. the male then lowers itself slowly into the slight depression and assumes the scraping posture shown in Fig. 11(a) & (b)

FIG.11 SCRAPE-CEREMONY



(a) Lateral view



(b) Anterior view - note tail position

3. in this posture the male then begins a scraping movement with the legs, which functions in enlarging the nest depression and gaining the attention of the female.

4. when the scraping is completed the male assumes a standing posture and commences "flicking" towards the nest - site.

The immediate reaction of the female seems to depend on whether or not she accepts the nesting - site. If the nest - site is accepted the female joins with the male in "flicking" behaviour, which then has functioned significance in lining the nesting depression. If the female is unreceptive to this behaviour both birds resume normal activity.

The scrape - ceremony has been observed in Lapwings (Rinkel, 1940; Spencer, 1953; Steifel, 1964;) and is very similar to the Spurwinged Plover scrape - ceremony in form and function. Rinkel (loc. cit.) claimed in the Lapwing scrape - ceremony that the female is attracted to the nest - scrape by the chestnut coloured upper tail coverts which are revealed by the male during the scrape-ceremony. This was further substantiated by Spencer (loc. cit.) and Steifel (loc. cit.).

In the Spurwinged Plover the upper tail coverts are white and are not easily distinguished against the white background

of the rectrices. The combination of white tail and tail cover appears to function as the nest - site release signal for the female. It is interesting that a juvenile plover which was observed to assume the scrape - ceremony posture in a flock was promptly attacked by the dominant male in the flock.

The scrape-ceremony has been observed to occur in Lapwings at night (Steifel loc. cit.). It would be expected that at night the white rectrices would be more functional than the chestnut upper-tail coverts and it is possible as a signal/that the white tail, rather than the upper-tail coverts, as the nest - site release signal in the lapwing.

DEFENCE OF NEST & BROOD

In many ground nesting birds, e.g. charadriid plovers (Williamson, 1948, Simmons, 1952, 1953 & 1955) Lapwings (Rinkel 1940, Spencer 1953), specific behavioural patterns have been developed for the defence of eggs and chicks against predators. Most of these patterns are in the form of passive defence which focus the attention of the predator on the adult bird in an attempt to distract the predator from the nest - site or the concealed chicks.

Passive defence, such as distraction - display, is characteristic of the small charadriid plovers and many shore birds (Simmons, 1955) and appears to represent a lower intensity of the aggressive drive in these species.

Some behavioural patterns have definite aggressive components which result in direct confrontation of the potential predator. In many larger species, like the bittern (Botarus stellaria), the agressive drive is so strong that predators are attacked vigorously by the bird in defence of its nest (Hinde, 1961, p.396).

In the Spurwinged Plover, parental defence of the eggs and chicks against potential predators involves several characteristic behavioural patterns and postures which are not performed outside the breeding season. The increase in the reproductive drive is associated with an increase in the aggressive drive which appears to reach a maximum level on or slightly before hatching of the eggs. During this period, overt aggression occurs against any territorial intrusion but may be especially intense if the eggs or chicks are directly approached. This level of aggression is maintained throughout the fledging period but wanes rapidly after fledging.

In nest defence, as in all other aspects of behaviour in Spurwinged Plovers, the male is more aggressive than the female and it seems possible that larger and more aggressive Spurwinged Plovers in the breeding season become the dominant and subdominant flock birds during the non-breeding season.

Four sequences of behaviour were observed in association with nest defence. These sequences, as described below, are not in any chronological sequence because the onset, duration

and intensity of the nest defence behaviour was extremely variable between pairs of plovers.

DIVE ATTACK DISPLAY:

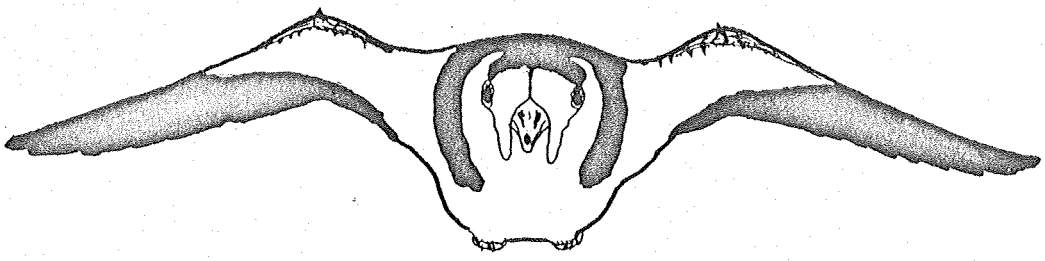
Dive attack displays are not peculiar to Spurwinged Plovers. They have been described as a form of nest defence in many bird species including the herring gull (Tinbergen, 1953); oyster-catcher, Lapwing, Black-tailed Godwit and the European Curlew (Simmons, 1955). Dive attacks occur uncommonly in some charadriid plovers e.g. Ringed, Little Ringed and Kentish Plovers, but Simmons (loc. cit.) states that these are"less pressed home "than in the larger waders.

In the Spurwinged Plover dive attack aggression is the commonest method of nest and chick defence and the components of this particular behavioural sequence are extremely stereotyped even though there may be variation in the intensity of the attack.

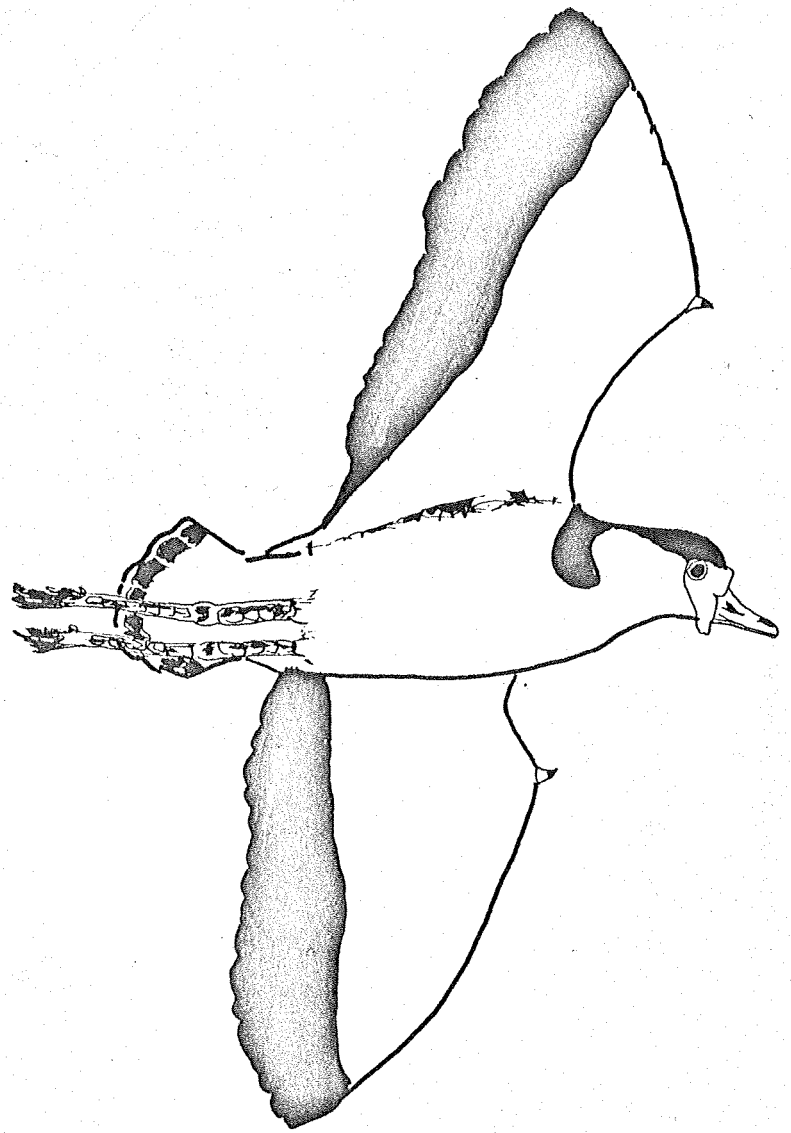
The dive attack usually commences from the ground and in the first element of attack the plover makes a low altitude flight at the head of the potential predator. It then turns away abruptly prior to impact and climbs at a steep angle until an altitude of approximately 50 to 100 feet is reached. This altitude is the "ceiling" for future dives. Occasionally, plovers may omit this first element of attack and fly to the "ceiling" altitude for the beginning of the first attack. The behavioural pattern which follows the initial attack is very similar the "swoop - and soar"

behaviour described in gulls (Moynihan, 1955; Tinbergen, 1960). The bird begins the "swoop" and gains speed by vigorous wing-beats. As the "predator" is approached the line of attack becomes increasingly more horizontal until finally the bird, in a horizontal plane, ceases wing movements and continues the approach with spurs and bill directed at the predator and the wings and body forming an inverted "V" (Fig.12(a)). This posture is maintained for a short distance past the predator and then the attacking bird begins a steep ascent with tail fanned and rapid wing beats (Fig.12(b)) until it reaches approximately the same altitude at which the attack dive began. The fanned tail appears functional in aiding the steep ascent and possible also as a behavioural signal. If the stimulus for attack is maintained, further attack dives occur, but if not, the bird lands and assumes the "low - forward" threat posture. This threat posture has a low aggressive component and it appears that birds assuming this posture are in a continual conflict of attack and escape drives.

If movements of the predator further stimulate the aggressive drive of the defending bird it assumes the upright aggressive posture (i.e. increase in the aggressive drive) and continually utters the threat call. The calling increases in intensity and frequency until again the attack threshold is attained and the bird resumes aerial aggression.



(a) Position at the end of the dive



(b) "Climbing" posture with tail fanned and elevated

The threshold level of the aggressive drive associated with the dive attack displays varies greatly between individuals and also within an individual, depending upon the stage reached in the breeding cycle.

In some individuals the threshold level was very low and these birds performed highly aggressive attacks on predators even before the eggs were hard-set (i.e. in the late stages of embryonic development). Other individuals having high thresholds performed incomplete attack-dives throughout the fledging period.

Female Spurwinged Plovers were always observed to have a lower aggressive drive than the males. This was indicated by the female attack-dives being much more shallow than the male's, and performed at higher distances above the predator.

During the study some observations were made on the dive attack display of the Banded Plover (Vanellus tricolor). This species performed a very similar dive attack display to the Spurwinged Plover except that during the approach flight the body and wings were rolled about the horizontal plane revealing the white wing stripes. These wing stripes appear to be incorporated into many displays of the Banded Plover but further observations are necessary to elucidate their functional significance as social signals.

FORWARD DISPLAY: (Fig.13(a-b))

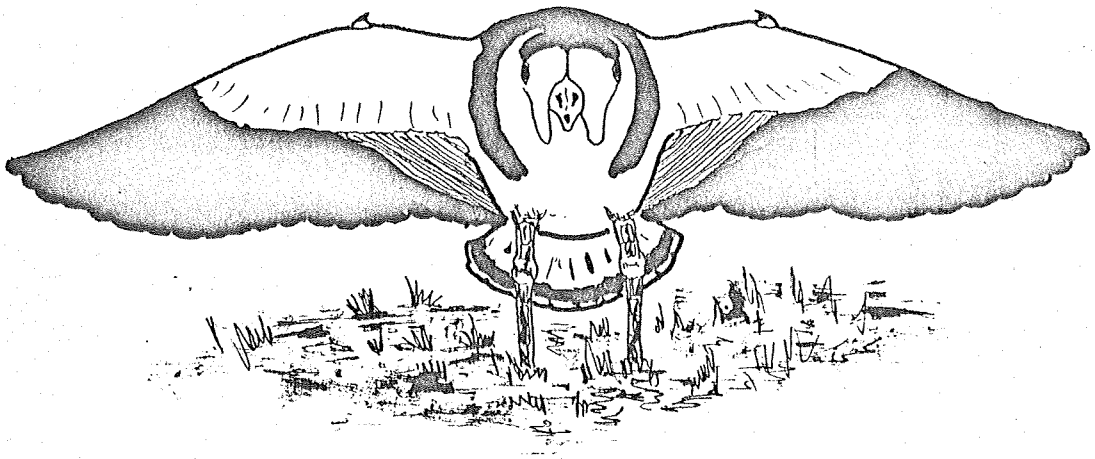
Two forms of the forward display occur during defence behaviour. In both forms the body is held horizontally, the legs are slightly bent and the neck is stretched to a varying extent. The bill is pointed horizontally forward or slightly down. The two postures differ only in wing and tail positions.

In the higher intensity form the wings are outspread and the tail is lowered and fanned (Fig.13). The posture is accompanied by a deep gutteral call which is similar to the call given during choking. I have only observed this high intensity forward - display four times and each time when I was crouching over hard - set eggs. In this forward posture the adult bird has a high aggressive drive and may advance within several feet of the intruder but making no attempt to strike it.

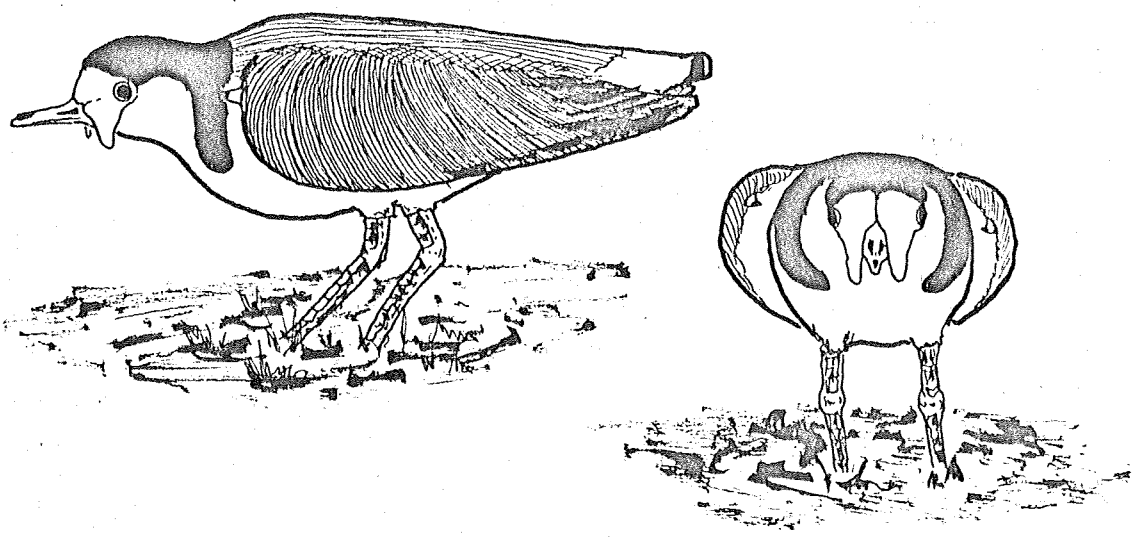
Predator recognition has not been studied in Spurwinged Plovers and it is not possible to indicate the reason for the absence of dive - attacks on resident livestock which may approach nest - sites. It is possible that the high intensity forward display is an aggressive posture used against livestock approaching near the nest.

In the low intensity forward display the wings are opened slightly, baring the spurs, and the tail is maintained in the normal closed position (Fig.13(b)). Plovers in this posture

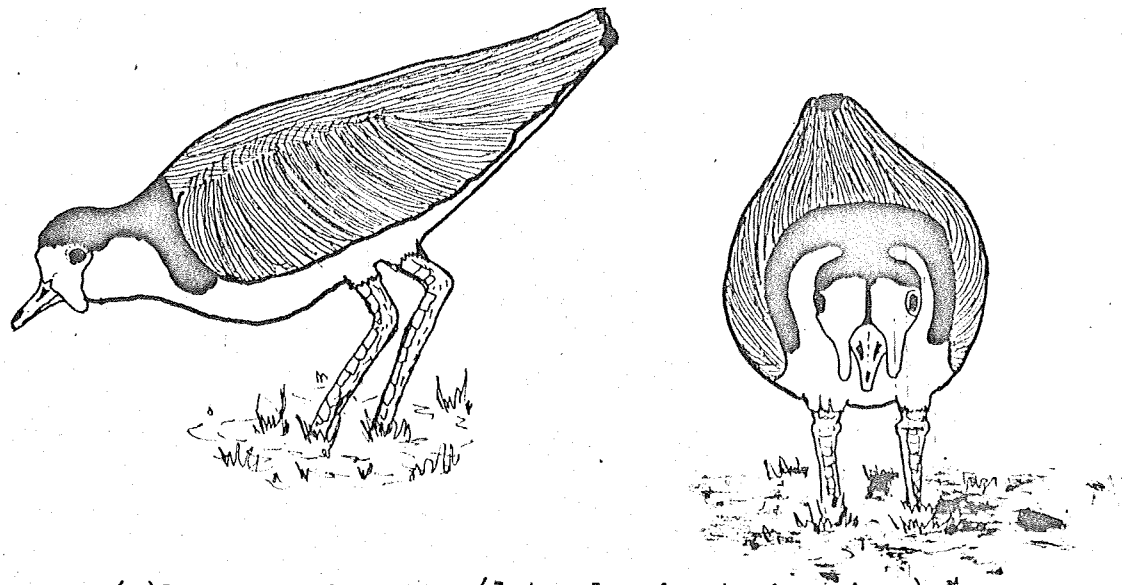
FIG.13 NEST DEFENCE POSTURES



(a) High intensity forward posture



(b) Low intensity forward posture(lateral and anterior views)



(c)Low forward posture (lateral and anterior views)

rarely approach as close to intruders and show a higher escape drive when compared with birds in the high intensity form.

An interesting observation was made in which a plover in the low intensity forward display was apparently at the threshold level of the high intensity form. This bird made many attempts to hold its wings outstretched but finally reverted to the low intensity display.

In both these postures the wattles were inflated, indicating a high aggressive drive.

LOW FORWARD DISPLAY (Fig.13(c))

This posture is a common form of threat used in nest and chick defence and is characteristic in having the lowest aggressive component of all the defence postures previously discussed.

The body is held at approximately 30° to the horizontal plane and the legs are slightly bent. The neck is retracted and the bill position varies from horizontal to vertically downward. The wings are kept tightly against the body, concealing the spurs.

The low intensity of the aggressive drive associated with this posture is evident from the rapid transition of this posture into the normal fleeing posture if the bird approaches too close to the intruder, or if the intruder makes a sudden movement.

Plovers assuming this posture rarely approach as near to potential predators as birds in the high and low intensity

forms of the forward display. This is evidence that the low forward display is a low intensity threat posture.

Distraction - display

In the Spurwinged Plover distraction - displays are apparently rare. During the present study only one distraction display was observed, which was in the form of a "broken wing" display. The apparent rarity of distraction - displays in the Spurwinged Plover is interesting when compared with the lapwing which also only occasionally performs these displays (Spencer 1953). Similarly, during brief studies of nest defence in the Banded Plover no distraction - displays were observed.

Displacement behaviour

Two forms of displacement behaviour were observed in Spurwinged Plovers during nest defence:

(i) displacement feeding

(ii) displacement brooding

Displacement feeding is commonly observed during threat displays in Spurwinged Plovers. A discussion of the drives involved in displacement feeding is given by Simmons (1955). Simmons states that displacement feeding occurs "at critical periods in those species which only at best occasionally perform distraction - display (e.g. lapwings)".

Displacement brooding, as described by Simmons (1955), is the only displacement activity known to occur exclusively during the breeding season. In Spurwinged Plovers displacement brooding

is common and is most frequently performed by birds in the low - forward posture. Spencer (1953) stated that displacement brooding was uncommon in Lapwing.

FLOCK BEHAVIOUR

Flock formation

At the end of the breeding season reconstitution of the flocks is rapid and is usually completed by early December. (Fig.14).

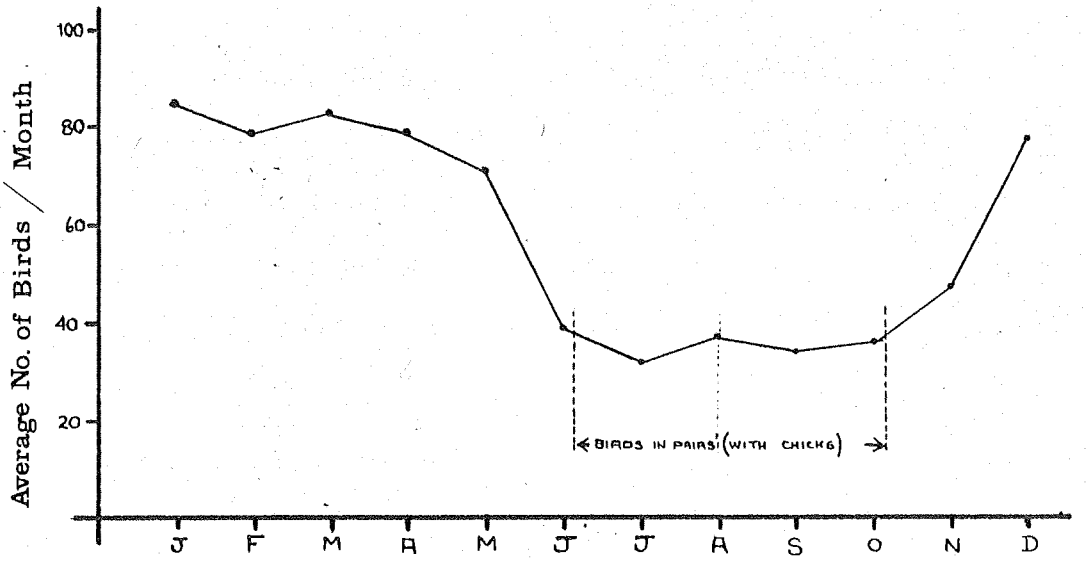
Flock size is variable and aggregations of more than one hundred birds are not unusual, although flocks of twenty to fifty birds are more common.

The flocks are stable in composition and they appear to alternate between one or two selected areas, one of which is at close proximity to permanent water. During early and late months of flocking, paired birds may return to territories after dusk but normally flock birds remain together during day and night.

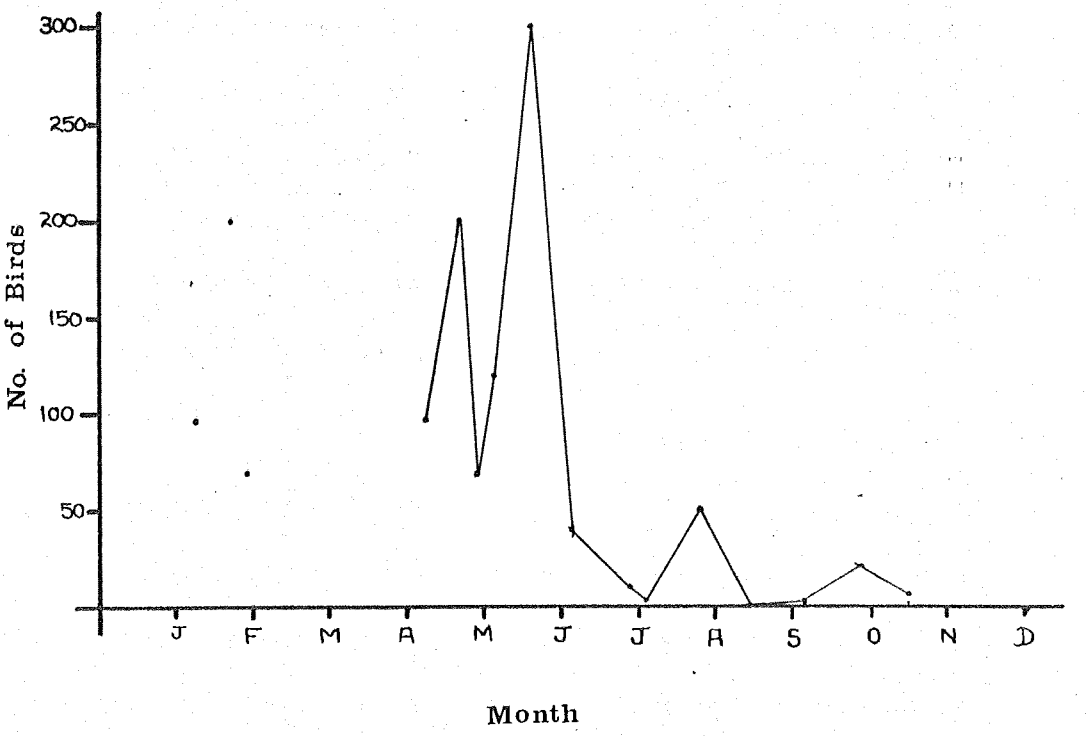
At the Kingston Beach study area flock formation was observed in more detail than in the other two areas and it was found that in the flocking season the resident population of approximately thirty plovers which had occupied territories in the preceding breeding season were joined by an influx of approximately fifty birds from the surrounding districts. Fig.14(a) shows the change in plover population during 1963 at the Kingston study area. Yasin (1967) was able to show a similar trend at Grant Lagoon. (Fig.14(b)).

FIG. 14

(a) FLOCK SIZE — Kingston Study Area — 1968



(b) — Granton Lagoon — 1967
(Yasin, 1967)



Thomas (in press) observed flocks of non-breeding birds during the breeding season but in the present study I found no evidence of "non-breeding" flocks. Spencer (1953) claimed that Lapwings attempted breeding in the first year and I consider that breeding in Spurwinged Plovers occurs in first - year birds. However, this could only be demonstrated by an extensive banding programme.

During the breeding season flocks of breeding birds were observed to aggregate on "neutral" grounds close to permanent water for bathing, preening and resting it is possible that these associations of breeding birds could be mistaken for "non-breeding" flocks.

Diurnal Rhythm:

Although no extensive observations were made on time budgets of Spurwinged Plover flocks, daily activity patterns were recorded on many occasions.

The flocks spend the early mornings and late afternoons foraging in small aggregations of one to three birds, which remain associated with the flock. Often birds may return to their territories to forage but generally the flock structure is maintained .

In the middle of the day during hot or windy weather the birds aggregate in tighter flock formation to rest and preen. These two activities predominate but are interspersed with occasional bickering and foraging. In cold and wet weather foraging may continue throughout the day.

In the evening flocks aggregate near water to bathe and drink and it is usual for them to remain in these areas throughout the night. Nocturnal flock movements have been observed in Spurwinged Plovers but the reason for this activity is not known. Nocturnal activity does not seem to be correlated with phases of the moon as has been shown for the lapwing (Spencer, 1953). Clearly, more observations are needed to determine the reasons for flock movements at night. At Ralph's Bay, South Arm six flocks of between 50 and 100 birds were observed to fly in at dusk from different areas on South Arm and aggregate in a large flock of approximately 500 birds. This large flock dispersed in the early morning into the original component flocks and these were observed to move back to forage in their own selected feeding grounds.

Social Organization.

The only attempt at determining social organization in Spurwing Plovers was made with a small flock of eighteen birds resident on the campus of the University of Tasmania. This was not a detailed investigation because it was not possible to identify, individually, all birds in the field.

However it was possible to identify some birds by certain morphological characters e.g. body size, wattle shape and size and characteristic differences in the black shoulder patches.

From the observations of flock behaviour it became apparent that one pair of birds were dominant over the remainder of the flock. The male of this pair was visibly larger in all external features than any of the other birds and considerably more pugnacious. It was the only bird in the flock in which the wattles, when fully inflated during aggression, formed an unbroken yellow shield across the forehead. It seems likely that other birds in the flock were able to "recognize" the dominant male by his external characters.

The dominant male was the only bird in the flock which reacted to birds flying to rejoin the flock from foraging areas. The intensity of the reaction seemed dependent upon the social status of the approaching bird and the high intensity upright aggressive posture was only performed to two other male birds. These two birds, I consider, were subdominant males and both were continually challenging the dominant male in displays of overt aggression.

The females of these pairs were not as aggressive as the males but seemed to adopt the social status of their mates. This phenomenon has also been observed in corvids (Lorenz 1952). However, it appeared that the dominant female was only dominant in the presence of the dominant male, and in his absence was often observed to flee from the more aggressive sub-dominant males.

The organization and status of other birds in this flock was not elucidated because of the difficulty of recognising the remaining individuals.

However it is apparent that a social hierarchy exists and more intensive study of social organization in Spurwinged Plovers would require that a complete flock be colour banded for the purposes of individual identification. This was not possible during the present study because no successful method was devised to trap plovers out of the breeding season.

Discussion

The most important fact brought out by these behavioural observations is the similarity of the postures and behavioural sequences of the Spurwinged Plover in comparison with those observed in the Lapwing (Rinkel, 1940; Spencer, 1953; Steifel, 1964;) and an African Spurwinged Plover, Vanellus spinosus, (von Helversen, 1963; Steifel, 1964).

Similarities were especially apparent in behaviour associated with aggression, mating, scraping and nest defence, but further studies of other vanelline plovers throughout the world are necessary before generic significance can be inferred from the observed behaviour. However, the results of the present study of the Spurwinged Plover appear to substantiate the generic reclassification of this bird by Bock (1958) from the genus Lobibyx to Vanellus. It is likely that this will also apply to the conspecific Masked Plover which apparently has similar behavioural patterns to the Spurwinged Plover and has been observed to hybridize with it (van Tets et al 1967).

The similarity of many behavioural sequences observed in the Spurwinged Plover with those described in many species of the related charadriiform family, the Laridae (Tinbergen, 1953; Moynihan, 1955; Tinbergen, 1959; Moynihan, 1962; Nelson, 1968) has enabled the use of much of the larid behavioural terminology in describing Spurwinged Plover behaviour. However, no phyletic relationships are implied from the apparent behavioural similarity between the larids and the vanelline plovers which have been studied. Further observation are necessary to demonstrate whether these behavioural similarities are a result of convergence or of similar phyletic origin.

The only behavioural posture observed in the Spurwinged Plover which requires further discussion is the choking posture and its origin. Tinbergen (1959), in describing the probable origin of choking in gulls, stated that choking was probably a combination of two movements. The primary movement is the taxonomically widespread movement of bending down, as in bending over the nest site prior to incubation. The second movement arises from the bird being in a conflict situation (as it is when in the presence of either a female or an opponent) in which it is likely to perform any movement facilitated by this initial movement, such as rhythmical regurgitation or depositing (similar to "flicking" in plovers). Choking, as usually described in gulls, consists of rhythmical movements of the head though to be derived from regurgitation movements observed during parental feeding of gull chicks (Tinbergen, 1959).

The absence of rhythmical head movements in the choking display of Spurwinged Plovers seems readily explained because on no occasion during the fledging of the chicks are they fed by regurgitation. In fact, regurgitation seems absent in all charadriids and the chicks usually feed themselves within 24 hours of hatching, although this seems dependent on the size of the yolk reserve absorbed into the stomach during hatching. The "flicking" movement which sometimes occurs during hostile choking is probably a displacement activity which is derived from nest-site choking. However, in some hostile situations in which "flicking" is absent from choking, the posture, with head and bill pointed towards the rival, appears to be more an overt aggressive posture, as described in the Lapwing by Lind (1957), than a displacement activity. Further observations on this particular display may elucidate its exact function in the Spurwinged Plover.

It is disappointing that no recent comprehensive studies have been made on comparative ethology of the genus Vanellus, or even the related genus Charadrius, because elucidation of their taxonomic relationships seems dependent upon such studies. In fact, Bock (1958) in discussing the taxonomic importance of ethological studies of plovers in his generic review of the Charadriidae stated that;

"Despite the fine work that has been done on the behaviour of several species ....., the comparative ethology of plovers is still in its beginnings and of no help to our understanding of the specific relationships of the plovers at this time ..... the relationships within the large genera, Charadrius and Vanellus, and perhaps even between them will be understood only after their behaviour is well known,..... "

FOOD AND FEEDING BEHAVIOUR

Introduction

Numerous comprehensive analyses have been made of food requirements of bird species (Frith, 1959, Frith & Davies, 1961; Frith, 1965; Holmes et al, 1968). However, there have been few studies of the food requirements of vanelline plovers.

Spencer (1953) in discussing food studies of the Lapwing, Vanellus vanellus, states:

"..... the results of 69 stomach analyses were 89% animal matter, 11% vegetable matter. Animal matter: about 64% insects, 10% Mollusca, 10% worms, 5% miscellaneous. Insects include Dermaptera...., Hemiptera...., Lepidoptera...., Coleoptera...., Hymenoptera...., Diptera.... Also Arachnida...., Crustacea...., Annelida...., Mollusca...., Vegetable matter include .... grass, cereals, leaves, moss and algae, etc. Gizzards often contain several tiny quartz stones .... Lapwings take practically all their food off the ground...."

Cotton (1960) listed the mollusca species found in stomach and crop contents of many species of South Australian birds, including the Spurwinged Plover. He recorded three species of freshwater Gastropoda in the Spurwing Plovers which were examined:

(i) Peplimnea lessoni Deshayes, 1830

(ii) Lenameria tenuistriata Sowerby, 1873

(iii) Glyptamoda ciliciae Reeve, 1862.

Green (1966), from examination of stomach contents, compiled food lists for twenty-two birds species, including two specimens of the Spurwinged Plover. The bird species were collected from dry Sclerophyll and savannah woodland areas in the Tasmanian midlands. In the two Spurwinged Plover stomach contents which were examined, the following invertebrates were recorded:

(i) pasture cockchafer beetles, Aphodius tasmaniae and A. pseudotasmaniae

(ii) ants, Pheidole sp.

(iii) weevils, Desiantha sp.

(iv) click beetle larvae, family Elateridae.

(v) dung beetles, Ontophagus australis

(vi) grasshopper, Austroicetes vulgaris

Fragments of beetles (Order Coleoptera), moths (Order Lepidoptera) and grasshoppers (Order Orthoptera) were partially digested and could not be identified further.

A brief examination of the stomach contents of Spurwinged Plovers was made during the present study.

Methods.

The stomach contents of twenty-eight Spurwinged Plovers were examined. These included five birds which had been shot while feeding on intertidal mudflats at Ralph's Bay.

No quantitative analysis of the food content was attempted in this study and many invertebrate food species were not identified below the taxonomic level of Order.

Food lists were constructed for the birds shot on agricultural land and those shot on intertidal mudflats.

Observations of feeding behaviour were made in conjunction with other behavioural observations.

Results and Discussion

Stomach Analyses.

(1) Agricultural land

The stomach contents of birds shot on agricultural land contained numerous invertebrates and also some plant material. The following invertebrates were identified:

Phylum Arthropoda

CLASS Insecta

ORDER Coleoptera

FAMILY Scarabaeidae: dung beetles (Ontophagus spp.)

FAMILY Elateridae: click beetles and larvae

FAMILY Curculionidae: weevils, species not known.

Numerous specimens of partially digested coleopterans could not be classified further than Order Coleoptera.

ORDER Hymenoptera:

FAMILY Formicidae: two plovers had stomach contents comprising only an ant species, possibly Pheidole spp. (Green, 1966).

ORDER Diptera: an unidentified dipteran was present in one stomach.

Phylum Annelida

CLASS Oligochaeta: unidentified species of oligochaete worms were present in some stomach contents. On numerous occasions Spurwinged Plovers were observed feeding on oligochaetes in the field.

Many of the stomach contents contained a small amount of plant matter which was not identified. It is possible that some plant material was consumed accidentally while birds were foraging for invertebrate species.

(ii) Intertidal mudflat environment.

The stomach contents of birds shot on intertidal mudflats at Ralph's Bay consisted wholly of marine species. The most common organisms present were two species of gastropod molluscs. A list of the species present in the stomachs examined is given below:

Phylum: Mollusca

CLASS Gastropoda

FAMILY Nassidae:

Parcanassa pauperata Lamark, 1822 - most individuals of this species eaten by the Spurwinged Plovers were less than 3/8" in spite of the normal size being approx. 3/4" long. It appears that there is selective feeding by plovers for shell sizes not exceeding approx. 3/8".

FAMILY Amphibolidae:

Salinator fragilis Lamark 1822 - the normal size of this species is approx. ½" (MacPherson & Gabriel, 1962) and here again shell size appears to be selected by the Spurwinged Plover, because the maximum size of S. fragilis shells found during the stomach analyses was 5/16".

Phylum: Annelida

CLASS Polychaeta: - some unidentified species of polychaete worms were present in the stomach contents of two plovers. During field studies of feeding behaviour on tidal flats, many birds were observed to take polychaetes.

As observed in Lapwings (Spencer, 1953), most stomach contents of the Spurwinged Plovers which were examined contained quartz fragments. These appear to be utilized in the mechanical breakdown of food material.

These results indicate the dietary diversity of the Spurwinged Plover. Its ability to occupy a variety of habitats seems facilitated by a dietary flexibility which enables Spurwinged Plovers to adapt to and survive on various food sources occurring in each habitat.

The fact that Spurwinged Plovers feed on marine organisms seems to suggest an efficient mechanism for salt regulation. Physiological and ecological studies of salt tolerance, salt regulation and water balance in the Spurwinged and Banded Plovers

may elucidate the selective factors which allow a wide distribution of the Spurwinged Plover yet confine most of the Banded Plover populations to drier inland areas.

Feeding Behaviour:

Foraging and feeding behaviour in the Spurwinged Plover is similar to many other avian surface and subsurface feeders. Foraging occurs throughout the day and has also on several occasions been observed at night. The periods of maximum foraging activity are in the early morning and late afternoons.

The only facet of feeding behaviour which requires discussion is the paddling action (Cotton, 1960) or "pattering" (Spencer, 1953). Pattering, consists of the bird extending its foot just above the ground and vibrating the leg rapidly.

Spencer (1953) observed pattering in the Lapwing and suggested that:

"pattering action undoubtedly has the effect of raising earthworms to the surface of the soil".

However, I consider that, in plovers, this action mainly facilitates dislodgement of surface invertebrates which are then much more easily seen by the foraging bird. This hypothesis seems to be supported by the high proportion of surface invertebrates eaten by Spurwinged Plovers and Lapwings.

A form of "displacement pattering" was observed in resting Spurwinged Plovers but its motivation and function remain unknown.

Pattering has been observed in many bird species, especially shorebirds, and it appears to have no taxonomic significance within the charadriids.

BREEDING BIOLOGY.

INTRODUCTION.

Few aspects of breeding biology have been studied in species of the genus Vanellus.

Klomp (1951) investigated the laying mechanism and egg production capacity of the Lapwing, Vanellus vanellus, in Holland to determine the reason for its apparent decline. He concluded that the recuperative powers of Lapwings after egg predation were of interest because of their stabilising effect on annual production.

Spencer (1953) discussed, in detail, all phases of nidification in the Lapwing in Britain.

Only one comprehensive study has been made of the breeding biology of Australian Vanelline plovers. Thomas (in press) studied aspects of nidification of Spurwinged Plovers in south-eastern Tasmania.

The present study was initiated in January 1968 at the Kingston Beach Golf Course but the main period of the investigation was from May to November. Many aspects studied were similar to those discussed by Mr. D.G. Thomas (Thomas, in press) and, where applicable, I have checked my findings with his results; I am grateful for his co-operation.

STUDY AREA. (Fig. 16)

The study area, Kingston Beach Golf Course, is located at Kingston approximately nine miles from the University of Tasmania.

Kingston Beach Golf Course is at sea level, except for the northern area which has an elevation of approximately 50 feet. Brown's River passes through the study area and during the study provided bathing and drinking facilities for resident plovers and plovers which were resident in areas of close proximity to the golf course.

The mouth of Brown's River is within ¼ of a mile of the study area and the tidal flats associated with it were often frequented at low tide by groups of plovers from the study area, especially during the non-breeding season.

A small island and an associated area of river flats at the river bend near the second green are exposed during low tide. This area is commonly frequented by residentbirds, especially during the breeding season, and utilised for resting and maintenance activities (e.g. bathing, preening, etc.)

A "neutral" area was associated with this part of the study area (see Fig.15). Here groups of breeding Spurwinged plovers aggregated, especially in late afternoon, to rest or preen. Agonistic behaviour was uncommon in this area.

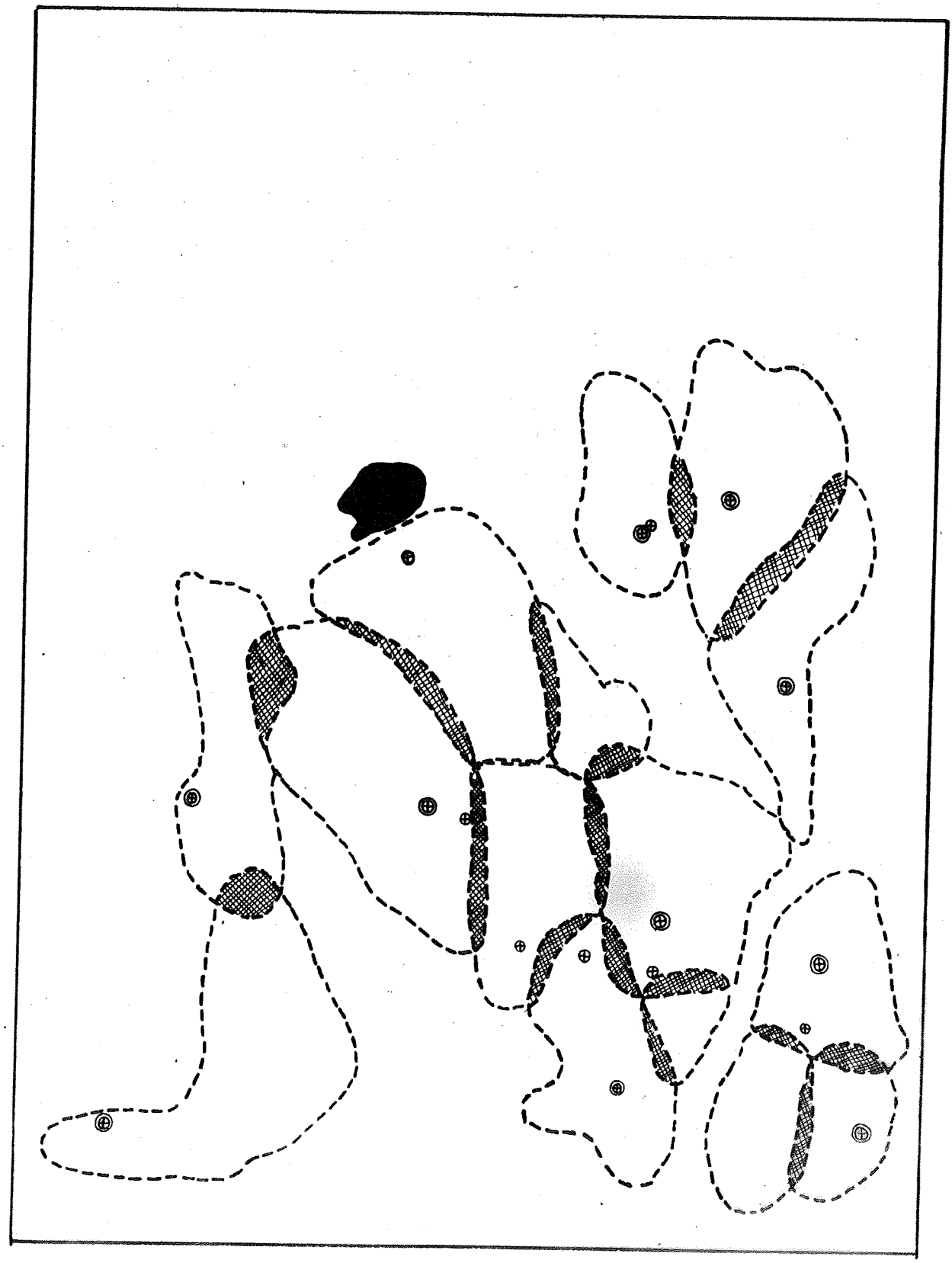
During spring tides margins of the study area close to the river are covered by up to 2" of water. Most of the areas prone to flooding correspond to areas of tussocks in study area (see Fig.16).

The river forms the boundary of the south and eastern edges of the study area and the Channel Highway delimits much of the west and north-west edge. The north and north-eastern boundaries are provided by a wet sclerophyll forest association with Eucalyptus obliqua the dominant tree.

The vegetation and physical features associated with the study area are shown in Fig. 16

The open woodland consited of Eucalyptus viminalis with a sparse understory of Acacia dealbata and ground cover of native grasses (Poa spp.). The borders of the open woodland merge into fairway rough. The grass species comprising the fairway "rough" were maintained at a

FIG. 15



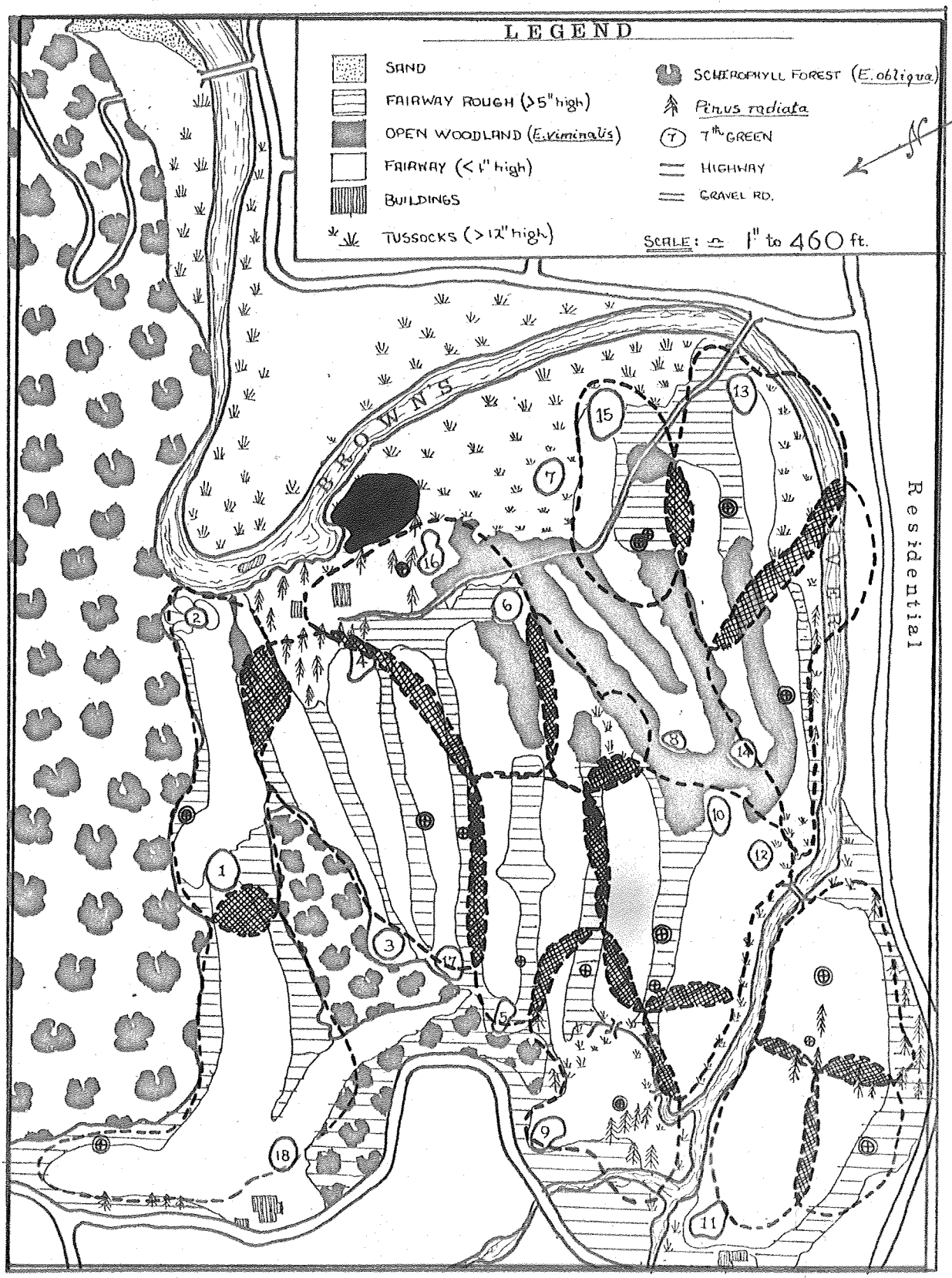
1968 TERRITORY

Territorial Boundary
Unproductive Nests
Overlap
Productive Nests
Neutral Ground

FIG.15

FIG.16

STUDY AREA — KINGSTON BEACH GOLF COURSE



1968 TERRITORY

Territorial Boundary
Unproductive Nests
Overlap
Productive Nests
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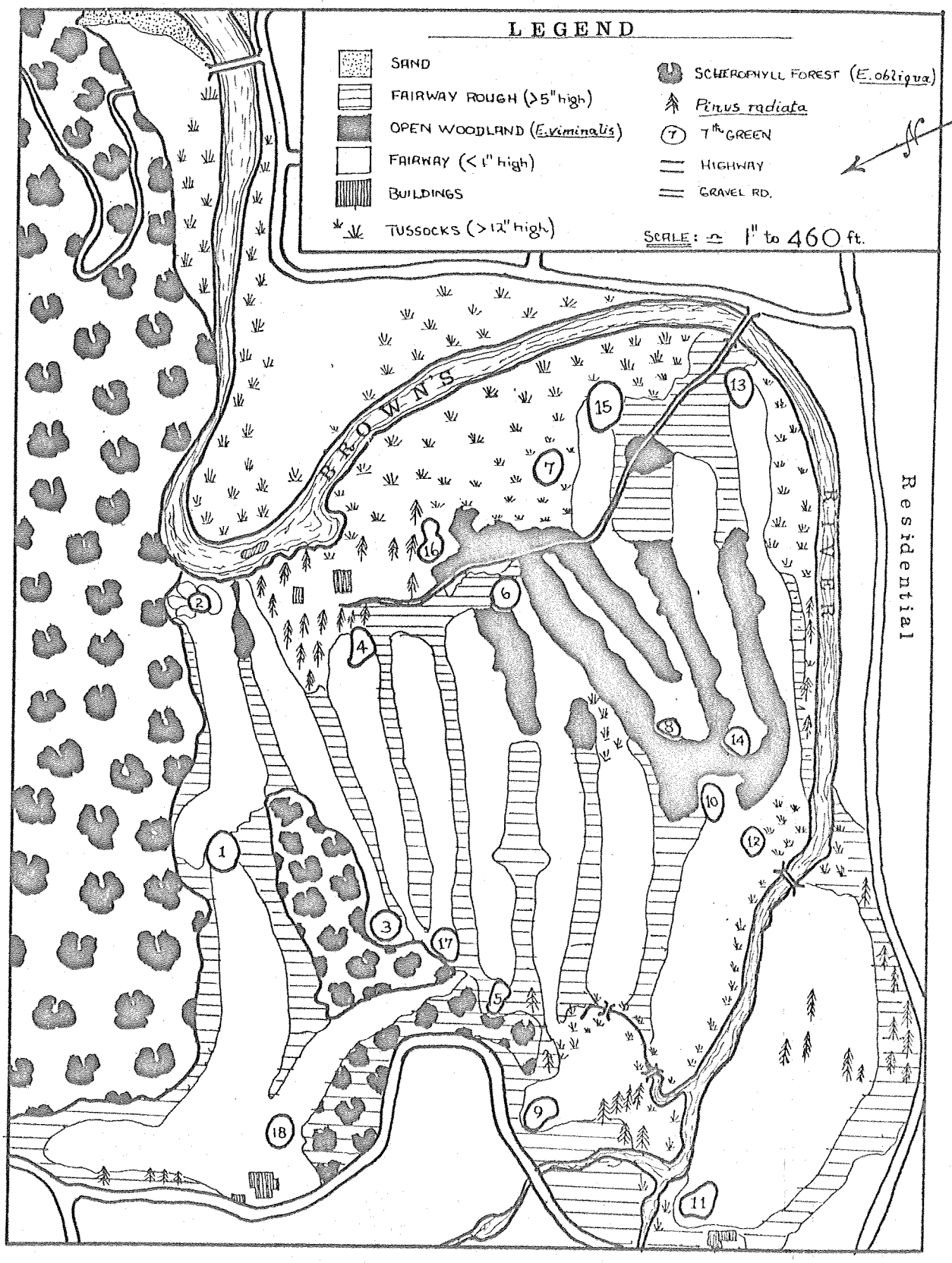
FIG. 16

STUDY AREA — KINGSTON BEACH GOLF COURSE



height of approximately 5". The areas of fairway "rough" were used mainly by the resident Spurwing population for resting and nest-site selection.

Feeding in the study area occurred mainly on the fairways. These comprised imported grass species maintained at a height of approximately 1". The fairways were constantly watered and provided ideal soil conditions for sub-surface feeding. Plovers feeding in the " rough" were usually observed to take surface invertebrates.

The Kingston Beach Golf Course provided an ideal study area for Spurwinged Plovers because of the high population density of resident birds throughout the year. Also, Spurwings in this area were more accustomed to human intrusion, than individuals resident in rural areas and much closer observations of behaviour were possible.

METHODS.

Trapping.

It was necessary, if any detailed results on individual birds were to be obtained, that as many resident Spurwinged Plover as possible in the study area should be trapped and colour banded for field identification.

Two unsuccessful trapping methods were attempted.

The first method involved the use of a funnel trap commonly used in trapping waterfowl. This was unsuccessful because no suitable bait was found which could entice plovers into the trap.

The second method attempted was netting at night by means of a ring net and spotlight. This also was unsuccessful, mainly because at night it was difficult to approach close enough to the birds to net them.

The only successful trapping method used was the nest-trap method described by D'Andria (1965). This method was adopted too late in the breeding season to trap large numbers of birds and only two adult S purwinged Plovers were caught and banded in the study area during the year in nest traps.

However, many birds were recognizable in the field during the breeding season and observations of the movements of many birds were made.

Banding & Colour Dyeing.

The two plovers trapped in the study area were given a different colour-combination of three celluloid bands. These colour bands were commercially manufactured spiral pigeon bands, and were slightly enlarged to fit the plover tarsus. All bands were still present on both plovers at the termination of observations. However, field identification of the banded adults was often difficult because the bands were obscured by ground vegetation.

Twenty-two plover chicks which hatched during the 1968 breeding season were also colour-banded using three-band combinations of red, white, blue and green bands. Re-captures of the surviving chicks during the fledging period enabled a study of growth rates and plumage changes. There was no loss of bands observed in any chicks and no evidence of colours fading.

Captured adults and chicks were colour-dyed using alcohol-soluble d yes. In the two adults, dyes were applied in broad bands across the white breast. These remained visible for a pproximately three weeks. In the chicks, the white upper-neck down was dyed. This region was selected because it was observed to be concealed during crouching. It was, therefore, expected that dyeing of this region would not

create increased predation due to interruption of the cryptic colouration of the chicks. However, colour dyeing the chicks was not successful because the colours faded rapidly and were not visible after approximately one week.

Weights and Measurements of Fledglings.

During the study of growth rates in fledgling Spurwinged Plovers the following measurements were taken:

(i) Weight.
(ii) Bill length.
(iii) Bill width.
(iv) Tarsus length.
(v) Wattle length.

The method of measurement in the chicks was identical to that described for adults. (See Morphology P. 27). Only chicks of known age were measured.

Many aspects of the breeding biology of Spurwinged Plovers were observed in the study area.

RESULTS & DISCUSSION.

Breeding Season.

Thomas (inpress) has interpreted the start of breeding in the Spurwinged Plover as the date on which the first egg was laid. However, he gives no further criteria for delimiting the breeding season.

It was decided from observations made during the period of the present study, to define the breeding season as the period during the year in which paired birds maintain exclusive territorial limits during day and night.

Thomas (loc.cit.) has stated that some Spurwinged plovers maintain territories throughout the year, but that these are not

common.

Observations during the year indicate that birds which seemed to maintain "territories" during the non-breeding season defended them less vigorously against intraspecific intruders and tended to rejoin the flocks for long periods during the day, especially in the middle of the day.

Observations on the campus of the University of Tasmania show that birds maintaining "territories" during the non-breeding season join flock birds during the day and only occupy "territories" in the evenings and early mornings.

Territoriality was used as the criterion for defining the limits of the breeding season in Spurwinged Plovers because in birds, selection and defence of territory appears closely related to hormonal changes in the body. These hormonal changes are responsible for the initiation of the sexual drive which subsequently leads to copulation, nest building, development of the gonads and the incubation drive. A diagramatic representation of breeding chronology in Spurwinged Plovers is given in Fig. 17

The breeding season in Spurwinged Plovers was observed to extend from May to November.

Pair formation.

Little information was obtained concerning pair formation and duration of the pair bond.

Spencer (1953) reported that pair formation usually occurs after males have selected a territory, in the Lapwing.

Steifel (1964) discussed pair formation behaviour in the Lapwing and described pair formation behaviour in which the male

FIG.17 A diagramatic representation of breeding chronology in the Spurwinged Plover

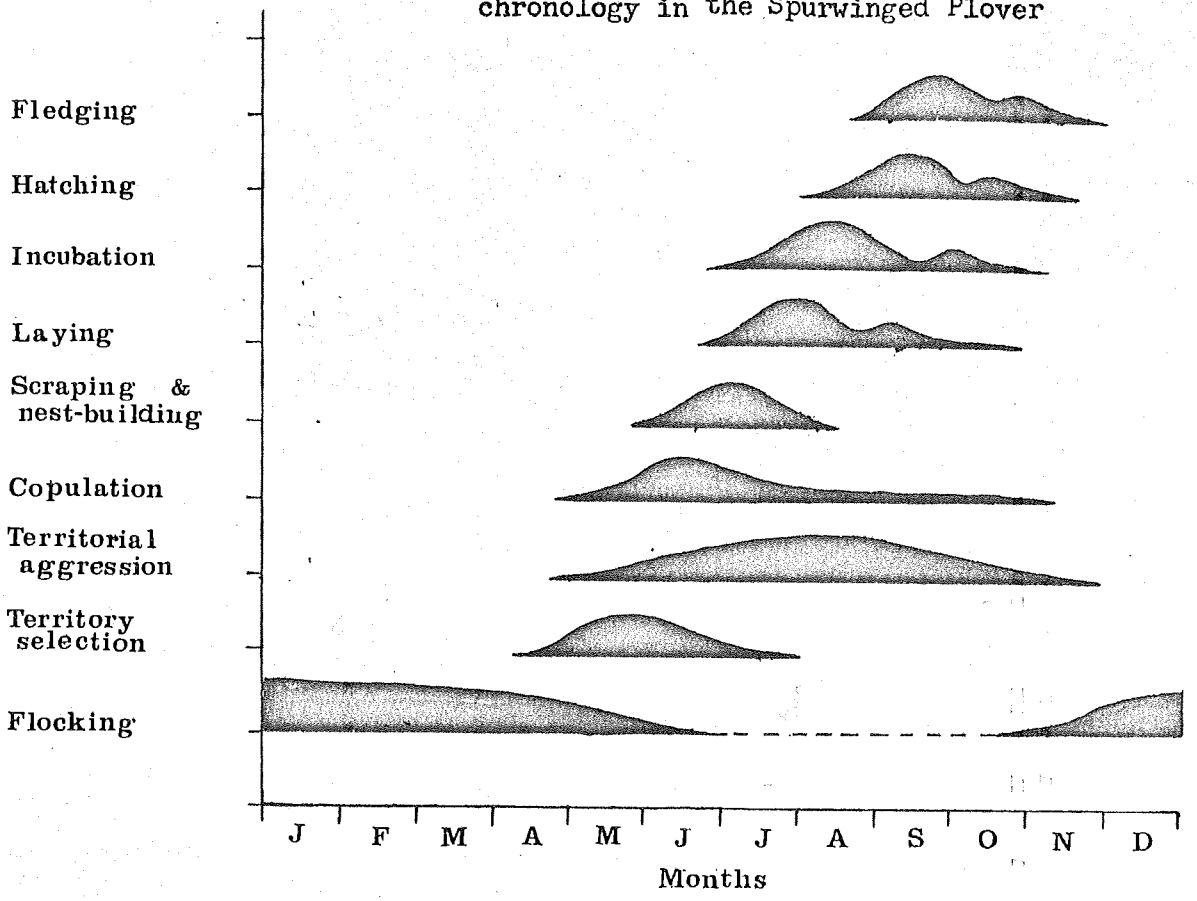
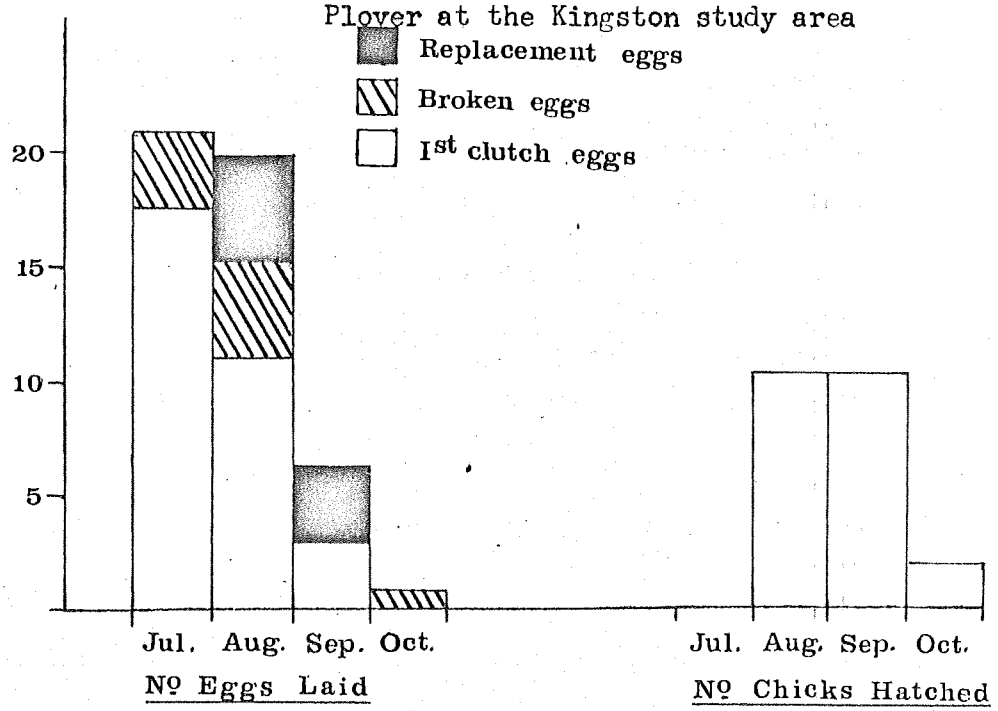


FIG.18 The laying and hatching success of Spurwinged Plover at the Kingston study area



moves in circles around the female.

In Spurwinged Plovers, observations seem to indicate that birds are paired within the flocks and that the pair-bond is maintained throughout the year. In fact, there have been reports of the same pair of plover occupying a similar nest site for at least three years (Allen, 1967), but this has not been confirmed.

It is possible that the pair-bond is maintained until the death of one of the pair birds in Spurwinged Plovers, but confirmation of this would require a large-scaled colour banding scheme and detailed observations.

Territory.

Hinde (1956) defined territory as "a defended area". However Schoener (1968) considered the definition of territory as "an exclusive area", by Pitelka (1959, cited in Schoener, 1968), a preferable concept. Pitelka (loc.cit.) states that

"the fundamental importance of territory lies not in the mechanism (overt defence or any other action) by which the territory becomes identified with its occupant, but the degree to which it is in fact used exclusively by its occupant."

Pitelka's definition of territory was adopted in this study because in Spurwinged plovers there was observed a continuum of behavioural acts, from vocal display through the various forms of threat display to overt fighting, which served to maintain the exclusive nature of the territory.

In the study area at Kingston fifteen pairs of plovers maintained territories but breeding was attempted only in twelve of the territories.

The limits of all territories were determined by plotting the

position and movements of paired birds, and the areas in which conflict between adjacent pairs occurred.

The territories of pairs of Spurwinged Plovers in the study area during 1968 are shown in Fig. 15 The sizes of the territories vary considerably and appear directly related to the intensity of aggression in the territorial males. It was interesting that the pairs occupying the three smaller territories in the study area did not breed during 1968, but maintained territorial limits throughout the breeding period.

Territory in Spurwinged Plovers provides an exclusive feeding area, in addition to a nesting area, and most plovers were never observed feeding outside territorial limits. In fact, the territories were unoccupied only during the late afternoons when plovers moved to the river flats to bathe, drink and preen.

Nesting and Laying.

(i) Nest construction:

The selection of nest-sites by Spurwinged Plovers has previously been discussed (see BEHAVIOUR: Nest-site selection) and Thomas (in press) has described in detail the position and construction of nests in this species.

Thomas (loc.cit.) found that of 110 nests which were observed 98.6% occurred on drainage ridges, small mounds or irregular surfaces and flat areas, and only 1.4% in hollows. He attributed this to a habit evolved to avoid nest flooding or ensure unrestricted visibility for the incubating bird. However, I consider that the position of the nest is determined by a combination of these two factors, with an emphasis on unrestricted visibility for the incubating bird. The latter seems substantiated by the fact that all nests observed during

the breeding season were associated with areas of open ground which had unrestricted visibility within a radius of at least ten yards.

Most nests occurred near "a distinctive feature such as a clump of thistles, stand of rank weeds, piece of wood or large stone". (Thomas, loc.cit.). This may function as a recognition signal for the nest-site as has been observed in the Herring Gull, Larus argentatus (Tinbergen, 1953a).

Lining of the nest commenced after the selection of a nest-scrape by the female, and both male and female plovers were involved. The only materials used in lining were those available near the nest and therefore the lining varied greatly between different nest-sites. It was observed, as discussed by Thomas, that the amount of nest lining was related to nest material availability near the nest.

Materials used in the nest lining included; various grasses and herbage, animal droppings, twigs, eucalypt leaves, pine needles and small stones.

The use of lining materials available within close proximity of the nest was functional in blending the nest-site into its immediate background, resulting in low nest-site visibility.

Fig. 16 shows that most of the nests constructed in the study area were confined to the areas of fairway "rough" rather than the fairways.

The apparent reasons for this were:
(i) the lack of suitable nesting materials on the fairways
(ii) the constant intrusion of golfers
(iii) the regular ground maintenance in these areas (e.g. watering, cutting grass etc).

The areas of fairway "rough" were less disturbed and the grass rarely cut below a height of 5".

(ii) Laying:

Because of prolific copulation observed between pairs prior to laying it was impossible to determine the time interval between copulation and egg laying.

Also, little information was obtained on the interval between the laying of successive eggs because constant observation of the nests was impossible during the present study. However, four intervals of approximately 24 hours and one of 48 hours were recorded. It seems reasonable to assume that laying intervals vary greatly between individual females.

Thomas (loc.cit.) has correlated commencement of laying in the Spurwinged Plover with annual temperature and rainfall fluctuations and explained this in relation to the increased abundance of insects. This is consistent with Lack (1954,1966) who stated that egg development in birds is dependent on food supply.

No attempt at correlating onset of laying with environmental factors was made during the present study.

(iii) Eggs:

The form, colour and variations in plover eggs have been described in detail by Oliver (1955), Sharland (1958), Serventy and Whittell (1962) and Thomas (in press).

Visible differences in egg colouration and egg size occurred within and between clutches.

Thomas (loc.cit.) observed no tendency for eggs to correspond to the colouring of the background, as has been found in the Indian vanelline plover, Vanellus malabaricus. Although this is technically correct, it was observed that in some nests in damp situations the effect of constant turning of the eggs during incubation resulted in

eggs assuming a similar colour to the background. This was particularly noticeable on eggs in North-West Tasmania which were laid on red krasnozem soils. These invariably assumed a reddish-brown colour.

During the breeding season dimensions of 245 eggs were recorded from northern and southern areas of Tasmania. The means and standard deviations of these measurements were determined separately for northern and southern eggs.

Southern eggs	n = 108	Northern eggs.	n = 136
Length: 50.35 ±	2.37 mm.	Length: 47.44 ±	8.45 mm.
Breadth: 36.47 ±	0.44 mm.	Breadth: 34.59 ±	6.11 mm.

The mean dimensions of the southern eggs compare favourably with the dimensions calculated by Thomas (in press) of 51.33 ± 2.25 mm. and 37.44 ± 1.24 mm. The dimension of the northern eggs showed a much greater variability than those in the south. The reason for this variation is not known but it may be an indication of clinal variation in egg dimension.

Incubation and Hatching.

(i) Incubation:

The commencement of incubation was observed to vary between individual plovers. As observed by Thomas (loc.cit) some birds began incubation with the laying of the first egg and in others incubation commenced only after completion of the clutch. This variation in onset of incubation is interpreted as being due to variations in the incubation drive between individual birds. Some birds were observed to assume incubation postures before any eggs were laid. In this context, because of the incomplete form of the incubation posture assumed by these birds, it was considered that this was displacement

behaviour.

The approximate incubation period of four clutches of eggs in the study area were calculated as 28 ± 1 days; 28 ± 2 days; 30 ± 1 day and 30 ± 4 days. The last figure was higher than the others because the nest was not checked regularly during the latter stages of incubation.

From these figures it appears that the approximate incubation period for Spurwinged Plover eggs is four weeks.

(ii) Hatching:

Synchronous hatching of clutches is common in many ground nesting birds and was observed to occur in most Spurwinged Plover clutches which hatched in the study area.

Although the eggs were laid over a period of approximately eight days (in a clutch of 4 eggs) hatching was completed usually within 24 hours, depending on the clutch size.

Synchronous hatching appears to be effected by birds delaying the onset of incubation until the clutch is completed. However, two clutches hatched synchronously even though incubation commenced with the laying of the first egg. No definite explanation of this phenomenon is possible but experiments designed to measure the temperature of incubated eggs, e.g. by using thermistors, could indicate that, initially, the brooding bird applies very little heat to the incomplete clutch, thus retarding embryonic development in eggs laid before completion of the clutch.

Eggs shells were removed by the parental birds after hatching and deposited away from the nest.

Usually within a few hours of hatching chicks were observed to

leave the nest-site with parent birds and move toward regions of denser vegetation in the territory. These areas (e.g. tussocks, borders of woodland areas, etc.) provided the necessary cover and background for maximum concealment during crouching (See Plate II) and were inhabited by chicks until they became fully fledged.

Observations of individual family units during the fledging period showed that, although these units were quite mobile within the territorial limits, there was no evidence of movement across territorial boundaries as was observed by Thomas (loc.cit.).

Chick development.

(i) Changes in Weight and Dimensions:

Twenty-two chicks were colour-banded initially and the surviving birds were weighed and measured as regularly as possible.

All chicks were measured infrequently because of the difficulty of locating fledglings after they had assumed the concealment posture in dense vegetation. However, the results of the measurements obtained indicate trends in growth rates of the fledglings.

The results are presented in Figs. 19 & 20.

The results show large variations because of the differences in growth rates of individual fledglings of similar ages.

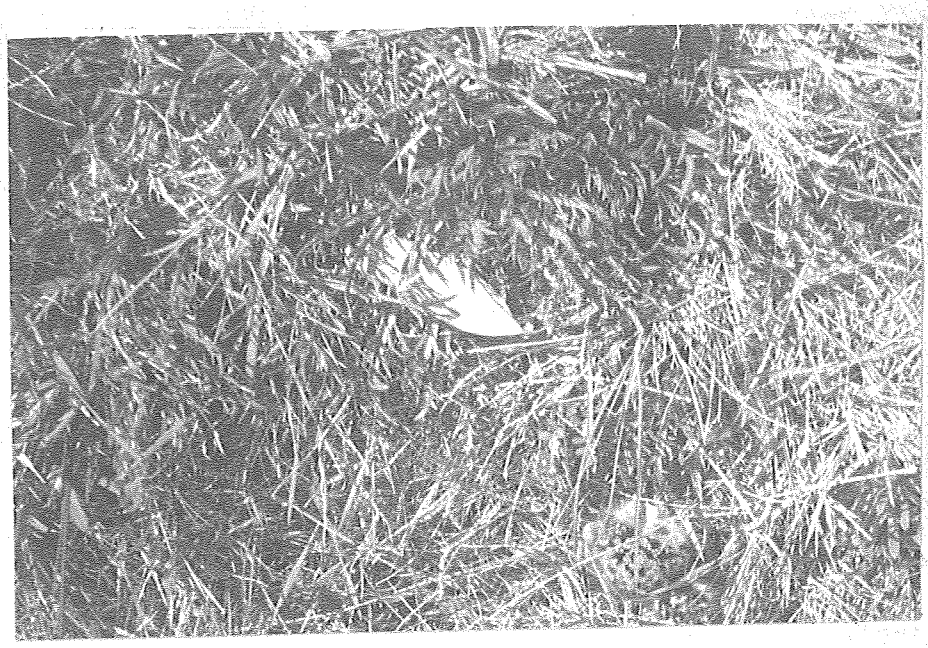
(ii) Plumage change. (See Appendix II).

Observations of plumage and colouration changes in fledglings were made in conjunction with the weighing and measuring programme and thus, were also infrequent. However, general trends were evident.

The nesting down of newly hatched chicks is shown in Plate III (Appendix II).

The crown and upper dorsum were the first areas in which juvenile

PLATE II



(a)

(b)

(a) This photograph demonstrates the effective concealment of a chick provided by its cryptic colouration. The chick was crouching, at a distance of 4' (see upper left).

(b) Close up photograph of the chick in (a) - distance 6"

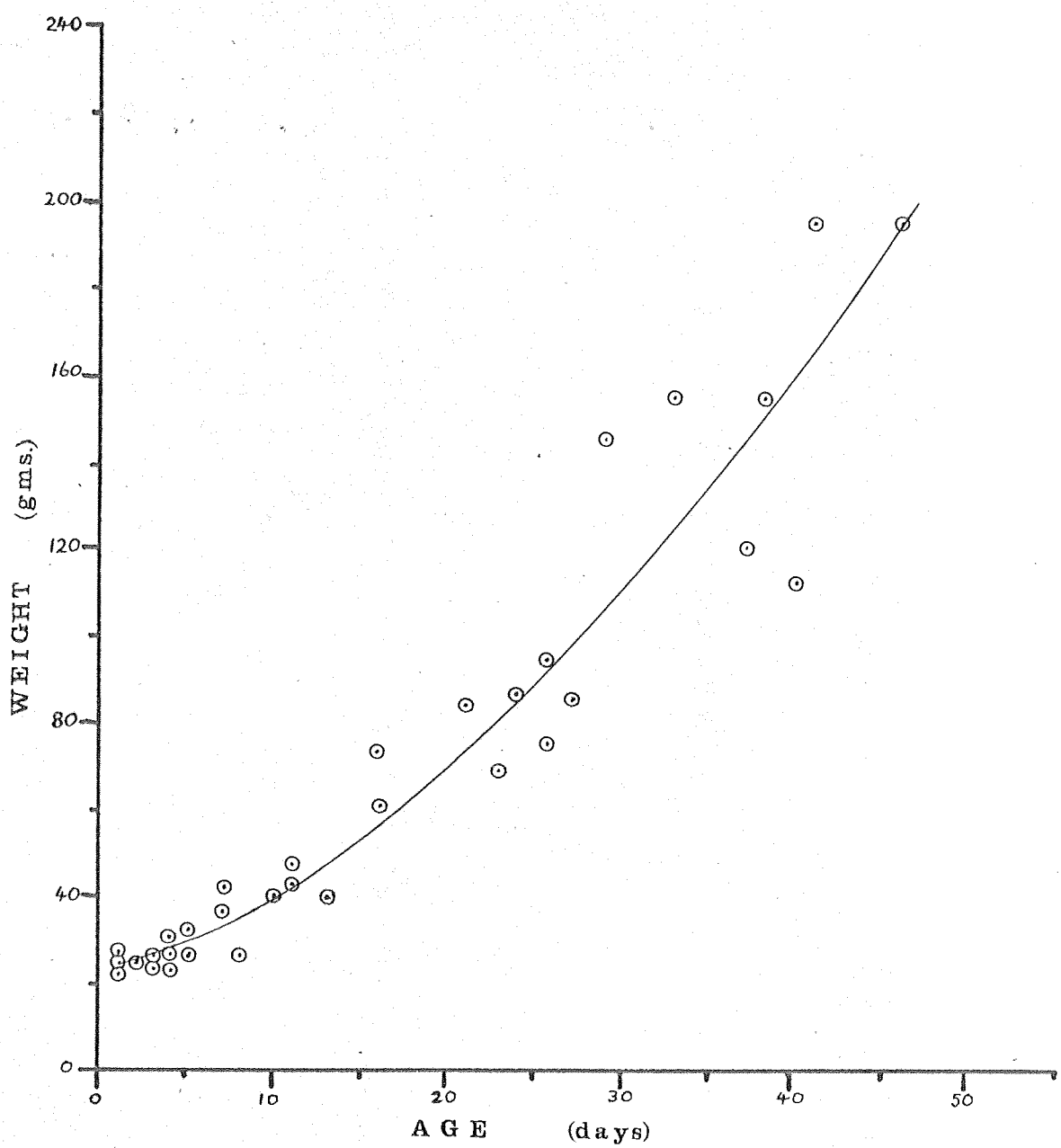


FIG.19 Chick development: - regression of weight against age

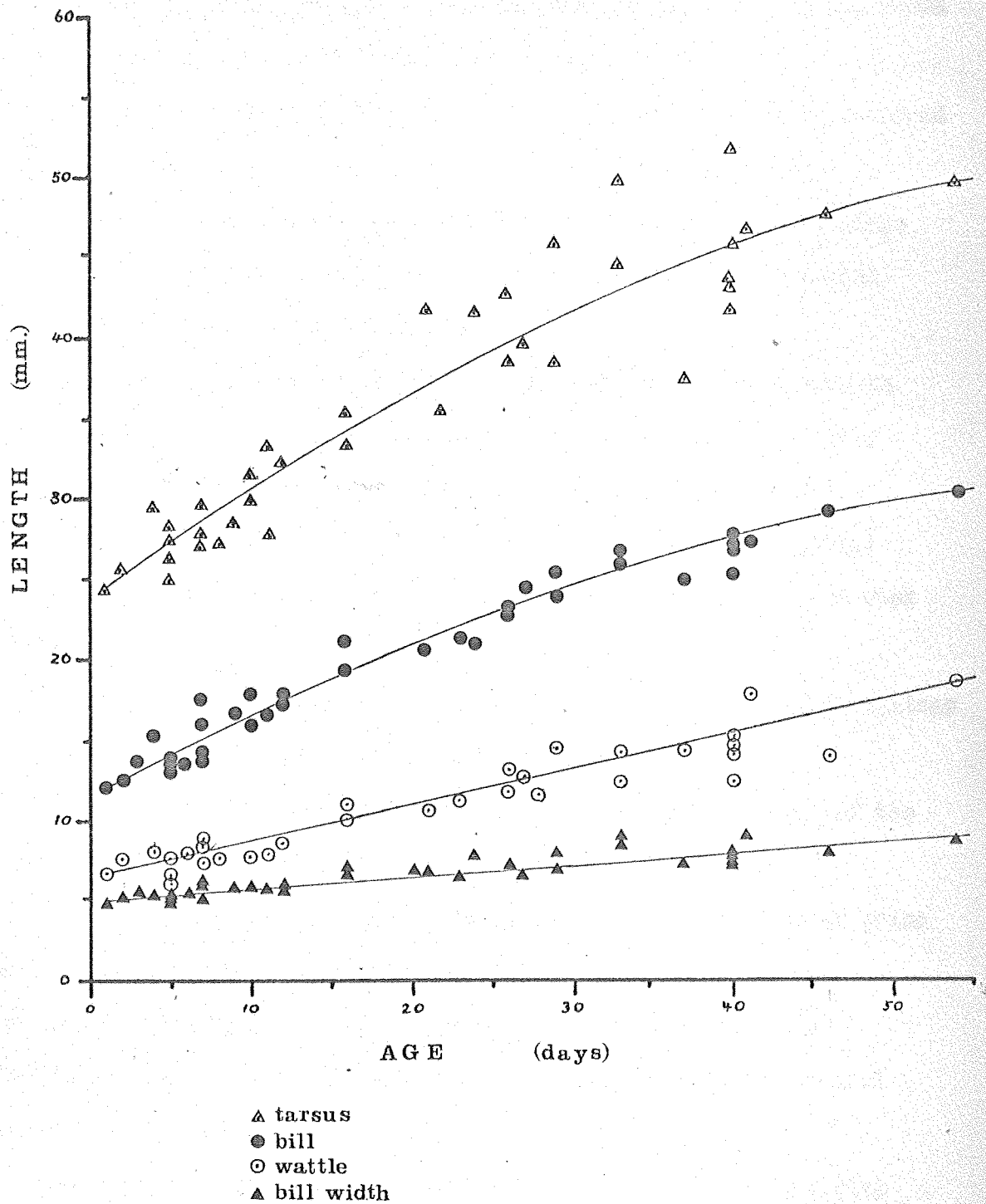


FIG.20 Chick development: - regressions of tarsus length, bill length, wattle length and bill width against age

plumage became evident, and this occurred at approximately 10 days old.

Juvenile plumage gradually replaced the nestling down on the crown by radial outward growth from the crown apex.
Complete replacement of down by juvenile plumage in this region occurred within 5½ weeks of hatching.

The replacement of the nestling down on the upper dorsum, wings and ventrum was in phase with replacement on the crown and was also complete within 5-6 weeks of hatching.

The development of the rectrices and remiges and their coverts was evident 2 - 3 weeks after hatching. These feathers were fully developed at 6 - 7 weeks of age when the fledglings began flying.
A fledgling period of 6 - 7 weeks was recorded by Thomas (loc.cit.) who stressed that there were sometimes variations of at least one week between attainment of flight in fledglings of similar ages.

The black shoulder feathers became evident in 3 week-old fledglings but remained rather diffuse until after fledging.

The nuchal crest and the lower dorsum were the last areas of the body to develop juvenile plumage.

A diffuse black colouration was evident in the nuchal crest prior to fledging but field observations indicate that attainment of a completely black nuchal crest occurs approximately 6 weeks after fledging. Even then, it is not comparable with the well-defined nuchal region in adult birds.

The lower dorsum remained covered by nestling down at fledging and there is no evidence of the period necessary for complete replacement by juvenile plumage.

The bill and irises are dark grey at hatching but gradually

acquire a dull yellow pigmentation which increases in intensity as fledging is approached. The colour change in the bill and irises is paralleled by a similar change in the wattles. (see MORPHOLOGY:Wattles).

The difficulty involved in trapping birds prevented any detailed observation of plumage and colour changes after fledging.

Breeding Success.

Breeding success has been determined in Spurwinged Plovers by Allen (1963) and Thomas (in press).

Allen (1963) recorded a total breeding success of 8 young raised to the free-flying stage per 150 eggs laid (5.3%).

Thomas (in press) estimated the breeding success of Spurwinged Plovers in south-eastern Tasmania as 8.1% (1964), 6.8% (1965) and 4.8% (1966).

During the present study the following breeding statistics were obtained for the population of 15 pairs breeding on the Kingston Beach Golf Course.

Total number of eggs laid	49
Total number of eggs broken	22 (44.9%)
Total number of eggs infertile	1 (2.0%)
Total number of eggs deserted	2 (4.0%)
Total number of eggs hatched	24 (49.1%)
Total number of chicks fledged	11 (45.8%)
Total breeding success	11/49 (22.8%)

The breeding success was considerably higher than determined by Allen (1963) or Thomas (inpress).

It appears that the high fledging rate is due to an abundance of food in the study area. This seems evident from the number of birds

resident in the study area throughout the year and the large influx of plovers during the non-breeding season from areas near the golf course. Obviously, in birds which have to feed themselves immediately after hatching, the mortality rate of chicks will be higher in areas with a less abundant food supply.

No direct observations were made of predation on plover chicks and the causes of chick mortality were not ascertained. It seems possible that chick mortality is associated with adverse environmental conditions, rather than actual predation in the study area. It was observed that plover chicks were very susceptible to cold stress and that young chicks separated from parental birds during cold conditions rapidly became torpid and unable to react to the parents "regrouping" calls.

Experiments on the effect of cold stress in Spurwinged Plover chicks may demonstrate a common source of mortality.

VOCALIZATION STRUCTURE

Introduction

Bird species, in general, are characterized by a wide variety of calls which are species - specific and incorporated into many aspects of behaviour. The structure of calls varies from the complex song of the Gouldian Finch, which appears to have three vocal mechanisms operating simultaneously (Thorpe, 1961), to the rather simple, short vocalisations of various oscines (Thorpe, loc. cit.).

Thorpe (1961) made extensive studies of bird songs, with special reference to variation within and between species of birds, functional significance and ontogeny.

Much work has been done in some families of the order Passeriformes, especially the Paridae (Lemon, 1968) and the Fringillidae (Thompson, 1968) but no structural investigation of calls in the order Charadriiformes have been published.

Spencer (1953) described phonetically the calls of the Lapwing, Vanellus vanellus, but this is of little use in a comparative sense because of its subjective interpretations.

Van Tets (pers. comm.) has prepared sound analyses of species of Australian vanelline plover but these are, as yet, unpublished.

This study was a preliminary sonographic analyses of some of the calls of the Spurwinged Plover. It was not possible to record any calls during the breeding season because of technical difficulties with recording equipment and some of the calls recorded were not duplicated.

Methods:

All calls were recorded in the field using a Grampian DP 4/L dynamic microphone in a 24" Grampian parabolic reflector. This was coupled through a preamplifier to a Fi-cord 202A tape recorder.

All recordings were made at a tape speed of $7\frac{1}{2}$ i.p.s.

The vocalizations recorded were sonographed on a Kay Electric Company 661-B Sonograph so that variations in the structure analysis of call could be demonstrated. The sonagraph analysed call frequencies from 85 cycles/sec. to 8 kilocycles/sec.

Results and Discussion:

The results of the sonographic analyses are presented in Figs. 25 & 26 in Appendix III.

Because of the brief nature of this aspect of the study, it was not possible to analyse fully the vocal repertoire of the Spurwinged Plover.

However, results indicate the calls are relatively complex in structure with each syllable comprising at least three harmonics. The frequency structure of syllables in many of the calls were found to be similar and it appears that vocal communication in Spurwinged Plovers is associated more with the intensity and the frequency of repetition of each syllable than with tonal variations.

This, as previously stated, is only a preliminary study and more detailed research into vocal communication in the Spurwinged Plover and other Vanellus species would provide an interesting comparative study.

GENERAL DISCUSSION

This study revealed the need for more detailed research into all aspects of the biology of the genus Vanellus, especially, as stated by Bock (1958), ecology and behaviour. The complete lack of information on many vanelline species made a comparative study, using results of the Spurwinged Plover research, almost impossible. As discussed previously in this work, the only vanelline plover which could be considered for comparative analysis with the results obtained during various aspects of the present study, was the European Lapwing, Vanellus vanellus.

Research made into distribution, status and selected habitats of the Spurwinged Plover and the related Banded Plover, Vanellus tricolor, reveal interesting results. These results confirmed the views of Sharland (1958) and Thomas (in press) that Spurwinged Plovers in Tasmania were numerous and widely distributed and contrasted markedly with Banded Plovers, which appeared to be distributed in localized regions in certain parts of the state.

Banded Plover distribution appeared to coincide mainly with areas of native grassland in drier regions. It seems that the decline in numbers of Banded Plover in Tasmanian during the last three decades is a result of agricultural development of native grasslands during this period. This has considerably reduced the natural habitat of Banded Plovers in Tasmania.

The increased human population and the extension of urban development into country areas may also have effected a decline in the Banded Plover because it apparently has not the same ability to coexist with human populations as the Spurwinged Plover. Although some Banded Plover frequent the "fringe" of urban areas (e.g. Penna near Hobart) most now occur in the more remote rural areas of the state which are rarely subjected to human interference (e.g. Montagu, Cape Portland and the Ouse district).

The results from the survey concerning habitats of Spurwinged Plovers indicate that it is able to inhabit a wider range of habitats than the Banded Plover and has benefitted greatly from the increased primary productivity of agricultural land.

It is interesting that the correlation between the increase in the Spurwinged Plover population and the increase land development in Tasmania closely parallels the population increase of Lapwings in Britain during the Saxon period, when large scale clearing of forests created new agricultural areas (Spencer, 1953 p.9).

Further studies of ecological requirements of both species, especially in relation to comparative food requirements and interspecific competition, may elucidate the reasons for the present distribution of both species in Tasmania.

Behavioural observations of the Spurwinged Plover indicate the use of the spurs and wattles in certain behavioural postures,

especially in agonistic displays. The role taken by these morphological features in behavioural sequences is not clear. Further experimental studies designed to obtain evidence on the release function of spur, wattles and other morphological characters may clarify their use in behaviour, especially in relation to social structure with in flocks. Observations of copulation in Spurwinged Plovers demonstrate that there is apparently no utilisation of the wattles in "courtship displays" as suggested by Beck (1959).

The behaviour observed in Spurwinged Plovers during the course of this study appeared to be very similar to that described for the Lapwing (Rinkel, 1940; Spencer, 1953; Steifel, 1964) and an African Spurwinged Plover Vanellus (= Hoplopterus) Spinosus (von Helversen, 1963). However, further behavioural studies of other vanelline plovers are necessary before a large scale ethological comparison of the genus Vanellus can be made in the same detail as has been done in gull species of the family Laridae (Tinbergen, 1959; Moynihan, 1967).

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The Kingston Beach Golf Club Committee gave permission for use of its land during the study and the Department of Physics allowed me access to its sonograph for analysis of plover calls.

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APPENDIX I

TABLE 4

SPUR-WINGED & BANDED PLOVER SURVEY (WINTER 1968).

.....*

Would you please tick which ever answer seems appropriate.

1.	Does the .....* occur in your district‡ ?.....	(a) No (b) rarely (c) occasionally (d) frequently (e) constantly.
2.	(a) Have you seen flocks of ....* in your district this winter?	(a) No (b) Occasionally (c) Constantly.
	(b) Roughly how many birds are in the flocks?	1 - 10 10 - 20 20 - 50 50 - 100 more than 100
3.	Roughly how many birds are in your district now?.....	1 - 10 10 - 20 20 - 50 50 - 100 more than 100
4.	Can you indicate which habitat(s) the ....* mainly.... occupies in your district?	(a) margines of lakes (b) seashores (c) lightly timbered areas (d) dry paddocks (e) wet paddocks (f) cultivated land
5.	Is there any further information which you consider may be useful for this survey (e.g. local distribution, behaviour, abundance in surrounding areas, nesting sites, etc.,).	

‡ N.B. "district" - within a radius of five miles of your school

.....* Spurwing or Banded Plover inserted here.

FIG.21

OCCURRENCE of SPURWINGED PLOVER in TASMANIA

(1968)

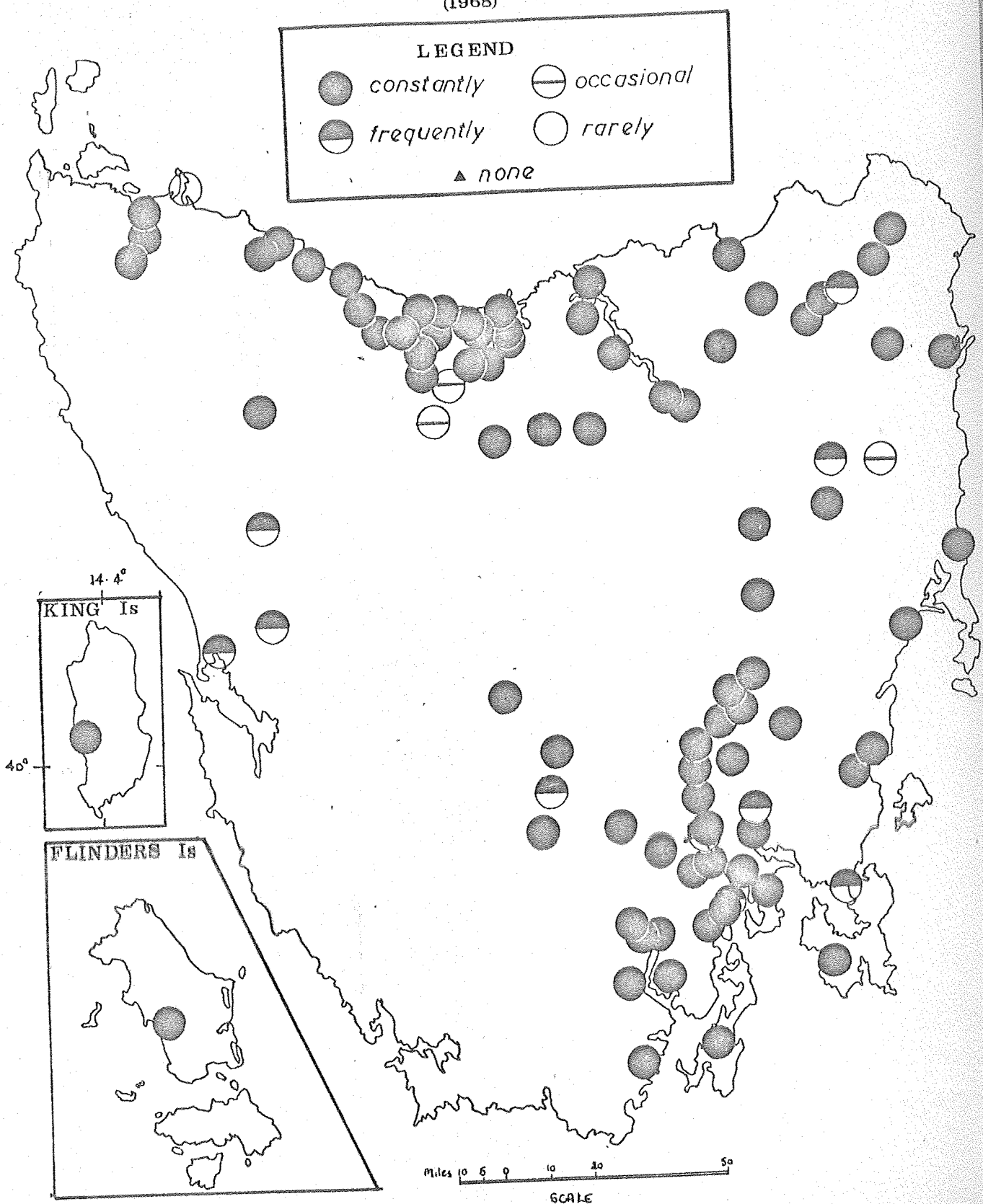
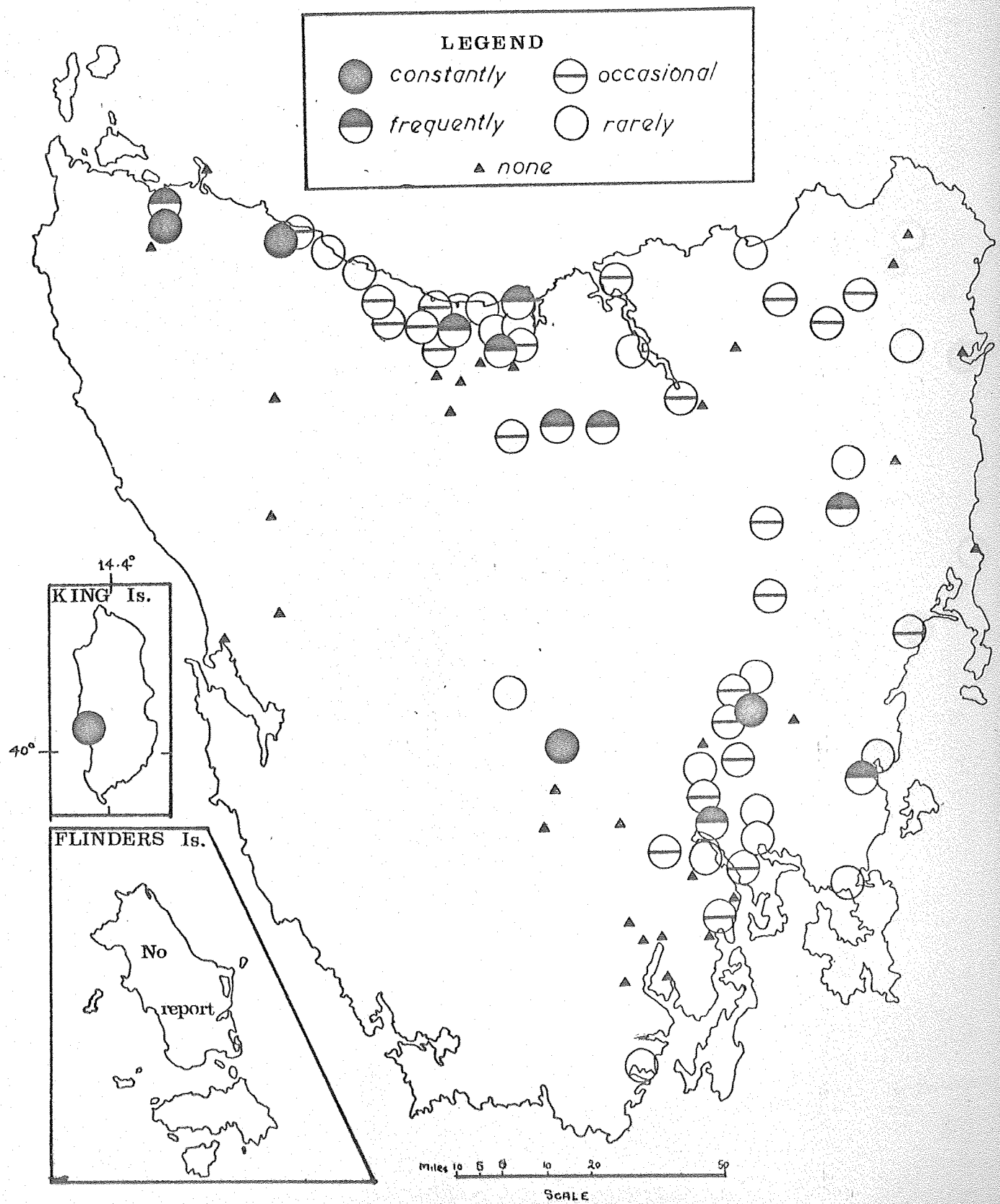


FIG.22

OCCURRENCE of BANDED PLOVER in TASMANIA



ABUNDANCE of SPURWINGED PLOVER in TASMANIA

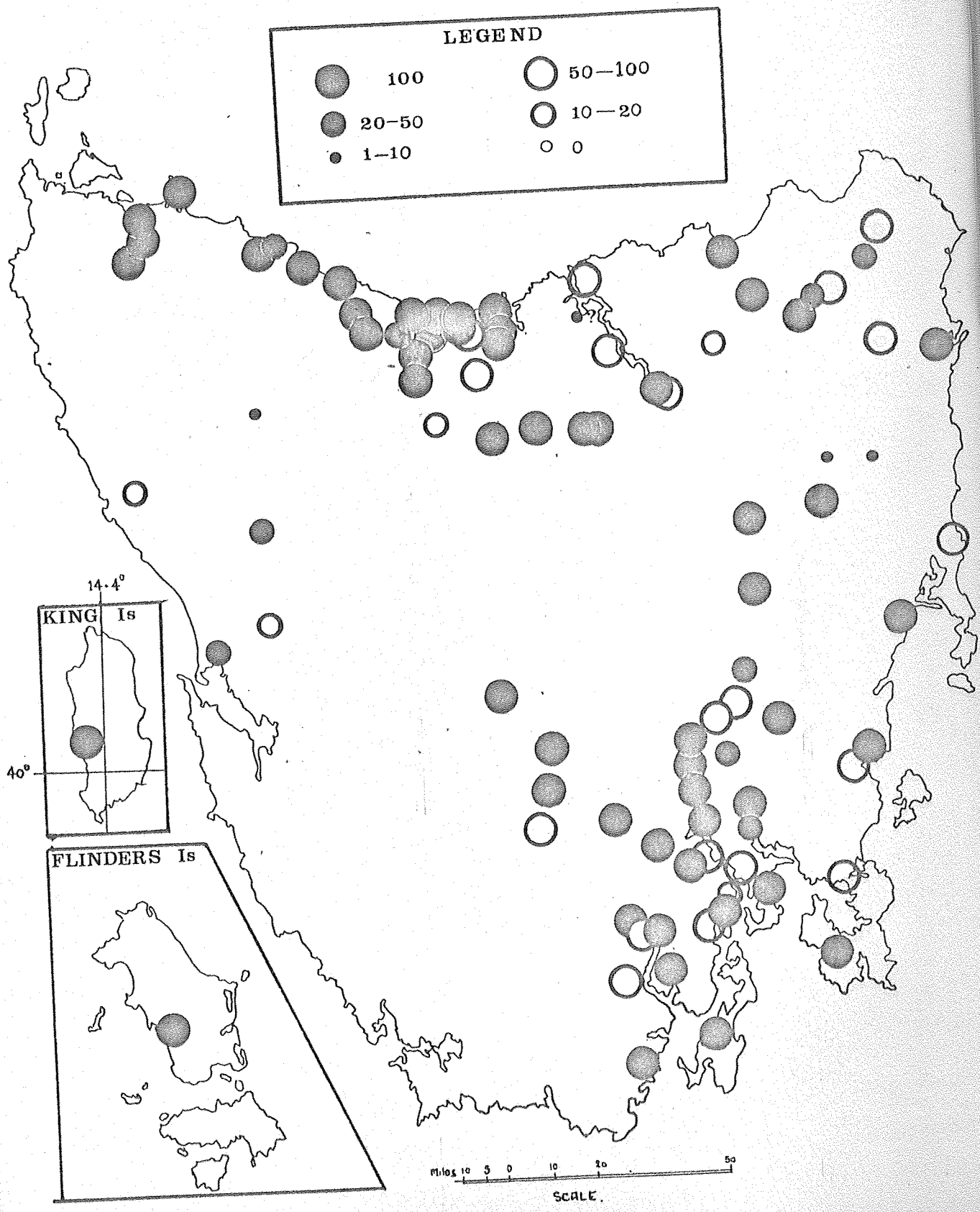
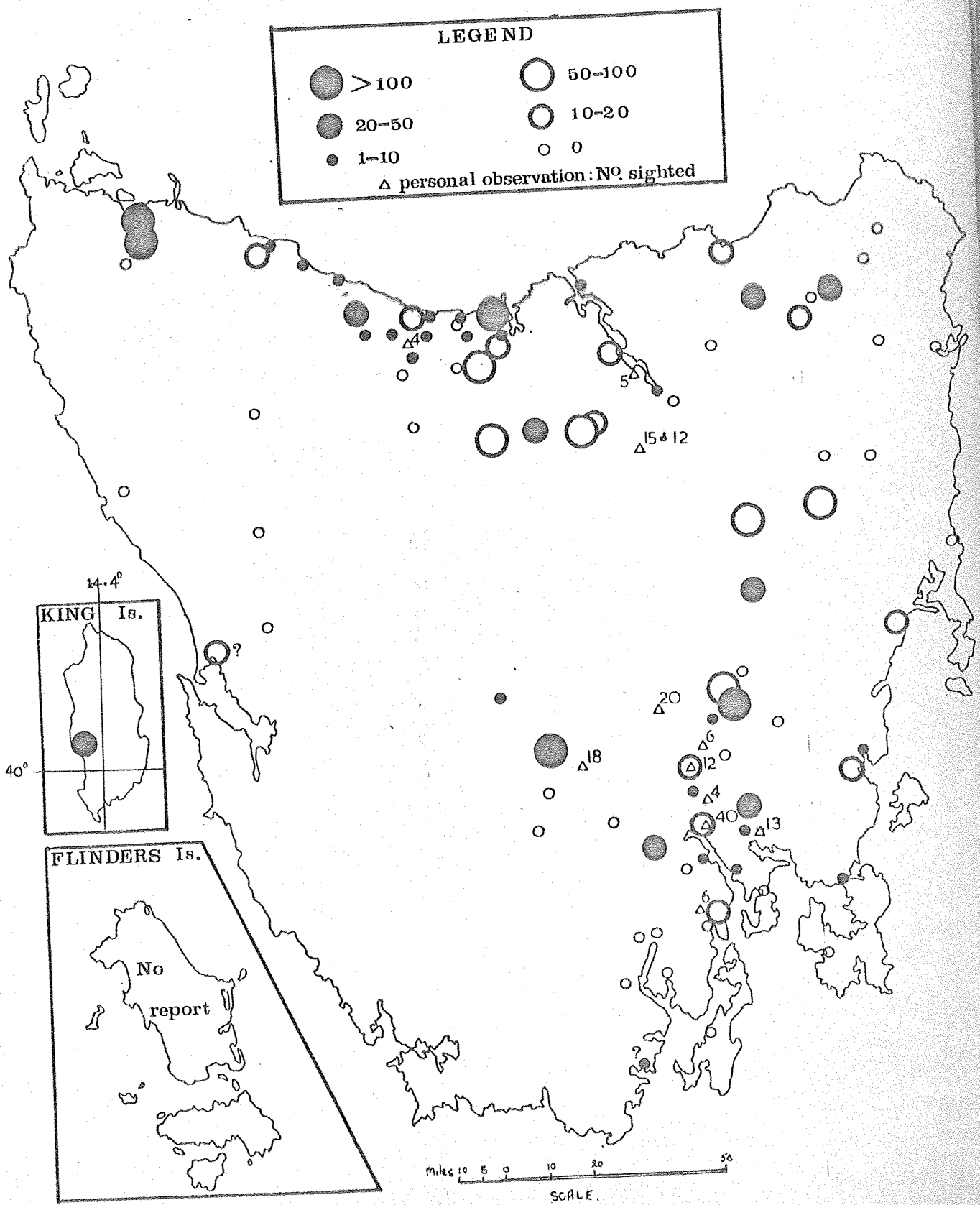


FIG. 24

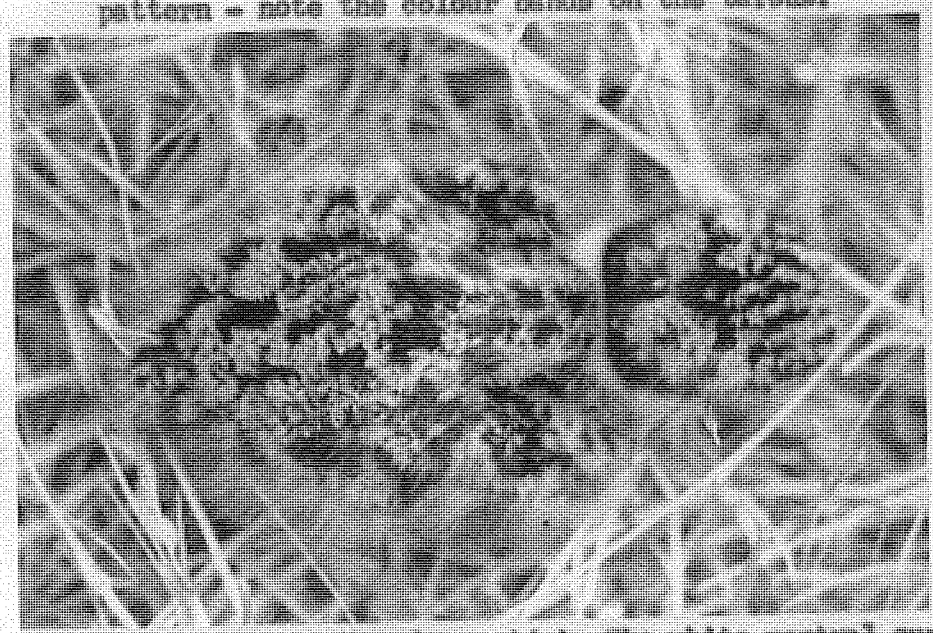
ABUNDANCE of BANDED PLOVER in TASMANIA



APPENDIX II

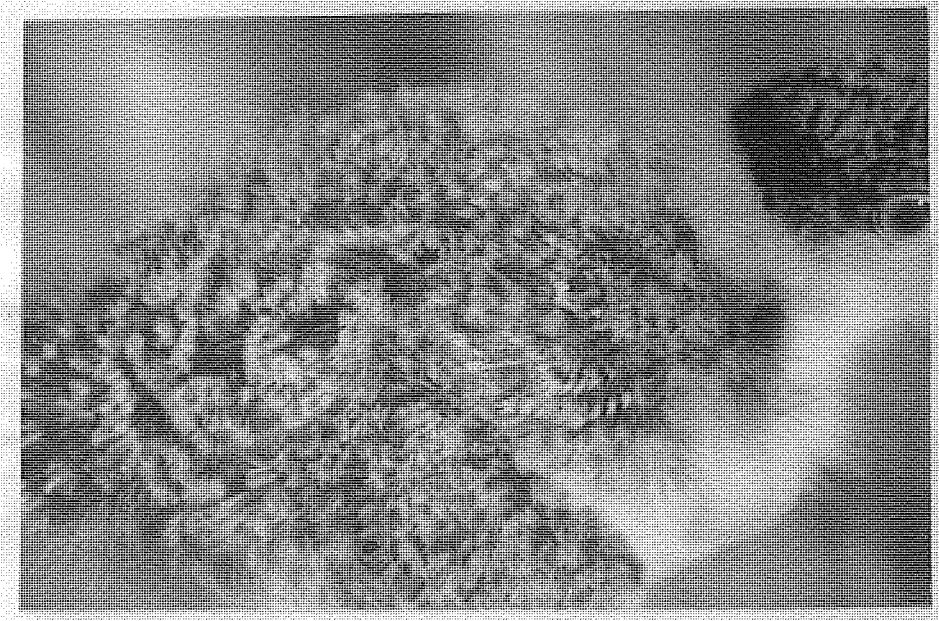
PLATE III

(a) Lateral view of a 48 hour-old Spurwinged Plover chick in a crouched posture. The white ventral down and the mottled dorsal down form a disruptive pattern - note the colour bands on the tarsus.

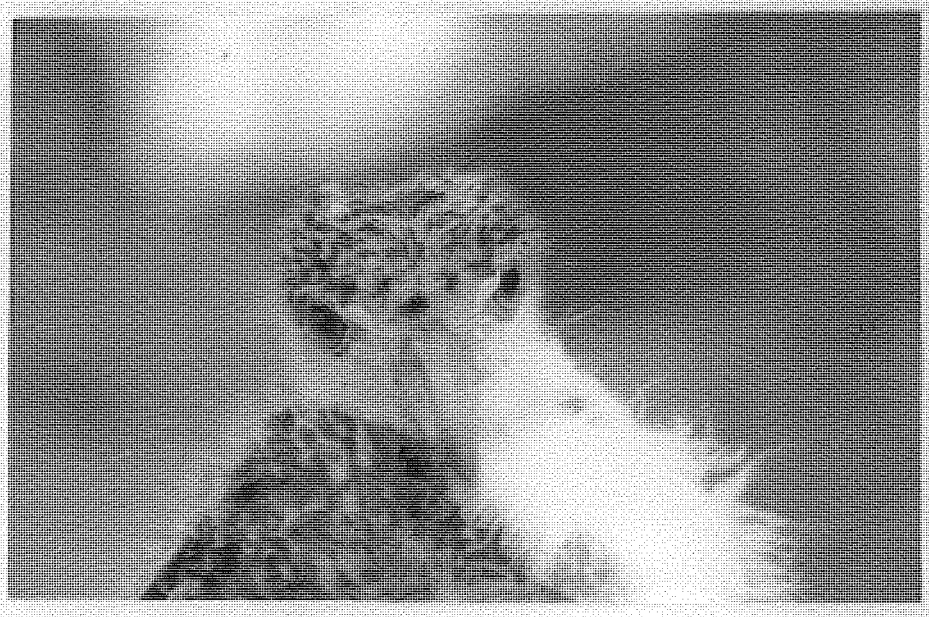


(b) Dorsal view of the above chick. The white ventral surface is not visible and the white neck collar is hidden by the retraction of the neck. The tarsi and bill are also hidden to maintain the disruptive pattern.

PLATE IV



(a) Two week-old chick showing the development of juvenile plumage in the upper dorsum region.



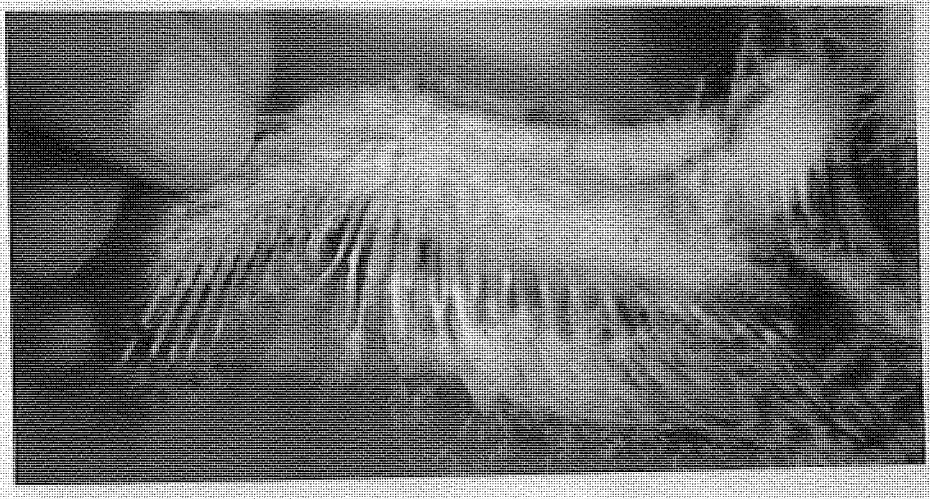
(b) An anterior view of the above chick showing the radial out-growth of juvenile plumage on the crown

PLATE V

These photographs indicate stages in the development of the primary and secondary wing feathers (rectrices) and their coverts, in fledgling Sparrowhawk Nisaetus.

(a) 23 hour-old chick :

(b) 2 week-old fledgling : - the primaries are in the quill stage.



(c) 4 - 5 week-old fledgling : - primaries have almost completely unfeathered.

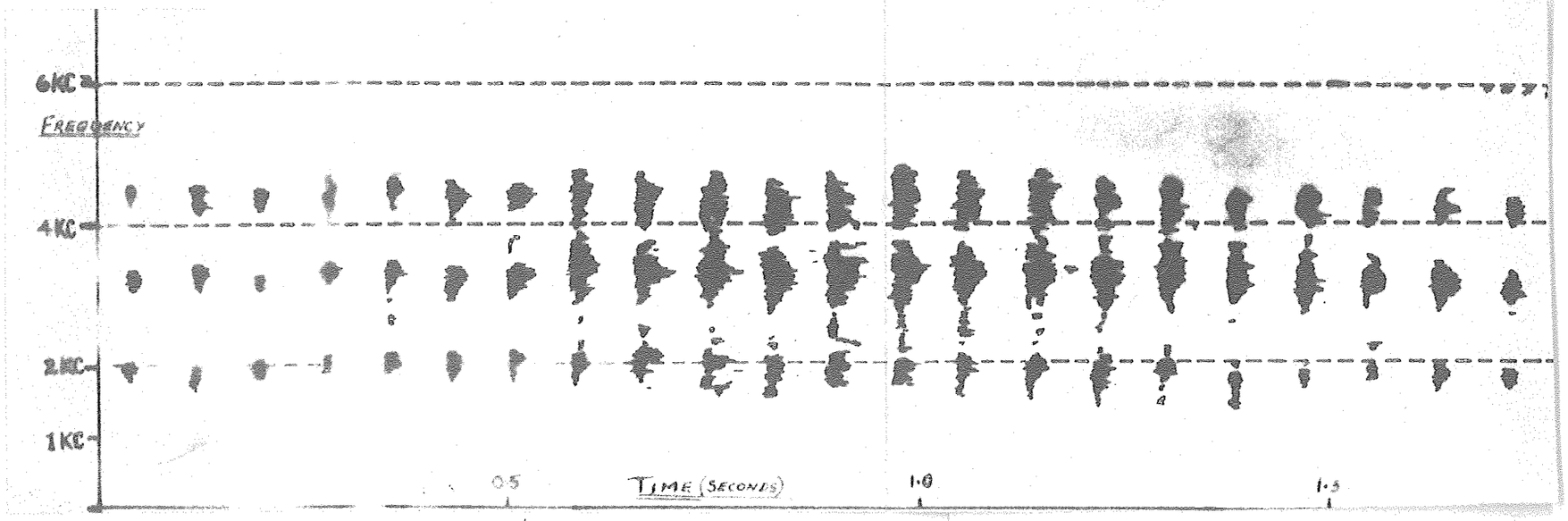
(a) 3 week-old fledgling : - dorsal view , showing juvenile plumage on the upper dorsal surface and the retention of nestling down o n the lower dorsum.

(b) 5 week-o ld fledgling : - the photograph shows the shape and size of the wing spur in juvenile birds.

FIG.25

(a) THE PRE-COPULATORY CALL

This call is uttered by the male during the pre-copulatory "run-up"



(b) THE O OUNO CHALLENGE CALL

This uttered by paired birds during choking and its preliminaries. This call is only given during aggressive choking.

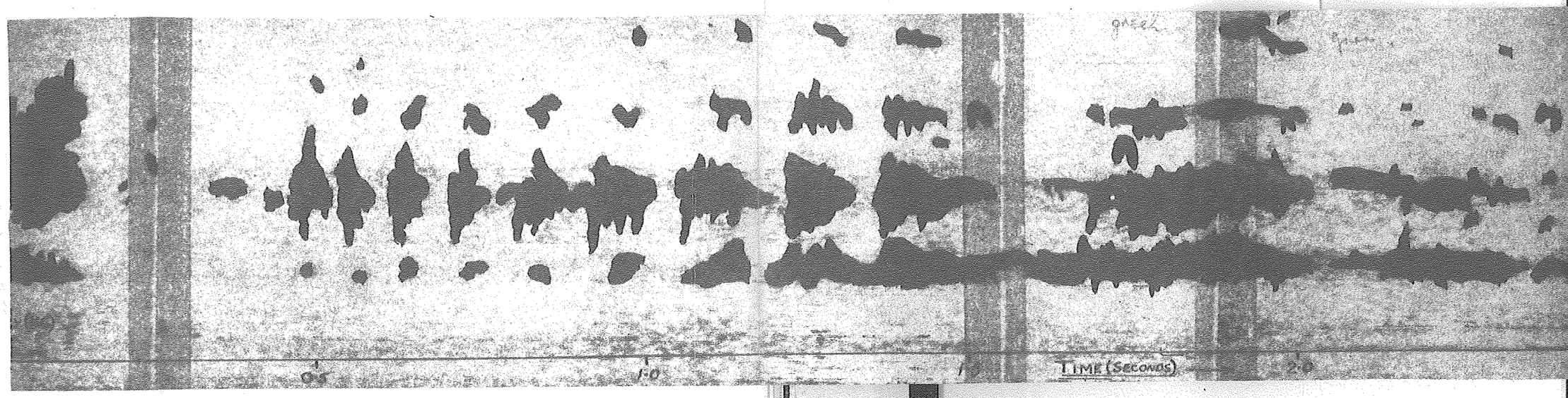
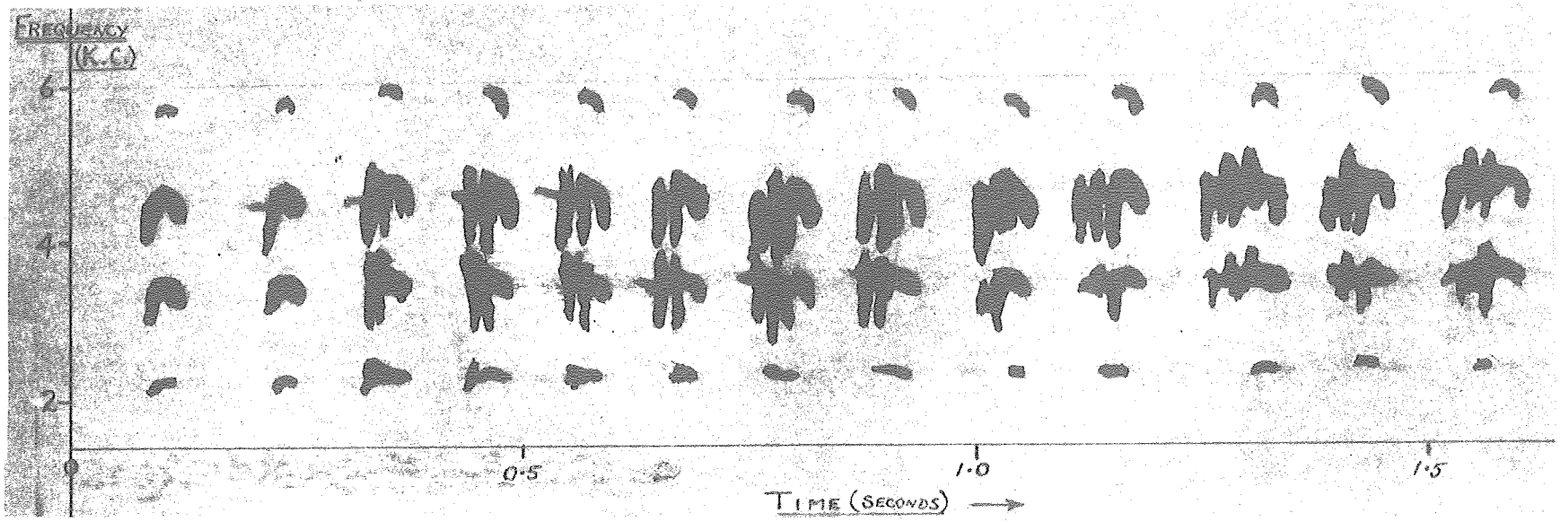


FIG.26

(a) THE ALARM CALL.

This call is given by alarmed plovers which have assumed the anxiety posture.



(b) THE TERRITORIAL CALL.

This is uttered by plovers during territorial intrusions and in other aggressive situations.