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ASPECTS OF THE BIOLOGY OF THE SPUR-WINGED PLOVER

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(*Vanellus miles novaehollandiae* STEPHENS 1819)

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A thesis presented in partial  
fulfilment of the requirements for the degree  
of Master of Science in Zoology  
at Massey University

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December 1981



PLATE 1: ADULT SPUR-WINGED PLOVER

## ABSTRACT

Spur-winged plovers in the coastal region of the Manawatu were studied from July 1979 until January 1981. Taxonomy and nomenclature are reviewed. Dispersal throughout New Zealand and the study area are mapped. The population of the species within New Zealand appears to be derived from a northern Australian population. Behaviour, both in the flocks and territories, was studied and compared with other vanelline plovers and with the Australian population of spur-winged plovers. A previously undescribed display flight was observed similar to the song flight of the lapwing (*Vanellus vanellus*); differences were ascribed to differences in the morphology and ecology of the two species. The population density in the study area is low and no contact fighting was observed. Breeding success was 34.5%, and the average number of chicks fledged by each successful pair was 1.6 in 1979, and 1.7 in 1980. The breeding season extended from June to January. Mean clutch size was 3.6, mode 4. Rapid evolution of egg size may have occurred; egg size was significantly smaller than in Southland ( $P < 0.001$ ). Territoriality, nesting, and flock behaviour were correlated with environmental factors, chiefly the level of the water table. Territories were significantly larger ( $P < 0.01$ ) than in Australia (4.3 Ha. vs 2.4 Ha.). Thirty eight chicks were captured and banded. In 1980 chick growth was recorded. Flock size, movement and behaviour were observed. Changes in behaviour from month to month and seasonally are discussed.

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\* Taken by Mr. Dennison

## CHAPTER 1

### INTRODUCTION

The Australian spur-winged plover (*Vanellus miles novaehollandiae*) was first reported in New Zealand in 1886, then in 1892 (Soper 1972), but it did not establish here until 1934, when five birds were observed near Invercargill (Barlow 1972). Subsequently the population increased rapidly, and spur-winged plovers are now found throughout the South Island and in many areas of the North Island.

Spur-winged plovers are monogamous, ground nesting birds. Most adults weigh between 350 and 400 grams. During the breeding season pairs establish large territories which are aggressively defended. Most territories are in pasture with some rough cover and a source of water. Clutch size is usually four, both parents incubate, and re-nesting after nest destruction is common. The chicks are nidifugous and take about seven weeks to fledge. Parents do not feed the young but brooding, especially at night, continues for two to three weeks after hatching. During the non-breeding season the birds congregate in flocks. Spur-winged plovers live for up to twelve years (Barlow 1978).

#### 1.1 Taxonomy

Plovers belong to the family Charadriidae, order Charadriiformes. Most Charadriiformes are small to medium size waders or shorebirds.

Prior to 1800 the species of plovers were placed in two large genera, *Charadrius* or *Vanellus*. In the next century many new genera were proposed, almost to the extent of having one genus for each species (Bock 1958).

Seebohm (1888) suggested that a monotypic generic

concept was impractical and proposed a conservative classification in which the plovers were placed in three genera *Charadrius*, *Vanellus* and *Lobivanellus*. Bock (1958) thought that the genera *Vanellus* and *Lobivanellus* were artificial, but considered Seebohm's classification more acceptable than the classification in use at the time of his own review.

Sharpe (1896) divided the plovers into many genera which Bock (1958) considered unnatural and not confirmed by the data.

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). Lowe based his classification primarily on degree of ossification of the skull and on dorsal colour. He proposed that those species with least ossified skulls and light dorsal colour arose from a primitive ancestor. They were the "Pre-Charadriinae", genera *Squatarola* and *Leucopoliis*. Species with more ossified skulls and dark dorsal colour arose from an advanced Charadriinae descendant, genera *Pluvialis* and *Charadrius*.

Bock (1958) showed that any classification based upon these features is artificial. Ossification increases until maturity, so skeletons must come from birds of known age. Salt content of the environment affects size of the nasal glands and hence the morphology of the roof of the skull. In general the greater the water salinity the larger the nasal glands and the less ossified the supraorbital rims and the lachrymal bones. Dorsal colour generally corresponds with soil colour and is of little use in generic classification.

Peters (1934) corrected some of Lowe's errors; mainly by shifting several misplaced genera from the Vanellinae to the Charadriinae; but generally he used

Lowe's conclusions, including most of Lowe's misinterpretations. Thus his two subfamilies (Charadriinae and Vanellinae) contain far too many genera.

Bock's (1958) generic review of the Charadriidae was based on osteology, external morphology and habitat. He studied museum specimens of skins and skeletons, re-evaluated Lowe's data, and studied many of the published papers on Charadriids to discover range and habitat. He could not use behaviour in his classification because of the lack of data on this aspect of the ecology of plovers. Bock decided that the presence or absence of wattles, wing spurs and hind toes were not correlated with generic differentiation. The series of skeletons he studied was not large enough to discover any useful osteological characters to differentiate genera. He found colour pattern useful in allying large groups of species.

Bock suggested that there are 56 species of Charadriid and places these in six genera:

Genus <i>Vanellus</i>	-	comprising	25	species
" <i>Charadrius</i>	-	"	24	species
" <i>Pluvialis</i>	-	"	4	species
" <i>Anarhynchus</i>	-	"	1	species
" <i>Eudromies</i>	-	"	2	species
" <i>Pluvianellus</i>	-	"	1	species

The vanelline plovers have a common wing and tail pattern; but wattles and spurs vary. Bock regards these as species specific recognition signals. Their habitat is generally inland in dry grasslands, marshes, or at stream and lake margins. Range is world-wide with the exception of North America. Bock places the centre of distribution in northern Africa, where the largest number of species are found.

Three vanelline plovers are found in Australia, the banded plover (*Vanellus tricolor*), the masked plover

(*Vanellus miles miles*), and the spur-winged plover (*Vanellus miles novaehollandiae*) Peters (1934) regarded the spur-winged plover and the masked plover as distinct species, *Lobibyx novaehollandiae* and *Lobibyx miles* respectively. Bock (1958) regarded them as conspecifics, as the only major differences are in the extent of the black crown and cape, wattle and body size. They are similar in all other features and were apparently allopatric. He considered that they must be regarded as distinct species if their range overlapped, and would constitute a super-species. In his review they were given the sub-specific status of *Vanellus miles novaehollandiae* and *Vanellus miles miles*.

Cooper (1966) observed an overlap in distribution of masked and spur-winged plovers in South Australia and south western New South Wales. He found no hybridization and used Peters' (1934) terminology which acknowledged specific status.

Van Tets et. al. (1967) observed that, where the ranges of spur-winged and masked plovers overlapped in Townsville, Queensland, plovers intermediate in the extent of black on neck and shoulders, and in the shape and size of wattles existed. Where the ranges overlapped in Western Australia mixed flocks were seen. The two types reacted to each other as conspecifics, and a few mixed pairs were seen. Van Tets et. al. (1967) considered that meeting of nesting ranges may have taken place after clearing of rain forest on the Queensland coast, and increased irrigation in central Australia. They concluded that Bock (1958) was correct in regarding the two types as sub-specific, and agreed with his grouping of the vanelline plovers into one genus.

Braithwaite and Van Tets (1975) noted that the spur-winged plovers in New Zealand resemble birds in the Queensland population. Dann (1977) supported their conclusions by comparing egg size at different latitudes, and showed that the New Zealand population produced eggs of comparable size to the Queensland population. These authors state their affirmation of Bock's nomenclature.

Van Tets (pers. comm. 1980) states that the plumage pattern of spur-winged plovers examined in the field, and in museum collections, matches that of birds from Mackay, Queensland, southwards, and has less black than birds from Canberra south to Tasmania. The type painting of *Vanellus miles novaehollandiae* at Sydney, New South Wales, is clearly of the northern type as in Queensland. The birds in New Zealand correspond to the northern population; therefore this is the name I use. There is no scientific name for the southern form.

## 1.2 Plumage and Morphology

### Size:

Dimensional statistics are summarized in table 1.1. As only one adult was captured during this study the results of Dann (in press) and Temple-Smith (1969) are also displayed. Temple-Smith's data demonstrate that there is no significant dimensional sexual dimorphism.

### Plumage:

The plumage of spur-winged plovers is similar in both sexes and shows no apparent seasonal variation. Adults have a light brown mantle and white breast. The crown is black extending back to form a nuchal crest which joins black bars on the sides of the breast. The tail is white with a broad subterminal black band and white or greyish tips to the outer feathers. The primaries and their coverts are black. The greater coverts have a narrow edging of white on the inner webs (Plate 2).

Juveniles differ from adults in that the crown is initially brown barred with black and the back also contains some black (Plate 3). The nuchal crest is poorly developed but the black breast markings are well defined. The back quickly becomes the adult colour, but juveniles can still be differentiated from adults for several weeks after fledging because of lighter cap colour.



PLATE 2: VENTRAL PLUMAGE (SIX WEEK CHICK) .



PLATE 3: DORSAL PLUMAGE (SIX WEEK CHICK) .



TABLE 1.1: SPUR-WINGED PLOVER MEASUREMENTS

SOURCE	TEMPLE-SMITH (1969)		DANN (in press)	THIS STUDY
	Male	Female		
Number of birds	20	8	28	1
	Mean S.D.	Mean S.D.	Mean S.D.	
Weight (gms)	390 + 30 -	360 + 39 -	378* + 44.5 -	420
Tarsal length (mm)	67.9 + 5.2 -	67.1+ 1.7 -	73.6 + 2.0 -	72
Culmen length (mm)			33.2 + 1.8 -	34
Wattle length (mm)	30.0 + 3.5 -	23.3+ 4.34 -		22.2
Spur length (mm)	16.2 + 2.4 -	13.1+ 3.4 -		13.6
Wing length (cm)	24.3 + 8.0 -	23.8+ 7.0 -		
Tail length (mm)	101.5 + 3.6 -	95.5+ 5.0 -		

\* Number of birds = 10

### Leg Colouration:

Chicks legs are a dark slaty blue, but on maturity the legs turn dark crimson.

### The Wing Spur:

The spur situated at the proximal end of the metacarpel has been investigated by Temple-Smith (1969). The tip is deciduous, probably being shed each year at the same time as wing moult, as in *Vanellus armatus* (Rand 1954). The spur has a bony core attached to the metacarpel and a bright yellow germinative layer which produces a transparent horny keratinous layer. Only the keratinous tips are shed.

Spurs are exposed by flexing and lowering the carpels. Raising the head allows the yellow tips to be prominently displayed against the white flanks.

In chicks the spurs first appear about the third week, they are initially grey, but gradually turn yellow. In some chicks the spurs are pale yellow at fledging, in others they remain grey.

## 1.3 The Study Area

The study area selected forms the central part of a large coastal embayment extending from west of Wanganui southwards 130km to Paraparaumu Beach (Fig. 1.1). The majority of the study was conducted within the intensive study area, comprising the Tangimoana Lands and Survey Block (Fig. 1.2).

### Geological and Geomorphological History:

Structurally the area is part of the Wanganui Basin and has been affected by epeirogenic uplift since the mid-pleistocene. During late Quaternary time sediment has been delivered to the coast by rivers. Some sediment is of volcanic origin arising from the Egmont and Central Volcanic areas, but most consists of quartzo-feldspatic

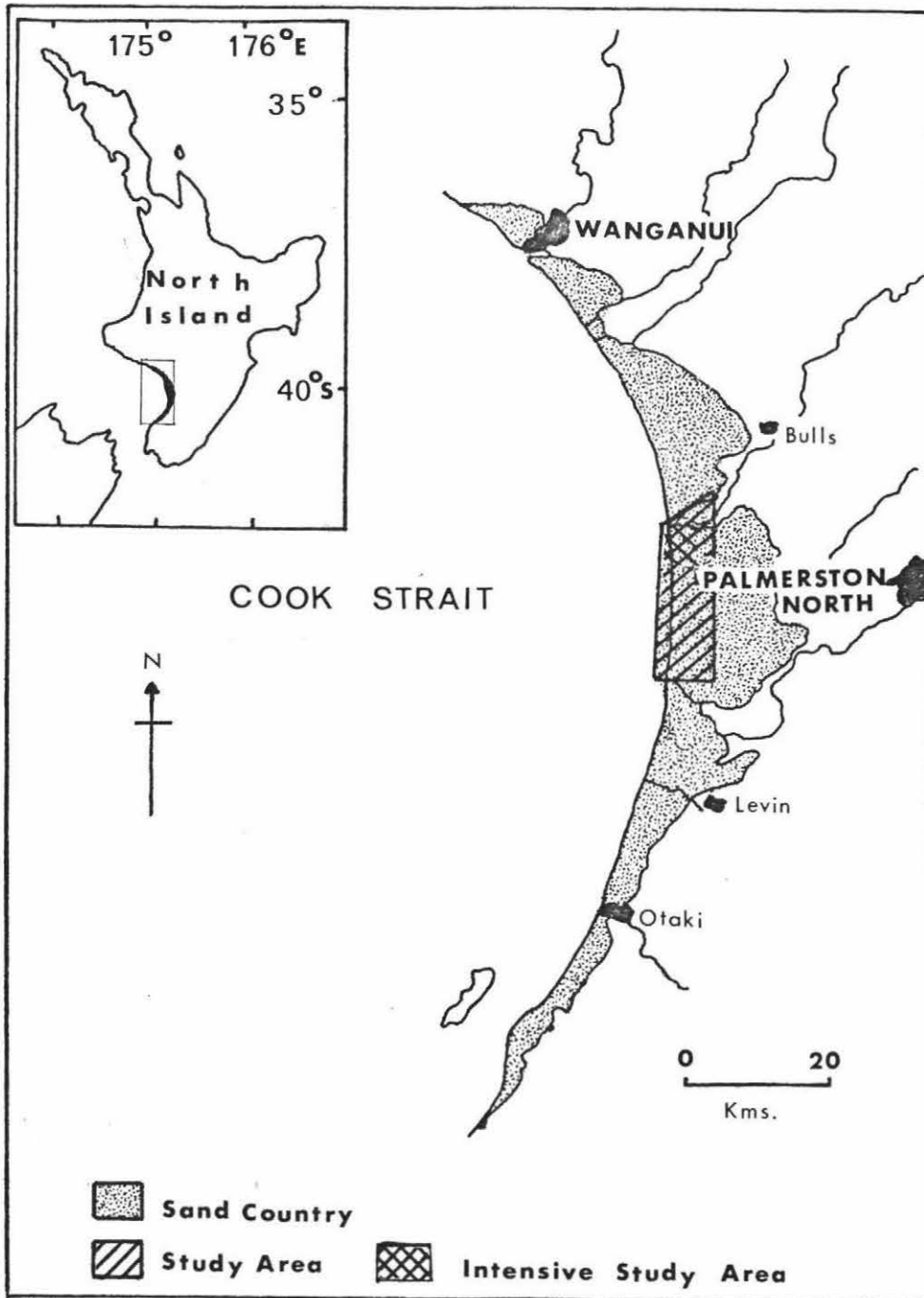


FIGURE:1.1 LOCATION: WEST WELLINGTON COAST.

Source: Gibbard 1972

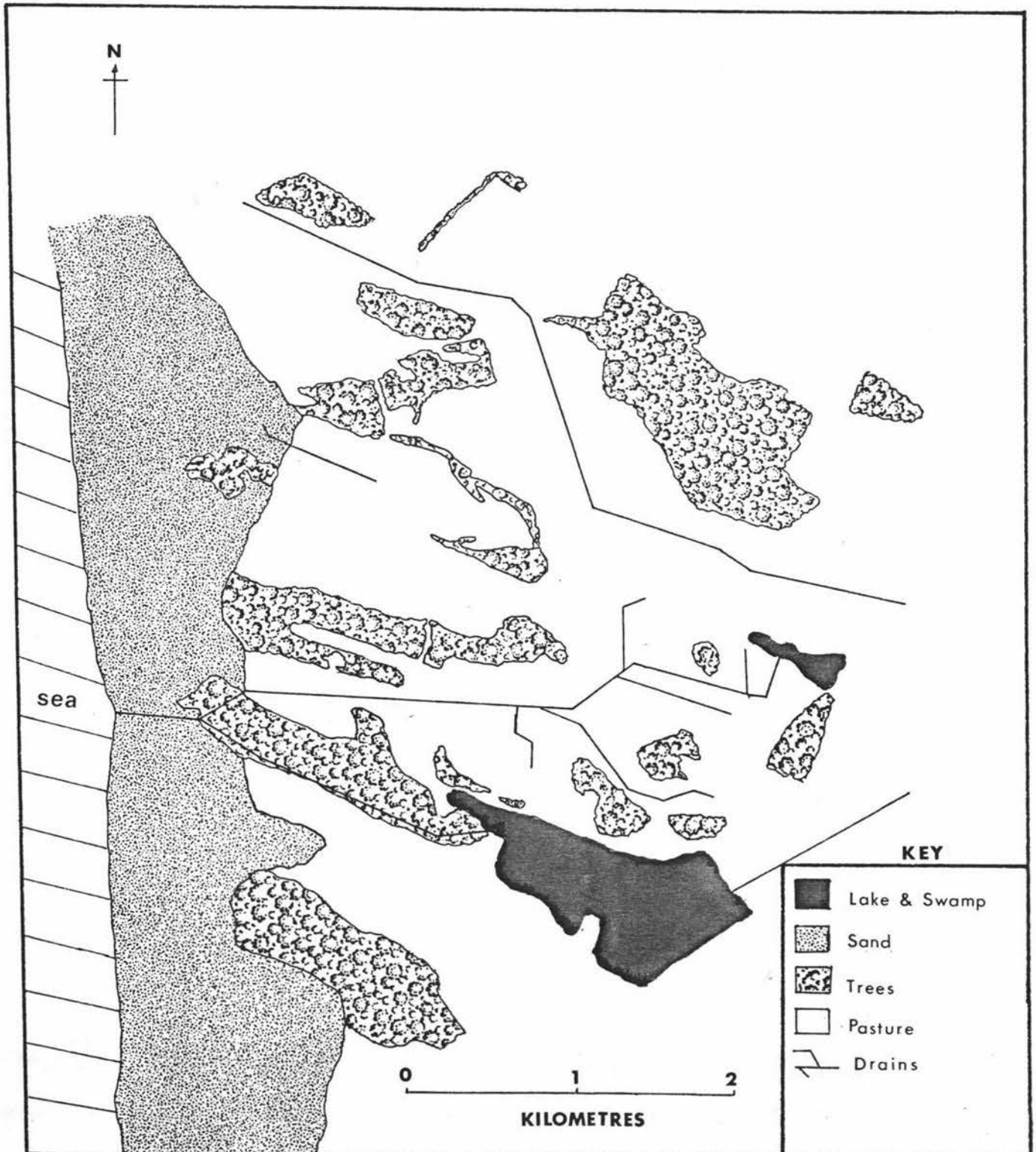


FIGURE:1.2 LOCATION: TANGIMOANA LANDS & SURVEY BLOCK .

material from the greywacke ranges to the east (Shepherd 1979).

The bulk of the coastal deposits consist of sand of uniform size. The Rangitikei River has also delivered some gravel to the coast, and a gravel bed lies within the Tangimoana Lands and Survey Block. The sand country extends from Paekakariki north for 192km. to Patea, with a maximum inland extension of 19km. at Rangiotu, and covers an approximate 312km<sup>2</sup> (Reaburn 1978) (Fig. 1.1).

Cowie (1963) distinguishes four dune building phases:

The Koputaroa Phase:- of limited extent and much older than succeeding phases (c. 10-20,000 yrs. B.P.).

The Foxton Phase:- 3.2 to 6.4 k.m. wide (c. 6,000 yrs. B.P., Hesp and Shepherd 1978).

The Motuiti Phase:- attributed to Maori destruction of vegetation on previously stable dunes (1,000-500 yrs. B.P.).

The Waitarere Phase:- occurs as a belt up to 3km. wide throughout the sand country, and as small patches where previously stable sand plains and dunes of the Motuiti Phase have been wind eroded. This phase has been attributed partly to accelerated erosion inland, causing increased accumulation of sand along the beaches, and partly to over-grazing and burning of the original vegetation on previously stable dunes. There are still some mobile dunes along the coastline, most have been stabilised by an afforestation programme, as well as marram (*Ammophila arenaria*) and lupin (*Lupinus arboreus*) planting.

#### Soils:

Soils were examined in detail by Cowie et. al (1967) who described them as characterised by a thin topsoil and subsoil on a base of sand.

### Topography:

The sand country slopes gently inland from sea level to a maximum height of 50m. Longitudinal dunes have encroached inland in a west-northwest direction, between the dunes are sand plains caused by deflation to the level of the water table. The boundary of the Waitarere and Motuiti dune phases is characterized by a series of lakes, formed because of restriction of runoff by encircling dunes (Fig. 1.3).

### Climate:

For the purpose of this study four seasons were recognised; Summer (December, January, February); Autumn (March, April, May); Winter (June, July, August), and Spring (September, October, November). Meteorological data were obtained from the Ohakea station 16km. northeast of the study area, and the Wildlife Service Station at Pukepuke Lagoon within the intensive study area.

Winds on the west coast are predominantly from the west-northwest. Average wind speeds in the Manawatu are 9 - 10 knots, with gale force winds commonly occurring in Spring and Summer. Shepherd (1979) considers the wind pattern to have been similar for the last 1,500 years, this conclusion is based on dune orientation and position.

Temperatures oscillated between a low in Winter and a high in Summer (Fig. 1.4). Mean monthly temperature ranged from 5.8°C. in July, 1979 to 17.7°C. in January, 1980. Forty two days of ground frost were recorded during the study (Fig. 1.4).

Rainfall over the study period appears to have been unusually distributed. Cowie (1967) using the thirty year averages (1931-61) states:

"There is a well defined increase in rainfall from March the driest month to June the wettest month, followed by a decrease to September a marked increase in October and a decrease over the summer months."

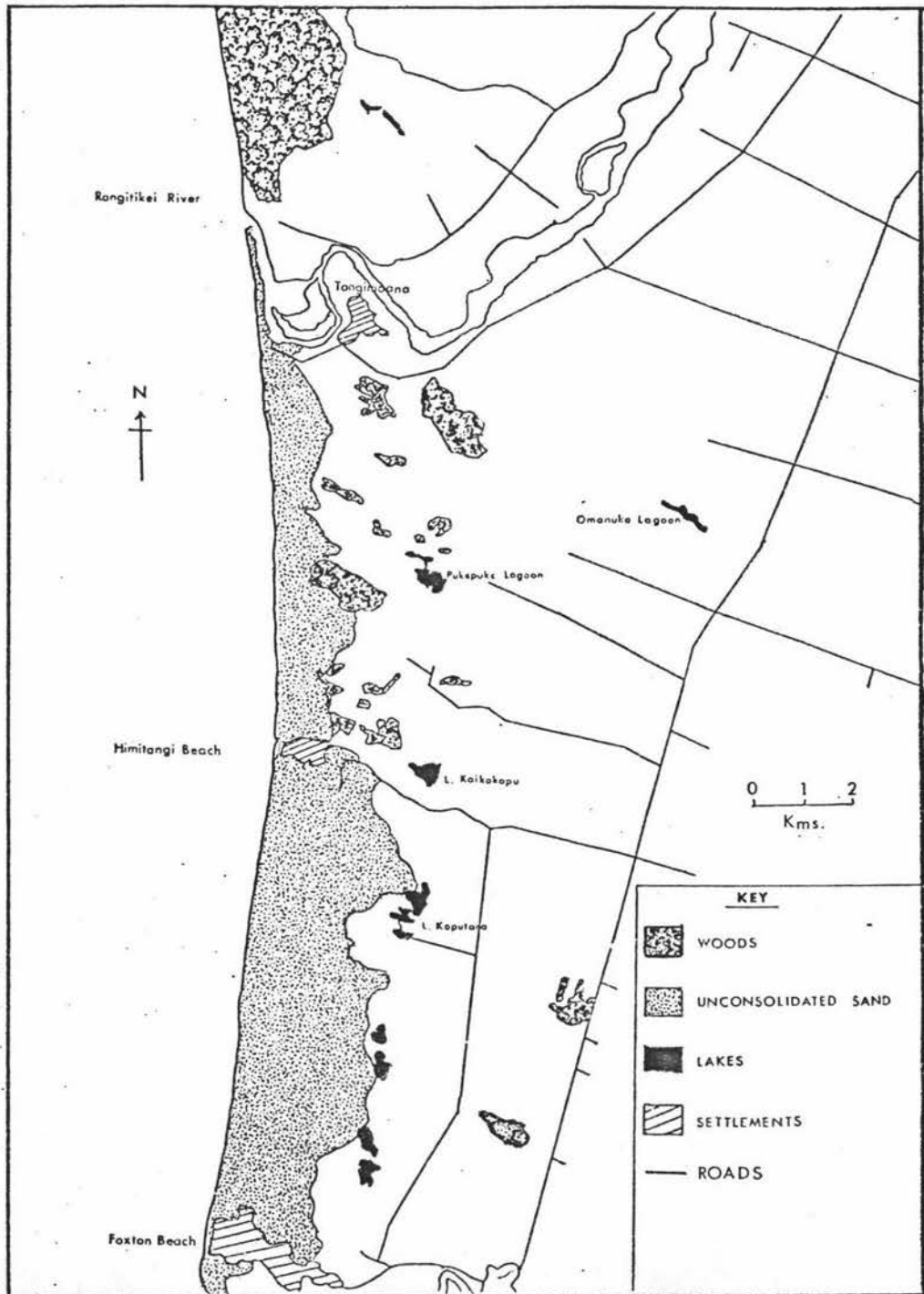
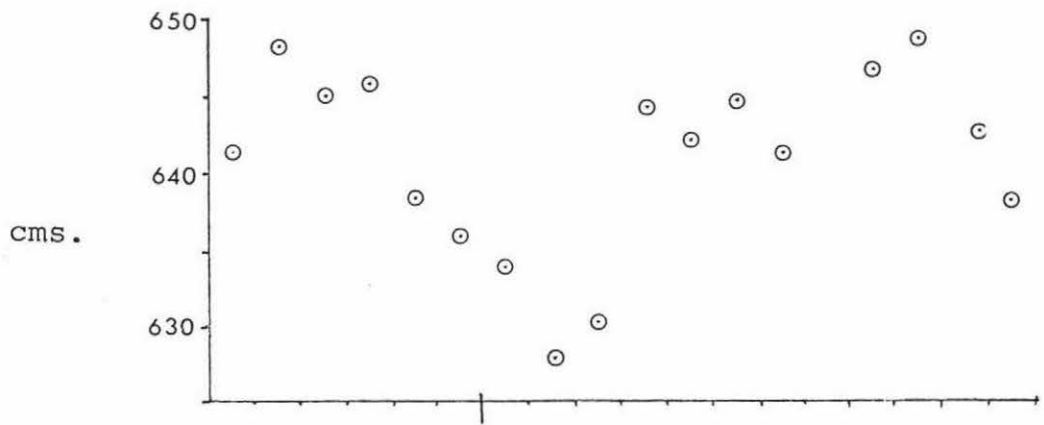
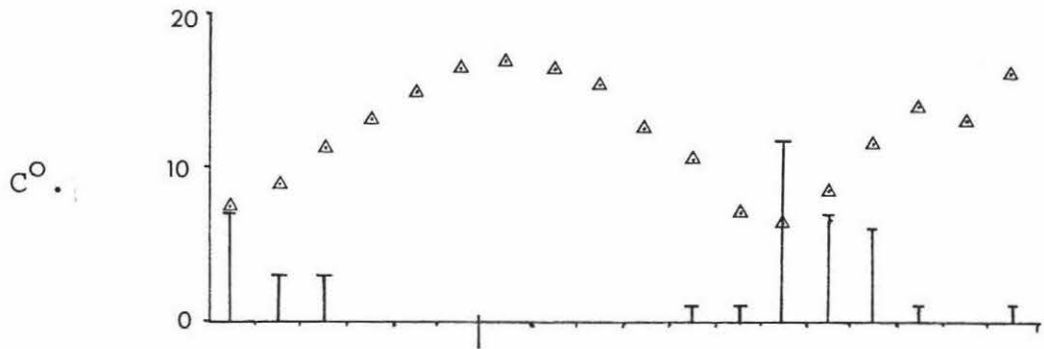


FIGURE:1.3 LOCATION: COASTAL MANAWATU



Mean monthly water table (height above sea level)



Mean monthly temperature and number of days ground frost

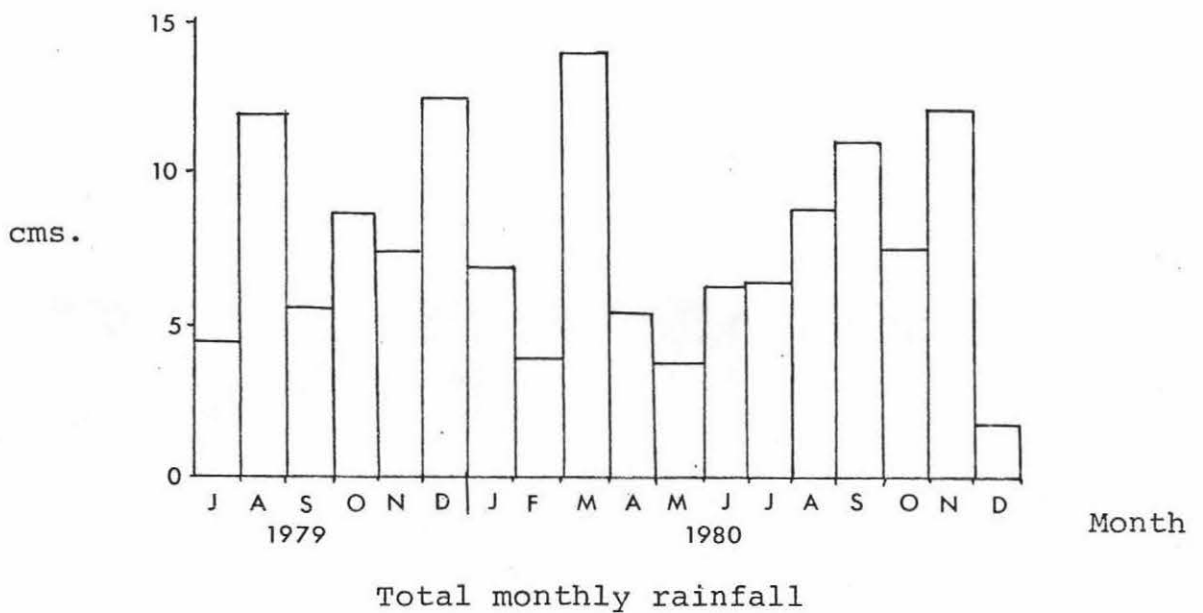


FIGURE 1.4: ENVIRONMENTAL DATA



For 1979 and 1980 no such recurring pattern was evident (Fig. 1.4). The water table in the study area was high in Winter and Spring and areas of ephemeral water were present within most pastures in the intensive study area during these seasons.

#### Vegetation:

Successional stages on dune ridges have been described by Carnahan (1957), and Esler (1964, 1978) has described the pre-European and European vegetation of the Manawatu. Most native vegetation has been replaced by introduced plant species. The hardy sand binding, salt resistant spinifex (*Spinifex hirsutus*) and pingao (*Desmoechoenus spiralis*) are still present on the foredunes along with the introduced marram (*Ammophila arenaria*). These species occur on dunes throughout the Waitarere dune phase. Also on these dunes are shrubs such as tauhinu (*Cassina leptophylla*), sand coprosma (*Coprosma acerosa*), pimelea (*Pimlea arenaria*) and tree lupin (*Lupinus arboreus*). Large stands of radiata pines (*Pinus radiata*) have been planted to stabilize some dune complexes. A few small stands of maritime pine (*Pinus pinaster*) and macrocarpa (*Cupressus macrocarpa*) still exist but are being logged and replaced by radiata pines.

Sand gunnera (*Gunnera arenaria*) is the pioneer plant of the dune hollows and is succeeded by red rush (*Leptocarpus simplex*) which is later replaced by toetoe (*Cortaderia toetoe*) and flax (*Phorium tenax*). Further inland farm pastures begin, although stiff club rush (*Juncus articulatus*) is still a dominant plant in wetter areas, few other native species are found outside swampy areas around lakes. Pasture plant species include ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*), and subterranean white clover (*Trifolium repens*), with crested dogtail (*Cynosurus cristatus*) on sand plains. Wetter areas include the species timothy (*Phleum pratense*), white, red and strawberry clover; (*Trifolium repens*, *T. pratense*, *T. fragiferum*) respectively.

In the past some dune forest and semi-swamp forest existed in the Foxton dune phase complexes. The dominant trees were mahoe, titoki, *Dodonaea* and ngaio, with tawa prominent in parts. There may also have been some totara (Esler 1978). Very little (approximately 4%) is left of these forests, remaining examples are Whites Bush and Himatangi Bush.

Semi-swamp forest was found in some areas of the Motuiti dune phase especially around Pukepuke Lagoon and at Round Bush. Dominant trees were kahikatea (*Podocarpus dacrydoides*), pukatea (*Laurelia novae-zelandiae*), and tawa (*Bielschmieda tawa*). Some forest occurred on the better drained sand plains and it is unlikely that kahikatea and pukatea were very prominent (Esler 1978).

Most of the swamps have been drained and turned into pasture. In undrained swamps raupo (*Typha orientalis*), flax (*Phoridium tenax*), and cabbage trees (*Cordyline australis*) are dominant. Raupo has spread very rapidly in recent years, efforts are being made to reduce its spread at Pukepuke by spraying with herbicide. Isolated cabbage trees still exist in wetter pastures.

Manuka (*Leptospermum scoparium*) and bracken fern (*Pteridium aquilinum*) are common on dunes of the Motuiti phase.

#### Fauna:

The interactions of spur-winged plovers with other animals in the study area are considered in chapter 2.

#### Land Use and History:

The coastal dune complexes were useful areas for initial European settlement. Early land use was limited to cattle grazing. The cattle removed much of the vegetation, especially the palatable spinifex on the fore-dunes. Burning to open up the country for mustering was probably even more damaging.

Wind erosion due to overgrazing was soon evident. Destructive activities were maintained and by 1900 sand dunes had encroached into large areas of farmland. In 1911 Doctor L. Cockayne was hired to solve the problem. He recommended a stabilisation programme involving fore-dune rebuilding, marram planting, and the planting of tree belts sufficiently large to protect inland farms. The programme was initiated in the Tangimoana area.

Since the 1950s sand country management policy has been concerned with the reclamation of as much land as possible for farming. Sufficient areas of productive forestry are being left to provide shelter and form the basis for a self supporting industry.

The pilot area at Tangimoana is now the Tangimoana Lands and Survey Block. The sand plains are used for mixed sheep and cattle grazing, at relatively low density to prevent wind erosion. Many dunes have been stabilised by pine planting. A narrow band of loose sand near the coast is at present being stabilised by marram, spinifex, and forest planting.

#### 1.4 Dispersion and Distribution

Before European settlement of Australia and New Zealand spur-winged plovers were confined to Tasmania and south-east Australia. Their native habitat was grass and shingle areas near rivers, lakes and estuaries (Thomas 1969). The conversion of forest, brush, and shrub to pasture; as well as the draining of swamps and the irrigation of dry land; enlarged their available habitat enabling the species to spread as far north as Townsville, Queensland and west into South Western Australia (Thomas 1969).

Barlow (1972) mapped the spread of spur-winged plovers in New Zealand up to 1970 (Fig. 1.5). Distribution has been updated by use of the Classified Summarised Notes from *Notornis* (Fig. 1.6). Distribution within the study area was surveyed in 1979 and 1980 and an assessment of the breeding area in 1975 based on interviews with local

farmers (Fig. 1.7).

The rapid spread of the species indicates that they either utilise a previously unused food resource or are outcompeting another species. Sharland (1943) observed that in Tasmania, where the spur-winged plover population had increased markedly, magpie (*Gymnorhina tibicen*) numbers had decreased so that:

".....where big flocks of plovers are seen, the magpie has practically disappeared."

But this decrease may have been due to introduced starlings. The behavioural interactions of spur-winged plovers and magpies observed in this study did not indicate the presence of interspecific competition. Spur-winged plovers feed on a wide variety of invertebrates (Temple-Smith 1969, Dann in press) and so are able to inhabit a diverse habitat and feed opportunistically on what is available.

Barlow (1972) distinguished two types of dispersal. Young birds may establish breeding territories at the periphery of an established breeding area, or migrate to a totally new area which may be many kilometres from the natal area. Young birds also take up territories left vacant by the death or movement of older birds, thus population density is maintained.

At the present rate of dispersal spur-winged plovers will be common throughout pasture in New Zealand in 10 to 20 years.

### 1.5 Methodology

The study period extended from July, 1979 until January, 1980. From November, 1979 an average of three days a week were spent in the field.

One day each week was used to observe flock behaviour and compile time budgets of major activities. Time

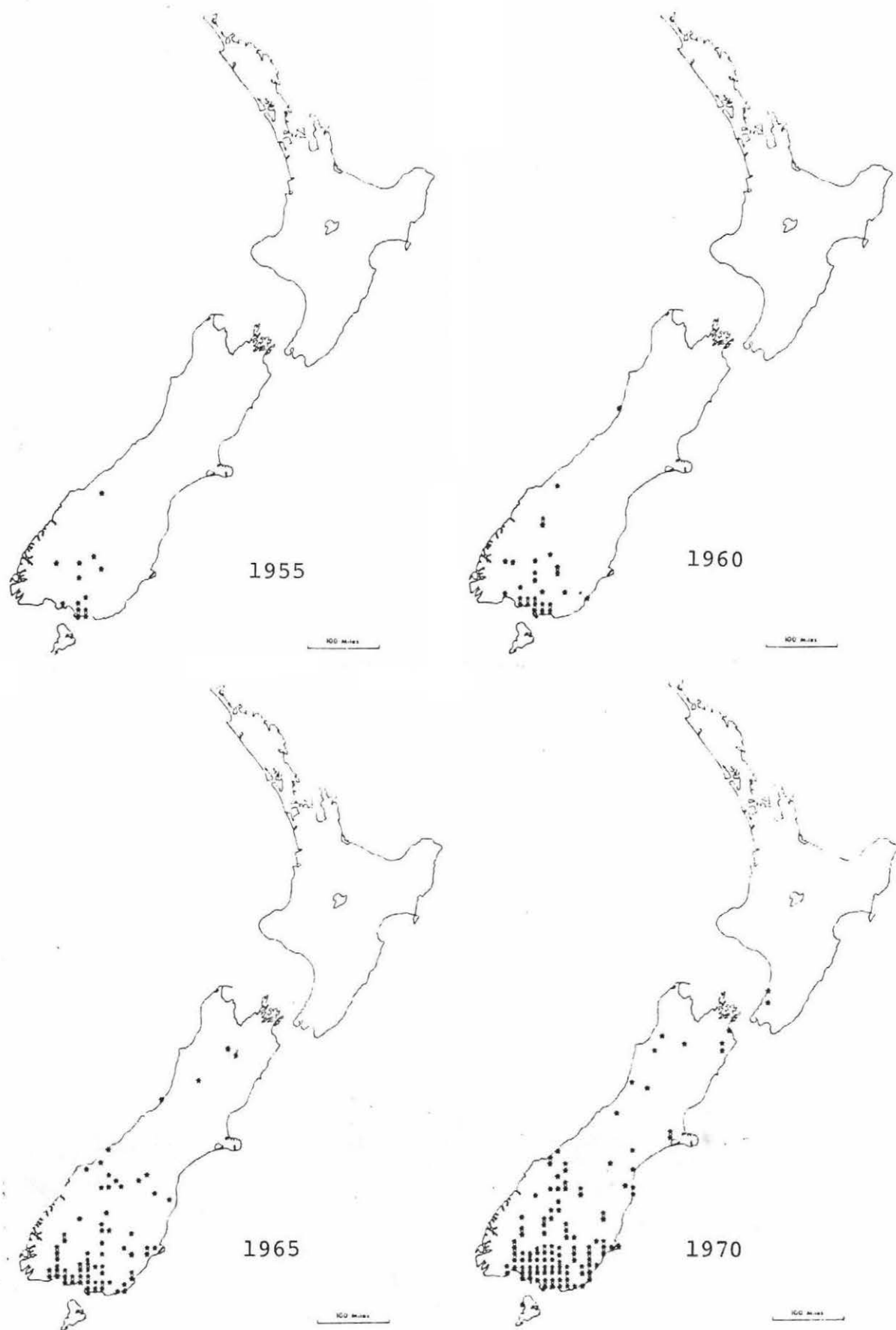


FIGURE 1.5: DISTRIBUTION OF THE SPUR-WINGED PLOVER WITHIN NEW ZEALAND; 1955-1970.

Source : Barlow 1972

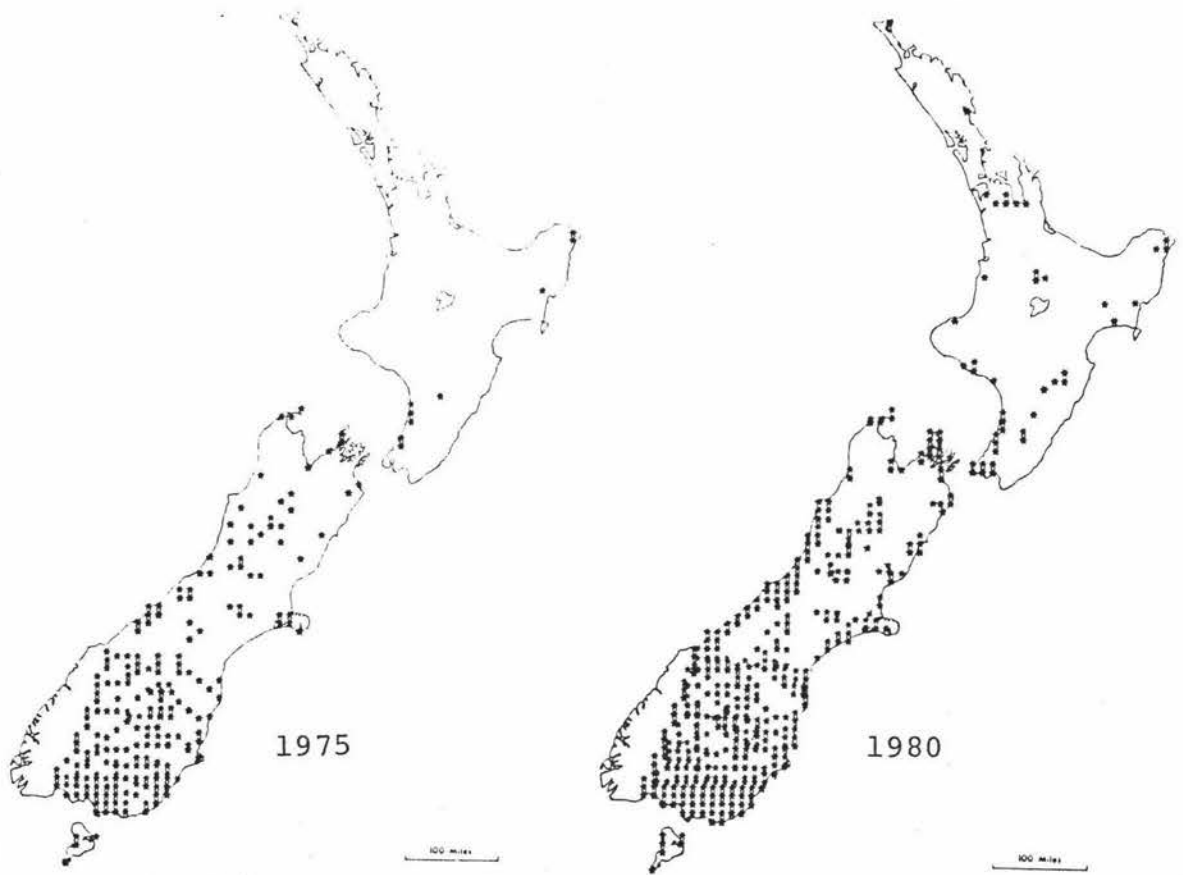
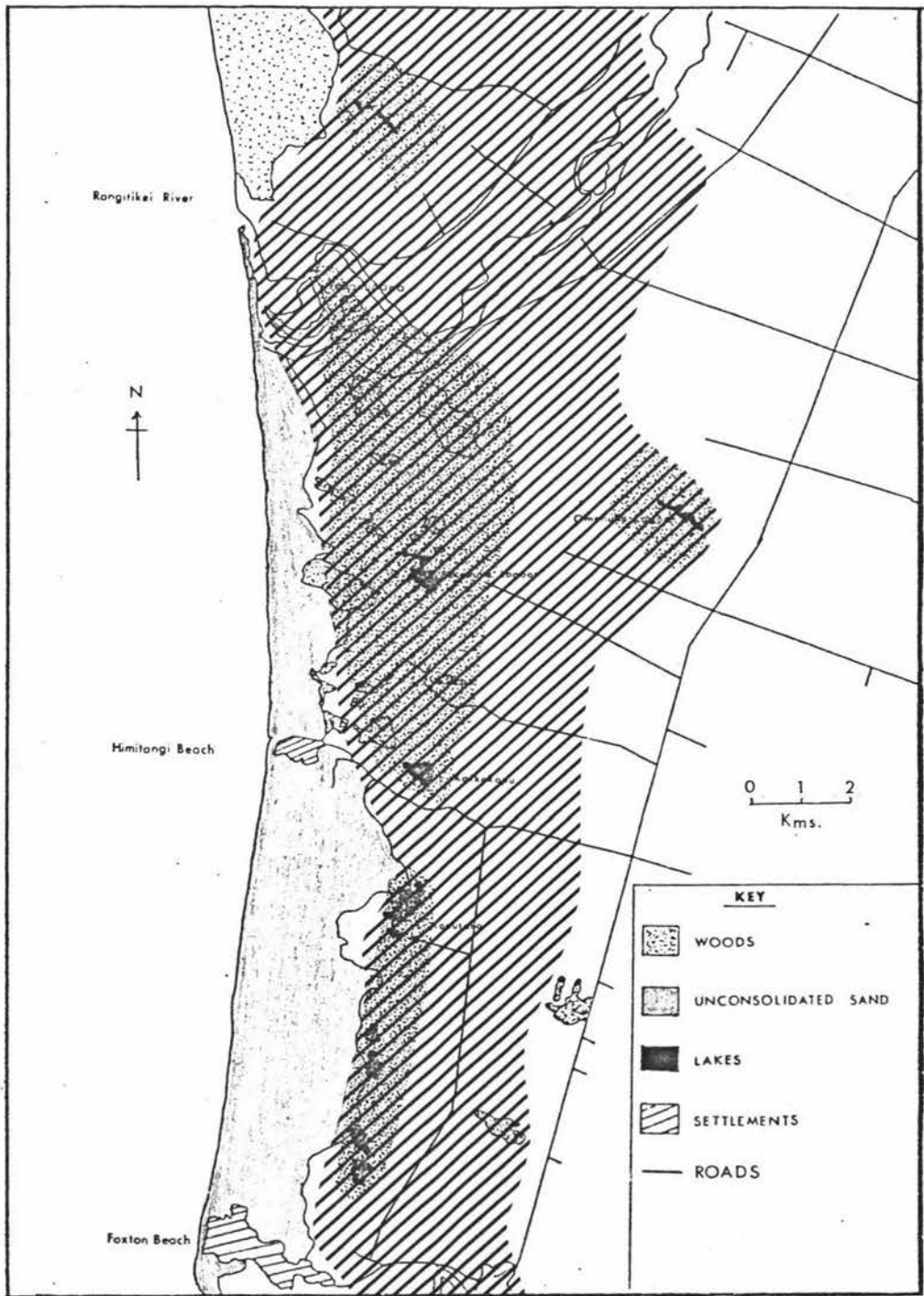


FIGURE 1.6: DISTRIBUTION OF THE SPUR-WINGED PLOVER  
WITHIN NEW ZEALAND; 1975-1980



Distribution in 1975



Distribution in 1980



FIGURE 1.7: DISPERSAL OF THE SPUR-WINGED PLOVER WITHIN THE STUDY AREA; 1975-1980

budgets were compiled by scan sampling (Altmann 1974) at ten minute intervals. The birds were studied from a car at a distance of approximately 100m. using 16 x 50mm. binoculars.

The other days in the field were used to study territorial behaviour, collect breeding data and survey distribution.

#### Trapping:

Various methods of trapping adult birds were attempted. Mist netting and the use of bait were unsuccessful. Cannon netting was not used because of the risk of injury to the birds. A drop trap over the next succeeded in capturing one adult. This method may have curtailed breeding success and was terminated. Chicks were captured by hand.

#### Morphometric Measurements:

Birds were weighed in a 1.5gm. net bag using 100, 200 and 500gm. spring balances. Vernier calipers accurate to 0.02mm. were used to measure exposed culmen, tarsus, wattle length, and spur length. Exposed culmen and tarsus were measured as recommended by Gurr (1947). Wattles were measured from the most antero-dorsal part of the upper lobe to the most ventral part of the lower lobe (Temple-Smith 1969). Spurs were measured from the junction at the metacarpel to the tip.

#### Banding:

From November, 1979 chicks were colour banded after reaching the age of two weeks. The E bands used were not retained by younger chicks.

#### 1.6 Objectives of Study:

1. A comparative study of the breeding biology of an expanding population with equilibrium populations. All other researchers have investigated populations at equilibrium with the environment the population in the Manawatu is rapidly increasing.



2. Description of the behaviour of spur-winged plovers and comparison with the behaviour of other species in the genus *Vanellus*

3. Study of flock behaviour, size and movement over the course of a year.

## CHAPTER 2

BEHAVIOUR2.1 Introduction

The comparative approach developed by Lorenz (1941, 1950, 1953) and Tinbergen (1959) still plays a fundamental role in research on social behaviour. Tinbergen (1963) distinguishes four kinds of questions asked about behaviour: causation, development, function, and evolution. Usually comparative studies use both functional and causal aspects simultaneously and this poses many difficulties (McKinney 1978). Many studies, for example those of Moynihan (1955a, 1958a + b, 1962) on gulls, attempt to interpret display repertoires in terms of tendencies to behave in different ways. McKinney (1978) points out two major difficulties in applying motivational concepts to behaviour. Firstly, they call for increasingly detailed and penetrating causal analysis yet remain untested until physiological experimentation takes place. Secondly, there is a temptation for behaviour, particularly in conflict situations, to be explained in terms of a presumed motivational state of the bird. Thus the concept of displacement behaviour, once widely used, is now recognised as indistinct, to be used cautiously (Hinde 1970). It may still be invoked where out-of-context behaviour is observed. Modern ethology concentrates on the functional approach, where emphasis is placed on displays as evolved mechanisms for signalling rather than as expression movements for drive states, and the possible benefits of apparently irrelevant activities are investigated.

In comparative studies the method of ecological correlation has become important in linking research on ecology with ethology. Crook's (1964) study of weaver birds is a model for this approach. He demonstrated that the social organization of ploceine weaver birds was correlated with diet and/or habitat. The analysis of social organization has been extended to include all bird species, by Crook (1965) and Lack (1968), showing that

similar selection pressures act over a wide taxonomic range.

Critiques of Wynne-Edwards' (1962) group selection theory by Crook (1964), Lack (1966), Wiens (1966), and others focused attention on the individual as the selective unit. Optimization theory (MacArthur and Pianka 1966, Emlen 1966) allows us to predict goals in behaviour more accurately. The basic rationale is that animals will, as a result of evolutionary selection pressures, maximise inclusive fitness. The most damaging criticism of optimization theories is that they are untestable. Maynard Smith (1978) states:

"There is a real danger that the search for functional explanations in biology will degenerate into a test of ingenuity."

However, he concludes that the concept of optimization is applicable to biological models.

In this chapter the displays of the spur-winged plover are described and compared with the displays of other species within the genus *Vanellus*. Unfortunately the lapwing (*Vanellus vanellus*) is the only vanelline plover on which a considerable behavioural literature exists, so a wide ranging comparative study is impractical.

Temple-Smith (1969) described many of the displays of spur-winged plovers. His terminology is derived from the studies of Tinbergen (1953, 1959) and Moynihan (1955a, 1962) on the Laridae, the family of gulls and terns, also in the order Charadriiformes. Many of the displays used by gulls are similar to those seen in spur-winged plovers, therefore this terminology is used where appropriate.

Temple-Smith (1969) studied a population at high density equilibrium. The differences in behaviour between this population and the recently established, rapidly expanding, Manawatu population are examined and discussed.

## 2.2 Pair Formation

Barlow et. al. (1972) observed that the pair bond was usually maintained until one of the partners died, although one case of "divorce" was recorded. Coulson (1966), working on the kittiwake (*Rissa tridactyla*), found that pairs that stay together generally show enhanced reproductive success as a result of their accumulated experience, but will break up and find new partners following a season of low reproductive success. Spur-winged plovers may follow a similar pattern.

Pair formation occurs in the flock, but it is difficult to observe because the birds are not sexually dimorphic. Most birds are already paired and are readily distinguished within the flock because partners stay close together when feeding and roosting. Courtship has not been described in this species, I identified two displays. These displays were only observed in May, suggesting that this is the period when most pair bonds are formed.

Most waders perform song flights during the breeding season. Male lapwings perform a song flight around the territorial boundaries, both spontaneously and after aggressive interactions. This advertises the territory and aggressively dissuades intruders (Dabelsteen 1978). Lind (1961) suggested that the song flight of waders has its origin in an aggressively dominated conflict behaviour, which after ritualization is still partly aggressively motivated.

In spur-winged plovers the display flight took place in circles around where the flock was feeding or roosting, many of the birds on the ground adopted an alert upright posture and several called. The displaying individual took off emitting the characteristic flocking call which continued throughout the flight. The bird flew rapidly in a semicircle around the flock less than three metres above the ground. It then ascended several metres and dived, revolving rapidly around the longitudinal axis,

ending the dive very close to the ground. Low erratic circling followed, with rapid changes in direction, more ascents and dives occurred. The whole display lasted approximately five minutes.

This display was only seen three times. On two occasions when the performing bird landed it chased another bird a short distance on the ground, then returned to its prospective mate and a choking ceremony occurred. On the other occasion the performer approached a pair and was chased off by one of the partners. It resumed the display and then approached the same pair but was chased off again.

The display flight I observed contained the alternating, ascent and dive components of the song flight of the lapwing (Dabelsteen 1978). Other components may be present but were not seen. It was probable that only male birds perform this display as in the lapwing.

Dabelsteen (1978) found that lapwings perform the song flight more often, and for longer periods, when males or predators were present than when only a female was present. He considered that the display originated mainly from ritualization of aggressive behaviour, and is aggressive in nature. The dive resembled an attack dive and alternating flight was similar to that found in a chase or aerial fight. In female situations the take off was accentuated and the "butterfly flight" was performed towards the female. The male then attempted to copulate with the female or perform a scrape ceremony (2.7). Thus the flight also contained sexual elements.

In spur-winged plovers the display flight is only observed in the context of courtship. The species probably mates for life, hence the rarity of this display and its simplicity when compared with the song flight of the lapwing. As in the lapwing, the flight is adapted to its signal function. It can be seen over large distances in open terrain and contains possibilities of transmitting several types of information simultaneously.

Another display which may be part of pair formation behaviour was similar to a display in the lapwing in which the male moved in circles around the female (Steifel 1964). In spur-winged plovers a display in which the pair circled each other emitting a guttural call, with the body horizontal was observed. On several occasions this occurred after the performance of the aggressive upright by one of the pair towards an intruder. The display was sometimes followed by choking. The display could be involved with pair bond maintenance.

Many interactions could not be fully interpreted as most of the birds in the flock were unmarked. Changes in relationships over time were difficult to assess and interpretations in terms of signal functions and conflicting motivation were necessarily vague. Otte (1974) showed that functions and effects of displays were likely to be confused when studying an unmarked population. Multiple functions may not be detected (Beer 1975), and the interests of males and females were unlikely to be assessed properly (McKinney 1978). Thus pair bonding behaviour in spur-winged plovers will not be properly interpreted until an in-depth study on a marked population is undertaken.

### 2.3 Fighting

Temple-Smith (1969) reported incidents of contact fighting in the flocks during the major period of territory selection, May - July. He distinguished two types of attack:

(a) The aerial attack; where the aggressor flew swiftly to the rival and delivered a wing blow to the head or body. The rival could avoid the attacker by crouching or retreating and sidestepping.

(b) The ground charge; which occurred when two rivals both adopted aggressive upright displays and neither assumed the submissive posture. The birds then charged, buffeted each other with rigid wings and pecked. Occasionally birds lost feathers during particularly severe bouts.

I never observed direct contact during a fight. One bird always retreated and aerial or ground chases ensued. Usually the chase lasted a few seconds but if the intruder persisted a lengthy pursuit of up to fifteen minutes could occur. After a long chase the choking ceremony was often performed when the pursuer returned to its mate.

The absence of contact fighting observed in this study was probably related to low population density. There was a surplus of suitable nesting habitat and therefore a decreased competition for space.

#### 2.4 Upright Postures

The upright posture was variable. The two extremes were the aggressive upright and the anxiety upright. Lind (1957) recorded upright postures in the lapwing that were similar to those of the spur-winged plover. Many charadriids perform uprights, the posture was originally observed in gulls (Tinbergen 1953, 1959 Moynihan 1955a, 1958a).

The aggressive upright:

The body was held upright bill pointed down, wattles inflated, neck stretched upward or forward and thickened by muscular contraction, wings flexed and slightly lowered so that the yellow spurs were displayed against white flanks (Fig. 2.1). This was a common threat display and was seen in both flocks and territories.

In territories the territorial bird faced and advanced towards the intruder which, unless it was a bird from a neighbouring territory, always retreated. A short ground or aerial chase followed and continued until the intruder left the territory. Temple-Smith (1969) observed that the male was more aggressive than the female and in many cases of territorial intrusion it was the only partner to perform this display.

In flocks both antagonists could adopt the aggressive

upright but one individual always assumed the hunched submissive posture. In this situation, and when a territorial intruder retreated before a performer could reach it, redirected aggression in the form of grass pulling was observed.

#### The anxiety upright:

Similar to the aggressive upright but differing significantly in several aspects. The neck was fully lengthened, body and bill more horizontal, plumage flattened, spurs hidden, and body orientated away from the source of disturbance (Fig. 2,1) In highly alarmed birds head bobbing occurred and was usually followed by flight. This posture was adopted in response to an alarm call by nearby birds.

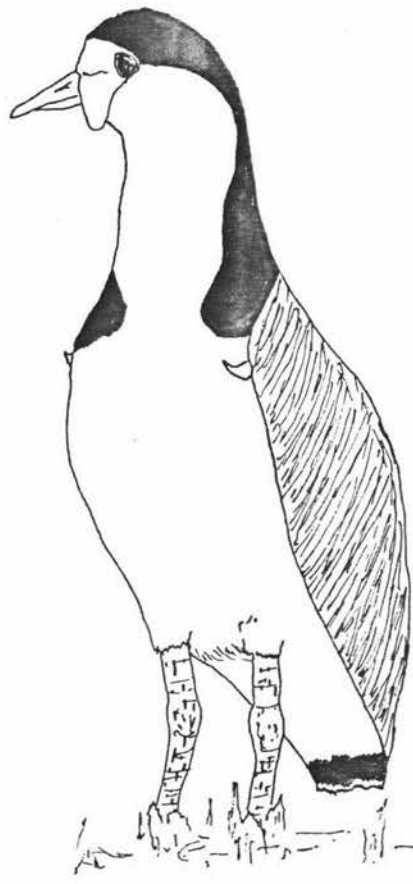
There is a marked similarity in the upright postures of a wide range of species, little ritualization appears to have taken place. In spur-winged plovers the aggressive upright prominently displays the white breast which can then be seen at a distance. The yellow wattles and spurs are also displayed. The bill and wings are positioned so that an adversary can be easily struck. The performer attracts attention by calling. This display is thus a valuable threat signal, especially for territorial birds. By contrast in the anxiety form of the upright the back is turned toward an aggressor or predator and the individual is not immediately obvious.

#### 2.5 Choking

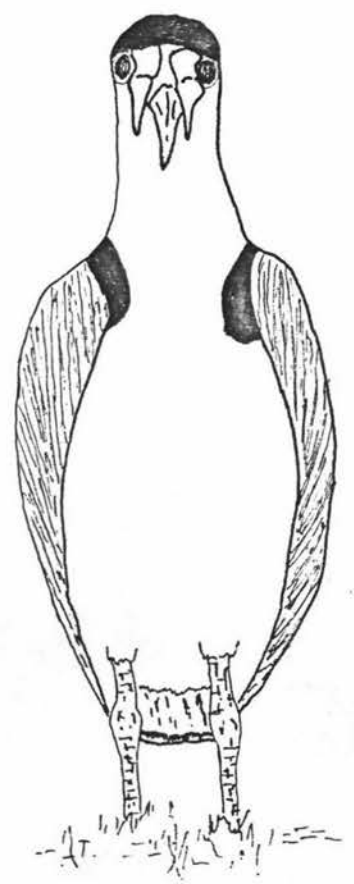
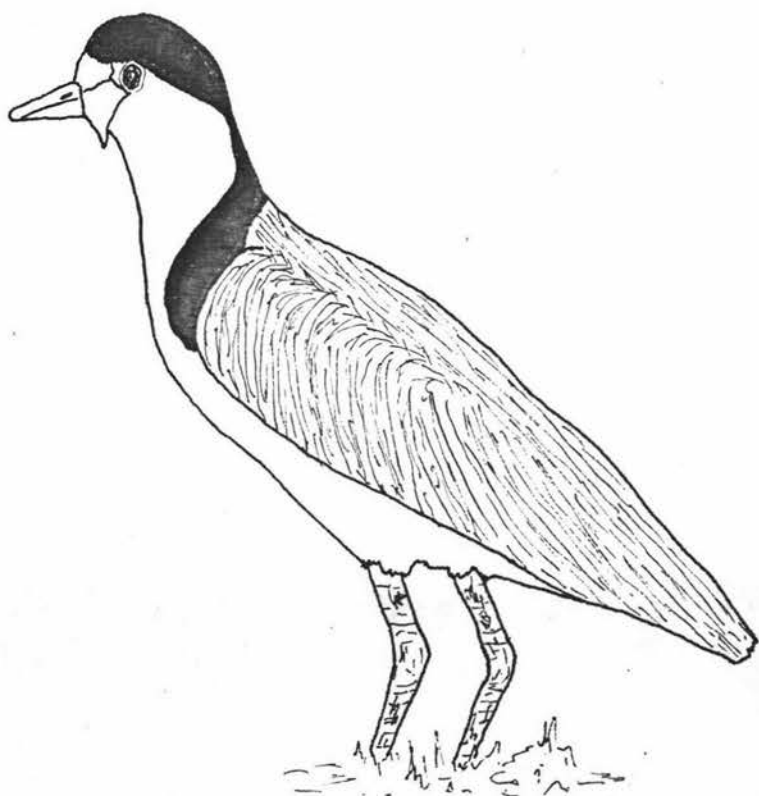
Choking is a pair display similar in form to choking in gulls (Tinbergen 1953, 1959 Moynihan 1955a, 1958a, 1962). It was seen in flocks but was usually observed in the territories.

Aggressive choking was preceded by the pair running, side by side, towards the intruder. The body was horizontal, head upright but not fully retracted (Fig. 2.2). If the





(a) The aggressive upright



(b) The anxiety upright

FIGURE 2.1: UPRIGHT POSTURES

intruder flew off as the pair approached they stopped, lowered their breasts and raised their hind quarters, at high intensity the body was almost vertical (Fig. 2.2). The head and bill were pointed down, or if the rivals were fleeing, up towards the intruders. The legs were bent and a guttural call was emitted.

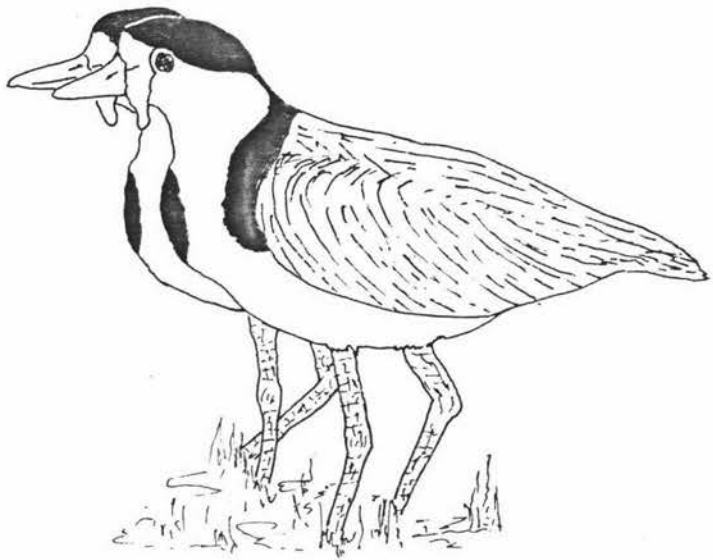
In the flocks, and at territorial boundaries, confrontations occurred. Both pairs assumed the aggressive upright, in the flocks one pair then chased the other pair a few metres. At territorial boundaries prolonged choking by opposing pairs was usually followed by both pairs retreating to feed well within their own territories.

Temple-Smith (1969) observed choking directed away from an opponent. This appeared to have an inhibitory effect on aggression. Lind (1957) observed this behaviour in lapwings and described it as a submissive posture. I did not observe this type of choking.

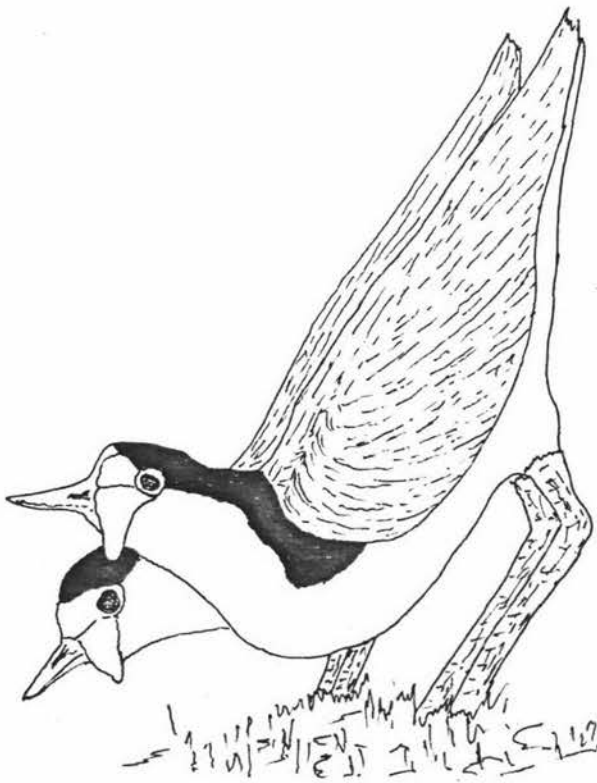
Non aggressive choking was performed by both sexes during nest site selection. This was accompanied by flicking behaviour in which both birds picked up material and threw it towards the nest site.

Aggressive and sexual forms of choking have been observed in some gull species (Noble and Wurm 1943, Tinbergen 1953, 1959, Moynihan 1955a, Beer 1975). Choking in spur-winged plovers appears in similar contexts. Tinbergen (1953, 1959) and Moynihan (1955a) considered aggressive choking to be displacement behaviour derived from nest building and chick feeding. Moynihan (1955a, 1958) also described choking in terms of intention movements. The criticism of motivational explanations in behaviour by McKinney (1978) are pertinent here.

Temple-Smith (1969) considered that choking in spur-winged plovers was a low intensity threat because the spurs were not bared or the wattles fully inflated. The initial run certainly appeared to function as a threat towards an



(a) Running posture of pair towards an intruder



(b) Choking posture

FIGURE 2.2: CHOKING BEHAVIOUR

Source: Temple-Smith 1969

intruder. It appeared that the rest of the display served to advertise the pair bond. The display may play a role in pair bond maintenance and formation. This may explain the significance of choking seen during nest site selection.

## 2.6 Copulation

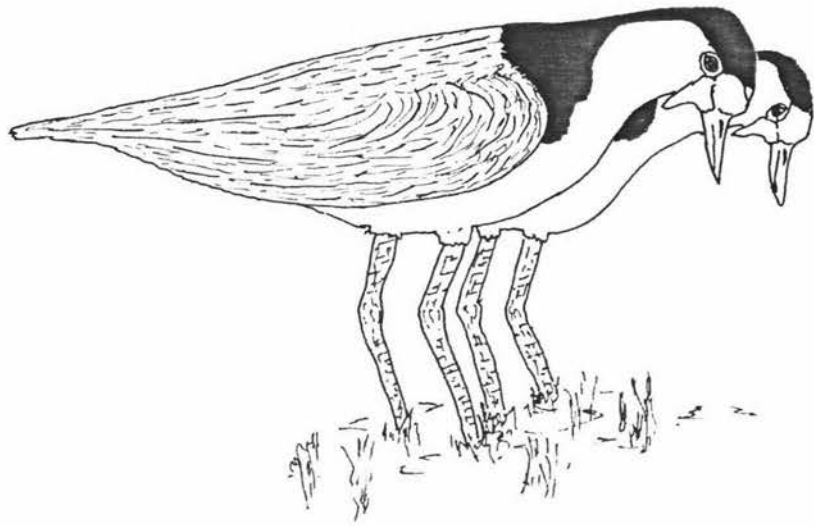
As Temple-Smith (1969) described copulation in detail, the major components are only briefly given here.

Copulation occurred both in the flocks and in the territories. However, I only observed it three times in the flocks while it occurred frequently before nest site selection and egg laying in the territories. I did not observe copulation after commencement of incubation.

Mating behaviour was highly stereotyped. The male uttered a highly distinctive staccato call heard only in the precopulatory context. The male ran after the female, both held the body horizontally, and the male call increased in intensity. The female crouched with the tail to one side and the cloaca exposed. The male stopped calling and mounted, copulation took about five seconds. After the male dismounted both birds adopted a post-copulatory posture similar to head flagging in gulls (Moynihan 1955a, 1962). It consisted of a high intensity aggressive upright with the head facing away from the mate.

Occasionally after the head flagging highly ritualized "false feeding" was observed. The birds angled the body as in feeding and touched the bill to the ground, the body and neck were then raised to a horizontal position with the head still pointed towards the ground. They then quickly lowered the head by angling the neck and body again, this continued for up to five seconds. The pair were side by side but faced either the same or opposite directions (Fig. 2.3).

Temple-Smith (1969) did not record false feeding after copulation. The courtship run is comparable with that



(a) Parallel false feeding



(b) Opposite false feeding

FIGURE 2.3: POST-COPULATORY FALSE FEEDING .

seen in the lapwing (Spencer 1953) and the golden plover (*Pluvialis apricaria*) (Williamson 1948). It always occurred and was an integral part of mating behaviour. If the female did not crouch copulation was not attempted, the crouch appeared to be an explicit acceptance signal by the female. The courtship run and staccato call may have multiple functions, e.g. signalling readiness to mate on the part of the male; mutual stimulation.

Tinbergen (1959) and Moynihan (1958a, 1958b) considered post copulatory head flagging in gulls to be an appeasement posture. The function of the post copulatory displays in spur-winged plovers was probably similar to head flagging in larids.

### 2.7 The Scrape Ceremony

Similar in form and function to the scrape ceremony performed by lapwings (Spencer 1953, Steifel 1964), the European spur-winged plover (*Vanellus spinosus*) (Steifel 1964), and many gulls (Moynihan 1955a, Tinbergen 1953). Temple-Smith (1969) described this display in detail. An outline is presented here.

The male selected a nest site and indicated the choice to the female by "flicking" material towards it and choking. The male then lowered his breast into the selected depression with the tail tilted well upward and shuffled in a circle with the legs. If the female accepted the nest site she joined the male in flicking material towards the nest, this had the function of providing lining material for the nest. If the female did not react the male stopped flicking and both birds resumed feeding.

### 2.8 Appeasement

The only appeasement posture I observed consisted of the attacked bird sitting down with the back to the aggressor. This was only seen six times, the aggressor always ceased the attack and violent grass pulling was observed. I considered this to be redirected aggression. The appeasement posture was similar to the hunched posture of some

gulls (Tinbergen 1959, Moynihan 1958b).

### 2.9 False Feeding

The highly ritualized false feeding seen after mating has been described. False feeding was commonly seen during aggressive interactions within the flock. It was most often performed after the aggressive upright and before a ground charge. Usually both birds in a pair performed simultaneously, the false feeding was always directed towards the antagonists. False feeding in chicks is discussed later.

Simmons (1955) noted that "displacement feeding" was a common displacement activity in many species of wader. His specific examples were the lapwing and the little ringed plover (*Charadrius dubius*). He explained it in terms of a conflict between attack and escape drives. As stated in the introduction, this terminology is now unacceptable.

The contexts in which this display was seen indicate that it was a high intensity threat signal. Since it was seen after courtship and was often performed by a pair in aggressive situations there could be some pair bond maintenance or advertisement function.

### 2.10 Incubation Behaviour

Two pairs were studied for a day during incubation. The sexes were recognized by slight differences in plumage pattern observed during copulation. Both sexes incubated for similar periods during the daylight hours (Fig. 2.4). Barlow et. al. (1972) noted that it was usual for the male to take over incubation just before nightfall, and saw males with frost on their backs incubating at dawn. Both males I watched took over incubation at dusk. This indicated that the male may incubate for most of the night.

The "off-duty" bird remained in the territory feeding and watching. Thomas (1969) saw the off-duty bird leaving the territory to feed. I never observed this.

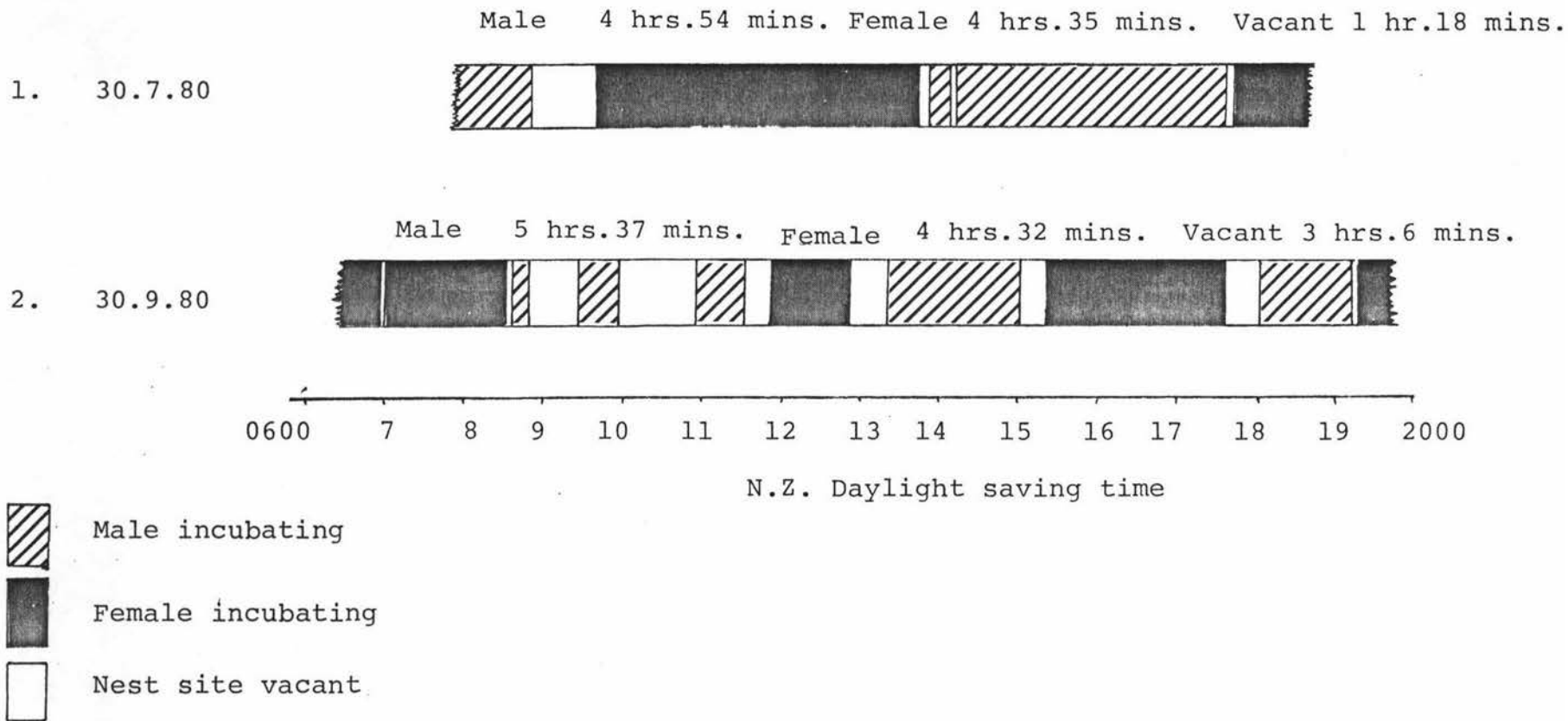


FIGURE 2.4: INCUBATION BEHAVIOUR



When the off-duty bird observed the approach of a predator it gave the alarm call. The incubating bird responded by running quickly away from the nest. Both birds then fed well away from the nest and gave no indication of its existence. The nest and eggs were well camouflaged and difficult to find.

In the usual change over the incubating bird left the nest and joined its mate, after a short period (Fig. 2.4) the other bird started incubating. When approaching and leaving the nest the birds ran quickly with the body horizontal, legs bent and head low. The white breast is not exposed. This is adaptively significant in concealing the nest site.

### 2.11 Distraction Displays

Many of the smaller charadriids perform elaborate distraction displays (Simmons 1955). Spencer (1953) observed that these "broken wing" displays were rare in the lapwing. I did not observe this type of display, but Thomas (1969) and Temple-Smith (1969) reported that it occurred rarely in spur-winged plovers.

### 2.12 Interspecific Interactions

Several explanations for interspecific aggression have been proposed. First, competition, especially for food (Orians and Wilson 1964, Orians 1971). Second, predator defence, either directly (Graul 1975, Harvey and Greenwood 1978), or indirectly by reducing density of prey for predators shared by the aggressive species and those species aggressed against (Myers 1980). Third, mis-directed intraspecific aggression (Murray 1971, Walters 1979).

The interspecific threat displays of spur-winged plovers have been discussed by Temple-Smith (1969), and only a brief description is given here.

The dive attack display in which the plover dived repeatedly at potential predators (Plate 4). The predator

may be in the air or on the ground. The plover passed very close to the potential predator but contact was not observed.

The forward display in which the body was held horizontal, legs slightly bent, neck stretched, and wattles inflated. At high intensity the wings were outspread, tail lowered and fanned, and a guttural call similar to that in choking was produced. This display was usually used in nest defence.

Plovers were also observed running toward and directing pecks at some birds. The incidents of aggression are listed in table 2.1. These types of threat displays are common among many species, particularly the larger charadriids (Simmons 1955, Tinbergen 1953, Graul 1975, Walters 1979). Therefore little taxonomic significance can be attached to these displays.

Walters (1979) identified three types of interspecific relationships between long-toed lapwings (*Vanellus crassirostris*) and other bird species. Totally excluded were blacksmith plovers (*Vanellus armatus*), harriers (*Circus spp.*) and coucals (*Centropus superciliosus*). Long-toed lapwings and blacksmith plovers established mutually exclusive territories. Walters thought that this was due to competition. As the species are similar and share many displays misdirected intraspecific could be a cause. Harriers and coucals were predators and were excluded by repeated dive attacks. These were considered to be direct anti-predator attacks.

Other species that were only occasionally attacked, and not excluded or only partially excluded, may have been a threat to eggs, fed on a similar diet to lapwings and, with one exception, were the same size as lapwing chicks and vulnerable to predation while on the substrate. Lastly, species which were tolerated were unlikely predators and a different size from lapwing chicks or adults.

TABLE 2.1 INCIDENCE OF INTERSPECIFIC AGGRESSION

Display	Dive Attack	Forward	Peck
Species Threatened			
Australasian Harrier ( <i>Circus approximans gouldi</i> )	63	0	0
Australasian Bittern ( <i>Botaurus stellaris poiciloptilus</i> )	2	0	0
Dominican Gull ( <i>Larus dominicanus</i> )	10	0	0
Magpie ( <i>Gymnorhina tibicen</i> )	0	2	4
Starling ( <i>Sturnus vulgaris vulgaris</i> )	0	1	2
Cow ( <i>Bos taurus</i> )	0	7	0
Sheep ( <i>Ovis aries</i> )	0	4	0
Cat ( <i>Felix domesticus</i> )	2	0	0
Dog ( <i>Canis familiaris</i> )	1	0	0
Man ( <i>Homo sapiens</i> )	1	0	0

In this study harriers (*Circus approximans*) and bitterns (*Botaurus stellaris*) were always excluded from territories by use of the dive attack display. Gulls (*Larus dominicanus*) were driven off by use of this display if they landed near the nest or chicks. The three attacks on gulls in the air were all against juveniles, they may have been mistaken for harriers. All the species which were dive attacked were potential predators of eggs and chicks. The display was extremely effective and the attacked individual invariably retreated.

Cattle (*Bos taurus*) and sheep (*Ovis aries*) were ignored unless they came within three metres of the eggs or chicks. When they came closer than this one or both of the parents adopted the forward display. The display was usually effective and sheep always retreated. However, three nests were destroyed by cattle despite use of the forward display. On three occasions plovers flew up towards the face of stock after performing the high intensity form of the forward display without effect. This was successful in driving off a sheep on one occasion and a bullock in other, but on the other occasion the bullock became excited and the nest was lost.

Magpies (*Gymnorhina tibicen*) and starlings (*Sturnus vulgaris*) were usually present in plover territories. The forward display was observed three times each time the magpie or starling was within one metre of the nest. On two occasions in the territories adult plovers directed pecks at starlings which had approached within fifty centimetres of their chicks. The other instances in which pecks were directed at magpies or starlings occurred in the flocks. One of these was initiated after copulation the male chased and directed a peck at a nearby starling. On the other occasions the plovers pecked at a nearby bird when it had approached within fifty centimetres.

Magpies were observed diving at and chasing spur-winged plovers on four occasions. Generally magpies, starlings and spur-winged plovers did not interact and foraged within

close proximity of each other. In response to the displays or attacks of the plovers the magpies and starlings moved, usually less than five metres, and continued feeding.

There is a slight overlap in the food resources of these species and magpies are potential predators of eggs and very young chicks.

Spur-winged plovers were not observed interacting with other bird species present in the study area. Species in this category which were commonly seen in plover territories, or feeding close to plover flocks were: hedge sparrow (*Prunella modularis occidentalis*), house sparrow (*Passer domesticus*), greenfinch (*Carduelis chloris chloris*), chaffinch (*Fringilla coelebs gengleri*), goldfinch (*Carduelis carduelis britannica*) and white-faced heron (*Ardea novaehollandiae*). Species occasionally or rarely observed in association with spur-winged plovers were: cattle egret (*Bubulcus ibis coromandus*), black swan (*Cygnus atratus*), paradise duck (*Tadorna variegata*), mallard (*Anas platyrhynchos*), New Zealand shoveler (*Anas rhynchos variegata*) pukeko (*porphyrio porphyrio melanotus*), pied stilt (*Himantopus himantopus leucocephalus*) kingfisher (*Halcyon sancta vagans*) and welcome swallow (*Hirundo tahitica neoxena*). These species are not potential predators and, although they fed in plover territories, were not observed within one metre of spur-winged plovers.

### 2.13 Chick Behaviour

Chicks fed near the parents for the first two weeks and were often brooded in this period. Older chicks fed in a more dispersed pattern, adults fed up to two hundred metres apart with the chicks between them.

When adults sighted approaching danger they uttered the alarm call. Some newly hatched chicks, one or two days old, failed to respond and continued to move around. Chicks

of this age came out of hiding while the adults were still alarm calling, they were therefore susceptible to predation. The usual chick response was to flatten on the ground with the head down and the eyes open (Plate 5). The white breast was concealed and the cryptic dorsal colouration camouflaged the chicks from potential predators. Chicks emerged when the adults ceased alarm calling and uttered a soft "regrouping" or "all clear" call. Chicks older than four weeks tended to run to a patch of cover, usually rushes, before adopting the concealment posture. On three occasions chicks very close to fledging, about seven weeks old, continued to run rather than hiding. The concealment posture and running before concealment in older chicks is common in ground nesting birds (Simmons 1955, Tinbergen 1953). Chicks did not develop any of the adult display patterns until after they fledged.

False feeding was seen when chicks were released after banding or measurement. Simmons (1955) recorded this in a number of species, and interpreted it as displacement feeding. If the chicks were chased they stopped false feeding and ran faster. The functional significance of this behaviour was unclear, it slowed the escape and thus appeared to be non-adaptive.

#### 2.14 Flock Behaviour

The changes in flock behaviour over time are considered in detail in Chapter 4. The main behavioural difference was that flocks birds were less aggressive toward other species than were those in territories. The composition and size of flocks changed on a daily basis. No dominance hierarchy was observed in any of the flocks. In contrast the flock studied by Temple-Smith (1969) had a stable composition and a dominance hierarchy. This may have been an anomalous situation as the dominant male bird was visibly larger than all other birds present.

#### 2.15 Discussion

Bock (1958) considered that comparative ethology was the key to understanding the taxonomy of the vanelline

ployers. The concept of using behavioural homologies in taxonomy is not new. Atz (1970) stressed the difficulties and considered the application unsound until the underlying structure was morphologically and physiologically known. Baerends (1975) and McKinney (1978) considered this view, but found a place for behavioural homologies in understanding evolutionary relationships provided they were applied cautiously. The value of blending ethological, ecological and evolutionary approaches was demonstrated by the work of Tinbergen (1959) on gulls, Crook (1964) on weaver birds, Nelson (1970) on sulids and McKinney (1970) on anatidae.

There is a marked similarity of behaviour in the vanelline plovers studied so far. Displays which may have evolved independently many times are unsuitable for use in homologies. These displays occur in a wide range of species and there is little interspecific difference. Examples are upright, forward and dive attack displays.

Mating and courtship displays function as isolating mechanisms. There are differences even between closely related species which can be used to clarify taxonomy. Useful displays for constructing homologies in this genus are courtship, scrape ceremonies and display flights. Choking may be of some value although it is common in the order Charadriiformes. Differences in vocalizations are likely to be useful, as in the case of anatidae (McKinney 1970).

Bock (1958) considered that the ancestral origin of the genus *Vanellus* was northern Africa. His tentative evolutionary pathways indicated that *Vanellus vanellus* and *Vanellus miles novaehollandiae* were two of the most distantly related species in the genus. The morphology and plumage was markedly different. Lapwings were sexually dimorphic. They also formed a new pair bond each year. However, both species were territorial in the breeding season, lived in similar environments and foraged for similar food. The largest differences occurred in pair

bonding and display flight situations.

Unfortunately the true implications of the differences between the two species will not become apparent until other vanelline plovers are ethologically described. It is probable that the courtship and mating displays, which act as isolating mechanisms, will be the most significant in constructing the homology.





PLATE 4: DIVE ATTACK DISPLAY



PLATE 5: CHICK IN CONCEALMENT POSTURE

## CHAPTER 3

BREEDING BIOLOGY3.1 Introduction

The breeding biology of spur-winged plovers has been studied in Australia by Thomas (1969), Temple-Smith (1969), and Dann (in press). Barlow et. al. (1972) studied the species in Southland.

A preliminary discussion of territoriality is required because there is no generally accepted definition. Noble's (1939) standard definition of "a defended area" was modified by Hinde (1956) to "a topographically localized defended area". Pitelka (1959) defined territory as an "exclusive area" while Brown and Orians (1970) proposed the restrictive definition "a fixed exclusive area with the presence of defence to keep out rivals". At the other extreme Davies (1978) recognises a territory "whenever individual animals, or groups, are more spaced out than would be expected from a random occupation of suitable habitat". The appeal of this definition is its statistical nature, but it is so broad that it includes all mechanisms by which animals space out.

The definition of territory I use is a defended exclusive area. Where defence need not be by overt aggression but may be maintained by any form of communication.

3.2 Breeding Season

The breeding season was taken as the date of laying of the first egg until the date of fledging of the last chick. In 1979 the date of laying of the first egg was assumed to be 11 weeks prior to the fledging date of the first chick. The breeding season in 1979/1980 extended from June 10 until January 7, and in 1980 from June 26 until December 19; which was 212 and 176 days respectively.

The number of nests started peaked in July for both 1979 and 1980, while the number of nests incubated peaked in

August (Figs. 3.1, 3.2). The number of territories peaked in September 1979 and August 1980. Nesting and territoriality was correlated with the various environmental factors on a monthly basis (Table 3.1). Multiple regression analysis showed that the number of territories was most highly correlated with water table level, temperature and day length. (Multiple coefficient of determination 77.2%). The level of the water table was the best predictor of territoriality (Appendix 1). The best predictor of nesting was temperature, but the coefficient of determination was only 49% (Appendix 1).

### 3.3 Territory

Spur-winged plovers defend large territories during the breeding season. The displays used in territorial defence are described in chapter 2. Some pairs formed territories several weeks before nesting and maintained them for some weeks after the chicks fledged; others set up the territory one day before nesting and left immediately the chicks fledged (Fig. 3.1).

Twenty eight territories were established in the intensive study area during 1980. Seventeen of these were in the same areas as territories of the previous year. It was not known if the same pairs occupied these territories in both years because adults were not banded. Nor was it known if those pairs which set up territories early in the breeding season, but did not breed, were the same birds that established late territories and did breed. Twenty five territories were identified in 1979, but the study did not start until July 13, 1979 so there may have been other territories set up and abandoned before this date.

During 1980 territory size was determined by plotting the position and movements of territorial occupants. Intra-specific conflict was most useful in determining territorial boundaries. Territories varied widely in size (range 1.5 - 15.6 ha.) and length of maintenance (range 4-37 weeks). Territories in which chicks were successfully fledged were

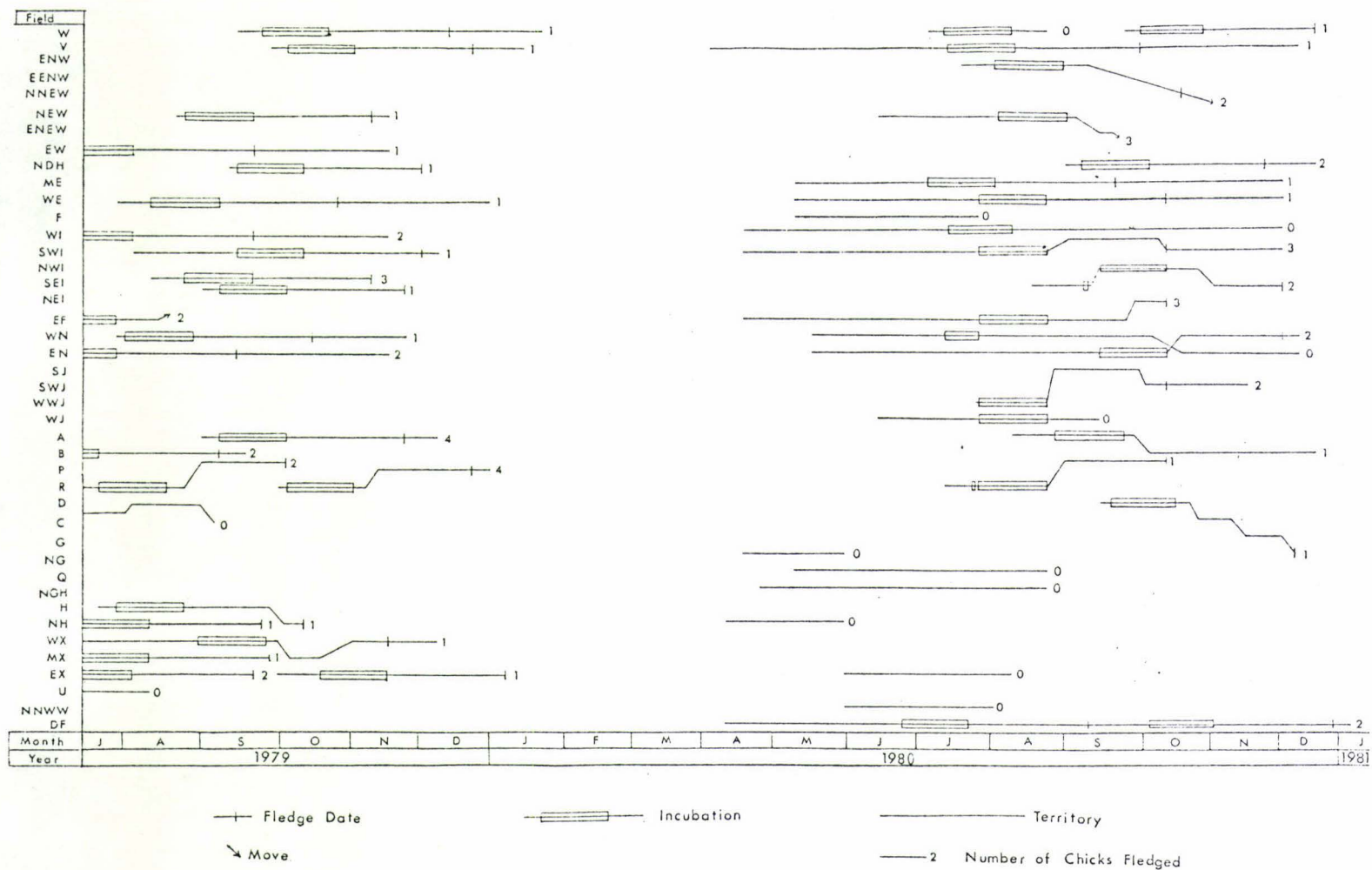


FIGURE 3.1: DIAGRAMMATIC REPRESENTATION OF SPUR-WINGED PLOVER BREEDING BIOLOGY WITHIN THE INTENSIVE STUDY AREA.

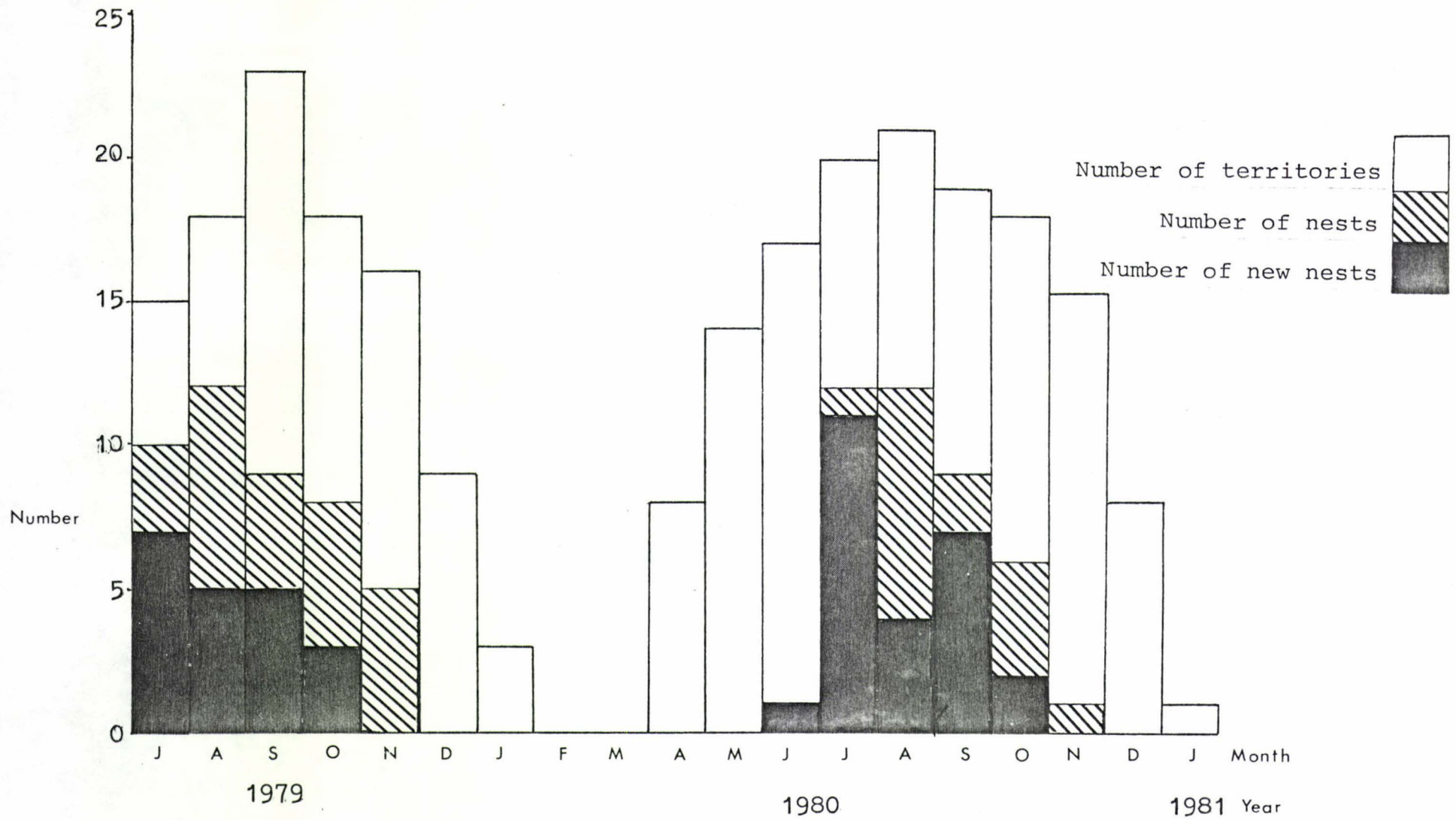


FIGURE 3.2: NEST AND TERRITORY NUMBERS WITHIN THE INTENSIVE STUDY AREA

significantly larger and were maintained for a significantly longer period than unsuccessful territories (Table 3.2). However, there was no significant correlation between territory size or length of territorial occupancy and number of chicks successfully fledged.

Site attachment and tolerance of disturbance varied. Pairs moved their territories for several reasons:

1. Grass growth, so that the average height of the ground cover was over fifteen centimetres.
2. Disturbance, by large numbers of stock or humans.
3. Lack of some longer cover, such as patches of thistles or rushes, to conceal older chicks.
4. Flooding of the initial territory.

Because of the low density of the plover population in the study area pairs were not constrained from moving by neighbouring territories. Only four pairs had close neighbours with which they interacted regularly (Fig. 3.3). Four pairs did not maintain stable territories, and moved with their chicks for much of the period prior to fledging. These pairs still defended a large area around the chicks, and were considered to be defending moving territories. I concur with Thomas (1969) that once the eggs have hatched spur-winged plovers defend an area around the chicks rather than a fixed area. This may explain the apparently larger size of successful territories.

Two territories in 1979 were in a grazed chou moellier crop, and one of the moving territories in 1980 was in a similar crop for three weeks; all the other territories within the intensive study area were in rough pasture (Plate 6) In the whole study area a few pairs were seen or reported in grazed chou moellier or turnip crops or new grain crops, but most were in areas of rough pasture. Territories were not found in improved pasture, perhaps because of high stock numbers and a lack of cover.

During nesting and for the first five weeks after hatching

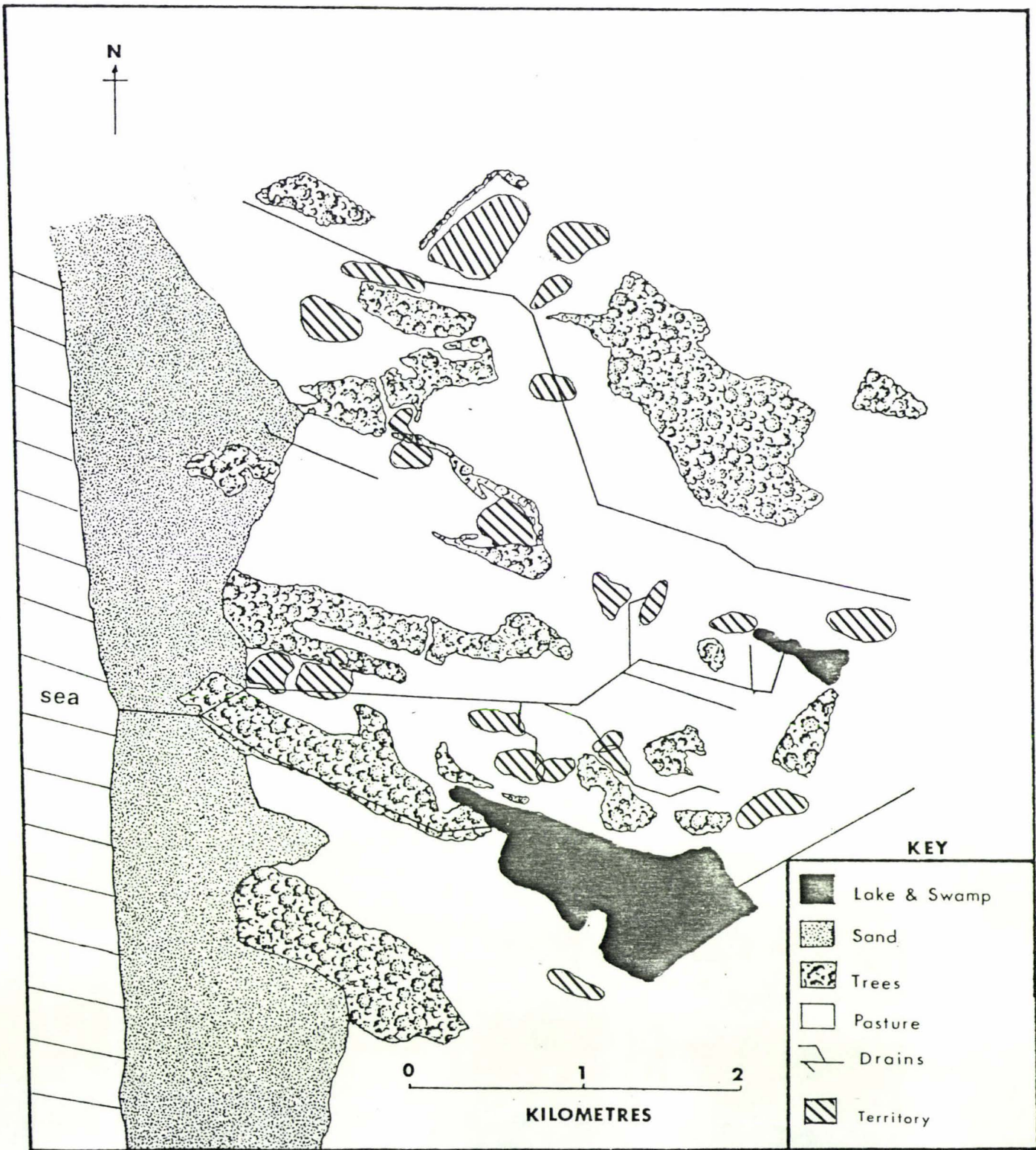


FIGURE 3.3: TERRITORIES WITHIN THE INTENSIVE STUDY AREA, 1980

TABLE 3.1: CORRELATION MATRIX OF TERRITORIES AND NESTING WITH ENVIRONMENTAL FACTORS ON A MONTHLY BASIS

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	Territory Numbers	Nests Started	Nests Extant	Water Table	Day length	Temp- erature
Nests started	0.613					
Nest Extant	0.749	0.867				
Water Table	0.836	0.423	0.565			
Daylength	-0.449	-0.571	-0.476	-0.441		
Temperature	-0.668	-0.702	-0.657	-0.610	0.905	
Precipitation	0.006	0.019	0.125	0.058	0.203	0.114

Based on 18 months data from July 1979 until January 1981

Significant values of the correlation coefficient with 16 degrees of freedom.

Significance	0.1	0.05	0.02	0.01	0.001
Correlation Coefficient	0.4000	0.4683	0.5425	0.5897	0.7084



TABLE 3.2: TERRITORY SIZE AND LENGTH OF OCCUPANCY

Successful Territories			Unsuccessful Territories	
Size (Ha)	Weeks Maintained	Chicks Fledged	Size (Ha)	Weeks Maintained
15.6	35	1	3.8	29
9.2	16	2	3.5	11
5.7	29	1	3.4	13
5.4	29	1	3.1	15
5.1	12.5	1	2.9	7
4.8	25	3	2.6	32
4.1	30	2	2.4	9
4.1	18	1	2.3	17
4.1	12	1	2.3	10
3.7	32	3	1.8	6
3.5	15	2	1.5	7
M	15	2	?	4
M	18	3		
M	11.5	1		
M	11.5	2		
?	37	1 + 1*		

- +	- +	- +	- +
X - s.d.	X - s.d.	X - s.d.	X - s.d.
6.0 <sup>+</sup> <sub>-</sub> 3.6	21.7 <sup>+</sup> <sub>-</sub> 9.1	2.7 <sup>+</sup> <sub>-</sub> 0.7	13.3 <sup>+</sup> <sub>-</sub> 8.9

M = pairs that moved their territories two or more times.

\* = double brood

? = territory size not mapped.

1. Successful territories were significantly larger than unsuccessful territories (Mann-Whitney U = 118.5,  $P < 0.001$ )
2. Successful territories were maintained for significantly longer periods than unsuccessful territories (Mann-Whitney U = 151.5,  $P < 0.01$ )
3. Territory size and length of occupancy were correlated (Spearman product moment rank correlation 0.4909  $P < 0.05$  with 20 degrees of freedom).

4. Territory size and number of chicks fledged were not significantly correlated (0.2685,  $P < 0.1$ , 9F)
5. Length of territorial occupancy and number of chicks fledged were not significantly correlated (0.1120,  $P < 0.1$ , 15F)

adults were never observed outside the territory. Pairs remained on the territory while chicks were weighed and measured. In the week prior to fledging some adults would leave the territory for up to one hour if disturbed. At this age chicks remained in the concealment posture until the adults returned.

### 3.4 Nesting

Nest site selection is described in chapter 2. Eighteen nests were discovered, two in 1979 and sixteen in 1980. Nests were lined with a variety of materials from around the nest site, mostly dead grasses (Plate 7). Two of the nests were not lined and consisted of depressions in the ground. Most nests were situated close to rushes or other cover such as dead wood, which provided camouflage for the incubating bird and nest. A distinctive feature near the nest may also act as a recognition signal.

All nests were on a slight rise or flat ground and the incubating bird had unrestricted visibility for a minimum distance of 5 metres. During the breeding period the level of the water table was high, most fields contained areas of ephemeral water and all nests were within 50 metres of open water. Sixteen nests were in areas accessible to stock.

Only two successful nests were found before egg laying began. The eggs were laid at intervals of approximately 24 hours, except for the final egg in one clutch which was laid after an interval of at least 48 hours. Incubation began after the laying of the third egg in this nest. The late laid fourth egg did not hatch. Incubation lasted 28 and 29 days.

Egg colour is olive green with markings of black, grey and dark brown. The olive green background colour is variable both within and between clutches (Plate 8). During incubation the eggs darken due to staining.



PLATE 6: TERRITORY HABITAT



PLATE 7: NEST

Forty six eggs were measured. The average size was 45.8mm. (s.d.  $\pm$  1.58) x 33.3mm. (s.d.  $\pm$  0.85), ranges 43.1 - 50.5 and 31.8 - 35.2mm. respectively. Weight on laying was approximately 30g. thus a modal clutch of 4 eggs represented nearly one third of a female's body weight. Eggs were weighed during the course of incubation and their densities calculated using the technique of Wooler and Dunlop (1980). Four eggs which did not hatch were measured volumetrically by water displacement in a 250cm<sup>3</sup> measuring cylinder (Table 3.3). Densities were then calculated using 0.52 as the constant in place of the 0.496 used by Wooler and Dunlop. Egg density over time was plotted (Fig. 3.4), but was only useful as a rough guide in ageing of eggs because of the large variability.

Five of the 18 nests found were destroyed, all the others successfully hatched chicks representing a success rate of 72.2%. Only two of the unsuccessful nests were completed clutches, these nests were trampled by cattle. Each contained three eggs and incubation had been in progress for over two weeks. Both pairs maintained their territories for several weeks after nest destruction but neither pair renested. In the three cases where incomplete clutches were destroyed the pairs renested immediately. One of these nests was trampled by cattle after only one egg had been laid. The pair renested less than 10 metres away and a further four eggs were laid. The second nest contained one egg when it was destroyed by a farm vehicle. This pair then laid three more eggs in a nest less than one metre from the old site. The third nest was flooded after two eggs had been laid. The pair then moved about 500 metres and produced another clutch.

Average clutch size in the 15 completed clutches was 3.6, 9 nests contained four eggs and 6 three eggs. The true average clutch size was probably a little higher as some clutches were found after the first week of incubation and some eggs may have been lost. One pair on a dairy farm to the north of the intensive study area produced a

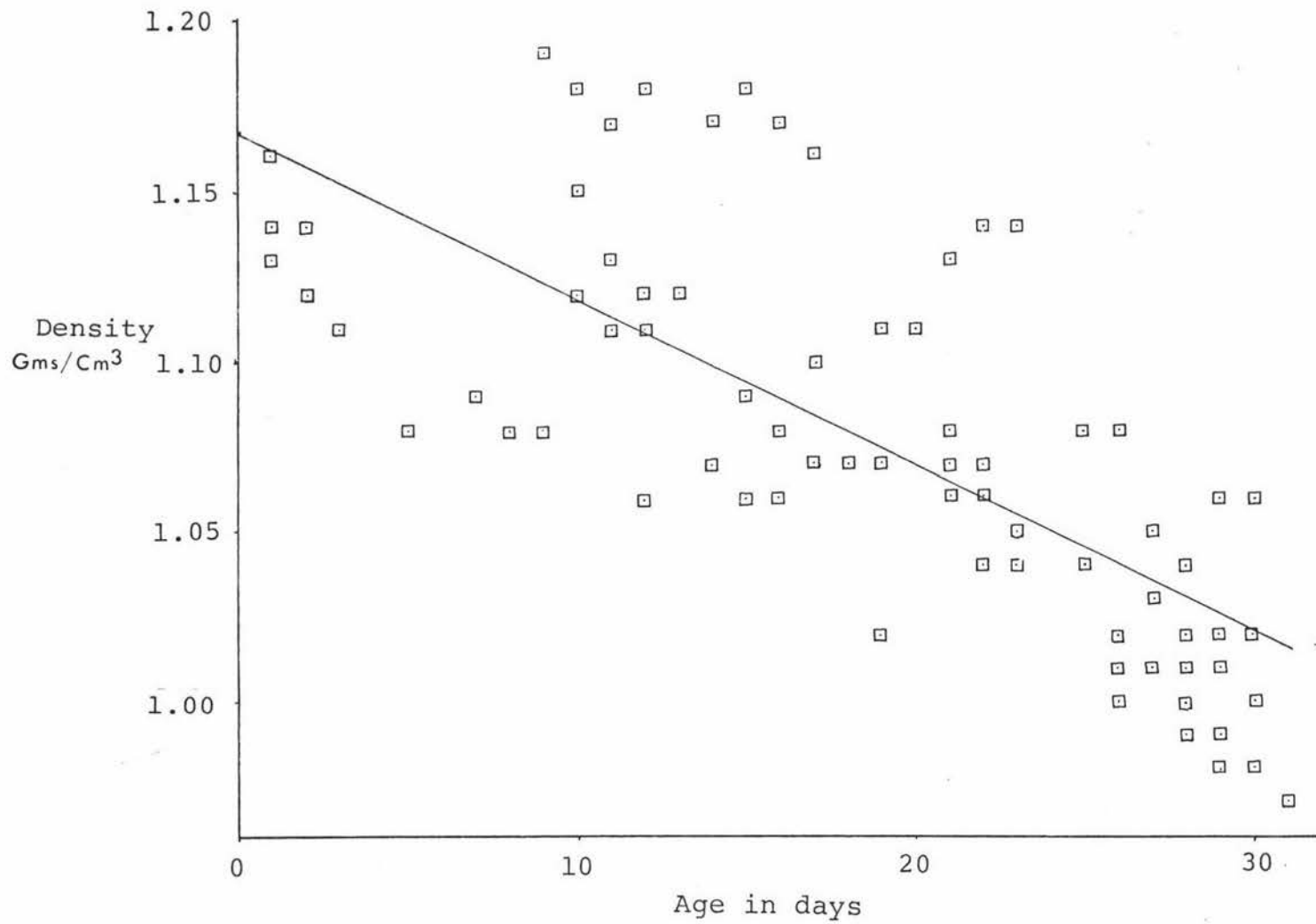


FIGURE 3.4: EGG DENSITY DURING THE COURSE OF INCUBATION

TABLE 3.3: MEASURED EGG VOLUMES

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Egg Size	Volume	$K_V$
46 x 32 mm.	24.5 cm <sup>3</sup>	0.52
44.6 x 33.4 mm.	26 cm <sup>3</sup>	0.52
45.7 x 33.4 mm.	26.5 cm <sup>3</sup>	0.52
43.8 x 31.8 mm.	23 cm <sup>3</sup>	0.52

Where  $K_V$  is the constant in the equation:

$$V = K_V LB^2$$

V = Volume      L = Length      B = Breadth of an egg.

double clutch. This pair was the first to nest in 1980 and three weeks after successfully fledging one chick, renested and reared another chick to fledging.

Hatching was observed at 6 nests. Three days may elapse from first piercing of the shell to final emergence. In each case the chicks hatched within a 24 hour period of each other. At one nest all 4 chicks hatched within a 2 hour period. Parents removed broken eggshells from the nest and deposited them over 10 metres away. The parents and chicks left the nest within one day.

### 3.5 Chick Development

14 chicks were captured and banded in 1979 and 24 in 1980. All chicks captured in 1980 were of known age and were recaptured up to three times. The measurements are recorded in Table 3.4 and Figures 3.5, 3.6, 3.7, 3.8, 3.9, 3.10. Changes in plumage were also recorded (Plates 9, 10, 11, 12, 13).

Chicks fledged at about 250g. which was 60% of adult bodyweight. This was a logarithmic phase of weight increase (Fig. 3.6). Tarsal and culmen growth were almost completed by the date of fledging. Wattle length was 60% of that found in adults at fledging. The spurs were less than 50% of adult length at fledging. The spurs first appeared at 16 days old and were originally bone grey in colour. At fledging they were either pale yellow or grey.

Juvenal plumage gradually replaced nestling down and first became evident about 9 days old. At fledging the only areas where down remained were the nuchal crest and lower dorsum (Plate 12). The bill, irises and wattles were all grey at hatching (Plate 10) but become yellow from the fifth week (Plate 12).

Juveniles remained with their parents for up to six months after fledging. Many family groups joined the flocks in November and December. The last groups to join the flocks did so in early February. Families were



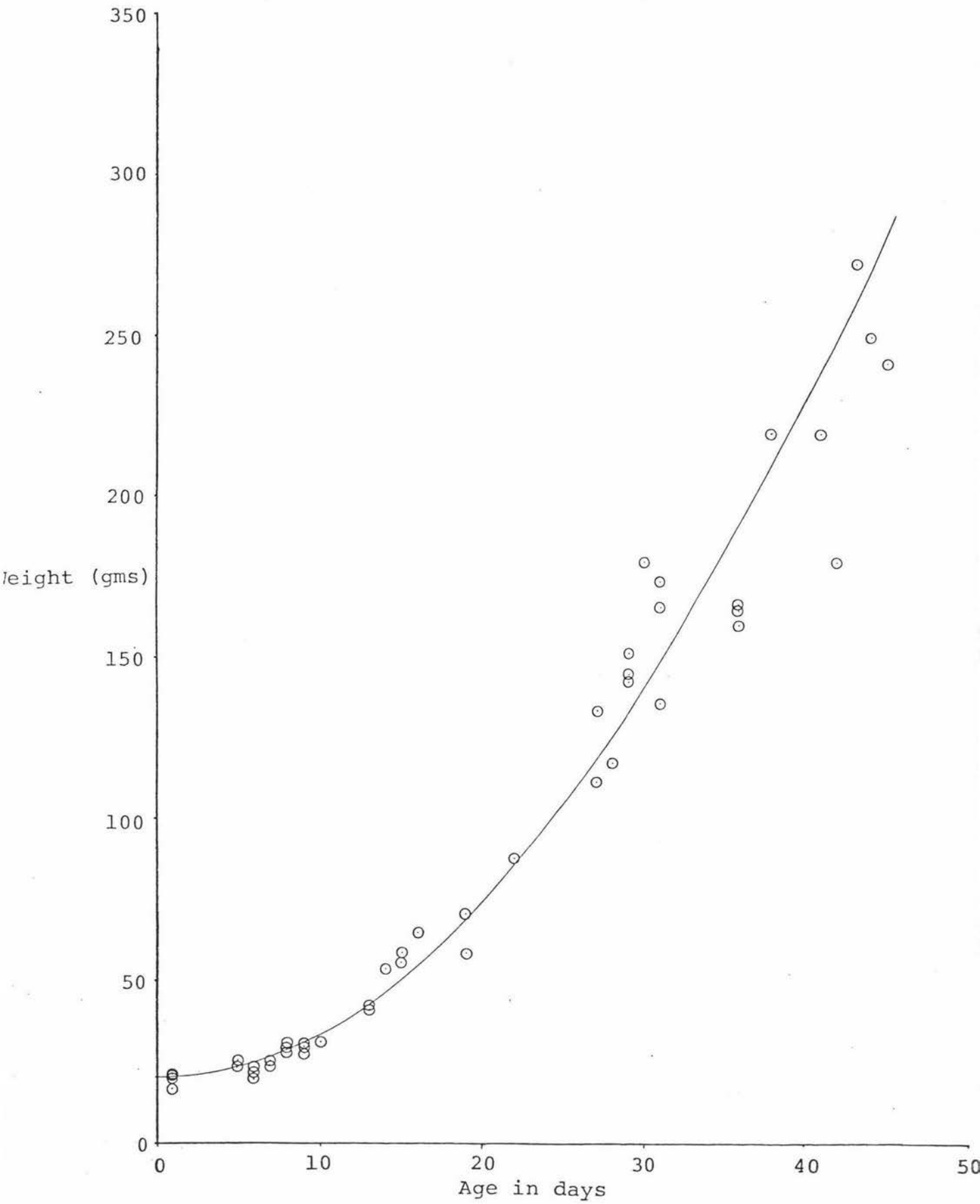


FIGURE 3.5: WEIGHT GROWTH CURVE OF SPUR-WINGED PLOVER CHICKS

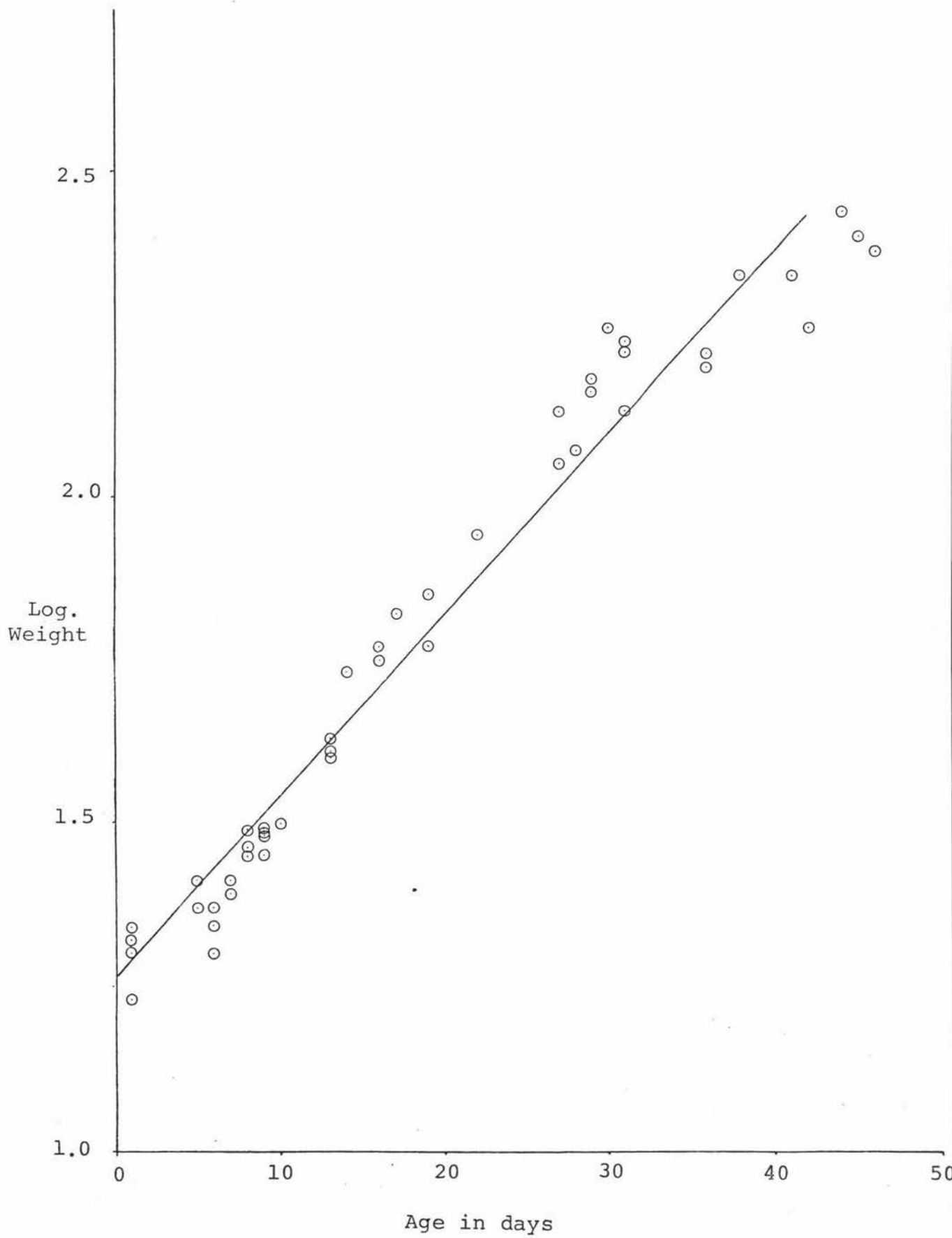


FIGURE 3.6: LOGARITHMIC WEIGHT GROWTH OF SPUR-WINGED PLOVER CHICKS

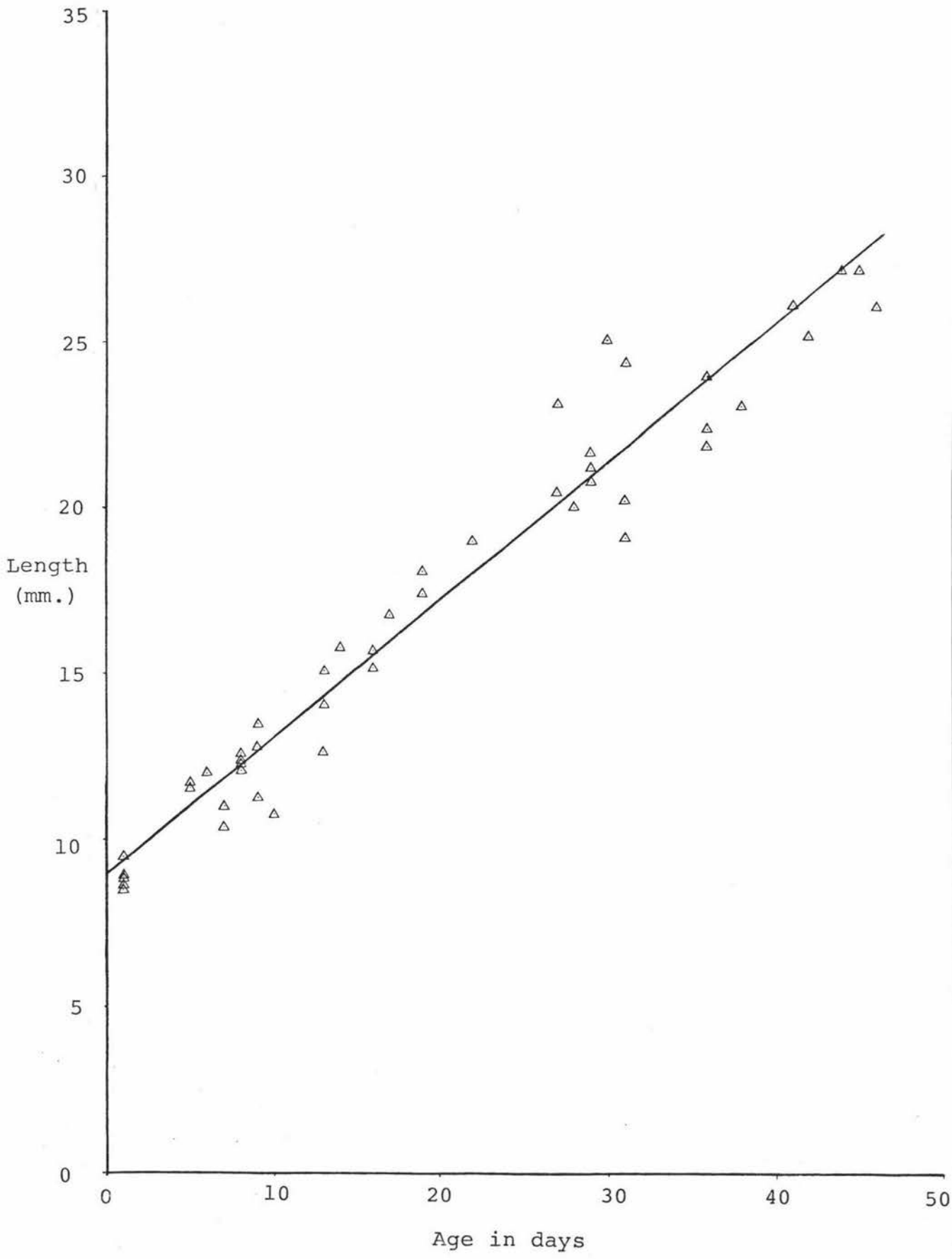


FIGURE 3.7: GROWTH OF EXPOSED CULMEN IN SPUR-WINGED PLOVER CHICKS

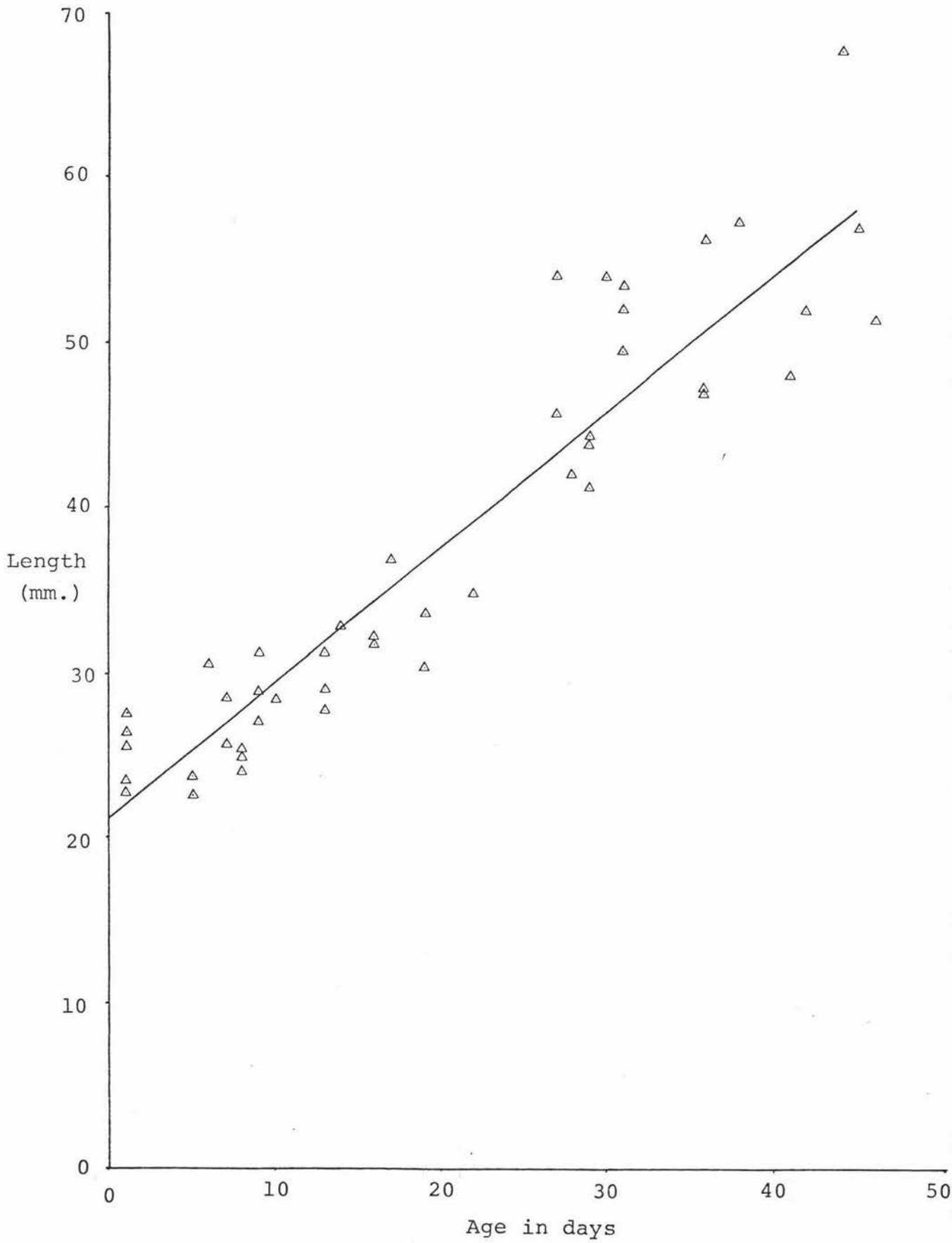


FIGURE 3.8: GROWTH OF TARSUS IN SPUR-WINGED PLOVER CHICKS

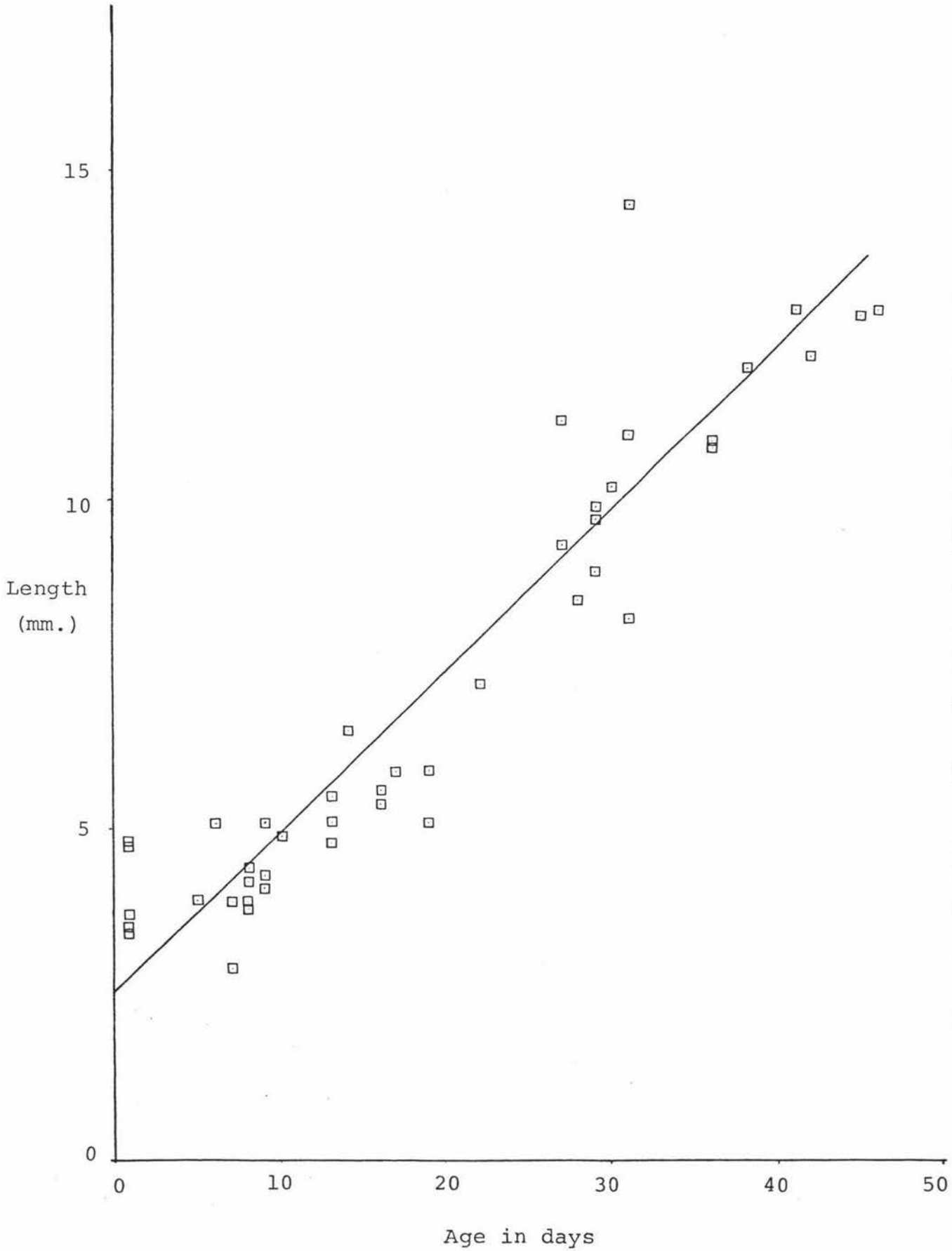


FIGURE 3.9: GROWTH OF WATTLE IN SPUR-WINGED PLOVER CHICKS

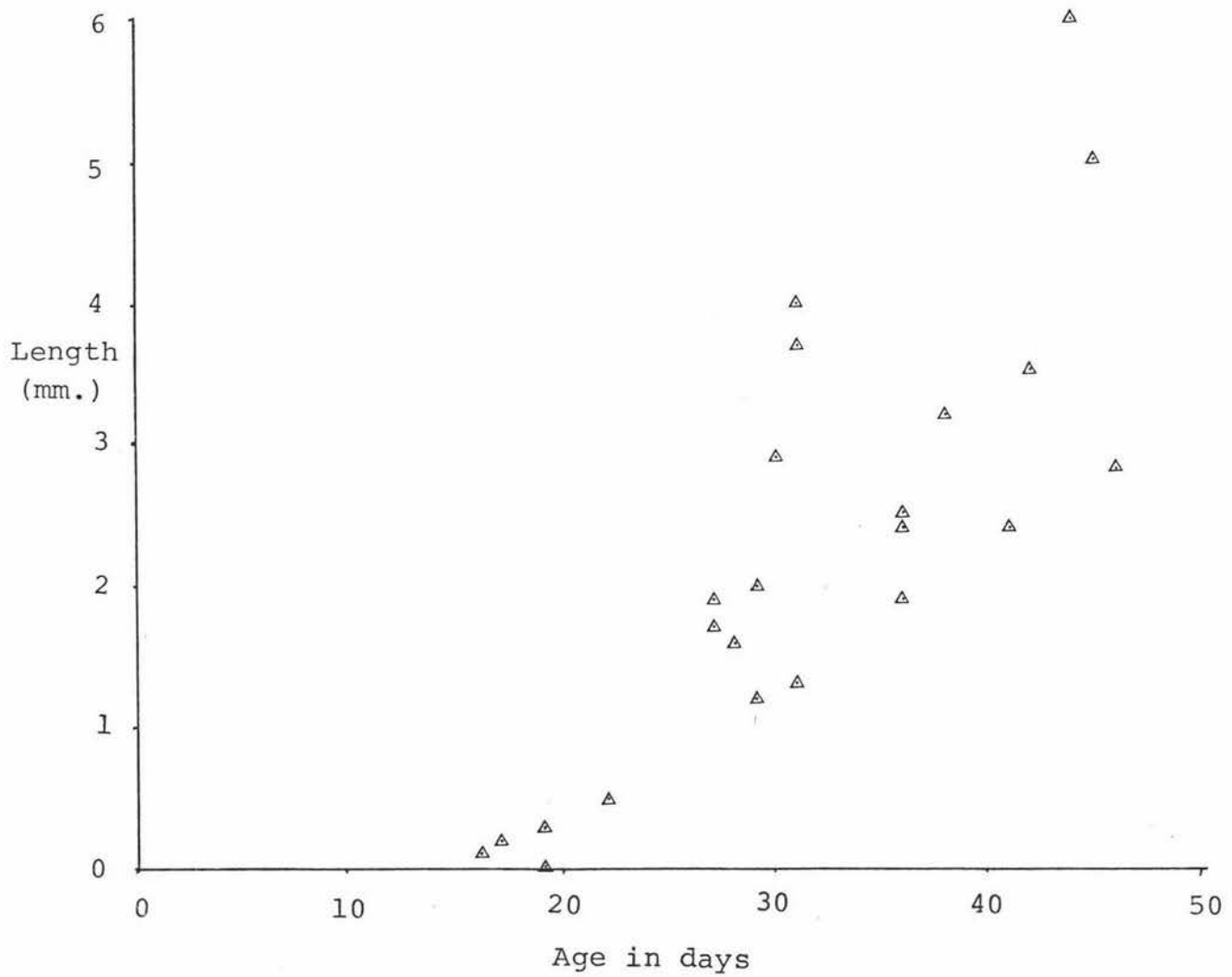


FIGURE 3.10: GROWTH OF SPUR IN SPUR-WINGED PLOVER CHICKS

TABLE 3.4: CHICK MEASUREMENTS

Field	Age (days)	Weight (gms)	Exposed Culmen (mm)	Tarsus (mm)	Wattle (mm)	Spur (mm)
A	1	20	8.5	27.5	3.5	0
A	1	21	9.0	26.3	3.7	0
W	1	22	9.5	22.7	4.8	0
D	1	17	8.7	23.4	3.4	0
DF	1	20	8.9	25.5	4.7	0
SI	5	23.5	11.6	22.5	3.9	0
SI	5	25.5	11.7	23.7	3.9	0
ENW	6	20	-	-	-	-
ENW	6	23.5	-	-	-	-
V	6	22	12.0	30.5	5.1	0
SJ	7	25.5	11.0	28.4	3.9	0
SJ	7	24.5	10.4	25.6	2.9	0
EF	8	29	12.3	24.9	4.2	0
EF	8	31	12.6	25.3	3.9	0
EF	8	31	12.4	24.9	4.4	0
EF	8	28	12.1	24.0	3.8	0
NEW	9	28	11.3	27.0	5.1	0
NEW	9	30	13.5	28.8	4.3	0
NEW	9	31	12.8	31.2	4.1	0
FR	10	31.5	10.8	28.4	4.9	0
SJ	13	41	14.1	27.7	5.5	0
SJ	13	43	15.1	29.0	5.1	0
WE	13	40.5	12.7	31.2	4.8	0
ENW	14	54	15.8	32.8	6.5	0
WI	16	59	15.2	31.7	5.4	0.1
WI	16	56	15.7	32.1	5.6	0.1
ME	17	65.5	16.8	36.9	5.9	0.2
SJ	19	71	18.1	33.5	5.9	0.3
SJ	19	59	17.4	30.3	5.1	0
EF	22	88	19.0	34.8	7.2	0.5
V	27	134	23.1	54.0	11.2	1.9
DF	27	112	20.5	45.7	9.3	1.7
DF	28	118	20.0	42.0	8.5	1.6
EF	29	145	21.7	41.2	9.9	1.2

TABLE 3.4: CHICK MEASUREMENTS Cont'd

Field	Age (days)	Weight (gms)	Exposed Culmen (mm)	Tarsus (mm)	Wattle (mm)	Spur (mm)
EF	29	143	21.2	43.8	9.7	2.0
EF	29	152	20.8	44.3	8.9	2.0
B	30	180	25.1	54.0	10.2	2.9
C	31	136	21.2	49.5	8.2	1.3
SEI	31	174	19.1	53.4	11.0	3.7
N	31	166	24.4	52.0	14.5	4
EF	36	160	24.0	56.2	10.8	1.9
EF	36	165	22.4	47.2	10.9	2.5
EF	36	167	21.9	47.0	10.9	2.4
SEI	38	220	23.1	57.3	12.0	3.4
WI	41	220	26.1	48.0	12.9	2.4
WE	42	180	25.2	52.0	12.2	3.5
W	44	273	27.2	67.7	17.4	6.0
ME	45	250	27.2	57.0	12.8	5.0
WI	46	242	26.1	51.4	12.9	2.8

Adult	420	28.3	72	22.2	13.6
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Degrees Freedom	Correlation of	Correlation Coefficient	Significance Level
45	Weight/Wattle	.9646	< 0.001
45	Weight/Culmen	.9496	< 0.001
45	Weight/Tarsus	.9525	< 0.001
23	Weight/Spur	.9045	< 0.001



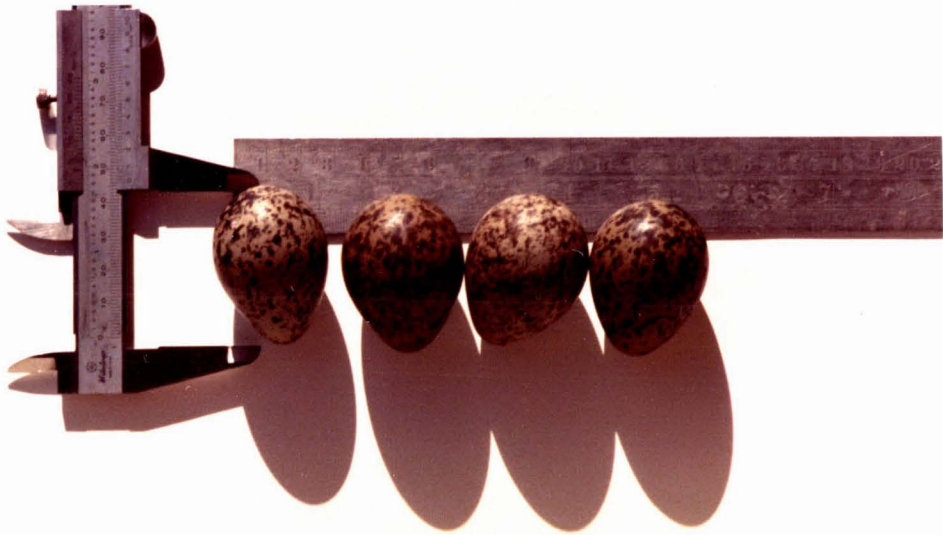


PLATE 8: EGG COLOUR VARIATION



PLATE 9: NEST AND NEWLY HATCHED CHICK



PLATE 10: ONE DAY OLD CHICKS



PLATE 11: THREE WEEK OLD CHICK



PLATE 12: SEVEN WEEK OLD CHICK



PLATE 13: FAMILY GROUP WITH FLEDGED CHICKS

distinguishable as units within the flocks until late April. They fed in groups and parents continued to attack harriers (*Circus approximans gouldi*) until late April.

One bird banded as a chick in 1979 established a territory in 1979 but the pair did not breed. Another chick was present as a paired bird in the non-breeding flock. One juvenile was still with its parents in June 1980 when they established another territory. The parents became increasingly hostile towards the young bird, which left four weeks after the territory had been set up. Only two of the 14 young banded in 1979 were present in the intensive study area at the end of 1980. Two of the others were observed 8km. south near Lake Koputara. The rest of the previous year's chicks were not seen and had presumably left the study area.

### 3.6 Breeding Success

The history of the 58 eggs discovered was:

Number of eggs destroyed	11	19.0%
Number of eggs infertile	2	3.4%
Number of dead embryos	2	3.4%
Number of chicks hatched	43	74.1%
Number of chicks fledged	20	46.5%
Total breeding success	20/58	34.5%

All chicks which died before fledging were lost in the first two weeks. Predation of plover chicks was not observed, but cattle killed two chicks by trampling. A feral cat was observed unsuccessfully attempting to kill chicks.

The total breeding success for the intensive study area was not known. In 1979 23 pairs successfully fledged 37 chicks giving an average clutch size on fledging of 1.6. In 1980 15 pairs successfully fledged 26 chicks, an average clutch size on fledging of 1.7. In addition, four pairs nested but did not fledge chicks in 1980. At

least three of these pairs did not renest. The greatest number of adult birds within the intensive study area, including flock birds, during August was 60 in 1979 and 41 in 1980. The number of chicks fledged, expressed as a percentage of the resident population, was 61.7% in 1979 and 63.4% in 1980.

### 3.7 Discussion

The breeding season observed in this study was comparable with the breeding season observed in other studies. Thomas (1969) thought that the onset of laying in the Hobart region was probably correlated with both temperature and rainfall but did not present an analysis. He considered that nesting in the more arid regions of New South Wales could have been correlated with flooding.

Dann (in press) observed that spur-winged plovers feed primarily on beetle larvae and earthworms. Earthworms migrate to deeper soil as the surface dries out (Edwards and Lofty 1972), and their numbers increase as soil moisture increases (Duweini and Ghabbour 1965). Thus, the largest number of earthworms will be found near the surface when the water table is high. The high correlation between territoriality and water table in this study indicates that spur-winged plovers establish and maintain breeding territories when food is most readily available.

Perrins (1970) noted that there was a lag period between surplus food availability and nesting in which gonadal development and egg formation took place. Barlow et. al. (1972) noted that after nest loss a period of 6 - 28 days elapsed before renesting. After brood loss, when the gonads had presumably regressed further, 19 - 21 days elapsed before renesting. Gonadal development does not explain the period between territorial establishment and nesting, 14 weeks in one case.

The correlation between onset of laying and temperature was not high. Barlow et. al. observed spur-winged plovers breeding successfully in Southland while there was still

snow on the ground. This study was not long enough to determine which factors were most closely related to nesting. Bourke (1953) observed early nesting in spur-winged plovers as an apparent response to increased water table level. The pair then renested within the normal breeding season. The pair which produced a double clutch in this study were also the first pair to breed.

These observations agree with Lack's (1966) hypothesis, that the immediate factor initiating laying in birds is the female's obtaining enough food to lay eggs while termination of laying relates to when the young can be raised. Immelmann (1971) noted that the most important ultimate factor for nearly all bird species is the availability of an adequate food supply, and breeding coincides with maximum food availability. Thus climatic factors are usually indirectly related to breeding through changes in food supply.

Thomas (1969) noted that some spur-winged plovers maintained territories throughout the year, but these were uncommon. Temple-Smith (1969) noted that where these territories occurred there was less intraspecific defence during the non-breeding season and territorial owners tended to join the flocks for long periods during the middle of the day. I observed no territoriality in February and March. Territories within the study area were significantly larger than those within Temple-Smith's study area (Mann-Whitney  $U = 252$ ,  $= t_s = 2.694$ ,  $P < 0.01$ ). The population he studied was at equilibrium and all suitable habitat within the study area formed parts of territories during the breeding season. The average territory size he observed was 2.4 Ha. (s.d.  $\pm 1.1$ ). The study area comprised a golf course.

In contrast Barlow et. al. (1972) noted that no nesting occurred on a golf course or an airfield within their study area. It was suggested that, although the areas were suitable for nesting, regular pedestrian movement prohibited its occurrence. Territory size ranged from 8.4 to 19.4 Ha.

(Mean 14.5) for 9 territories measured in Southland and there were large spaces between territories. There was some doubt about the validity of the territorial measurements. They also noted that only 31 of 222 nests were started in areas accessible to stock. This suggests that the Southland population had not reached peak density and sub-optimal habitat was not utilised, but numbers were stable from 1965 to 1970.

At high density space appears to limit the breeding population but pairs still maintain areas larger than necessary for foraging. I postulate that the major function of breeding territories in spur-winged plovers is to decrease the probability of chick or nest predation. Eggs and chicks are cryptically coloured and Tinbergen et. al. (1967) demonstrated that when predators search for camouflaged prey selection favours spacing-out. Krebs (1971) showed that great tit (*Parus major*) nests were more susceptible to predation when they are closer together. To assess the importance of spacing-out as an anti-predator strategy in spur-winged plovers further study of high density populations is needed.

If space is limiting the breeding population in high density populations the maintenance of a territory all year would ensure an optimum breeding area. This might explain why some territories are defended all year in Australia.

Different authors cite varying periods of incubation from 27 to 32 days. Thomas (1969) observed that some birds start incubation from the laying of the first egg. Considering the synchronous hatching it is unlikely that this is true incubation causing development of the embryo. Therefore commencement of apparent incubation before clutch completion may partially explain the different periods that have been observed. Environmental temperature may also be important in length of incubation. Drent (1972) showed that exposure of eggs results in rapid heat loss. The recovery period required to return the eggs to the initial equilibrium

temperature is quite lengthy. At lower temperatures heat loss will be greater and the subsequent recovery period longer. Lind (1961) observed that the black tailed godwit (*Limosa limosa*) covers the eggs at night in the laying phase, particularly at low air temperatures when there is a danger the embryos might freeze. Barlow et. al. (1972) observed an average incubation period of 30-31 days in Southland, and this may be explained by cooler air temperatures during the breeding season than in this study area.

Thomas (1969) and Dann (1977) have compared egg sizes of populations from different latitudes. The increase in egg width with latitude in the populations studied by these researchers conforms with Bergmann's rule. Dann noted that there was no significant difference between the egg width of the Invercargill population and the New South Wales population. He ascribed this difference in the expected trend to the derivation of the New Zealand population from a northern Australian population. He assumed that the New Zealand population had not been established long enough for change in egg size from the ancestral stock to become evident.

The variation of egg size with latitude is presented in Table 3.5. The data collected by Temple-Smith (1969) in southern Tasmania conforms with the latitudinal variation observed by Dann (1977). The egg width is significantly larger than that of the Hobart population and significantly smaller than the Phillip Island's population ( t-test  $P < 0.001$  for both comparisons). Because of the large variation in size within the northern Tasmanian eggs there is no significant difference between the egg size of this population and that of the Phillip Island population or the Invercargill population. (t-test  $P < 0.1$ ). Egg width at Puke Puke is significantly smaller than at Invercargill (t-test  $P < 0.001$ ). This indicates that egg size changes rapidly in response to changing environment and egg size should not be used to indicate latitudinal



TABLE 3.5: EGG SIZE VARIATION IN SPUR-WINGED PLOVERS WITH LATITUDE

Locality and Latitude	N.	Mean Length	Mean Width	Source
Invercargill, Southland 46°24'	60	49.4 ± 2.00	35.3 ± 1.00	Barlow et. al.1972
Hobart, Tasmania 42°55'	171	51.33 ± 2.25	37.44 ± 1.24	Thomas 1969
Southern Tasmania 42°-43°30'	108	50.35 ± 2.37	36.47 ± 0.44	Temple- Smith 1969
Northern Tasmania 41°-42°	136	47.44 ± 8.45	35.59 ± 6.11	Temple- Smith 1969
Pukepuke, Manawatu 40°19'	46	45.8 ± 1.58	33.3 ± 0.85	Present Study
Phillip Is. Victoria 38°30'	82	48.78 ± 1.93	35.78 ± 0.90	Dann 1977
L. Bathurst, New South Wales 35°2'	16	49.0	35.4	Thomas 1969

location of the ancestral stock of the New Zealand population.

The average age of birds within the study area is probably low because the population is recently established. Coulson (1966) observed that egg size increases with age in Kittiwakes (*Rissa tridactyla*), Davis (1975) noted a similar correlation in the herring gull (*Larus argentatus*). Thus the small egg size could be partially explained by a generally young breeding population in the Manawatu.

The adaptive significance of clutch size in birds has been discussed by Lack (1954, 1966, 1968), Cody (1966), Klomp (1970), and Charnov and Krebs (1974). MacLean (1972) considered that the maximal clutch size of four in the Charadrii had not been adequately explained. Sharland (1943a, b) saw spur-winged plovers successfully incubating clutches of 5 and 6; therefore they are not limited by the number of eggs they can cover. The ability to lay repeat clutches after nest destruction indicates that 4 eggs is not the physiological limit.

Safriel (1975) proposed a model for the determination of clutch size in birds with nidifugous young using predation pressure as the primary limiting factor. He showed that when clutches were experimentally increased to 5 in the semipalmated sandpiper (*Calidris pusilla*) they were significantly more susceptible to predation. The model provides a feasible explanation of clutch size in spur-winged plovers.

Tinbergen et. al (1967) noted that egg-shell removal is common in several ground nesting species. They demonstrated that the behaviour aided the concealment of camouflaged nests and functioned as an anti-predator device. Egg-shell removal in spur-winged plovers aids concealment of eggs during incubation if breakage occurs. It has little value in protection of chicks as they leave the nest within hours of hatching.

Sharland (1943b) saw two spur-winged plovers sitting on a clutch of 7 eggs with one off duty bird in attendance. Barlow et. al. (1972) reported a clutch of 6 eggs associated with three adults. Emlen (1978) noted that most species of co-operatively breeding birds exist in relatively stable environments where all suitable habitat is utilised. In many cases the inclusive fitness of both breeders and helpers is increased, because the helpers aid relatives to increase reproductive success and simultaneously gain experience. The long period of post-fledging dependence in spur-winged plovers could promote the evolution of co-operative breeding. Chicks often remain with their parents until the start of the next breeding season. (Barlow et. al. 1972).

Ricklefs (1968) reviewed the type and significance of growth patterns in birds, but was primarily interested in altricial species. Weight growth curves are usually sigmoid, but in nidifugous species the young normally fledge before attaining adult weight. Spur-winged plovers are no exception and only the logarithmic phase of growth is completed before fledging.

It is significant that the tarsus and culmen are almost fully grown by the date of fledging. These structures are essential to survival and at full size allow more effective foraging. In contrast the spurs are poorly developed. They are only used in highly aggressive situations and courtship. Adults continue to defend young from predators after fledging. Thus it is probable that the spurs are not fully developed until sexual maturity. The wattles may have some thermoregulatory function as they are highly vascular. Temple-Smith (1969) noted that in hot weather they appear red indicating increased blood flow. Weight and wattle length have the highest correlation coefficient (Table 3.4), both are 60% of that found in adults at fledging.

The growth rate of chicks observed during this study were comparable with those Temple-Smith (1969) recorded.

Lines were drawn by model I linear regression, growth of the culmen most nearly approximated a straight line (Table 3.6). The overall growth patterns are likely to be curves (Ricklefs 1968).

It was expected that some of the young banded in 1979 would breed in 1980. Barlow et. al. (1972) observed breeding in some one year birds. In low density, increasing populations selection will favour early reproductive output. Due to the high emigration rate early breeding was not observed. Both of the banded birds which remained in the intensive study area were paired in 1980 and one was territorial, and this suggests that some of the previous year's young bred in 1980.

Comparative breeding success is tabulated in Table 3.6. The figures given for this study relate to the eggs which were found. Clutch size is similar in all studies, as is average brood size at fledging in the Manawatu and Tasmania. Nest and hatching success are related; both are over 20% higher in this study than any other study. There are three possible explanations for the difference. Firstly, failure to find unsuccessful nests. The quantity of time spent in the field in 1980 was greater than in most of the other studies. Therefore, there is little likelihood that success in nest discovery was significantly lower. If the two nests discovered in 1979 are ignored nest success was 68.75% and hatching success was 72%. Secondly, different degrees of disturbance of breeding birds. Barlow et. al. (1972) noted that interference during laying or hatching promoted nest desertion. The use of a drop trap over the nest may inhibit breeding success. Only Barlow et. al. used this method of trapping extensively. The degree of interference by other observers would be comparable with this study. Thirdly, there was little competition for space. All territories were in optimum habitat, stock numbers were low and breeding density was low. In addition there are fewer potential predators in New Zealand than in Australia. This could also explain

TABLE 3.6: COMPARATIVE BREEDING BIOLOGY DATA

Source	Period of Study	Study Area	Average Clutch Size	Nest Success (%)	Hatching Success (%)	Fledging Success of Chicks (%)	Average Brood Size at Fledging	Broods that Fledge Young (%)	Breeding Success (%)
Thomas 1969	1964-1966	Tasmania	3.53	44, 49, 50			1.52, 1.68, 1.75	20, 32, 37.9	4.8, 6.8, 8.1 * * *
Temple-Smith 1969	1968	Tasmania			49.1	45.8			22.8
Barlow et. al. 1972	1965-1969	South-land	3.75	49.8		25.0 *			9.2
Dann In Press	1975	Victoria	3.58	44.4	45.0	19.3			8.9
Moffat	1979-1980	Manawatu	3.60	72.2	74.1	46.5	1.66	86.7	34.5

\* Approximate

the higher than average fledging success. However, this does not explain the difference between Manawatu and Southland. The population in Southland appeared to be at a similar density to that in the Manawatu. It is possible that temperature differences between the two study areas are important, along with the increased interference due to drop trap capture of incubating birds.

The fledging success in this study is comparable with that observed by Temple-Smith (1969). He postulated that chick mortality was primarily associated with adverse environmental conditions. Chicks less than 2 weeks old are susceptible to cold and rapidly become torpid if separated from the parents in cold conditions. I observed that parents return rapidly to chicks of this age after disturbance and brood them. As the chicks feed in a group at this age they are unlikely to become separated from their parents.

In all studies the majority of chick mortality occurred in the first two weeks. Thus Temple-Smith's hypothesis is plausible. The behaviour of very young chicks (cf 2.13) means that they are more susceptible to predation, but adults are most aggressive during this period and chase potential predators from the territory. Ricklefs (1972) noted that nest predation is the most important mortality factor for small land birds, but larger birds such as seagulls were relatively immune to predators.

Accidental trampling by stock is probably a major cause of chick mortality. At least two chicks were killed by cattle in this study. Disease may also be important. One chick weighed only 68g. at 4 weeks and did not survive to the following week. The morphological data from this chick is not included in the growth data.

Boyd (1962) reviewed mortality and fertility of European Charadrii. Adult mortality rates based on banding surveys ranged from 15.7% to 51.9% with most in the

range 30 - 45%. Death rate and bodyweight were inversely correlated and closely related species tended to have similar mortality rates. Adult death rate in the Lapwing (*Vanellus vanellus*) was 34.3%. Most Charadrii had a hatch success of 66 - 96% and a fledging success of 40 - 80% which varied from year to year. These figures are comparable with the results of this study. However, the low values obtained in other studies indicate that adult mortality in spur-winged plovers was less than 30%. A breeding success of less than 10% maintained populations at equilibrium, although Temple-Smith (1969) observed a breeding success of 22.8% in an equilibrium population.

The high breeding success in the study area explains the rapid rate of increase in plover numbers within the Manawatu, and other recently colonised areas in New Zealand.

## CHAPTER 4

FLOCK ECOLOGY4.1 Introduction

Many species of birds are gregarious for parts of the year (Orians 1971). The study of flocking in spur-winged plovers has been largely neglected. Temple-Smith (1969) described some of the behaviour of birds in the flocks, but other authors only noted flock size in the non-breeding season. There are several advantages of flocking behaviour. These are analysed and discussed.

4.2 Habitat

Flocks were observed on tilled land, young crops, grazed crops, river flats, hay and grain stubble, rough and improved pasture. They did not utilise areas where the average height of the ground cover exceeded fifteen centimetres. When flocks foraged in areas of uniformly short cover, such as tilled land or improved pasture, they moved to areas of longer cover to rest e.g. ungrazed grass along fence lines or adjacent fields containing rushes, thistles or similar cover. Thus flocks used a much wider range of habitat than breeding birds.

4.3 Flock Size and Movement

During the non-breeding season spur-winged plovers aggregated into flocks of variable size (Figs. 4.1, 4.2 and Table 4.1). In September only a few non-breeding birds remained in the flocks. They were nomadic during the breeding season (Table 4.1), and seldom remained in the same area for more than a few hours.

In November flock size increased as family groups and territorial pairs joined the flocks. By the end of January all of the birds had left their territories and were in the flocks. From January until May the numbers in flocks were relatively stable. One flock used an



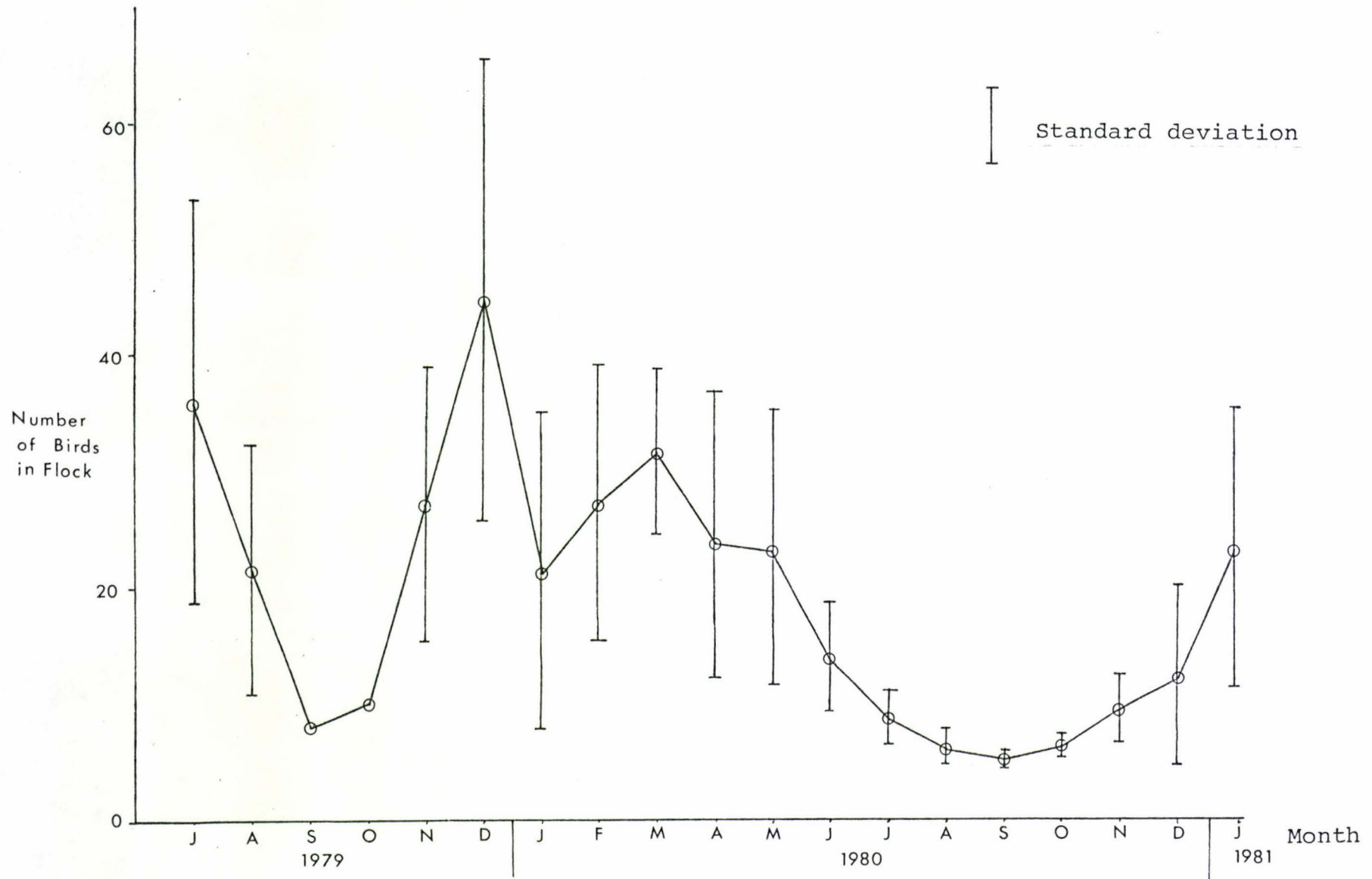


FIGURE 4.1: AVERAGE FLOCK SIZE DURING THE STUDY PERIOD

TABLE 4.1: FLOCK MOVEMENT AND SIZE

Date	Area*	Land Type	Range of Flock Sizes
13.7.79- 31.8.79	1 + 2	Rough pasture	14-69
1.9.79- 13.11.79	Nomadic	All types of field with cover < 15cm.	8
13.11.79- 11.12.79	3	Old chou moellier	22-42
11.12.79- 8.1.80	4,5,6	Rough and improved pasture, river flats	40-75
18.12.79- 18.1.80	7	Hay stubble short grass	
29.1.80- 16.6.80	8	Rough pasture + tilled land + chou moellier	8-39
18.1.80- 5.2.80	1,3,4,5, 7,9,10	Rough pasture, hay stubble + river flats	6-17
5.2.80- 21.2.80	11	Hay stubble	20-40
26.2.80- 28.4.80	12	Tilled land + newly planted grass	
2.5.80- 16.7.80	1,2,7,13 12	New grass, rough + improved pasture	8-23
16.7.80- 31.7.80	1 + 7	Rough pasture	5-8
1.8.80- 11.11.80	Nomadic	All types of field with cover < 15cm.	5
11.11.80- 6.1.81	14 + 2	Rough pasture + hay stubble	7-21
20.11.80- 6.1.81	8,15,16	Rough pasture	8-19
25.11.80- 10.12.80	Entire study area	Various	5-17
10.12.80- 6.1.81	4	Rough pasture	21-35

\* See Figure 4.2

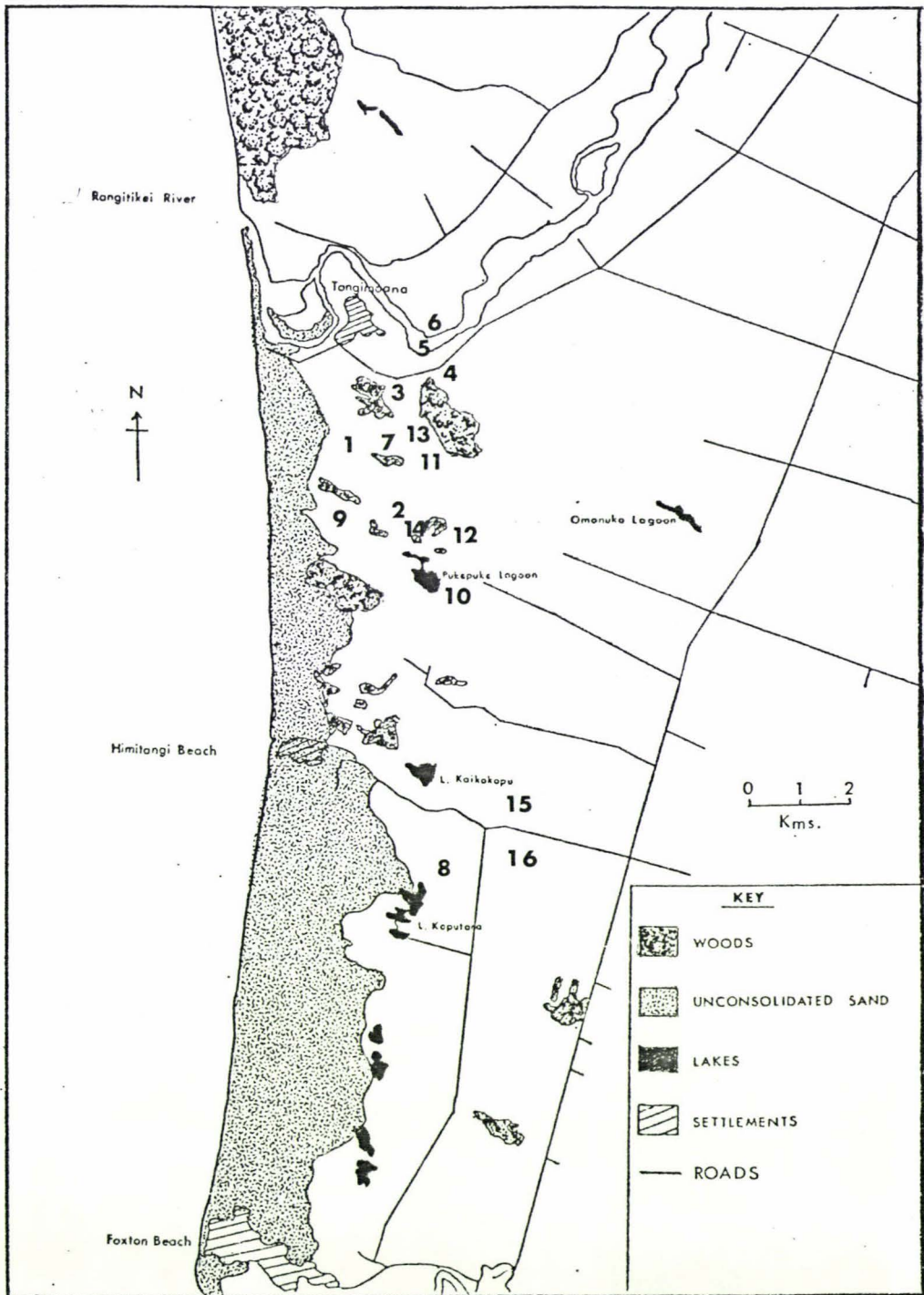


FIGURE 4.2: DISTRIBUTION OF FLOCKS WITHIN THE STUDY AREA

area near Lake Koputara (Fig. 4.2) for more than four months. There was daily interchange of individuals between flocks.

In May when the water table rose the flocks began to split up. Pairs left to establish territories and the smaller groups became increasingly mobile.

In December 1979 most of the ground cover in the intensive study area was longer than fifteen centimetres prior to hay cutting. The plovers congregated in one of the few fields with vegetation less than 15cm. The largest flock consisted of seventy five birds. Some families with banded young flew south and joined the flock near Koputara where the cover was generally shorter. The large flock split up when hay stubble became available.

During summer the level of the water table dropped. The only surface water in pasture was in stock water holes or drains. Plovers used these for drinking and bathing but rivers and lakes were also used. Extensive areas of surface water existed in fields during the rest of the year and all drinking and bathing was accomplished in the foraging areas.

#### 4.4 Time Budgets

Time budget data for September 1979 could not be collected because of the increased mobility of the flock. Five types of behaviour were recorded:

1. Foraging: consisted of drinking, eating and search time. Pairs and families fed in distinct groups and the flocks dispersed over the foraging area (Plate 14). The flock did not advance across pasture in a group, as starlings (*Sturnus vulgaris*) or rooks (*Corvus frugilegus*) do. Groups moved randomly throughout the foraging area. Flocks of thirty to forty individuals foraged over areas of up to five hectares.

2. Resting or loafing: in the middle of the day, especially in spring and summer, many of the individuals in a flock grouped together in an area of longer cover. They stood or sat relatively stationary for considerable periods, some roosted for a few minutes. Paired birds in the resting group sat or stood within a few centimetres of each other. Distance between individuals was usually about one metre; thus a group of thirty to forty resting birds grouped in an area of about one tenth of a hectare.

3. Preening: no ritualized preening was observed. All preening was concerned with plumage maintenance. Bathing was considered to be a type of preening.

4. Flying.

5. Aggression/Courtship: grouped together because much of the aggression appeared to be related to pair bond maintenance.

The number of hours of daylight varied. Therefore both percentage and amount of time spent in each activity over the course of a year were graphed (Figs. 4.3, 4.4). The number of hours spent feeding was inversely correlated at the 0.001 level with water table level (Table 4.2). From December to March, when the water table was low, nine to ten hours a day were spent feeding. This was also the period when nearly all the birds were in the flocks. From April to October six to eight hours a day were spent feeding. Multiple regression analysis demonstrated that feeding was most highly correlated with a combination of water table level, temperature and day length. The coefficient of determination was 81.4%.

The number of hours used in preening was relatively constant throughout the year. More time was spent in preening from October to December when family groups joined the flocks. The activity was correlated at the 0.02 level with day length (Table 4.2), and the largest

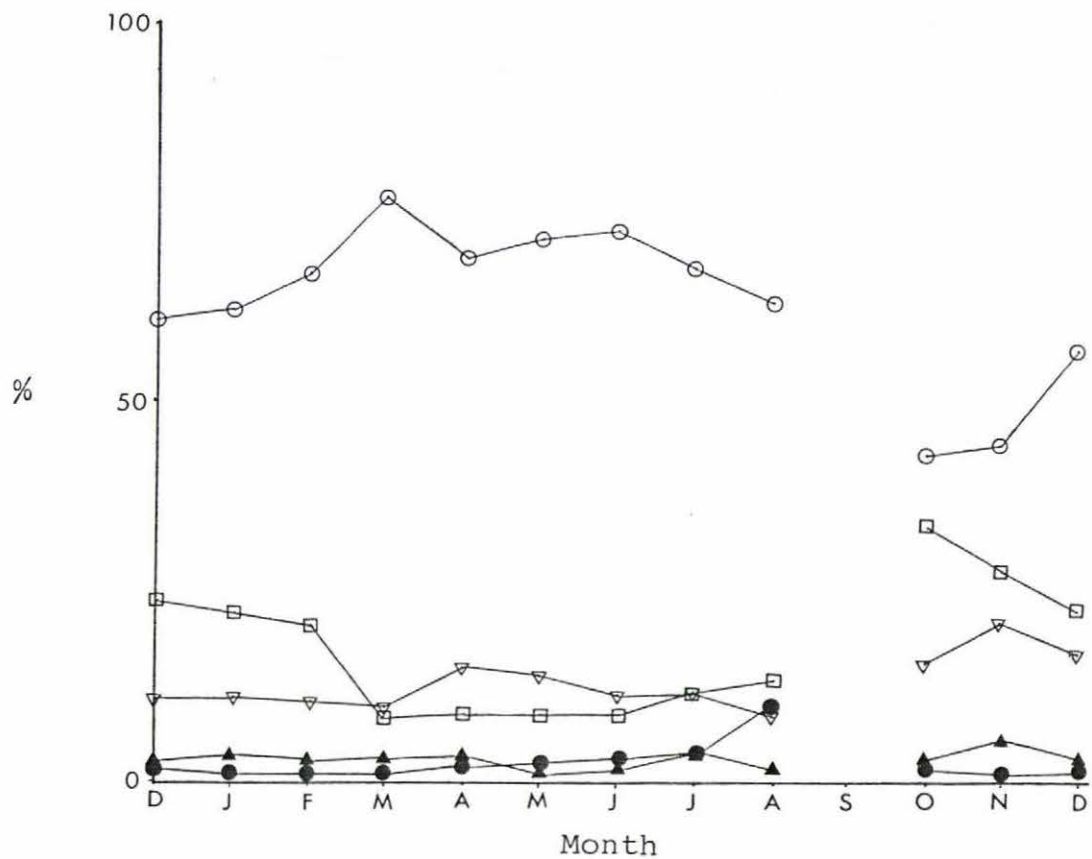


FIGURE 4.3: FLOCK BEHAVIOUR OVER TIME (PERCENTAGES)

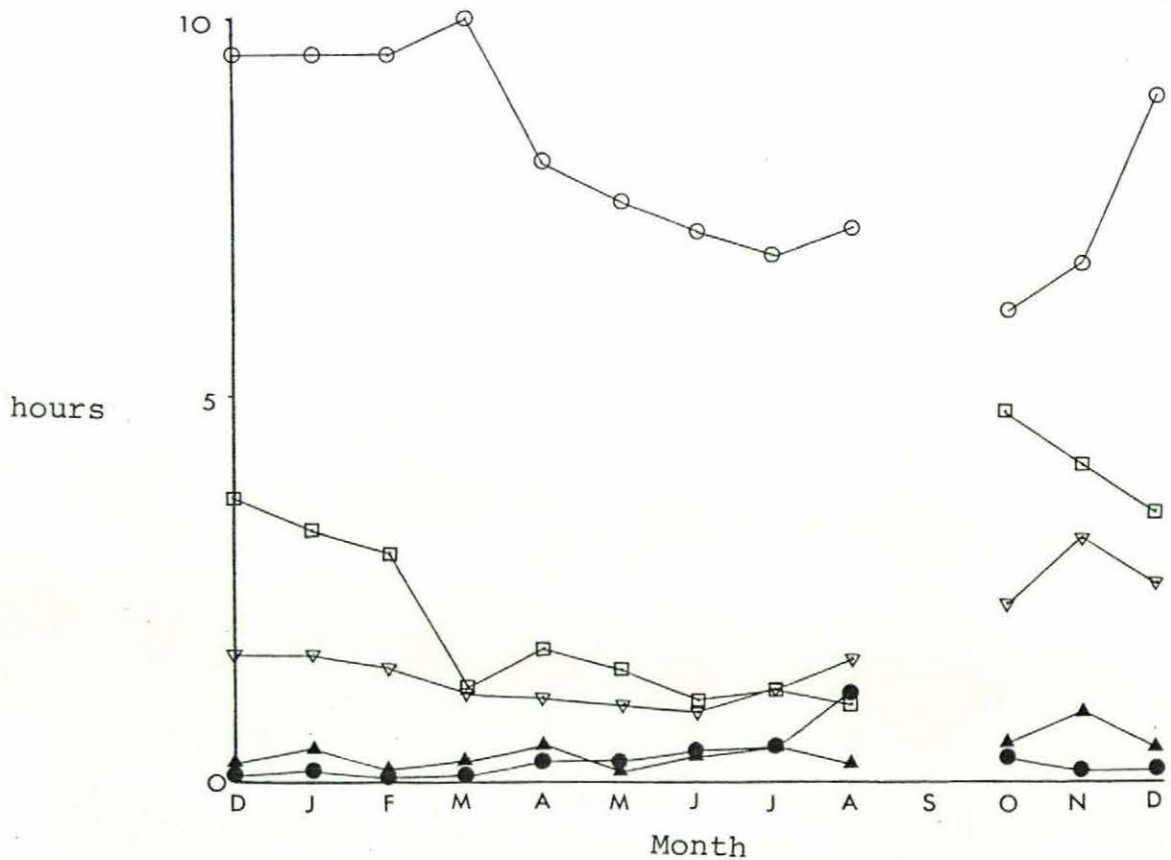


FIGURE 4.4: FLOCK BEHAVIOUR OVER TIME (DAILY HOURS)

Feed ○ Preen ▽ Rest □ Fly ▲ Aggression/Courtship ●

coefficient of determination was obtained by regression with water table and day length (Appendix 2).

Resting was correlated at the 0.001 level with day length. Regression with water table and day length gave a coefficient of determination of 83.0% (Appendix 2). Loafing peaked in October and then gradually declined to February. From March to August very little resting occurred during the day.

Time spent flying was not significantly correlated with any environmental factor (Table 4.2). Throughout most of the year little time was spent in flying. The flocks were most mobile in September and this is the reason for the lack of time budget data in that month. The increased mobility of flocks during July and August is not reflected in my data because the most stable flocks were studied.

The level of aggression and courtship within the flocks increased markedly in August but during the rest of the year was very low. There was a correlation with temperature at the 0.05 level (Table 4.2) but no significant multiple regressions (Appendix 2).

The percentage of time utilised in feeding, resting, and aggression was correlated with day length (Table 4.3). The number of hours spent preening was positively correlated at the 0.01 level with resting and flying. The percentage of time spent feeding was inversely correlated with preening, resting and flying. The correlation coefficient between feeding and preening was  $-0.920$  which is highly significant. The percentage of time spent preening was correlated with the percentage of time spent flying (Table 4.3).

The diurnal rhythm of flock birds varied from season to season (Fig. 4.5 and Appendix 3). When day length and food availability (as reflected in water table level) allow, there were two distinct peaks of foraging activity separated

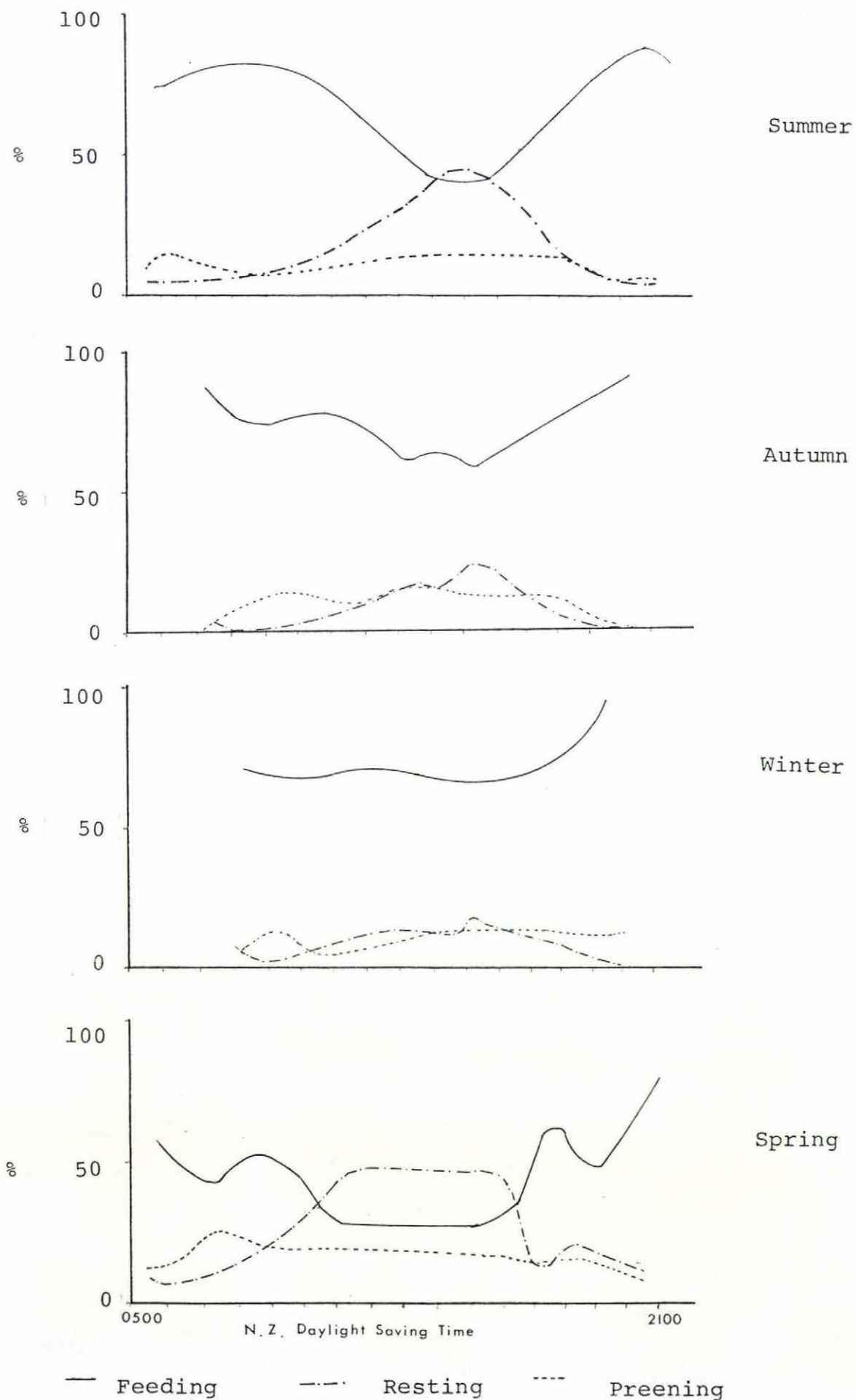


FIGURE 4.5: SEASONAL VARIATIONS IN DIURNAL RHYTHM



TABLE 4.2: CORRELATION MATRIX OF FLOCK BEHAVIOUR WITH ENVIRONMENTAL FACTORS

	Feeding	Preening	Resting	Flying	Aggression/ C
Preening	-0.153				
Resting	-0.021	0.746			
Flying	-0.263	0.788	0.536		
Aggression	-0.477	-0.393	-0.233	-0.286	
Water Table	-0.893	0.178	-0.009	0.211	0.505
Day length	0.495	0.660	0.835	0.440	-0.459
Rainfall	0.135	0.077	0.181	0.358	0.098
Temperature	0.723	0.440	0.605	0.193	-0.591

TABLE 4.3: CORRELATION MATRIX OF PERCENTAGE OF MONTHLY TIME UTILISED IN VARIOUS ACTIVITIES WITH ENVIRONMENTAL FACTORS

	Feeding	Preening	Resting	Flying	Aggression/ C
Preening	-0.677				
Resting	-0.920	0.456			
Flying	-0.528	0.636	0.310		
Aggression	0.098	-0.369	-0.273	-0.174	
Water Table	-0.379	0.457	0.081	0.301	0.477
Day length	-0.571	0.278	0.753	0.170	-0.559
Rainfall	-0.141	-0.084	0.146	0.382	0.037
Temperature	-0.254	0.084	0.511	-0.076	-0.681

SIGNIFICANCE LEVEL OF CORRELATION COEFFICIENTS WITH 10° OF FREEDOM

P <	0.1	0.05	0.02	0.01	0.001
Correlation Coefficient	.4973	.5760	.6581	.7079	.8233



PLATE 14: FLOCK BIRDS FEEDING



PLATE 15: FLOCK FLYING

by a resting period in the middle of the day. Preening occurred at a similar level throughout the day although it was noted that preening bouts lasted longer during a loafing period. Flying and aggression were scattered throughout the day.

#### 4.5 Discussion

Presumably flocking has evolved because it increases Darwinian fitness. Two major advantages of flocking are increased foraging efficiency and decreased predation. In an environment with patchy or unpredictable food resources flocking may enable birds to exchange information about food sources (Ward and Zahavi 1973). Although this is the most likely functional explanation of the large communal roosts of birds such as starlings, herons and seabirds, it is difficult to test (Bertram 1978).

It is probable that the advantages of increased predator protection are the primary ultimate factor for flocking in many species (Orians 1971). Kenward (1978) demonstrated that woodpigeons (*Columba palumbus*) were less susceptible to predation in flocks because of increased predator detection. Spur-winged plovers probably benefit in a similar manner. Within the study area there were no potential predators of flying spur-winged plovers. When a potential predator was spotted by a flock member, the alarm call was uttered and this alerted the rest of the flock, especially resting birds. If the predator continued to approach the whole flock would take off and fly about as a distinct unit until the predator left (Plate 15). In response to prolonged disturbance the flock flew to another foraging area.

Plovers within flocks are able to rest for large portions of the day because some members of the flock are active and therefore vigilant. The correlation between feeding and water table adds further evidence to the hypothesis discussed in Chapter 3. that more food is available when the water table is high. The strong inverse

correlation between the percentage of time spent feeding and the percentage of time spent resting suggests that when food is plentiful the time saved is used in resting, so minimizing energy cost. Pyke (1979) found that golden-winged sunbirds (*Nectarinia reichnowi*) behave so that energy cost is minimized, and suggested that this type of behaviour maximized fitness. Flocking in spur-winged plovers is also likely to maximise fitness because it allows resting.

The improved detection benefit of being in groups does not increase with increasing group size indefinitely. However, larger groups may increase individual fitness by decreasing the chance of being the prey (Hamilton 1971). Optimal group size, especially in temporary associations such as spur-winged plover flocks, is dependent on the relative strengths of different selective pressures. The most important ultimate factor that reduces group size is probably the food supply of an area. In large groups increased competition for food will decrease individual fitness. Large groups may also attract more predators.

Most flocks within the study area during the non-breeding season consisted of 20 to 30 birds. The small groups were probably due to low population density. Temple-Smith (1969) recorded flocks of 70 to 80 birds, Thomas (1969) saw flocks of up to 500 birds, and Sharland (1943a) saw a flock of over 750.

Territorial birds are restricted to areas with patches of longer cover to camouflage unfledged young. This explains why flock birds can use a wider range of habitat. It is significant that flock birds still move to areas of longer cover to rest, where they are camouflaged. Areas where the average ground cover is over 15cm. may not be utilised for several reasons. Detection of ground predators would diminish and locomotion would be impeded. Visual communication within the flock and especially between pairs and family groups may be important and would be

impaired by long vegetation.

The highly mobile nature of the small non-breeding flocks present during the breeding season is probably the result of two major factors. Firstly, much of the optimum habitat is defended by territorial birds. When flock birds land in a territory they are promptly evicted by the residents, therefore being forced to move. Secondly, most of the birds in the flocks are paired and could be searching for suitable territories.

The increase in preening in late spring and early summer is probably due to the influx of young into the flocks during this period. In these recently fledged birds, nestling down is not fully replaced by feathers, and preening efficiency may be lower in young birds, therefore taking longer. Additionally, the long day length and high food availability allow more time for activities other than feeding. This is indicated by the inverse correlation of feeding with resting, preening and flying. As the amount of time spent flying increases, it is logical to assume that the amount of time spent preening will also increase, as expected the two activities are correlated.

The increase in aggression/courtship from June to a peak in August was caused by courtship interactions before territorial establishment. Increased aggression between pairs was one of the results. Parents also chased off the previous years chicks if they were still present during this period.

Harcourt (1978) observed that peaks of feeding in the morning and the evening separated by a midday rest period are common in many diurnal animals. Individuals are usually closer together during rest periods than foraging periods. These observations are also true of spur-winged plovers. Harcourt demonstrated that patterns, as well as frequencies, of social interaction change according to the predominant group activity, and these can be important

in correctly interpreting social relationships of the study animals.

I did not observe a change in patterns of aggression between feeding and resting periods. The spur-winged plover flocks were temporary, non-hierarchical, changeable groups whereas Harcourt was studying stable family hierarchies. Social interactions in a hierarchy are integral to the group structure and more frequent than in a transient group. Therefore, patterns of social interactions will be more important in this type of group.

It could be expected that aggression and flock size would be related but this was not apparent. However, the scan sampling technique only records the amount of time spent in each activity. As aggressive interactions are of short duration, significant seasonal fluctuations may have been missed.

Spur-winged plovers were often heard calling both on the ground and in the air at night, especially if there was a bright moon. This nocturnal activity could have important effects and may partially invalidate conclusions drawn from time budgets during daylight.

## CHAPTER 5

SYNTHESIS

Spur-winged plovers have benefited from the advent of European farming practices in Australia. This allowed the population to increase and lead to the spread of the species (Thomas 1969). Similarly, in New Zealand the replacement of bush by pasture made large areas of suitable habitat available. The poor utilisation of pasture by indigenous bird species has resulted in the rapid increase and spread of introduced birds in this type of habitat. I consider that the increase in the spur-winged plover population in this country is the result of high breeding success.

MacArthur and Wilson (1967) noted that augmentation of the intrinsic rate of increase is likely to be found in the earliest stages of colonization. It is probable that this increase occurs because of a decrease in density-dependent limiting factors. In this study area the breeding success of spur-winged plovers was significantly higher than in Australia. This was primarily due to an increase in nest and hatching success, fledging success was also enhanced. As a consequence of the low population density, territory size was enlarged. Most pairs established territories, but there was still large spaces between the majority of territories. Territories were only established in areas of relatively low stock density with patches of longer cover. Greater spacing in optimal habitat reduced the probability of predators finding the nest or chicks (cf. Tinbergen et. al. 1967). Because of the low stock density the chance of accidental trampling of nests was reduced.

Other agents may be important to the increased breeding success besides stochastic factors. There is usually a decrease in interspecific competition on islands allowing niche diversification (MacArthur and Wilson 1967). There are fewer potential predators in New Zealand than Australia

and there are several climatic differences.

In Australian populations some territories are defended throughout the year. This was not observed during this study; probably reflecting a lack of competition for space. The absence of contact fighting in the flocks was probably a result of the unstable nature of the flocks and absence of a dominance hierarchy. This was also a consequence of the low population density. Stability of flock composition would lead to increased social interactions and development of dominance hierarchies, as observed by Temple-Smith (1969). However, the much larger size of the dominant bird in the flock he studied may have led to an anomalous situation. Further research is required to clarify the point.

Some displays of spur-winged plovers serve multiple functions (Table 5.1). The upright, choking, and false feeding displays were observed in different contexts. Beer (1975) noted that many displays include elements of both hostility and courtship. Many territorial birds were sexed by observation of copulation, but the sex of intruders and flock birds could not be determined because of the lack of sexual dimorphism. Thus it was difficult to interpret interactions and quantitative data were not obtained.

The sex ratio may be about unity as only one unpaired bird was observed during the breeding season. Incubation and brooding of the young is shared. Therefore, mortality should be comparable and both parents are necessary for fledging of the young (Barlow et. al. 1972). The reported instances of co-operative breeding occurred in high density populations where space could have limited breeding (Sharland 1943a,b). The inclusive fitness of the parents may have been increased by allowing female offspring to remain in the territory and breed. The rarity of co-operative breeding implies that population density has to be extremely high before it is advantageous



TABLE 5.1: DISPLAYS OF SPUR-WINGED PLOVERS  
AND CONTEXTS IN WHICH THEY OCCUR

	Non-social disturbance	Rivalry	Courtship	Copulation	Nest-site selection	Defence of Nest	Defence of Brood
Upright	X	X	X				
Choking		X	X		X		
False Feeding	X	X	X	X			
Display Flight			X				
Facing Away				X			
Pre-Copulatory				X			
Scrape					X		
Dive Attack						X	X
Forward						X	X

Variations in the length and timing of the breeding season from year to year are correlated primarily with water table level. The ultimate factor is probably the availability of food for the female. Dann (in press) has correlated laying with invertebrate biomass. The evolution of a long breeding season and protracted post-fledging dependence are probably adaptations to the original, rather than the present breeding habitat. The original habitat, in Tasmania and south eastern Australia, has unpredictable weather; so asynchronous nesting would increase the probability of some chicks surviving.

Amongst the vanelline plovers only the lapwing has been studied in detail, which makes a comparative review of the taxonomy of the genus based on behaviour impossible. In comparing the behaviour of spur-winged plovers and lapwings, the most apparent differences in the displays are in courtship. The reasons for these differences are probably related to differing morphology and life histories. Lapwings are sexually dimorphic and form a new pair bond each year. They use the song flight to advertise territorial boundaries.

Less than 50 years have passed since the arrival of the founding members of the New Zealand population of spur-winged plovers. This is a very short period in evolutionary terms and little or no change from the parent population was expected, but there has apparently been a rapid change in egg size. This may be due to the founder effect (Mayr 1963), but it is doubtful if this effect is very important. There has been a conspicuous absence of change in many species introduced into New Zealand in small numbers. Part of the observed difference may be because of a relatively young breeding population. Also further immigration from more northerly Australian populations may have taken place (Barlow 1972, Sutton pers. comm. 1980).

The observed differences are enough to throw doubt on the validity of the use of egg size in determining the

derivation of the New Zealand population. Similarity in plumage pattern between the northern Australian population and the New Zealand population is the best evidence of the source of the population in this country. Further data on variation of egg size with latitude within both countries is required before definite conclusions can be reached.

## APPENDIX 1

TABLE 1A: TERRITORIES, NESTS, AND ENVIRONMENTAL FACTORS

Year	Month	Territories	Nests started	Nests Extant	Level of water table (height above sea level) (centimetres)	Mean day length (hours)	Total rainfall (millimetres)	Mean Temperature (degrees celsius)
1979	J	15	7	10	641.5	9.62	44.6	7.4
	A	18	5	12	648.7	10.57	119.3	8.7
	S	23	5	9	645.2	11.83	57.0	11.2
	O	18	3	8	646.0	13.17	87.5	12.9
	N	16	0	5	638.2	14.35	75.2	15.0
	D	9	0	0	636.1	15.00	125.3	16.4
1980	J	3	0	0	633.9	14.68	64.0	16.9
	F	0	0	0	627.9	13.65	40.0	16.4
	M	0	0	0	630.5	12.35	139.1	15.3
	A	8	0	0	644.4	11.02	55.1	12.6
	M	15	0	0	642.5	9.90	37.3	10.6
	J	17	1	1	645.0	9.35	61.7	7.1
	J	20	11	12	641.4	9.62	64.1	6.7
	A	21	4	12	644.0	10.57	86.8	8.6
	S	19	7	9	646.7	11.83	114.5	11.6
	O	18	2	6	649.2	13.17	75.1	13.7
	N	15	0	1	643.1	14.35	120.7	12.8
	D	8	0	0	638.2	15.00	33.1	15.9

In subsequent tables the t ratio is equal to the partial correlation coefficient divided by the standard deviation of the partial correlation coefficient. The significance level of all t values can be obtained from a table of Student's distribution. t values which are significant at the 0.01 level are marked with an asterisk. D.F. stands for degrees of freedom.  $r^2$  is the coefficient of determination adjusted for degrees of freedom. The coefficient of determination is the square of the correlation coefficient (r). It is the amount of variation in x which is explained by y.

TABLE 1B: MULTIPLE REGRESSIONS OF TERRITORY NUMBERS WITH ENVIRONMENTAL FACTORS

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	t ratio	t ratio	t ratio
Water table	3.49*	3.57*	4.07*
Day length	2.15	2.17	
Rainfall	-0.42		
Temperature	-2.75	-2.81	-1.74
D.F.	13	14	15
$r^2$	75.8%	<u>77.2%</u>	71.6%

$r^2$  for water table vs. territory numbers = 69.9%

TABLE 1C: MULTIPLE REGRESSIONS OF NESTS STARTED WITH ENVIRONMENTAL FACTORS

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	t ratio	t ratio	t ratio
Water table	-0.35	-0.33	
Day length	0.78	0.89	0.86
Rainfall	0.37		
Temperature	-2.04	-2.15	-2.44
D.F.	13	14	15
$r^2$	38.0%	41.8%	45.2%

$r^2$  for temperature vs. nests started = 49.3%

TABLE 1D: MULTIPLE REGRESSIONS OF NESTS EXTANT  
WITH ENVIRONMENTAL FACTORS

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	t ratio	t ratio	t ratio
Water table	0.59	0.66	
Daylength	1.03	1.21	1.54
Rainfall	0.68		
Temperature	-1.93	-2.04	-2.94
D.F.	13	14	15
$r^2$	40.0%	42.3%	44.4%

$r^2$  for temperature vs. nests extant = 43.2%

## APPENDIX 2.

TABLE 2A: MEAN DAYLIGHT HOURS AND PERCENTAGE DAYLIGHT HOURS SPENT BY FLOCK BIRDS IN MAJOR ACTIVITIES

Year	Month	H o u r s					P e r c e n t a g e				
		Feeding	Resting	Preening	Flying	Aggression/ Courtship	Feeding	Resting	Preening	Flying	Aggression/ Courtship
1979	D	9.5	3.7	1.7	0.3	0.23	61.5	24	11	2.0	1.5
	J	9.5	3.3	1.7	0.53	0.08	62.5	22	11.5	3.5	0.5
	F	9.45	2.98	1.5	0.2	0.03	66.5	21	10.5	1.5	0.5
	M	10.00	1.21	1.27	0.36	0.15	77	9	10	3	1
	A	8.13	1.08	1.76	0.44	0.25	69.5	9.5	15	3.5	2
	M	7.6	1.0	1.5	0.2	0.2	72	9.5	14.5	1.5	2
1980	J	7.2	0.95	1.5	0.25	0.33	73	9.5	11.5	2.5	3.5
	J	6.9	1.2	1.2	0.4	0.4	68	12	12	4	4
	A	7.3	1.6	1.0	0.2	1.1	64.5	14	9	2	10
	S										
	O	6.2	4.9	2.3	0.5	0.4	43.5	34.5	16	3.5	2.5
	N	6.8	4.2	3.1	0.91	0.15	45	27.5	20.5	6	1
	D	9.0	3.5	2.6	0.4	0.16	57.5	22.5	16.5	2.5	1

The subsequent tables of multiple regressions utilise environmental data tabulated in Appendix 1, Table 1A.

TABLE 2B: MULTIPLE REGRESSIONS OF FLOCK FEEDING BEHAVIOUR WITH ENVIRONMENTAL FACTORS

	H o u r s			P e r c e n t a g e		
	t ratio	t ratio	t ratio	t ratio	t ratio	t ratio
	t	t	t	t	t	t
Water Table	-3.49*	-3.78*	-4.26*	-3.36*	-3.64*	-5.06*
Day length	-1.14	-1.17		-3.87*	-4.23*	-5.92*
Rainfall	0.31			0.21		
Temperature	1.74	1.81	1.59	1.30	1.36	
D.F.	7	8	9	7	8	9
$r^2$	79.1%	81.4%	80.7%	77.8%	80.5%	78.6%

Water table versus feeding behaviour (hours),  $r^2 = 79.7\%$

Day length versus feeding behaviour (percentage),  $r^2 = 32.6\%$

TABLE 2C: MULTIPLE REGRESSIONS OF FLOCK PREENING BEHAVIOUR WITH ENVIRONMENTAL FACTORS

	H o u r s			P e r c e n t a g e		
	t ratio	t ratio	t ratio	t ratio	t ratio	t ratio
	t	t	t	t	t	t
Water table	2.05	2.8	2.94*	1.99	2.64	2.75
Day length	2.17	4.4*	4.61*	1.09	2.28	2.28
Rainfall	-0.46	-0.46		-0.58	-0.61	
Temperature	-0.20			-0.07		
D.F.	7	8	9	7	8	9
$r^2$	56.2%	61.4%	64.8%	24.7%	34.1%	38.6%

Day length versus preening behaviour (hours),  $r^2 = 43.5\%$

Water table versus preening behaviour (%),  $r^2 = 20.9\%$



TABLE 2D: MULTIPLE REGRESSIONS OF FLOCK RESTING BEHAVIOUR WITH ENVIRONMENTAL FACTORS

	Hours			Percentage		
	t ratio	t ratio	t ratio	t ratio	t ratio	t ratio
	t	t	t	t	t	t
Water table	2.06	2.25	3.25*	1.88	2.06	2.99*
Day length	3.79*	4.09*	7.45*	3.00*	3.20*	5.67*
Rainfall	-0.32			-0.36		
Temperature	-0.65	-0.63		-0.62	-0.59	
D.F.	7	8	9	7	8	9
$r^2$	79.4%	81.7%	83.0%	67.9%	71.4%	73.4%

Day length versus resting behaviour (hours),  $r^2 = 69.7\%$   
 Day length versus resting behaviour (percentage),  $r^2 = 56.7\%$

TABLE 2E: MULTIPLE REGRESSIONS OF FLOCK FLYING BEHAVIOUR WITH ENVIRONMENTAL FACTORS

	t ratio	t ratio	t ratio	t ratio	t ratio	t ratio
	t	t	t	t	t	t
	Water table	1.07	1.78	1.76	0.91	1.48
Day length	1.45	2.02	2.31	0.54	0.87	
Rainfall	0.84	1.01		0.65	1.24	1.49
Temperature	-0.59			-0.38		
D.F.	7	8	9	7	8	9
$r^2$	20.3%	26.8%	26.6%	0.0%	8.3%	10.8%

Day length versus flying behaviour (hours),  $r^2 = 19.4\%$   
 Rainfall versus flying behaviour (percentage),  $r^2 = 14.6\%$

TABLE 2F: MULTIPLE REGRESSIONS OF AGGRESSION/  
COURTSHIP WITH ENVIRONMENTAL FACTORS

	H o u r s			P e r c e n t a g e		
	t ratio	t ratio	t ratio	t ratio	t ratio	t ratio
Water table	0.55	0.67		0.20	0.15	
Day length	0.13			0.15		
Rainfall	0.63	0.74	0.74	0.49	0.32	0.61
Temperature	-0.74	-1.38	-2.35	-1.04	-1.22	-2.91*
D.F.	7	8	9	7	8	9
$r^2$	9.0%	20.2%	25.1%	20.2%	27.8%	37.1%

Temperature versus aggression/courtship behaviour (hours)  
 $r^2 = 34.9\%$

Temperature versus aggression/courtship behaviour (percentage)  
 $r^2 = 46.4\%$

## APPENDIX 3

TABLE 3A: FLOCK DIURNAL BEHAVIOUR SUMMER (DECEMBER-JANUARY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
0520	0	0	0	0	22	2	0	0	78	7
0530	0	0	0	0	74.5	64	7	6	18.5	16
0540	2	2	0	0	88	86	7	7	3	3
0550	0	0	0	0	81	81	15	15	4	4
0600	0	0	0	0	82.5	84	13.5	14	4	4
0610	0	0	0	0	81.5	79	15.5	15	3	3
0620	6	8	1.5	2	73.5	95	16.5	21	2.5	3
0630	4.5	6	0	0	78.5	110	14.5	20	3	4
0640	7.5	11	0	0	74	108	15	22	3.5	5
0650	2.5	4	0	0	83	131	7.5	12	7	11
0700	0	0	1.5	2	75	117	16.5	26	7	11
0710	5.5	9	0	0	81	135	9.5	16	4	7
0720	2	3	3.5	6	76	125	8	13	13	18
0730	4.5	7	1.5	2	85.5	133	3	5	6	9
0740	11.5	20	0.5	1	75.5	129	5.5	9	7	12
0750	4	8	1	2	80.5	152	9.5	18	5	9
0800	2	4	0.5	1	84.5	163	7.5	14	5.5	11
0810	0	0	3.5	7	78.5	150	11.5	22	6.5	12
0820	1.5	3	0.5	1	86	155	3.5	6	8.5	15
0830	0	0	8.5	16	81.5	154	4	8	6	11
0840	1	2	4	6	77	119	6.5	10	11.5	18
0850	0	0	1.5	2	85.5	138	2	3	11	18
0900	0	0	0	0	89	132	7.5	11	3.5	5
0910	0	0	45	75	45.5	76	4	7	5.5	9
0920	0	0	0	0	86.5	145	8.5	14	5.5	9
0930	5	9	0	0	79	146	12	22	4.5	8
0940	0	0	0	0	74.5	156	13.5	28	12	25
0950	0	0	0	0	83	178	9.5	20	7.5	16
1000	0	0	0	0	78.5	174	10.5	23	11.5	25

TABLE 3A: FLOCK DIURNAL BEHAVIOUR SUMMER (DECEMBER-JANUARY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1010	0	0	0	0	72.5	162	8.5	19	19	42
1020	1.5	4	2.5	6	76.5	189	7.5	19	11.5	29
1030	0	0	0	0	84	278	4	14	11.5	38
1040	0	0	0	0	80.5	240	6.5	19	13	39
1050	0.5	2	1	3	77	220	7.5	21	13.5	39
1100	0	0	0.5	1	75.5	217	5.5	16	18.5	53
1110	0	0	0.5	1	60	147	14	34	25.5	63
1120	0	0	1	3	70.5	175	7.5	19	20.5	51
1130	1.5	4	0	0	73.5	198	11.5	31	13.5	37
1140	1.5	4	7	19	64	174	10	27	17.5	48
1150	0	0	0	0	75.5	187	6	15	18	45
1200	2	4	13	29	68.5	154	9.5	21	7.5	17
1210	2	4	4	9	62	138	11	24	21.5	48
1220	2	4	0	0	55	109	16.5	33	26.5	52
1230	2	4	0	0	41	85	21	44	36	75
1240	3	5	0	0	46.5	82	19	34	31.5	56
1250	2.5	4	3	5	48	77	15.5	25	31	50
1300	0	0	0	0	56	81	14	20	30.5	44
1310	0	0	0	0	56.5	103	11.5	21	32	59
1320	3	6	2	4	51	108	14	30	30	64
1330	2.5	6	0	0	54.5	137	14	35	29	73
1340	1	3	0	0	54	145	10.5	28	34.5	92
1350	0	0	0	0	52	154	11.5	34	36.5	108
1400	0	0	8	26	42	134	10.5	33	39.5	127
1410	0	0	2	8	39.5	140	15	54	43.5	154
1420	0	0	0	0	40.5	151	14.5	54	45	169
1430	1	4	0	0	40	136	12.5	42	46	156
1440	0.5	2	0	0	35	123	15.5	55	48.5	170
1450	0	0	0	0	37.5	135	15	54	47.5	171

TABLE 3A: FLOCK DIURNAL BEHAVIOUR SUMMER (DECEMBER-JANUARY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1500	0	0	8	29	48.5	175	11	40	32.5	118
1510	0	0	7.5	29	46.5	181	12.5	49	33	129
1520	0	0	0	0	42.5	160	20.5	77	37	138
1530	0	0	4	15	38	145	18	69	40	154
1540	0	0	0	0	40.5	165	17.5	71	42	172
1550	0	0	0.5	3	49	221	12	55	38.5	174
1600	0	0	0	0	49.5	214	11.5	50	39	169
1610	0	0	0	0	45.5	196	15.5	68	38.5	167
1620	0	0	8	40	43	211	12	60	37	182
1630	0.5	2	0	0	50.5	250	18.5	91	30.5	152
1640	0.5	2	0	0	49.5	233	16.5	78	33.5	159
1650	0	0	0	0	55	257	11.5	53	33.5	156
1700	0	0	1.5	7	61.5	266	12	52	24.5	106
1710	5	21	12	53	51.5	224	12	52	20	87
1720	5.5	22	0	0	58	226	15.5	61	21	83
1730	0	0	0	0	64.5	265	14.5	59	21.5	88
1740	0	0	0	0	73	270	9	34	18	66
1750	0	0	0	0	72	245	11.5	39	16.5	57
1800	0	0	0	0	71.5	196	12.5	34	16	44
1810	0.5	1	0	0	82.5	172	5.5	12	11.5	24
1820	2	4	0	0	74.5	158	16	34	7.5	16
1830	1	2	0	0	76.5	160	16.5	34	6	13
1840	6	11	0	0	69.5	129	11.5	21	13.5	25
1850	0	0	0	0	80	152	11.5	22	8.5	16
1900	0	0	0	0	78	155	8.5	13.5		27
1910	1.5	3	0	0	87	171	4	8	7	14
1920	0	0	2.5	5	88.5	179	4.5	9	4.5	9
1930	4	7	0	0	84.5	157	3	6	8.5	16
1940	3.5	6	0	0	77	130	8.5	14	11	19

TABLE 3A: FLOCK DIURNAL BEHAVIOUR SUMMER (DECEMBER-JANUARY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1950	0	0	0	0	91.5	151	5.5	9	3	5
2000	1	2	0	0	93	155	4	7	2	3
2010	1	2	0	0	88	146	3	5	8	13
2020	0	0	0	0	93	154	4	7	3	5
2030	0	0	0	0	90.5	162	9	16	0.5	1
2040	0	0	0	0	90	81	6.5	6	3.5	3
2050	0	0	0	0	85	86	6	6	9	9
2100	0	0	2.5	2	83	63	4	3	10.5	8

TABLE 3B: FLOCK DIURNAL BEHAVIOUR AUTUMN (MARCH-MAY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
0700	0	0	0	0	100	12	0	0	0	0
0710	0	0	0	0	63.5	14	0	0	36.5	8
0720	0	0	7.5	5	89	58	3	2	0	0
0730	2	2	0	0	82	83	9	9	7	7
0740	1.5	2	0	0	85	103	8.5	10	5	6
0750	0	0	0	0	89	88	11	11	0	0
0800	1.5	2	7.5	10	81.5	106	7.5	10	1.5	2
0810	5	6	5.5	7	80	99	9.5	12	0	0
0820	5	8	13	21	72	116	9.5	15	0.5	1
0830	4.5	7	18.5	30	69.5	112	7.5	12	0	0
0840	8.5	13	6	9	75	116	9.5	15	1.5	2
0850	3.5	5	5	7	74	107	16	23	2	3
0900	1.5	2	6.5	9	75.5	106	15.5	22	0.5	1
0910	3	4	5	7	65.5	90	21	29	5	7
0920	1.5	2	0.5	1	73.5	100	15.5	21	9	12
0930	2.5	4	2.5	4	76.5	128	15.5	26	3	5
0940	4	7	6.5	12	73	131	13	23	3.5	6
0950	3.5	6	2	3	74	124	16.5	28	4	7
1000	2.5	4	2.5	4	65	109	24.5	41	6	10
1010	0	0	0	0	81	139	14	24	5.5	9
1020	3.5	6	0	0	76	123	15.5	25	5	8
1030	0	0	4.5	8	77.5	140	10	18	8.5	15
1040	1	2	0	0	80.5	133	12.5	21	5.5	9
1050	1	2	0.5	1	83.5	168	12	24	3	6
1100	1	2	0	0	80.5	171	12	26	6.5	14
1110	1	2	2	4	78.5	174	11	24	7.5	17
1120	3	6	0	0	75.5	148	11.5	23	9.5	19
1130	1.5	4	0.5	1	86.5	203	7	17	4.5	10
1140	1	2	1	2	83.5	194	8	19	7	16
1150	1	2	0	0	76.5	180	11.5	27	11.5	27

TABLE 3B: FLOCK DIURNAL BEHAVIOUR AUTUMN (MARCH-MAY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1200	1	2	2.5	7	74	190	13	33	9.5	25
1210	1.5	4	3.5	8	68.5	167	14.5	35	12.5	30
1220	2.5	6	5	12	76	192	12.5	31	4.5	11
1230	4	10	2.5	6	68	169	14.5	36	11.5	28
1240	1.5	4	1	2	69.5	178	15	39	13	33
1250	1	2	2.5	6	67.5	172	16.5	42	13	33
1300	1	2	3.5	8	59.5	133	15	33	21	47
1310	0	0	0	0	59.5	120	17	34	24	48
1320	0	0	4	7	58	107	15.5	29	22.5	42
1330	0	0	4.5	8	63.5	112	18	32	13.5	24
1340	2.5	4	0	0	66.5	117	17.5	31	13.5	24
1350	1	2	0	0	69.5	117	19.5	33	9.5	16
1400	0	0	0	0	71.5	112	15.5	24	13.5	21
1410	0	0	2.5	4	69.5	114	12	20	16	26
1420	1	2	4.5	8	63.5	116	16.5	30	15	27
1430	4	7	1	2	62	108	15.5	27	17	30
1440	0	0	2	3	62.5	97	12.5	19	23	36
1450	2	3	1	2	62.5	103	12	20	22.5	37
1500	2	4	0	0	54.5	118	15.5	34	28	60
1510	0	0	0	0	57.5	123	13	28	29.5	63
1520	2.5	6	0	0	65.5	164	12.5	32	19.5	49
1530	1	2	0	0	66	164	13	32	20	50
1540	1	2	1.5	4	66	172	11	29	20.5	54
1550	2	4	3	7	61	139	13	30	21	48
1600	1	3	3.5	9	67.5	176	12.5	33	15	39
1610	1	2	1	2	67.5	170	16.5	41	14.5	37
1620	1	2	0	0	72.5	187	11	28	16	41
1630	2.5	6	5	13	73	183	12.5	31	7	17
1640	1	2	5	12	72	173	13.5	33	8.5	21
1650	0	0	6	14	76.5	173	10.5	24	6.5	15



TABLE 3B: FLOCK DIURNAL BEHAVIOUR AUTUMN (MARCH-MAY)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1700	1	2	0	0	75.5	178	17	40	7	16
1710	0	0	2.5	6	76.5	184	13	31	8	19
1720	1.5	3	6.5	15	73.5	174	14.5	34	4.5	11
1730	1.5	4	10	23	70.5	164	13	30	5	12
1740	3	6	2.5	5	75	154	13	27	7	14
1750	0	0	0	0	90	180	8.5	17	1.5	3
1800	2	4	0	0	88	190	8.5	18	2	4
1810	2.5	6	2.5	6	86	190	7	16	2	3
1820	2	4	1.5	3	90	190	6.5	14	0	0
1830	2	4	0	0	92	187	6	12	0	0
1840	2	4	1.5	3	92	165	3.5	6	0.5	1
1850	3.5	6	5.5	9	85.5	138	3.5	6	1	2
1900	2	3	1.5	2	94	141	1.5	2	1.5	2
1910	3.5	4	19.5	23	75	88	1.5	2	0	0
1920	0	0	9	9	87	86	3	3	1	1
1930	0	0	4	4	95	95	1	1	0	0
1940	0	0	10.5	8	89.5	20	0	0	0	0
1950	0	0	12.5	10	87.5	70	0	0	0	0
2000	2.5	2	0	0	97.5	72	0	0	0	0

TABLE 3C: FLOCK DIURNAL BEHAVIOUR WINTER (JUNE-AUGUST)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
0800	10	1	0	0	90	9	0	0	0	0
0810	18	2	0	0	72.5	8	0	0	10	1
0820	18.5	10	0	0	61	33	7.5	4	13	7
0830	5	4	7.5	6	70.5	55	5	4	11.5	9
0840	8.5	7	3.5	3	71.5	60	13	11	3.5	3
0850	14	14	3	3	69	68	12	12	2	2
0900	11	10	15.5	14	54.5	49	15.5	14	3.5	3
0910	10.5	9	1	1	70	61	17	15	1	1
0920	0	0	17.5	16	64	59	14	13	4.5	4
0930	2.5	2	6	5	64.5	53	22	18	5	4
0940	6.5	5	22	17	60.5	47	5	4	6.5	5
0950	9	6	0	0	71	47	9	6	10.5	7
1000	9	6	0	0	74	48	7.5	5	9	6
1010	3	2	0	0	84	57	6	4	7.5	5
1020	13	10	13	10	61.5	48	10.5	8	2.5	2
1030	18	14	5	4	69	53	4	3	4	3
1040	14.5	13	0	0	71	63	4.5	4	10	9
1050	10	9	3.5	3	70.5	64	3.5	3	13	12
1100	0	0	10.5	9	71.5	60	3.5	3	14.5	12
1110	8.5	8	1	1	66.5	63	10.5	10	13.5	13
1120	3.5	3	3.5	3	75	69	5.5	5	13	12
1130	7.5	7	0	0	65.5	61	13	12	14	13
1140	6	6	9	9	63	62	8	8	14	14
1150	0	0	6.5	6	71	66	8.5	8	14	13
1200	0	0	0	0	69.5	62	10	9	20	18
1210	2	2	0	0	80	76	6.5	6	11.5	11
1220	2	2	8	8	70	72	8.5	9	11.5	12
1230	0	0	0	0	69.5	64	10	9	20.5	19
1240	0	0	0	0	70.5	58	8.5	7	20.5	17
1250	0	0	2.5	2	75.5	62	6	5	16	13

TABLE 3C: FLOCK DIURNAL BEHAVIOUR WINTER (JUNE-AUGUST)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1300	7	6	0	0	67.5	56	12	10	13.5	11
1310	2.5	2	4.5	4	79.5	69	8	7	5.5	5
1320	2	2	0	0	69	64	14	13	15	14
1330	2	2	4	4	65.5	63	8.5	8	20	19
1340	3.5	3	0	0	68.5	63	15	14	13	12
1350	3	3	1	1	77.5	72	8.5	8	9.5	9
1400	2	2	0	0	66	65	18	18	14	14
1410	0	0	5	5	70	67	15.5	15	9.5	9
1420	7	6	1	1	70	61	14	12	8	7
1430	2	2	3.5	3	70.5	65	13	12	11	10
1440	2.5	2	0	0	56	48	13	11	29	25
1450	2.5	2	0	0	57	46	21	17	20	16
1500	4.5	4	3.5	3	50	43	18.5	16	23.5	20
1510	2.5	2	0	0	72	62	14	12	11.5	10
1520	9.5	8	0	0	68.5	57	11	9	11	9
1530	0	0	7	5	65	48	15	11	13.5	10
1540	3.5	3	10.5	9	53.5	46	20	17	13	11
1550	2.5	2	0	0	65.5	55	18	15	14.5	12
1600	7	7	0	0	67	66	13	13	13	13
1610	8	8	1	1	71	69	9.5	9	10.5	10
1620	8	7	0	0	74.5	67	6.5	6	11	10
1630	0	0	0	0	74.5	78	12.5	13	13.5	14
1640	0	0	2.5	2	65	61	14	13	19	18
1650	2.5	2	2.5	2	62	53	20	17	14	12
1700	6	6	3	3	66.5	69	12.5	13	12.5	13
1710	4	4	2	2	74	75	14	14	6	6
1720	0	0	2	2	85	86	11	11	2	2
1730	2	2	0	0	78.5	76	11.5	11	8	8

TABLE 3C: FLOCK DIURNAL BEHAVIOUR WINTER (JUNE-AUGUST)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1740	2	2	0	0	84	83	11	11	3	3
1750	4	4	2	2	78	78	9	9	7	7
1800	0	0	0	0	85	86	9	9	6	6
1810	0	0	0	0	81	80	10	10	9	9
1820	4.5	2	0	0	74.5	32	16.5	7	4.5	2
1830	0	0	0	0	90.5	19	9.5	2	0	0
1840	0	0	0	0	100	11	0	0	0	0
1850	0	0	0	0	100	6	0	0	0	0
1900	0	0	0	0	50	3	16.5	1	33.5	2
1910	25	1	0	0	50	2	25	1	0	0
1930	0	0	0	0	100	4	0	0	0	0

TABLE 3D: FLOCK DIURNAL BEHAVIOUR SPRING (SEPTEMBER-NOVEMBER)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
0530	0	0	12	2	29.5	5	12	2	47	8
0540	0	0	0	0	61	14	8.5	2	30.5	7
0550	0	0	0	0	86.5	26	10	3	3.5	1
0600	0	0	3	1	56.25	18	34.5	11	6.25	2
0610	0	0	20	7	51.5	18	20	7	8.5	3
0620	0	0	11	4	67.5	25	8	3	13.5	5
0630	0	0	45.5	16	40	14	3	1	11.5	4
0640	8.5	4	33.5	16	35.5	17	14.5	7	8.5	4
0650	0	0	31	14	44.5	20	11	5	13.5	6
0700	0	0	54.5	25	28.5	13	13	6	4.5	2
0710	8	3	2.5	1	57	21	16	6	16	6
0720	0	0	14.5	5	45.5	16	28.5	10	11.5	4
0730	0	0	11.5	5	42	18	32.5	14	14	6
0740	6.5	3	4.5	2	39	18	32.5	15	17.5	8
0750	4.5	2	4.5	2	47	22	34	16	10.5	5
0800	0	0	7	3	49	21	25.5	11	18.5	8
0810	8	3	5.5	2	35	13	29.5	11	21.5	8
0820	0	0	20.5	7	26.5	9	20.5	7	32.5	11
0830	5	2	2.5	1	60	24	15	6	17.5	7
0840	0	0	0	0	67.5	29	18.5	8	14	6
0850	0	0	0	0	60.5	23	15.5	6	23.5	9
0900	0	0	0	0	51.5	20	23	9	25.5	10
0910	0	0	0	0	48.5	19	23	9	28	11
0920	10.5	4	7.5	3	33.5	13	23	9	25.5	10
0930	0	0	12.5	5	50	20	15	6	22.5	9
0940	0	0	0	0	52.5	21	17.5	7	30	12
0950	5.5	2	5.5	2	44.5	16	19.5	7	25	9
1000	0	0	0	0	52.5	20	21	8	26.5	10
1010	0	0	0	0	61	22	14	5	25	9
1020	0	0	0	0	45	14	13	4	42	13

TABLE 3D: FLOCK DIURNAL BEHAVIOUR SPRING (SEPTEMBER-NOVEMBER)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1030	0	0	0	0	30.5	11	25	9	44.5	16
1040	0	0	16.5	6	22	8	22	8	39	14
1050	0	0	0	0	39	14	19.5	7	41.5	15
1100	0	0	12	5	46.5	19	24.5	10	17	7
1110	0	0	0	0	26.5	9	26.5	9	47	16
1120	0	0	0	0	20.5	7	23.5	8	56	19
1130	0	0	0	0	29.5	10	14.5	5	56	19
1140	0	0	0	0	32.5	11	20.5	7	47	16
1150	0	0	0	0	38	13	29.5	10	32.5	11
1200	0	0	2.5	1	31	12	28	11	38.5	15
1210	0	0	0	0	25.5	10	15.5	6	59	23
1220	0	0	5	2	17.5	7	27.5	11	50	20
1230	0	0	0	0	20.5	8	31	12	48.5	19
1240	0	0	0	0	33.5	13	13	5	54	21
1250	0	0	17	7	34	14	0	0	49	20
1300	0	0	0	0	41.5	17	10	4	49	20
1310	0	0	0	0	34	14	24.5	10	41.5	17
1320	0	0	2.5	1	24.5	10	27	11	46.5	19
1330	0	0	0	0	35	16	15	7	50	23
1340	0	0	0	0	25.5	11	14	6	60.5	26
1350	0	0	0	0	28	12	25.5	11	46.5	20
1400	0	0	0	0	26	11	26	11	47.5	20
1410	0	0	4.5	2	32.5	14	16.5	7	46.5	20
1420	9.5	4	2.5	1	31	13	9.5	4	47.5	20
1430	0	0	7	3	37	16	9.5	4	46.5	20
1440	0	0	20	8	22.5	9	20	8	37.5	15
1450	0	0	0	0	42.5	17	15	6	42.5	17
1500	0	0	16.5	7	35.5	15	19	8	28.5	12

TABLE 3D: FLOCK DIURNAL BEHAVIOUR SPRING (SEPTEMBER-NOVEMBER)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
1510	0	0	0	0	36.5	15	17	7	46.5	19
1520	0	0	0	0	18	8	29	13	53.5	24
1530	0	0	0	0	22	10	22	10	55.5	25
1540	2	1	0	0	35.5	16	20	9	42	19
1550	6.5	3	0	0	38	17	24.5	11	31	14
1600	0	0	0	0	29	13	22	10	49	22
1610	0	0	0	0	31	14	24.5	11	44.5	20
1620	0	0	2.5	1	46.5	19	22	9	29.5	12
1630	4.5	2	2.5	1	49	21	14	6	30	13
1640	0	0	2	1	68	32	10.5	5	19	9
1650	0	0	6.5	3	69.5	32	8.5	4	15	7
1700	0	0	0	0	78	35	11	5	11	5
1710	0	0	0	0	66.5	30	22	10	11	5
1720	0	0	2.5	1	54.5	24	20.5	9	22.5	10
1730	0	0	12.5	5	57.5	23	15	6	15	6
1740	0	0	0	0	67.5	25	16	6	16	6
1750	0	0	0	0	54	20	21.5	8	24.5	9
1800	0	0	0	0	69	27	13	5	18	7
1810	0	0	0	41.5		17	24.5	10	34	14
1820	9	4	2	1	42	19	20	9	26.5	12
1830	8.5	4	4.5	2	43.5	20	21.5	10	21.5	10
1840	4.5	2	0	0	51	22	28	12	16.5	7
1850	9.5	4	0	0	60.5	26	16.5	7	14	6
1900	0	0	2.5	1	69	29	16.5	7	12	5
1910	2.5	1	0	0	60.5	26	16.5	7	21	9
1920	0	0	0	0	65	28	11.5	5	23.5	10
1930	0	0	0	0	71	29	10	4	19.5	8
1940	0	0	0	0	66	27	22	9	12	5
1950	0	0	0	0	69	29	24	10	7	3

TABLE 3D: FLOCK DIURNAL BEHAVIOUR SPRING (SEPTEMBER-NOVEMBER)

N.Z. Daylight Saving Time	Aggression/ Courtship		Flying		Feeding		Preening		Resting	
	%	N	%	N	%	N	%	N	%	N
2000	0	0	0	0	90	37	7.5	3	2.5	1
2010	10.5	4	7.5	3	56.5	22	7.5	3	18	7
2020	0	0	0	0	89	15	16	3	5.5	1
2030	0	0	0	0	84	16	5.5	1	10.5	2
2040	0	0	0	0	83.5	10	16.5	2	0	0



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