The Maintenance and Reproductive Behaviour of Black Stilts (*Himantopus novaezealandiae*) in Captivity, and Implications for the Management of this Rare Species.

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Master of Science in Zoology

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ABSTRACT

In an effort to conserve New Zealand's rarest endemic wading species, the black stilt (Himantopus novaezealandiae), eggs were removed from the wild in October 1979 for establishment of a captive breeding population. Eight chicks fledged following artificial incubation and hand-rearing at the National Wildlife Centre near Masterton. At two years of age, these tentatively sexed stilts were formed into pairs and housed in large outdoor enclosures.

I studied their behaviour from December 1982 until February 1986, aiming to i) collate an ethogram for the species under the restrictions of a captive environment ii) describe and quantify behavioural activity, especially that of reproductive behaviour and breeding biology iii) describe vocalisations and iv) on the basis of observed behaviour, examine captive breeding as a management option for black stilts.

A repertoire of 38 context-specific behavioural patterns were observed throughout the year and a further 15 stereo-typed species-typical nest-building, copulatory, incubation and chick-rearing patterns occurred during the breeding season. Time-budget analysis of a focal pair of stilts showed foraging and immobility to be the predominant daily activities, peaking during the pre-nesting period. A bimodal diurnal distribution of foraging activity was observed, peaking in the early morning and mid-late afternoon. Time allocated to foraging and immobility was inversely related to the time spent in incubation.

While all stilts showed incipient breeding behaviour, only one pair bred. Multiple laying of this focal pair was induced by subsequent clutch removals. This pair produced 10 clutches of eggs over three breeding seasons, with a maximum of five clutches being laid in one season. Laying spanned the period from 18 September to 28 January. The mean clutch size was 3.27 and the mode was 4.0. Fertility was 90.6% in captivity and 95.6% in the wild. Following egg removal, re-laying took place within 8-13 days (mean and mode 9 days).

The male did the most incubating, especially in the first five days after initiation of egg-laying by the female.

Eight chicks were reared successfully by this pair over the three years. Captive chick growth was faster than that of wild chicks and they fledged earlier (at 35-36 days). They exhibited similiar antipredator behavioural patterns to wild chicks and their response depended on age of the chick and type of predator.

Eleven adult and four juvenile vocalisations were structurally described. These categories were both intergraded or discrete and call parameters were variable within and between call types. Variation within one call type (alarm yap) was greater between individuals (wild and captive) than within individuals. Interspecific variation between pied stilt (H. himantopus leucocephalus) and black stilt alarm calls was also greater between species than within them. Hybrids of the two stilt types were intermediate in call structure, but considerable structural overlap with that of pied and black call parameters was evident.

Based on the observed behaviour and breeding biology of captive stilts, I propose a novel management strategy which involves the establishment of a captive breeding facility for this species within their natural range in the Upper Waitaki Basin.

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TABLE OF CONTENTS

Page

CHAPTER ONE - Introduction and Methods

1.1 Introduction

1.3 Methods

1.3.4 Sexing

1.4 Discussion

CHAPTER TWO - Non-Breeding Behaviour

2.2 Methods

2.3 Results

2.4 Discussion

CHAPTER THREE - Breeding Behaviour and Performance

3.2 Methods

3.3 Results

CHAPTER FOUR - Parental Behaviour,
Juvenile Growth and Ontogeny.

4.3.2 Ontogeny of behavioural patterns

4.4 Discussion

CHAPTER FIVE - Vocal Behaviour

5.3.1 Description of the vocal repertoire

A. Adult calls

CHAPTER SIX - Synthesis and Options for Management

6.2 Management options and associated problems

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER ONE

INTRODUCTION AND METHODS

1.1 Introduction

1.1.1 Black stilts

The black stilt (Himantopus novaezealandiae) is New Zealand's rarest endemic wader species, existing as a single population of less than forty adult birds (13 pairs) and breeding only on the riverbeds and associated wetlands of the Upper Waitaki Basin, South Canterbury (figure 1.1).

They are considered (Fleming 1962, Pierce 1984a) to be the first of two separate invasions to New Zealand of an Australian form of the genus Himantopus (Order Charadriiformes, Family Recurvirostridae). As has occurred following first invasions of other taxa to New Zealand, the first influx of stilts became melanistic (black stilt) after colonisation (Fleming 1962, Kearton 1976) and morphologically distinct from Australian ancestral stock (Pierce 1982). A second invasion of Himantopus himantopus (the black-winged stilt) possibly in the early nineteenth century, underwent speciation before or during colonisation of New Zealand, giving rise to H. h. leucocephalus-the pied stilt.

The taxonomy of black stilts has been confusing. Full species, subspecies and colour morph status, have all been applied to New Zealand stilts (Pierce 1984b). Hybridisation occurs within the area of range overlap of the two types of New Zealand stilts and this has contributed further to the confusion over nomenclature.

Recently Pierce (1984b) reviewed the historical taxonomy of stilts and concluded that on the basis of;

- i) his experimental demonstration of positive assortitive mating in black stilts;
- ii) morphological, ecological and behavioural differences between pied and black stilts; and
- iii) in view of their present taxonomic position;

they should " retain their full specific status".

In contrast to the highly successful colonisation of New Zealand farmlands and riverine systems by pied stilts in the past century or more, the black stilt has dramatically declined in numbers from its widespread distribution in the nineteenth century (Pierce 1984a).

The reasons for the decline of black stilts include an inability to adapt to man-induced changes (particularly introduction of predators and habitat disruption through wetland drainage, damming, water abstraction, etc.) and reproductive compatability with the pied stilt (Pierce 1982).

Efforts to conserve this endangered species have focussed on the provision of predator-free breeding sites, cross-fostering of eggs to pied and hybrid foster nests and the establishment of a captive population. Progeny from captive birds were to be returned back into the wild population.

1.1.2 Establishment of a captive population

In October 1979, officers of the New Zealand Wildlife Service (Department of Internal Affairs) removed eight fertile black stilt eggs from three nests in the Waitaki Basin. The eggs were transferred to the National Wildlife Centre at Mount Bruce near Masterton (figure 1.1) and "incubator-hatched". Before these clutches were transferred, Mount Bruce staff had successfully experimented with pied stilt eggs to perfect the incubation temperature, humidity and hand-rearing techniques for stilt chicks. All transferred eggs hatched successfully and the eight healthy chicks were initially held in brooders and fed on aquatic invertebrates. A supplementary food supply of chopped oxheart (containing a vitamin/mineral mix) was also provided and the amount progressively increased until it constituted the complete food source for the young chicks.

From fledging until two years of age, the stilts were kept as three separate sibling groups in small concrete-floored aviaries (section 1.3.2). These birds were tentatively sexed at twenty months old. As a result of preliminary sexing (section 1.3.4), three male-female pairs and one female-female pair were moved to outdoor enclosures and housed separately during October 1981.

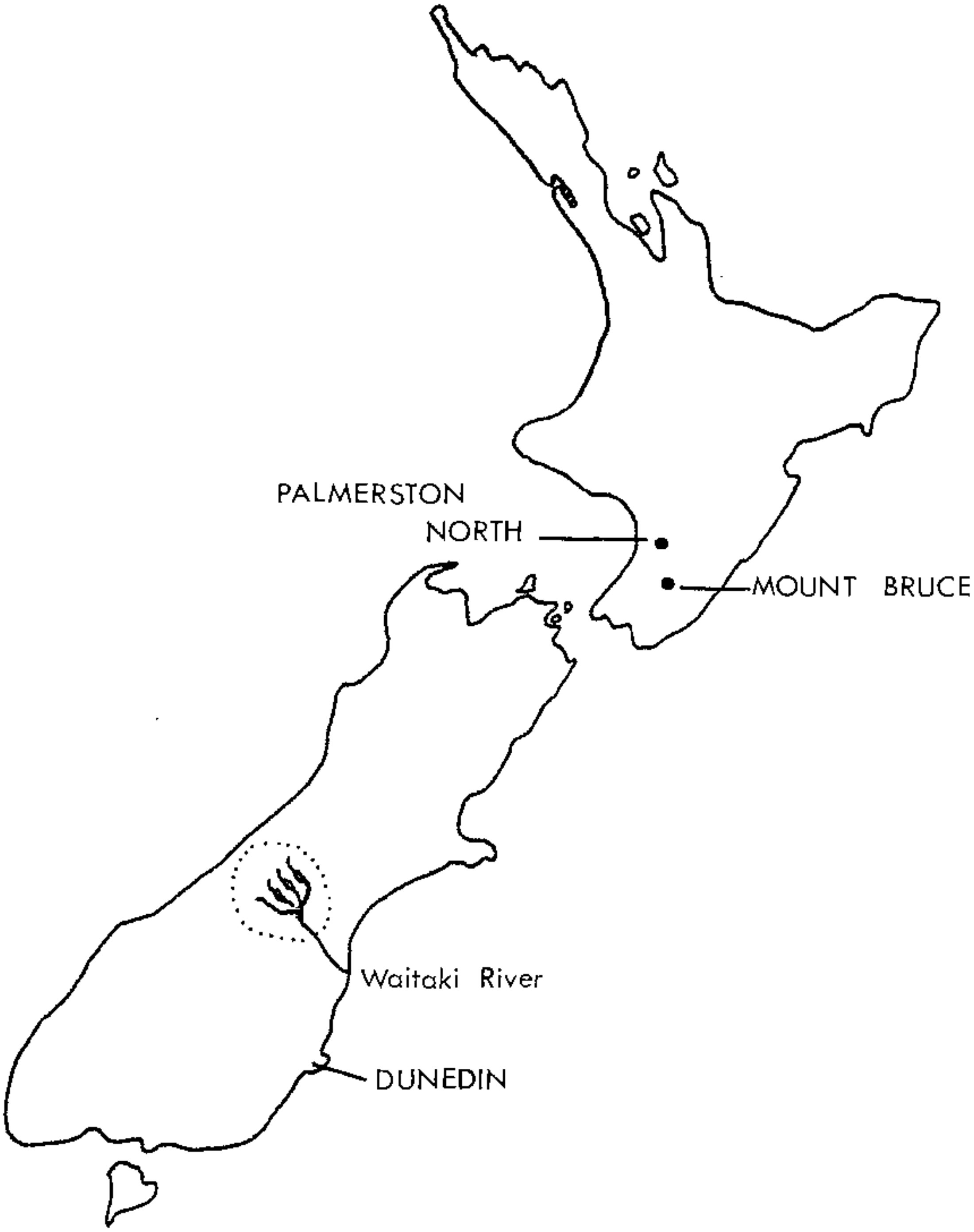


FIGURE 1.1 Breeding range of black stilts

They fed on invertebrates of an artificial stream and this food supply was supplemented by a mixture of chopped oxheart, vitamins and minerals. Incipient breeding patterns were observed by Wildlife Service staff before the initiation of my study, but none of these birds had bred.

1.1.3 Other Recurvirostridae in captivity

The Family Recurvirostridae contains about 14 forms of avocet and stilt (Gruson 1976) distributed widely across the world (figure 1.2). Nomenclature of the Recurvirostridae has been treated in different ways by taxonomists (appendix one) but I shall refer to each of the 14 types as <u>forms</u> and not individual species of one of the three widely recognized (Kinsky 1970, Clements 1974, Condon 1975, Gruson 1976) genera occuring in this family; <u>Himantopus</u> (stilts), <u>Recurvirosta</u> (avocets) or <u>Cladorhynchus</u> (banded stilt). The genus <u>Ibididorhyncha</u> has been excluded (appendix one).

The <u>International Zoological Yearbook</u> (1975-1982) lists 28 institutions throughout the world which have bred and/or maintained recurvirostrids in captivity. Questionnaires (exemplified in appendix two) were sent to 24 of these institutions, to investigate the captive management of recurvirostrids other than <u>H. novaezealandiae</u>. Two New Zealand centres maintaining stilts but not listed in the yearbook, were also sent questionnaires. Fifteen of the 26 questionnaires were answered and returned.

A complete list of the 15 institutions (plus Mount Bruce; Bryant, pers comm.) is presented in table 1.1 and appendix three. Additional information from the questionnaires will be referred to in chapter six.

1.1.4 Studies of stilt/avocet behaviour

Since the late nineteenth century, general observations have been made on the distribution of black stilts and aspects of their breeding biology (Stead 1932, Oliver 1955, Soper 1967).

It was not until the late 1970's however, when black stilt numbers had decreased to less than 100 (Budgeon 1977), that ecological studies on this species began. Pilot studies of their feeding habitats (Merton

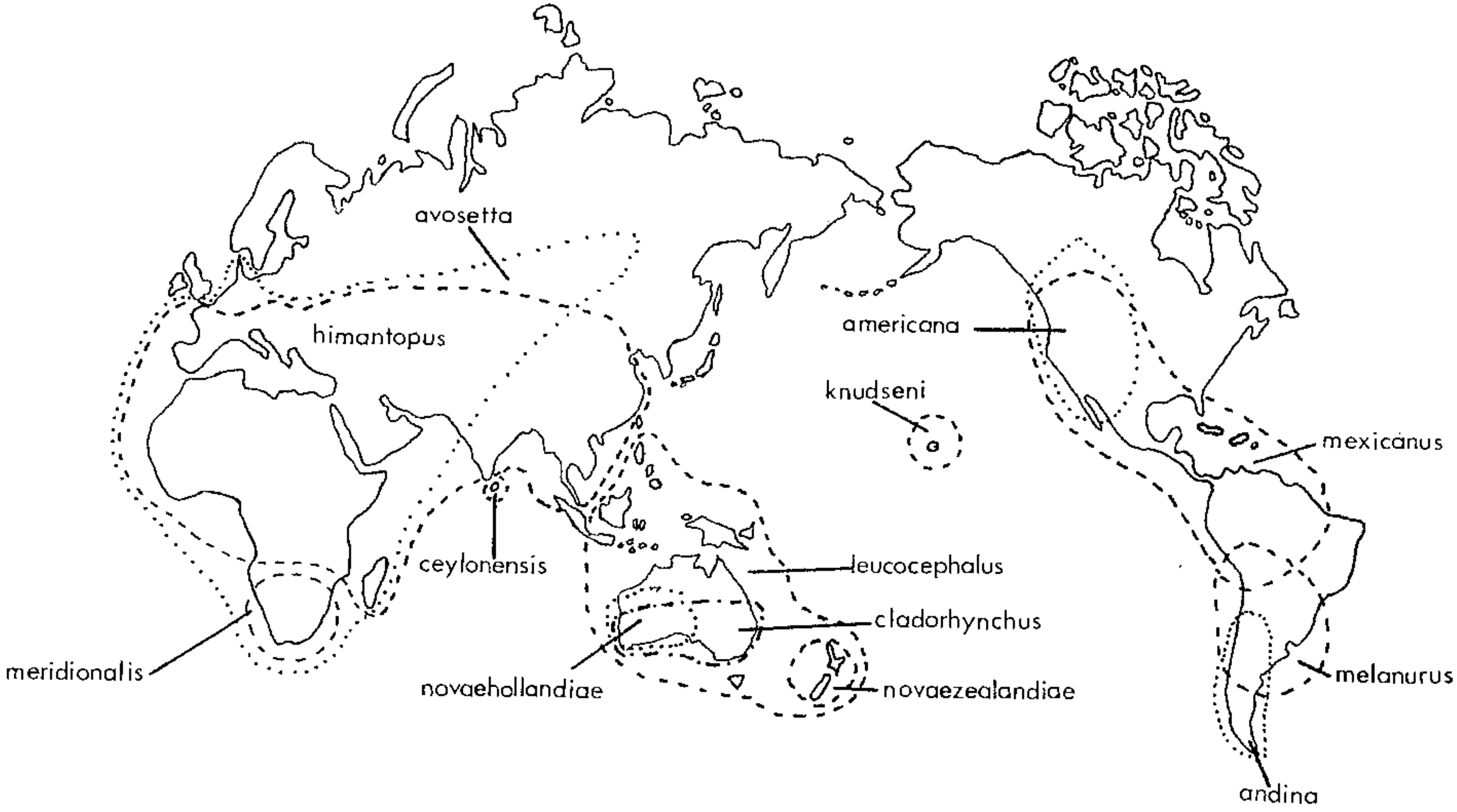


FIGURE 1.2 World distribution of the Recurvirostridae (from Pierce 1982)

Table 1.1 Recurvirostridae in captivity.

GENUS	FORM	COUNTRY	INSTITUTION *[1]
Recurvirostra	americana	U.S.A	6,7 *[2]
	avosetta	U.S.A	8
		Germany	12,11,9,10
		Holland	14,13
		Switzerland	15
		Hungary	16
	novaehollandiae	Australia	4*[3]
Himantopus	leucocephalus	New Zealand	2,3,1
		Australia	5
	himantopus	Australia	4
		Germany	12,11,9
		Switzerland	15
	mexicanus	U.S.A	6,7,8
Cladorhynchus	leucocephalus	Australia	4

*[1] KEY TO INSTITUTIONS: (see Appendix three for full address)

1 = Auckland
2 = Mount Bruce
3 = Otorohanga
4 = Perth
5 = Taronga
6 = Dallas
7 = Los Angeles
8 = New York Bronx
9 = Bochum
10 = Koln
11 = Rheine
12 = Wuppertal
13 = Emmen
14 = Amsterdam
15 = Bern
16 = Budapest

*[2] Breeding has occurred in underlined institutions only (number)

*[3] Fertile eggs laid but did not hatch

1977), breeding areas and general behaviour (Budgeon 1977) were carried out.

A comprehensive ecological and morphological study of black and pied stilts in South Canterbury has recently been completed (Pierce 1982). Pierce examined the general biology of the two species, seasonal movements, habitat choice, feeding behaviour, breeding biology, nesting success, hybridisation and taxonomy. These comprehensive ecological studies have provided valuable information for managing black stilts in the wild. However, except for feeding behaviour (Budgeon 1977, Pierce 1982), the species has been little studied behaviourally.

Studies on the behaviour of closely related species have been relatively comprehensive and quantitative. Breeding behaviour of pied stilts was studied in the Manawatu area of the North Island (McConkey 1971). Makkink (1936) attempted an early ethogram of the European avocet (*R. avosetta*). Hamilton (1975) published a quantitative behavioural comparison of the American avocet (*R. americana*) and black-necked stilt (*H. himantopus mexicanus*), relating behavioural differences to generic taxonomy. Since this publication, an increasing amount of work has been completed on the Recurvirostridae. Quantitative descriptions of juvenile behaviour have been highlighted in studies of antipredator behaviour (Sordahl 1982) and the ontogeny of feeding behaviour (Espin et. al., 1983). Time budgets of adults have been analysed for the American avocet (Gibson 1978), and Sordahl (1980) extensively studied adult antipredator behaviour in the American avocet and black-necked stilt.

Descriptive observation of the breeding behaviour of stilts (Goriup 1982) and avocets (Cooke 1977) continue to be the focus of some studies.

1.2 Objectives

Although black stilt ecology has been comprehensively studied (Pierce 1982), no complete ethogram for this species has yet been assembled. Vocal behaviour has also been ignored, with only a few calls anecdotally described (Stonehouse 1968, Pierce 1982, Falla et. al., 1982).

Behavioural studies of endangered New Zealand species held in captivity, have in the past been limited to general observations of kakapo (Strigops habroptilus) (Reid 1969) and takahe (Notornis mantelli) (Reid 1977). The role of captive breeding in management of rare species has not been examined fully for any of the New Zealand birds.

The main aims of the present study were;

i) to collate an ethogram of all observed behavioural patterns used by captive black stilts;

ii) to describe and quantify daily and seasonal activity, aggressive, breeding and parental behaviour of successful breeders and the physical and behavioural development of their progeny;

iii) to sample and describe vocalisations of captive stilts and investigate alarm calls of wild pied, black and hybrid stilts, testing for a) individual and b) species differences; and

iv) on the basis of described behaviour, to examine captive breeding as a management option for black stilts.

One assumption made throughout this study was that management of black stilts for conservation is an appropriate objective for the species.

1.3 Methods

1.3.1 Study area

All observations on captive birds were made at the National Wildlife Centre near Mount Bruce in the Wairarapa. Mount Bruce is located on State Highway 2, 25 km north of Masterton. Since 1962, this area has been administered by the New Zealand Wildlife Service as a wildlife reserve.

The reserve covers 56 ha in area, of which all but a few hectares are native podocarp/hardwood forest beginning at 305 m above sea-level and ascending to 716 m (top of Bruce Hill).

The average annual rainfall for the area is 2350 mm, with temperatures ranging from -5.0°C (extreme minimum June 1983) to 28.3°C (extreme maximum January 1983) during this study. Monthly rainfall and air temperatures recorded at Mount Bruce weather station (305 m above sea level) during this study, are presented in figures 1.3 and 1.4.

1.3.2 Aviaries

The study birds were kept in two outdoor enclosures (plate 1.1) at the initiation of this study in July 1982. The two enclosures covered an area of approximately 700 m^2 and 445 m^2 respectively, with an arched external frame reaching to a maximum height of 5-6 m. Each aviary was subdivided into two adjoining sections by a 12 mm mesh wire fence (plate 1.2) which could be raised if neccessary.

Water flow from the nearby Mount Bruce stream was diverted along a concrete channel to grills and a weir (plate 1.3). Flow into the two aviaries was controlled by removing or adding wooden boards to the weir, thereby lowering or raising the water levels. From the intake (plate 1.4), water moved slowly down a curved silt-covered gravel bed and exited through an outlet at the far end of the aviary. Figure 1.5 shows the depths of silt and the approximate dimensions of the stream and aviary banks.

Permanent vegetation was sparse along the gravel banks and consisted mainly of tussock and flax and Hebe shrubs.

Small (0.5 m x 0.5 m) and large islands (1-3 m x 0.5-1 m) were created mid-stream in each aviary, to provide nesting areas for the stilts. Smaller concrete-floored aviaries (plates 1.5 a,b) were used to house stilts later in the study. These rectangular aviaries (referred to below as "security aviaries") were 3 m high, 3 m wide, and 6 m long. They had an inside covered area (2.3 m x 3.0 m x 3.0 m) for shelter.

A mixture of minced oxheart, vitamins and minerals was the only food available to birds held within these aviaries.

1.3.3 Hides

A hide was erected near each of the two large outdoor enclosures, at a floor level of 1.1 m (aviary 1-2) and 1.9 m (aviary 3-4) above ground. Access to these hides was by way of a ladder to a rear entrance. The hides were placed 3.6 m and 8.3 m from the enclosures, permitting views

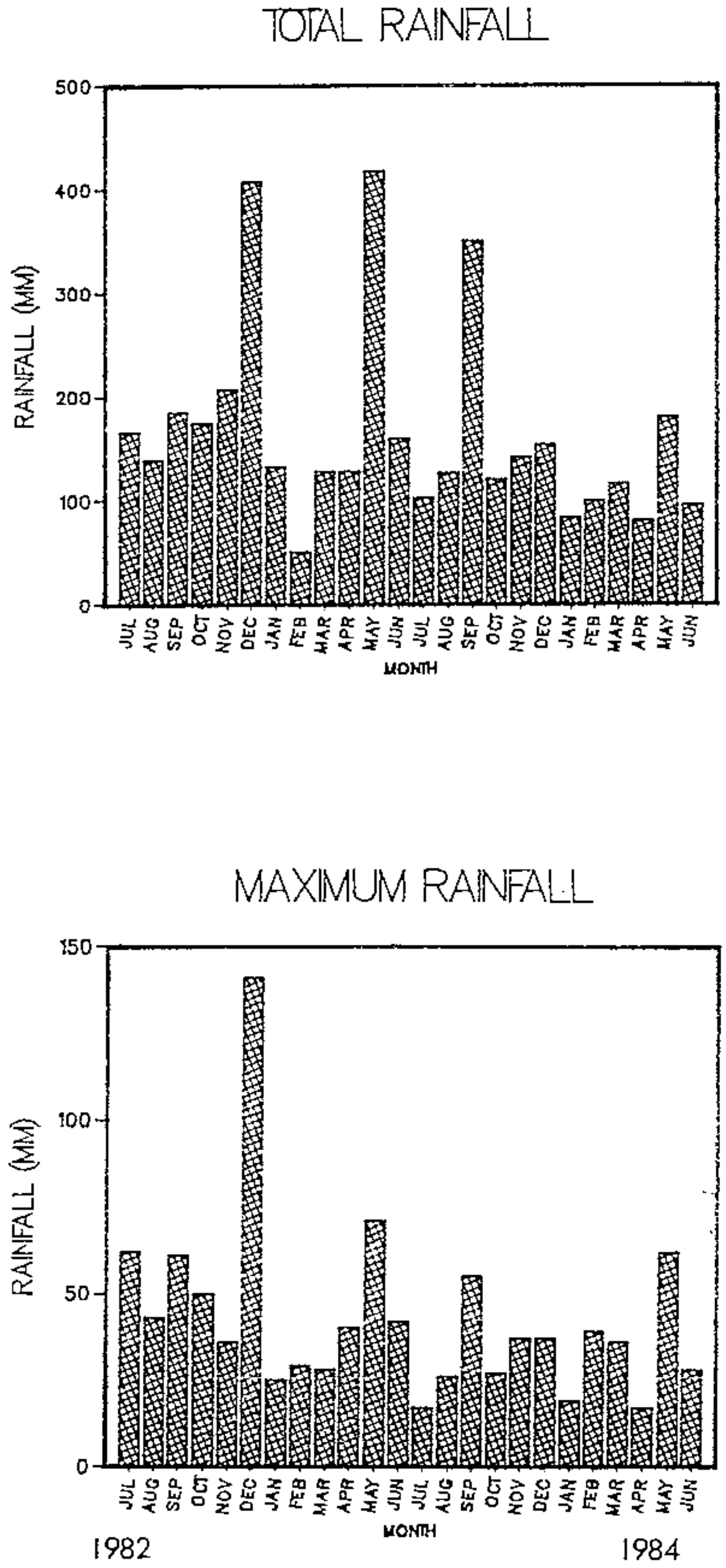


FIGURE 1.3 Monthly rainfall at Mount Bruce

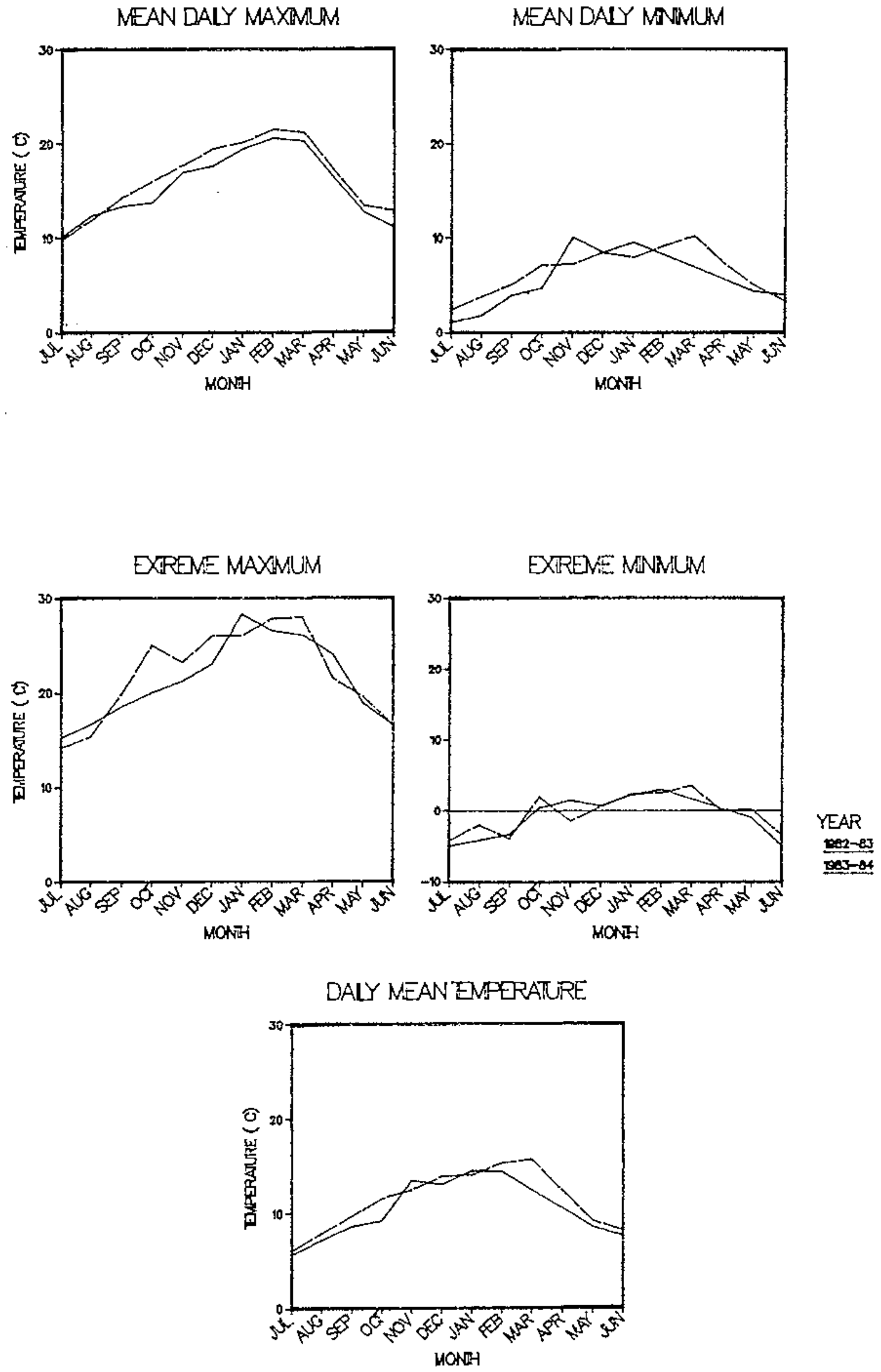


FIGURE 1.4 Monthly temperatures at Mount Bruce

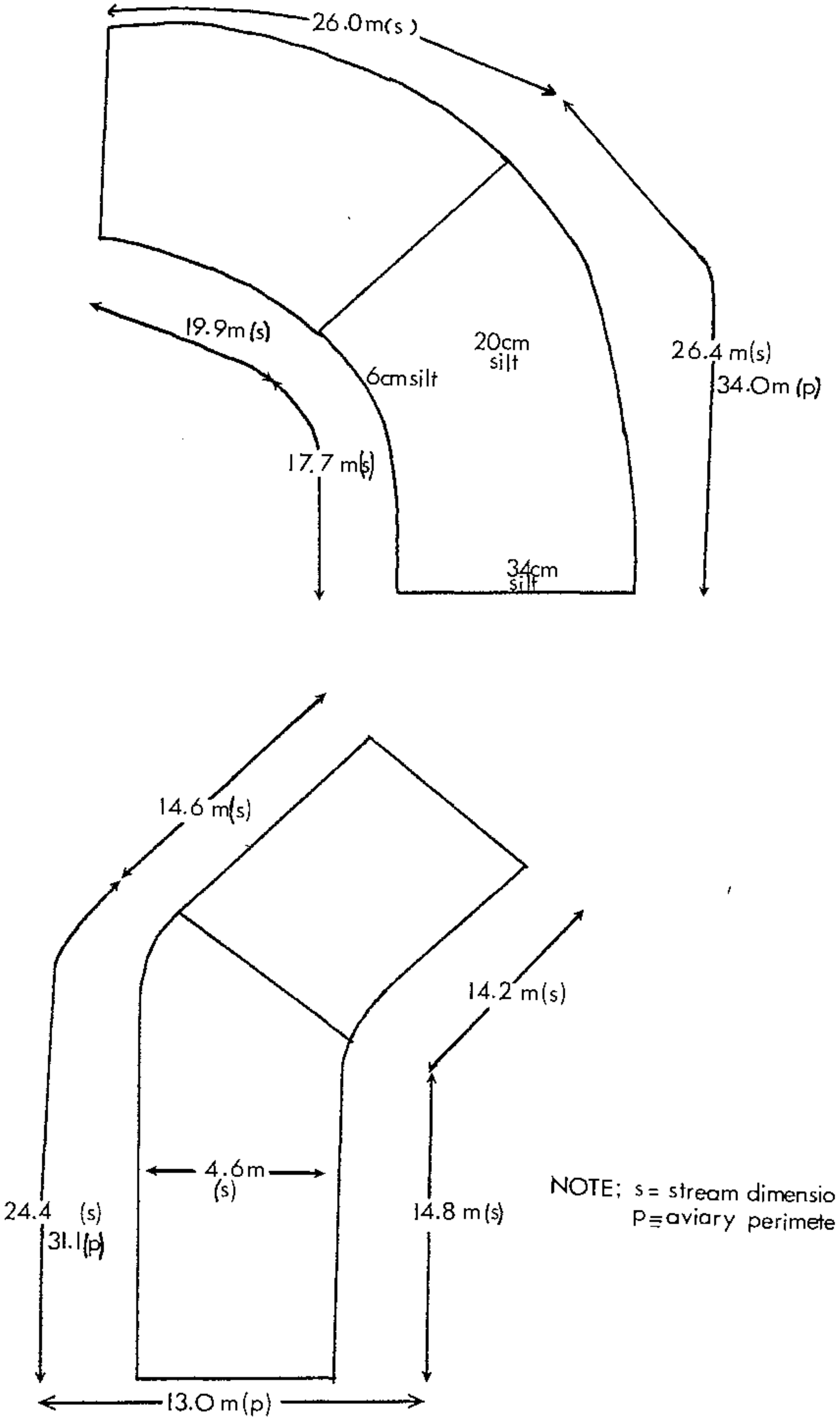


FIGURE 1.5 Dimensions of the two outdoor enclosures

PLATE 1.1 L-shaped outdoor enclosure (foreground)
Second enclosure in the background.

PLATE 1.2 Internal view of enclosure. Note median fence between aviaries.

PLATE 1.3 Grill and weir controlling water flow into enclosures.

PLATE 1.4 Water inflow pipe to an enclosure.

PLATE 1.5a "Security" aviaries
External view

PLATE 1.5b Internal view

of all but a small bank area in one enclosure.

Some observations and vocal recordings were made from inside a parked car, situated on a slightly elevated roadside, 4 m from the aviaries.

No hides were used during observations of the security aviaries, as there was too small an area in which to place them. The study birds held within these aviaries were frequently approached by visitors to the reserve and as a result, the birds were tolerant of my presence.

1.3.4 Sexing

1.3.4.1 Methods

A combination of sexing techniques was used in an attempt to establish the sex of individuals.

The five techniques yielding results were;

i) hormonal analysis of faeces,
ii) behavioural observation,
iii) tactile examination of the width between pubic bones,
iv) discriminant function analysis of morphometric measurements,
and v) autopsy.

These methods are elaborated upon below;

Hormonal analysis of faeces: Faecal samples were taken from each of the eight adult birds during August 1981. The samples were analysed by Professor G.C. Liggins (Postgraduate School of Ostetrics and Gynaecology, Auckland) for oestrogen and progesterone content. The procedure was repeated in September 1984 for four of these birds and again in October 1984 for eight adults and six sub-adults held at that time. The hormone ratios are presented in appendix four.

This method posed several problems;

i) repeated analysis of the same individual was not always consistent eg., 2608 (appendix four);
ii) there were problems assigning a cutoff limit to the oestrogen/progesterone ratio between males and females. G.C. Liggins considered this value to be 0.45, but

individuals which scored between 0.35 and 0.60 were unable to be reliably sexed; and

iii) hormonal levels varied with time of the year.

Behavioural observation: Individuals (recognised by metal and colour-bands) were appointed female status if they were observed adopting the pre-copulatory posture described in section 3.3.1.1. Confirmation of female sex was made through observation of egg-laying. Stilts were classed as behaviourally male, if they performed the pre-copulatory walk (section 3.3.1.1) around another stilt or if they imitated the male copulatory posture (section 3.3.1.2).

Tactile examination of pubic bone width: Tactile examination of the width between the pubic bones of each stilt, was carried out by I. J. Bryant (Senior Wildlife Officer at Mount Bruce). This method was relatively consistent with other results in table 1.2.

Sexing based on morphology : Although sexual dimorphism in plumage occurs in other Recurvirostridae, (eg.,*H. himantopus*; black-necked stilt and black-winged stilt), both sexes of the study species are entirely black except for crimson legs and irises. Pierce (1982) described a greenish gloss to be more prominent on the back of the male, but this was not a reliable feature for sexing captive birds. Of the standard body measurements, sexual dimorphism is significant only in the length of the tarsus (Pierce 1982), males having longer tarsi than females (but with much overlap).

Two sets of four measurements equivalent to those made by Pierce, were taken in captivity from each of the eight adult birds and four juveniles (hatched in captivity later in the study), as an aid to preliminary sexing. The exact method of measurement and one set of results, are given in appendix five.

Four parameters were measured;

i) tarsal length ii) wing length
iii) bill length and iv) weight.

A discriminant function analysis was performed on each set of measurements, using the tarsal length of three birds of known sex (2605, 2611 and 2612) as a basis for grouping birds of unknown sex.

Each analysis yielded the same result for each of the eight adult birds (table 1.2).

Autopsy: Two sub-adults and one five year old adult were reliably sexed by autopsy, after being humanely killed following injury. The stilts were sexed by M.C. Vickers (M.V.Sc), veterinarian with the Ministry of Agriculture and Fisheries (Palmerston North).

1.3.4.2 Synthesis of sexing results

The most consistent results for each individual were provided by a combination of behavioural observation, tactile examination of pubic bone width and faecal steroid analysis (table 1.2). Except for known breeders or autopsied birds, sexes of all other individuals can only be classified as "probable" or "unknown".

The least consistent method of sexing in relation to results obtained from all other techniques, was discriminant function analysis of morphometric measurements. The three birds constituting a reference set for this analysis were a very small sample size. The two discriminant function analyses themselves were consistent for each unclassed individual, but in some cases (eg., 2606 and 2609), the results did not agree with other methods.

1.3.5 Equipment

Observations were made from hides through Zeiss 8 x 30 mm binoculars. A 60 mm spotting scope was used for observing young chicks and the foraging and incubation behaviour of captive adults. All observations in the wild were made through a telescope.

Vocalisations were recorded onto a Nagra IV-D tape recorder through a Sennheiser transistorized condenser, directional microphone. The recordings were run at a 19.05 cm/sec tape speed, on low noise setting. Tapes were played through a Kay Electric Co. spectrographic vibralizer model no.7030, on a wide band setting at 80-80,000 Hz.

Photographs were taken with a Pentax K1000 camera, using 50 mm and 350 mm lenses in captivity and a 500 mm lens (courtesy R. Pierce) in the wild population.

Table 1.2 Methods of sexing *[1]

	1	2	3	4	5	6	7	8	Probable sex
Individual									
2605	m	nr	m	m	m	m	m	-	male
2606	f	m	f	f	f	m	m	-	female
2607	f	-	f	f	m	f	f	fA	female
2608	f	-	m	f	f	f	f	-	female
2609	f	-	f	f	f	m	m	-	female
2610	m	-	m	m	m	m	m	-	male
2611	m	m	m	m	m	m	m	mB	male
2612	f	f	f	f	f	f	f	fB	female
5107	-	-	-	f	-	-	-	fA	female
5108	-	-	nr	f	m	-	f	-	unknown*[2]
5109	-	-	m	nr	m	-	f	-	unknown*[2]
5110	-	-	m	m	m	-	m	-	male
5111	-	-	-	m	-	-	-	mA	male
5112	-	f	f	f	f	-	f	-	female
5113	-	m	m	f	f	-	f	-	unknown*[2]
5114	-	nr	m	m	m	-	f	-	male
2632	-	-	-	-	m	-	-	-	unknown*[2]

*[1] KEY:1 = hormonal analysis (1)
2 = hormonal analysis (2)
3 = hormonal analysis (3)
4 = behavioural observation
5 = pubic bone width
6 = discriminant analysis (1)
7 = discriminant analysis (2)
8 = actual sex

m = male
A = autopsy
f = female
B = breeder
nr = no result
- = not tested

*[2] = sex unknown; insufficient or conflicting results.

1.4 Discussion

1.4.1 Limitations in sample size

The population of eight black stilts held at Mount Bruce at the beginning of this study, represented approximately 16-20% of a total world population of less than 50 birds (Nilsson 1983). Working with not only a small original population, but also with an even smaller representative captive sample, posed problems in sample sizes for quantitative analysis of behaviour.

Individual members of a species may vary in their behaviour, both amongst themselves (i.e., between subjects) and in the case of a single individual, with time (i.e., within subjects). The results of scientific studies should have both internal validity (limited variation within a sample due to extraneous factors) and external validity (allow generalisation from the sample to a larger population of subjects) (Campbell and Stanley; cited in Still 1982). External validity can be obtained through proper experimental design and sampling (Still 1982), but when small samples are involved as in the case of captive studies, the results may lack "power" (i.e., minimization of error due to rejecting a true hypothesis or accepting a false one). Much of the study reported here involved only one pair of birds. The interpretation of quantitative analyses of their behaviour required therefore, particular care when making inferences about the wild stilt population. The internal validity of sampling during this study was increased to some extent by estimating the variation over as many observations of the same subject as possible.

1.4.2 Behavioural constraints

With captive animals, one can never know for certain how much of their behaviour is altered by the abnormal conditions of their confinement (Lorenz 1981). Deficiencies in the social environment of captive species can inhibit behaviour which may otherwise occur in the natural environment of a wild population. For example, many species have been transferred from the wild into zoos but have failed to breed. This failure may have resulted in part, from a lack of knowledge of the natural history and social behaviour of the species (Kear 1977). Kakapo (Strigops habrobtilus) exemplify this, having been transferred to Mount Bruce in 1961 and 1967 (Reid 1969) but failing to survive longer than one year. Even if this endangered bird had survived in captivity, the later discovery that it was a lek species and that females probably range widely in search of potential mates during the pre-breeding season, led to the conclusion that captive breeding of this highly specialised breeder may not be possible (Merton 1975). A background knowledge of the behaviour of an endangered species is vital then, before proceeding with their captive propagation (Eisenberg and Kleiman 1977).

Individuals were also behaviourally constrained by the amount of space available to them. No avenue of escape from the influence of neighbouring birds or cagemates was available, except after human intervention.

The frequency of performance of some behavioural acts may have been influenced by the conditions of captivity, e.g., a lone bird will show little agonistic behaviour, whereas crowded birds may show an increased or decreased frequency of such behaviour (Dilger 1962). The form of behavioural patterns however, should not have been much affected (Dilger 1962). The positive observation of a complex behavioural pattern performed by a captive animal, justifies an assertion that the pattern is characteristic of the species (Lorenz 1981). Conversely however, concluding that a particular behavioural pattern is not present in a species on the basis of captive observation only, is not advisable (Lorenz 1981). Observations of animals in a natural habitat then becomes neccessary. During this study I have therefore set out, not to collate a behavioural repertoire for black stilts as a whole, but to describe only the behavioural patterns observed under the restrictions of a captive environment. These observations are compared to some extent with personal observations of black stilts in the wild population.

CHAPTER TWO

NON-BREEDING BEHAVIOUR

2.1 Introduction

A precise catalogue of all the behavioural patterns of a species (i.e., an ethogram) is the basis for any ethological investigation (Eibl-Eibesfeldt 1975). Defining units of behaviour for an ethogram is not clear cut. The behaviour of an organism is a complex continuous succession of changes. Natural units can be considered to occur as either states (ie., of appreciable duration) or events (ie., instantaneous) (Altmann 1974).

The way in which an animal apportions its time and energy will ultimately influence its survival and reproductive success (Maxson and Oring 1980). Therefore, for any given set of environmental conditions, there is presumably an optimum time and energy budget. Natural selection will favour individuals which exhibit this "optimal" budget (Maxson and Oring 1980).

From an ecological point of view, time spent foraging is probably the most interesting and important aspect of a birds time budget (Gibson 1978). The proportion of daily time allocated for feeding will be determined either directly or indirectly by factors which include an individuals needs (Gibson 1978); ambient temperature (Verbeek 1964,72, Verner 1965, East 1980); photoperiod (King 1974); activity levels (Verner 1965, Gibson 1978); availability, quality and quantity of prey (Verbeek 1972, King 1974, Gibson 1978); egg production, moult, migration or other energy expensive activities (King 1974, Gibson 1978); body weight (Gibson 1978); intensity of competition and predation (King 1974) and type of social system (Maxson and Oring 1980). These physical, biological and biotic factors are not independent of one another, eg., food availability tends to increase with increased environmental temperature and photoperiod (Verner 1965). Energy needs tend to increase with decreasing temperatures (Verbeek 1964,72). Time-activity budgets however, are only roughly equivalent to energy budgets, because different activities will have different energy requirements (King 1974) and search rates, pecking rates and handling times will be variable within foraging bouts of equal length

(Goss-Custard and Rothery 1976). Time-budgets can however, provide comparative insights into time and energy allocation within and between species, that are not yet available through energy budgets (King 1974).

The fulfillment of energy requirements through foraging could be expected to be of central importance before and during the breeding season. During this period, the allocation of time toward maintenance activities could be affected by seasonal time requirements for breeding activities eg., incubation, chick rearing.

In this chapter, the repertoire of maintenance, aggressive and alarm behavioural patterns of captive adult black stilts is described. The similarities and discrepancies between behavioural patterns described for captive black stilts and those of the American avocet, black-necked stilt (Hamilton 1975), European avocet (Makkink 1936), pied stilts (McConkey 1972) and wild black stilts (Budgeon 1977, Pierce 1982) will be discussed. The daily time budget of a focal pair of stilts is also presented to i) quantitatively illustrate how these individuals apportioned their total available daylight hours between activities and; ii) examine any reallocation of time to foraging, preening and resting during the breeding season.

2.2 Methods

2.2.1 Description of behavioural patterns

From July to September 1982, behavioural observations of eight adult black stilts were made from hides overlooking two outdoor enclosures (section 1.3.3). During this time, one arbitrarily formed pair was housed on either side of a division fence within each enclosure. A total of four "pairs" were housed within these two large enclosures. A seasonal inventory of maintenance, aggressive and alarm behaviour was collated. A combination of sampling methods was used to collate an ethogram. Most behavioural pattern occurrences were noted during ad-libitum sampling (Altmann 1974), because quantitative comparisons were not being made (eg., comfort movements such as stretching). All-occurrence sampling (Altmann 1974) was used for behavioural patterns which were either i) rare eg., aggressive interactions or ii) which occurred as states rather than events eg., bathing (data later used in time budget analysis). The behavioural inventory collated was added to and checked against subsequent observations over the remaining two years of the study (1983/84).

2.2.2 Diurnal time budget analysis

Collection of data for a daily time-activity analysis of a focal pair of stilts was initiated in November 1982 and continued until July 1984. Observation periods spanned daylight hours from one-half hour after sunrise to one-half hour before sunset. Observations were divided into six periods, three from dawn to mid-day and a further three from mid-day to dusk (Verner 1965). The days were divided in this way to show diurnal variations in time budgets and to make observations at different times of the breeding season more comparable. Even "blocks" of time over the day and throughout the two years were therefore created. Individual activity was recorded by instantaneous sampling of selected animals at 30 sec intervals (Altmann 1974). Because time budgets deal with the state of an animal rather than with events (Altmann 1974), the predominant behavioural state of each animal over the half minute period was noted. This method did tend however, to bias overall estimates towards the most frequently performed activity. The percentage of time spent by an individual in a given activity was estimated from the percentage of samples in which that activity was recorded (Altmann 1974).

Activity of the focal pair was divided into 12 behavioural categories for analysis, three of which were behavioural patterns restricted to the nesting season (and therefore presented in section 3.3.4). A further three were observed only during the parental care period and are presented in section 4.3.7. The remaining six categories of maintenance and alarm behavioural patterns were observed throughout the year.

These categories were;

a) foraging - searching for and consumption of prey;

b) immobility - either i) resting ie., standing on one or both legs for a period longer than one minute;
    or ii) standing ie., transitory state of immobility less than or equal to one minute in duration and occurring between other activities.

c) preening - bathing and manipulation of body feathers;
d) oxheart consumption - includes time spent at oxheart trays only;
e) walking/wading - non-specific locomotion; and
f) attention/alarm - reaction to predators and other disturbance.

2.2.3 Seasonal time budget analysis

A seasonal time budget was obtained by dividing time budget data into four stages (Gibson 1978) for each of two breeding seasons. These stages were;

1) Pre-nesting, which began with the initiation of pre-copulatory behaviour (eg., adoption of the female precopulatory posture) and continued until laying of the first egg (approximately 8-10 weeks) during season one. The pre-nesting period of the second breeding season began after the first seasons progeny had been removed and continued until egglaying (3.5 weeks later);
2) Incubation, which included time from laying the first egg of each clutch (clutches were multiple) until that clutch was taken or hatched (4-7 and 24-26 days respectively);
3) The period of parental care of chicks from hatching to fledging (a period of 35-40 days); and
4) Parental care of chicks from fledging until breakup of the family party (a period of 4-5 months).

Table 2.1 presents the time span covered by each stage of the two breeding seasons.

Table 2.1 Duration of breeding stages

STAGE	1982/83 SEASON	1983/84 SEASON
One	22.07.82 - 19.12.82	26.08.83 - 12.09.83
Two	6.01.83 - 12.02.83	20.09.83 - 21.10.83
Three	20.02.83 - 6.04.83	8.11.83 - 12.12.83
Four	11.05.83 - 17.08.83	17.12.83 - 6.06.84

2.3 Results

2.3.1 Description of behavioural patterns

498 hours of behavioural observations were accumulated between July 1982 and February 1985. These involved eight adult black stilts and totalled 1178 stilt hours of observation. Behavioural patterns observed throughout the year (i.e., not restricted to the breeding season) were then classified according to context and primary function and are presented under the headings of i) maintenance behaviour ii) attention/alarm behaviour and iii) aggressive behaviour.

2.3.1.1 Maintenance behaviour

a. Foraging

Peck: Pecking was the most common method employed by captive black stilts in taking prey. The bill was directed downwards into the water and as far as the silt bottom. When prey were caught, the head and bill were raised above water level in a single jerking movement. This resulted in swallowing of prey and repositioning of the head for the next peck. Stilts foraging in water 4-6 cm deep immersed their entire head and neck for up to 3-5 sec at a time, while tugging at an object or prey item.

Probe: During probing, the head was tilted sideways so that both the bill and head were at an angle to the horizontal. The bill was then directed toward a stone and moved along its surface or through surrounding silt. More than one probe was usually made before food was located. This was the most commonly used method when feeding on land and along the water margin where silt was shallow or absent.

Scything: Scything was another tactile method of foraging used by captive stilts. The bill was swept in an arc through silt in shallow or exposed areas in a sideways movement of the head and bill. This method was occasionally used when stilts foraged in deep water (8-10 cm), but was more often and most intensively used on exposed silt surfaces or areas with only a shallow water covering. When aviary water levels were dropped once to implement vegetation control, intensive scything activity was carried out by juvenile and adult stilts through the exposed mud surfaces and small pools which remained.

Snatching: This was a method of catching insects on the wing or on vegetation. Visually located flying insects were pursued briefly and rapidly taken by an upward thrust of the head and opened bill. This was only observed as a successful attempt to catch flying prey once, when a moth was taken on the wing by a juvenile stilt. Snatching was a more successful method of catching insects when the prey was taken off vegetation along aviary banks. A blue-bottle fly (Family Calliphoridae) was the only identifiable insect seen being snatched by a stilt, in one instance off vegetation from near an oxheart shelter. Once caught, the fly was carried to water where it was immersed and then eaten. Other smaller insects were snatched, but they were too small to be identified by me.

b. Oxheart consumption

All stilts obtained some food from trays containing minced oxheart. Pecking was the only method used to consume oxheart pieces, a peck being directed at an angle above the horizontal toward a tray positioned at breast height. As when foraging, the head was jerked backwards to swallow. Pieces of oxheart which had dropped to the ground were also taken by pecking. Large pieces which could not be swallowed immediately, were worked up toward the mouth by rapidly opening and closing the bill and then swallowing in a similiar manner (Plate 2.1). Oxheart was often carried within the tip of the bill from the tray to water, where it was immersed and then eaten.

c. Drinking

Captive stilts drank when standing or slowly moving forward in water, by lowering the bottom mandible to skim beneath the surface. The bill was raised above the horizontal, allowing water to run down along the inside of the lower mandible before swallowing. Stilts frequently drank after consuming oxheart.

d. Resting

Captive stilts spent a large proportion of their time immobile (section 2.3.2.4), and most of these bouts followed preening bouts. One or more of five resting positions were used during a period of immobility;

Stand two legs: Stilts stood on both legs, with the head and neck brought downward into the shoulder while the head remained facing forward. Both eyes were open.

Stand two legs, head in: Both legs remained in contact with the ground but the bill was tucked beneath the stilt's wing. In this position which was observed only rarely, the eyes remained open and the bird was alert to its surroundings.

Stand one leg: On leaving water to rest on land, stilts shook one or both of their legs to remove excess water. While continually being shaken, one leg was drawn upward to fold lengthwise along the lower body. With the tarsus and tibia tucked in beneath the body, only the metatarsus remained visible for a short time, after which it too was brought up into the body. Stilts would occasionally preen their metatarsus before completely tucking it underneath body feathers. Once in this position, immobile stilts were reluctant to place this leg on the ground again if disturbed and so moved and regained balance by hopping. The head and bill faced forward and were brought back into the shoulder. Both eyes were fully or partly opened (Plate 2.2).

Stand one leg, head in: As above, one leg was tucked into the lower body, but the bill was placed beneath the wing and covered to the nasal feather line. This was the most commonly used position for resting, during which the eyes were partly or fully closed for short durations. The body was faced into the wind and stilts pivoted on one leg to change direction (Plate 2.2).

Sit: During hot weather or when ailed by a leg injury (i.e., resulting from bands in two cases and from abrasion on rocks in another), a sitting position was used in resting. The lower body was brought into contact with the ground and both legs were folded in beneath the body. The head was pulled in toward the shoulder or the bill tucked in beneath the wing. In the latter case, the eyes were closed for short periods.

PLATE 2.1 Oxheart consumption

PLATE 2.2 Resting positions

e. Bathing

Stilts bathed in water approximately 6-8 cm deep, crouching over the surface so that the lower body made contact with water. By rocking its body forward and backward, a stilt's head and bill was dipped rapidly below water and raised again, resulting in droplets of water running over the neck and back (Plate 2.3). During initial dipping, the wings remained closed and in contact with the side of the body. As the head was raised from beneath water, a single "tw-ink" call was emitted (section 5.3.1.1). Dipping of the head and emission of this sound was repeated 4-8 times before the neck was brought up along the back in a sideways "S"-shape movement, to rub the head over the upper mantle (Plate 2.4). Dipping was then resumed in a forward rocking motion with the wings held out from the body. Both wings were flapped up and down below the water surface and with a sideways dip of the body, each wing alternately immersed in water. Flapping and sideways rocking were interspersed with forward dipping and rubbing of the head along the mantle. Side-dipping became vigorous as water was thrown over the entire body. On three occasions, I observed bathing stilts fully immersing in a forward dive and resurfacing almost 1 m forward of their original position. Bathing was completed by an upward spring into the air as both wings were flapped to remove excess water (Plate 2.5). An entire body shake followed and bathing was terminated with a tail shake. Bathing by one stilt was sometimes followed with bathing by a second stilt. This was especially the case for juveniles within a family group, when up to four different individuals were observed to bathe in succession.

f. Preening

Preening took place on land (either on aviary banks or mid-stream islands) or in shallow water along bank and island margins. Preening frequently followed a bathing bout and preceded immobility. Initially the neck was stretched upward, allowing the bill to be brought down and back toward the chest. Quick pecks were made with the bill tip at breast feathers and those beneath the leading and trailing edge of the wing. If preening had been preceded by bathing, tips of the primary feathers on one wing were continuously rubbed together with those on the opposite wing. One wing was then held away from the body with the leading primary stretched downwards and the bill was used to preen inside the wing feathers (Plate 2.6). Stilts alternated quick pecks to the breast, lower body and wing feathers before rubbing the side of the head over the lower back and uropygial gland. The head was rubbed vigorously over the entire back and wings, spreading oil collected from the gland over these regions. Preening activity was variable in duration, from a few sec during a foraging bout to 20 min before switching to other activities. Preening also varied in pattern and context (eg., preening during precopulatory activity, section 3.3.1.1) but generally followed that described above.

Injured individuals released into outdoor enclosures after a period of inside confinement, immediately went into water to bathe and repeated the bathing/preening sequence 2-3 times before switching activities.

g. Comfort movements

Stretch two wings: Stilts stretched both wings by raising them upward to their full extent before returning them to their original position. The head was lowered slightly toward the ground and the bill pointed downward. This movement sometimes occurred simultaneously with defaecation.

Stretch one wing: Observed only rarely, a single wing stretch was achieved by taking weight off one leg while it remained in contact with the ground and stretching the same side wing horizontally backward toward the tail.

Stretch wing and leg: One leg and wing were unilaterally stretched backward and parallel with the ground (Plate 2.7). In this way the wing was fully extended to follow the line of the corresponding leg. The head was brought down into the shoulder but maintained at mantle level.

Scratch head: Head scratching occurred mainly during preening by dropping one wing out and down from the side of the body. The leg on the corresponding side was brought back, and then forward over, the carpel joint of the wing. The head was held downward and tilted sideways as the metatarsus was brought up toward it (Plate 2.8).

Shake: Shaking occurred after bathing, during preening, or as an

PLATE 2.3 Bathing - body dipping

PLATE 2.4 Bathing - head rubbing

PLATE 2.5 Bathing - spring and flap

PLATE 2.6 Preening inside wing feathers

PLATE 2.7 Stretch wing and leg

PLATE 2.8 Scratch head

PLATE 2.9 Upright posture

isolated event upon leaving water for land. Feathers of the head, neck, chest, back and wings were raised as the stilt made a quick shaking movement of the head and body.

Gape: Gaping was a momentary opening and closing of the bill while resting or standing on land. The upper and lower mandibles were opened and separated up to 2 cm, then rapidly closed after one to two secs.

Defaecation: Defaecation occurred on land and only once was it observed to occur while a stilt foraged in water. Stilts foraging in the stream frequently left the water to walk up an aviary bank or mid-stream island to defaecate. They then returned to water and resumed foraging or moved toward the oxheart tray.

2.3.1.2 Attention/alarm behaviour

Upright posture: When alarmed by low-flying birds, passing mammals, the intrusion of humans or by other disturbances, stilts adopted an upright position in which the neck of the alarmed stilt was extended vertically and slightly forward of the shoulder. Both eyes were widely opened, exposing the entire red iris and the head was turned to the direction of the disturbance (Plate 2.9). Loud "yap" calls were usually given in rapid succession (section 5.3.1.6.a) until the intruder left or the disturbance ceased.

Forward posture: This attentive position was similiar to the "upright posture" described above, except that the neck and head were held further forward, forming an almost straight line with the body and tail. The bill and head were directed downward, resulting in a curved lower neckline (Plate 2.10). The breast feathers were raised which gave the impression of a broader chest. Feathers of the nape and neck were also raised and a repetitive "tip" call was given (section 5.3.1.2). This position was observed in four different contexts (in each case, the posture was repeatedly adopted during a single observation period);

i) when an adult male stilt stood over a nest site;
ii) as a subordinate female stood cornered in its aviary by an aggressive male;
iii) when three juveniles and an adult male stood over an elver (*Anguilla* sp.) as it moved through the silt bottom

of the aviary stream; and

iv) by a yearling bird toward two stilts in an adjacent aviary.

Tilt head: Stilts reacted to aerial predators, particularly the harrier hawk (Circus approximans), by elongating the neck and holding the head on a 30-40° angle to the vertical (Plate 2.11). This cocking movement resulted in one eye being directed toward the sky. Both the head and neck were pivoted to follow the flight path of the observed predator while the stilt's body remained stationary.

Walk fence: Stilts alarmed by ground disturbances outside their enclosures walked the fenceline facing the disturbance. After walking, or at times running parallel to the fenceline for approximately 2-10 m, an alarmed stilt turned towards the wire fence and walked off in the opposite direction to which it had been moving. This "to and fro" movement continued for up to 20 min on several occasions but the cause of the disturbance was not always obvious to me.

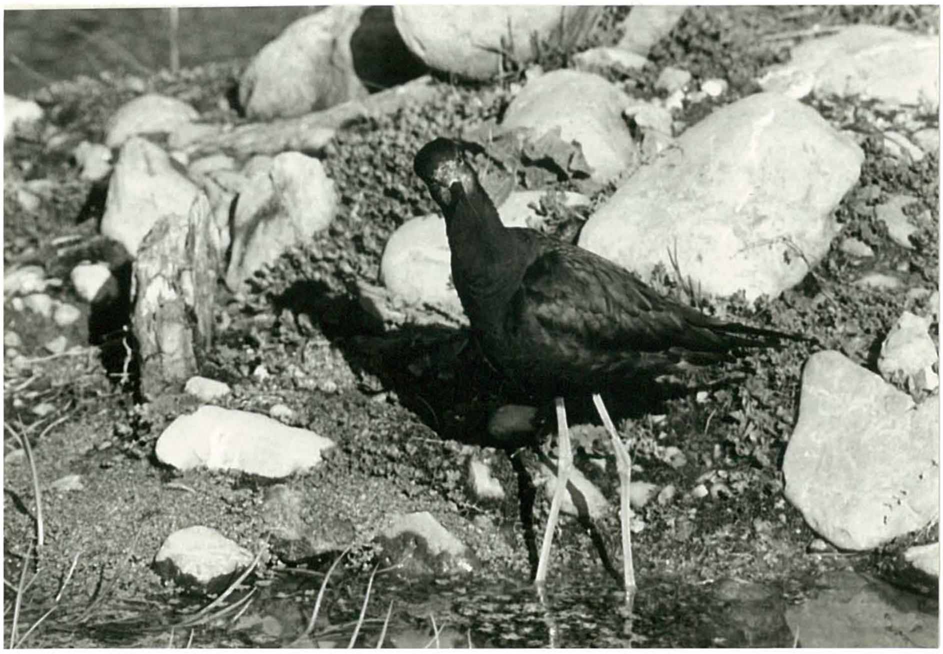
Head bob: When excited, stilts often bobbed their head repeatedly up and down, extending the neck only a few cm. Head bobs also occurred when approaching oxheart shelters for feeding from trays. No alarm calls were emitted but a moderate volume "yap" call (section 5.3.1.6.a) was often given when walking along the bank in front of oxheart shelters.

Intention bob to fly: I observed an intention movement to fly only on four occasions. The alarmed stilt which displayed this pattern ran along an aviary bank or along a median fence between aviaries, in a semi-crouched position with both knees bent and with the body forward of its usual stature. After running 2-3 m, the stilt stopped and in a single bobbing movement, lowered its body further toward the ground and then returned to its semi-crouched position before moving off again. During the lowering of the body, the wings were held close to the body and slightly forward of their normal position.

Flight: When alarmed by passing humans, dogs or aerial predators, stilts left the ground and flew around the aviary, frequently hitting the top and side wire of the enclosure. The legs were held straight out behind the body while the wings were flapped. Repetitive loud "yap" calls were emitted (section 5.3.1.6.a). On returning to land,

PLATE 2.10 Forward posture

PLATE 2.11 Tilt head



"yapping" continued and an alert upright posture was assumed while running along the aviary bank. Calling and running continued until the disturbance subsided.

Run and hide: I twice observed stilts running for cover to hide from a harrier flying overhead. On both these occasions, the same two stilts were involved (one male, one female). As a harrier flew directly over the aviary within 10 m of the top wire, these two birds ran to a shrub (*Hebe* sp.) providing overhanging vegetation, under which they hid.

2.3.1.3 Aggressive behaviour

Aggressive upright: When two territorial stilts were either side of a median fence between adjacent aviaries, they walked parallel to each other, adopting a very erect posture in which both necks were fully extended vertically (Plate 2.12). This upright position was similiar to that described in 2.3.1.2 (upright posture), except that the neck was stretched upward and the head held further back in line with the shoulder. Both stilts dropped their wings slightly and held them back from the shoulder. Primary feathers of the wing were extended rigidly backward. The feathers of the neck were raised and the chest lifted upward, which allowed increased head height above the ground.

Tug fence: During agonistic encounters of the type described above, a stilt often turned from an aggressive upright position toward the median fence and delivered a quick peck toward it (Plate 2.13). As a stilt held on to the wire above eye level, its slightly opened bill was used to tug the fence. This hold was maintained for 3-10 sec, during which further tugs were sometimes made. After the hold was released, the stilt resumed an upright aggressive posture or turned away from the fence.

Tug vegetation: Grass pulling occurred during aggressive interactions along the median fence. Stilts walked forward with the head and bill directed downward and body parallel to the fenceline, while pecking at small stones and loose vegetation. A peck was directed at rooted vegetation and the hold maintained 2-10 sec. During this time, further tugs at the grass were usually made. When the hold was released, material was sometimes pulled up with the bill and either dropped or thrown backward along the side of the body (below).

Sidethrow: Vegetation lying near the median fence was picked up with the bill and thrown backward with a sideways flick of the head through 45-90°.

Squat: Two female and three male stilts were observed to squat during aggressive interactions at the fence between aviaries. By bending both knees, the body was lowered chest first toward the ground, although not always contacting it. Sidethrowing was observed after most squats. If the body had been lowered completely to the ground, scraping (below) then followed this behavioural pattern.

Scraping: After crouching completely so that the body was lowered to the ground, both legs were brought up and out behind the body while body weight was centered forward on the chest. Both tibia pointed upward at an angle of 45-70° to the ground and the tarsi were almost vertical. The wings were also directed upward, following the line of the tibia and the feet were used to dig out gravel and vegetation from behind the stilt.

Aggressive pursuit: Aggressive stilts frequently chased their cagemate(s). A hunched posture was adopted, with the head lowered to shoulder height and brought back into the chest while the stilt ran quickly after the subordinate bird (Plate 2.14).

Head low, run sideways: Subordinate stilts being pursued ran with a lowered head which was turned in the direction of the pursuer. This resulted in running sideways rather than forward. Both "aggressive pursuit" and "head low, run sideways" occurred mainly in front of oxheart shelters, when a subordinate stilt had approached the tray to consume meat and was chased off again.

Intention-peck or peck: After chasing a subordinate bird, a pursuing stilt briefly increased its speed for approximately 0.5-1.0 m and directed its bill forward in a lunging peck at its opponent. It was difficult for me to distinguish between an actual peck and a misdirected peck or intention movement to peck. On one occasion though, physical contact was observed between adult stilts when an aggressive stilt held on with its bill to the bird being chased. On a second occasion, an adult female pinned down and physically pecked a 5 day old chick (section 4.3.6)

PLATE 2.12 Aggressive upright

PLATE 2.13 Tug fence

PLATE 2.14 Aggressive pursuit
(hunched bird in foreground)

PLATE 2.15 Fly and drop

Fly and drop: The most intense and physical pattern displayed by stilts during aggressive interactions was one in which they sprang into the air and dropped down on a nearby stilt. The drop was made with both legs extended downward and the wings held upward to "float" down on the crouching opponent (Plate 2.15). Physical contact was often made between the two birds. If standing in water, an attacked stilt crouched down, submerging its lower body. Repetitive swoops were made by one or both birds, before settling in different parts of the aviary.

2.3.2 Diurnal time budget

A total of 307 hours (614 stilt hours) of raw data (i.e., total number of minutes of sample time spent in each activity) was accumulated between July 1982 and June 1984 for time budget analysis of a focal pair of captive black stilts. The distribution of data collection over the four stages of the breeding season and six periods of the day is presented in Tables 2.2 and 2.3.

The sampling distribution of raw data collected over the two breeding seasons was non-normal. A greater proportion of the total observation hours were between mid-morning and mid-afternoon during stages two and four, than at other times and stages of the day/season. To "correct" the non-normal distribution of data sampling and equalise variance within and beween i) time periods and ii) stages, raw data were expressed as percentages of the total sample time and were normalised using square root transformation (Hinkle et. al., 1979). Six two-way analyses of variance within and between scores of the dependent variable (time spent in activity) over three independent variables i) breeding stage ii) period of the day and iii) individual, were performed using the analysis of variance (ANOVA) procedure. ANOVA allowed testing of the equality of all the mean percentage times spent in an activity over four breeding stages and six time periods, while maintaining the type I error (i.e., error of rejecting a true hypothesis) at the 5.0% significance level for the entire set of comparisons (Hinkle et. al., 1979). The null hypotheses tested were "that the proportion of time spent in an activity was equal for i) both individuals, ii) all six time periods and iii) all four stages of the breeding season". An interaction amoung independent variables was present when the effect of the levels of the first independent variable on the dependent variable was not the same across the levels of the

Table 2.2 Diurnal distribution of time budget sampling

	TOTAL NUMBER OF SAMPLING HOURS		
PERIOD	SEASON ONE	SEASON TWO	TOTAL
One	13.7	18.8	32.5
Two	29.5	27.0	56.5
Three	34.9	30.0	64.9
Four	36.2	31.8	68.0
Five	24.5	34.0	58.5
Six	8.2	18.4	26.6
TOTAL	147.0	160.0	307.0

Table 2.3 Breeding stage distribution of time budget sampling

	TOTAL NUMBER OF SAMPLING HOURS		
STAGE	SEASON ONE	SEASON TWO	TOTAL
One	23.0	21.2	44.2
Two	78.7	61.6	140.3
Three	15.2	22.2	37.2
Four	30.1	55.0	85.1
TOTAL	147.0	160.0	307.0

second independent variable (Hinkle et al 1979). For example, an interaction between the effects of time of the day and individual for the activity immobility, would mean that individuals differed significantly in the period(s) of the day during which each spent immobile.

Tables 2.4 and 2.5 indicate for which activities, an ANOVA test rejected (denoted x) or accepted (denoted +) the null hypotheses, at the p = 0.05 significance level (two-tail test).

Results of the above tests for individual, time period and stage of the breeding season differences in time budget will each be further elaborated below. Seasonal differences in time budget between years will also be reported.

2.3.2.1 Individual time budget analysis

An ANOVA test of the null hypothesis that "there was no difference between individuals in the total proportion of sample time spent in each of the six activities", was rejected in each season for three activities; oxheart consumption, walking and immobility. The null hypothesis was accepted for the three remaining activities; preening, attention/alarm and foraging.

There was no interaction between the effects of individual and time period for any of the activities. The interaction between the effects of individual and stage of breeding season was significant only for foraging, oxheart consumption and immobility (season one), preening and attention/alarm (season two).

The male consumed significantly more oxheart than the female in season two (Figure 2.2 d), but the reverse applied during the first season (Figure 2.1 d). The male spent a greater proportion of sample time walking than did the female (Figures 2.1 e, 2.2 e). In contrast, the female remained immobile for a larger proportion of time than the male (Figures 2.1 c, 2.2 c), especially during season one. The two stilts spent approximately the same time as each other in attention/alarm (Figure 2.1 f, 2.2 f), preening (Figures 2.1 a, 2.2 a) and foraging (Figures 2.1 b, 2.2 b) during both seasons.

Table 2.4 Summary of ANOVA tests (1982/83 season)

ANOVA TEST	PREEN	WALK	ALARM	IMMOBILE	OXHEART	FORAGE
Individual	+	x	+	x	x	+
Time	x	+	x	x	+	x
Indiv*Time	+	+	+	+	+	+
Stage	x	x	x	x	x	x
Indiv*Stage	+	+	+	x	x	x
Time*Stage	x	+	x	+	+	x

Table 2.5 Summary of ANOVA tests (1983/84 SEASON)

ANOVA TEST	PREEN	WALK	ALARM	IMMOBILE	OXHEART	FORAGE
Indiv	+	x	+	x	x	+
Time	+	+	x	x	x	x
Indiv*Time	+	+	+	+	+	+
Stage	x	x	x	x	x	x
Indiv*Stage	x	+	x	+	+	+
Time*Stage	x	+	x	x	x	x

KEY Ho: Level is independent of treatment
+ = accept the null hypothesis
x = reject the null hypothesis
* = interaction of individual, stage or time period

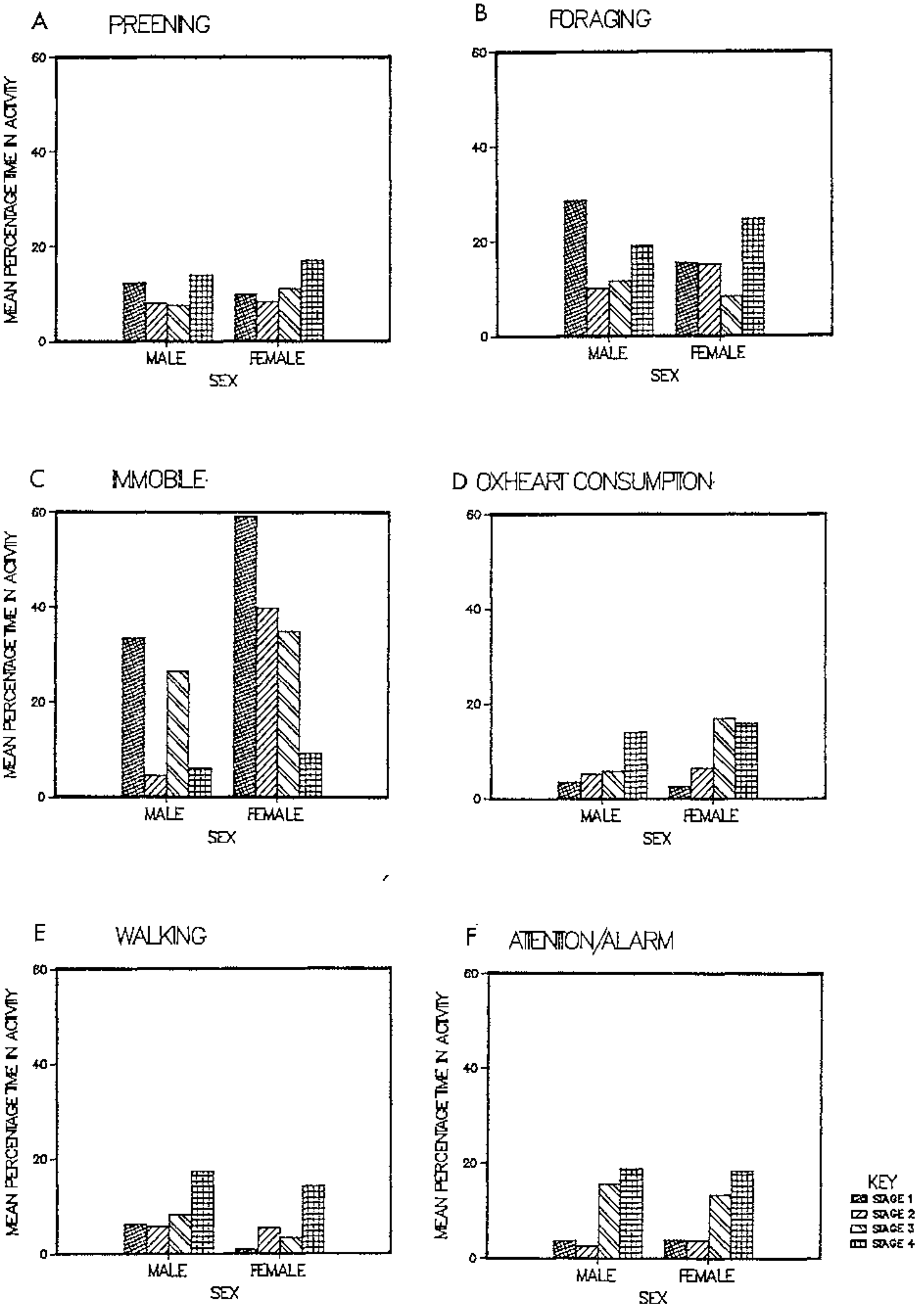


FIGURE 2.1 Individual time-budget (by stage) 1982/83 breeding season

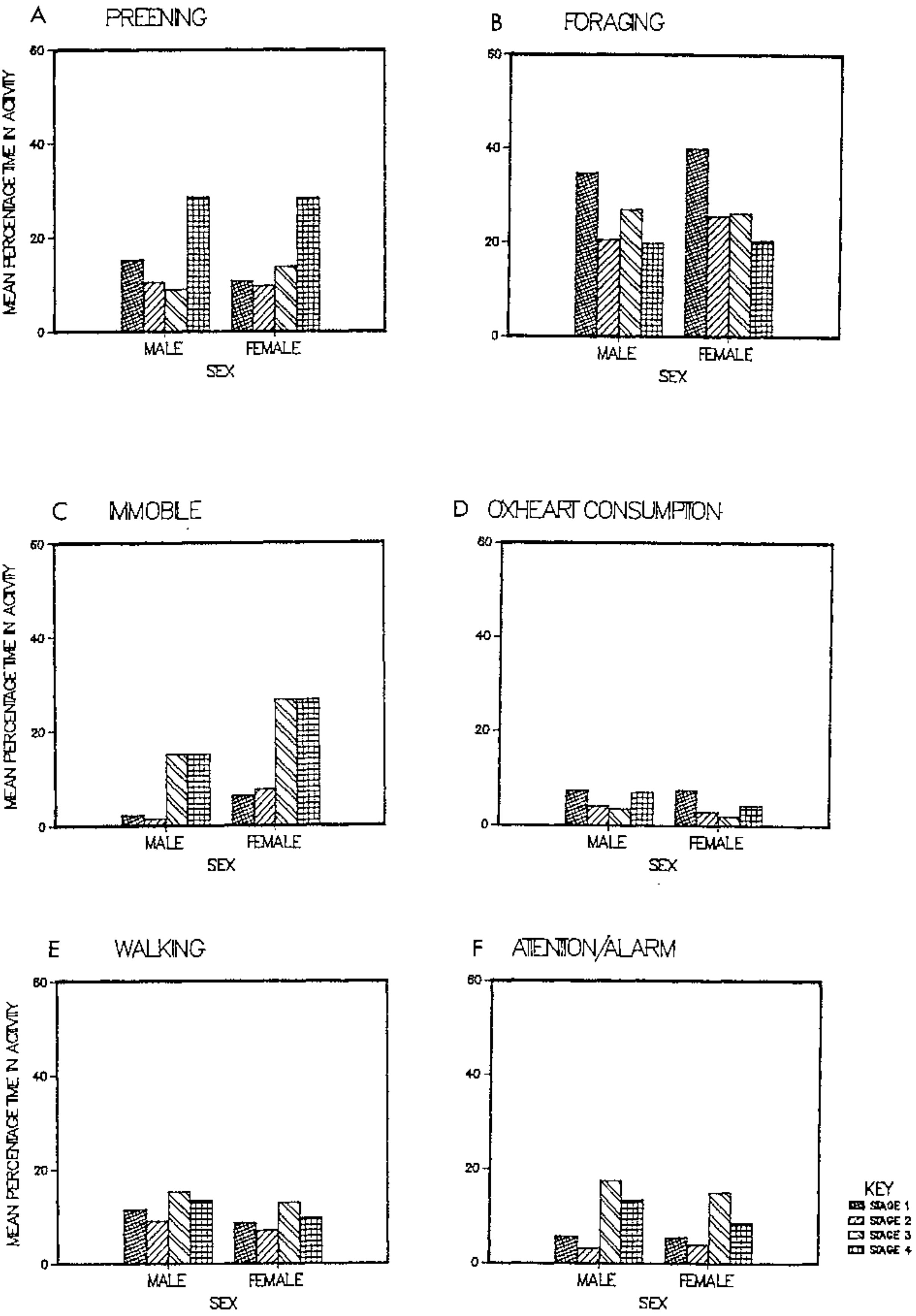


FIGURE 2.2 Individual time-budget (by stage)
1983/84 breeding season

2.3.2.2 Diurnal time budget analysis

There were no individual differences in the proportion of time allocated to an activity over each of six diurnal time periods (i.e., the effects of the interaction between time period and individual were not significant). Data from the two individual time budgets were combined for each season to produce a diurnal budget of each activity. An ANOVA test of the null hypothesis that "the proportion of time spent in an activity was equal for all time periods", was rejected for all activities except oxheart consumption and walking (season one), preening and walking (season two).

The percentage of observation time that the stilts spent in each activity over six time periods is presented in Figures 2.3 and 2.4 for the two seasons data.

When data from all four stages of the breeding season were combined (Appendix six), the following diurnal activity peaks were evident;

i) Immobility peaked at period 5 (mid-afternoon) during season one and at period 4 in season two.

ii) Diurnal attention/alarm activity followed a bimodal distribution, peaking during early-mid afternoon and again in the late afternoon.

iii) Peaks in foraging activity occurred at periods 1,3 and 4 during separate stages of the breeding cycle in season one (Figure 2.3 b). The combined data from these stages therefore, showed a prolonged peak in foraging activity from period 1 to 4 (Appendix six). Foraging data from season two clearly indicated a bimodal distribution of activity, peaking in the early morning and again in the mid to late afternoon (Appendix six).

iv) Preening activity peaked during period 4 in season one but remained consistent over time for season two.

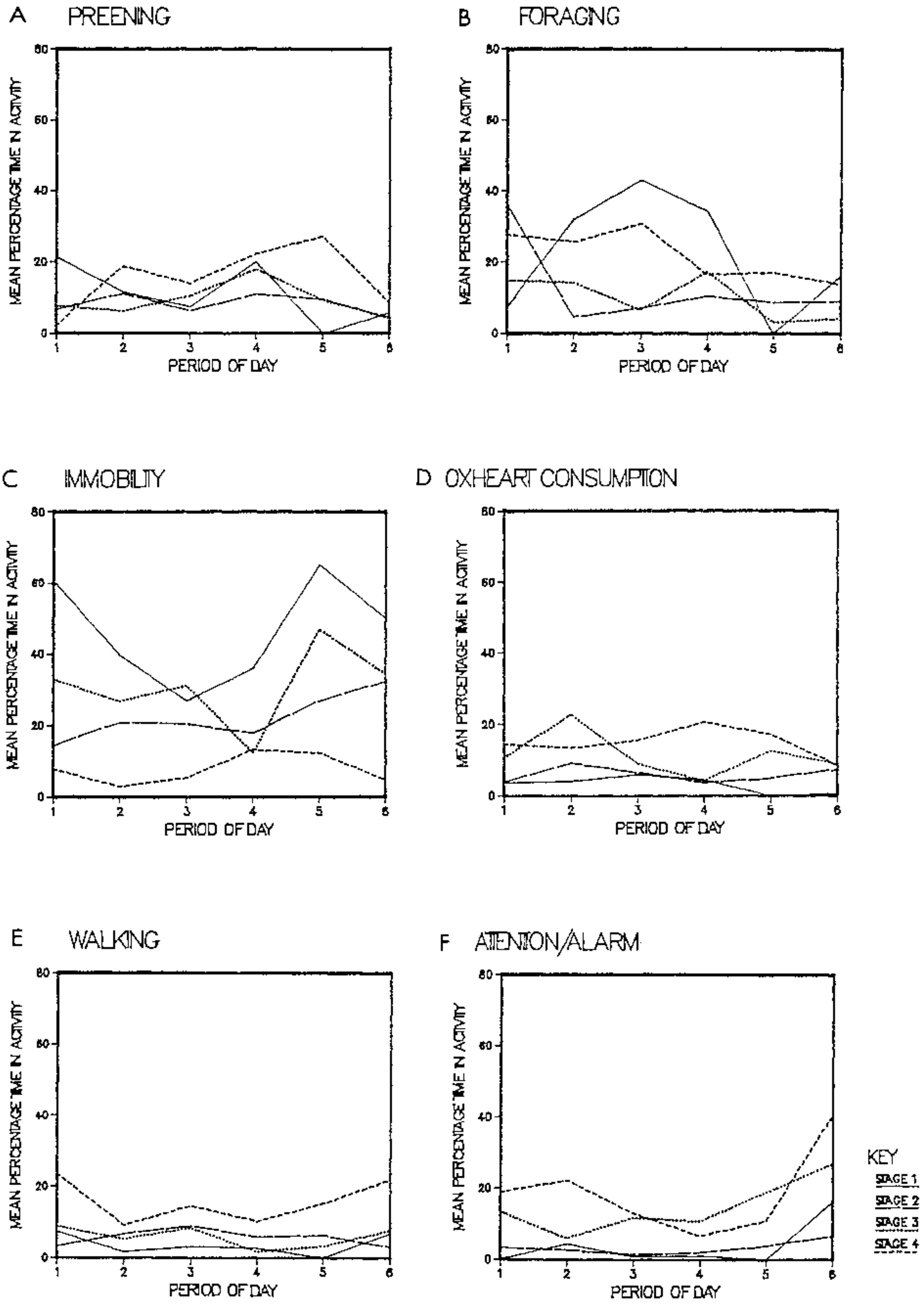


FIGURE 2.3 Diurnal time-budget (by stage) 1982/83 breeding season

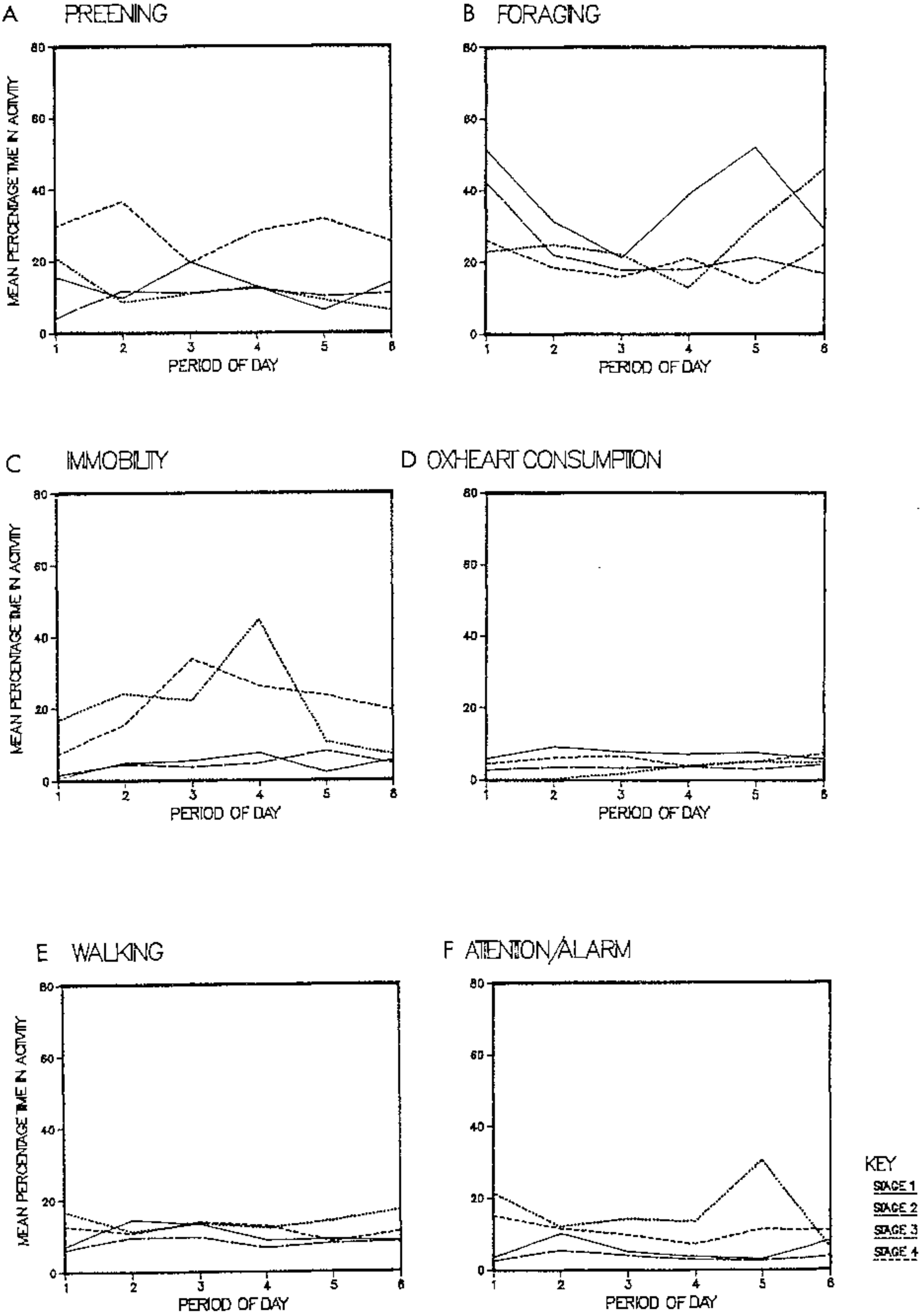


FIGURE 2.4 Diurnal time-budget (by stage) 1983/84 breeding season

2.3.2.3 Breeding stage time budget analysis

The null hypothesis that "the proportion of sample time spent in an activity was independent of the stage of the breeding cycle", was rejected for all activities in both seasons. Figures 2.5 and 2.6 indicate the mean percentage of total sample time spent in each activity for the four breeding stages (combined male and female data).

Foraging activity peaked during stage one (pre-nesting) of both seasons (Figures 2.5 b, 2.6 b) and again during stage 4 (post-fledging parental care) in season one (Figure 2.5 b). The second peak of season two was lower than the first and occurred during the pre-fledging parental care stage of the breeding cycle.

Oxheart consumption peaked during the parental care period of the first season (Figure 2.5 d). In the second season however (Figure 2.6 d), lower peaks were evident during the post-fledging parental care and pre-nesting stages. Walking occurred primarily during the two parental care stages of both seasons (Figures 2.5 e, 2.6 e), as did attention/alarm activity (Figures 2.5 f, 2.6 f). Preening activity of the focal pair peaked (Figures 2.5 a, 2.6 a) after their chicks had fledged (stage four). A lower second peak occurred during the pre-nesting stage of both seasons. Immobility followed dissimiliar patterns over the two seasons. For the first three breeding stages of the first season (Figure 2.5 c), immobility was the predominant overall activity of the female (35-60% of observation time). The male however, spent a maximum of 35% of observation time immobile prior to nesting and 25% during early chick-rearing of this season. During the second season (Figure 2.6 c), less time was spent immobile by either bird. Peaks in immobility occurred during both stages of the parental care period, with higher immobility again for the female than for the male.

2.3.2.4 Breeding season time budget analysis

Figure 2.7 presents the mean percentage of total sample time spent in each activity over the two seasons (individual and stage of breeding data combined).

Foraging was the activity to which the greatest proportion of time was allocated by the stilts during season two, representing 26.7% of total

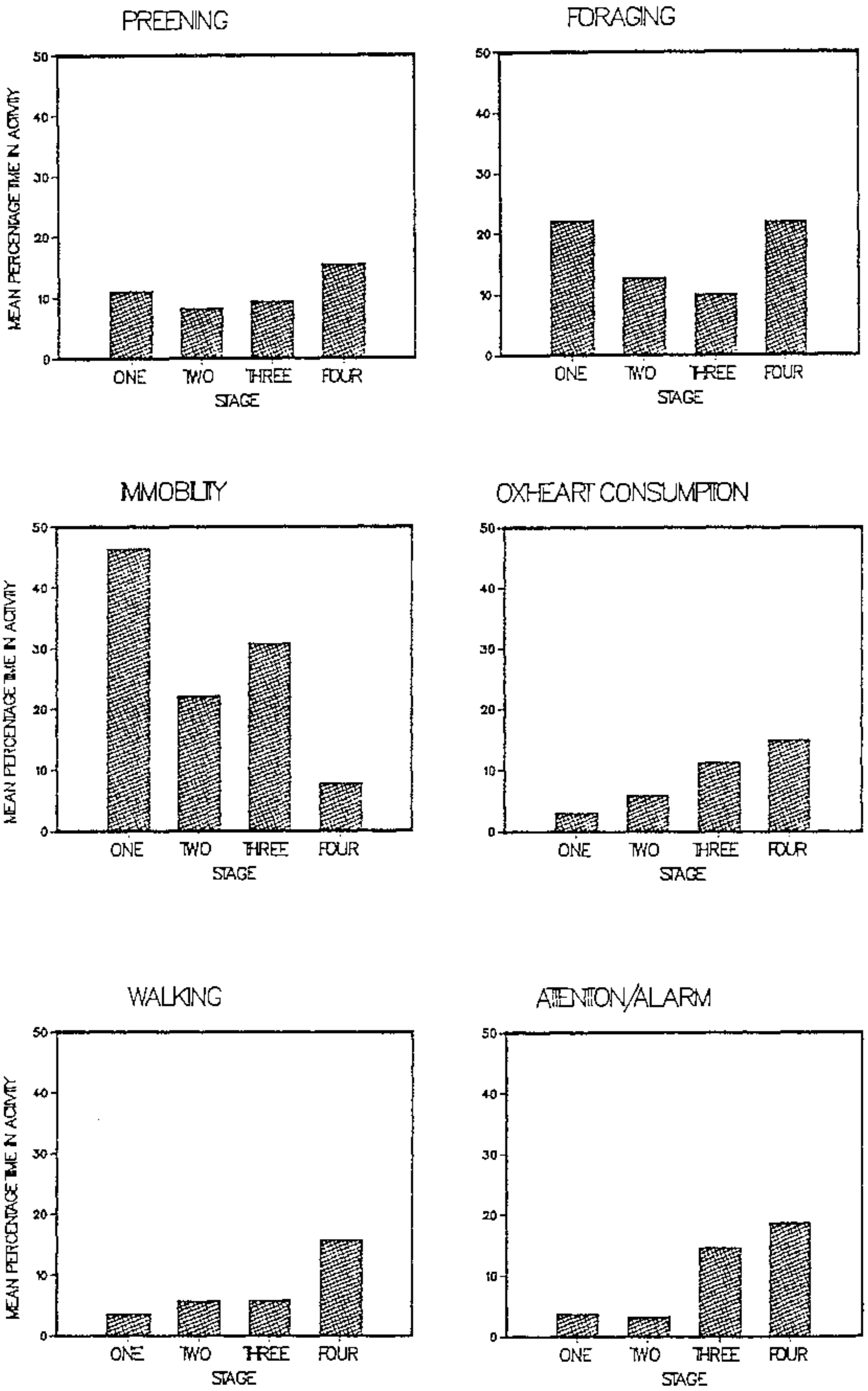


FIGURE 2.5 Breeding stage time-budget 1982/83 breeding season

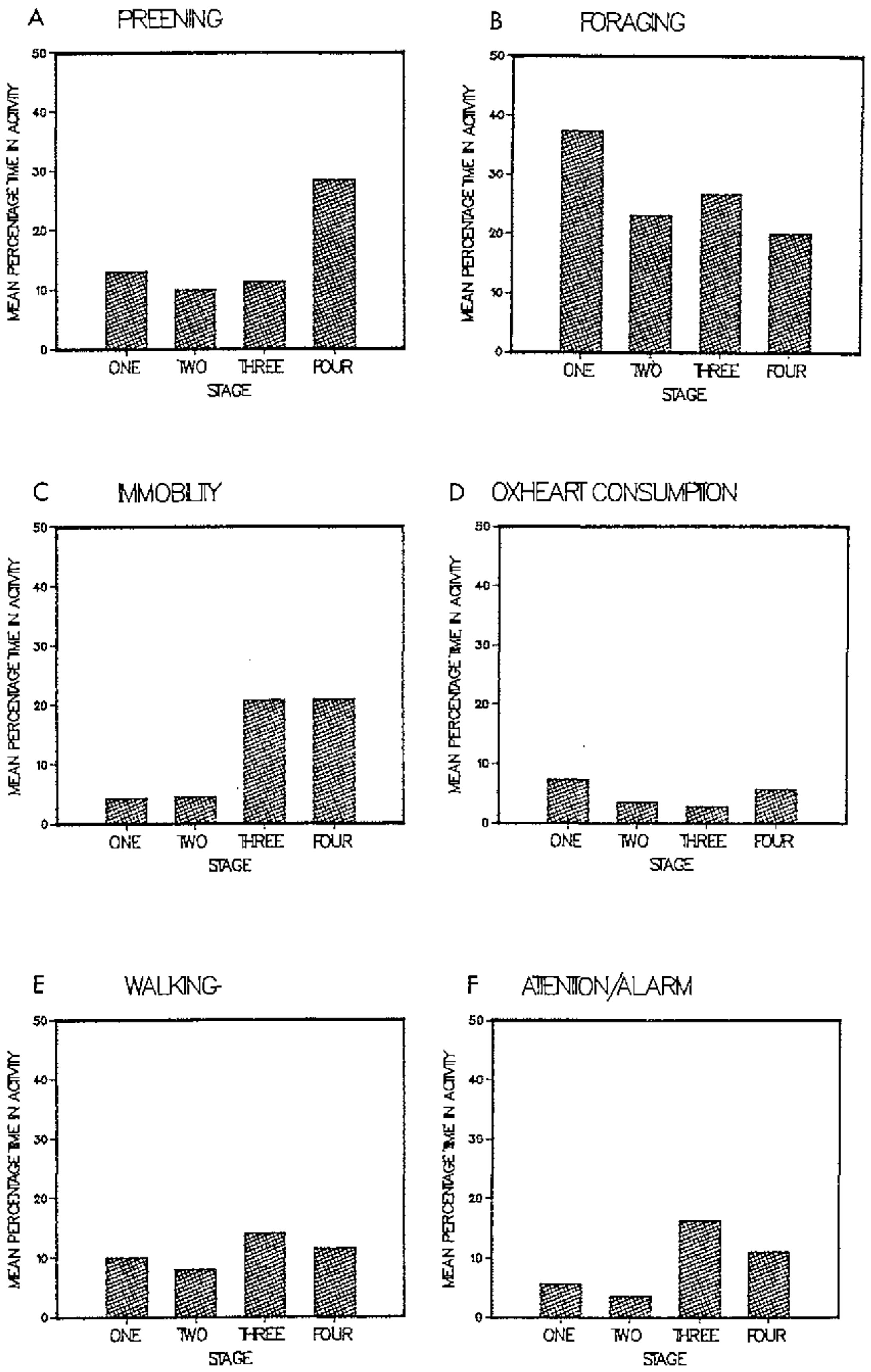


FIGURE 2.6 Breeding stage time-budget 1983/84 breeding season

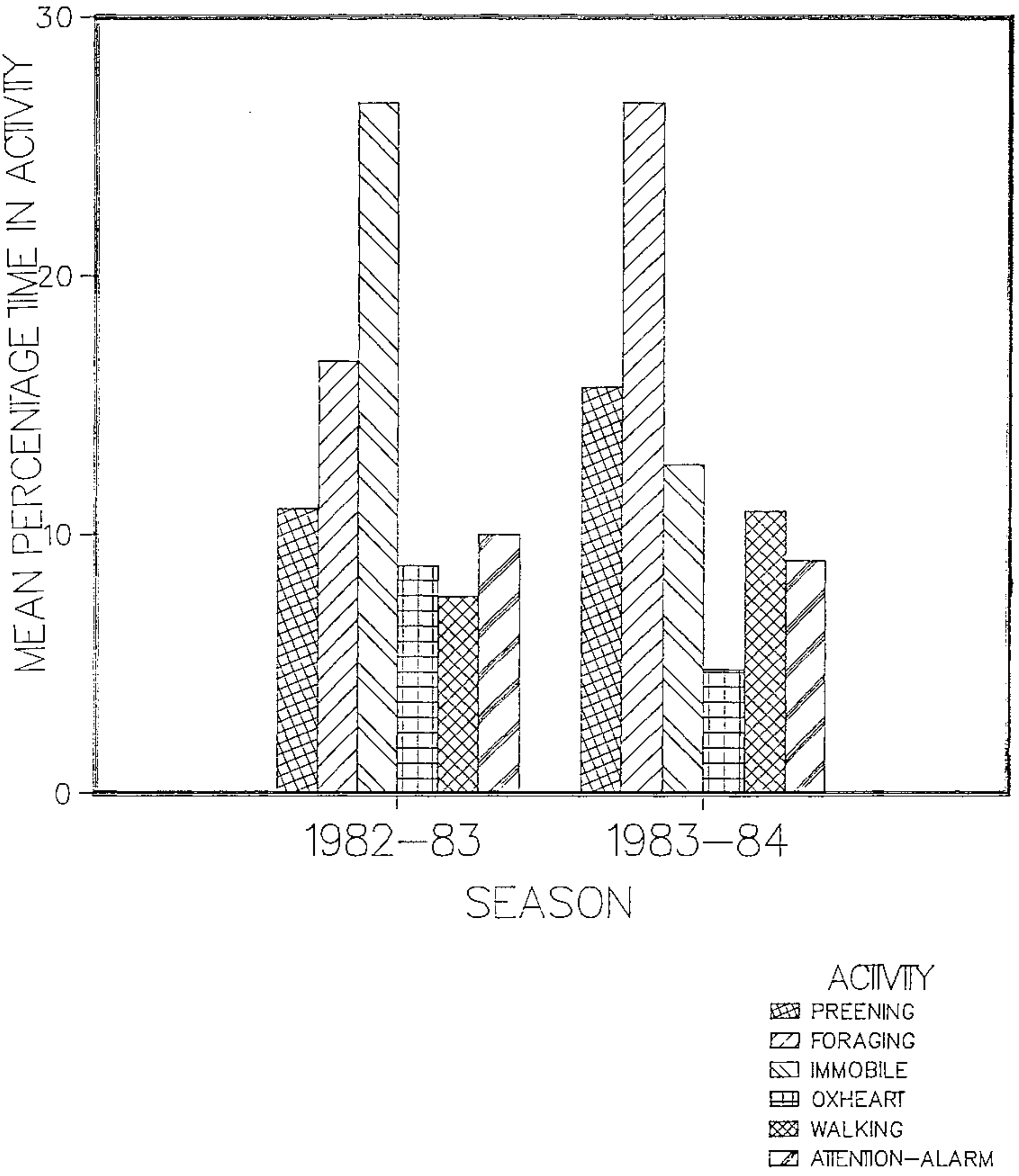


FIGURE 2.7 Total time spent in each activity (combined individual and stage data)

observation time during that season. During season one, foraging was the second most common activity, occupying 16.7% of total observation time.

Immobility was the predominant activity over the first season (26.7% of total sample time) and the third most common activity during season two (12.6%). The percentage of time spent preening was 15.7% (season two) and 11.0% (season one) of the total observation time.

2.4 Discussion

2.4.1 Description of behavioural patterns

Many of the maintenance, comfort, aggressive and alarm behaviour patterns performed by captive black stilts are also shared by other members of the Family Recurvirostridae. During foraging for example, captive black stilts primarily used pecking to locate prey. Pecking was also the most common method employed by black-necked stilts (Hamilton 1975), black-winged stilts (Goriup 1982), wild black stilts (Budgeon 1977, Pierce 1982) and pied stilts (McConkey 1971). Pecks were directed primarily at motile prey, visually located in water (Pierce 1982). This method was used mainly at water depths of 0-0.5 cm (Budgeon 1977) or during terrestrial (Hamilton 1975, Budgeon 1977, Pierce 1982) and subsurface foraging. Complete immersion of the head while pecking in water of greater than tarsus depth has been described by Hamilton for American avocets and black-necked stilts as "plunging". Budgeon (1977) noted that black stilts used this type of method mainly in water of 9-18 cm in depth. The distinction between plunging and pecking may be arbitrary (Hamilton 1975), the former merely being the reaching for prey at greater depth than during pecking.

Black stilts use a wide range of visual and non-visual feeding methods besides pecking (Pierce 1985). One of these non-visual methods is probing, which is the tactile location of prey hidden beneath riverbed stones (Pierce, in press). This method was used also by captive stilts. By repeatedly probing under stones with the bill inclined at an angle to the vertical (multiple lateral probing), wild black stilts dislodged prey into view before catching them with a quick peck (Pierce 1982). The lateral probing ability of black stilts is suggested by Pierce to be a reason for their ability to remain in the MacKenzie

Basin during winter, after lentic feeding areas have partly frozen over. Their ability to dislodge less active prey from beneath stones was not shared by pied stilts which migrate out of the basin in late summer (Pierce 1982).

An interesting element of stilt feeding behaviour was the immersion of snatched prey into water. This behavioural pattern has been reported in the black-winged stilt (Goriup 1982) and has been previously observed being performed by wild black stilts (Budgeon 1977). Food-washing has also been described in other waders (Harber et. al., 1947). Immersion of prey appears to function in removal of mud and vegetative debris (Harber et. al., 1947). This may be a likely explanation for its use by wild black stilts feeding in the very soft muddy substrate of Glenmore Tarn (Budgeon 1977). Captive stilts however, were observed washing mainly oxheart and insects snatched off vegetation. It is unlikely that these food items contained debris, but washing may have aided in swallowing the comparatively "dry" prey. This possibility is supported by the frequency of which the study birds drank water after consuming oxheart. Drinking has been described for American avocets (Hamilton 1975), but this is the first record for stilts.

The chief secondary activity of captive stilts was immobility. Resting (i.e., remaining immobile for longer than one minute) was predominant over standing. Long periods of inactivity frequently followed bathing and/or preening. Synchronization of resting, bathing or preening activity was observed. Hamilton (1975) suggested that activity synchronization implies some social function or context for these patterns. The sight of one bird bathing for example, may stimulate others to bathe.

In addition to the bodily maintenance and social functions of resting and preening, the postures involved have been observed by other authors in quite different contexts. Makkink's (1936) "pseudo-sleeping" attitude of the European avocet (resembling the "stand two legs, head in" posture described in section 2.3.1.1d), was adopted by avocets involved in intraspecific conflicts. In situations such as that described by Makkink, "pseudo-sleep" is probably a displacement activity (i.e., an activity which appears irrelevant to either tendency of a conflict situation (Hinde 1970)). In captivity, as with pied stilts (McConkey 1971), the context in which this posture was adopted by black stilts was more one of general watchfulness toward intraspecifics or approaching humans.

Comfort movements such as the two-wing stretch, scratch head and stretch wing and leg, have a primarily physiological function (Hamilton 1975). Stretching and yawning probably aid in circulation of oxygen and activation of breathing after periods of inactivity (Sauer and Sauer 1967). Head scratching by birds may be accomplished indirectly (i.e., over wing) or directly (i.e., foot straight to the head), either as a basic autonomic response to irritation on the head or at an extended level, as part of the feather maintenance system integrated with behaviour such as displacement (Simmons 1961). Only indirect scratching was observed in captivity and appeared only in the first context applied by Simmons. Head scratching is a potentially useful taxonomic characteristic, as the method of scratching is generally uniform in related birds, at least up until family level (Simmons 1961). If this is indeed so for the Family Recurvirostridae, the omission of direct head scratching from the captive black stilt repertoire may be due to a low frequency of occurrence and therefore low probability of observation.

Leaving water to defaecate on land has been observed in many wading birds (Brackbill 1966, Hamilton 1975), including black stilts (Budgeon 1977), black-necked stilts and American avocets (Hamilton 1975). Only once was defaecation by captive black stilts observed over water. Defaecation occurred usually after coming up on land from foraging, before moving to oxheart trays to feed. Similiarly, Hamilton noted defaecation to occur while stilts were on land for other purposes. Defaecation on land has the advantages of not clouding water (important since stilts are primarily visual feeders) and avoiding direct infestation of water with parasites (Hamilton 1975). Standing in water may also be physiologically or psychologically inhibitory to defaecation (Hamilton 1975). This behavioural pattern has also been reported in what Hinde (1970) would term a "displacement context". Hamilton reports a "false" motion to defaecate on land by a stilt involved in intraspecific interaction. In this context though, the underlying causal stimuli eliciting the defaecation response may not have been irrelevant to those stimuli which "normally" determine its occurence (Hinde 1970). Autonomic responses such as defaecation during conflict are more often measures of "anxiety" or "emotionality" (Hinde 1970), rather than displacement.

In captivity, displacement activities were more common during intense aggressive encounters, especially at the median fence between adjoining aviaries. Activities normally occuring during nest building such as scraping and sidethrow (chapter three), were observed in aggressive encounters between neighbours. Most agonistic encounters between individuals however, involved paired aggressive upright postures. The orientation of the stilt's body during these interactions was thought by Hamilton to be "important signals for the motivational state of individuals". If rivals faced toward one another, there was a tendency to attack. Facing away indicated appeasement (Hamilton 1975). Upright postures thus may serve as an appeasement signal, originating from a conflict between opposite tendencies (i.e., to attack or to flee) (Baerends 1975). Hamilton terms a similiar posture to the aggressive upright, a "giraffe" posture (comparable to the captive black stilt's "forward posture" described). A distinction of context between this posture and the aggressive upright needs to be made for captive stilts at least. Hamilton's observations of the giraffe posture occurred as black-necked stilts walked towards their opponents. He concluded that it appeared to serve as a threat to peck the opponent and was used frequently during intraspecific interactions. This was not the case for captive stilts, which appeared to adopt the aggressive upright posture more in an appeasement (eg., by a subordinate cornered by an aggressive cagemate) or anxious (eg., toward an elver in the aviary stream) context, rather than one of threat toward an intraspecific individual.

Hamilton (1975) gave a functional explanation for the parallel aggressive upright position, suggesting that it aids in striking the opponent with the wing and allows quick retreat or attack. Wing-striking of an opponent was not observed being performed by captive birds, most aggressive interactions terminating in a tug fence gesture. Hinde terms the "direction of a motor pattern appropriate to one of the conflict tendencies onto an object other than that which initially initiated it" as redirection activity. Captive black stilts in aggressive situations, often directed pecks toward the median fence or toward vegetation beside it. Pecks were even directed at cagemates, following aggressive inter-pair encounters (chapter three). It may be argued that grass-pulling is redirected aggression, but McConkey (1972) suggests that other elements such as settling and sideways-throwing may be due to sexual excitement over ownership of a territory. On the other hand, the elements contain criteria for displacement activities i.e., they occur as irrelevant acts in conflict situations and are often not complete (McConkey 1971). The distinction between redirection activities, displacement activities and responses to suboptimal stimuli is not always clear cut (Hinde 1970). This was especially so for displays occuring during captive black stilt bouts of aggression.

The most intense aggressive display observed between black stilts in the same enclosure, was "fly and drop" (equivalent to Hamilton's "head and legs down flight", McConkey's "parachuting", Makkink's "spring and flap" and "treading upon another birds body"). Pied stilts recently disturbed by a human intruder or predator may indulge in parachuting behaviour (McConkey 1971). This was perhaps due to the breakdown of individual distance and its re-establishment after the disturbance had ceased. It may also have been due to a lowered attack threshold resulting from increased levels of excitement (McConkey 1971). Intrapair aggression was also observed following human intrusion near captive birds. The aggressor approached it's cagemate primarily in a hunch pursuit posture, or occasionally flew toward and dived down on it. Aggressive activity usually diminished slowly as intruders retreated.

During the non-breeding season, intraspecific interactions were generally limited to low intensity hunch pursuit postures. It was not until the beginning of the breeding season (mid-June), that aggressive encounters became more intense. For completeness of description of aggressive behavioural patterns however, these more intense aggressive displays have been included in discussion of non-breeding behaviour. Their occurrence outside the breeding season was occasionally noted but these instances were comparatively rare. Similiarly, captive stilts were noted on rare occasions during the non-breeding season to attack other species trapped within the breeding enclosure (i.e., either a house sparrow Passer domesticus or New Zealand shore plover Thinornis novaeseelandiae housed in an adjoining aviary). McConkey (1971) observed interspecific aggression at no stage during the non-breeding season of pied stilts.

2.4.2 Time budgets of a focal pair

The foraging time budget presented in section 2.3.2 for a captive pair of black stilts was a measure only of the relative proportions of time spent in this, compared to other activities. Relative prey abundances throughout the year, search rates, handling times and pecking rates of stilts were not monitored. Therefore seasonal and diurnal variability in energy uptake over equal length foraging periods was unable to be calculated. Similiarly, except for mean monthly temperatures and rainfall which were recorded at Mount Bruce, fluctuations in the physical factors of the environment (i.e., wind, water temperature, etc.) in which stilts were placed were unknown.

In the light of work by other authors dealing with avian time budget studies though [and particularly that of Gibson (1978) who constructed a seasonal and diurnal time budget of the American avocet], some remarks and likely explanations may be proposed for diurnal and seasonal allocation of time by this focal pair of black stilts.

There was a pre-nesting peak in the proportion of time in which the male spent foraging. A similiar peak in the pre-nesting period was observed for the female during the second season only. Perhaps the two most important factors contributing to these peaks may have been i) high energy demands of egg production (female), nest-building (male and female - chapter three) and agonistic interactions (male) and ii) lower environmental temperatures in turn affecting prey availability (below).

Energy requirements of birds tend to increase at low temperatures, while abundance of some prey species tends to decrease (East 1980). The time spent feeding then, may increase with a drop in temperature. Verbeek (1964) certainly found this to be the case with the Brewer blackbird (Euphagus cyanocephalus). Temperatures at Mount Bruce during the pre-nesting stage of season one were the second lowest of the four breeding stages (minimum temperatures occurred during the post-fledging parental care period over winter). During the second breeding season, this stage experienced the lowest mean temperatures (although lower minimum temperatures occurred late in stage four). Peaks in foraging activity during the pre-laying period have been observed in semipalmated sandpipers Calidris pusilla (Ashkenazie and Safriel 1979), spotted sandpipers Actitus macularia (Maxson and Oring 1980) and yellow-billed magpies Pica nuttali (Verbeek 1972). Verbeek attributed this peak in energy uptake to a requirement for energy toward egg-laying. American avocets also demonstrate high feeding levels during the prenesting stage, a pattern brought about by low environmental temperatures, low food abundance, high activity levels and high energy requirement for egg production (Gibson 1978).

Captive black stilts were not limited by the amount of food present for consumption since supplementary oxheart was always available, but food quality (ie. invertebrates rather than oxheart) may have become important toward breeding. The focal pair certainly spent most of the time devoted to food consumption foraging in the stream rather than at the oxheart. Heaviest use of oxheart was during the parental care period, especially during the winter months after the chicks had fledged.

The high peak in female immobility and relatively lower foraging peak (c. f. male) during this stage of the first season, resulted in part from sampling error. The number and length of observation periods were few and short respectively during this period of the study. Observation periods were also biased toward the time of day during which immobility predominately occurred (ie. early-mid afternoon). Time budget data were taken mainly during December, a month of moderately warm temperatures (0.6-23°C, mean = 13°C). Sampling error does not account however, for the remaining high frequencies of female immobility during the incubation and early chick rearing stages of this season. The female contributed less toward incubation than did the male (15% observation time c.f. 50% for the male). If time spent in immobility and incubation are combined, the male actually spent as long immobile as the female (season one-male 55%, female 54%; season two-male 42%, female 37%). In a similiar manner, Gibson (1978) established that stage differences in immobility could be eliminated by combining time spent on the nest with time spent immobile.

The decrease in the proportion of time allocated by the male toward foraging during incubation in season one and by both birds in season two reflected the proportion of time spent spent sitting on the nest (chapter three). Incubation cannot however, be invoked as a causal explanation for the decrease in proportion of time spent foraging during this stage. Although the ANOVA procedure treated each activity independently, there was no strict independence between activity classes. For example, time spent foraging was in part influenced by time available for this activity, before or after time demands of breeding activity had been or were met. Gibson attributed a similiar decrease in American avocet foraging during incubation to higher ambient temperatures, reduced activity levels and greater prey abundance. These factors (in addition to increasing photoperiod), may also have accounted to some extent for the observed decrease in captive stilt foraging during stage two. It appears however, that as in the spotted sandpiper (Maxson and Oring 1980), time spent foraging and incubating by these stilts was inversely related.

Diurnally, foraging did not differ between the sexes. Season two clearly indicated a bimodal distribution of foraging activity, with a large peak in early morning and another toward mid-late afternoon. Morton (1967) observed a bimodal feeding pattern in white-crowned sparrows (Zonotrichia leucophrys gambelii), with morning and afternoon peaks. Schartz and Zimmerman (1971) noted however, the conspicuous lack of a modal feeding pattern in dickcissels Spiza americana. Wild black stilts exhibited two main feeding peaks, one from early morning and another in the late afternoon (Budgeon 1977, Pierce 1982). Early morning foraging was probably a response to hunger after the previous nights fast. A late afternoon peak probably prepared a bird for the night ahead i.e., lower temperatures and fasting (Gibson 1977, Pierce 1982). In captivity, high diurnal peaks in foraging activity occurred during pre-nesting and post-fledging parental care, but those peaks were muted during incubation and early chick rearing. This may have resulted from higher demands on time for incubation and care of the young but again a causal explanation based on non-independent observations is not appropriate. This pattern was also present in American avocet time budgets (Gibson 1978). Peaks in diurnal feeding also generally corresponded to troughs in immobility behaviour and vice versa.

Time allocated toward preening was greatest during the post-fledging parental care period of both seasons, with a smaller peak during the pre-nesting stage of the breeding season. Throughout its range, Himantopus himantopus moults twice annually, a complete post-nuptial moult and an incomplete pre-nuptial moult (Pierce 1982). The peaks in preening by captive stilts correspond with times of moult. Diurnally, there were no peaks in preening activity during the second breeding season, except during stage four when peaks occurred during mid morning and afternoon. Preening peaks during season one, generally preceded immobility peaks.

Alarm behaviour peaked in frequency during the parental care period of both seasons but was less frequently observed than either foraging, immobility or preening. The high peaks of walking during this period probably resulted from a combination of vigilant behaviour and "guarding of chicks".

CHAPTER THREE

BREEDING BEHAVIOUR AND PERFORMANCE

3.1 Introduction

Among the problems likely to arise in captive breeding of an endangered species are those stemming from a lack of knowledge of the animal's social behaviour (Eisenberg and Kleiman 1977). In attempting to determine why a captive pair of birds do not breed for example, one needs a behavioural profile of stilt breeding behaviour for comparison. Captive study provides a "norm" from which deviations (including those of wild birds) can be measured (Eisenberg and Kleiman 1977).

Chapter Two described maintenance, aggression and alarm behaviour of stilts held in captivity. In this chapter, intra-specific and intra-pair social interactions are described. Breeding performance of a focal pair of stilts is monitored and compared to breeding behaviour reported for wild black stilts (Pierce 1982).

3.2 Methods

3.2.1 Description of behavioural patterns

Between August 1982 and March 1983, I collated the repertoire of breeding behavioural patterns of a focal breeding pair of stilts. Supplementary observations of pre-copulatory behaviour were made on the six other adult birds. Methodology of description followed that described in section 2.2.1 for non-breeding behaviour. These behavioural pattern descriptions were also added to in subsequent observations over two later breeding seasons (July to November 1983 and July 1984 to January 1985). Descriptions were aided by the use of photographs and 8 mm colour cinefilm.

3.2.2 The effect of neighbours on intra-pair activity

During September 1982, three of the four black stilt pairs were manipulated in an attempt to form new pair bonds. During these manipulations, the fourth (focal) pair was subjected to five changes of neighbours in the adjacent aviary (treatments). Prior to these manipulations, the focal pair was kept next to two female stilts and had been engaging in pre-copulatory behaviour but had not successfully copulated. They also had not demonstrated any intra-pair aggression.

Heavy sacking was tied along the length of the median fence between aviaries, creating a 1 m high visual barrier during two of the five treatments. The treatments were;

i) two female neighbours - no visual barrier;
ii) three females, one male - with visual barrier;
iii) three females, one male - no visual barrier;
iv) one male, one female - with visual barrier; and
v) no neighbours.

The length of observation and treatment periods varied throughout these manipulations (Table 3.1). Over an observation period, an all-occurrence count (Altmann 1974) was taken for four types of social interaction within the focal pair;

i) aggressive pursuit of a mate;
ii) sidethrowing nest material (section 3.3.1.3);
iii) pre-copulatory activity (section 3.3.1.1); and
iv) copulation (section 3.3.1.2).

Once all neighbours were removed (treatment five), the focal pair remained isolated by a minimum distance of 25 m from all other stilts.

3.2.3 Breeding performance

Nest sites: Observations of the focal pair were made at weekly intervals during the pre-nesting period of three breeding seasons; i/ November 1982 - February 1983, ii/ September 1983 - December 1983 and iii/ September 1984 - December 1984. I noted the dates of first occurrence of nesting activity and the location of nest sites.

Copulatory activity: During visits made to the study area during the pre-nesting and egg-laying phases of the breeding seasons, the occurrence of copulations and attempted copulations were noted. Four other parameters of copulatory activity were recorded to supplement descriptive results; i) duration of the copulatory bout (i.e., number of seconds from adoption of the female pre-copulatory posture until the end of copulation or the females' relinquishment of this position), ii)

Table 3.1 Effect of neighbours treatments

TREATMENT	DATE OF TREATMENT	LENGTH OF TREATMENT	LENGTH OF OBSERVATION	DAY(S) OF OBSERVATION
One	22.7.82-10.9.82	40 days	217 minutes	15,17,21.8.82
Two	10.9.82-12.9.82	45 hours	168 minutes	10,11.8.82
Three	12.9.82	2 hours	30 minutes	12.8.82
Four	12.9.82-28.9.82	16 days	127 minutes	12,18,22,23.8.82
Five	28.9.82-20.9.84	24 months	195 minutes	28.9.82

the number of times that the male walked from side to side around the female (section 3.3.1.1), iii) the side from which he mounted and toward which he dismounted at copulation and iv) the location of the female when she assumed the pre-copulatory posture (i.e., on land, in open water or on the waters edge).

Egg-laying: Observations intensified from the onset of egg-laying, spanning sunrise to sunset from laying of the first to the last egg of each clutch (where possible). I recorded the time at which eggs were observed being laid and the first appearance of other eggs. Checks were made at the nest soon after I arrived each morning at the study site and again 2-3 times during the day. No visits were made at night. To keep disturbance of the stilt pair to a minimum, my observations were made from outside the aviary or during daily changes of oxheart trays. All nests and eggs were easily visible from outside the aviary and the disturbed birds usually returned quickly to the nest after I had moved away.

The first clutch produced by this pair during the 1982/83 season was removed for artificial incubation, in a successful attempt to induce relaying. During the following two breeding seasons, first and successive clutches were also removed until a final clutch was left with the parent birds.

Fertility of cross-fostered eggs was checked by R. Nilsson (N.Z. Wildlife Service).

Incubation: Observations during the egg-laying and incubation phases of the pairs' nesting cycle were made from a hide. The duration of an incubation bout was noted precisely, from the time an incubating stilt first sat, until it stepped or flew off the nest. The sex of the incubating bird was also recorded.

3.3 Results

3.3.1 Description of behavioural patterns

Fifteen breeding behavioural patterns noted during 498 hours of observations were grouped on the basis of context and function into five activity types;

i) pre-copulatory; ii) copulatory;
iii) nest-building; iv) egg-laying and
v) nest maintenance/incubation behaviour.

These patterns of behaviour are presented in sections 3.3.1.1 to 3.3.1.5.

3.3.1.1 Pre-copulatory behaviour

Pre-copulatory posture (female): Five female black stilts were independently and repeatedly observed adopting a horizontal posture in the presence of a male or female stilt in the same or adjoining aviary. This female posture occurred only between mid-July and late February (1982-1985) and always preceded copulation (although copulation did not always occur after a female had adopted the posture). Before adopting the pre-copulatory posture, the female walked in shallow water near her mate in a hunched body position and made sideways flicks of her bill beneath the water (Plate 3.1). The head and bill were then raised and held in line with the body at an angle of 35° to 45° with the water surface. Bill dipping continued until the female was approached by a cage-mate. The head and bill were raised higher, resulting in the line of the body becoming parallel with that of the water. A low soft call (section 5.3.1.7) was usually emitted by a female maintaining this position. Only one female stilt adopted the position while standing in water. Four other female stilts independently adopted an identical posture and although water was available to them, these stilts assumed the posture only when standing on land (Plate 3.2).

Four different types of social interaction were observed preceding the adoption of the pre-copulatory position;

i) A male and female walked slowly past each other in a hunched posture, with their heads held upright but drawn back in toward the shoulder. As the two stilts neared one another, walking slowed in pace and the tarsi were lifted out of the water in a higher stepping action. This type of interaction was observed in two pairs (one of which later successfully bred).

ii) Stilts in adjoining aviaries spent much time interacting at the median fence. Two stilts were observed together either side of the division wire, throwing nest material and crouching on the bank. Low staccato calls (section 5.3.1.8) were also heard before the female adopted the pre-copulatory posture.

iii) Two female stilts standing on an island and manipulating nest material separately adopted this position within a five minute period as they stood adjacent to each other. No calls were given.

iv) One female was aggressively pursued by a male until she assumed a pre-copulatory posture. The pursued female ran sideways up an aviary bank in a head-low posture and adopted the pre-copulatory position when cornered by the aggressive male. Once the female was immobile, the male walked a side to side path behind her (below).

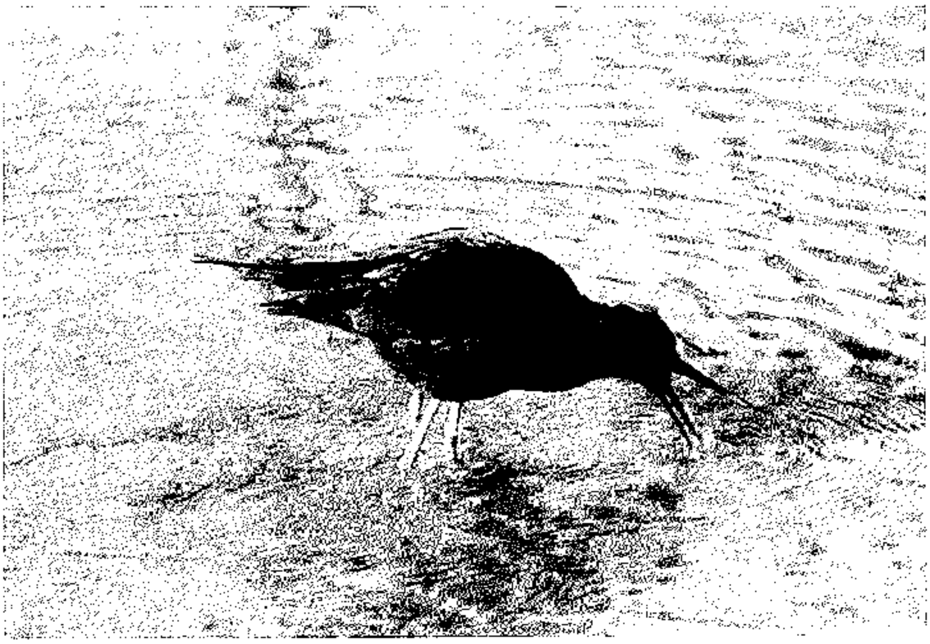
Side to side walk (male): When a female assumed the pre-copulatory posture described above, the male walked in a U-shaped path behind her. As he became parallel and shoulder to shoulder with the female, the male dipped his bill below the water surface and splashed water upward (bill-dipping) (Plate 3.3). This activity was often followed by flicking of the bill briefly in under the wing and upper body feathers, or by quickly preening the breast feathers (false-preen) (Plate 3.4). Side to side walking was resumed, the male again stopping to bill-dip and false-preen in the same position on the opposite side of the female. During the male display, the female turned her head toward the side on which the male had approached. If the male attempted to walk around in front of her, she pivoted her body to face away from him. As he became increasingly excited, the males' body and neck feathers were raised, bill-dipping became exaggerated and the head was held high between bill-dips (Plate 3.5).

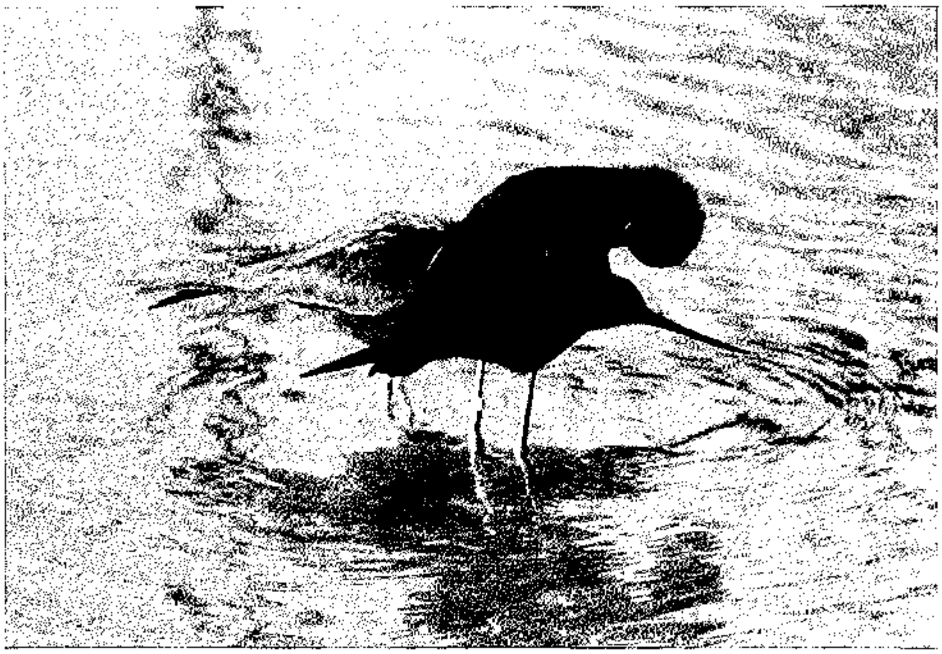
PLATE 3.1 Bill-dipping before assuming the female pre-copulatory posture

PLATE 3.2 Pre-copulatory posture adopted on land

PLATE 3.3 Male bill-dipping beside horizontal female

PLATE 3.4 Male false-preening





3.3.1.2 Copulatory behaviour

Copulation: Courtship led to copulation in only the one black stilt pair. The male sprang upward into the air, landing on the female's mid-back or shoulders. Upon landing, he raised both wings to attain balance and edged up the females back to grip with his feet just forward of her wings (Plate 3.6). As the male lowered his cloacal region down and beneath that of the female, the wings were also brought down and held partly folded above his back (Plate 3.7). During coition, the female moved her head rapidly from side to side horizontally. The male dismounted and both stilts stood upright with necks extended vertically and bills crossed (Plate 3.8). One wing of the male was brought over and around the females' back, while the other wing was trailed in water. The female lowered the leading edge of both wings down behind her and the pair walked forward for 2-5 m in this position before separating (Plate 3.9).

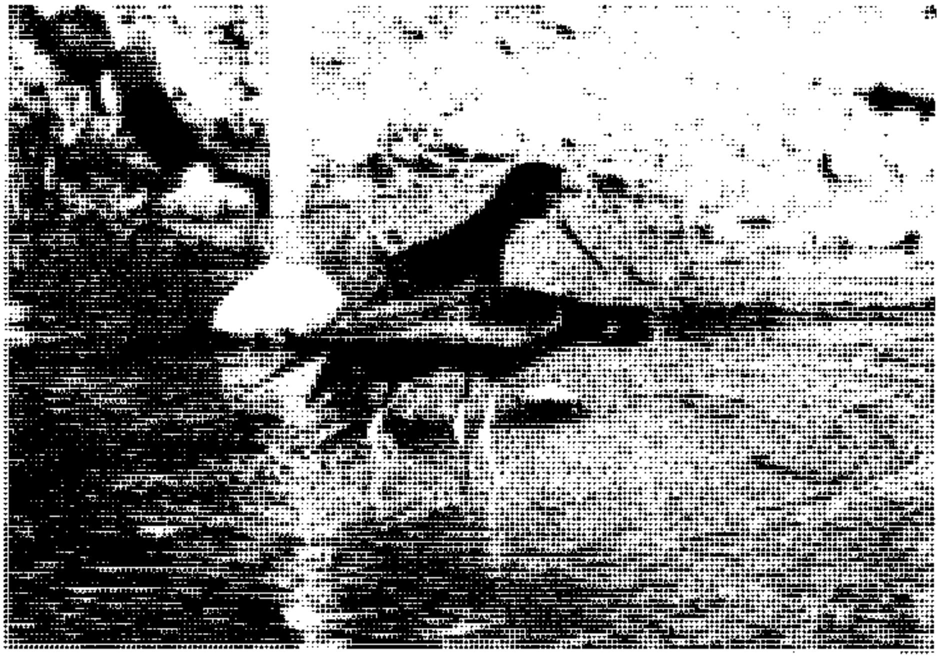
Simulated copulation: Two male black stilts attempted to copulate with inanimate objects. One of these individuals was an aggressive male which continually harrassed and pursued its female cagemate. During observations of July 1984, this stilt approached a mid-stream island and squatted over several large stones. He sat in a crouched position with the tarsi lying horizontally over the uneven surface. Both wings were raised upward to their full extent and the tail was lowered and moved from side to side above the stones (Plate 3.10). The wings were then brought down and held above the back. In 8 of 28 observations of this activity, the bill was lowered forward of the island and dipped below water 2-5 times while the stilt remained in a sitting position. After a period of between 5 and 60 sec (mean=22, n=19), the stilt stood up and walked away from the island. In a further 4 of the 28 observations of this activity, grass material was picked up and thrown sideways while walking away from the island. During "simulated copulations" performed by the male, the female rested or foraged at least 6-7 m away. If approached by the female, he ceased this activity and departed from the island. Male aggression toward the female decreased during the period in which this behavioural pattern was observed.

Simulated copulations performed by this male were also observed on a second site. After pursuing the female up an aviary bank until she adopted a pre-copulatory posture, the male began side to side walking around behind her. This pre-copulatory walk continued interspersed with false-preening and bill-dipping, for approximately 2 minutes before the male attempted to mount the female. He was unsuccessful in his attempt and immediately upon landing, he lowered his abdomen to the ground beside the female and stretched his wings upward. He remained in that position for approximately 5 sec. He then stood upright and both birds extended their necks upward with their heads turned toward each other. Without crossing bills, the two stilts moved slowly forward before separating.

A second male black stilt was observed copulating with an inanimate object on two occasions. This stilt had been arbitrarily paired with a female which had been previously held in an adjacent aviary during September 1984. Within 2-3 days of being placed together, this pair had built a well-constructed nest in their concrete-floored aviary (section 1.3.2). Some pre-copulatory activity was observed but copulation had not taken place. During one observation period, the female stood immobile 3 m away from her cagemate, as he walked near the nest site in a hunched posture. His neck, breast and body feathers were raised and the bill was dipped toward the ground. After a series of bill-dips, the male turned in a tight circle, rotating his body 360° before bill-dipping again. This activity continued for approximately 30 sec before the male sprang sideways and up a distance of 6 cm to land on the nest margin. The male then lowered his abdomen down toward the nest and stretched both wings upward. The wings were lowered slightly and the stilt remained in this position for 5 sec before "dismounting". Bill-dipping and body rotation resumed for a further 2-3 minutes before the stilt sprang back up onto the nest site and repeated the simulated copulation. During two separate observation periods which followed the one described, this stilt was again observed bill-dipping and turning tight circles on land but was not seen to simulate copulation again. On these occasions however, he sprang forward and raised both wings, landing a few centimetres forward of his takeoff point. While in mid-air, the stilt lowered its abdomen slightly toward the ground. This pattern was repeated several times and was interspersed with bill-dipping.

PLATE 3.5 Male holds his head high between bill-dips

PLATE 3.6 Mounting of the female,
wings stretched upward.



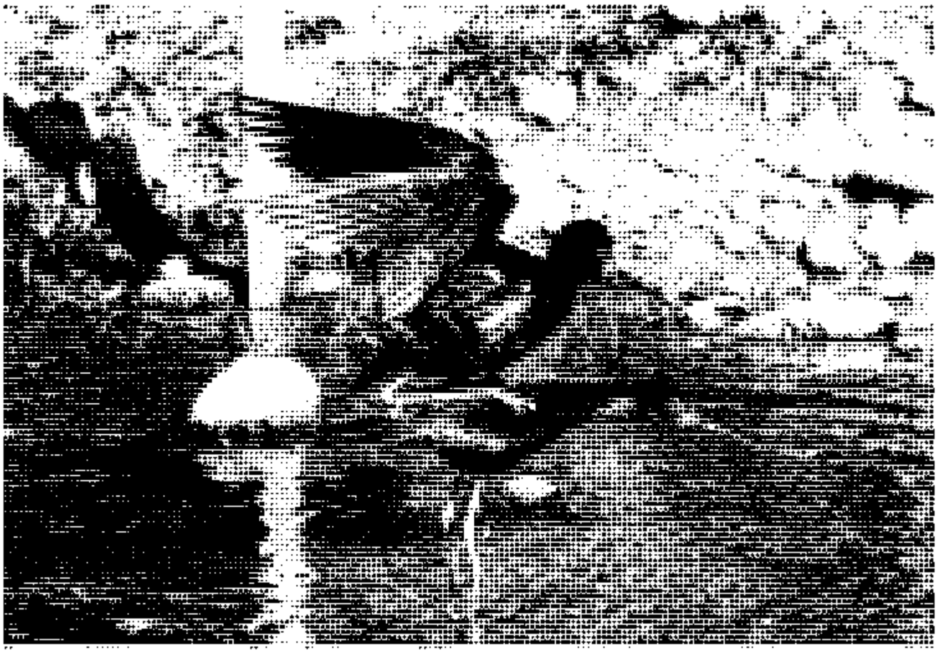


PLATE 3.7 Wings of the male lowered before coition.

PLATE 3.8 Bill-crossing (male on right)

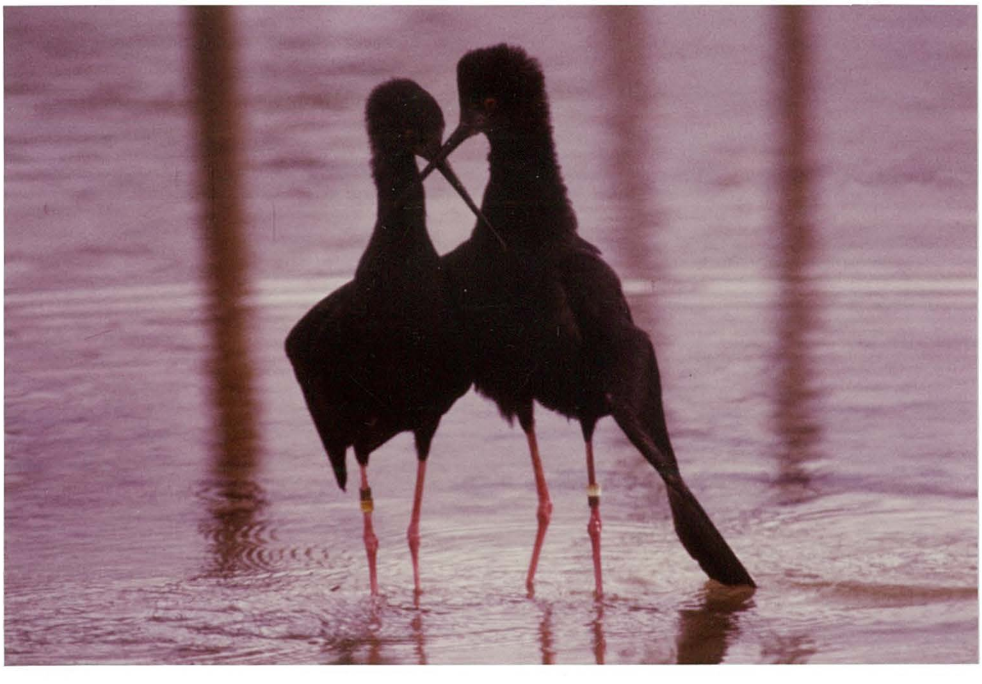
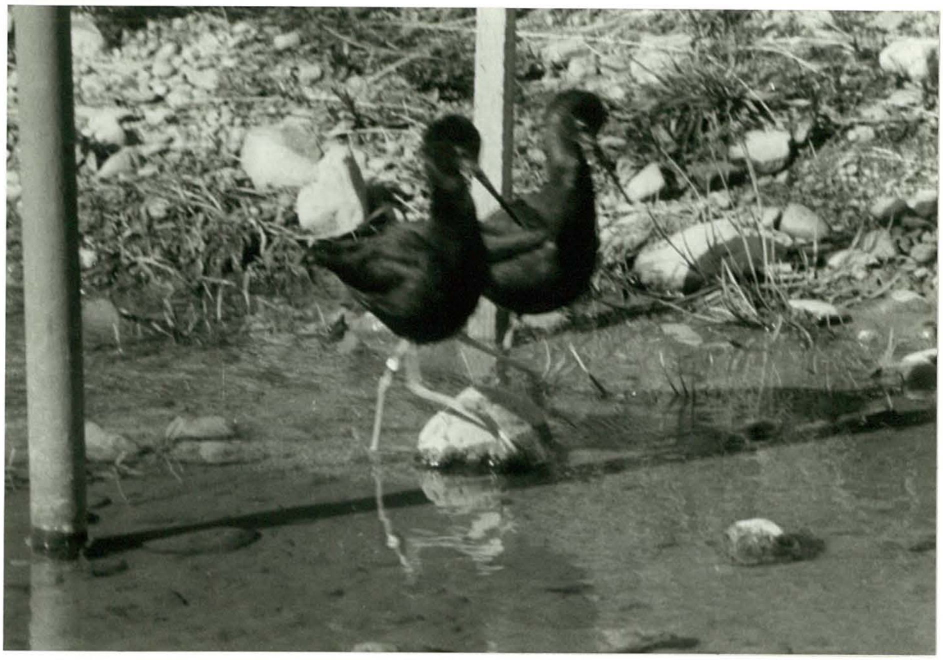
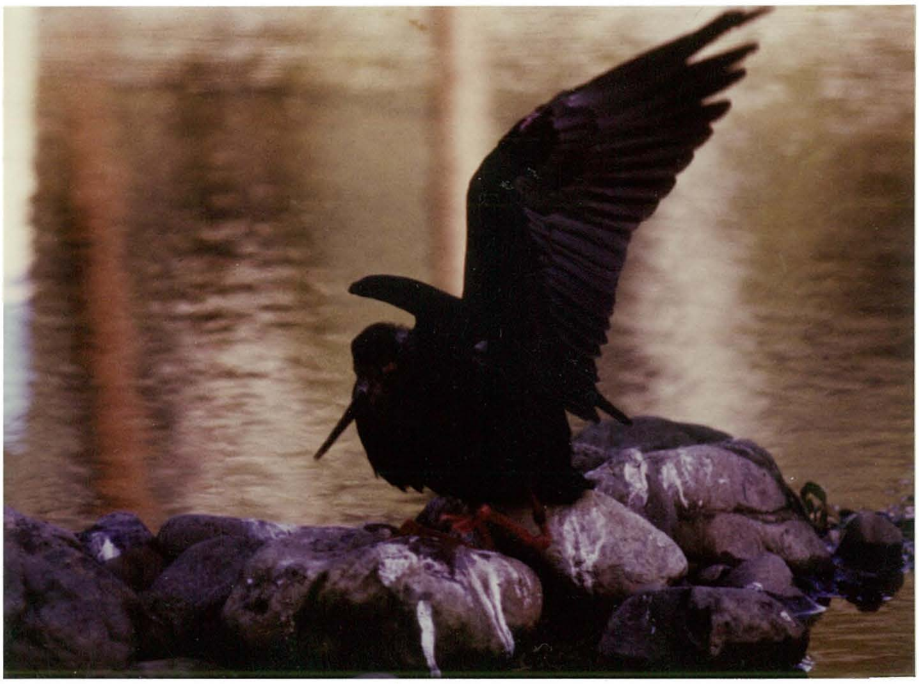


PLATE 3.9 Walking forward after bill-crossing

PLATE 3.10 Simulated copulation





3.3.1.3 Nest building behaviour

Side by side ground peck (both sexes): During early nest-site selection activity, stilts approached a preliminary nest site in a hunched posture with the bill directed downward (Plate 3.11). The neck was contracted to bring the head back toward the shoulder. The bill, back and tail were held in a straight line at approximately 45° to the horizontal. Soft staccato calls (section 5.3.1.8) were emitted and when approached by its mate (who assumed the same posture), the stilt increased the volume of the call and calling of the two stilts temporally overlapped (section 5.3.1.8). Grass material was picked up with the bill and thrown sideways at, or near the proposed nest site (below). More than one site (and up to 4 or 5 simultaneously) was investigated by a pair of stilts before nest building began. Even after a nest had been completely constructed, this behavioural pattern was exhibited at other sites.

Sidethrow (both sexes): As above, grass material was thrown backward along the stilts body as it faced away from the nest site, resulting in grass being placed closer to the nest. On several occasions however, this material was thrown in the opposite direction to the nest. Immersed algae and roots of grasses were also tugged up from below the water surface and thrown toward land (Plate 3.12). Whenever one stilt threw nest material near a nest site, it was usually joined by its mate who also participated in the activity.

Crouch/Semicrouch (both sexes): Stilts crouched over preliminary nest sites by bending the knees and lowering the chest completely to the ground or semi-crouched by flexing the knees slightly and lowering the body only part way to the ground. Crouching often preceded scraping (below) or manipulation of nest material.

Scraping (both sexes): When in a sitting position, a stilt brought both legs out behind the body, held the tarsi vertically and dug out a nest depression in the gravel with its feet (Plate 3.13). After 5-10 sec of scraping, the stilt stood up and turned around on the site, repeating the activity.

Sideways-build (both sexes): While sitting on the nest, stilts reached forward and picked up vegetation in the bill, placing it to the side of the body or down in front of the chest (Plate 3.14).

3.3.1.4 Egg laying

Only one captive female stilt produced eggs during the period of this study, with laying being observed on four occasions. The stilt sat on the nest for a period of between 10 and 20 minutes, before raising her body to semi-crouch above it. A foot was placed either side of the nest and while standing in this crouched position, the stilt manipulated eggs within the nest with her bill. After 2-3 minutes, the female stepped off the nest and threw back material toward it. During this sequence, the point at which an egg had been laid was not obvious to me.

3.3.1.5 Nest maintenance and incubation

Both individuals of the focal pair contributed to maintenance of the nest and incubation of eggs.

Nest changeovers: Changeovers at the nest occurred in three different manners;

Type i) The incubating stilt stood up and moved off the nest while its partner was engaged in an activity away from the nesting area. The latter stilt moved directly toward the nest to incubate or continued its present activity for a short period before approaching. During the period of egg-laying, the breeding pair often copulated between bouts when this type of changeover occurred;

Type ii) An incubating stilt alarmed by an outside disturbance flew directly up off the nest to land at least 2 m away from it. Its mate usually began the next incubation bout;

Type iii) As an incubating bird sat on the nest, its partner approached and began walking around the nest site. While circling its mate, the relieving bird shook each leg alternately to remove excess water and then stood near the nest margin (Plate 3.15). If no motion to stand was made by the incubating stilt, the bird attempting to incubate either resumed circling or attempted to walk onto the nest (Plate 3.16). The incubating bird was almost "pushed" off the nest in these instances. During one nest changeover observed, the male had circled the female for 4-5 minutes without inducing her to leave the nest. He finally approached his sitting mate and semi-crouched above her, which resulted in the female quickly vacating the nest. Following this type of changeover a relieving bird sat almost immediately and its mate picked up and threw back nest material as it left the nest area (Plate 3.17).

Egg rolling: Before commencement of incubation by a newly arrived bird on the nest, the eggs were sometimes manipulated first. The stilt stood semi-crouched over the nest and directed its bill downward, placing the underside of the lower mandible upon the far-side of the egg furtherest from it. By gently moving the bill, an egg was rolled toward the centre of the nest. The stilt then changed the direction in which it faced by approximately 45° and manipulated the next egg, rolling each egg in succession.

Nest scraping: This behavioural pattern was identical in form to that described in 2.3.1.3 except that the stilt sat further forward on the nest. Most of the stilts' weight was placed on its chest and the feet were used to scrape out substrate near the periphery of the nest, after first rolling the eggs toward the centre.

Settling on the nest: Once egg manipulation had been completed, the incubating bird lowered its body, chest first, toward the ground as the chest feathers were raised to expose the brood patch. After the lower body had contacted the nest, the feathers of the back, wings, chest and lower body were raised as the bird shuffled its body laterally. This action brought the brood patch into close contact with the eggs and settled the stilt closely into the nest.

Sideways building: Stilts continued maintenance of the nest structure (as described in 3.3.1.3) while sitting on the nest.

3.3.2 Effect of Neighbours

Between 15 August and 28 September 1982, 737 minutes of focal pair observations were accumulated over 10 days, under five different

PLATE 3.11 Side-by-side ground peck

PLATE 3.12 Tugging up immersed vegetation

PLATE 3.13 Nest-scraping

PLATE 3.14 Sideways building (bird on nest)

PLATE 3.15 Nest changeover (Type 3)
- circling and leg shaking

PLATE 3.16 - walking onto the nest

PLATE 3.17 - relieving bird sits

neighbour treatments. Figure 3.1 summarises the rates of display per hour of the four types of male-female interaction being monitored; pre-copulatory activity, nest material manipulation (sidethrow), aggression and copulation. The null hypothesis that "there was no difference in the rate of participation in an activity over the five treatments" was accepted for sidethrow (Kolmogorov-Smirnov goodness of fit test, $D = 0.288$, $p>0.05$ for the male; $D = 0.251$, $p>0.05$ for the female), pre-copulatory activity ($D \approx 0.282$, $p>0.05$ for both birds), copulation and female aggression ($p>0.05$).

The null hypothesis was rejected for male-initiated aggression ($D = 0.369$, $p<0.05$). Male aggression toward the female occured at a low rate (rate = 0.4/hour) during treatment one (two female neighbours, no visual barrier). Aggression ceased temporarily when visual isolation from neighbours was enforced, despite the addition of one further male and one female to the adjoining aviary (treatment two). When the visual barrier was removed, aggression by the male toward its mate increased to a rate of 8 attacks/hour. Aggression was also observed within the original female-female pair of neighbours (from before and during treatment one). This pair had previously never displayed any intra-pair aggression. Two neighbouring females were removed, leaving one male and one female and the barrier was re-erected (treatment four). The rate of aggressive approaches of the male toward the female decreased to 4.7/hour but aggression did not cease until all neighbours were removed (treatment five).

Although pre-copulatory activity was observed before experimental manipulation and during all treatments except treatment 3, copulation did not take place until all neighbours were removed (treatment five). No aggression was observed again within this pair until after completion of this study when neighbours (two unsexed yearling stilts) were once again introduced during September 1985.

3.3.3 Breeding Performance

Nesting behaviour of the focal pair was observed from November 1982 to February 1983, September to December 1983 and September to December 1984. 376 hours of observations were accumulated during stages one (pre-breeding) and two (egg-laying and incubation) of the three breeding seasons.

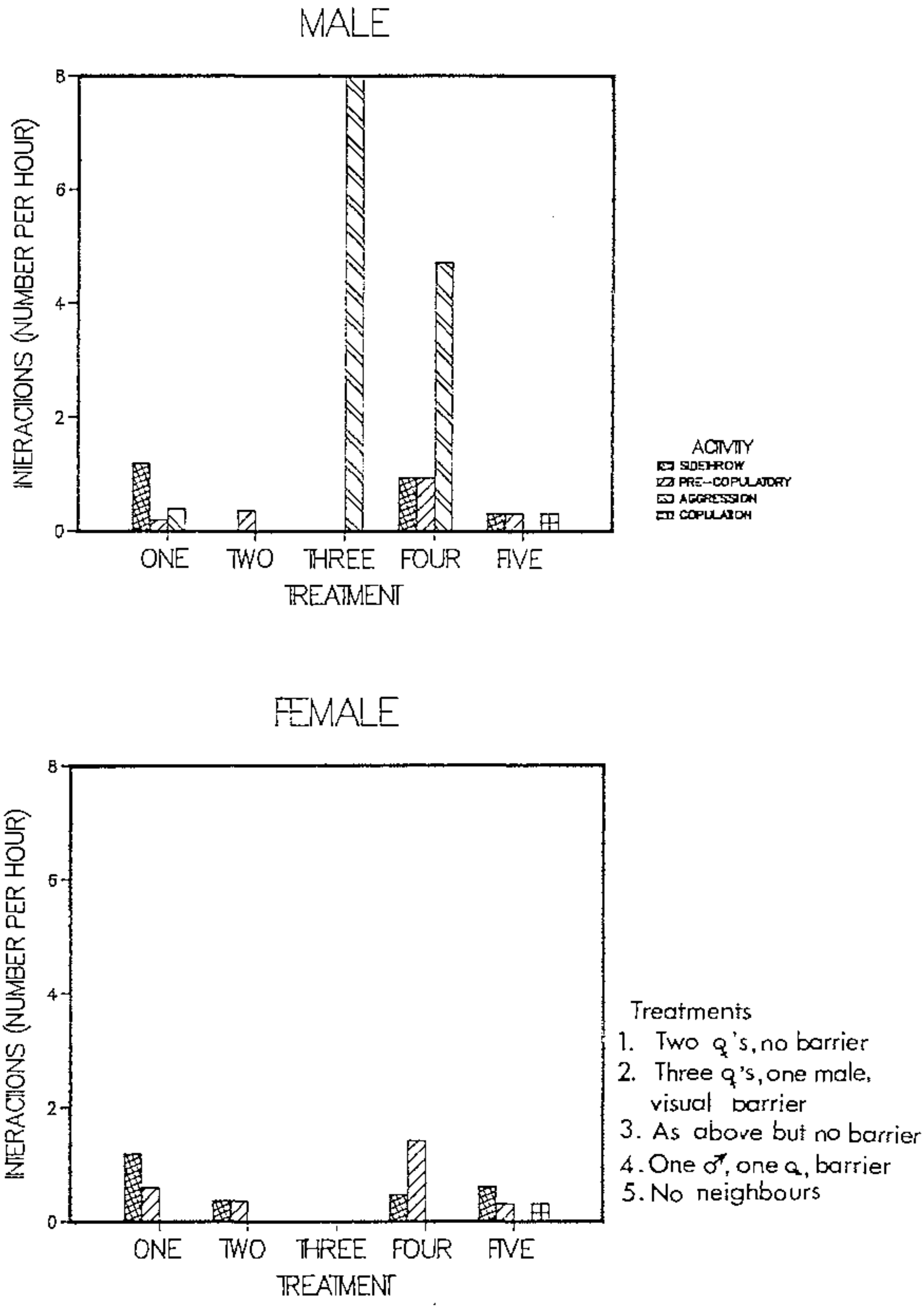


FIGURE 3.1 The effect of neighbours on intra-pair activity

3.3.3.1 Nest sites

Six different nest sites within three localized areas were selected and utilized by the focal breeding pair between January 1983 and December 1984. Two of these nests were used in relaying further clutches during the second and third breeding seasons (1983/84 and 1984/85). The first nest site used in the 1982/83 breeding season was located up one bank of the breeder's aviary, approximately 3 m from the oxheart shelter (Plate 3.18). After eggs of this clutch had been removed for artificial incubation, the nest was abandoned and a second area for nesting was chosen. This area was a large mid-stream island (section 1.3.2), upon which an approximately 1 m^2 piece of turf had been placed. The turf had been brought in from outside the aviary to provide an additional source of nesting material. The large island was the main area used for nesting by the focal pair, the top of the island being the site of three nests in which a total of five separate clutches were laid.

The third area within which nest sites were located was a smaller island (section 1.3.2), 6 m from the first. Vegetation was prevalent on this island during the 1983/84 season and provided cover for nests. This nesting area was used during one breeding season only, when three clutches of eggs were successively laid in one nest site. A second nest constructed on this island was only 6 cm from the first and was used only once.

The time taken to construct a near-completed nest varied from 24 hours to 4-6 weeks. Nest material manipulation occurred at one site for 6 weeks before laying. During construction of this nest, most of the incorporated material was built into the nest borders overnight, only 5 days before laying.

In addition to the breeding pair, two other pairs of stilts built nests. During late October/early November 1982, a male black stilt built a nest upon a mid-stream island within the second outdoor enclosure (section 1.3.2). Although the female manipulated some material around the nest site, aggression by the male toward the female resulted in the nest being constructed solely by the male. A nest scrape was evident and the nest had a well defined grass material lining and border, but no eggs were laid by the female of this pair. A

PLATE 3.18 Nest containing three eggs

PLATE 3.19 Incomplete nest

second pair of stilts placed together in a small concrete aviary (section 1.3.2) late in the 1984 breeding season built an incomplete nest on the edge of a concrete-based, water-filled area used for bathing and drinking (Plate 3.19). Large amounts of dry material were incorporated into the nest but despite active social interaction within this pair, they also did not breed.

3.3.3.2 Copulatory activity

a. Seasonal activity: Copulations of the focal pair were observed between mid-July 1982 and late November 1984. The first and last copulations observed and dates of first adoption of the pre-copulatory posture by the female are presented in Table 3.2 for each of the three breeding seasons.

Copulatory activity ceased on day 2-3 after laying the first egg of each clutch and resumed again either upon removal of eggs to induce relaying, or in the following July after rearing progeny from the final clutch of the previous season. Copulations increased in frequency until laying (Table 3.3), peaking at days 2 or 3 after laying the first egg. Differences in copulatory activity between time period categories were not statistically significant (using Kolmogorov-Smirnoff goodness-of-fit at $p = 0.05$) for either copulations ($D = 0.238$, $n = 2.3$, $p > 0.50$) or total copulations plus attempts ($D = 0.186$, $n = 4$, $p > 0.05$).

b. Diurnal timing: 82 copulations performed by the focal pair were observed during the study. A further 57 observations were made of attempted copulations (i.e., a pre-copulatory posture was assumed by the female and although the male responded to varying extents, copulation did not occur). 73 of the observed copulations and 30 attempted copulations formed the data set for an analysis of diurnal frequency of copulatory activity. Copulations were grouped into periods of the day in which they had been observed and are presented as a frequency (number/time) in Figure 3.2. There was a bimodal peak in frequency of copulations during the day, one from early to mid-morning (0600-1000 hours) and a larger peak in the early afternoon period (1200-1400 hours) (combined data from three seasons). A peak in attemped copulations was also observed during the early morning period, with a second smaller peak in mid-afternoon observations. However,

Table 3.2 Length of the copulatory period

	FIRST OBSERVED PRECOPULATORY POSTURE (FEMALE)	FIRST OBSERVED COPULATION	LAST OBSERVED COPULATION
Season one	22.07.82	29.09.82	26.01.83
Season two	31.07.83	05.08.83	21.10.83
Season three	11.08.84	11.08.84	26.11.84

Table 3.3 Seasonal frequency of copulation

DAYS BEFORE LAYING	OBSERVATION TIME (HOURS)	FREQUENCY COPULATION (NO./HOUR)	FREQUENCY ATTEMPTS (NO./HOUR)	TOTAL FREQUENCY (NO./HOUR)
41-50	6.43	.15	.31	.46
31-40	13.00	.23	.15	.38
21-30	4.34	.69	.00	.69
11-20	14.10	.49	.35	.85
1-10	11.32	.79	.53	1.32

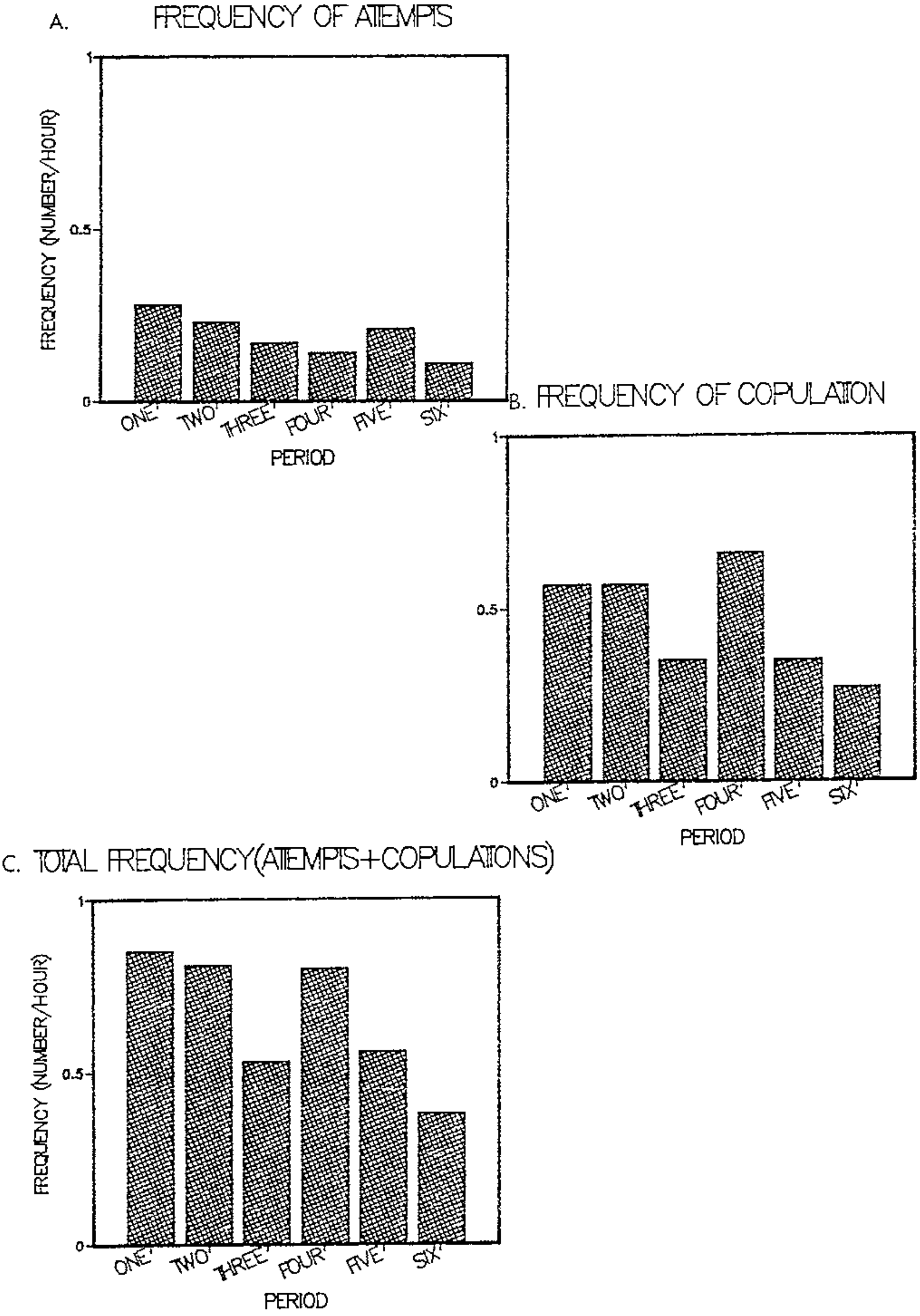


FIGURE 3.2 Diurnal frequency of copulation

these copulatory frequencies were not significantly different between diurnal time-periods (Kolmogorov-Smirnoff, p = 0.05; d = 0.109 for copulations, d = 0.094 for attempts plus copulations).

c. Time between copulations: The shortest interval observed between successive copulations was 20 minutes, occurring in this instance on the second day after laying the first egg of a clutch. On this observation day, 11 copulations were observed within a period of 480 minutes, the highest frequency encountered during the study. The mean interval between successive copulations for continuous sampling periods was 69 minutes (n=21), with 8 of the observations being less than 1 hour apart.

d. Pattern of copulatory activity: The mean length of a copulatory bout (section 3.2.3) was determined for both completed and attempted copulations. The length of a completed copulatory bout ranged from 23-265 sec (mean = 79.9, n=67). Bouts of attempted copulations ranged from 14 to 675 sec in duration (mean= 130.24, n=42).

The number of side to side walks performed by the male (section 3.3.1.1) around behind a female adopting the pre-copulatory posture was counted for both completed and attempted copulations. From combined results of the three breeding seasons, the mean number of side to side walks was 16.7 for completed bouts and 21.7 for attempted copulatory bouts (n=20, range = 0-107).

After side to side walking, the male mounted the female from her left side (n=26 of 26 observations) and dismounted either to her left (n=9 of 18 observations) or right (n=9 of 18 observations).

e. Location of copulatory activity: With two exceptions, copulations took place only while the female stood in water of ankle to mid-tarsus depth. The two copulations observed occurring on land were both early in the first breeding season. One of these copulations occurred near a nest site, mid-way up the aviary bank. The copulatory form was not complete, as no crossing of bills was observed when the male dismounted. A second copulation was observed on the same bank, but occurred very close to the water's edge. In addition to these two land copulations, a further 25 attempted copulations were initiated on land. Seven completed and six attempted copulations were observed on the water's edge and on seven occasions, the female adopted a pre-copulatory posture in open water. During the following two breeding seasons, all but three of the attempted and completed copulations occurred in shallow water of 2-8 cm in depth. The female adopted the pre-copulatory posture on land on three occasions, but copulation did not occur in any of these cases. Consecutive copulations often occurred on a single site favoured by the female. These areas were usually right on the water margin, either near the mid-stream islands or aviary bank. Under these circumstances, the male walked around the female both on land and in the water.

3.3.3.3 Egg-laying

a. Seasonal timing: Over the three breeding seasons, the earliest egg laid was on the 18 September and the latest was laid on the 28 January. During the first breeding season, the breeding female laid a late first clutch from January 5 and a second clutch 13 days after removal of these eggs.

Egg-laying began earlier in the second and third breeding seasons (18 September and 7 October respectively). Removals resulted in three clutches being laid during the second breeding season and five clutches in the third season. Egg-laying concluded on the 21 October and 10 December respectively (Table 3.4). The parent birds were left to incubate, hatch and rear the final clutch in each breeding season.

b. Diurnal timing: Accurate times of egg-laying were known only from four observations of egg deposition by the female. These observations were made at 0915 hours, 0800 hours, 1445 hours and 1430 hours. Two other eggs were found on the nest soon after laying (one at 0630 hours and the other at 0620 hours) and were recognised by their lighter green colouration which slowly faded to a dull olive-green 2-3 hours later. From first observations of the appearance of 10 other eggs during the course of the study, it appeared that seven were laid in the late evening/early morning (2000-1000 hours), three in the mid/late afternoon (1400-1700 hours) and one between 1030 and 1145 hours.

c. Inter-clutch intervals: The number of days from removal of a full clutch of eggs until laying of the first egg of the next clutch is shown in Table 3.5 for the three breeding seasons. The median and mode

Table 3.4 Seasonal timing of egg-laying

	CLUTCH NUMBER				
	1	2	3	4	5
Season one	Jan 5-7	Jan 24-28	-	-	-
Season two	Sept 18-22	Oct 2-5	Oct 18-21	-	-
Season three	Oct 7-12	Oct 25-29	Nov 6-10	Nov 23-26	Dec 6-10

Table 3.5 Number of days between egg removal and relaying.

	REMOVAL NUMBER			
	1	2	3	4
Season one	13	-	-	-
Season two	9	9	-	-
Season three	9	8	11	9

were both 9 days between clutches.

d. Inter-egg intervals: The interval between laying of two successive eggs was not easily determined unless both eggs were observed being laid or were found soon afterward. This situation arose only once during the study, when a light green egg was found on the nest at 0630 hours and the next egg was observed being laid 26 hours later at 0800 the following morning. In only three of the 10 clutches were all eggs of the same clutch laid on successive days. There was usually a break in laying between either the first and second, or the third and fourth eggs. Three-egg clutches had a break in laying between the second and third eggs.

e. Clutch size: Ten clutches comprising a total of 36 eggs were laid by the breeding female between January 1983 and December 1984. Four of these clutches contained three eggs and the remaining six clutches had four eggs each. In addition, one shell-less egg was found 5-6 m from the nest but is not included in this total. The mean clutch size was 3.27 and the mode was 4.

f. Fertility: The fertility of eggs laid at Mount Bruce by the focal pair is reliably known from 32 of the total 36 eggs (R. Nilsson pers. comm.) The remaining four eggs were chilled in early incubation and did not develop. Of the 32 eggs, 29 (90.6 %) were fertile. All but two of these eggs hatched out healthy chicks, the exceptions being two embryos which died in early incubation.

In comparison, the number of fertile eggs laid within the wild population from September 1982 until January 1985 was 175 of a total 183 eggs (95.6 % -data: R.Nilsson). Four eggs from a single clutch were not included in a total of eight infertile eggs from the Waitaki Basin, because of the possibility that they were from a same-sex pair. The hypothesis that the fertility rate was the same in the two populations could not be rejected, using a test of ranks.

3.3.3.4 Incubation

Incubation behaviour was observed for eight of the ten clutches produced by the focal pair between January 1983 and December 1984.

Four null hypotheses were tested using the ANOVA procedure on transformed (arcsin) incubation data collected from days 1-9 after laying the first egg of each of eight clutches;

i) "that the mean proportion of sample time in which the eggs were incubated by either bird was independent of clutch number and day after initiation of laying";

ii) "that the mean proportion of sample time spent by the male on the nest was independent of clutch number and day after laying";

iii) "that the mean proportion of sample time spent by the female on the nest was independent of clutch number and day after laying"; and

iv) "that the mean number of minutes between incubation bouts was independent of clutch number and day after laying".

A fifth null hypothesis was also tested by ANOVA using data from days 2-5 only;

v) "that the mean length of an incubation bout was independent of individual (male, female), day after laying (2-5) and clutch number (1-8)".

The results of each ANOVA procedure are presented in Table 3.6 for the five hypotheses and are elaborated below.

a. Total incubation: The proportion of total sample time spent on the nest by either bird was significantly different between clutches (Figure 3.3 a) and over the nine days sampled (Figure 3.3 b).

Daily data from combined clutches indicated an approximately linear increase in the proportion of sample time during which the nest was covered by either bird from day one (43.3%) to day seven (98.2%). A plateau was reached around 98.0% during days seven to nine (Figure 3.3 b).

Five of the eight individual clutches (Figure 3.3 a) were incubated for an approximately equal percentage of total sample time (range = 60.8 - 70.3, mean = 66.1). The other three clutches were incubated for 95.9, 52.3 and 82.3% of sample time.

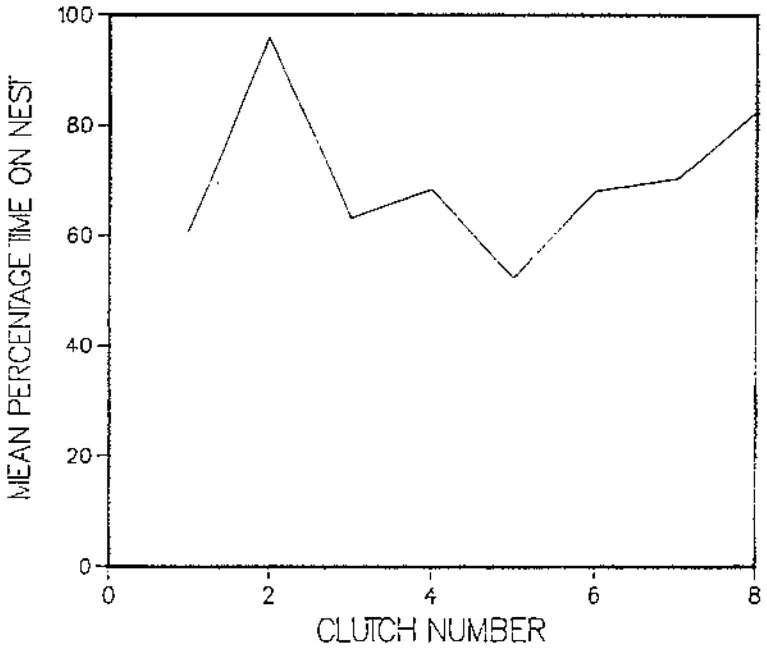
b. Male incubation: There were no significant differences in the

Table 3.6 Summary of ANOVA tests on incubation data

HYPOTHESIS	TEST		
	DAY AFTER LAYING	CLUTCH NUMBER	INDIVIDUAL
i) Total incubation	x p=.008	x p=.043	-
ii) Male incubation	+ p=.429	+ p=.082	-
iii) Female incubation	x p<.001	x p=.010	-
iv) Inter-bout period	x p<.001	x p=.020	-
v) Length of bout	x p<.001	x p<.001	x p=.003

KEY: x = reject the null hypothesis
+ = accept the null hypothesis
- = not tested

A. PERCENTAGE TIME ON NEST—BY CLUTCH



B. TOTAL PERCENTAGE TIME ON NEST

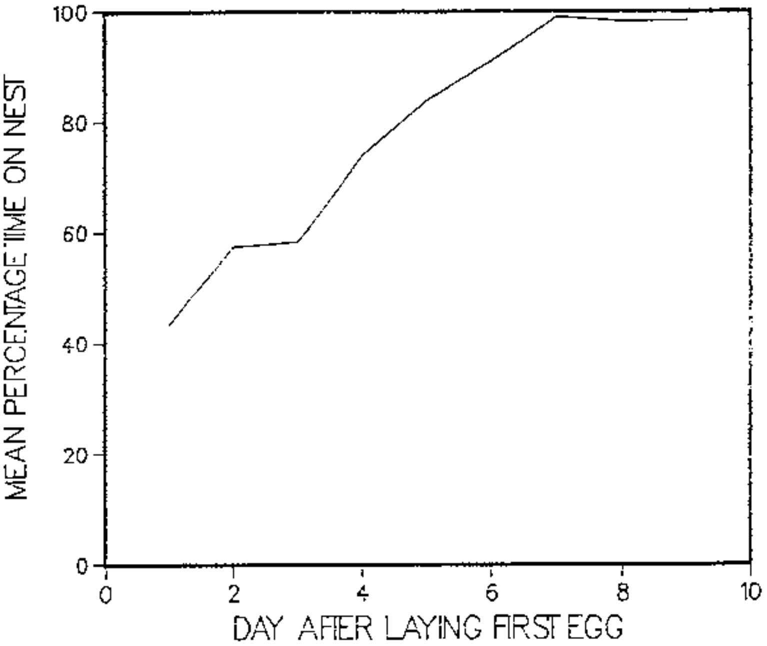


FIGURE 3.3 Percentage sample time spent on the nest (by clutch, and day after laying first egg)

proportion of daily time allocated by the male toward incubation over the nine sample days (Figure 3.4 a) or between the eight clutches (Figure 3.4 b).

Between 39.2 and 48.4% of the male time budget over days 1 to 9 after initiation of egg-laying by the female (combined clutch data) was spent sitting on the nest (Figure 3.4 a). Although male incubation remained approximately consistent in terms of the proportion of sample time in which it was observed, his contribution to total nest coverage (Figure 3.4 c) actually decreased from day 1 (90.5%) to day 8 (42.9%). During this time, the female contribution progressively increased (below).

Of the eight clutches, seven were covered by the male for between 36.9% and 47.1% of sample time, the final clutch (clutch two, season one) reaching a peak at 58.3% (Figure 3.4 b).

c. Female incubation: The proportion of sample time spent by the female on the nest differed significantly between clutches (Figure 3.4 b) and over days after laying (Figure 3.4 a). Her contribution was low during early egg-laying (4.1% at day one) but increased linearly as incubation progressed (Figure 3.4c), to approach and approximately equal that of the male at day five (male 43.7%, female 40.3%). From days five to nine, the contribution to incubation was similiar for both sexes, each individual incubating for approximately 50% of total sample time. The female spent slightly more time on the nest on days eight and nine than did the male.

The proportion of time that each clutch was covered by the female was more variable than that observed for the male (Figure 3.4 b). Peaks in female coverage of the nest occurred at clutches 2,4 and 8 (39.5%, 37.6% and 45.8% respectively). The remaining clutches fell within a range of 19-29.7% of observation time (mean = 24.7).

d. Inter-bout period: The mean duration between consecutive incubation bouts by either bird decreased linearly as incubation proceeded from day one (8.3%) to day seven (0.3%) (Figure 3.5 a).

The mean inter-bout period was approximately equal for six of the eight clutches (Figure 3.5 b), falling within a range of 2.25-4.36 minutes (mean = 3.38). In addition, a peak of 5.76 minutes occurred during

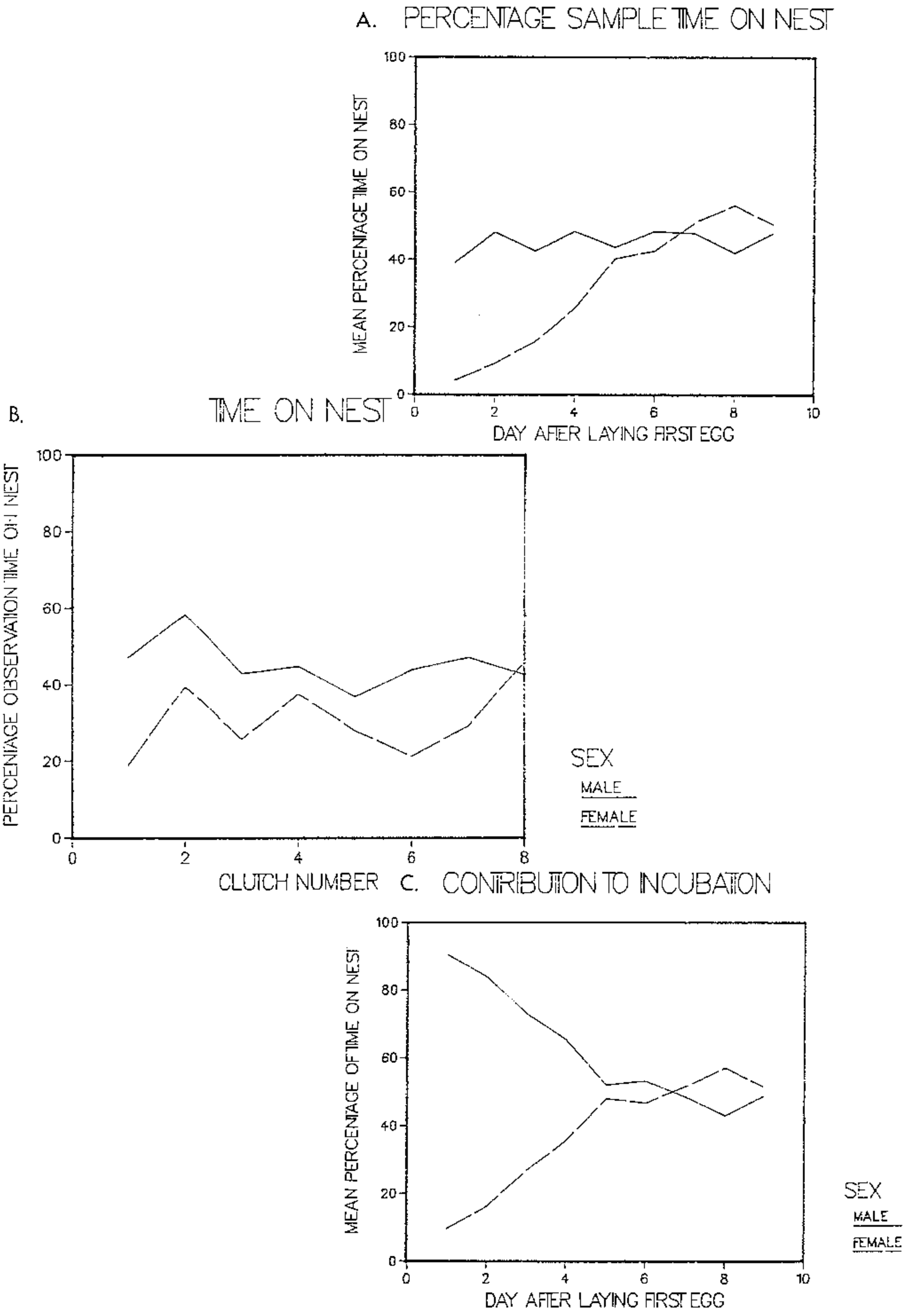
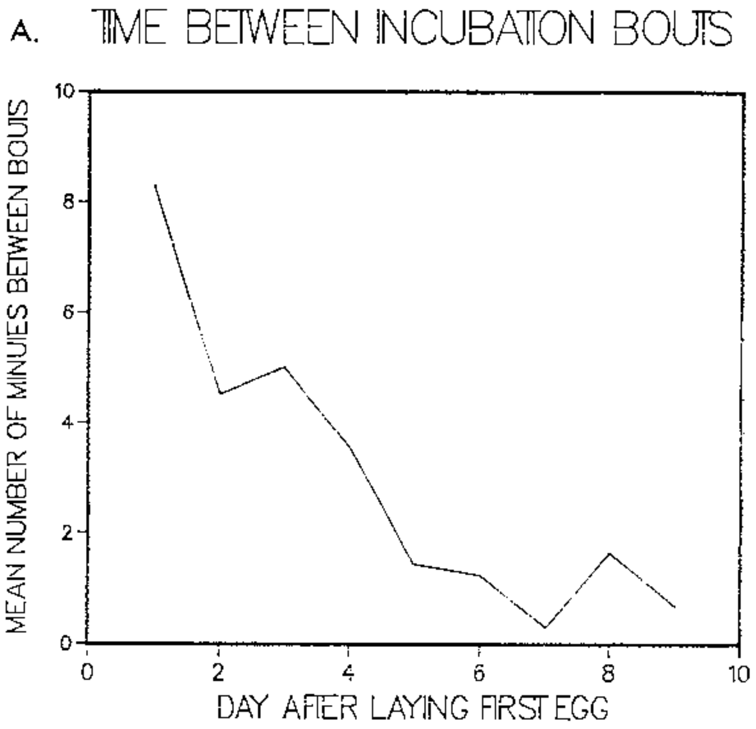


FIGURE 3.4 Time spent by each individual in incubation (by clutch, and day after laying first egg)



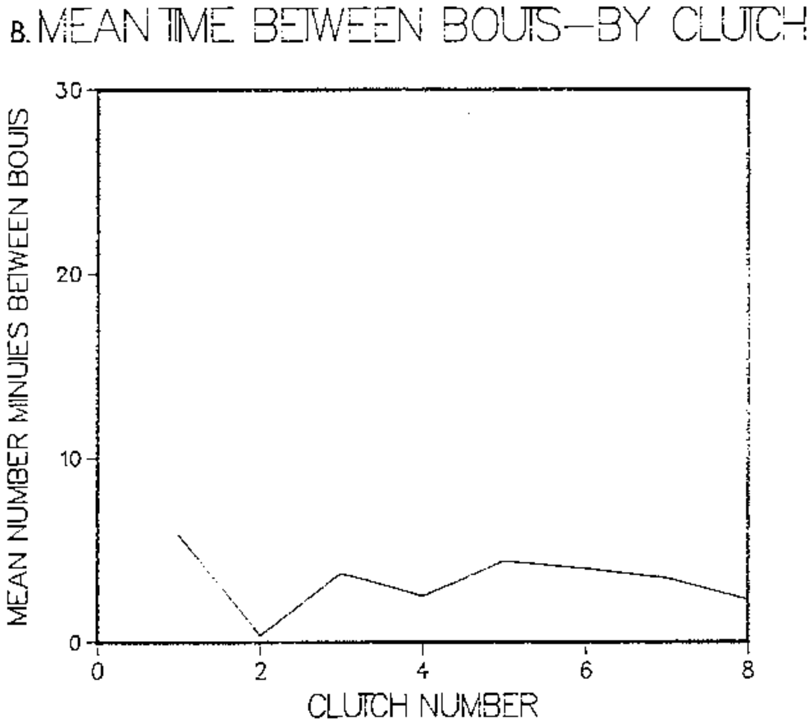


FIGURE 3.5 Length of inattentiveness on the nest (by clutch, and day after laying first egg)

clutch one (season one) and a low of 0.32 minutes during clutch two of the same season.

e. Bout length: The mean length of an incubation bout was significantly different over day (Figure 3.6 a) and clutch (Figure 3.6 b) and between individuals. The overall mean male bout length (combined clutches and days) was 12.0 minutes and that of the female was 9.3 minutes.

The mean bout length of the male was greater than that of the female for all days except days four and five (Figure 3.6 a). Day four showed an approximately equal mean bout length between individuals (male = 14.5%, female = 14.6%) while during day five, female bout length was greater (male = 10.6 minutes, female = 11.3). Both individuals increased the mean length of their incubation bouts as incubation proceeded (Figure 3.6 a).

3.3.3.5 Progeny produced

Two of the ten clutches produced in captivity by the focal pair (section 3.3.3.3) were left for the parent birds to rear (clutch 2 season one, clutch 5 season three). One further clutch (clutch 3 season two) was switched for a clutch of four from the wild in an attempt to increase genetic variability of captive stocks. These eggs were also successfully incubated, hatched and reared by the breeding pair.

Six clutches were transported to the Waitaki Basin (Table 3.7) where they were cross-fostered to dark hybrid and pied stilt pairs.

One clutch only was artificially incubated and hand-reared at Mount Bruce. Of the four clutches reared in captivity, eleven juveniles survived to fledging and eight of these birds were still alive February 1985.

3.3.4 Breeding Time Budget

Daily time budgets incorporating three breeding activities of the focal pair; 1) nest-building/nest-maintenance 2) copulation and 3) sit nest/incubation were collated between November 1982 and July 1984.

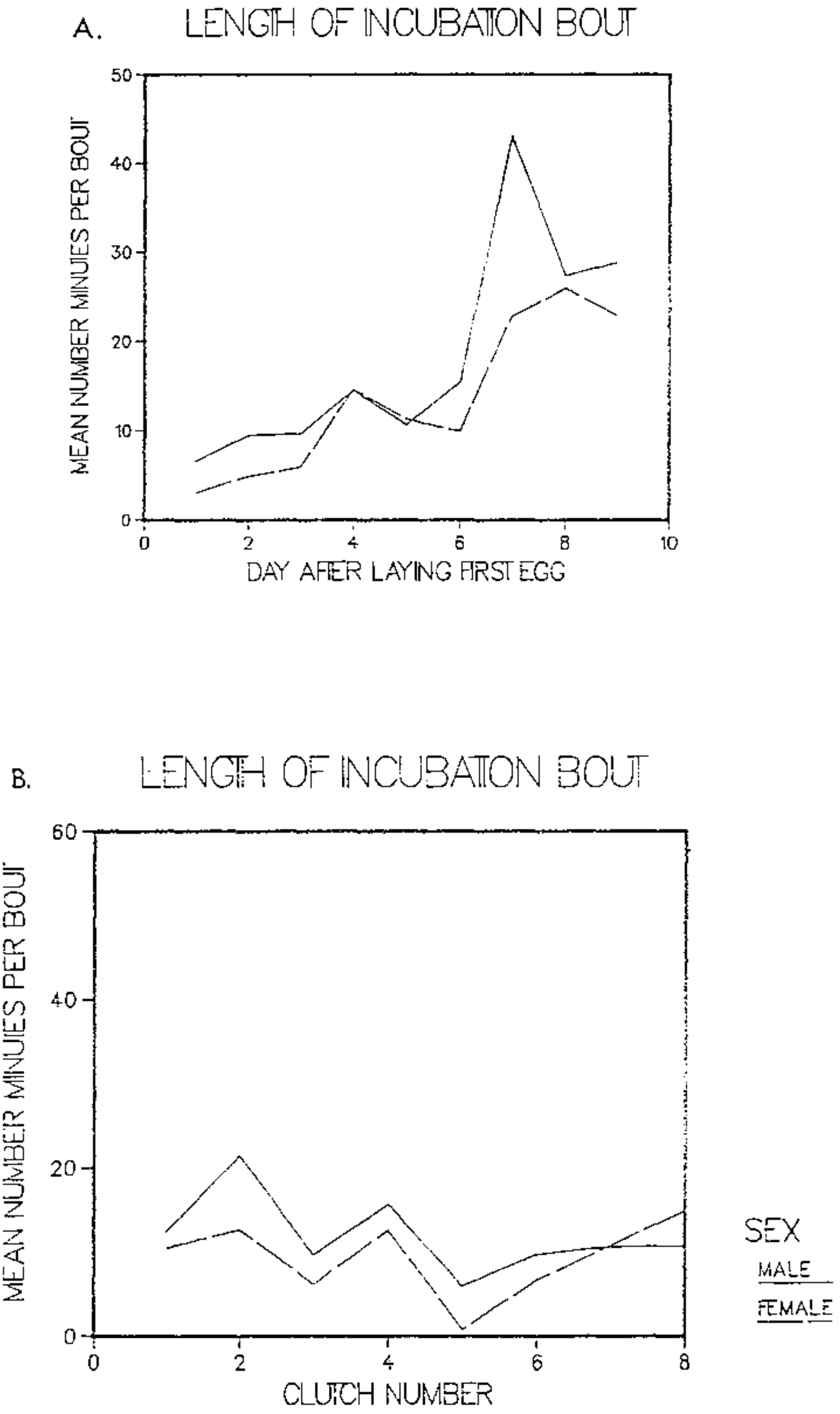


FIGURE 3.6 Mean bout length during male and female incubation (by clutch, and day after laying first egg)

Table 3.7 Fate of captive-reared progeny

Season	Clutch number	No.fertile eggs	Date hatched	Fate of Progeny
1	1	3	4.2.83 artif-cially	one died in early incubation one humanely killed 13.3.83 one surviving (5108)
	2	4	20.2.83	two killed after hitting wire two surviving (5109,5110)
2	1	3	17.10.83	cross-fostered to wild
	2	3	29.10.83	cross-fostered to wild
	3	4	8.11.83	swapped for clutch of four from the wild. one died in incubation three surviving (5112,5113, and 5114)
3	1	2	3.11.84	cross-fostered to wild
	2	4	22.11.84	cross-fostered to wild
	3	3	7.12.84	cross-fostered to wild
	4	4	15.12.84	cross-fostered to wild
	5	3	3.1.85	one died during incubation two surviving (2632-red, unbanded yellow)

Data from activities 1 and 2 (n = 307 hours) were collected over all four stages of two breeding seasons (section 2.2.3). Activity 3 however, occurred only during stage two so collection of data involving this activity was restricted to that time period (n = 140 hours).

The number of minutes spent in each activity per hour of observation was treated as described for non-breeding behaviour in section 2.3.2 and was tested using the ANOVA procedure.

Copulatory data showed no individual difference and so were combined for analysis.

Three null hypotheses were tested;

i) "that the proportion of time spent in nest-building/maintenance was equal for both individuals, all time periods and stages of the breeding season",

ii) "that the proportion of time spent in copulation was equal over all time periods, stages of the season and between seasons", and

iii) "that the proportion of time spent sitting on the nest was equal for both individuals, both seasons and over all time periods".

Tables 3.8, 3.9 and 3.10 indicate for which activities an ANOVA test rejected (denoted x) or accepted (denoted +) each null hypothesis. Results from each activity will be further elaborated in sections 3.3.4.1 to 3.3.4.3.

3.3.4.1 Nest-building/nest maintenance

In both seasons, the male spent a greater proportion of daily time in nest-building activity than did the female (Figures 3.7 a,3.8 a), although this result was only statistically significant during the first breeding season.

Stage differences in the proportion of time spent in this activity were significant for each of the two seasons. Nest-building peaked during stage one (pre-nesting) of the 1983/84 season (Figure 3.8 b) but peaks differed between the two individuals during the 1982/83 season (Figure 3.7 b) i.e., stage one (female) and stage two (male). A low rate of nesting activity was observed early in stage three (hatching to

Table 3.8 Summary of ANOVA tests for nest building/maintenance

	1982/83	1983/84
Time	x	x
Stage	x	x
Time*Stage	x	x
Individual	x	+
Time*Indiv	+	+
Stage*Indiv	+	+

Table 3.9 Summary of ANOVA tests for copulation

Time	x
Stage	x
Time*Stage	+
Season	+
Time*Season	+
Stage*Season	x

Table 3.10 Summary of ANOVA tests for sit nest/incubation

Time	+
Individual	x
Time*Indiv	+
Season	+
Indiv*Season	x
Time*Season	+

KEY: + = accept the null hypothesis
x = reject the null hypothesis
* = interaction of individual, time, season or stage.
- = not tested

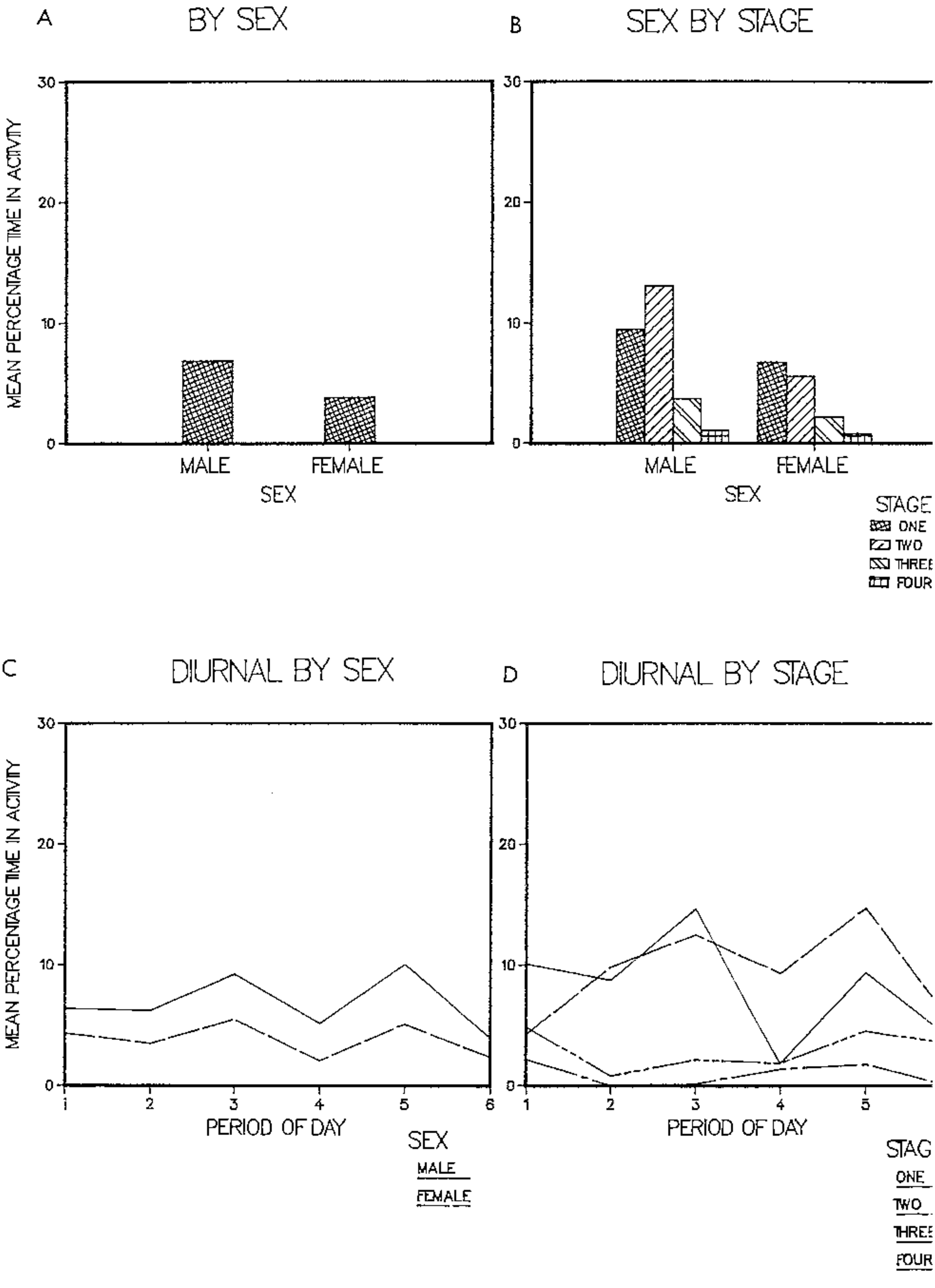


FIGURE 3.7 Nest-building/nest maintenance time-budget 1982/83 breeding season

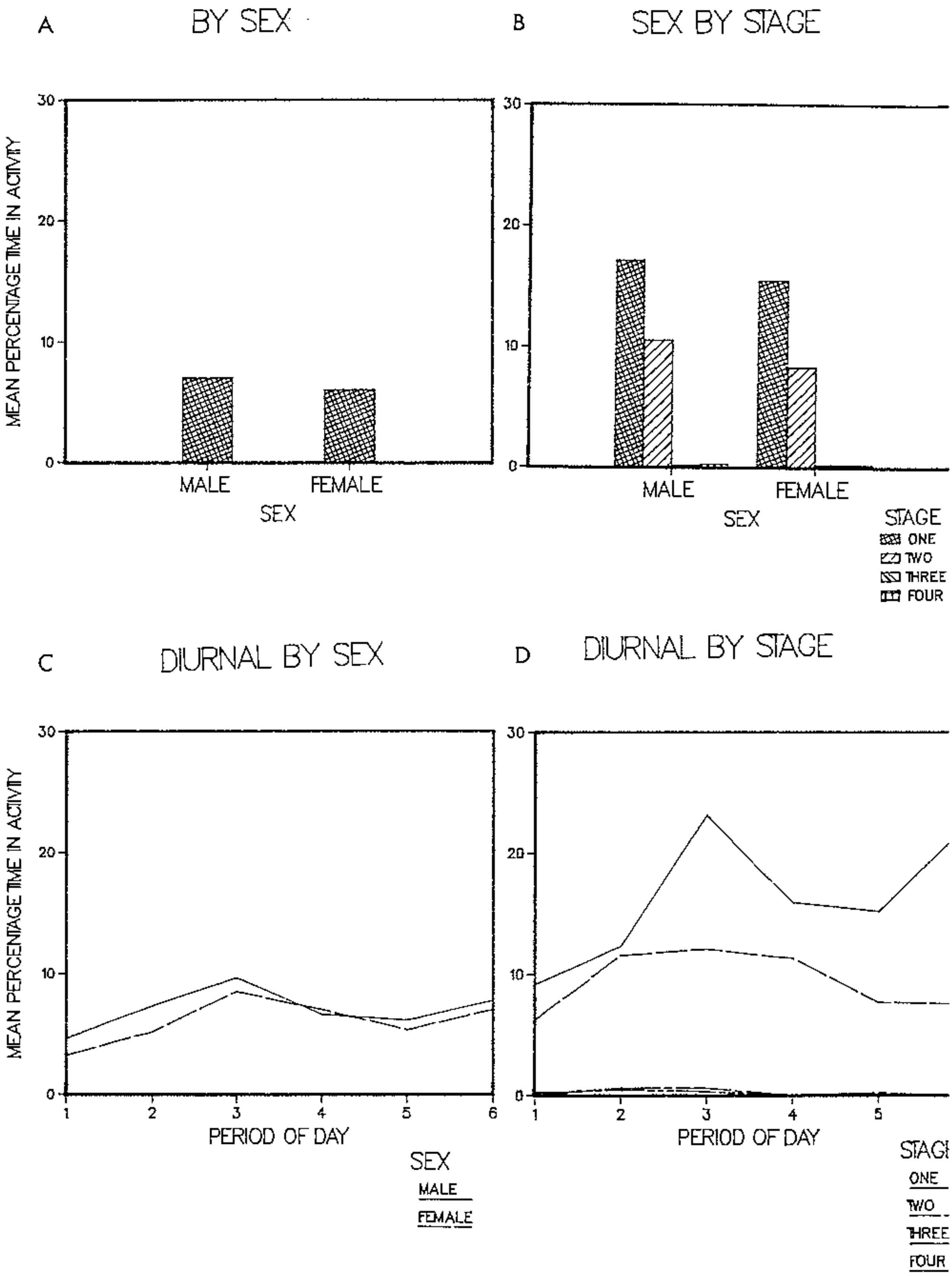


FIGURE 3.8 Nest-building/nest maintenance time-budget 1983/84 breeding season

fledging of chicks), as not all eggs hatched synchronously and so the parent birds remained on the nest after chicks had left it. Stage four also included nesting activity toward June/July, immediately before break-up of the family group.

Diurnally, nest maintenance activity followed a bimodal distribution, peaking during period three of both seasons (Figures 3.7 c,d and 3.8 c,d) and again in period five (season one) or period six (season two).

3.3.4.2 Copulation

The proportion of time spent in copulatory activity was significantly different over the six time periods and over the four stages of the breeding cycle. Between season differences were not significant however (Figure 3.9 a).

Copulation peaked during stage one of each season (Figure 3.9 b) and diurnally peaked at periods 2 and 5 (Figure 3.9 c). Diurnally, the proportion of time spent in copulatory activity was not significantly different between the four breeding stages (Figure 3.9 d).

3.3.4.3 Time on the nest

The male spent significantly more time on the nest than the female over all time periods and both seasons (Figure 3.10 a,b,c). There was no significant diurnal difference in the proportion of time spent on the nest (both individuals combined) (Figure 3.10 c,d) over the six time periods. Seasonal differences were also not significant (combined individuals and stages)(Figure 3.10 d).

3.4 Discussion

The courtship, copulatory, nest-building, egg-laying and incubation behaviour of a focal pair of stilts was described in section 3.3.1. Formation of this pair had occurred before initiation of this study. Pairing in the Family Recurvirostridae appears to be a result of the persistent association of a female with a male until all initial aggression ceases (Hamilton 1975). In the wild, this appears to take 20+ days for black and a minimum of 3-4 days for pied stilts (Pierce 1982). Pair formation in captive black stilts was problematic.

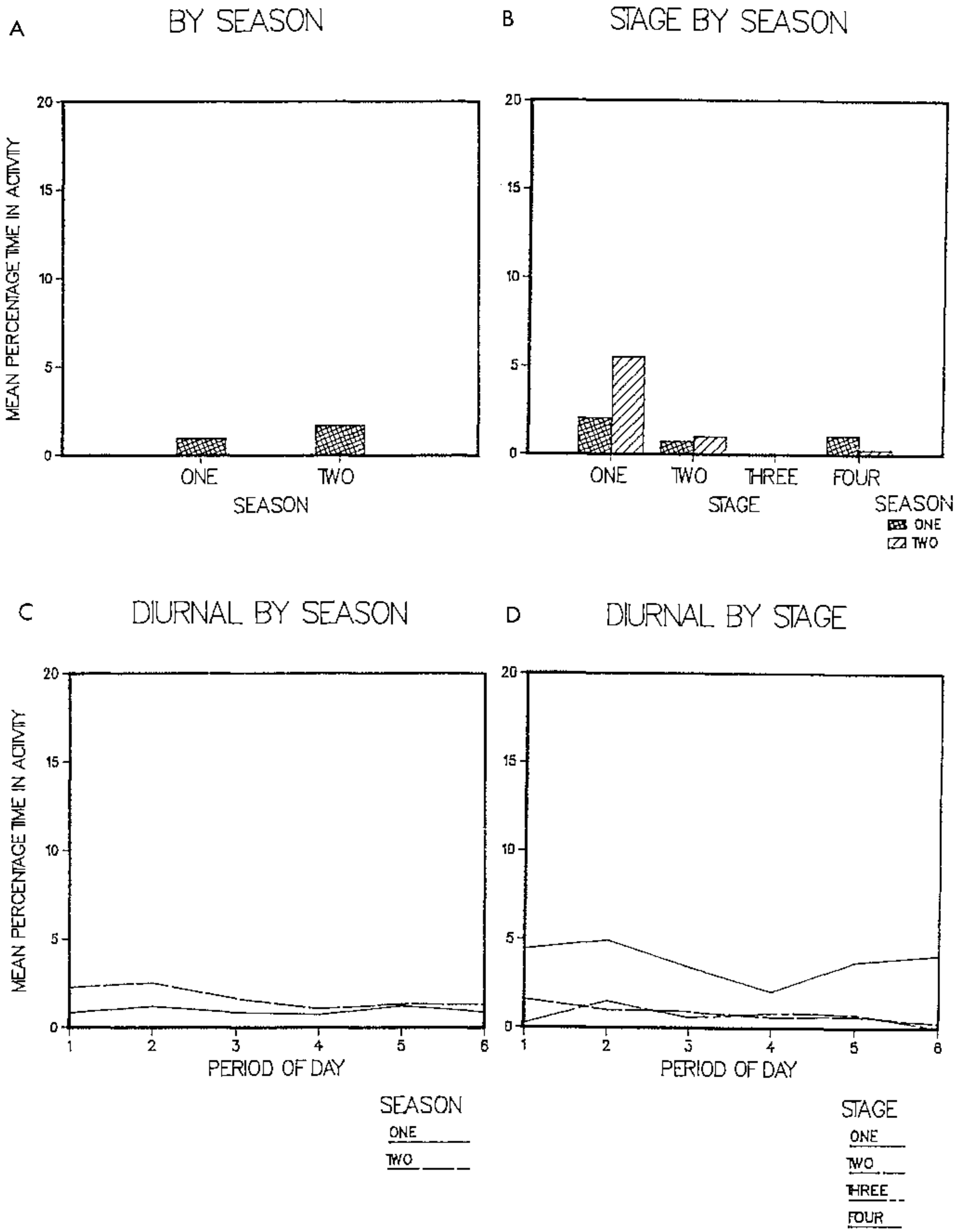


FIGURE 3.9 Copulatory activity time-budget 1982/83 and 1983/84 breeding seasons combined

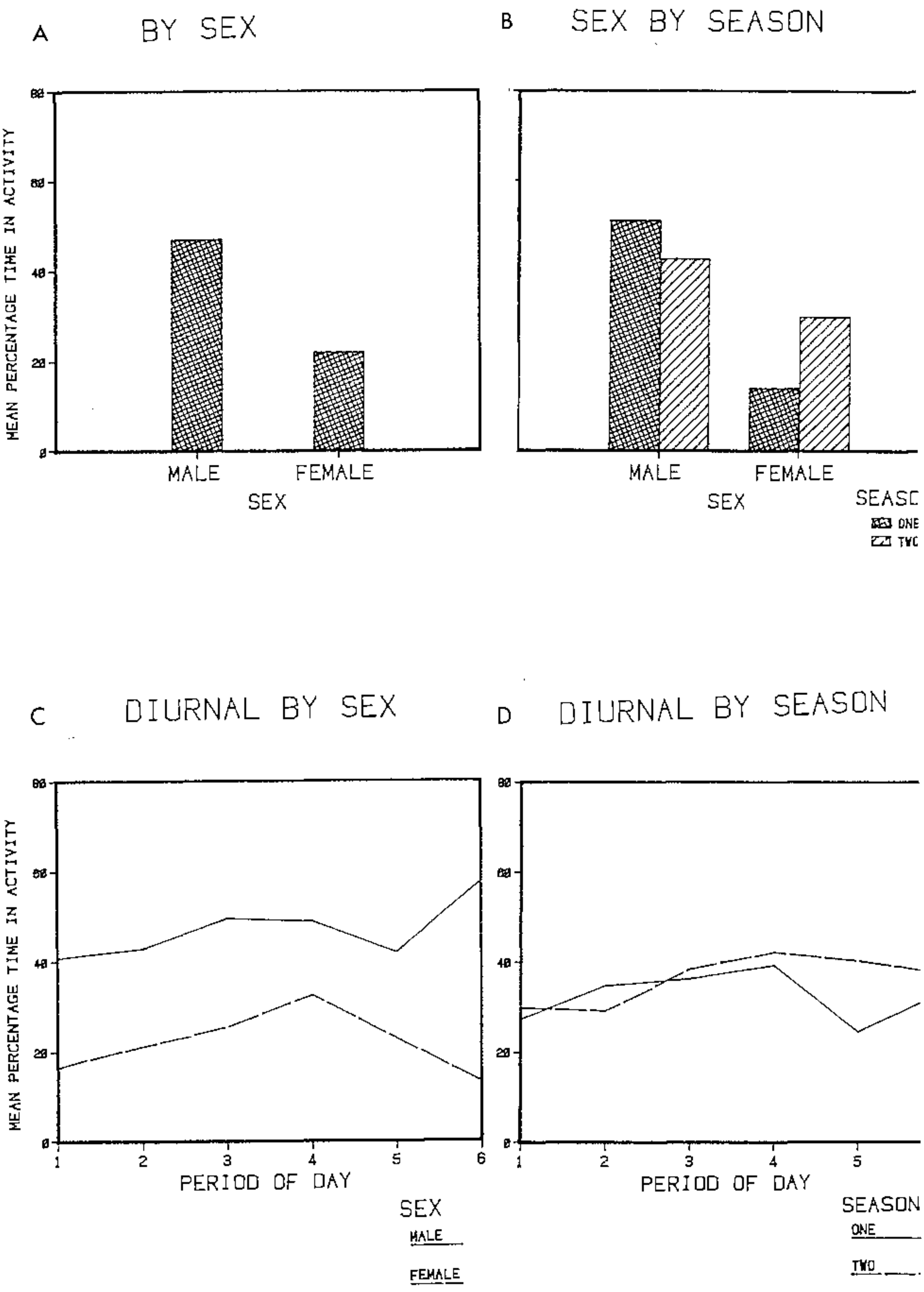


FIGURE 3.10 Incubation time-budget (by individual and season)

Individuals of opposite (probable) sex who demonstrated little agonistic behaviour toward each other were housed as pairs. Usually these birds initiated nesting and pre-copulatory activity. Copulation took place in only the focal pair. Intra-pair aggression eventually developed between all other male-female pairs, so individuals were repeatedly manipulated in attempts to form new pair bonds. An effect of neighbouring birds on intra-pair activity, particularly that of aggressive interaction was experimentally evident during pair manipulations. Redirected aggression within the focal pair was most intense while one male and three female stilts were housed within an adjoining aviary. In this instance, there was redirection of motor patterns (aggressive pursuit or peck) appropriate to one tendency within a conflict situation (attack), onto an individual other than that which elicited it (i.e., a mate rather than a neighbour). This type of aggression has been observed in flocking birds where one individual is supplanted at a food source by a superior and instead of retaliating, turns its aggressiveness onto a subordinate bird (Hinde 1970). Captive stilts were unable to physically contact neighbours through a median fence and this may have resulted in redirection of aggressive motor patterns onto a mate. Copulation by the focal pair of captive black stilts did not take place until the day following removal of all neighbouring birds.

Pair formation and strengthening of the pair bond appeared to involve one or more activities not different from copulation, fighting and nesting activity since these were the only performances that stilts and avocets (Makkink 1936) appeared to display. Feeding side by side, driving intruders out and selecting a nest-site together, may all contribute to cementing the pair bond (Gibson 1971). Ritualized preening before pre-copulatory activity has been suggested by some authors (Makkink 1936, Gibson 1971, McConkey 1971, Hamilton 1975) to play some part in pair formation and "courtship". Preening before adoption of the female pre-copulatory posture was not observed in captive (pers.obs.) or wild black stilts (Pierce 1982). Rather, pre-copulatory activity took place following foraging or wading. There were subtle vocal and visual communications between individuals of the captive focal pair just before adoption of the pre-copulatory posture by the female. These took the form of hunched postures and high slow stepping actions as the two birds approached one another.

As previously noted for black (Pierce 1982) and pied (McConkey 1971, Pierce 1982) stilts, copulations peaked prior to egg-laying (although this was not statistically significant). The prolonged period between the first copulation of the season and egg-laying (eg., October 1982 and January 1983 respectively) may play some part in strengthening the pair bond and synchronize gonad maturation (McConkey 1971). With two exceptions, all successful copulations took place while both birds stood in water. The stimulus of foot contact with water may have been important for successful performance of pre-copulatory displays such as bill-dipping and false-preening by the male. Black-winged stilts (Gibson 1971) and pied stilts (McConkey 1971) have also been described copulating only in water. Copulatory attempts early in the first breeding season were initiated primarily on land and were longer than copulations performed over water.

Copulation with inanimate objects as observed during this study and termed "simulated copulation", have also been reported for European avocets (Makkink 1936) and black-necked stilts (Hamilton 1975). Makkink termed this behavioural pattern "eruptive copulation". Movements were made by males toward objects of approximately female size, with little if any pre-copulatory or post-copulatory display. In two of the three observations by Makkink of this pattern, no female acted "adequately". He concluded that "the emotional state (of the male) increased in such a degree that it boiled over and gave rise to the act apart from an adequate object". The two captive male stilts which exhibited this behavioural pattern were both housed with a female bird, each of which had adopted the pre-copulatory posture, but the males had independently failed to mount. Simulated copulation only once followed unsuccessful attempts at copulatory activity. Copulations directed toward non-appropriate forms have also been described for many other species including Fischers lovebird *Agapornis fisheri*, the wood thrush *Hylocichla mustelina* and American redstarts *Septophaga ruticilla* (Ficken and Dilger 1960), robin *Turdus migratorius* (Young 1949, cited in Ficken and Dilger 1960), sage grouse *Centrocercus urophasianus* (Simon 1940, cited in Ficken and Dilger 1960) and the New Zealand Kakapo *Strigops habroptilus* (Merton et. al., 1984). In all cases of copulations with inappropriate objects observed by Ficken and Dilger, a female was present although not always available. It appears that these copulations were redirected activity in response to subnormal stimuli (Hinde 1970).

Earliest laid eggs were observed on 18 September (1983) and the latest laying date of the focal female was 28 January (1983). The first eggs of the 1982/83 season were laid very late compared to the natural distribution of egg-laying in the wild [mid-September to early December (Pierce 1982)]. All wild black stilt clutches laid after the 15 October were second attempts (Pierce 1982). The time between successive clutches laid in captivity was much shorter than clutches found in the wild (mean = 9.7 days, n = 7 for captive stilts; mean = 19-22 days, n = 6 for wild stilts (Pierce 1982)). Laying during the second breeding season in captivity began much earlier but was delayed slightly in the third season, probably as a result of temporarily housing the focal pair indoors several weeks prior to breeding.

There was then, considerable variation in laying dates both within captive laid clutches and between captive and wild ones. Several factors have been proposed to account for variation in laying dates, clutch sizes and breeding success in avian species (Perrins 1970). Food supply is often cited as a proximate as well as an ultimate factor influencing these three parameters (Kallander 1974, Hogstedt 1981, Newton and Marquiss 1981, Ewald and Rohwer 1982). Supplementary feeding has been found to advance the onset of laying in Agelaius phoeniceus (Ewald and Rower 1982), especially if provided early in the pre-breeding season. Food-enriched territories also supported more nesting females than control territories. Similarly experimental pairs of the magpie Pica pica laid earlier, had larger clutches and produced more fledlings than control pairs (Hogstedt 1981). Sparrowhawks Falco sparverinus (Newton and Marquiss 1981) and great tits Parus major (Kallander 1974) also laid earlier in food enriched territories.

Apart from the effect of abundant food, other reasons for why some individuals of a species breed earlier than others are the age and experience of the breeding individuals (Perrins 1970). Age of the breeding female has been reported to affect laying date of many species eg., great tits (Perrins and McCleery 1985), red-winged (Agelaius phonenicus) and yellow-headed (Xanthocephalus xanthocephalus) blackbirds (Crawford 1977). In all three species, young birds laid later than older individuals.

It was unlikely that age was an important single factor in delayed breeding by the focal black stilt pair during the first season, since as first-time breeders they were already three years old. Wild stilts are known to breed at two years of age (Pierce 1982). An effect of female experience on breeding performance and success as demonstrated for Canada geese Branta canadensis moffiti (Aldrich and Raveling 1983) is a more likely explanation. Geese nesting for the first time were less attentive on the nest and began incubation at lower body weights than experienced birds (even when the latter were younger individuals). Nest inattentiveness was much higher during the first stilt breeding season, especially so for the female. Chilling of eggs during one long inattentive period after the onset of incubation of the very first clutch may have been partly responsible for embryo death of one egg.

The pair bond may also affect date of laying (Perrins 1970). Coulson (1966) showed that kittiwake pairs (Trissa tridactyla) which have mated for successive years lay earlier than those which are first-time pairs. It is likely that courtship is facilitated and accelerated if individuals have previous experience of one another (Coulson 1966). Similiarly Perrins and McCleery (1985) found pairs of great tits breeding together for the first time laid later and smaller clutches than average and had a lower breeding success. The effects of pair bond retention and experience were probably the two most important factors contributing to earlier laying of the captive black stilt pair during their second and third breeding seasons. It remains unknown however, whether either disturbance from neighbouring birds or food supply primarily influenced the delay in laying during the first season.

The total number of clutches laid per season was higher during the 1983/84 season (n = 5) than that known from any wild pair. Pierce reported one pair of black stilts which produced three clutches during 1980 and a second pair which laid four clutches during 1982.

As in wild pairs (Pierce 1982), the captive pair exhibited high site fidelity during re-laying. Only six nests within three localities were used to lay 10 clutches of eggs. Nest sites were primarily located on mid-stream islands, a feature common to pied stilts and some black nests (Pierce 1982). Nesting on islands has the advantage within the wild population of lessening the risk of nest location and destruction by predators. Other captive stilt pairs constructed nests but did not lay eggs in them. Nest-building activities begun in aviaries and zoos by a large variety of birds seldom result in a nest characteristic of the species (Lorenz 1981).

Clutch size in the Recurvirostridae is almost invariably four (Maclean 1972). Maclean believed that this was also the ancestral clutch size of the Charadrii and that species occurring away from a proposed northern centre of origin lay less than the four egg-clutch (eg., banded stilt of Australia which lays only a three egg clutch). Four of the ten clutches laid by the captive female contained three eggs only. The mean clutch size of the captive pair (i.e., 3.27) was lower than that recorded for other recurvirostrids. Pierce (1982) recorded a mean clutch size of 4.0 for black and 3.82 for pied stilts. McConkey (1971) reported a mean clutch size of 3.91 for pied stilts and Gibson (1971) has described a mean clutch size of 3.9 for American avocets. Maclean's theory of reduced clutch sizes of Recurvirostridae in the Southern hemisphere was perhaps applicable to the mean clutch size of captive black stilts. But it did not hold when considering the mode clutch size of four observed in captivity and in the wild. Some abnormally large clutches of 6-8 eggs have been laid by wild black stilts, but these have usually been from female-female pairs and were generally infertile. Clutch sizes decrease as the breeding season progresses for many avian species (Ewald and Rohwer 1982). This results from either reduction in food supply, or breeding by younger females which tend to lay later and fewer eggs. The captive pair of stilts did not appear to follow this pattern, as the three 3-egg clutches were laid at the beginning or mid-way through the season. Reasons postulated for the limit of the normal clutch size in birds have been related to the number of eggs which parent birds can cover during incubation. This suggestion was dispelled by Shipley (1984) as an explanation for the American avocet's clutch size, since Shipley's experimentally augmented clutches hatched more young than control clutches of four. Gibson (1971) found however, that clutch sizes of 3-4 hatched a greater proportion of young than 2 or 8 egg clutches. In this case though, it was likely that two-egg clutches did not elicit a strong enough tendency to incubate and large clutches were too big to cover. So hatching success may be related to incubation for extreme size clutches only. Why only four and not five eggs are generally laid by shorebirds appears to be related more to the number of young that a pair can feed, brood or protect from predators. Safriel (1975) found experimental broods of five semipalmated sandpiper young (<u>Calidris</u>

pusilla) had a lower average survival of young. The precocial young were vulnerable to predation and adults could only offer limited protection. A clutch size of four then, may produce an optimal number of 2-3 young for successful rearing. During McConkey's study, pied stilts appeared to have an abundance of food over spring and summer but the average number of young per family group was only 2.4. Pied stilts (McConkey 1971) and the captive black stilt pair of this study laid only four eggs even when the first 3 were taken immediately after they were laid.

Incubation by recurvirostrids does not usually begin until the complete clutch has been laid or is near completion (Yeates 1941, Gibson 1971, Hamilton 1975, Cooke 1977, Pierce 1982). The captive pair began incubation after laying the second or third egg. The nest was not usually covered for over 80% of sample time until days 5-6 after initiation of egglaying. As in all other recurvirostrids, both sexes incubated. The male took the main role in this activity. Hamilton (1975) found female black-necked stilts incubated predominately over the day, for longer periods than the males. Gibson (1971) found the same but the small samples and large ranges of both these studies indicate considerable variation (Gibson 1971). This variation was noticable with change in day after laying of the focal captive pair. The male spent an approximately equal amount of daily time on the nest from day 1 to day 9 after laying, whereas the female progressively increased the proportion of daily time that she spent on the nest from day 1 to day 9 after egg-laying. This resulted in an overall increase in the time the nest was covered as incubation progressed. The proportion of male contribution to nest coverage actually decreased over the first 9 days after egg-laying. Gibson (1971) also found that male American avocets spent more time on the nest over the first 9 days after laying than did the female. As with captive laid black stilt clutches, American avocet clutches were characterized by high nest inattentiveness early in incubation. There is then, evidence for variation in relative contribution of the sexes to incubation over the incubation period, at least for the single captive black stilt pair and American avocets. Pierce (1982) did not find these sex differences between early and late incubation but females had longer bouts in both pied and black stilts, with males spending more time on the nest at night. McConkey found no sexual differences in bout length but nest coverage did increase as incubation proceeded. This increase over time was in all probability an indication of increasing tendency of pied stilts to incubate from initial egg-laying (McConkey 1971). With the captive pair however, this increase in "tendency" to incubate was a direct result of increased female participation after completion of egg-laying.

CHAPTER FOUR

PARENTAL BEHAVIOUR, JUVENILE GROWTH AND ONTOGENY

4.1 Introduction

A persistent controversy in the study of behaviour has been the relative contributions made by heredity and environment in determining the emergence of particular behavioural patterns (Melzack et. al., 1959). Stereotyped reactions occurring in the absence of prior experience of a particular stimulus makes it probable that such reactions depend on a genetic background i.e., they are innate.

Many behavioural patterns essential for survival could be expected to be innate. These might include reactions to predators and patterns involving care of young. Captive birds reared in the absence of parental influence provide interesting subjects for examination of some patterns which may be genetically determined.

In this chapter, the parental behaviour of a focal pair of stilts and the behavioural ontogeny of their chicks is described. In particular, adult patterns of behaviour elicited in the absence of prior experience are identified. Patterns of juvenile behaviour observed from hatching until fledging are described. Variability and changes in juvenile responses toward different types of predator, and the development of feeding behaviour with time/age are also examined.

4.2 Methods

Adult parental care: The collation of the repertoire of behavioural patterns related to parental care by the breeding pair followed the methodology of sections 2.2.1 and 3.2.1. Supplementary observations of adult antipredator behaviour were made within the wild population from 24 September to 5 October 1983 and 3-13 December 1984.

Egg-shell removal: In order to obtain a full description of this behavioural pattern and to investigate whether it could be elicited at a time other than immediately after hatching, an exploratory experiment was conducted. On November 28 1984, I placed one large fragment of black stilt egg-shell within a nest of newly laid eggs. A second fragment was placed 15 cm from the nest and a third 0.5 m away. The shells were positioned so that the light inner shell faced upward, which increased visibility of the fragment.

Juvenile behaviour: The form and first appearance of all behavioural patterns performed by the eight juvenile stilts reared successfully at Mount Bruce (section 3.3.3.5) was recorded and described between March 1982 and February 1985.

Observations on juveniles 5108, 5109 and 5110 (hatched February 1983), focussed on post-fledging behaviour up until 2 years of age. A second clutch of three juveniles (5112, 5113, 5114, hatched 8.11.83) were observed until they were 15 months old and a final clutch of two (2632-red, yellow; hatched 3.1.85) were followed until they fledged.

Age and foraging success: The same eight chicks comprised the study set of individuals for an examination of changes in foraging behaviour with age (from hatching until fledging).

Using focal animal sampling (Altmann 1974), counts were taken over a 30 sec interval of;

i) the number of pecks directed toward the water or substrate (strikes); and

ii) the number of successful captures, indicated by a backward jerk of the head when swallowing.

Counts were abandoned if activity switched before the 30 sec had elapsed. Repeated observations on these chicks were grouped into eight age-classes; 1-5, 6-10, 11-15, 16-20, 21-25, 26-30, 31-35 and 36-40 days. The data were log-transformed and one-way ANOVA tests (Nie et. al., 1975) performed on i) ageclass by strikes; ii) ageclass by captures and iii) ageclass by rate of successful capture (i.e., captures/strikes).

Chick growth: Chick growth from hatching until fledging was monitored for two clutches of captive reared progeny, each clutch having been reared in successive years by the breeding pair under semi-natural conditions. The chicks monitored were 5112, 5113, 5114 (1983/84 season) and 2632-red and yellow (1984/85). Each chick was colour-banded for individual identification at age 2-3 days. The length of the bill, tarsus and wing were measured using Vernier calipers to an accuracy of 0.1 mm (using measurement criteria outlined in Appendix 5). As wing length increased toward fledging, a wooden metric ruler was used for this measurement (to an accuracy of 1.0 mm). Chick weights were measured with 300 g and 500 g Pesola spring balances. Comparative morphometric data from chicks reared in the wild black stilt population were obtained during banding operations and made available for analysis by R. Nilsson (Wildlife Service). Additional morphometric measurements of wild black stilt chicks from hatching to fledging were made available by R.J. Pierce.

Juvenile antipredator behaviour: Reactions of these same five captive stilts to the presence of "natural" aerial and ground predators or alarm calling of their parents were noted from hatching until 67 days of age. The four classes of predator recorded were;

i) humans - including personnel entering the study aviary to feed or handle birds;
ii) harriers - which resided approximately 500 m from the aviaries and infrequently flew above or near the stilts;
iii) magpies - which roosted in tall podocarp trees approximately 300 m from the stilts and frequently flew back and forth over the aviaries to feeding areas; and
iv) others - included the black-backed gull *Larus dominicanus*, white-faced heron *Ardea novaehollandiae* and vagrant species of non-predators (eg., sulphur crested cockatoo *Kakatoe galerita*).

Comparative observations were made in the wild population of similiar-age chicks. Harrier and human intrusions into territories were observed and the immediate responses of black stilt chicks were recorded. Data were divided into two groups; i) pre-fledging responses (age 2-34 days) and ii) post-fledging responses (39-67 days).

Juvenile time budgets : Daily time-activity budgets for one clutch of three juveniles produced during season two and one clutch of two during season three were collected from hatching until family break-up (age 6 months). The method used in data collection and analysis has been previously described in section 2.2.2.

4.3 Results

Behavioural patterns of the focal pair and their young during stages three and four of the breeding cycle are described in section 4.3.1. These observations are supplemented by observations of black stilts in the wild population and by some on other captive birds. Section 4.3.2 outlines the first appearance of juvenile behavioural patterns. The effect of age on foraging success is also examined in this section. Physical growth of captive-reared chicks is presented in section 4.3.3 and is compared with growth of similiar-age wild chicks. Changes in juvenile time-budgets and antipredator behaviour with age are examined in sections 4.3.4 and 4.3.5 respectively. Aggressive interactions within the family unit are described in section 4.3.6, and the allocation of time by the focal pair toward this and two other parental activities is presented in section 4.3.7. Finally, in section 4.3.8, the break-up of the family party is described.

4.3.1 Description of behavioural patterns

A/ Parental behaviour

A total of 143.5 hours of observations were accumulated during the parental-care periods of three breeding seasons. 45.3 hours of observations were made between 20 February and 17 August 1983, 77.2 hours between 8 November 1983 and 6 June 1984, and finally 21 hours during the pre-fledging period of season three (3 January to 2 February 1985).

Eight behavioural patterns performed by either of the parent birds were grouped according to context and function.

4.3.1.1 Removal of egg-shells

The removal of egg-shells from a nest after chicks had hatched was observed only once during the study (C.Veltman - pers.comm.). The breeding female sat on the nest for 20 min before she stood and picked up a fragment of egg-shell with her bill. She flew with the egg-shell to the corner of the aviary which was farthest from the nest, before dropping the fragment upon the ground. She then flew to the nest. Approximately 15 minutes after dropping this egg-shell, she returned to the area and briefly manipulated the fragment with her bill. The male repeated this "nibbling" activity 30 minutes later, before both birds finally abandoned the broken shells.

An experimental attempt to elicit this pattern of activity was attempted on 28 November 1984. Egg-laying had been completed the day before this experiment. Five minutes after I had deposited the egg-shell within and around the nest, the male returned to the area and attempted to resume incubation. He crouched over the nest briefly, before picking up the egg-shell, and flew off to drop the fragment into water 2 m away. Neither of the other two shell fragments placed near the nest were removed by the stilts and after 45 minutes of observation, I retrieved these shells from the aviary.

4.3.1.2 Brooding

Both parents brooded the chicks in the first 4 weeks after hatching. The brooding bird squatted over the ground, placing its tarsus horizontally over the substrate while keeping the tibia vertical (Plate 4.1). One or more chicks approached the squatting bird from the front and pushed their way head first in under one wing, which the brooding bird held slightly out from the body. The adult and chicks remained in this position (Plate 4.2) until either the parent bird stood up and moved away, or the chicks walked out from cover. A favoured site for brooding chicks was along the flat 20 cm wide concrete base of the fence surrounding the aviary.

A non-breeding adult male stilt was also observed adopting this posture, 3-4 m from its resting mate and near a preliminary nest site. The posture was assumed for 2-3 minutes, three times during one observation period (Plate 4.3).

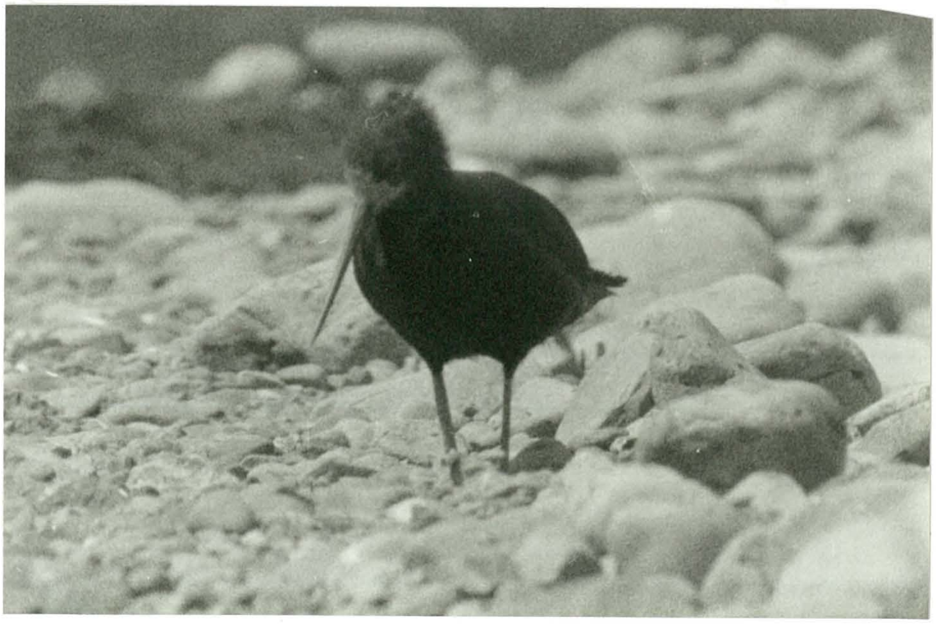
4.3.1.3 Guarding of chicks

After leaving the nest, the chicks were followed by their parents while they foraged along the waters edge. The adults emitted loud repetitive contact calls as they moved along the aviary bank, assuming a semi-hunched posture. Adult vocalisations and locomotory activity diminished and temporarily ceased when the chicks finished foraging and returned to land to rest.

PLATE 4.1 Brooding - adult squats and chicks approach

PLATE 4.2 Brooding - chicks tucked in under adult

PLATE 4.3 Non-breeding male in brooding position



4.3.1.4 Antipredator behaviour

Broken-wing display: Whenever a human intruder approached a nest of the breeding pair, the adults ran excitedly along the aviary bank giving loud "yap" calls (section 5.3.1.6). As the intruder neared and stood over the nest, the adult stilts held their wings horizontally outstretched with the primaries lowered toward the ground (Plate 4.4). This display continued in close proximity to the intruder and occurred primarily during incubation (although was also observed while chicks were nearby). The pattern of behaviour was accompanied by a change in call type from "yaps" to intense "eerr" calls (section 5.3.1.6).

Dive-swooping: The most common reaction of the captive stilt pair to human encroachment near a nest-site or chicks was a swooping dive down over the head of the intruder. A stilt approaching an intruder flew at an angle of approximately 45-60° to the vertical down toward it and passed just above the head. The performance of this pattern of behaviour was most easily observed in the more open environment of the wild population. Dives made by wild stilts were from a greater height than that made in captivity (i.e., 30-45°) to the vertical. Some horizontal approaches were made by these stilts, veering off to one side on nearing the intruder. Swooping stilts remained silent during descent toward the intruder and yap calls did not commence until the stilt began its ascent.

Run and crouch: Only once during the study was a captive stilt observed away from the nest site in a momentary sitting position resembling incubation. The male briefly ceased running toward the observer and squatted in a position similiar to that in section 3.3.1.5 for incubation. At the time of observation, the pair had young chicks which were being handled by the observer.

Tilt head/alarm call: As described in section 2.3.1.2, captive stilts tilted the head to observe avian predators which flew over or near the aviary. During incubation and early chick rearing, tilting the head was usually accompanied by an "url" call given by the male only (section 5.3.1.6). This pattern of behaviour occured while the stilt stood or walked on land but on one occasion was observed when the male was in a crouched position and brooding two chicks. At the time the call was being emitted, a harrier was gliding 30 m above the aviary.

PLATE 4.4 Broken-wing display

PLATE 4.5 Aggressive flight

Aggressive flight: A further reaction of captive stilts to human intruders near the nest or in the locality of chicks was to fly directly up toward the approaching human from a distance of approximately 15-20 m (Plate 4.5). In addition to human intruders, magpies were also a target for this type of approach by captive stilts, but no approaches were made toward harriers. In comparison, stilts of the wild population aggressively flew directly up toward harriers which were as distant as 120 m away. The "url" call was given during flight and upon reaching their target, one or more stilts (pied and/or black) swooped on the harrier and drove it off in the opposite direction to the nest area.

B) Juvenile behaviour

Patterns of maintenance, comfort and alarm behaviour of young stilts from hatching until just after fledging resembled those previously described for adults (section 2.3.1) The first appearance of these behavioural patterns and the ability of chicks to perform some of these patterns fully (eg., preening), was affected by their physical development.

Five additional patterns of behaviour were observed being performed by juveniles. These were;

i) one comfort pattern (brooding);
ii) one locomotory activity (swimming);
iii) one social interaction (allopreening); and
iv) two patterns of antipredator behaviour
(freeze; and seek cover and stand).

These five patterns are described in sections 4.3.1.5 to 4.3.1.8.

4.3.1.5 Brooding

Young chicks sought to be brooded frequently in the first week after hatching, particularly during cloud cover or rain. When a chick required brooding it approached one parent, lifted both its wings above the back and raised them up and down. Wing flapping became exaggerated as the parent stilt crouched down to face the chick. If the adult did not crouch but instead turned and moved off again, wing flapping ceased until the parent stilt turned toward the chick. Pursuit of the adult and wing-flapping continued until the chicks were brooded. Once under the adult wing, only the legs were visible (Plate 4.2). From the age of 6 days, one leg was often tucked up under the chick's body.

4.3.1.6 Swimming

During the first 1-2 weeks of life, the chicks swam the 3-4 m across the aviary from the mid-stream island toward a bank. As the chicks grew, they were able to reach the bottom of the stream and were not observed swimming again.

4.3.1.7 Allopreening

Chicks occasionally pecked with the bill at the back and wing feathers of a sitting sibling. Feather pecking ceased as the sitting bird stood up and moved away.

4.3.1.8 Antipredator behaviour

Freeze: When alarm calls were given by parent birds in response to predators flying above the aviary (i.e., harrier or magpie), the chicks crouched to lie immobile on the ground or ran a short distance before lying down and "freezing" their position (Plates 4.6, 4.7). Although the "freeze" position was observed almost entirely when chicks were of less than fledging age, one newly fledged chick of the wild population also remained motionless near cover after its foster parents had alarm called. As the human intruder approached within 10-15 m, this chick flew up and away from cover.

Seek cover and stand: From 2 weeks of age until just after fledging (approximately 40 days), captive chicks sometimes sought cover under overhanging shrubs when an aerial predator passed over the aviary. They remained motionless in a crouched position until the predator had passed and alarm calls of their parents ceased. A pair of non-breeding adult stilts also sought cover during two observations of harrier intrusions (described in section 2.3.1.2).

PLATE 4.6 Wild chick "freezing" its position during human intrusion.
- open sparse habitat

PLATE 4.7 - dense vegetation

4.3.2 Ontogeny of behavioural patterns

4.3.2.1 Age at first appearance of behavioural patterns

The age at first appearance of each juvenile behavioural pattern is presented in Tables 4.1, 4.2 and 4.3 under the categories of;

i) maintenance and comfort behaviour;
ii) alarm and antipredator behaviour; and
iii) behaviour involving social interactions.

Some behavioural patterns (indicated by * in Tables 4.1-4.3) of 1-2 week old juveniles differed in form from the corresponding adult pattern as follows;

*1 From the first day after hatching, young chicks waded up to 3 m away from the nest. For the first 3-4 days, they lacked coordination and balance, being very unsTable on their legs. When following parent birds around the aviary, they frequently fell over on the uneven surface of the aviary bank.

*2 Up until 2 weeks of age, the chicks preened while they crouched in a posture identical to that used by adults during brooding (section 4.3.1.2). Attempts by chicks of this age to preen while standing were short-lived as they lost balance and fell backward.

*3 From hatching until approximately 40 days of age, resting took place in a sitting position rather than standing as the adults primarily did.

*4 When prey was captured by chicks, it was worked up the bill by opening and closing the mandibles and moving the head slightly backward. Unlike the head-jerking action of the adults when swallowing invertebrates, the chicks flicked their bill and head quickly sideways.

The differences between adult and juvenile performance of the patterns noted above gradually diminished as the chicks increased in experience, physical strength and co-ordination. Adult and juvenile maintenance and comfort patterns were identical by the time the chicks had fledged.

Table 4.1 Age at first appearance of maintenance and comfort behavioural patterns.

Age of chick (days)	Behavioural patterns
1	Locomotion - unstable, frequent falls, swim. *1 Preening : pick at chest, side, wing feathers while standing (brief), between legs if squat.*2 Bathing : dip head, rub head on back, dip body sideways, flap wing stubbles. Brooding: frequent, flap wing stubbles. Comfort : scratch head while in water (brief) shake head, gape, sit to rest with head on side.*3 Forage : snatch prey off vegetation, peck in shallow water after period of dabbling.*4
2	Oxheart - infrequent consumption, frequent manipulation Brooding - preen afterward. Preening - above tail while standing (brief).
3	Forage - plunge.
4	Comfort - defaecate on land, scratch head on land, stretch one leg back, stand one leg and preen (brief) Brooding - infrequent. Locomotion - more stable. Preen - rub head over back, preen chest well. Bathing - shake afterward.
6	Brooding - one leg held up under flank feathers. Comfort - stretch wing stubble and leg back, stretch both wings upward, shake legs. Oxheart - eat larger pieces, carry to water.
7	Comfort - drink, wing stretch.
13	Comfort - stand one leg, lift wings while defaecating, fly upward after bathing, scratch head over the wing.
25	Forage - scythe. Comfort - sit with head in under wing, rest on one leg with bill in under wing.
27	Forage - wash captured invertebrate in water.
35	Locomotion - fly.
40	Comfort - rest more on one leg than sitting, stand on two legs with the bill under the wing.

Table 4.2 Age at first appearance of alarm and antipredator behavioural patterns.

Age of chick (days)	Behavioural patterns
1	alert upright freeze, run and freeze.
4	bob head, tilt head.
13	alarm call when chased, run head-low.
74	forward upright.

Table 4.3 Age at first appearance of behavioural patterns involving social interaction.

Age of chick (days)	Behavioural patterns
25	sibling aggression.
68	allopreening.
82	tussle over siblings' oxheart in water.
130	sidethrow at median fence between aviaries.
146	aggressive pursuit (of sparrow).
160 (season 1) 230 (season 2)	sidethrow nest material, sit and pull in material.
183	aggressive upright, tug fence.
552	pre-copulatory posture.

4.3.2.2 Age and foraging success

Black stilt chicks hatched in captivity were nidifigous and therefore able to peck-forage from the first day of leaving the nest (Plate 4.8). Bouts were short at first, the chicks frequently returning to their parents for brooding.

The number of successful invertebrate captures per attempts made over a 30 sec period was measured for known-age captive chicks and is presented in Table 4.4 for eight ageclasses.

Three null hypotheses that i) the mean number of strikes; ii) the mean number of captures; and iii) the rate of successful capture (i.e., captures/strikes) made over 30 sec were not different between the eight ageclasses, were all rejected at the $p<0.001$ significance level.

Ageclass 1 chicks (1-5 days) made fewer strikes and had a lower rate of capture than all other ageclasses. Rate of successful capture increased to a maximum at ageclass 7 (31-35 days), although mean number of captures and strikes both peaked at ageclass 2 (6-10 days).

4.3.3 Chick growth

Weight and lengths of bill, tarsus and wing of known-age captive and wild chicks from hatching until fledging are shown in Figure 4.1.

Three null hypotheses that i) bill length, ii) tarsus length and iii) weight were not different between same-age captive and wild chicks, were all rejected in an analysis of covariance on the two data sets ($p<0.001$). A fourth hypothesis that wing length was not different in same age captive and wild chicks was also rejected by this analytical method but at $.005<p<.0025$.

Captive chicks fledged at a younger age than wild chicks (Table 4.5). However statistical analysis of these data were not possible as sample sizes were too small.

4.3.4 Juvenile time budgets

Time budget data from three juveniles produced in the 1982/83 season

PLATE 4.8 Two-day old chick foraging

Table 4.4 Foraging success of chicks
(mean units/30 seconds±SEM)

AGECLASS (DAYS)	CAPTURES	STRIKES	RATE OF CAPTURE	N
1 (1-5)	5.65±0.84	9.61±0.83	.542±.045	26
2 (6-10)	22.58±2.01	26.44±1.72	.817±.033	29
3 (11-15)	15.66±2.03	21.66±1.61	.680±.054	15
4 (16-20)	12.26±1.74	15.46±1.72	.769±.028	15
5 (21-25)	10.00	14.00	.714	1
6 (26-30)	10.71±0.72	14.19±0.90	.763±.025	21
7 (31-35)	20.12±2.66	21.50±2.25	.920±.037	8
8 (36-40)	11.07±0.58	13.39±0.51	.819±.022	28

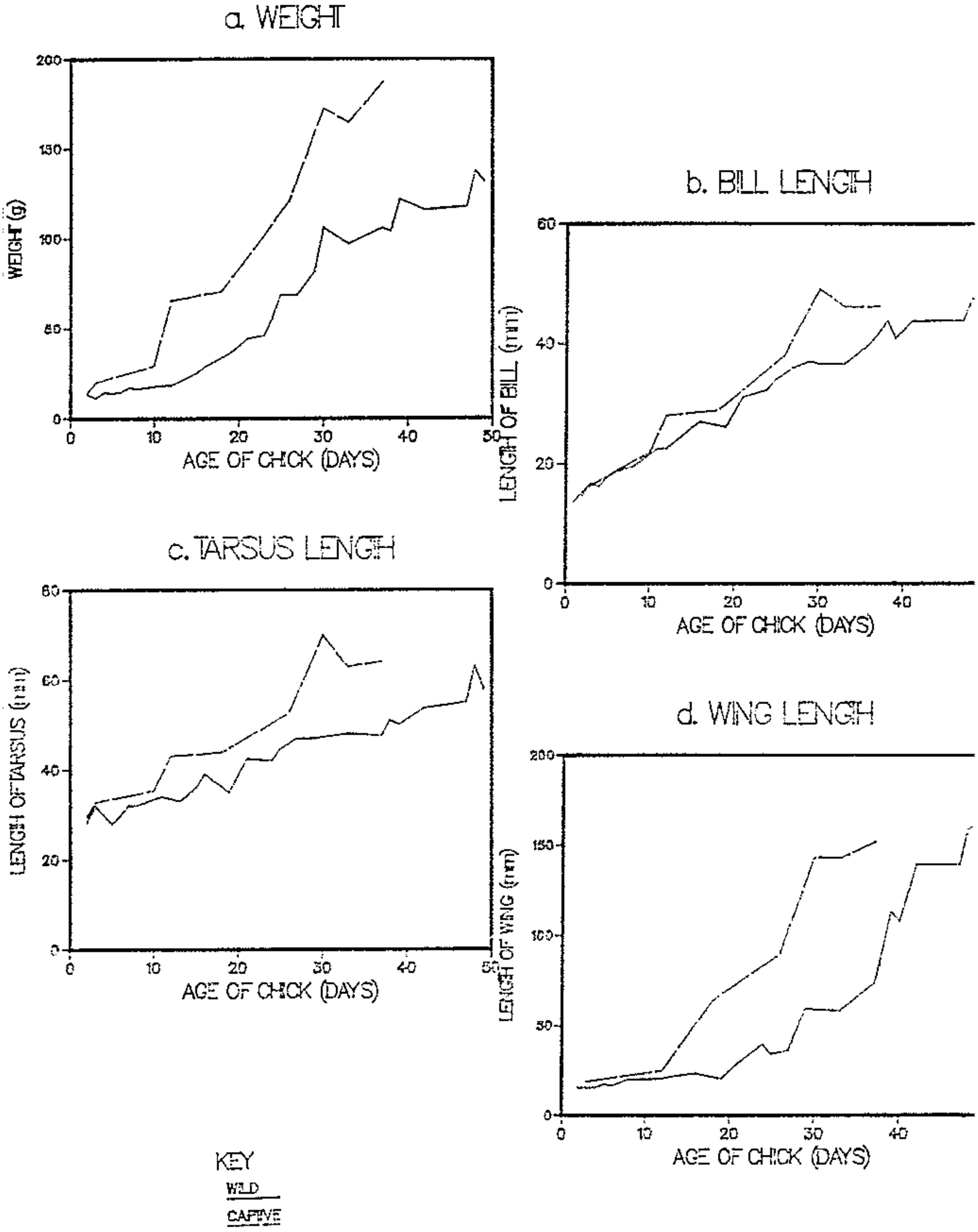


FIGURE 4.1 Growth of captive versus wild-reared black stilt chicks

Table 4.5 Age at fledging (days)

	SEASON 1	SEASON 2	SEASON 3
Captive chicks	-	35 (n=3)	35.5 (n=2)
Wild chicks	mean=47 (n=12) (r=41-55)[1]	mean=40 (n=5) [2]	mean=41 (n=5) (r=39-44)[2]

KEY: n = number of chicks

r = range of chick ages at fledging

[1] 1977-1980 (from Pierce 1982)

[2] data courtesy of R. Nilsson

and three in the 1983/84 season were collated and the data divided into 20 ageclasses for analysis (0-1 week old, 1-2 weeks old,...19-20 weeks old).

The null hypotheses that the percentage of sample time spent in an activity was more variable i) within individuals than between individuals, and more variable ii) within ageclasses than between ageclasses were tested by ANOVA for each years' data. The results of these tests on each of eight activities are presented in Table 4.6 for season one and Table 4.7 for season two. The mean values presented are from combined ageclass data and represent the overall percentage of sample time spent in an activity for each season.

Variance in sample time spent in an activity was less within ageclasses than between them, but the reverse applied within and between individuals.

Figures 4.2 and 4.3 present a summary of the mean proportion of time spent in each activity (three individuals combined) over the 20 weeks observation during the 1982/83 and 1983/84 seasons.

Four main features over the two seasons data were;

i) foraging was the predominant activity over the first 1-3 weeks after hatching;

ii) the proportion of sample time spent immobile increased from week 1 to a maximum at weeks 7-8 (when foraging was at a minimum);

iii) no oxheart was taken until approximately 2 weeks of age;

iv) brooding was observed only from week 1 until 4.

4.3.5 Juvenile antipredator behaviour

Seven types of response by captive chicks to the presence of predators and/or alarm calling of parent birds were observed (Table 1, Appendix 7). A sample of 93 pre-fledging and 83 post-fledging responses of captive chicks to the intrusion by one of four classes of predator; i) human, ii) harrier, iii) magpie or iv) other, are summarised in Appendix 7.

To test the null hypothesis that type of predator, age of chick and

Table 4.6 Summary of ANOVA tests on juvenile time-budget data (1982/1983 season)

ACTIVITY	TEST-AGE		TEST-INDIVIDUAL		RANGE	MEAN
Forage	x	p=.002	+	p=.436	12.3-66.5	41.1
Oxheart	x	p<.001	+	p=.205	0.0-24.7	9.7
Immobile	x	p<.001	x	p=.037	4.0-40.0	23.9
Preen [1]	x	p<.001	+	p=.081	3.7-42.2	13.8
Walk	x	p<.001	+	p=.176	0.0-16.4	6.8
Alarm	x	p<.001	+	p=.403	0.0-12.3	3.8
Run [1]	x	p=.003	+	p=.271	0.0-19.7	2.2
Brood [1]	x	p<.001	nr	nr	0.0- 3.5	0.3

Table 4.7 Summary of ANOVA tests on juvenile time-budget data (1983/1984 season)

ACTIVITY	TEST-AGE		TEST-INDIVIDUAL		RANGE	MEAN
Forage	x	p<.001	+	p=.693	13.1-82.8	43.4
Oxheart	x	p<.001	+	p=.496	0.0-12.8	4.8
Immobile	x	p<.001	+	p=.635	0.0-66.9	23.6
Preen	x	p<.001	+	p=.510	0.0-19.7	12.3
Walk [1]	x	p<.001	+	p=.397	0.0-11.8	5.6
Alarm	x	p<.001	+	p=.450	0.0-11.3	5.7
Run [1]	+	p=.040	+	p=.049	0.0- 1.5	0.2
Brood [1]	x	p<.001	+	p=.336	0.0-15.6	2.0

KEY: + = accept the null hypothesis
x = reject the null hypothesis
nr = no result
[1] = skewed data

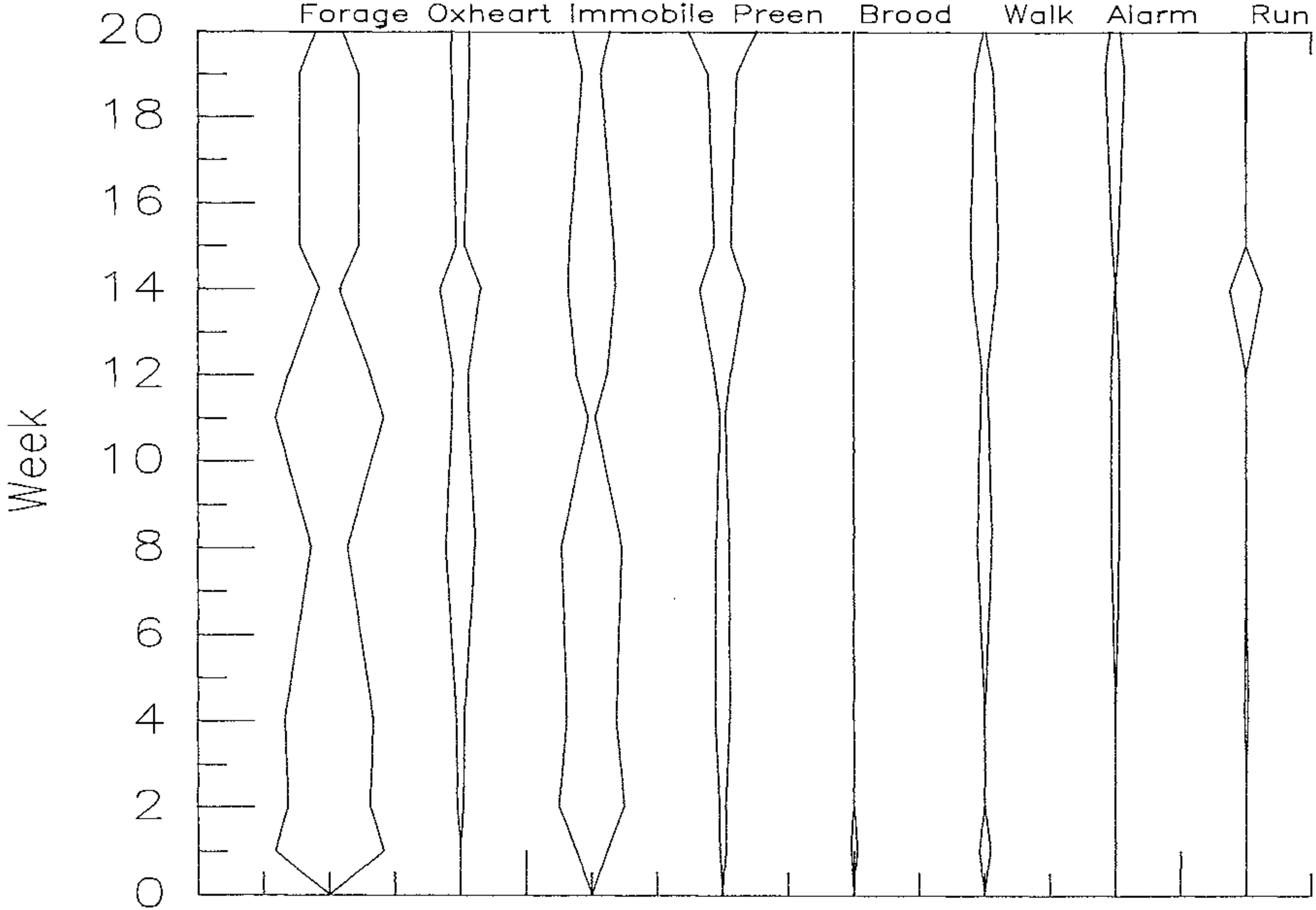


FIGURE 4.2 Juvenile time-budget 1982/83 breeding season

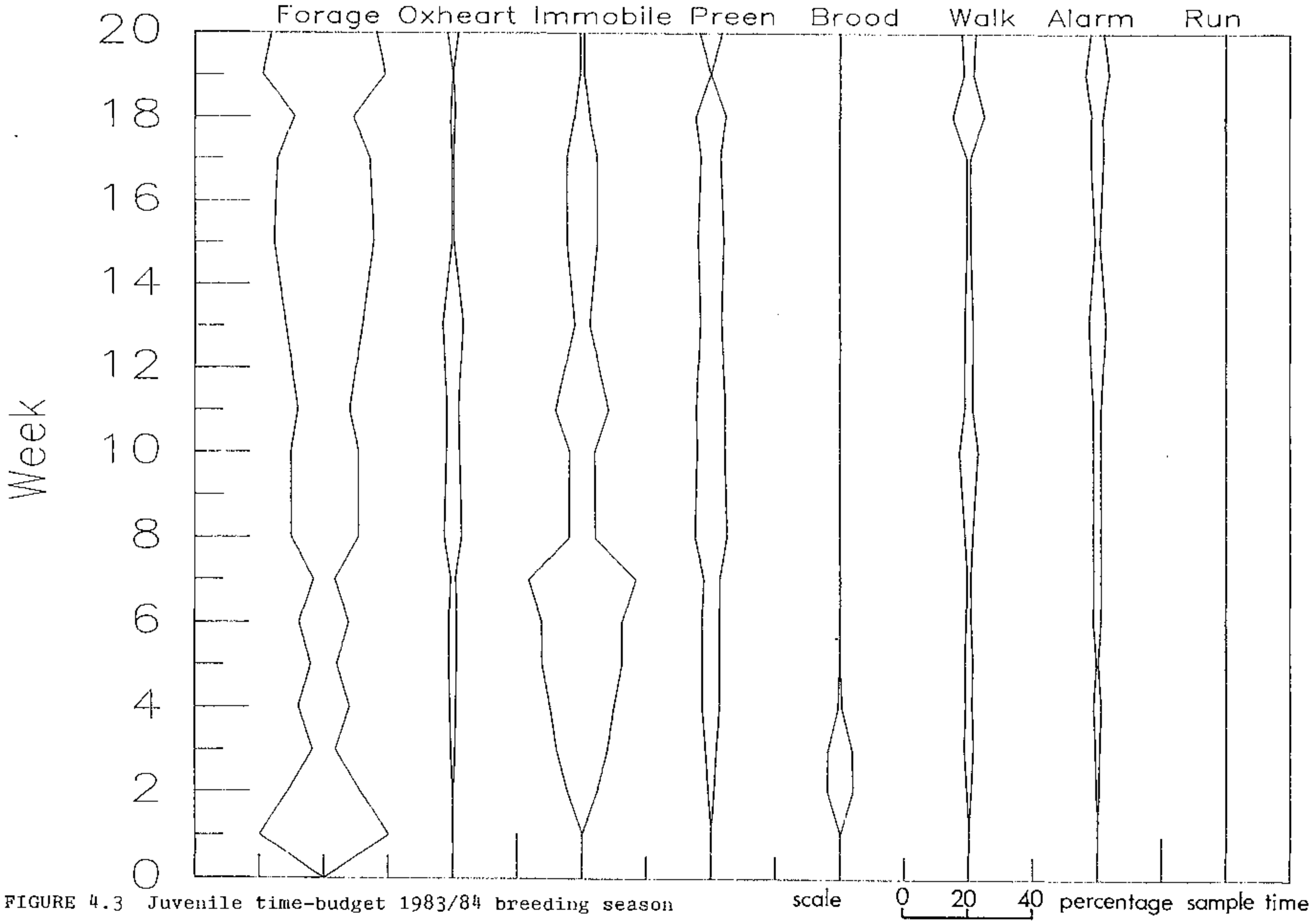


FIGURE 4.3 Juvenile time-budget 1983/84 breeding season

type of response were not mutually dependent in the population sampled the seven response types were grouped into two classes;

i) immobility (included all responses in which chicks attempted to remain or become motionless/inconspicuous);

ii) mobility (responses during which chick concealment and immobility was not obvious to me).

Predator type was also grouped into two classes;

i) aerial predators (harrier, magpie)   ii) humans

A three dimensional (2x2x2) contingency Table of the three variables; age of chick, response and type of predator is presented in Table 4.8 for the clumped data from Table 1 in Appendix 7. A test for mutual independence of these variables (Zar 1984) rejected the null hypothesis stated above ($p<0.001$). Three further hypotheses about the independence of variables;

i) that response was not dependent on age of chick,

ii) that response was not dependent on type of predator,

and iii) that predator type was not dependent on age of chick;

were all rejected at the $p<0.001$ significance level.

Comparative data from the wild population were collated from 19 responses of chicks to human intrusion and 2 responses to the presence of harriers. Sample size did not allow a statistical comparison of wild and captive chick antipredator responses, but the data are presented in Table 2 of Appendix 7 for general comparison with Table 1 of Appendix 7.

Three response types of wild chicks prior to fledging were identical to those observed in captivity (freeze, run and freeze, run). After fledging, one additional response of a wild chick was observed which was not seen in captive chicks (freeze then fly). The only other response of fledged wild chicks to humans was to stand alert/upright.

4.3.6 Intra-family aggression

A summary of aggressive interactions observed within the family group is presented in Table 4.9 for each of the three breeding seasons.

Discriminate aggression of the male towards specifically male juveniles

Table 4.8 Responses of two captive chick age classes to two predator types

	AGE 1		AGE 2		
TYPE OF PREDATOR	Aerial	Human	Aerial	Human	Total
RESPONSE					
Mobility	8(31)	60(90)	49(87)	27(100)	144(82)
Immobility	18(69)	7(10)	7(12)	0(0)	32(18)
Total	26	67	56	27	176

NOTE: Numbers in brackets denote the % occurrence of response type/predator type in the total number of observations

Table 4.9 Intra-family aggression

SEASON (period of chick rearing)	AGGRESSORS (adults)	RECIPIENT (chicks) i)BAND NO., ii)AGE, iii)SEX.	DATE AGGRESSION INITIATED.	FATE OF CHICK(S)	CLUTCH SIZE
1 (Jan.83- Aug 83)	male(predom) female *1	5110 20 days male?	12.3.83	removed	4
	male only	5111 84 days male	11.5.83	removed with other juveniles	3 (exclud. 5110)
2 (Nov 83- July 84)	male only *2	5114 67 days male?	14.1.84	removed with other juveniles	3
3 (Jan 85-)	female only *3	2632-red yellow 4 days sex unknown	6.1.85	still with adults	2

Note: see text for discussion of points *1 to *3 within the family party was observed during the first two breeding seasons. Aggression was severe enough only in the case of 5110 to warrant removal of the chick. Two further chicks aggressively pursued by the adult male (5114 and 5111), remained under parental care until break-up of the family unit.

The points indicated *1-*3 in Table 4.9 require further elaboration;

*1, *2 . Aggression was displayed by a sibling toward the harassed chick. On the 12 March 1983 and 2 July 1984, sibling aggression was observed only after parent birds had aggressively chased the recipient. Sibling aggression was terminated on its first appearance by removing the dominated individual from the aviary. On the second occasion, all aggression ceased after the removal of all juveniles from the parental aviary.

*3 The adult female was removed from the breeding enclosure (suffering a leg injury) when the chicks of the 1984/85 season were 2 days old. She was released again two days later on January 6, after bands causing the injury had been removed. Following release, the female approached and pecked each of the chicks. During aggressive approaches of the female toward the chicks, the male repeatedly interposed by running after and positioning himself between the female and their offspring. The frequency of aggressive attacks waned but did not completely cease over the weeks to fledging. The male took over all parental responsibilities until that time.

4.3.7 Parental care time budget analysis

Daily time budget data from the three parental care activities of the focal pair; i) brooding, ii) guarding of chicks and iii) aggression toward juveniles were tested by the ANOVA procedure (as in 2.3.2 and 3.3.4).

Brooding data were collected over stage three of the breeding cycle (parental care from hatching until fledging), as this was the only stage in which the activity occurred. Similarly, guarding of chicks occurred only during stage 3 of season one and stage 4 of season two. Aggression toward juveniles was observed during stages 3 and 4 of both seasons.

Three null hypotheses were tested;

i) "that the proportion of time spent in brooding was equal for both individuals, all time periods and between seasons";

ii) "that the proportion of time spent in guarding of chicks was equal for individuals, all time periods and between seasons"; and

iii) "that the proportion of time spent in aggression toward juveniles was equal for individuals, all time periods and over stages 3 and 4".

Tables 4.10, 4.11 and 4.12 indicate for which variable(s), the null hypotheses were rejected (denoted x) or accepted (denoted +) ($p = 0.05$). Results from each activity will be elaborated in sections 4.3.7.1 to 4.3.7.3.

4.3.7.1 Brooding

Overall data from combined time periods and seasons indicated a greater proportion of daily time was spent by the male in brooding than was spent by the female (Figure 4.4 a). This result was not statistically significant.

There was a significant interactive effect of individual and season, the male doing most of the brooding in season two and the female contributing more during season one (Figure 4.4 b). Male brooding activity bimodally peaked at periods 2-3 and again at period 6 (Figure 4.4 c). A single peak in female brooding activity occurred during period 1 (Figure 4.4 c). The interactive effect of individual activity with time period produced a similiar diurnal pattern in seasonal data (Figure 4.4 d). During season one when the female did most of the brooding this activity peaked at period one. During season two, the larger contribution of the male toward brooding produced the same bimodal peak at periods 3 and 6 as in Figure 4.4 c.

4.3.7.2 Guarding of chicks

The difference between individuals in the total proportion of time spent "guarding" chicks (combined seasons and time periods) was not significant (Figure 4.5 a). The male devoted only slightly more time to this activity than did the female.

Seasonal differences were significant, since guarding of chicks was only infrequently observed during season one (0.3% total observation time) but constituted 3.7% of observation time in the second season (Figure 4.5 b)

The difference diurnally between individuals was not significant but each data set indicated a significant bimodal peak at periods 2 and 6 (Figure 4.5 c). The same peak at periods 2 and 6 occurred in combined individual and time period data (Figure 4.5 d) for season one. A smaller peak at periods 5-6 occurred during the second season (reflecting the decreased frequency of chick guarding during that season).

4.3.7.3 Aggression toward juveniles

The mean percentage of observation time spent by the parent birds in aggressive approaches toward their own progeny (section 4.3.6) is presented for individual, seasonal, stage of the season and diurnal data (Figure 4.6 a-g).

Values obtained from combining data from the two seasons indicated that the male spent significantly more time than the female in aggressive activity (Figure 4.6 a), especially during stage four of the breeding cycle (Figure 4.6 c). There was a significant effect of individual on the observed frequency of this behavioural pattern during the two stages, with the male being the predominant aggressor during stage 4. Conversely, the female spent a greater proportion of time in this activity than did the male during stage 3 (Figure 4.6 c).

The proportion of time spent by either individual in this activity was greatest during the first season (4.3% of total observation time c.f. 0.26% in season two).

Diurnally, aggressive activity peaked at periods 2 and 5 in stage 3 (Figure 4.6 e) and in periods 3-4 of stage 4 (combined seasons data). These peaks directly corresponded to individual peaks in diurnal activity, the male at period three and the female at period two (Figure 4.6 f). From combined individual and stage data, a single diurnal peak in this activity occurred at period two (mid-morning).

Table 4.10 Summary of ANOVA tests for brooding (both seasons)

Time	x
Individual	+
Time*Indiv	x
Season	+
Time*Season	+
Indiv*Season	x

Table 4.11 Summary of ANOVA tests for guarding of chicks (both seasons)

Time	x
Individual	x
Time*Indiv	+
Season	x
Time*Season	x

Table 4.12 Summary of ANOVA tests for aggression toward juveniles

SEASON	1982/83	1983/84
Time	x	+
Individual	x	x
Time*Indiv	+	+
Stage	+	x
Time*Stage	+	+
Indiv*Stage	x	x

KEY: x = reject the null hypothesis,
+ = accept the null hypothesis
at the 0.05% significance level.

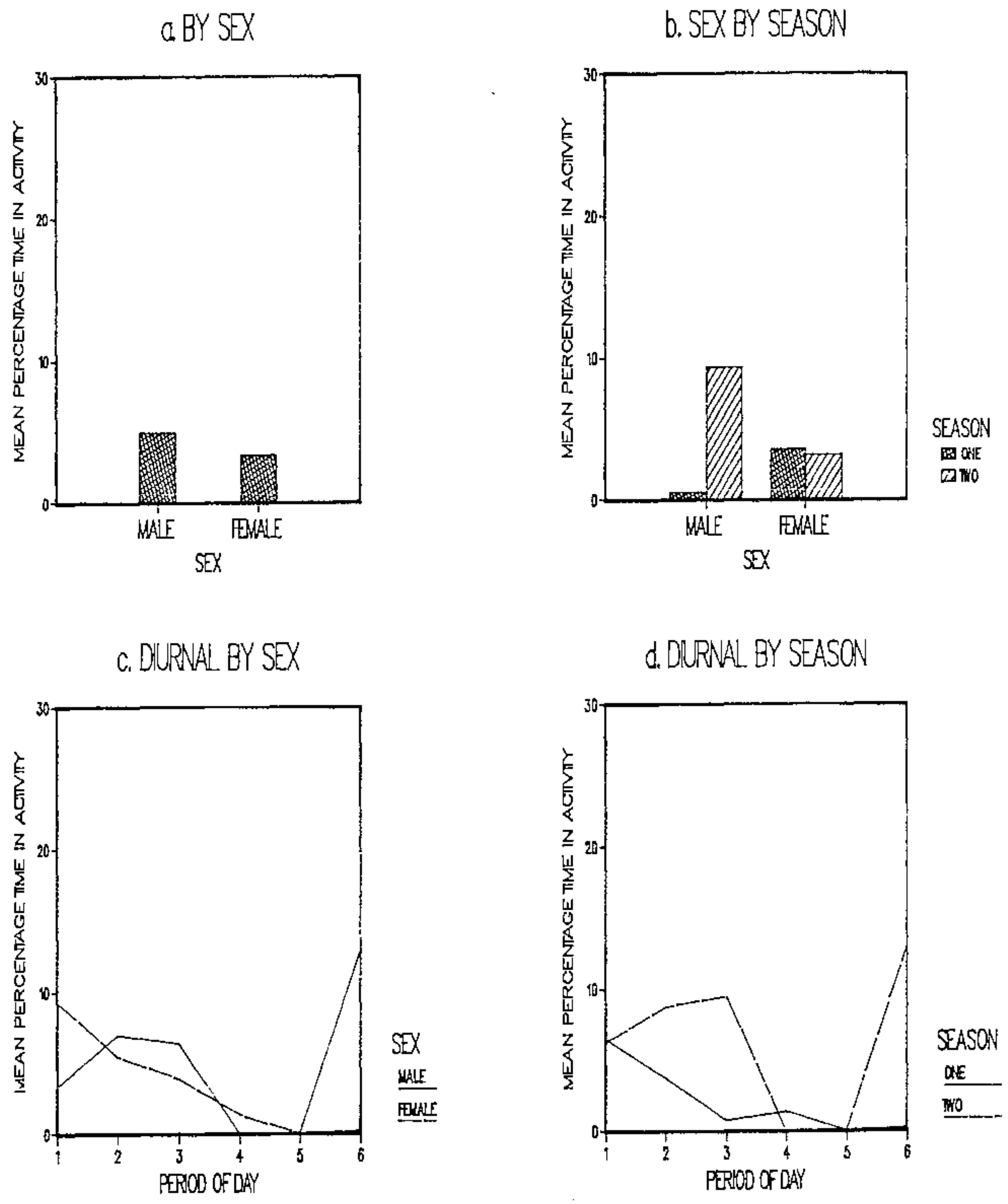


FIGURE 4.4 Adult 'brooding' time-budget (stage 3)
(by individual, season, and time period)

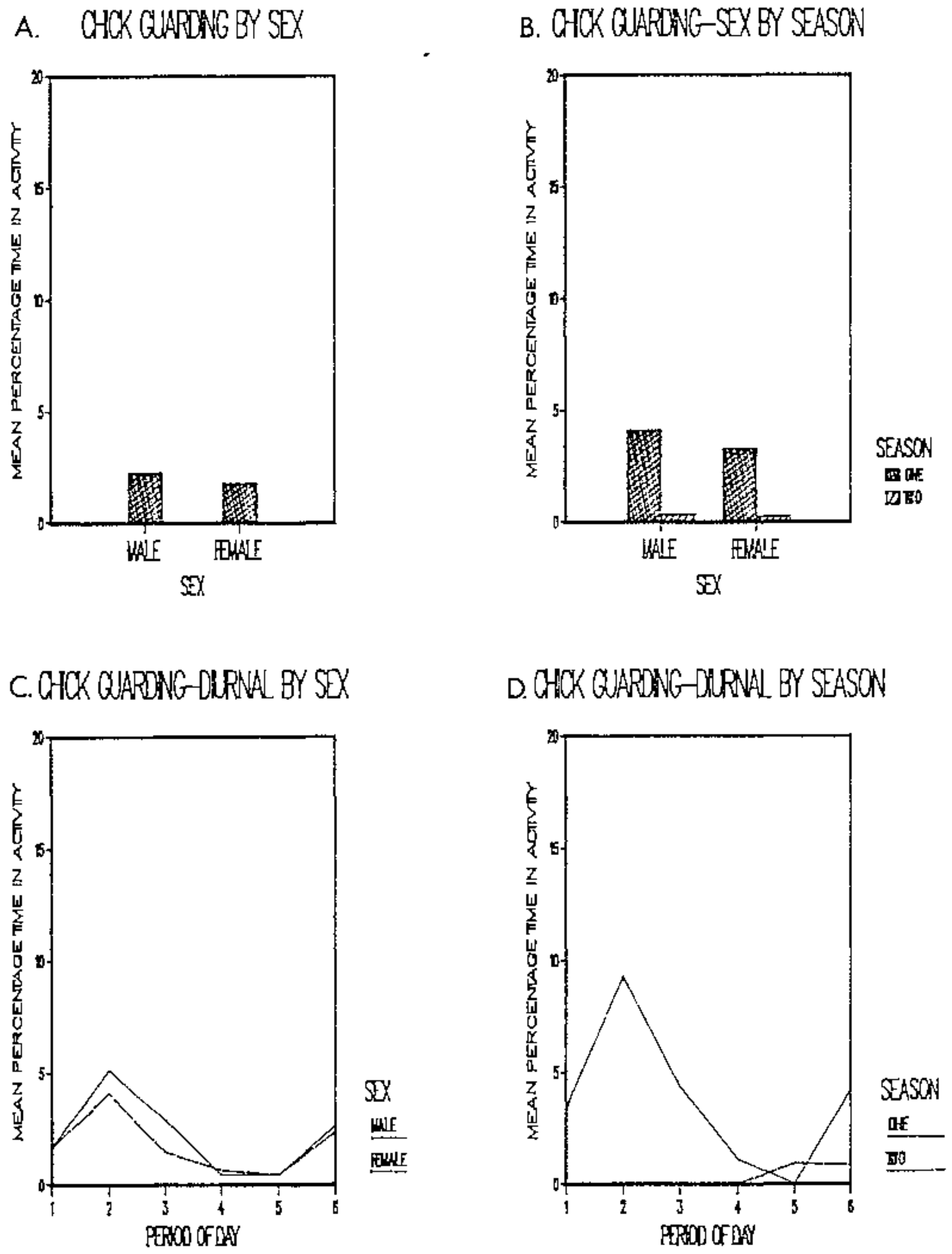


FIGURE 4.5 Adult 'guarding of chicks' time-budget (stage 3 - 1982/83 season, stage 4 - 1983/84 season)

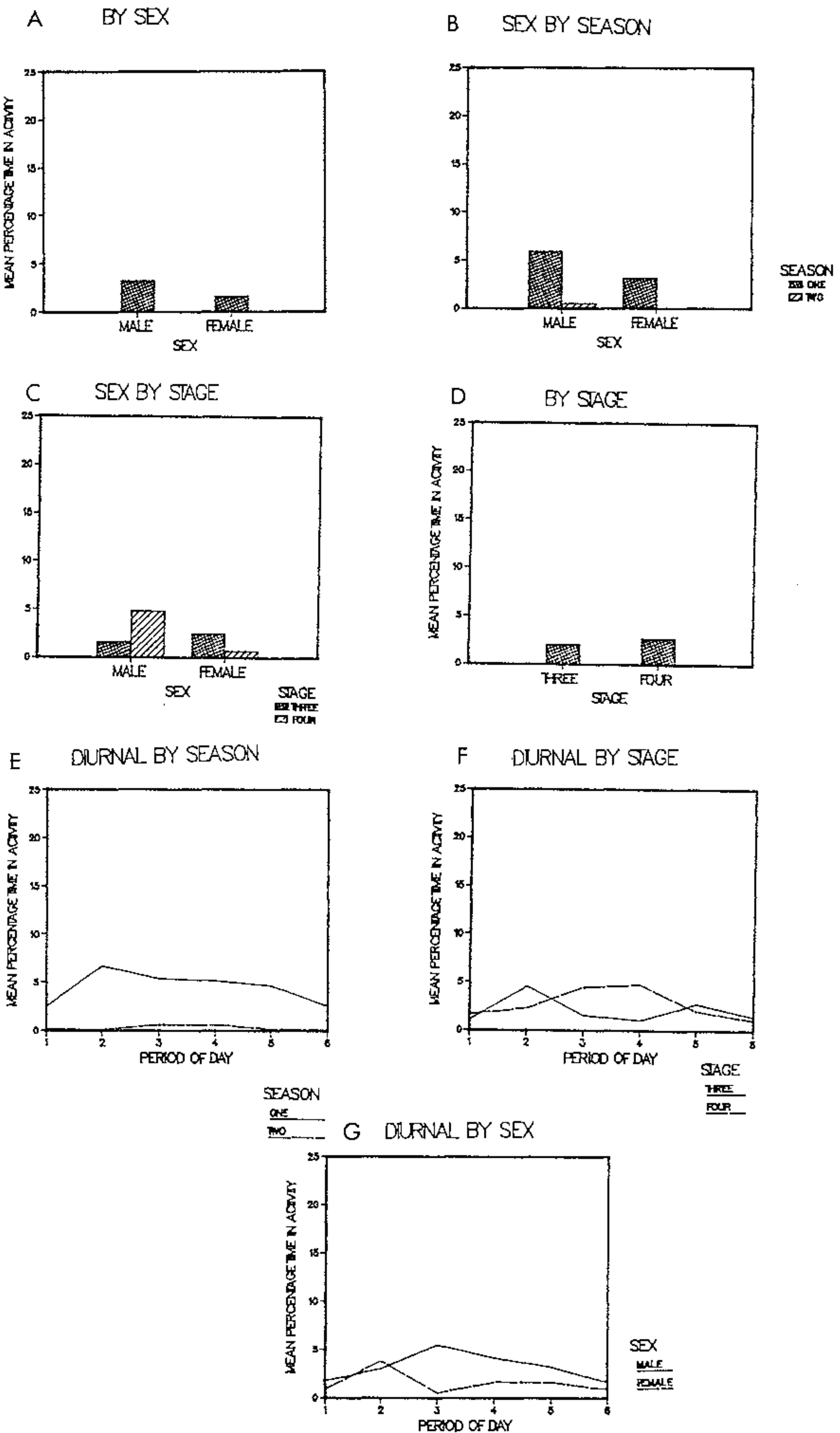


FIGURE 4.6 Adult 'aggression toward juveniles' time-budget

4.3.8 Family party break-up

The pattern of family break-up was similiar following the first and second breeding seasons. Intense aggression by the parent birds (predominantly the male) toward the respective seasons' progeny was apparent on the dates indicated in Table 4.13.

Bouts of male aggression were sporadic, with intervening periods of juvenile tolerance. On the 17 August 1983, aggressive approaches were made by the male toward three juveniles at the rate of 23/hour (observation time = 4.95 hours). All juveniles were removed from the parental aviary following these intense attacks. Adult nest-building activity increased upon removal of the juveniles.

Table 4.13 Timing of family breakup

Season	1	2
Date	17.8.83	2.7.84
Age of chicks	6 months	6 months

4.4 Discussion

4.4.1 Parental behaviour

The focal pair displayed several antipredator behavioural patterns during egg-laying, incubation and early chick-rearing which have been previously described for other recurvirostrid species. They included i) removal of egg-shell immediately after hatching of chicks; ii) distraction displays during incubation and chick-rearing; and iii) aggressive approaches toward intruders and overhead predators.

Egg-shell removal has been described not only for most recurvirostrid species (Makkink 1936, Gibson 1971, McConkey 1971, Sordahl 1980), but also for a wide range of avian species of many different families (Nethersole-Thompson and Nethersole-Thompson 1942). Some birds eat the egg-shells, others remove or trample fragments down or incorporate them into the nest. Attempts to experimentally elicit this behavioural pattern have included Tinbergen's authoritative study on egg-shell removal of black-headed gulls (Larus ridibundus L.) and Sordahl's (1980) experiments with black-necked stilts and American avocets. American avocets removed egg-shells placed in the nest before resuming incubation, as did the focal male of this study. Makkink (1936) has observed European avocets to pick up egg-shells perceived at some distance from the nest, even after the chicks had already left the nest area. The focal male removed only the shell placed within the nest and not those 15 cm and 50 cm away. Removal of egg-shell during this experiment was elicited 26-28 days before its normal occurrence (i.e., at hatching). Sordahl found that removal occurred throughout the incubation period of American avocets and black-necked stilts.

Removal of egg-shells may function in;

i) avoiding detection of the nest by predators. Egg-shells are usually white on the inside and hence conspicuous to visually hunting predators, leading them directly to a nest of newly hatched and unhatched young. Similiarly, damaged eggs may be a liability to the rest of a clutch and to parent birds, by attracting sight- or scent-oriented predators;

ii) later-hatching eggs may become encapsulated and trap hatching young;

iii) the edges of egg-shells may injure chicks; and

iv) organic material associated with egg-shells might lead to mould and bacteria in the nest (Sordahl 1980).

All four of these factors may have contributed to the evolution of removal behaviour by stilts and avocets (Sordahl 1980). Tinbergen showed that egg-shell-removal by gulls functioned in predator avoidance, as did Sordahl for black-necked stilts and the American avocet.

The two focal individuals possessed a second antipredator adaptation also observed in the wild, i.e., "broken-wing" display. This behaviour pattern was analogous to the "lure display" of pied stilts (McConkey 1971), "tight-rope display" of American avocets and black-necked stilts (Hamilton 1975), "distraction display" of wild black stilts (Pierce 1982), "injury-feigning" of European avocets (Makkink 1936) and "wing-displays" of American avocets and black-necked stilts (Sordahl 1980). Distraction displays comprise forms of conspicuous behaviour which have evolved to deflect potential predators from eggs or young, by presenting to these predators stimuli releasing and directing their hunting behaviour (Simmons 1955).

Thirdly, dive-swooping as displayed by the study birds, was analogous to "dive-bombing" of American avocets and black-necked stilts (Hamilton 1975, Sordahl 1980) and aggressive flight of pied stilts (McConkey 1971). Dive-bombing probably functions to intimidate a ground predator (Hamilton 1975) by passing closely above it.

Responses by the focal pair to aerial (harriers, magpies) and terrestrial (man, dogs) predators differed. The tilt head and alarm call was the most common reaction toward aerial predators during breeding stages 2 and 3. Grounded magpies and terrestrial "predators" outside the aviary (eg., man), elicited an excited running and calling activity. The focal pair responded to the presence of humans within their aviary with broken-wing displays and dive-swooping during these stages of the season. Sordahl (1980) also found that black-necked stilts and American avocets responded differently to aerial and terrestrial predators. The general response of both species to terrestrial predators was weak. The response to aerial predators involved mainly dive-bombing and chasing. Further discrimination not only within predator classes (i.e., terrestrial versus aerial), but also between predator species within each class, was demonstrated by Sordahl through presentation of four different avian predator models. McConkey (1971) found reactions of pied stilts to harriers was stronger than their reaction toward black-backed gulls. Responses of captive black stilts to harriers was much more intense than that to either magpies or non-predatory aerial species eg., white-faced heron. Antipredator responses of recurvirostrids have been shown to vary not only with proximity and type of predator, but also with stage of the reproductive cycle (Sordahl 1980, Pierce 1982). These two factors are not independent of one another as responses to potential predators have been found to peak at different stages of the breeding cycle of magpies Pica pica (Buitron 1983). Predators of eggs and nestlings for example, were attacked most intensely during incubation and early chick-rearing. Captive stilts occasionally flew aggressively toward magpies but never toward harriers, although this was the commonest reaction of wild stilts toward overhead harriers during the breeding season.

Aggression of the parent birds directed at one or more of their progeny occurred four times during the study. Makkink (1936), Gibson (1971), Hamilton (1975) and Sordahl (1980) have all reported aggression by avocets and stilts toward unrelated chicks. Explanations suggested for this pattern of behaviour in recurvirostrids include;

i) several parents vying for the same brood (Hamilton 1975);
ii) parents driving unrelated chicks away from their brood (Sordahl 1980);
iii) redirection of aggression that has arisen in another context (Makkink 1936);
iv) discipline by parents of young that respond too slowly in a dangerous situation, eg., presence of a predator (Makkink 1936);
v) adults attack and drive away unrelated chicks of any age because they attract predators that may prey on adults (Sordahl 1980); or
vi) unrelated chicks are driven away as a result of competition for resources (Sordahl 1980).

None of the above suggested explanations for aggression toward chicks appears to be appropriate to the contexts in which intra-family aggression in captivity was observed. Parent birds (particularly the male) drove away their own chicks, so explanations i), ii), v) and vi) were not applicable. Aggression toward juveniles was never seen in the context of adult interaction with neighbours (since all had been removed) nor was it observed following the intrusion of predators above or near the aviary. Two further explanations for the occurrence of this pattern of behaviour may be i) the inability of adults to recognise their own chicks and ii) discriminate aggression toward male juveniles which causes their early dispersal from natal areas. The first hypothesis is supported by observed aggression by the breeding female toward her own offspring, after a period of isolation from them. Herring gulls Larus argentatus do not recognise their own young until they are 35 days old (Holley 1984). They could only distinguish a strange chick if it showed inappropriate behaviour i.e., ran away. Intermingling of recurvirostrid broods have been reported by Makkink (1936) and Hamilton (1975). Makkink recorded one avocet taking care of five young without any hostility. Similiarly, Hamilton observed mixed broods of American avocets so often that he concluded it was "common and resulted from a lack of territorial behaviour and the inability of parents to recognise their own young". Gibson (1971) did not observe any mixed broods of American avocets and concluded that that would require intrusion of territorial boundaries. Chicks were attacked by other avocets if separated from their parents. It appeared that stilts may recognise their own chicks but if separated from them early in the chick-rearing period, this recognition may not develop or could be lost. Intra-family aggression directed by parent birds onto progeny by wild black stilts, acts as a mechanism for juvenile dispersal toward the break-up of the family unit in spring (Pierce, pers.comm.). This was also observed in captivity (August 1983 and July 1984). The reason for male parent aggression toward predominately male chicks is not clear. This pattern has not been described by other authors studying recurvirostrid behaviour.

4.4.2 Juvenile growth and ontogeny

The five black stilts chicks reared in captivity grew faster and fledged earlier (mean = 35.5 days, n = 5) than wild black stilts of the same age. Their growth rate was comparable to that of pied stilts which fledge at 34 days (range = 30-37, n = 17) (Pierce 1982). Black chicks in the wild fledged at 47 days (range = 41-55, n = 12). Growth of these chicks was seasonally variable however, with 1984/85 reared chicks fledging at only 41 days (range = 39-44). Faster growth and earlier fledging probably resulted from an abundance of invertebrates and the opportunity for chicks to forage longer during the mild weather of this season (Pierce pers. comm.). Wild black chicks took 5 weeks to reach 100 g weight and 100 mm wing length (Pierce 1982) whereas captive chicks had reached these growth parameters at 3.5 to 4 weeks of age. The faster growth rate of captive compared to wild chicks may be attributed to a constant unlimited food supply, milder night temperatures and to reduced movement and energy expenditure. Locomotory activity in response to harassment by i) intraspecifics ii) individuals of other species and iii) predators, was reduced in captivity. In comparison to the wide-ranging foraging behaviour of wild chicks (Pierce 1982), captive individuals could not move far in search of food. Food was easier to obtain under captive conditions however.

Growth rate affected the ontogeny of behavioural patterns (eg., preening, flight). Development of behavioural patterns under captive conditions may have been faster than that of wild chicks. Age of first occurrence of some infrequently observed behavioural patterns may have been underestimated. Young captive chicks left the nest within 1-2 days of hatching and foraged independently of parent birds. Parental feeding of chicks has not been observed in any of the recurvirostrid species (McConkey 1971, Hamilton 1975, Sordahl 1980, Pierce 1982) except three hybrid Himantopus melanurus x Himantopus mexicanus chicks reared by their parents at San Diego Zoo (Lint 1959). For the first 5-6 days, these chicks did not pick up any food from the ground or out of containers, but would only take insects from the parent's bill. They began to feed on their own at 10 days of age. Captive black stilts did not take supplementary food until they were between 6 and 12 days old, but these chicks had access to invertebrates within the aviary stream. Newly hatched chicks (1-5 days) made fewer peck movements, and the successful rate of capture was also lower during this period, indicating increasing foraging success with age and/or experience. Learning experience associated with foraging behaviour may continue up until the first winter of wild-reared black stilt chicks (Pierce 1982), when juvenile foraging success more closely resembles that of adults. Studies of herring gulls Larus argentatus (Greig et. al., 1983), little blue herons Florida caerulea (Recher and Recher 1969), ruddy turnstones Arenaria interpres (Groves 1978) and black-winged stilts (Espin et. al., 1983) have revealed lower successful rates of prey capture and/or slower peck rates of juvenile compared to adult birds. My study indicates that chick ability to locate and consume prey increased primarily over the first week of life. Search rate (eg., time taken to walk 10 paces), handling time (Goss-Custard and Rothery 1976) and the size and number of prey taken per peck were not measured. Therefore changes in actual food intake per unit time with age of chick were not discernable.

Young chicks of all the Recurvirostridae species crouch or hide motionless when danger threatens (Makkink 1936, McConkey 1971, Hamilton 1975, Pierce 1982, Sordahl 1980,82). They rely on the aggressive and diversionary behaviour of their parents to drive away predators. Responses of captive chicks toward predators varied according to i) age of chick, ii) distance of the predator from the aviary (which in turn affected intensity of response of the parent birds), iii) the ongoing activity of the chicks and iv) the type of predator. Age has been shown to affect the responses of American avocet and black-necked stilt chicks, who began to run rather than freeze at 2 weeks of age. Increasing strength and speed improved chances of chick escape, while increased size lowered chances of successful hiding (Sordahl 1982). Similiarly, captive black stilt chicks less than 13 days old "froze" when humans entered their aviary. From this time onward though, they remained in the open, moving toward the aviary stream while the parents gave alarm calls. Immobility of chicks in response to aerial predators continued up until 40 days of age. Age-related changes in the responses of captive chicks to both humans and aerial predators may have been ontogenetic or due to habituation.

Harriers flying closest to the breeding aviary elicited the strongest response from both the parent birds and chicks. Klump and Curio (1983) also found blue tits *Parus caeruleus* responded more intensely to life size models of sparrowhawks *Accipiter nisus* passing low over their cage, than to smaller models mimicking a hawk at greater height. Wild black stilt chicks also responded differently to my presence as a function of distance. If surprised by my approach from within 20-30 m, these chicks fled. If an approach was made from a greater distance (eg., 300-400 m), alarm calls were given and the chicks were immobile and hidden before I reached them.

The type of activity in which captive chicks were engaged prior to alarm calls being given also affected their behaviour. Sitting chicks generally remained sitting when aerial predators were sighted, or they ran and "froze" if previously engaged in locomotory activity. Humans evoked the opposite response, as sitting chicks (less than 2 week old) moved out into the open. Sordahl (1980) described stilt chicks swimming away from shore to avoid him, a response which would deter scent-oriented predators. This effect of current activity on response to predators has also been demonstrated in two species of voles, *Microtus agrestis* and *Clethrionomys britannicus* (Fentress 1968). Animals locomoting at the time of stimulus presentation were more likely to flee than animals engaged in other activities.

CHAPTER FIVE

VOCAL BEHAVIOUR

5.1 Introduction

Behavioural interactions within members of this species involve not only visual displays as already described in Chapters Two to Four, but also vocal modes of communication.

The first aim of this chapter is to describe and classify sounds emitted by captive adult and juvenile stilts into broad categories, indicating the context(s) in which each call type is heard.

Vocal communications of other bird species have usually been studied under one of three groups. That is, as a) song; b) calls or cries; or c) noises (Bremond 1963).

The distinction between bird song and calls is not clearcut in many species. The most useful working definition of song is "a vocalisation or set of vocalisations that is repeated in more or less continuous, regular patterns, often in sustained bouts" (John-Smith 1977). Calls on the other hand are "in most cases, mono- or disyllabic sounds which do not contain more than four or five notes. They are not organised into sequences or phrases of different length ... and are generally produced in a variety of situations..." (Bremond 1963).

Vocal and non-vocal sounds of shorebirds range from soft, short-range calls to loud nuptial aerial song that carries for miles (Miller 1984), however no song repertoires have been reported for any species of shorebird. Brief sounds or calls are generally a more common means of communication between members of this group (Miller 1984).

Classification of sound signals usually occurs within a structural and functional framework (Miller 1984). But these two factors do not necessarily correspond. For example, shorebird calls are not generally context-specific (Miller 1984), as a particular call may correspond to different behavioural elements and several calls to the same situation. Or a multitude of calls may appear in only one context.

Because of the complexities of inter-relating structure, context and function of calls, I have broadly classified vocalisations of captive stilts according to structure only. I have subsequently incorporated information on those contexts in which they were heard.

Bird sounds are commonly classified after inspection of sonagrams. On the basis of several measurements (eg., frequency of fundamental or duration of call), classes can be characterised quantitatively. I used this approach in classifying calls, after an initial subjective auditory discrimination of general sound types. One danger in classifying sonagrams subjectively is that we may subdivide a sample of calls whose acoustic morphology varies continuously. Most communication systems probably lie between those with discrete categories of signals and those with continuous variation (Miller 1979).

Extensive structural intergradation of sounds is refered to as "grading". If classification is difficult because of the presence of numerous sounds of intermediate form, the system is considered to be graded. Grading within and between sound classes was reported by Adret (1982) for adult avocets, vocalising during the hatching phase of the breeding cycle. He found some calls to progress structurally into others. Grading of calls is a feature not unique to avocets. Oring (1968) also indicated a structural gradient in calls of solitary and green sandpipers. Similiarly, Sordahl (1980) reported a graded vocal system for American avocets and black-necked stilts.

The second aim of this chapter then, is to illustrate the structural variation within and between captive black stilt call types.

Acoustic morphology varies amoung and within sound classes because of numerous proximate causes (i.e., anatomical, neural, endocrinological etc.) and correlates (eg., age, gender, individual, etc.,) (Miller 1984). The third aim of this chapter is to examine one of these correlates (i.e., variation within and between individuals), for a single call type.

Interspecific variation within this call type between the two closely related stilt species is also investigated. Pied and black stilts exhibit a combination of specific and sub-specific characters which places them as a subspecies by some authors (Pierce 1982). Isolating mechanisms between the two species include different plumage, length of appendages and selective mating (Pierce 1982). Hybrids of the two species tend to be intermediate in their plumage between that of parent birds (Pierce 1984b). Darker hybrids also demonstrate foraging patterns that are similiar to that of black stilts (Pierce 1982).

Vocalisations of pied, black and hybrid stilts could perhaps also be used as a diagnostic feature for the two species and their hybrids. This possibility is investigated and discussed.

5.2 Methods

Vocalisations of seven adult and seven sub-adult captive black stilts, were recorded and analysed using the equipment described in section 1.3.4. Calls not specifically associated with breeding were sampled ad. libitum (Altmann 1974) from each stilt. Breeding calls were recorded primarily from the focal pair and supplemented with recordings from two other pairs. Recordings were taken randomly with respect to time of day and month, from October 1982 until March 1985.

Alarm calls of wild black, pied and hybrid stilts were recorded during two visits to the MacKenzie Basin, South Canterbury i) 31 October-19 November 1983 and ii) 3-13 December 1984. I approached nesting territories of breeding pairs and recorded stilts as they flew around or toward me. Where possible, both individuals of a pair were recorded seperately and together on the same and consecutive tape tracks. I noted the plumage node (Figure 5.1) of each stilt being recorded. Supplementary pied and black stilt alarm call recordings were made available for sonagraph analysis by the Information Section, N.Z. Wildlife Service.

In an analysis of individual and inter-specific variation in alarm calls, fifteen "yap" calls were randomly selected from each of 47 stilts sampled (43 wild, 4 captive). Eight variables were measured for each call, to the nearest 0.5 mm (Figure 5.2). These were;

A) call duration;
B) fundamental frequency at initiation,
C) fundamental frequency at mid-point, and
D) fundamental frequency at completion of call;

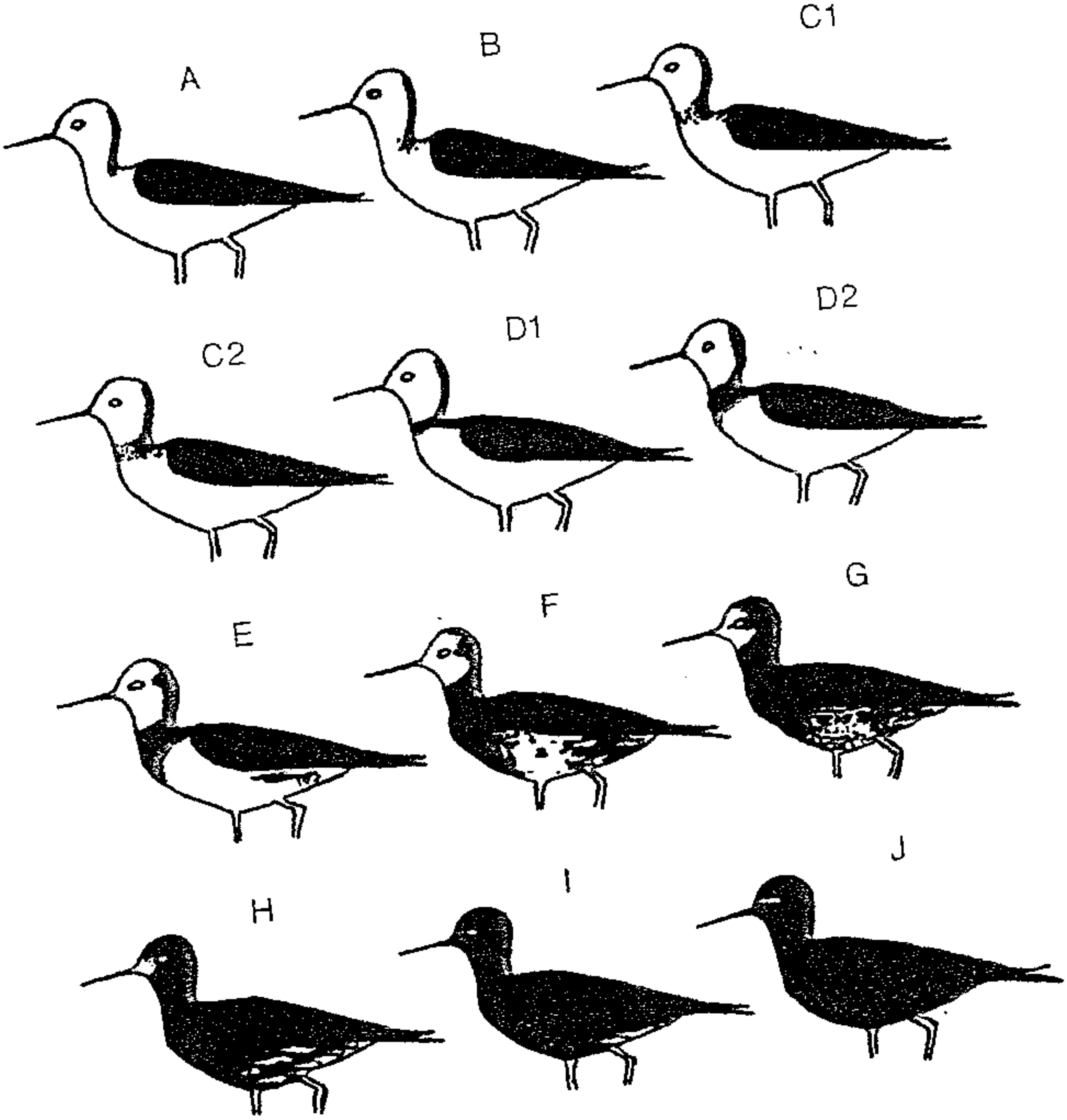


FIGURE 5.1 Plumage nodes of stilts (from Pierce 1982)

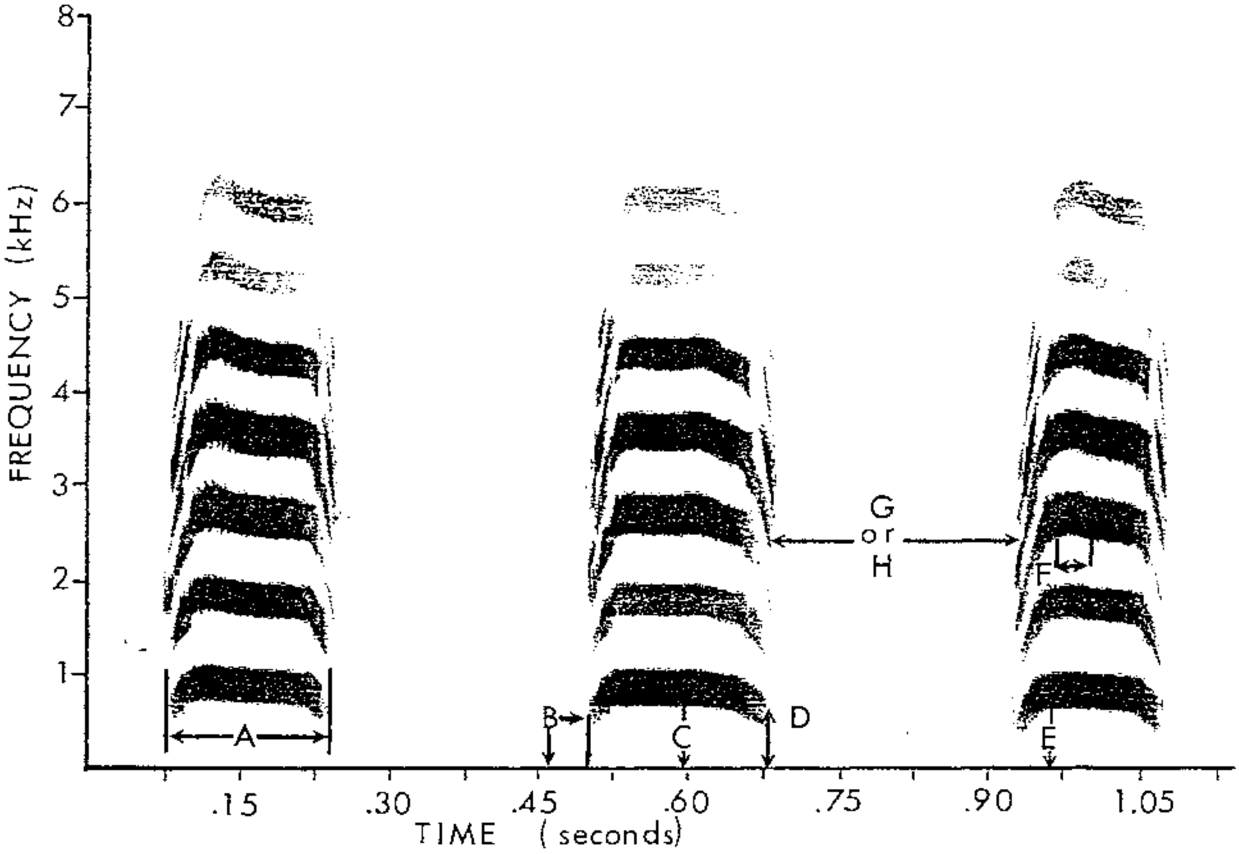


FIGURE 5.2 Variables measured from alarm calls

E) highest frequency of the fundamental;
F) point (in mm) to the left (-ve) or right (+ve) of mid-call, at which peak fundamental frequency was reached;
G) period between previous call completion and initiation of sample call; and
H) period between completion of sample call and initiation of next call.

Three further variables were extrapolated from these measurements. They were the differences in frequency between;

I) mid-point and completion of a call (i.e., C - D);
J) completion and initiation of call (i.e., D - B); and
K) mid-point and initiation of call (i.e., C - B).

Further variables used to describe calls of captive stilts, are defined and elaborated in section 5.3.1.

5.3 Results

5.3.1 Description of the Vocal Repertoire

5.3.1.1. "Tw-ink" call

STRUCTURE: The "tw-ink" call was a variable call, consisting of one or two notes. Five measurements were made from each of 17 calls of this type. These were;

i) duration of the complete call (variable A, above);
ii) fundamental frequency of the first note (variable L);
iii) fundamental frequency of the second note (variable M);
iv) duration of the first note (variable N); and
v) duration of the second note (variable O) (Figure 5.3).

These calls were sampled from the breeding male (7), breeding female (7) and another probable male (3).

Mean values are presented in Table 5.1 from combined individual data.

Table 5.1 Structure of the tw-ink call

3 individuals (combined mean, n = 17)

VARIABLE	UNITS	MEAN(±1 s.d)	RANGE
A	(msec)	44.4 ± 15.3	15.1 - 60.4
L	(Hz)	2877.9 ± 371.8	2618.0 - 3696.0
M	(Hz)	892.7 ± 89.1	693.0 - 1001.0
N	(msec)	22.9 ± 7.6	0.0 - 30.2
O	(msec)	26.4 ± 6.1	15.1 - 37.7

The first part of this call had a higher mean fundamental frequency, (i.e., L>M) and was of shorter duration than the second part of the call (i.e.,O>N). The former was more variable in length, being very short or absent during four of the 17 calls sampled (Figure 5.3).

CONTEXT: The "tw-ink" call was emitted by a bathing stilt as the bill was raised above water after head dipping (section 2.3.1.1e). It was repeated approximately 2-7 times, each time after a successive head dip. Calls primarily occurred early in the bathing sequence, decreasing in frequency and finally ceasing as bathing continued.

5.3.1.2. "Tip" call

STRUCTURE: Three individuals were recorded emitting this call;

i) 2609 (female, n = 13 calls)
ii) 5108 (unknown sex, n = 9) and
iii) 2607 (female, n = 4).

Measurements of two variables (A and C) from tip calls of these birds are presented in Appendix 8 for each individual . Data from Appendix 8 were combined and are presented in Table 5.2.

Tip calls were characterised by a low mean frequency of 554.7 Hz (n = 3 individuals) and a large number of harmonics (maximum = 15) up to 7700+ Hz in range (Figure 5.4). Some of these top harmonics may have been an artifact of recording levels however.

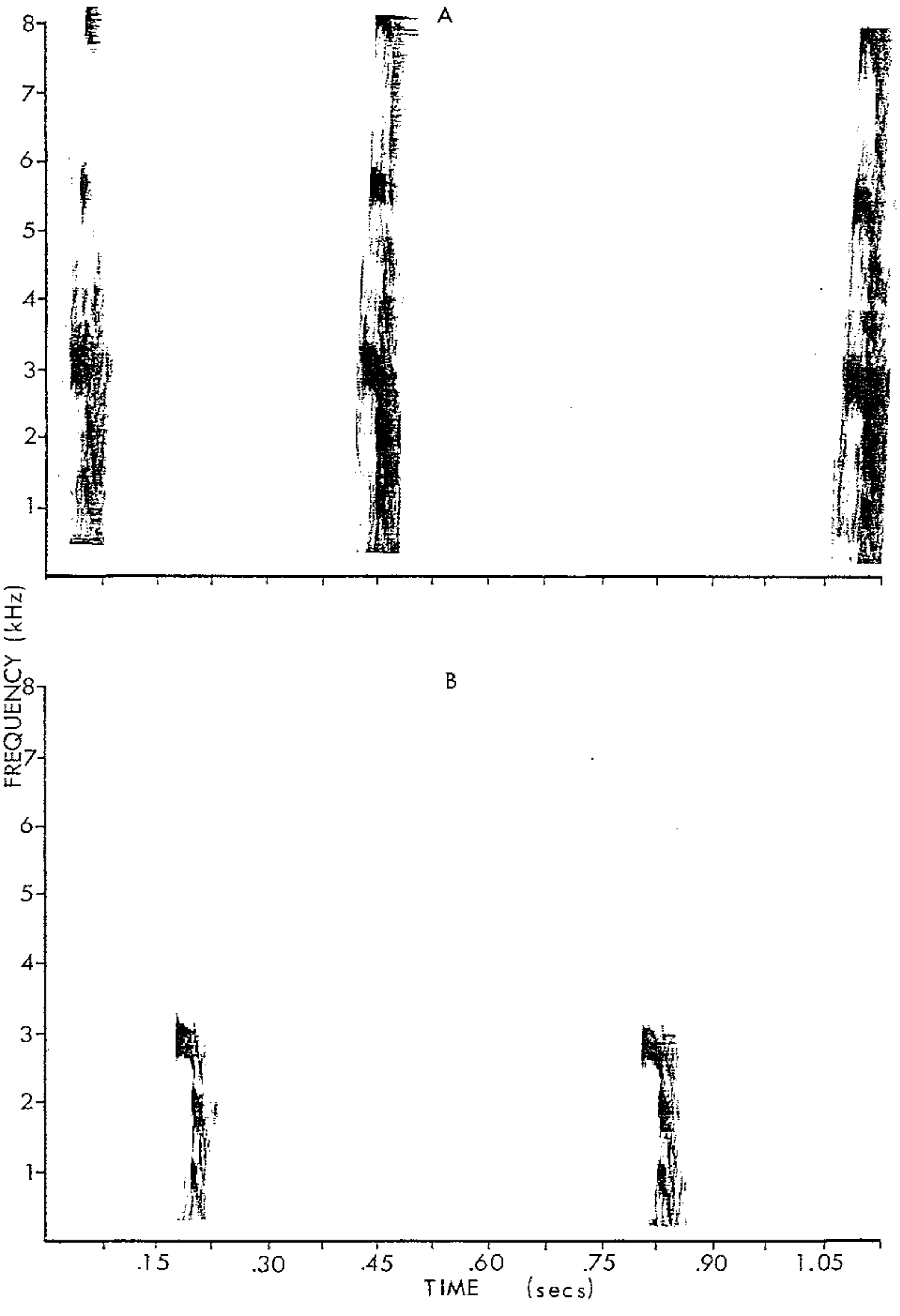


FIGURE 5.3 Adult tw-ink call

a. Parts one and two (captive breeding male)

b. Part two only (captive breeding female)

These calls were moderately loud and were of short duration (Table 5.2). The fundamental and/or fourth harmonics were emphasized.

Table 5.2 Structure of the tip call

All three individuals combined (n = 27 calls)

VARIABLE	UNITS	MEAN (±1 S.D)	RANGE
A	(msec)	523.5 ± 110.7	388.8 - 822.9
C	(Hz)	554.7 ± 80.0	462.0 - 731.5

CONTEXT: The "tip" call was heard only as a captive stilt stood an alert "forward posture" (section 2.3.1.2) over a nest-site or near neighbouring birds.

5.3.1.3. "Ruh" call

STRUCTURE: Four individuals were heard emitting the "ruh" call, the two stilts of the breeding pair and individuals 5108 and 5109 (a non-breeding pair). Recordings were taken only from the non-breeding pair. Table 5.3 presents the mean values of eight variables measured off 19 calls of one of these birds.

"Ruh" calls had a low fundamental frequency, 269-1080 Hz in range. This soft, moderately long call was repeated at a rate of approximately 2 per sec and had a mean duration of 200 msec. The fundamental, second and third harmonics were accentuated.

Within this class of call, two types were recognised;

i) type 1 (Figure 5.5a) which gradually ascended from approximately 330 Hz in frequency to peak at around 680 Hz near completion of the call;

ii) type 2 (Figure 5.5b) which was characterised by a more abrupt frequency change in mid-call, with a much higher fundamental frequency over the latter part of the call.

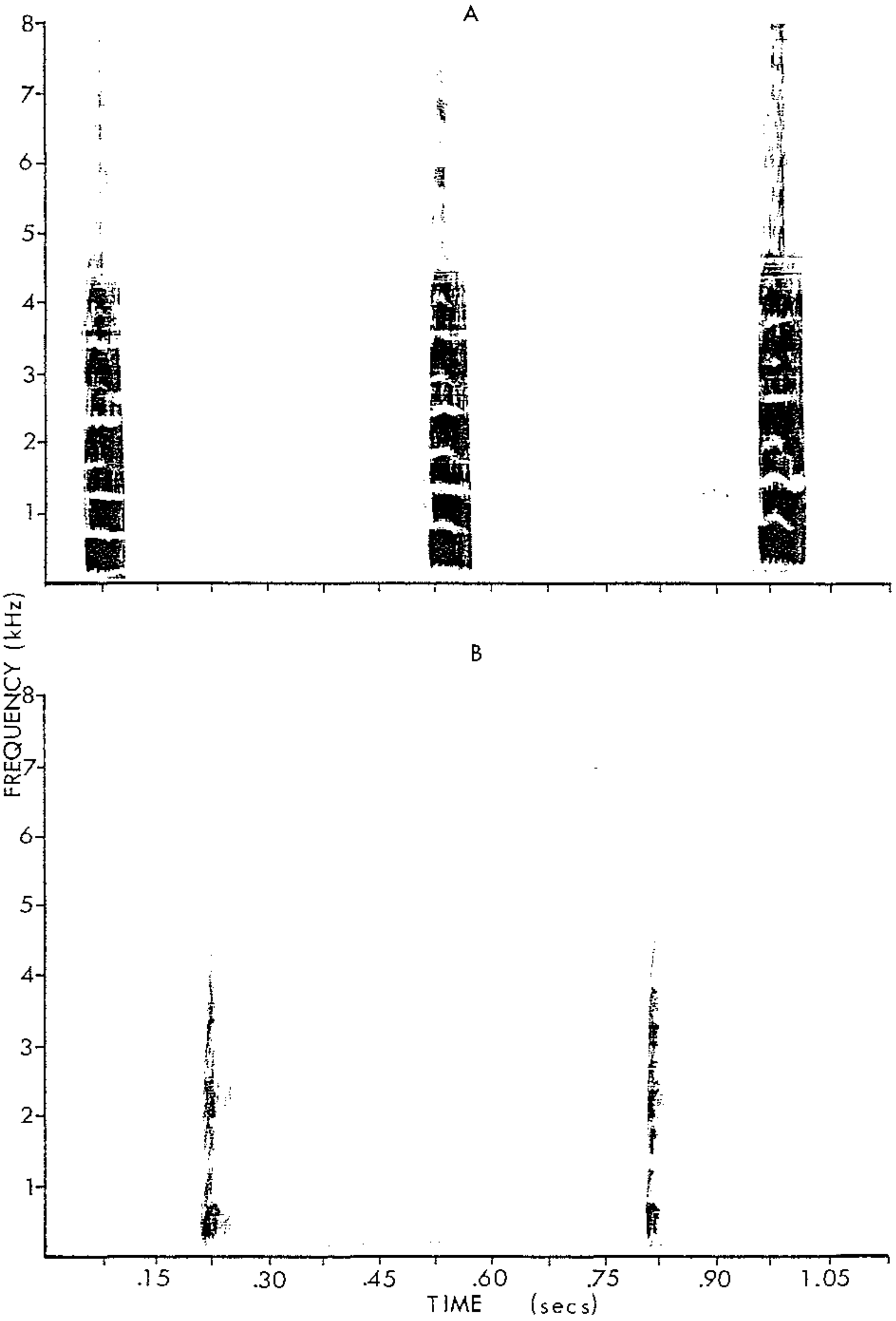


FIGURE 5.4 Adult tip call

a. Captive individual one

b. Captive individual two

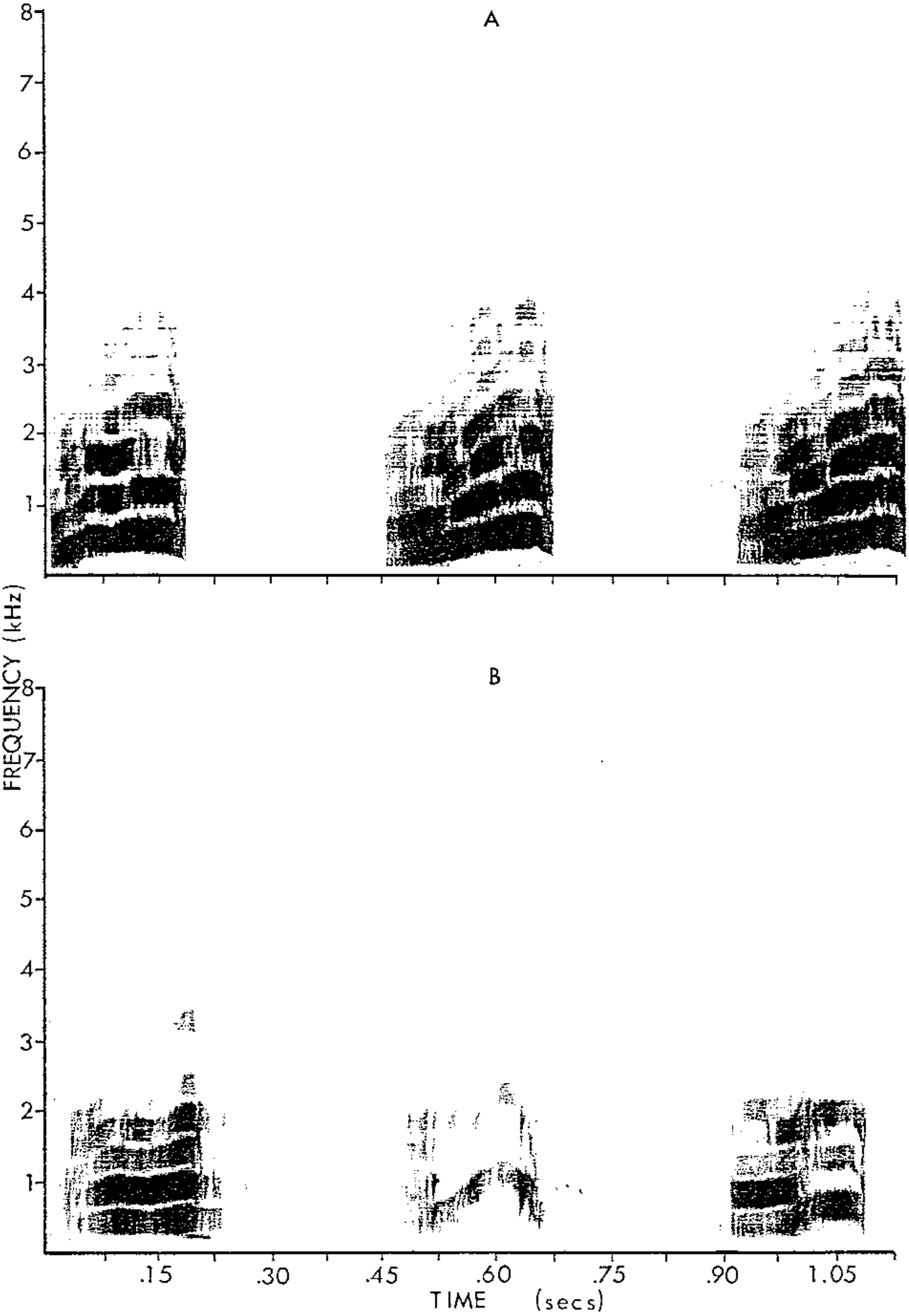


FIGURE 5.5 Adult ruh call

a. Type one

b. Type two

Table 5.3 Structure of the ruh call

Individual 5108 (n=19)

VARIABLE	UNITS	MEAN (±1SD)	RANGE
A	(msec)	198.9 ± 22.2	143.4 - 226.5
B	(Hz)	329.4 ± 37.8	269.5 - 385.0
C	(Hz)	522.8 ± 10.1	385.0 - 847.0
D	(Hz)	573.4 ± 77.9	462.0 - 693.0
E	(Hz)	680.8 ± 150.9	481.0 - 1078.0
F	(msec)	68.1 ± 17.7	22.6 - 83.0
G	(msec)	262.0 ± 22.6	226.5 - 302.0
H	(msec)	263.8 ± 20.8	226.5 - 302.0

CONTEXT: The breeding pair uttered a series of these calls as I entered the aviary to handle their chicks. The parent birds remained on the ground and ran around the intruders in a crouched, slightly forward stance (similiar to the intension flight posture described in section 2.3.1.2). The non-breeding "pair" of birds gave ruh calls when approached and cornered in their small "security" aviary (section 1.3.2).

5.3.1.4 "Yark" call

STRUCTURE: Yark calls were only recorded from individuals of the captive breeding pair. These calls were moderately loud, 120-160 msec in duration and ranged in frequency from 539 to 1000 Hz (Table 5.4). Yark calls emitted by the female were characterised by a sharp increase in frequency just after initiation of the call (Figure 5.6) and a gradual frequency drop toward the end of a call. Similiar calls of the male also increased sharply at the beginning and quickly dropped in frequency, with a pronounced frequency modulation at the termination of each call (Figure 5.6). The female call had a lower fundamental frequency than that of the male (although this was not statistically tested).

CONTEXT: These contact calls were given mainly as the parent birds walked around their aviary in a hunched posture, "guarding" chicks

Table 5.4 Structure of the yark call

Captive male (n = 14)

VARIABLE	UNITS	MEAN (±1SD)	RANGE
A	(msec)	140.7 ± 11.3	120.8 - 158.5
B	(Hz)	646.2 ± 58.8	539.0 - 770.0
C	(Hz)	918.5 ± 49.7	808.5 - 1001.0
D	(Hz)	737.0 ± 58.2	654.5 - 847.0
E	(Hz)	935.0 ± 32.7	885.0 - 1001.0
F	(msec)	-12.9 ± 22.0	-52.8 - 0
G	(msec)	1177.0 ± 156.0	1011.0 - 1321.0
H	(msec)	1260.0 ± 85.4	1200.0 - 1321.0

Captive female (n =5)

VARIABLE	UNITS	MEAN (±1SD)	RANGE
A	(msec)	137.4 ± 11.5	120.8 - 151.0
B	(Hz)	762.3 ± 32.2	731.5 - 808.5
C	(Hz)	831.6 ± 34.4	770.0 - 847.0
D	(Hz)	685.3 ± 42.1	616.0 - 731.5
E	(Hz)	870.1 ± 25.1	847.0 - 904.7
F	(msec)	-28.3 ± 26.4	-60.4 - 0
G	(msec)	-	-
H	(msec)	-	-

Combined individuals (n = 19)

VARIABLES	UNITS	MEAN (±1SD)	RANGE
A	(msec)	139.9 ± 11.1	120.8 - 158.5
B	(Hz)	704.2 ± 45.5	539.0 - 808.5
C	(Hz)	895.6 ± 59.9	770.0 - 1001.0
D	(Hz)	723.4 ± 58.2	616.0 - 847.0
E	(Hz)	917.9 ± 42.1	847.0 - 1001.0
F	(msec)	-16.3 ± 23.2	-60.4 - 0
G	(msec)	1177.0 ± 156.0	1011.0 - 1321.0
H	(msec)	1260.0 ± 85.4	1200.0 - 1321.0

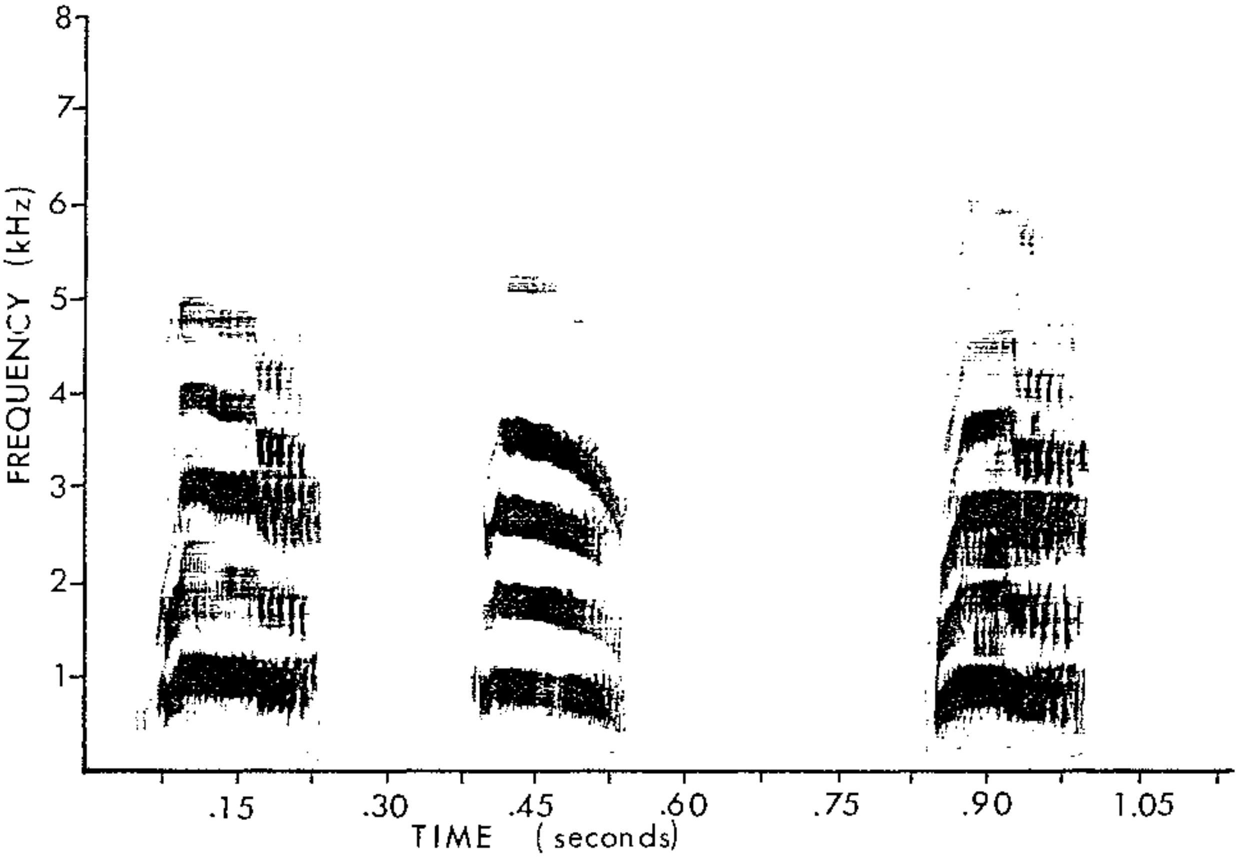


FIGURE 5.6 Adult yark call

Calls one and three are from the captive breeding male, call two is the female (section 4.3.1.3). However these calls were also heard outside the parental-care period.

5.3.1.5 Yak call

STRUCTURE: "Yak" calls were very similiar to both the yark (above) and yap (below) calls. A total of 33 yak calls were recorded from five stilts; the captive male (n = 3), a wild node D stilt (n = 3) and three wild black stilts (n =27). Two of the latter black stilts were identified as being female (individual parameter values of their calls are presented in Appendix 9). Variables A-H measured from sonagrams of these five stilts are presented as a combined mean in Table 5.5.

Yak calls of the captive male were shorter (83 to 94 msec) and of slightly lower fundamental frequency (mean = 911.2 Hz) than yark or yap calls. They differed from the former by a conspicuous lack of frequency modulation (Figure 5.7). Yak calls differed also from yaps in both amplitude and rate of emission, being quieter and not as frequently emitted.

CONTEXT: Given in the same type of context as the yark call.

5.3.1.6 Yaps

Yaps were graded in structure but were classified into four types on the basis of structure and aural distinctness (to me);

a.<u>Common "Yap"</u> call

STRUCTURE: Loud "yap" calls a) ascended and then descended in frequency, peaking at between 770 and 1155 Hz for captive birds (Table 5.6) or b) ascended and remained at a higher frequency until the end of a call.

These calls were of moderate length (75.5 to 120.8 msec) with a large number of harmonics. The fundamental, third and fourth harmonics were more accentuated than other harmonics.

Table 5.5 Structure of the yak call

Captive male (n = 3)

VARIABLE	UNITS	MEAN (±1SD)	RANGE
A	(msec)	86.8 ± 6.5	83.0 - 94.3
B	(Hz)	564.7 ± 58.8	500.5 - 616.0
C	(Hz)	911.2 + 22.2	855.5 - 924.0
D	(Hz)	731.5 ± 138.8	577.5 - 847.0
E	(Hz)	911.2 ± 22.2	885.5 - 924.0
F	(msec)	0	0
G	(msec)	288.8 ± 72.1	237.8 - 339.7
H	(msec)	288.8 ± 72.1	237.8 - 339.7

Individual 13 - wild node D (n = 3)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	95.6 ± 4.3	90.6 - 98.1
B	(Hz)	577.5 ± 0	577.5
C	(Hz)	693.0 ± 38.5	654.5 - 731.5
D	(Hz)	564.7 ± 22.2	539.0 - 577.5
E	(Hz)	693.0 ± 38.5	654.5 - 731.5
F	(msec)	0	0
G	(msec)	-	-
H	(msec)	-	-

Combined wild black females (n = 2 individuals, 22 calls)

VARIABLES	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	117.9 ± 6.0	105.7 - 128.3
B	(Hz)	540.7 ± 74.6	462.0 - 693.0
C	(Hz)	813.7 ± 63.2	731.5 - 924.0
D	(Hz)	707.0 ± 38.5	654.5 - 770.0
E	(Hz)	820.7 ± 63.0	731.5 - 924.0
F	(msec)	2.2 ± 8.8	-15.1 - 30.2
G	(msec)	387.5 ± 259.0	86.8 - 1049.4
H	(msec)	385.7 ± 241.2	86.8 - 1049.4

Combined wild black individuals (n = 3 individuals, 27 calls)

VARIABLES	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	111.3 ± 15.3	75.5 - 128.3
B	(Hz)	548.9 ± 72.1	462.0 - 693.0
C	(Hz)	825.6 ± 65.2	731.5 - 924.0
D	(Hz)	737.2 ± 76.0	654.5 - 924.0
E	(Hz)	832.7 ± 63.9	731.5 - 924.0
F	(msec)	4.0 ± 9.9	-15.1 - 30.2
G	(msec)	490.5 ± 368.9	86.8 - 1525.1
H	(msec)	478.2 ± 349.8	86.8 - 1525.1

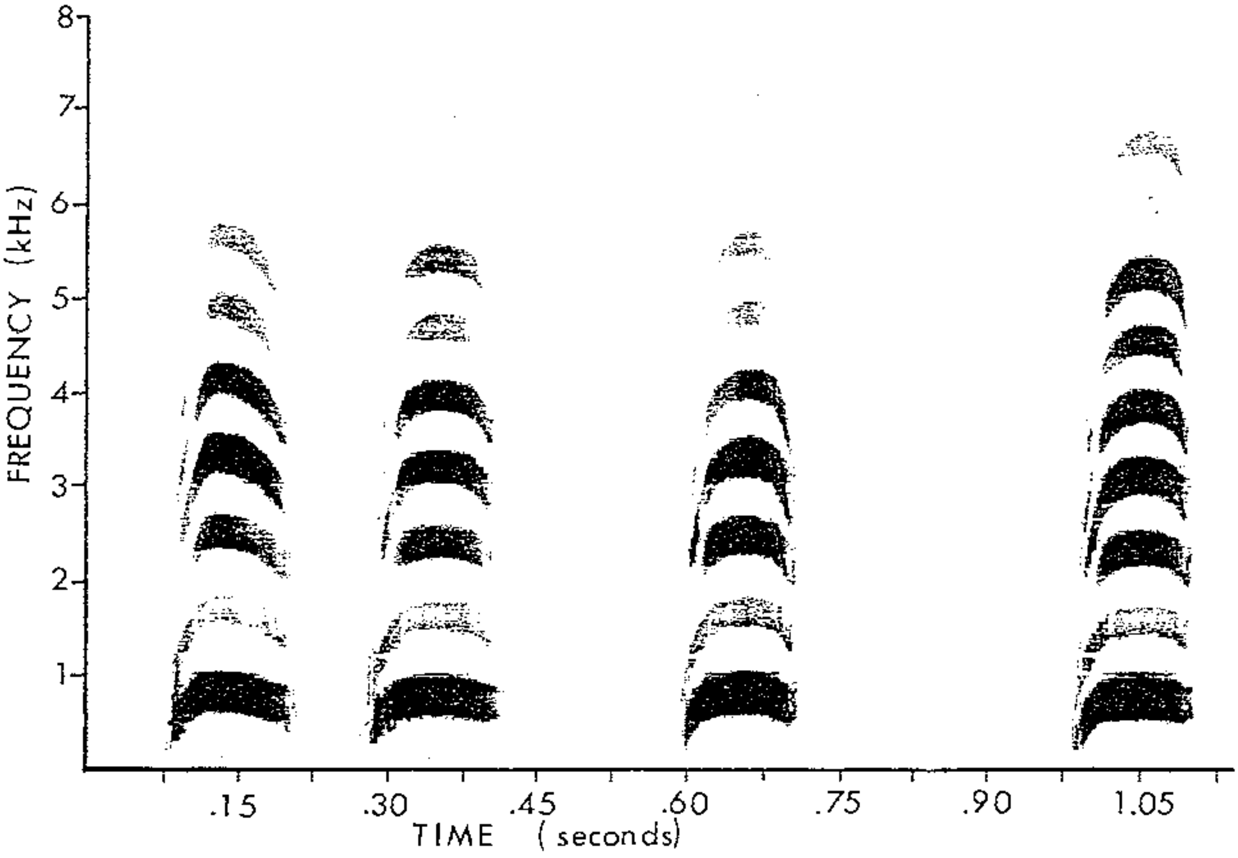


FIGURE 5.7 Adult yak call
(Wild black female)

Table 5.6 Structure of the common yap call

Captive male (n = 16)

VARIABLE	UNITS	MEAN (± 1 SD)	RANGE
A	(msec)	109.3 ± 5.7	98.2 - 120.8
B	(Hz)	584.4 ± 63.1	462.0 - 693.0
C	(Hz)	1118.8 ± 45.4	1001.0 - 1155.0
D	(Hz)	1003.3 ± 91.6	847.0 - 1116.5
E	(Hz)	1121.1 ± 39.3	1039.5 - 1155.0
F	(msec)	-10.0 ± 10.9	-26.4 - 0
G	(msec)	518.4 ± 93.2	422.8 - 732.3
H	(msec)	518.0 ± 92.9	422.8 - 732.3

Captive female (n =16)

VARIABLE	UNITS	MEAN (± 1 SD)	RANGE
A	(msec)	99.1 ± 15.3	75.5 - 124.6
B	(Hz)	579.8 ± 123.9	385.0 - 731.5
C	(Hz)	873.2 ± 90.9	770.0 - 1001.0
D	(Hz)	649.9 ± 126.3	462.0 - 924.0
E	(Hz)	847.7 ± 90.9	770.0 - 1001.0
F	(msec)	7.5 ± 16.3	0 - 60.4
G	(msec)	382.7 ± 187.0	188.7 - 804.1
H	(msec)	396.4 ± 197.7	188.7 - 804.1

The captive breeding female's call was of lower pitch (fundamental frequency, variables C and E) (Figure 5.8) and shorter duration (variable A) than that of the breeding male (Table 5.6).

These alarm calls were recorded from two further captive individuals and 17 black stilts from the wild population. Results from these recordings are presented in section 5.3.2.

CONTEXT: The "common" yap call given in captivity was elicited in

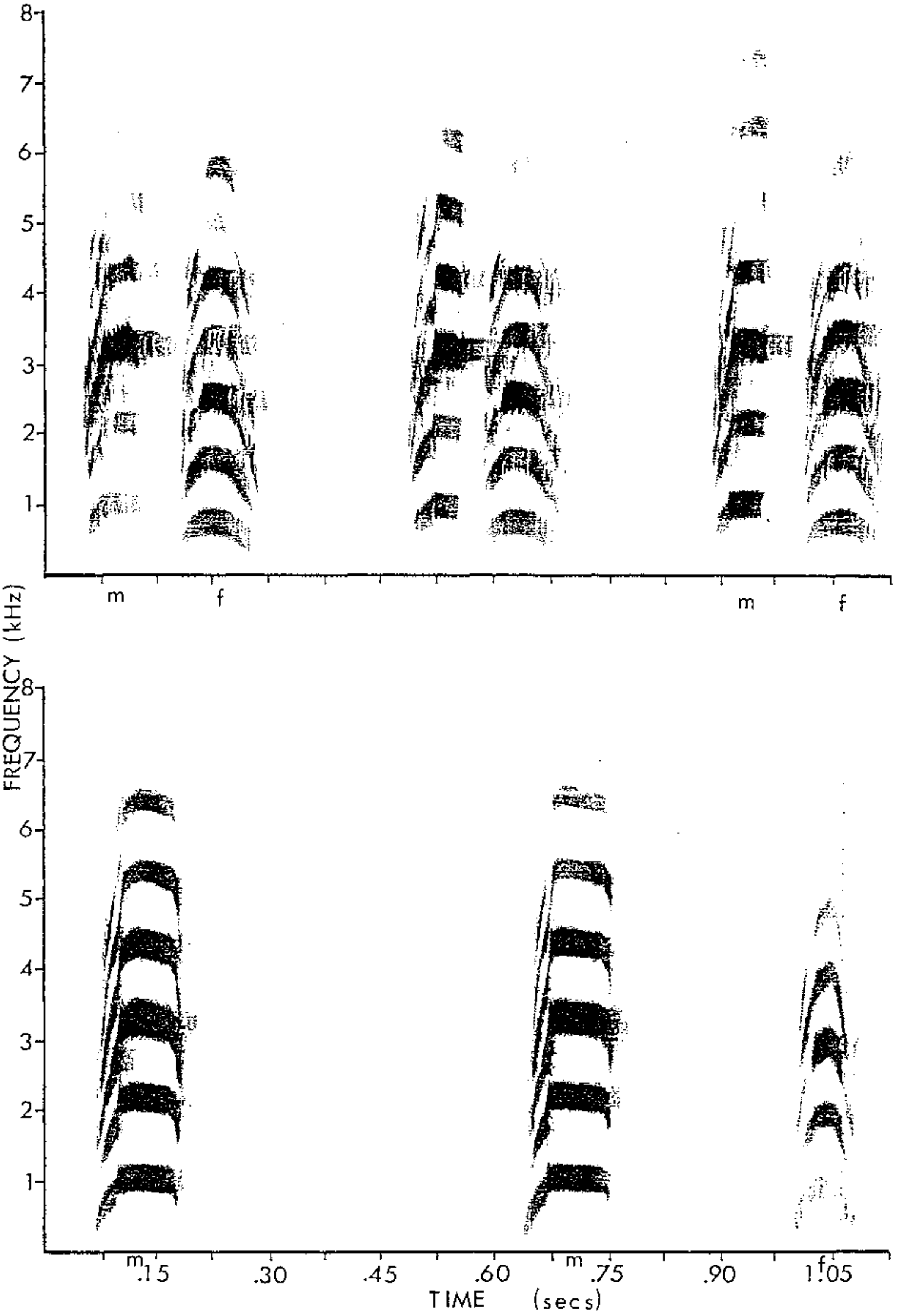


FIGURE 5.8 Common yap call

m = captive breeding male

f = captive breeding female

response to humans near or within the aviaries or by outside disturbance such as dogs, other stilts and passers-by.

b. "Url" call

STRUCTURE: "Url" calls were particularly graded calls, which both followed and preceded common yap calls. The url call was recorded from four individuals; the breeding captive male, a wild node D stilt and two wild black stilts. Recordings from wild stilts indicate a peak in frequency (to 1155 Hz) at the beginning to mid-call, decreasing in frequency toward the end. The position of peak frequency was variable in samples from the one captive bird. Calls of this individual were also shorter than wild calls (Table 5.7). Frequency modulation occurred near the end of some wild calls (Figure 5.9).

CONTEXT: The breeding male was the only captive bird heard giving the call. For all individuals, the context of the call remained the same. It was heard only during the incubation and chick-rearing phases of the breeding season, as one or more stilts flew toward an overhead aerial predator. Occasionally this "mobbing" call was given by a stilt as it remained on the ground with its head tilted up toward the sky (section 2.3.1.2). The latter was the case particularly with the captive individual, as this bird did not attempt to fly toward hawks or magpies which flew over the aviary but remained on the ground calling. Url calls were also given by wild stilts on the ground, just before they took off to "mob" aerial predators.

c. "Eerr" calls

STRUCTURE: The second highly graded alarm call of captive and wild stilts was long and variable in duration. Five stilts were recorded giving this call; the captive breeding male, one wild pied stilt and three wild node F stilts (Table 5.8). Mean measurements from calls of the three node F birds are given in Appendix 10 for each individual.

The calls of the pied stilt were of comparable length to the captive calls (151-283 msec). The mean length of node F calls was much greater, being up to 407 msec in duration. As in the url call, there was a peak in fundamental frequency near the beginning of these calls and a drop in frequency toward the end. The characteristic structural

Table 5.7 Structure of the url call

Breeding male (n =41)

VARIABLES	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	122.0 ± 13.8	86.8 - 154.8
B	(Hz)	621.6 ± 73.3	423.5 - 731.5
C	(Hz)	1007.1 ± 98.4	770.0 - 1155.0
D	(Hz)	844.2 ± 81.4	616.0 - 1001.0
E	(Hz)	1034.0 ± 87.9	847.0 - 1155.0
F	(msec)	0.7 ± 1.9	-3.7 - 4.4
G	(msec)	290.4 ± 134.6	135.9 - 830.5
H	(msec)	290.4 ± 134.6	182.8 - 830.5

Individual 5 - wild node D (n = 5)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msecs)	165.5 ± 30.5	139.7 - 211.4
B	(Hz)	716.1 ± 64.4	616.0 - 770.0
C	(Hz)	870.1 ± 64.4	770.0 - 924.0
D	(Hz)	770.0 ± 170.0	500.5 - 962.5
E	(Hz)	904.5 ± 121.7	693.0 - 1001.0
F	(msecs)	-33.2 ± 23.0	-60.4 - -7.5
G	(msecs)	351.1 ± 193.4	166.1 - 581.3
H	(msecs)	351.1 ± 193.4	166.1 - 581.3

Combined wild blacks (n = 2 individuals, 27 calls)

VARIABLES	UNITS	MEAN (± 1SD)	RANGE
A	(msecs)	180.4 ± 35.7	117.0 - 256.7
B	(Hz)	727.2 ± 55.8	616.0 - 847.0
C	(Hz)	919.7 ± 70.3	731.5 - 1039.5
D	(Hz)	709.7 ± 75.9	577.5 - 847.0
E	(Hz)	1063.7 ± 65.0	847.0 - 1155.0
F	(msecs)	-49.6 ± 19.9	-90.6 - -11.3
G	(msecs)	275.0 ± 137.5	120.8 - 770.1
H	(msecs)	300.6 ± 150.8	128.3 - 770.1

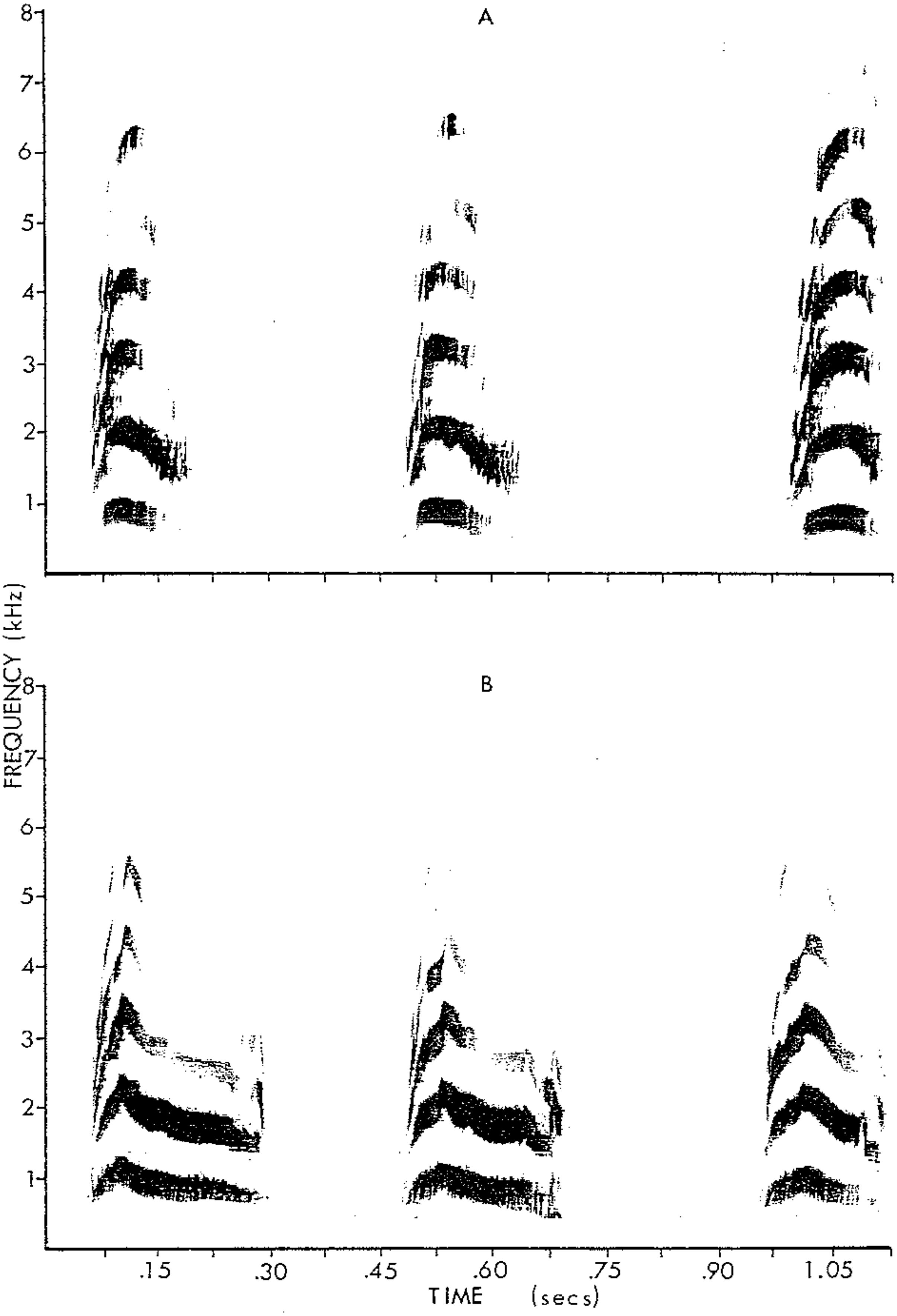


FIGURE 5.9 Adult url call

a. Captive breeding male

b. Wild black stilt

Table 5.8 Structure of the eerr call

Individual 18 - wild pied (n = 3)

VARIABLE	UNITS	MEAN	RANGE
A	(msec)	207.6 ± 44.5	158.5 - 245.4
B	(Hz)	680.2 ± 44.4	654.5 - 731.5
C	(Hz)	847.0 ± 0	847.0
D	(Hz)	757.2 ± 22.2	731.5 - 770.0
E	(Hz)	847.0 ± 0	847.0
F	(msec)	-56.6 ± 49.3	-90.6 - 0
G	(msec)	-	-
H	(msec)	-	-

Captive black male (n = 7)

A	(msec)	210.9 ± 55.4	151.0 - 283.1
B	(Hz)	704.0 ± 48.2	616.0 - 770.0
C	(Hz)	907.5 ± 110.8	808.5 - 1078.0
D	(Hz)	742.5 ± 82.3	616.0 - 847.0
E	(Hz)	940.5 ± 108.6	808.5 - 1165.0
F	(msec)	-4.8 ± 55.1	-83.0 - 75.5
G	(msec)	197.6 ± 26.6	151.0 - 218.9
H	(msec)	163.6 ± 46.9	83.0 - 207.6

Combined wild node F (n = 20 calls, 3 individuals)

A	(msec)	312.0 ± 67.3	158.5 - 407.7
B	(Hz)	592.9 ± 53.5	500.5 - 693.0
C	(Hz)	819.1 ± 44.8	731.5 - 885.5
D	(Hz)	681.4 ± 50.1	616.0 - 808.5
E	(Hz)	839.3 ± 42.5	770.0 - 904.7
F	(msec)	-40.0 ± 49.7	-128.0 - 37.7
G	(msec)	321.1 ± 168.9	162.3 - 679.5
H	(msec)	323.6 ± 167.0	162.3 - 679.5

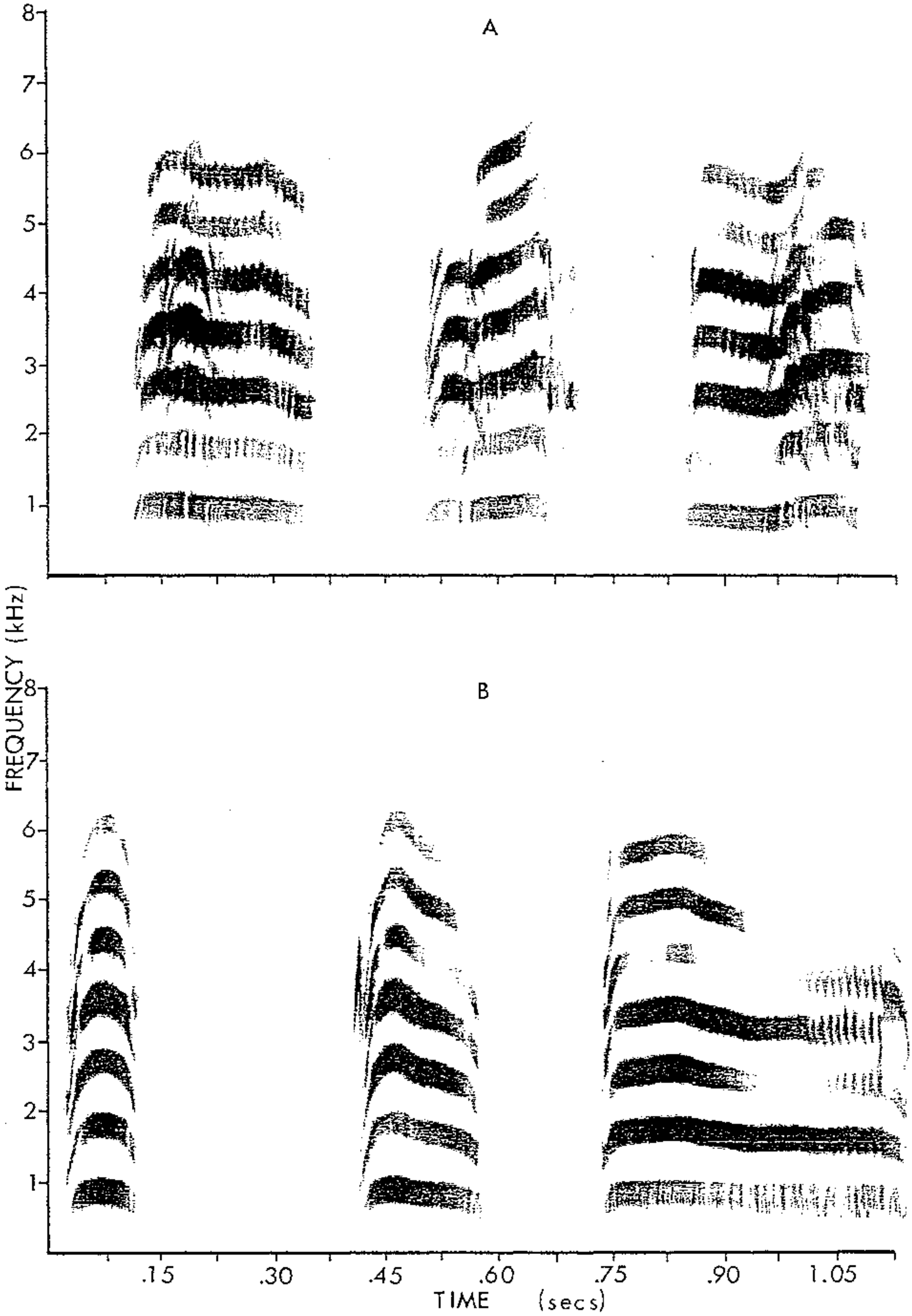


FIGURE 5.10 Adult eerr call

a. Captive breeding male

b. Wild node F stilt

(note: intergradation from alarm yap)

differences between the two call types, were frequency modulations throughout or toward the end of "eerr" calls (Figure 5.10) and less of an early frequency peak than that heard in url calls.

CONTEXT: "Eerr" calls were heard during human intrusion into territories of wild or captive stilts which were incubating eggs or rearing chicks (particularly the former). The nesting birds flew toward the intruder and then crouched on the ground with one or both wings out-stretched, rocking the body and fluttering the wings on the ground (i.e., "broken-wing" display as described in section 4.3.1.4). The body movement resembled that of an adult with a damaged wing.

d. Double-note calls

STRUCTURE: Only one individual (captive breeding male) was heard giving this call. These calls were short and repeated in very quick succession, often producing two notes of similiar frequency with an interval of 0-30 secs between them. Table 5.9 presents mean measurements of eight variables measured from double-note calls of this male.

The second part of each call was either i) a replicate of the first or ii) descended in frequency after an ascent in the first part of the call or iii) repeated the frequency ascent of part one but continued for a longer period and at a higher frequency (Figure 5.11). A maximum of three double-note calls were given per second by this bird.

The series of calls within which double-notes were heard varied in structure along a continuum that included "yap" and "eerr" calls.

Double-note calls were moderately loud with the third to fifth harmonics being of greatest energy.

Table 5.9 Structure of the double-note call

Captive male (n = 9)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	68.7 ± 18.4	37.7 - 105.7
B	(Hz)	680.2 ± 54.4	616.0 - 770.0
C	(Hz)	1001.0 ± 103.7	847.0 - 1116.5
D	(Hz)	988.2 ± 90.3	770.0 - 1078.0
E	(Hz)	1043.8 ± 55.9	962.5 - 1116.5
F	(msec)	8.8 ± 15.3	-15.1 - 30.2
G	(msec)	350.0 ± 23.7	320.9 - 385.0
H	(msec)	351.0 ± 26.4	320.9 - 385.0

CONTEXT: These calls were recorded from within the breeding pair's aviary during removal of a clutch of newly laid eggs.

5.3.1.7 "Pit" call

STRUCTURE: The very soft "pit" call of a hen bird was extremely short in duration (mean = 8.2 msecs) and was comprised of 4 to 5 clear harmonics above a moderate fundamental frequency of approximately 851.3 Hz (Table 5.10). The definition of harmonics above 4000 Hz became less precise. Variable P represents the highest frequency reached in this call type. "Pit" calls were given at a rate of approximately three per second (Figure 5.12).

Table 5.10 Structure of the pit call

Captive female (n = 18)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	8.2 ± 1.4	7.5 - 11.3
B	(Hz)	851.3 ± 90.4	731.5 - 1001.0
G	(msec)	333.8 ± 88.1	234.0 - 490.7
H	(msec)	333.8 ± 88.1	234.0 - 490.7
P	(Hz)	5732.2 ± 1840.1	2695.0 - 7700.0

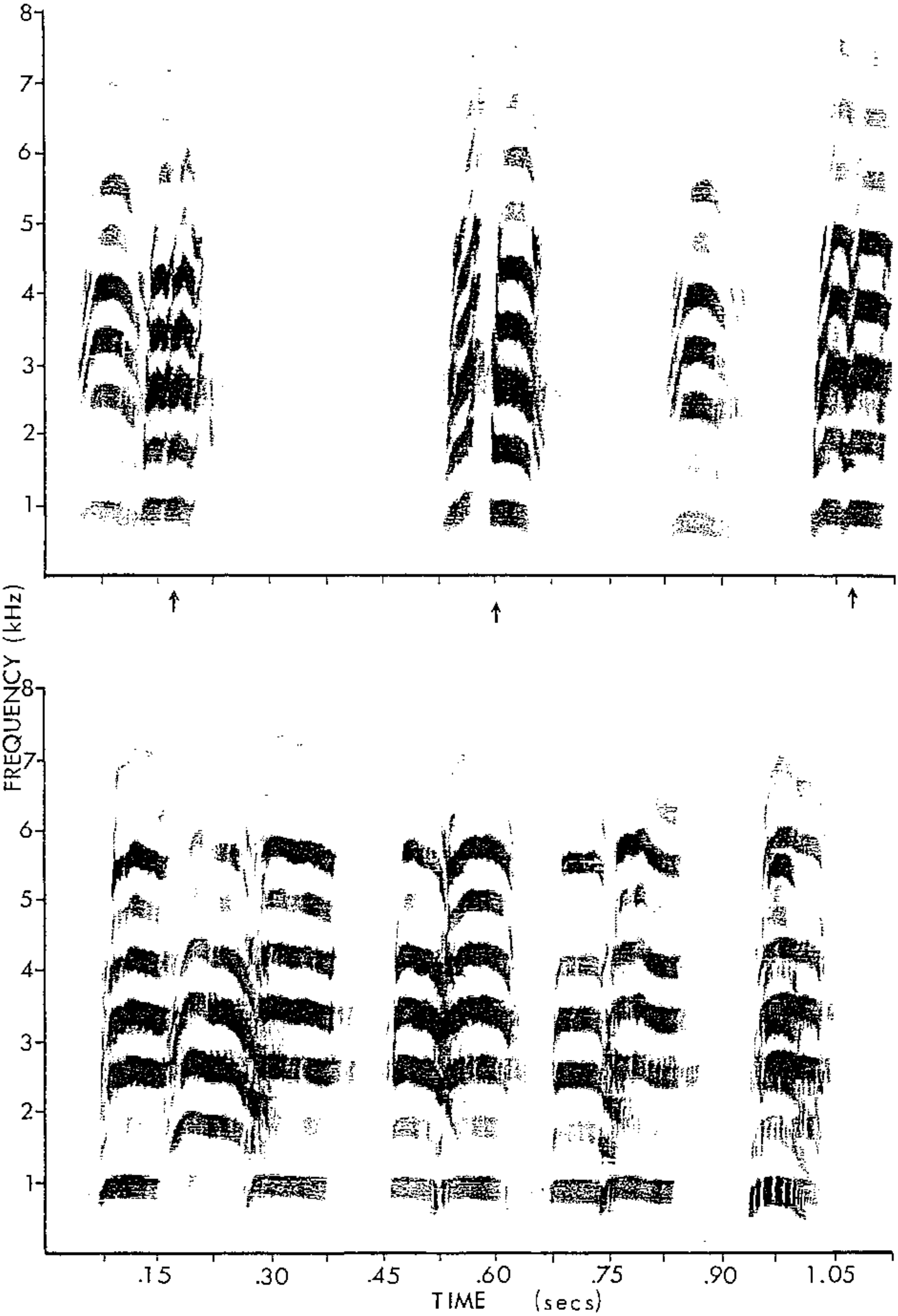


FIGURE 5.11 Adult double-note calls

Two series of calls from the male
and female of the focal pair
(double-notes indicated are from the male)

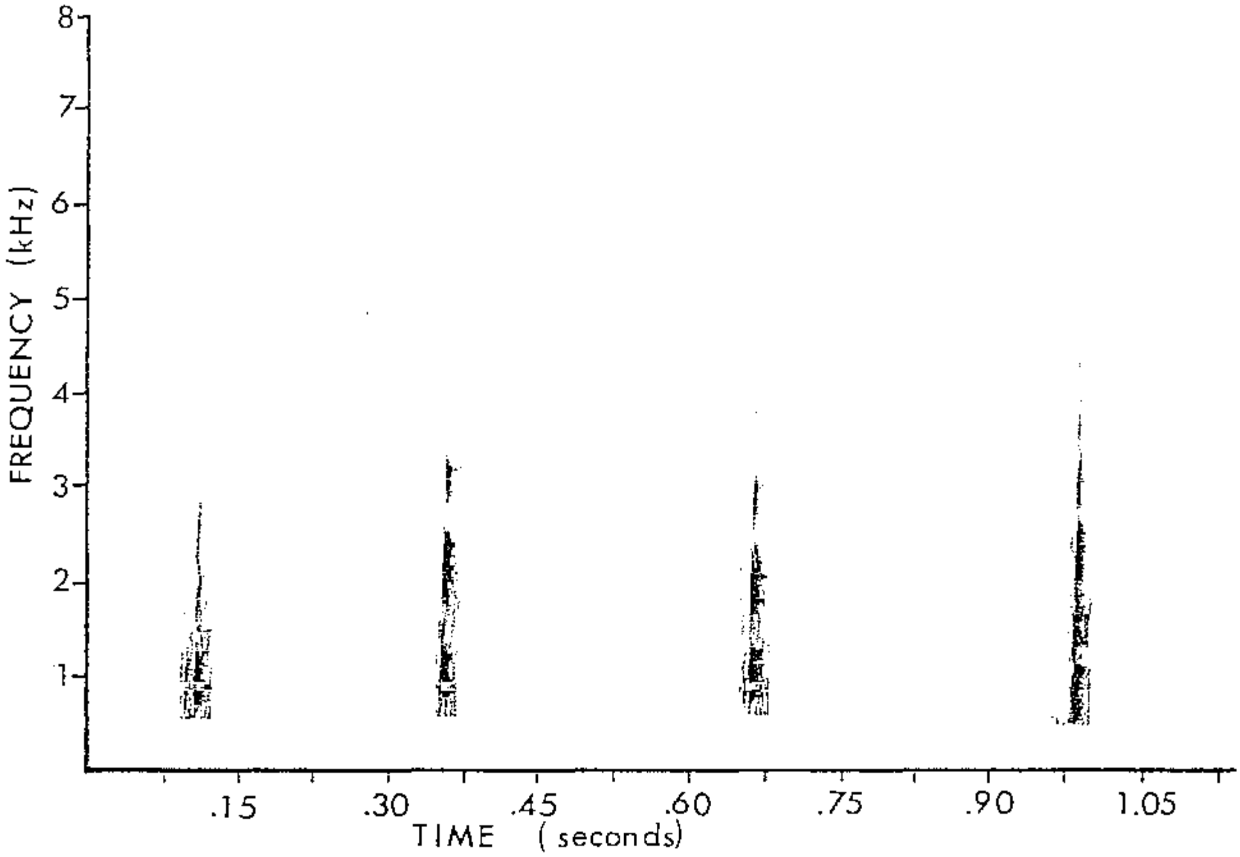


FIGURE 5.12 Adult pit call
Captive breeding female

CONTEXT: The pit call was heard and recorded from only the female of the breeding pair, as she stood in a horizontal pre-copulatory posture (section 3.3.1.1) near the male.

5.3.1.8 Staccato calls

STRUCTURE: Staccato calls were recorded from two pairs of stilts. They were variable in length (Table 5.11) and were classified (below) on the basis of this variability into three call types;

Type 1) Calls of 22.0-37.7 msec duration, which had a low fundamental frequency of between 462 and 616 Hz (Figure 5.13 a). These calls were rapidly emitted at a rate of about 10 per second, approximately 109 msecs apart. The inter-call period was variable;

Type 2) Extremely short notes of 7.5 to 22 msecs duration and of slightly higher frequency than type one calls (Figure 5.13 b). The diminuation of harmonics in higher frequencies resembled that of the female pre-copulatory call (section 5.3.1.7);

Type 3) Loud calls of longer duration (mean = 98 msec) and higher fundamental frequency (up to 1078 Hz) were given after several seconds of type 1 and/or 2 calls. Within this call type (Figure 5.13 c), the fundamental and second harmonics were amplified.

Table 5.11 presents the combined mean values for 5 variables measured off 217 calls of the two stilt pairs (from data in Appendix 11).

Table 5.11 Structure of staccato calls

Combined individuals (n = 217)

A	(msec)	24.6 ± 18.6	7.5 - 98.1
B	(Hz)	635.4 ± 107.8	462.0 - 1078.0
G	(msec)	109.3 ± 119.4	15.1 - 853.1
H	(msec)	108.6 ± 118.7	15.1 - 853.1
P	(Hz)	3772.7 ± 1210.4	1309.0 - 7700.0

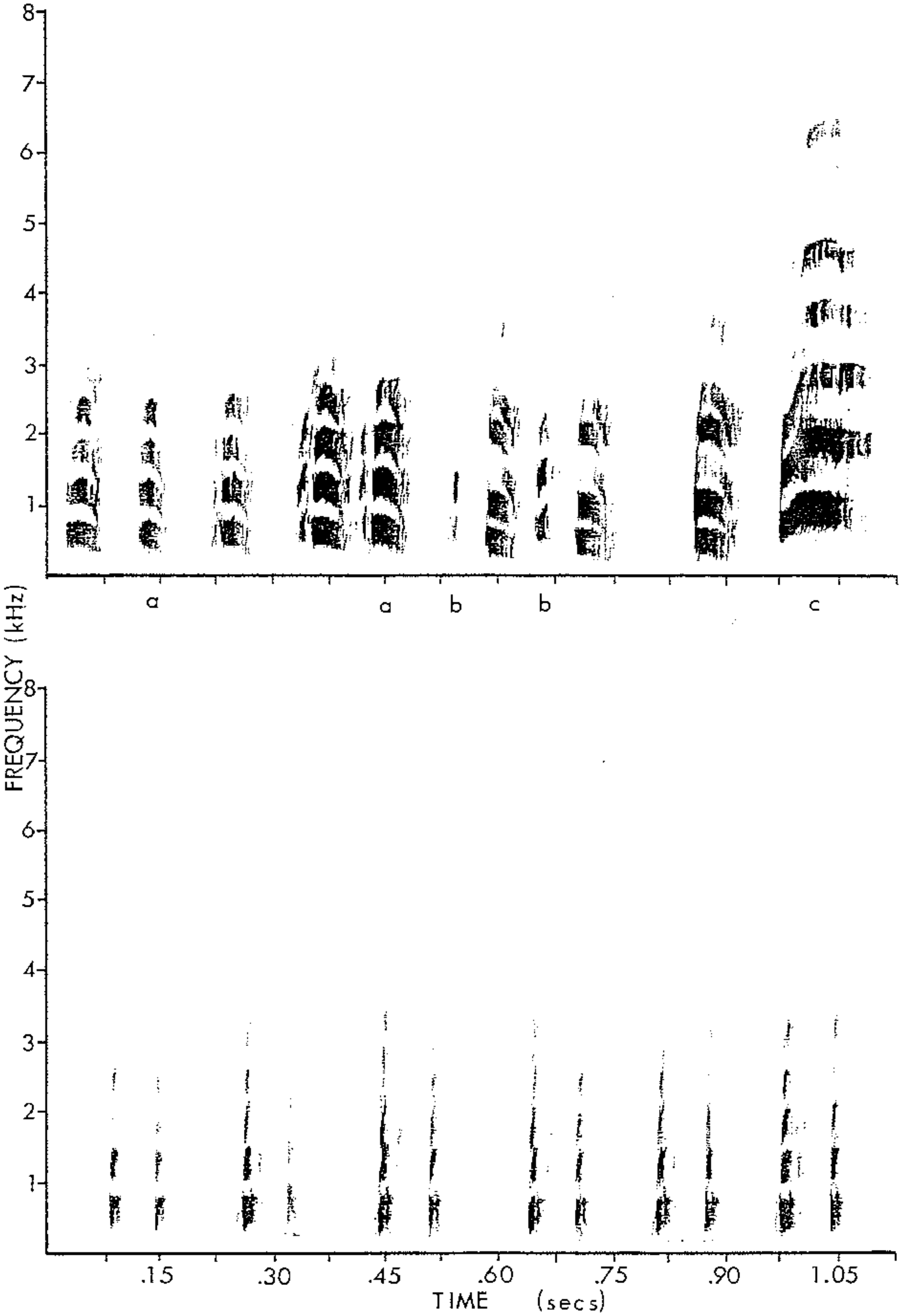


FIGURE 5.13 Adult staccato calls

i. Breeding pair

ii. Single non-breeding captive individual

a = type 1 note, b = type 2 note, c = type 3 note

CONTEXT: Calls over or near nest-sites were emitted as a series of short staccato notes, either by one individual or as part of a "simultaneous calling" with a second bird. Four pairs of stilts independently performed these temporally overlapping calls and recordings were made from three of these pairs. Overlapping staccato calls were usually initiated by one stilt as it stood with head and bill directed downward over an established or prospective nest-site (section 3.3.1.3). If the initiator was joined by the second member of the pair, these type 1 and 2 calls increased in rate of emission and calls of the two individuals overlapped temporally. Calling increased in amplitude and ceased after several louder type 3 calls were emitted.

In one calling series, one individual emitted type 2 calls as its cage-mate simultaneously emitted type 1 calls. In all other overlapping staccato calls recorded, it was not possible to distinguish the two individuals.

B/JUVENILE CALLS

5.3.1.9 Pipping

STRUCTURE: Recordings of "pip" calls were taken from one individual in the Waitaki Basin. These calls were soft and moderately long (mean = 60.7 msecs) with a very high fundamental frequency (Figure 5.14), rising and dropping over a large frequency range (Table 5.12).

Table 5.12 Structure of the pip call

One individual (n = 11)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	60.7 ± 9.5	45.3 - 75.5
B	(Hz)	1970.5 ± 347.3	1617.0 - 2618.0
C	(Hz)	3542.0 ± 592.4	2772.0 - 4581.5
D	(Hz)	1631.0 ± 144.3	1386.0 - 1848.0

CONTEXT: These calls were given by black stilt chicks from within eggs just prior to hatching.

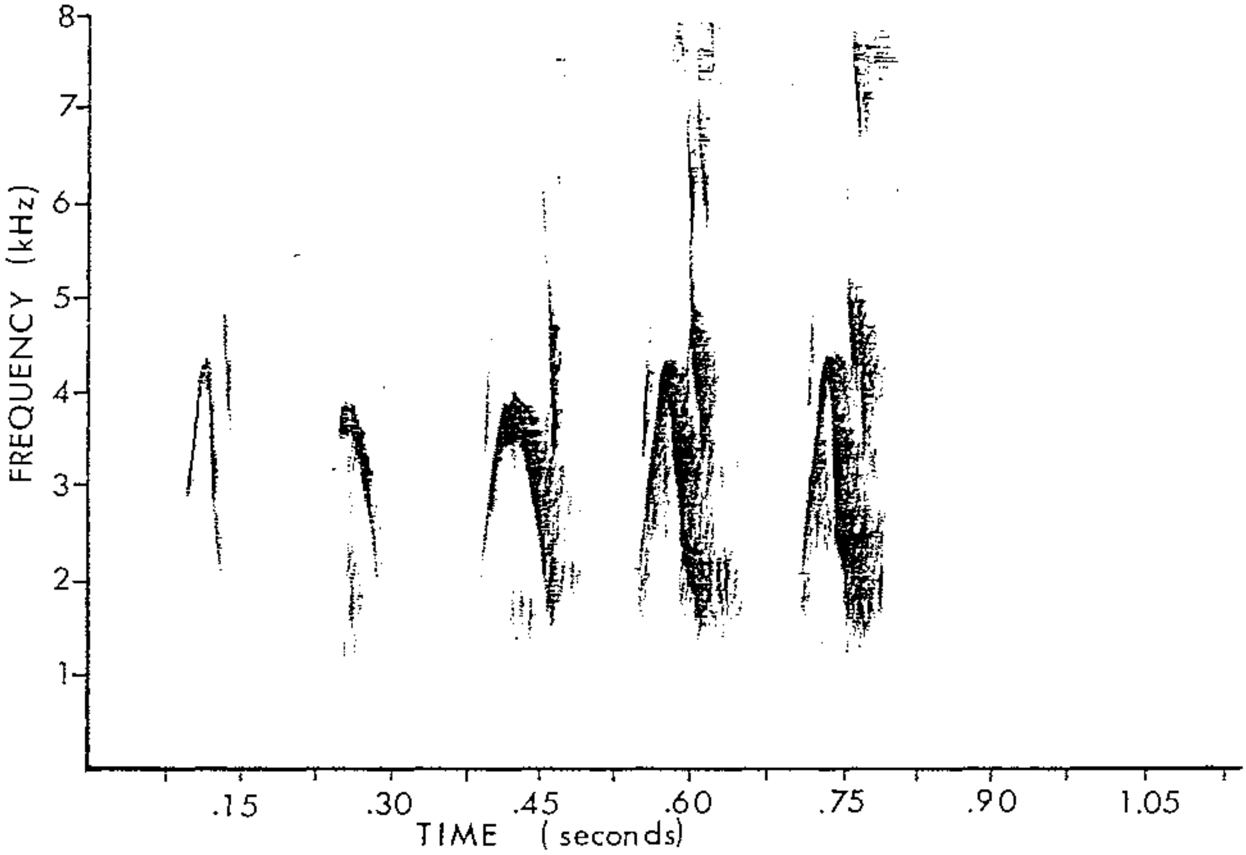


FIGURE 5.14 Within-egg pip call

5.3.1.10 "Yip" calls

Yip calls were recorded from a newly hatched wild chick and from two clutches of captive chicks near fledging age. Eight variables measured from these calls and not yet described, are illustrated in Figure 5.15.

<u>One-day old chick</u>

STRUCTURE: Yip calls of a single one-day old chick were of very high frequency and covered a large frequency range (Table 5.13). These were loud, two-part calls. The first part was longer and of higher fundamental frequency than the second.

Table 5.13 Structure of the yip call - One day old chick

One individual (n = 12)

Q	(Hz)	77.7 ± 3.0	71.7 - 83.0
R	(Hz)	1604.0 ± 122.1	1386.0 - 1809.0
S	(Hz)	6266.0 ± 243.6	5852.0 - 6737.5
T	(Hz)	1209.5 ± 440.3	770.0 - 1925.0
U	(msec)	1450.2 ± 47.4	1386.0 - 1540.0
V	(msec)	45.9 ± 2.7	41.5 - 49.0
W	(Hz)	26.1 ± 33.9	22.6 - 30.2
X	(Hz)	278.8 ± 8.2	266.0 - 294.0

CONTEXT: Calls of the particular individual recorded were given from inside an artificial brooding box, just prior to the chick being placed under foster parents. Captive chicks emitted yip calls from the first day after hatching, as they followed or foraged near parent birds.

5.3.1.11 "Chip" calls

STRUCTURE: Juvenile chip calls were simple in structure and very soft, with one to two harmonics which ascended and then descended in frequency over a short period of time (Table 5.14, Figure 5.16). Call frequency dropped approximately 1200 Hz toward the end of a call, from a mid-call peak of around 2000-3500 Hz (variable C).

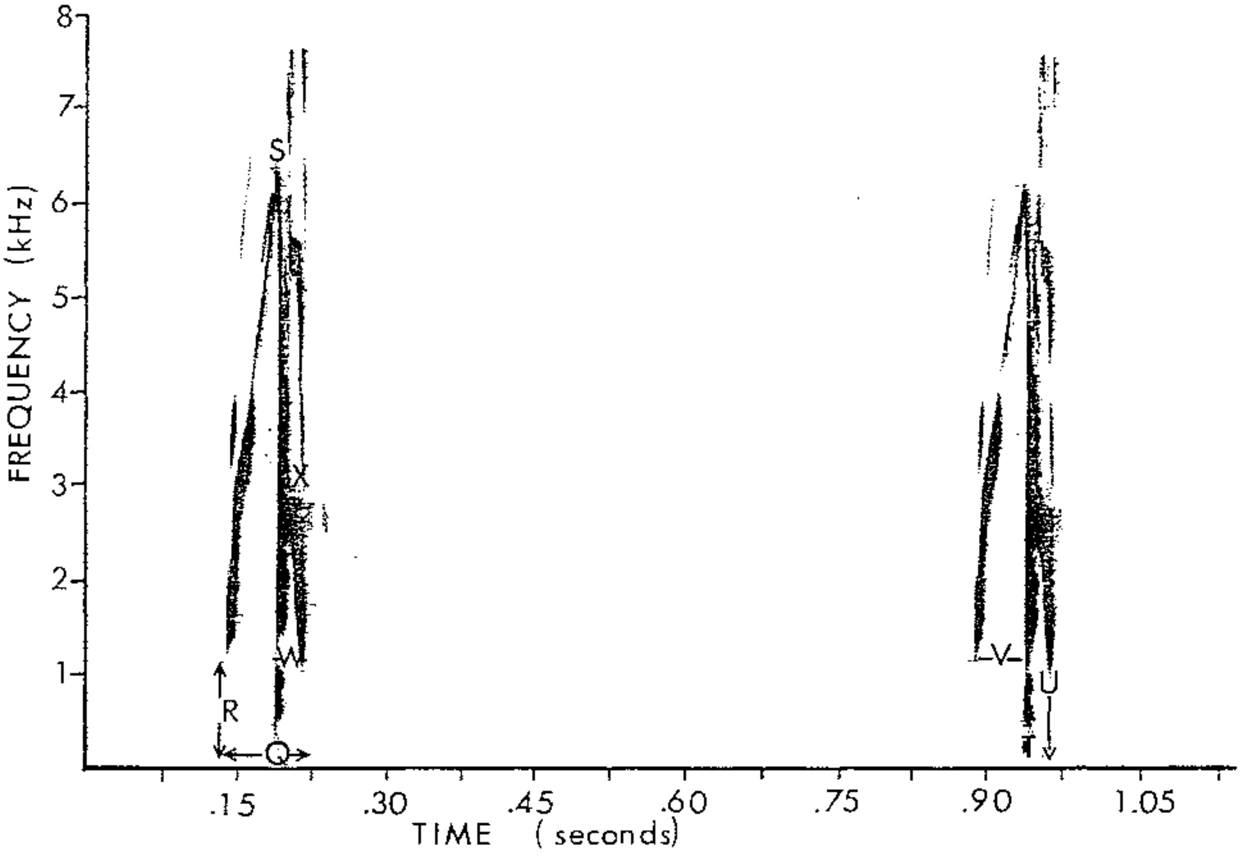


FIGURE 5.15 Juvenile yip call - one day old chick (indicating variables)

Table 5.14 Structure of the chip call

2632-red and yellow (n = 28)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	37.3 ± 6.6	26.4 - 52.8
B	(Hz)	2072.1 ± 266.7	1694.0 - 3080.0
C	(Hz)	2817.4 ± 417.9	2156.0 - 3465.0
D	(Hz)	1662.4 ± 90.7	1540.0 - 1848.0
E	(Hz)	2550.6 ± 330.4	2156.0 - 3041.5
F	(msec)	-1.9 ± 5.3	-7.5 - 7.5

CONTEXT: Chip calls were given by chicks as they foraged near parent birds or followed them around the aviary. These calls were too soft to hear being given by wild chicks, because of the long distances from which they were observed.

5.3.1.11 "Chap" calls

STRUCTURE: "Chap" calls were recorded from two captive juveniles (2632-red, yellow) (Appendix 12). Juvenile chap calls were of higher frequency and greater amplitude than chip calls. They were also longer (mean = 65.7 msecs) and of variable fundamental frequency (Figure 5.17). The fundamental and third harmonics were strongest in amplitude (Table 5.15).

Table 5.15 Structure of the chap call

Combined individuals (from Appendix 12) n = 46

A	(msec)	65.7 ± 15.1	41.5 - 98.1
B	(Hz)	1974.0 ± 256.9	1540.0 - 2618.0
C	(Hz)	3156.2 ± 192.3	2618.0 - 3465.0
D	(Hz)	1856.4 ± 319.8	1386.0 - 2926.0
G	(msec)	605.2 ± 404.1	147.2 - 1238.2
H	(msec)	589.2 ± 417.8	147.2 - 1238.2

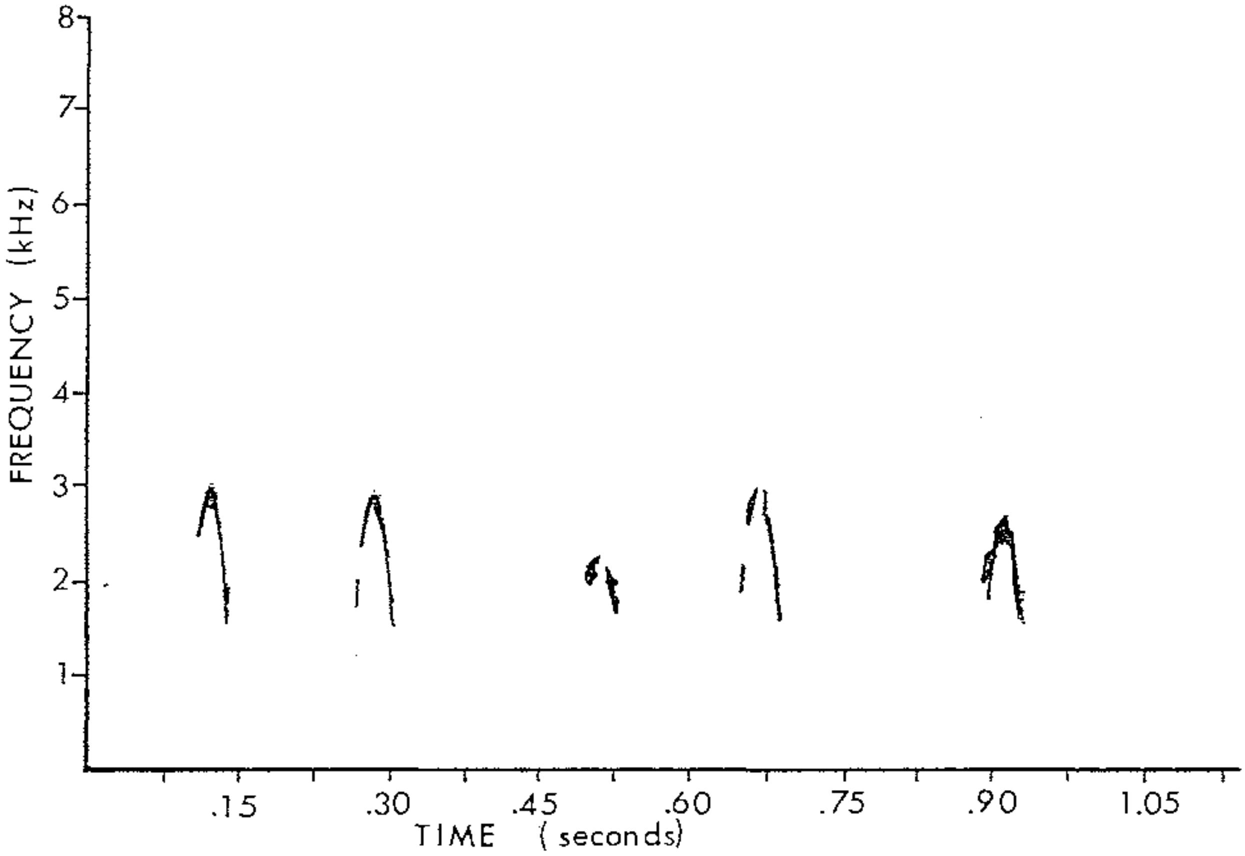


FIGURE 5.16 Juvenile chip calls (two captive chicks)

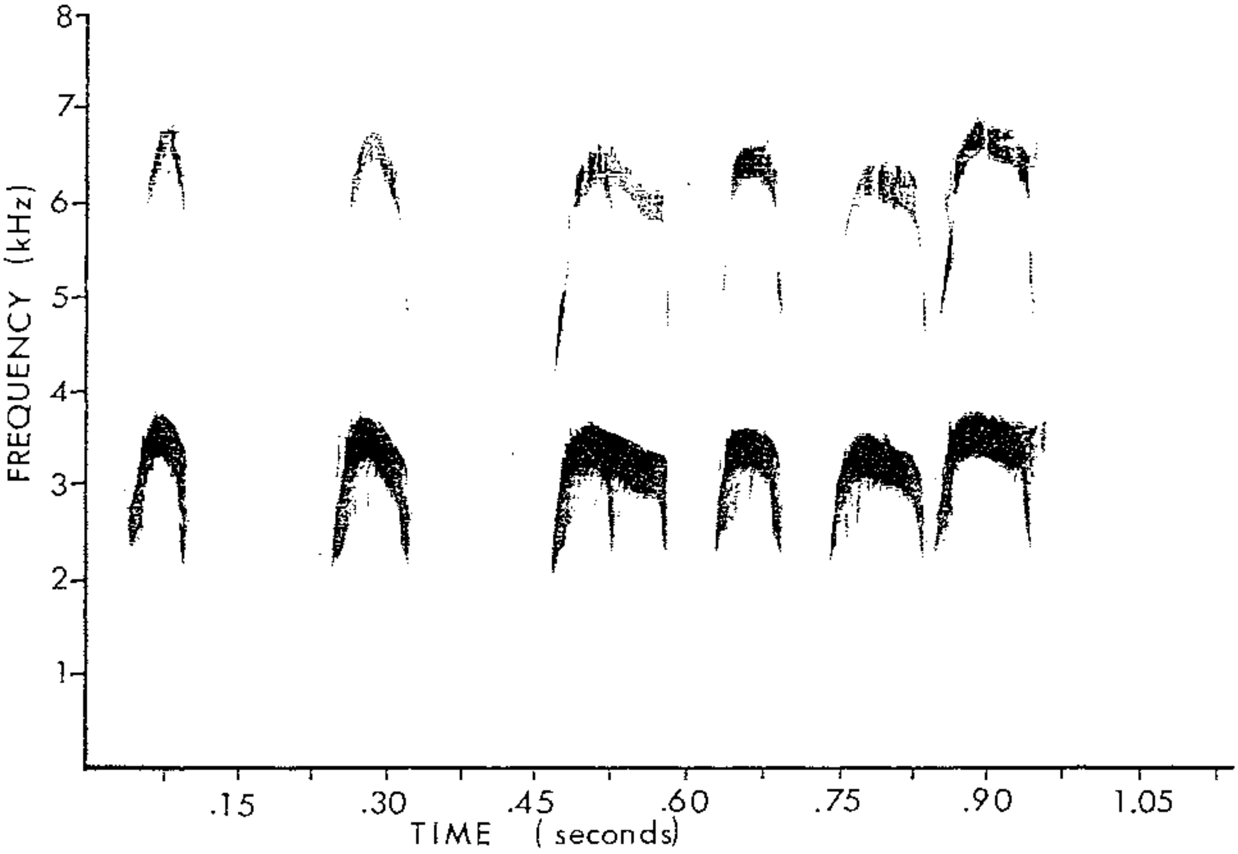


FIGURE 5.17 Juvenile chap calls (two captive chicks)

CONTEXT: These calls were given in association with adult common yap calls which were elicited during human intrusion or disturbance around aviaries. Older chicks (i.e., post-fledging) gave chap calls during flight around their aviary, even though adult birds remained undisturbed.

5.3.2 Variation in Alarm Calls

A sample of 77 sonagrams was prepared from alarm call recordings taken in the MacKenzie Basin and at Mount Bruce. The sonagrams contained a total of 946 alarm calls from 47 individuals (43 wild, 4 captive). 705 of these calls (15 per individual) formed the data set for an analysis of variation over 11 variables (A-K, section 5.2).

Variations within and between individuals (section 5.3.2.1), and within and between individuals grouped into plumage types (section 5.3.2.2) were examined.

Plumage nodes (Figure 5.1) were divided into four classes;

i) pied stilts (node A) (Plate 5.1);
ii) light hybrids (nodes B to E);
iii) dark hybrids (nodes F to I) (Plate 5.2); and
iv) black stilts (node J).

5.3.2.1 Individual variation

In an examination of individual variation in alarm calls within plumage classes, a separate ANOVA was conducted for each class, over 11 measured variables (parameters). Fifteen calls from each individual were examined and each of the 11 parameters was individually tested.

Sample size varied between plumage classes as follows;

Class 1 (pieds):	10 individuals;
Class 2 (light hybrids):	5 individuals;
Class 3 (dark hybrids):	11 individuals; and
Class 4 (blacks):	21 individuals.

The null hypothesis tested for each plumage class was "that variation of each of the measured parameters (A-K) was greater within, than between individuals".

PLATE 5.1 Pied stilt (node A)

PLATE 5.2 Dark hybrid (node E-F)

Table 5.16 summarises the results of the analyses (+ denotes failure to reject the hypothesis and x denotes rejection of the hypothesis) at the p = 0.05 significance level.

Table 5.16 Summary of ANOVA treatments on individual alarm calls

Plumage class	A	B	C	D	E	F	G	H	I	J	K
1	x	x	x	x	x	x	x	x	x	x	x
2	x	+	x	x	x	+	x	+	x	x	x
3	x	x	x	x	x	x	x	x	x	x	x
4	x	x	x	x	x	x	x	x	x	x	x

KEY: x = reject the null hypothesis
+ = accept the null hypothesis
at the 0.05 significance level.

The stated null hypothesis was rejected for all parameters in each plumage class, except B, F and H in class 2 (light hybrid). Therefore with the above exceptions, variability between individuals for each of these call variables, was greater than variability within individual calls. Variability within a series of calls from one individual is illustrated in Figure 5.18. Individual differences between members of a breeding pair are shown in Figure 5.19.

5.3.2.2 Interspecific variation

Variation of variables A-K within and between plumage classes was examined using a similiar ANOVA procedure, except that the 15 calls from each individual were treated as one unit. Grouping of the 15 calls of each individual into single values for each variable, provided a sample of 10 units (individuals) for node class 1, 5 units for class 2, 11 units for class 3 and 21 units for class 4.

The null hypothesis tested was "that variation for each of the

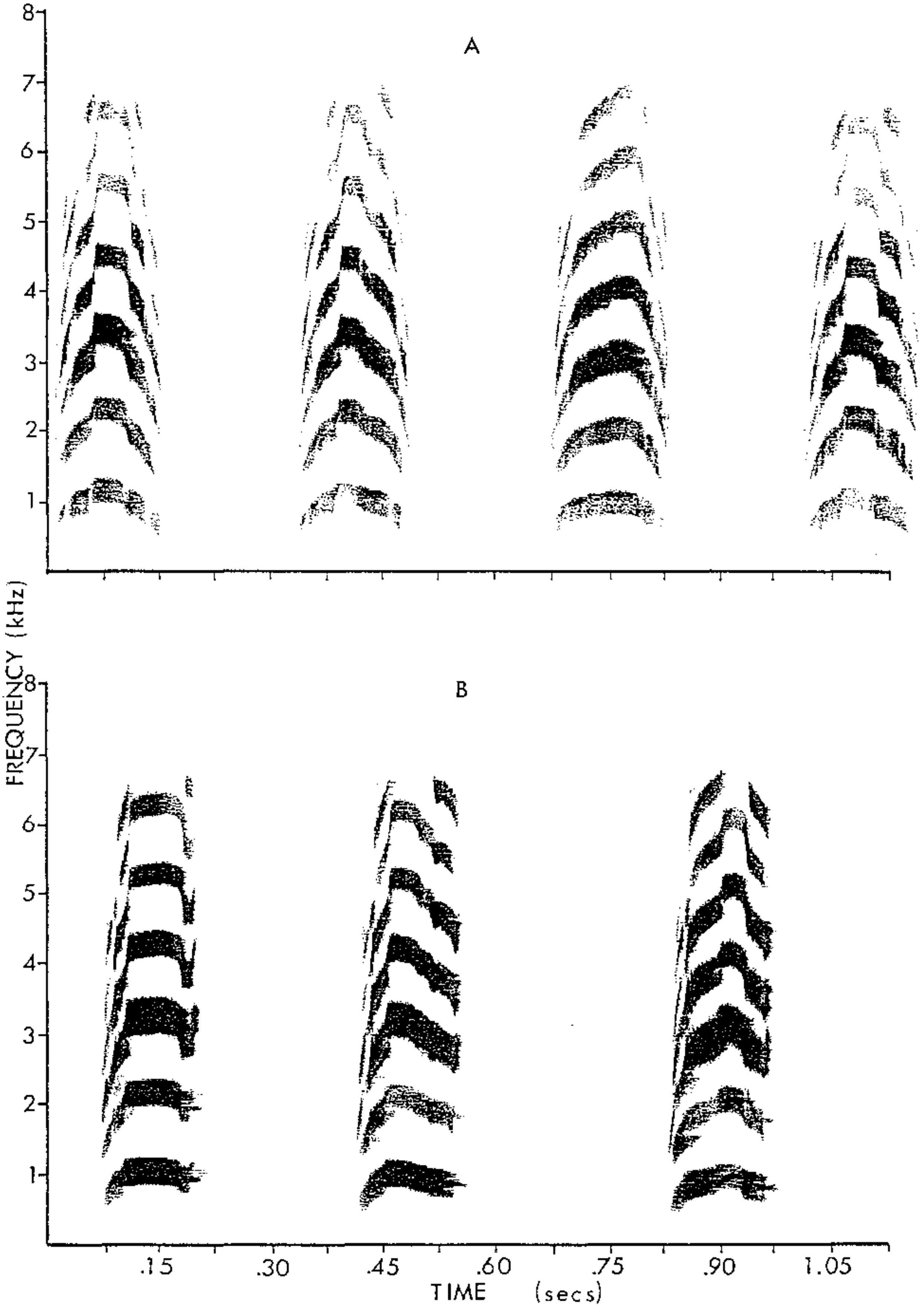


FIGURE 5.18 Variation in alarm call within individuals

a. Individual one, wild black

b. Individual two, wild black

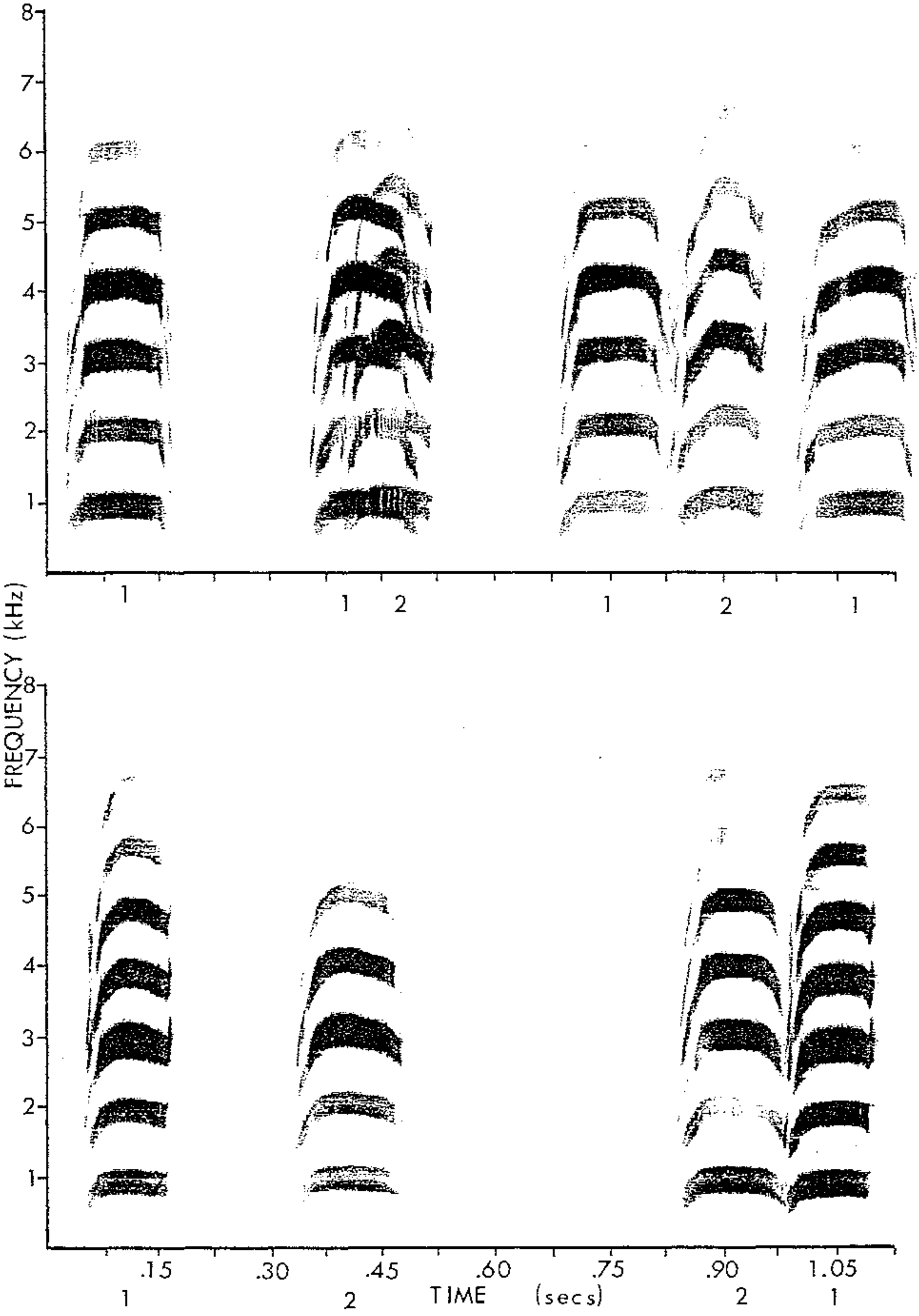


FIGURE 5.19 Variation in alarm call between individuals of a breeding pair

a. Two blacks, Lower Cass River

b. Two blacks, Ahuriri River

1 = Individual one 2 = Individual 2

variables (A-K) was greater within plumage classes than between plumage classes." Table 5.17 summarises the variables for which the null hypothesis was accepted or rejected in a test between all four plumage classes (+ = failure to reject the hypothesis, x = reject the hypothesis).

Table 5.17 Summary of ANOVA treatments within and between all plumage classes

VARIABLE

A	B	C	D	E	F	G	H	I	J	K
+	+	x	x	x	+	+	+	+	+	+

The null hypothesis was rejected only for variables C, D and E. The mean, standard deviation (sd) and range of each variable is presented in Table 5.18 for each plumage class. Mean values for each variable tended to progressively increase in a graded manner from the lightest node (1 - pied) through to the darkest node (4 - black) (Figure 5.20).

A second ANOVA was performed on these data, excluding plumage classes 2 and 3 (hybrids). Variation within and between the pied and black classes only were examined.

The null hypothesis stated in this instance was "that variation of each of the alarm call parameters measured (A-K), was greater within a species than between the two species". A summary of these treatments is given in Table 5.19.

Table 5.18 Mean values of measured variables for four plumage classes

	Pied		Light hybrid	
VARIABLE	MEAN (±1SD)	RANGE	MEAN (±1SD)	RANGE
A	111.5 ± 11.0	83.0 - 143.4	108.4 ± 18.6	86.8 - 169.9
B	609.8 ± 78.4	462.0 - 808.5	622.5 ± 31.9	539.0 - 731.5
C	899.4 ± 94.7	731.5 - 1078.0	924.3 ± 68.8	808.5 - 1078.0
D	752.4 ± 129.7	539.0 - 1116.5	820.0 ± 96.2	654.5 - 1039.5
E	905.5 ± 97.3	731.5 - 1116.5	926.2 ± 69.5	808.5 - 1078.0
F	1.3 ± 12.7	-30.2 - 52.8	-1.7 ± 8.7	-30.2 - 37.7
G	257.2 ± 154.1	120.8 - 1313.7	319.7 ± 78.1	218.9 - 641.7
H	244.4 ± 113.1	120.8 - 1034.3	312.1 ± 85.1	98.1 - 641.7

	Dark hybrid		Black	
VARIABLE	MEAN (±1SD)	RANGE	MEAN (±1SD)	RANGE
A	126.1 ± 23.5	79.2 - 181.2	122.3 ± 19.8	75.5 - 173.6
B	669.6 ± 79.8	462.0 - 885.5	653.1 ± 88.9	385.0 - 808.5
C	949.1 ± 61.3	770.0 - 1116.5	981.5 ± 93.7	770.0 - 1155.0
D	819.4 ± 96.1	539.0 - 1001.0	867.0 ± 122.1	462.0 - 1116.5
E	957.0 ± 60.1	770.0 - 1116.5	988.1 ± 94.7	770.0 - 1155.0
F	4.9 ± 21.2	-49.1 - 90.6	5.1 ± 17.3	-30.2 - 67.9
G	353.0 ± 171.5	90.6 - 1200.4	335.3 ± 167.4	120.8 - 1147.6
H	354.1 ± 169.7	90.6 - 1200.4	328.4 ± 159.7	120.8 - 1147.6

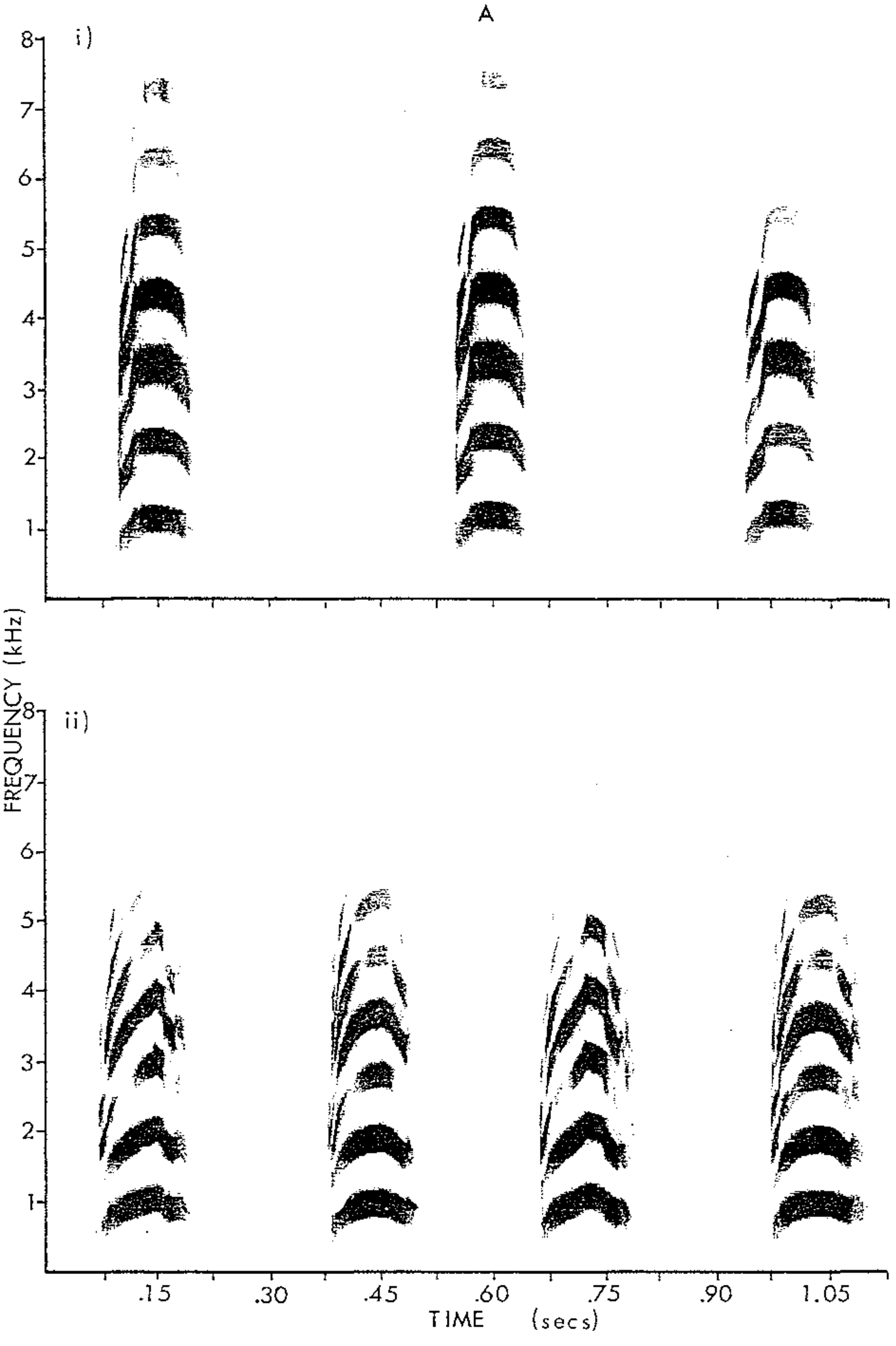


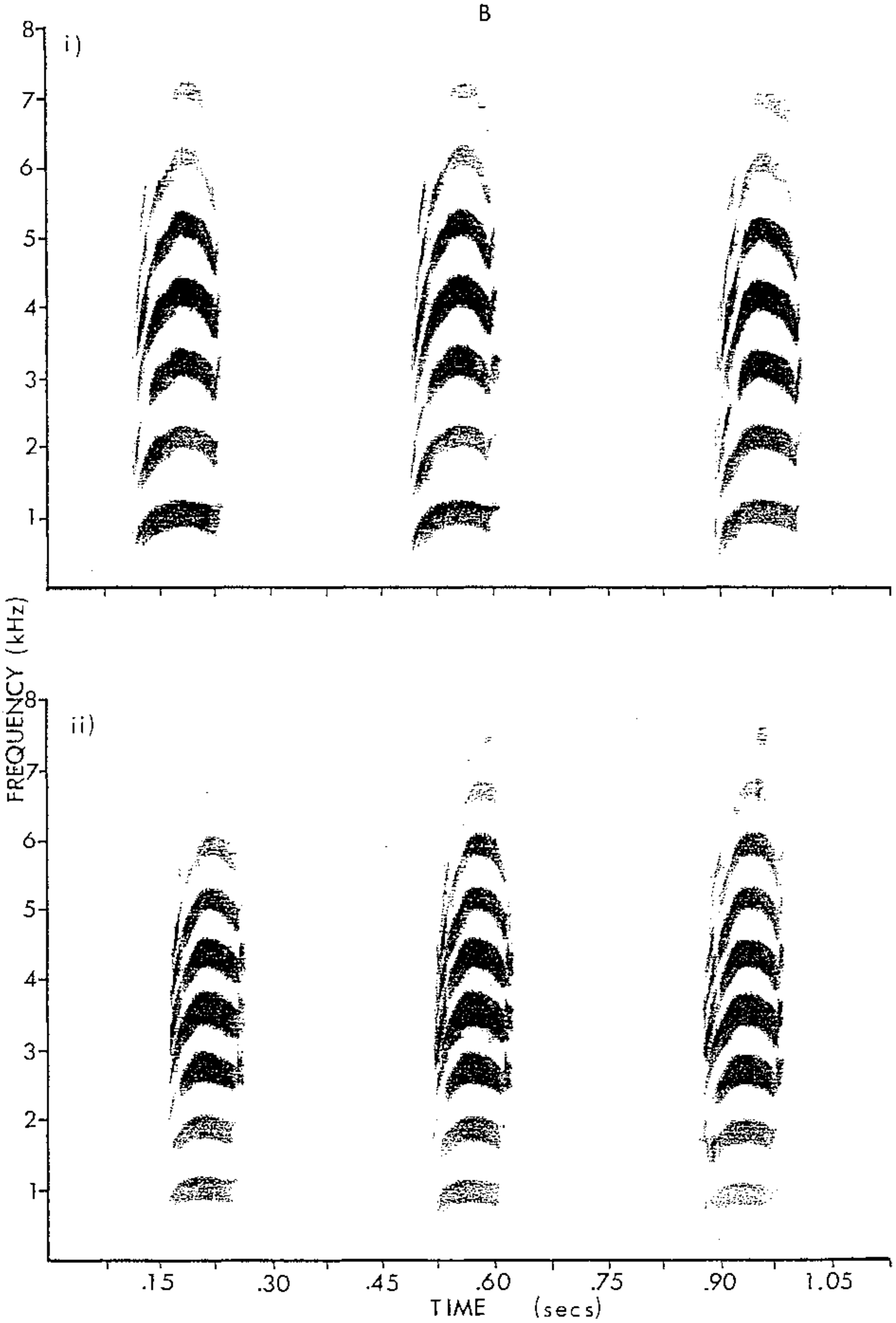
FIGURE 5.20 Interspecific variation in alarm calls of all plumage classes

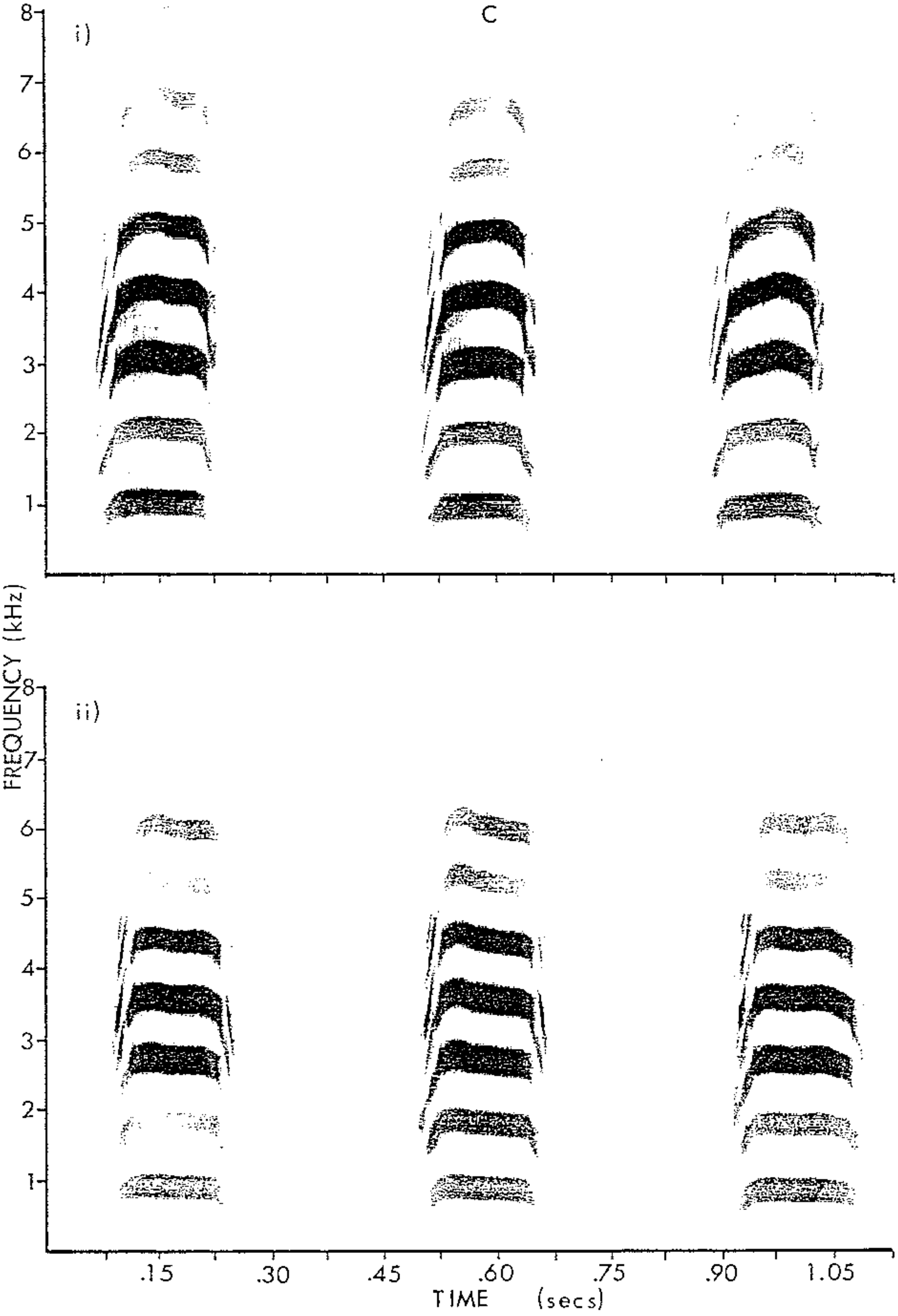
a. Pied stilts i) Individual one ii) Individual two

b. Light hybrids i) Node B/C ii) Node E

c. Dark hybrids i) Node F ii) Node G

d. Black stilts i) Individual one ii) Individual two


B
i)
ii)
8
7
6
5
4
3
2
1
FREQUENCY (kHz)
.15
.30
.45
.60
.75
.90
1.05
TIME (secs)


C
i)
ii)
FREQUENCY (kHz)
8
7
6
5
4
3
2
1
.15
.30
.45
.60
.75
.90
1.05
TIME (secs)

D

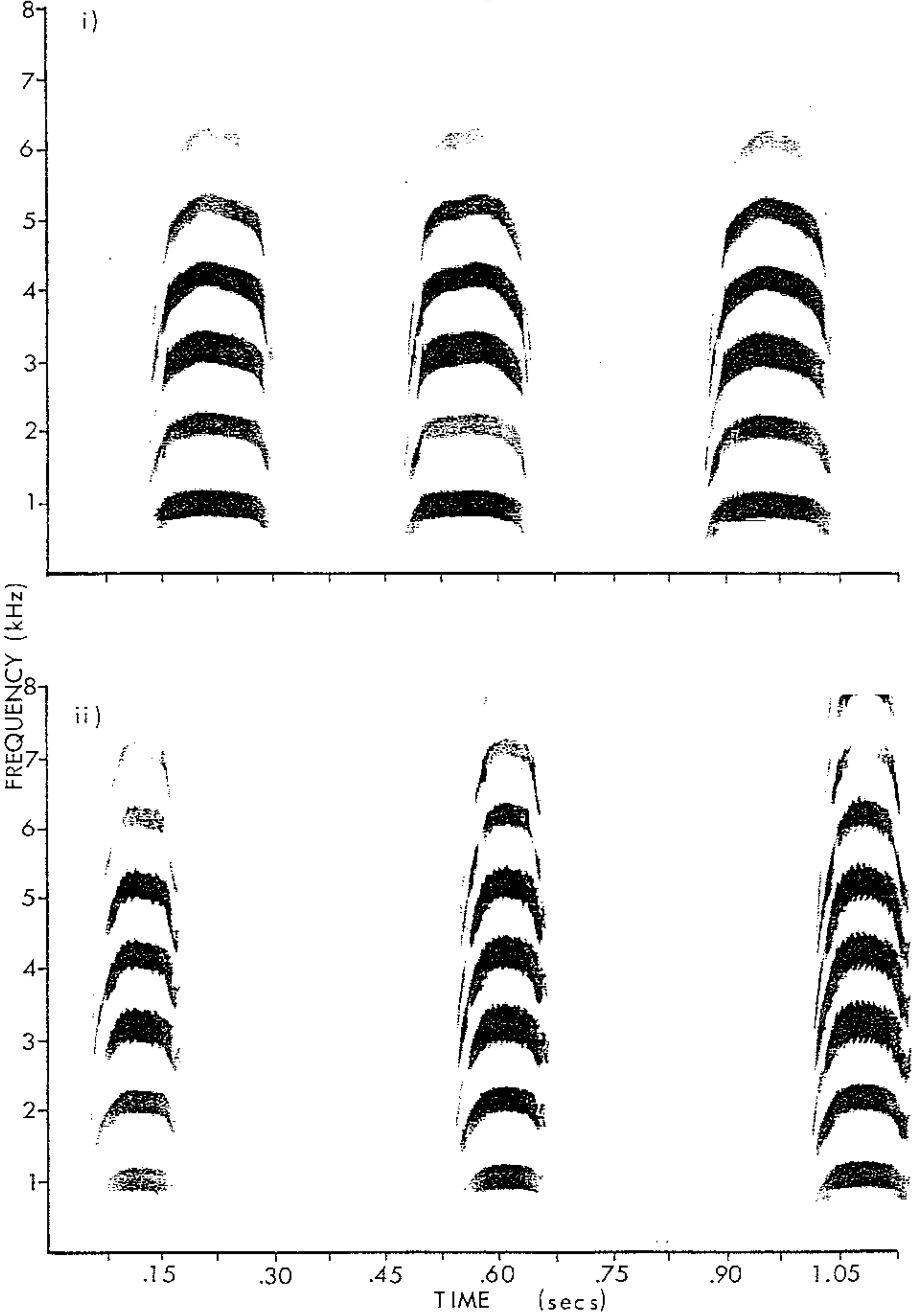


Table 5.19 Summary of ANOVA treatments (between pied and black only)

VARIABLE

A	B	C	D	E	F	G	H	I	J	K
x	+	x	x	x	+	+	x	+	x	+

KEY: x = reject the null hypothesis
+ = accept the null hypothesis
at the 0.05 significance level.

The stated hypothesis was rejected for variables A,C,D,E,H, and J but accepted for the remaining five variables.

Between-node variation was significantly greater than within-node variation for the first six parameters. Figure 5.21 illustrates calls of a black stilt and a pied stilt on one sonagram.

5.4 DISCUSSION

Eleven adult and four juvenile call types were identified and described for captive black stilts. The size of their call repertoire was comparable to that described for other recurvirostrids (Makkink 1936, Adret 1982, Goriup 1982, Cramp and Simmons 1983). Adret (1982) described ten distinct sound classes for the European avocet in the perinatal phase alone. Adret suggested that not all calls were independent as some progressed into others. Cramp and Simmons (1983) described eleven adult and three juvenile calls or variants for European avocets (based on Makkink's (1936) study). Four broad groups of stilt calls were also recognised (Cramp and Simmons 1983). The vocabulary of black-winged stilts (Goriup 1982) was not large, but was comprised of only a few single notes arranged more or less continuously according to circumstances.

All black stilt calls recorded in captivity and in the wild were structurally simple. They were of moderate or extremely short length, low in fundamental frequency (except juvenile calls) and generally rich

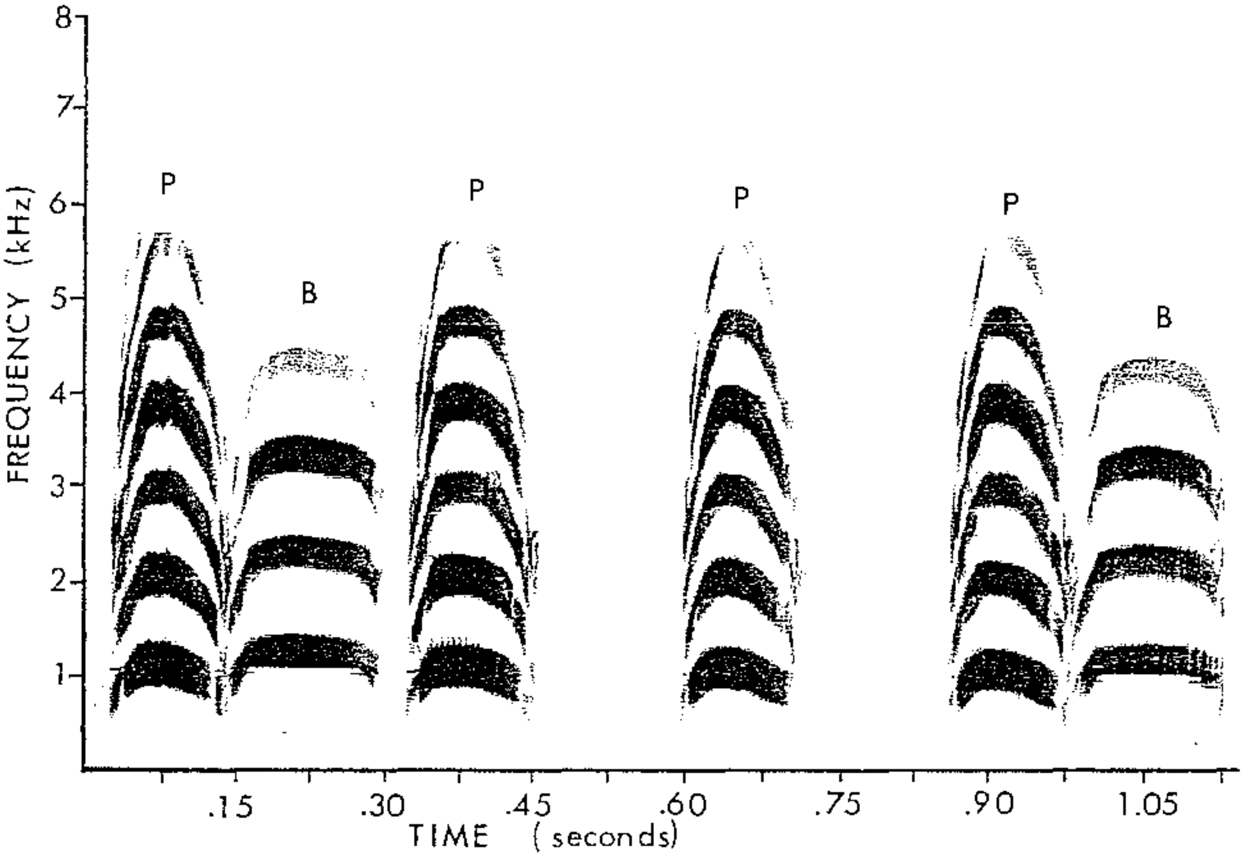


FIGURE 5.21 Comparison of pied and black stilt alarm calls
P = Pied stilt B = Black stilt

in harmonics. These structural characteristics are all typical of the calls of many shorebird species (Miller 1984), although there is considerable variation within and between species. Vocal signals propagated to cover long distances (such as the wide open lotic environment of the Waitaki Basin) are generally high in energy and low in frequency (Miller 1984). They tend also to be spectrally pure, with simple or no amplitude modulation. They are stereotyped and repetitive to compete with background noise and improve locatability of the sender (Miller 1984). Black stilt calls (particularly the yap and yark) appeared to correspond with at least these latter features (i.e., they were stereotyped, repetitive and low in frequency).

All call types were recorded primarily from the focal pair. Paired birds generally communicate with one another in numerous contexts such as changing over at the nest, maintaining contact during foraging and warning of potential dangers. Response or antiphonal calling is common amoung paired shorebirds (Miller 1984). Examples of these calls in the captive stilt repertoire were staccato notes. Although calls of paired birds overlapped temporally, they did not qualify as "duets" under criteria outlined by Farabaugh (1982).

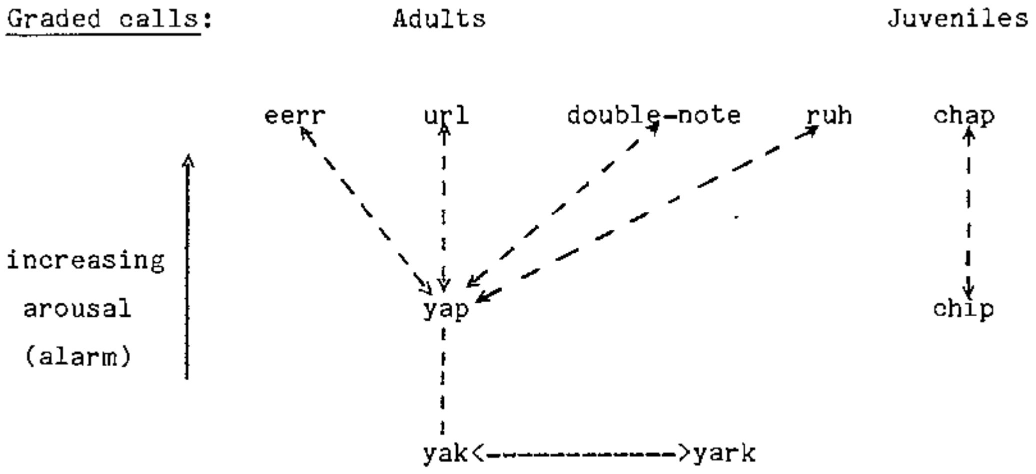
Various authors (Makkink 1936, Hamilton 1975, Goriup 1982, Cramp and Simmons 1983) have suggested or implied that avocets and stilts give distinctive calls during each behavioural display. Sordahl (1980) was convinced however, that the "American avocet and black-necked stilt at least, have a variable or graded vocal system which would be difficult to analyse functionally". A preliminary attempt by Wollemann and Olazy (1977) at analysis of European avocet alarm calls also indicated a graded nature of the system.

The calls of black stilts in captivity and in the wild exhibited the type of graded system referred to by these authors. A group of calls given predominately in an alarm context i.e., yap, eerr, url and double-note calls were most noticeably intergraded.

Variation of behavioural response of captive stilts toward aerial predators has been described in Chapter Four. Response differed with distance of the predator and therefore the degree of danger elicited by its presence. Grading of alarm calls followed the same pattern, with simple yaps progressing into eerr or url calls as humans or harrier hawks (respectively) moved closer to the caller. Alarm calls of black-winged stilts also differ as a function of predator distance from the caller. Wollemann (1978) described two kinds of alarm call of this species. A short, rapidly repeated sound was emitted as the "person or thing" releasing the excitement was farthest from the bird. A second, longer call repeated less often, was given as the "person" neared the vocalising stilt.

A similiar grading between yap, yark and yak calls was also heard. Without further analysis and larger sample sizes, the relationships of these calls to one another cannot be presently defined more than is simply illustrated in Figure 5.22.

Figure 5.22 Hypothetical relationships of black stilt call types



Discrete calls:

Adults	Juveniles
pit	pip
tw-ink	
tip	
staccato	

Some call types were relatively discrete entities eg., pit, tw-ink, tip and staccato calls of the adults and the pip call of hatching chicks. These calls were generally heard being given in one context only eg., tw-ink call during bathing, staccato notes by paired birds over a nest-site and ruh calls during close approaches of humans. In the absence of prior experience, the breeding pair emitted calls similiar to those heard in the wild population eg., staccato calls at nest-sites and url calls toward harrier hawks and magpies, indicating an innate basis to these vocalisations.

In addition to examining structural variation between call types, variation was also investigated within a call type of captive and wild stilts. I focussed on one particular call (the common alarm yap) and assessed the extent to which it was graded i) within and between individuals and ii) within and between the two closely related species (pied stilt, black stilt) and their hybrids.

Yap calls varied significantly more between individuals of the same plumage class than within individuals. The only exceptions to this were three parameters within the light hybrid class.

Forsythe (1970) showed by spectrographic analysis, that considerable variation existed in the calls of Numenius americanus, the long-billed curlew. Individual notes varied in length and spacing but not in frequency. Similarly, Baker (1982) found "purr" calls of adult Dunlins Calidris alpina to be individually distinctive and he suggested that this might aid parent-young recognition in a situation where mixing of broods during foraging activity was possible.

Even though the mechanism involved in across-individual variation in calls of similiar plumage was unknown, it was possible that individuality in calls aided in recognition of mates, offspring or adjacent neighbours. Individulity in alarm calls may also encode information about the characteristics of the caller. Variation might be due to a number of correlates including age, sex or pairing status of the caller, its geographic origin or mechanism of sound production i.e., physiological, anatomical and neural factors (Miller 1983).

Sordahl (1980) noted a tendency for female avocets for example, to have slightly higher voices than males, but individual variation and the graded nature of the calls led to considerable overlap. I was statistically unable to examine any potential sexual differences in call parameters of black stilts (as most sample birds in the wild population were unbanded and therefore unable to be sexed). It appeared (based on my auditory perception of calls and on that of other workers involved with black stilts) that there was a difference in call pitch between the two individuals of some breeding pairs (eg., the breeding female's alarm call in captivity had a slightly lower fundamental frequency than that of the male). Individual differences in frequency of the fundamental within wild pairs was also evident from sonagrams. A larger sample from known sex birds is required though, before this difference might be demonstrated to correlate with sex of the caller.

Between-individual differences and similarities of call characteristics as determined by the human ear or by technical analysis need not agree with perception as achieved by birds (Becker 1982). It is necessary to support these findings with tests using the reactions of individuals to calls of intra- and inter-specifics.

Interspecific variation between alarm yaps of pied stilts and black stilts was demonstrated in section 5.3.2.2, for six parameters of these calls. Although closely related sympatric species which live together in one area often differ markedly in their vocalisations (Becker 1982), marked convergence of calls has been demonstrated in some sympatric species eg., alarm and aggressive calls of Parus Major, P. caeruleus and P. palustris (Latimer 1977).

Pied stilts and black stilts exhibited significant species differences in alarm call parameters eg., frequency of the fundamental and call duration. There was considerable overlap across the two species in range of these parameters. This is perhaps not surprising, considering the graded nature of the yap call and the suggestion that both species are of similiar ancestral stock (Pierce 1984b). Mean values for these call parameters tended to progressively increase in a graded manner from the lightest plumage class (pied) through to the darkest.

The extent of melanism in stilts reflects the genetic background of these birds eg., F1 crosses of a pied and a black parent produced stilts which are intermediate in plumage and a black x a node E/F pairing produced birds of very dark plumage (node G-I) (Pierce 1982). In most cases of hybrid recoveries by Pierce, there were no throwbacks to parental plumage and inherited plumages were intermediate between the two parents (Pierce 1984b). If the melanism of individual plumage has a genetic basis as suggested by Pierce, it follows that progressive variation in alarm call parameters across plumage classes may also have a genetic link.

Most sounds in non-passerines appear to be innate (Becker 1982). Through prenatal or early post-hatching experience of parent vocalisations and through visual stimuli, the preference for species-specific sounds is increased (Becker 1982). Alternately, this preference can be masked through imprinting on another species. Busse (1977-cited in Becker 1982) showed that exchanges of arctic tern _Sterna paradisaea_ and common tern _S. hirundo_ chicks resulted in young birds becoming imprinted on sounds of the other species. This point has particular relevance in relation to imprinting of black stilt chick on calls of their foster parents. It is unlikely that this would be a problem in management of this species in the wild, although the possibility of imprinting on sounds of foster parents still exists (in conjunction with other features of imprinting discussed in Chapter Six). Considerable overlap in structure of yap calls between pied stilts, black stilts and their hybrids resulted in only subtle auditory differences (to the human ear). How stilts perceive these differences and whether young stilts could become imprinted on sounds other than that of their own species is unknown.

CHAPTER SIX

SYNTHESIS AND RECOMMENDATIONS FOR CAPTIVE MANAGEMENT

6.1 Introduction

6.1.1 Background

Eight eggs were removed in October 1979 from a dwindling population of less than 50 adult black stilts in the MacKenzie Basin, South Canterbury. These eggs were transferred to the National Wildlife Centre at Mount Bruce in the Wairarapa, in an attempt to establish a breeding population in captivity.

Although all eight eggs transferred to Mount Bruce successfully hatched and seven of these stilts still survive at six years of age, only the one pair originating from these eggs has successfully bred. Ten clutches were laid by this focal brother-sister pair during three breeding seasons (i.e., between January 1983 and December 1984). Of these ten clutches, six were transferred back into the wild population by cross-fostering to pied/hybrid parents. One clutch was hand-reared in captivity and the other three clutches were reared by the parent birds.

I collated an ethogram which included all observed behavioural patterns exhibited by the eight captive-reared birds between January 1982 and February 1985. In particular, the daily and seasonal activity and breeding biology of a focal pair of stilts was described and quantified. Eight chicks which were hatched and reared by this pair were monitored and their physical and behavioural development described. Finally, vocalisations of captive and wild stilts were recorded and categorised according to structure and were used to supplement observations on behavioural patterns.

Now that successful breeding (however limited) of this species in captivity has been achieved, the options for future management of captive-produced progeny need to be considered.

6.1.2 Future management options

There are three options for the management of captive-produced progeny;

i) The transfer of eggs to the MacKenzie Basin for cross-fostering to pairs of pied, black or hybrid stilts;

ii) Rearing of chicks in captivity, either by hand or by parent birds for subsequent release into the wild population as sub-adults; and

iii) Retention of progeny in captivity to increase existing breeding stock.

Figure 6.1 illustrates these three options. On the basis of my results presented in the first five chapters and with reference to related literature, I will elaborate each option (section 6.2). In particular, the unique problems associated with each management step are emphasized. Problems in establishing captive breeding pairs are also discussed (section 6.2.1). Results from the questionnaire to institutions holding recurvirostrids (appendix two) are incorporated into the discussion of pairing problems.

6.1.3 Management suggestion

Finally, I propose a novel strategy for inclusion of captive-reared progeny in the overall management of this species in the wild.

6.2 Management options and associated problems

6.2.1 Pair formation

> "How does one sex monomorphic species; what constitutes compatibility; and what are the species' essential requirements for food, shelter, and successful reproduction? With Whooping cranes, as with many other endangered species, success is often the hard-won fruit of several seasons and the insight of many biologists. It is still as much an art as science, and patience is an essential antidote to disappointment"
>
> (Kepler 1978)

One of the major factors limiting the formation of pairs and successful

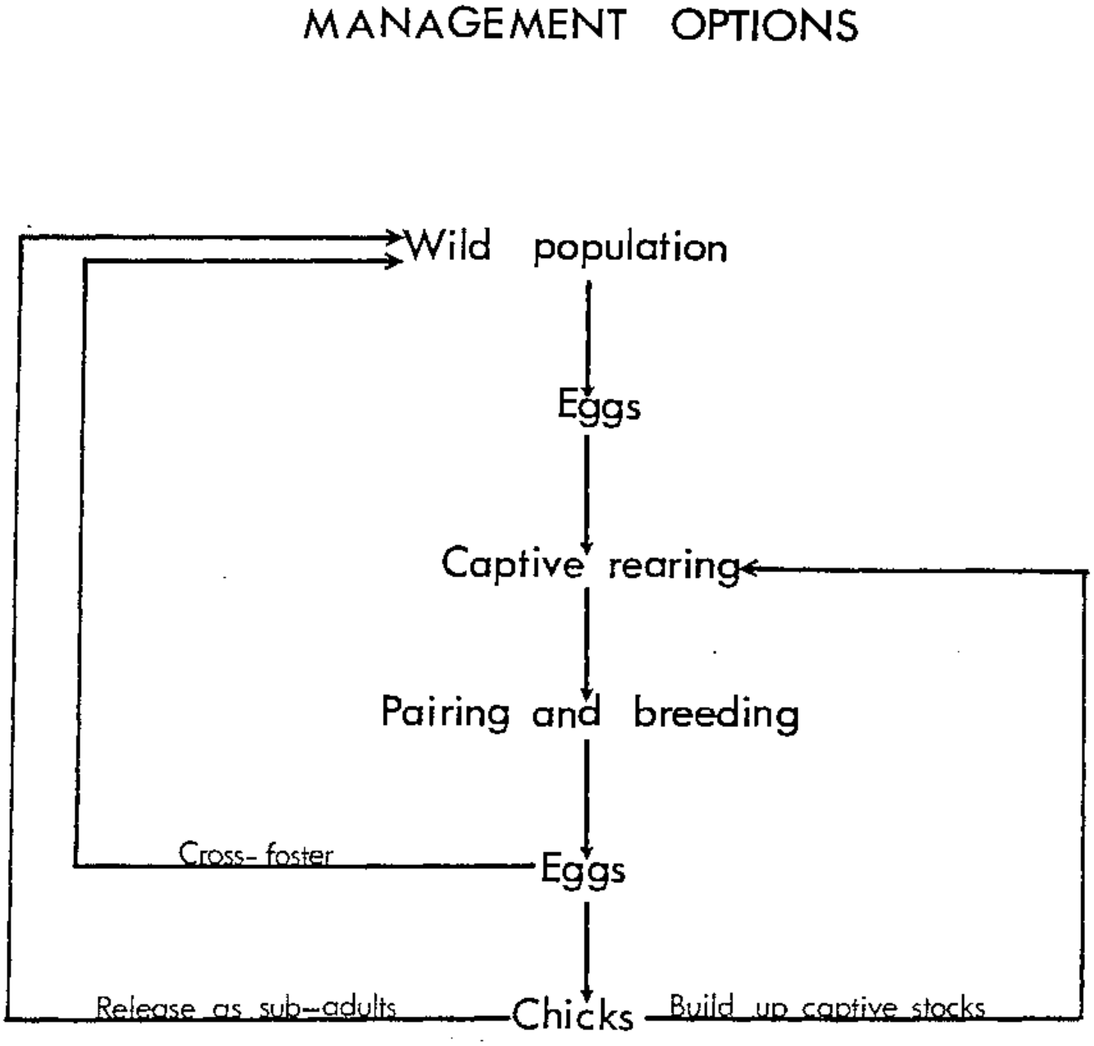


FIGURE 6.1 Management options for captive-reared black stilts

reproduction of rare species in captivity has been the inability of aviculturalists to accurately determine the sex of their birds (Mengden and Stock 1976). Sexual monomorphism, coupled with the tendency of birds in captivity to develop abnormal sexual patterns which mimic that of the opposite sex, have resulted in the use of many different techniques for determination of sexes. The three most reliable methods used in sexing other rare species have been laparoscopy, probing and chromosomal analysis (Mengden and Stock 1976). But each of these methods has associated problems and inaccuracies. Laparoscopy involves making an incision through the body wall to observe whether ovaries or testes are present. This method has been successfully used to determine sexes of Recurvirostridae held at the Dallas (Toffic, pers. comm.), Los Angeles, Taronga (Phipps, pers.comm.) and New York Bronx zoos. It carries however, the risk of injury or death from anaesthesia. This makes it impractical for use on black stilts unless used by workers familiar with their anatomy and practised in laparoscopy of similiar species.

Chromosomal analysis has been used to determine the sexes of cranes in captivity (Archibald 1974) and was also attempted with black stilts at Mount Bruce. Heteromorphism of paired chromosomes is indicative of the female sex in avian species, whereas males have identically paired chromosomal elements (Mengden and Stock 1976). Feather pulp or blood samples may be used in chromosomal preparations, both of which were unsuccessful in producing results for the study birds. Technical difficulties with these samples may be eliminated in future practice and could provide a more reliable method of sexing.

Analysis of faecal steroids reduces stresses involved in techniques such as laparoscopy and blood sample collection. This technique pioneered by Czekala and Lasley (1977), involving comparison of the amount of sexual steroids excreted by males and females in faecal material, has been used successfully in sexing the Indian jungle fowl (Gallus gallus murghi). Results from faecal steroid analysis of captive black stilts were relatively consistent with both behavioural observation and the tactile examination of pubic bone width. Application of faecal analysis in future would be aided by taking repeated samples throughout the year and from known sex birds, to determine a reliable cut-off limit for the ratio of oestrogen/testosterone in males and females.

Behavioural observations of the eight adult stilts were the most consistent and reliable sexing method over the period of this study. All stilts remained behaviourally consistent with the gender to which they were initially allocated. Sexing of recurvirostrids by behavioural observation has been used successfully in most zoos returning the questionnaire in appendix two.

Even though captive stilts were tentatively sexed, problems remained in their breeding management. Black stilts are an aggressive, territorial species which nest as solitary pairs (Pierce 1982). Pair formation occurs after a long (20+ days) period of persistent association with conspecifics of the opposite sex (Pierce 1982). Black stilts in captivity were initially housed as pairs on the basis of sexing results. Only one pair (from the same clutch) proved compatible, despite manipulations of all other birds to induce re-pairing. Intra- and inter-pair aggression was intense, especially during the breeding season. The housing of pairs in adjacent aviaries resulted in redirection of aggression toward a mate within two separate pairs. One pair copulated when all neighbours were removed. Aggression within this pair also ceased.

Shorebirds in captivity usually develop dominance relationships in which one bird assumes dominance over others and controls their access to food and water trays (Serventy et. al., 1962). Breeding by ringed plovers *Charadrius dubius*, spotted redshanks *Tringa erythropus* and common sandpipers *Actitis hypoleucos*, all necessitated the removal of conspecifics and other individuals from their aviaries due to intense aggression (Koivisto 1977). Similiarly, captive cranes require separation of pairs to avoid fighting (Sauey and Brown 1977, Kepler 1978). However, in some cases the presence of conspecifics in a flocking situation or as neighbouring birds stimulates reproductive activity. Courtship and reproduction in European avocets (a colonial species) (Salzert and Schelshorn 1979) and turnstones *Arenaria interpres* (Kovisto 1977) has been stimulated by the presence of neighbouring or flock birds. Vocal contact between visually separated whooping crane *Grus americana* pairs may stimulate courtship in adjacent birds (Sauey and Brown 1977, Kepler 1978). Housing which allows visual contact is avoided for cranes, because it tends to distract birds and impede reproduction (Sauey and Brown 1977).

Stimulation of breeding activity resulting from the presence of neighbouring conspecifics, has been demonstrated for captive takahe (Notornis mantelli). This species was held at Mount Bruce from 1958 until 1972 but no fertile eggs were laid during this time. Improvements in diet, social stimulation and in layout of enclosures, did not result in laying of fertile eggs. It was not until 1972 when a "neutral zone" was erected between adjacent aviaries, allowing territorial encounters of neighbouring takahe while gradually reducing fighting and trespassing, that the first fertile eggs were laid (Reid 1977).

Neighbouring groups of mammals in visual contact have been suggested by Eisenburg and Kleiman (1977), to exert inhibitory influences on one another, with one pair emerging dominant and exhibiting the only successful reproduction. Perth zoo (Gaynor, pers. comm.) reported some intra-pair but primarily inter-pair aggression when stilts were in sight of one another, particularly during the nesting season. Deficiencies in aspects of the social environment (eg., proximity, sex or number of neighbouring conspecifics) of this and other captive species can therefore inhibit behaviour which may otherwise occur under a different housing regime. Experimental demonstrations of deficiencies in the social unit of black stilts in captivity, were difficult to elicit during the study. Limitations on the number of study animals (1.4.1) and the availability of suitable aviaries, did not allow manipulation of social and environmental factors to induce breeding.

Dominance not only between pairs, but also within pairs has been shown to be an important variable affecting reproduction in captivity (Kepler 1978). Young cranes for example, become sexually retarded by dominance relationships which develop naturally in a flock, if these birds are penned together for more than three years. Aggression within pairs may result from overcrowding, forcing animals to violate anothers' "individual distance" (Innis et. al., 1985). The minimum area requirement for a number of individuals placed in an aviary is difficult to determine. An approximation of the amount of space desirable for a group of given size, might be based on observed minimum preferred distances between animals (Innis et. al., 1985). Wild black stilt pairs tend to nest several kilometres apart, although some pairs have nested within 100 m of other stilts (Pierce 1982). It is unlikely that this wide spacing pattern is neccessary for captive stilts. Two factors which may determine the size requirement of aviaries for housing stilt pairs may be food quality (since quantity was not limited) or minimum preferred distances between conspecifics. Neither of these aspects of the environment were investigated in this study.

Specific niche requirements are as important to successful breeding as sufficient aviary size (Eisenberg and Kleiman 1977). Breeding requirements are not always obvious and may require frequent manipulation of cage artifacts during cage design. The focal study pair tended to nest on islands surrounded by water and copulate over shallow water. It is possible that an expanse of water is a requirement for successful breeding. It is also possible that a natural food supply and particularly some component of it (eg., silt depth suitable for invertebrates) facilitates breeding.

Birds which are allowed to choose their own mates are more likely to form successful breeding pairs than those which are arbitarily paired. For example, avocet breeding pairs have proved easier to form in captivity than have stilt pairs. This stems mainly from housing avocets in groups since colonial nesting occurs naturally in the wild and individuals are able to have a mate choice. Stilts in captivity tend to be more aggressive if housed with conspecifics and pairs are usually separated as they form. Arbitrary pairing of <u>H. h. mexicanus</u> at Dallas zoo after surgical sexing was not successful in establishing productive pairs. The only pair to regularly breed there had been given a choice of mates. Flocking has also been the most successful method of establishing pairs of whooping cranes in captivity (Sauey and Brown 1977). The single breeding pair in this study, although paired on the basis of sexing results, were housed together from hatching until two years of age and therefore may have formed a pair bond prior to manipulation.

The future success in forming captive breeding pairs therefore appears to lie in;

i) accurate determination of the sex of individuals;

ii) housing of known sex birds in a situation which allows individuals to choose their own mates;

iii) detecting a balance in the social environment of pairs, between adequate inter-pair stimulation of breeding activity and the avoidance of redirected aggression as a result of the proximity to neighbours; and

iv) definition of minimal/optimal requirements of aviary size and design for breeding.

6.2.2 Cross-fostering of eggs

> "Cross-fostering is a technique that has great potential for extending the range of an endangered species into new areas or for re-establishing populations in vacant areas of a former range, where a suitable foster species exists... But depending on the species, cross-fostering can also result in maladaptive behaviours, and sexual imprinting on the foster species is certainly one of the most serious of these".
>
> (Cade 1978)

Cross-fostering has been successfully used as a management technique for whooping cranes (Drewien and Bizeau 1978, Kepler 1978), ospreys *Pandion haliaetus* (Spitzer 1978), other birds of prey (Fyfe et. al., 1978), yellow warblers *Dendroica petechia* (as a preliminary investigation for use with the closely related endangered Kirtlands warbler *D. kirtlandii*) (Brewer and Morris 1984), Newells race of the Manx shearwater *Puffinus puffinus newelli* (Vernon Byrd et. al.,1984) and the Chatham Island black robin *Petroica traversi* (Merton 1981).

Cross-fostering of eggs to pied and hybrid stilt foster parents has been employed by the New Zealand Wildlife Service as a management technique for black stilts since 1981. The merit of this method lay in the vulnerability of early nests to predation and flooding and the ability of black stilts to relay after egg removal (Pierce 1982). Annual reproductive output of the single black stilt population, has been increased by combining cross-fostering with successive clutch removals. Eggs produced in captivity have been included in the cross-fostering programme of the 1983, 1984 and 1985 breeding seasons.

Use of captive breeding pairs as a potential source of eggs for cross-fostering has particular merit for use in endangered species management. Intensive manipulation of these pairs is possible, resulting in higher productivity than may be achieved within the wild population. The single focal pair of this study produced five clutches of eggs in the 1984/85 breeding season and although fertility of these eggs was lower than that in the wild, these eggs still represented 20% of all eggs cross-fostered during that season. Eleven wild pairs produced the remaining 80% of eggs. Four clutches per season is the maximum that has been laid by any one wild pair (Pierce 1982) and usually only one or sometimes two clutches are removed (Nilsson 1983,84). Problems associated with wild pairs "disappearing" after egg removal and the limitations imposed by food availability as an energy requirement for production of further clutches are eliminated under captive conditions. The ability of the focal pair to produce five clutches within a season, was achieved partly as a result of short relaying periods (range = 8-13 days, mean = 9.7 and mode = 9) and a longer laying season. Supplementary feeding assisted in meeting the energy demands for production of eggs.

High productivity of whooping cranes in captivity has also contributed significantly to management of this species in the wild. In 1977, five captive pairs produced 40% of the total whooping crane eggs obtained that season, with seventeen wild pairs accounting for the remainder. One whooping crane pair was capable of producing five clutches per season (Kepler 1978).

"We may be able to increase production, but how much better off is the population having been manipulated, than if it was left alone?" (Cade 1978). Management of rare New Zealand species has concentrated in the past on increasing the recruitment of juveniles into the adult population. A wide variety of management techniques have been employed to accomplish this including predator control, translocation to predator free islands, captive breeding, inducement of multiple laying and cross-fostering of eggs. The technique which probably constitutes the greatest risk in terms of long-term behavioural characteristics of a population is that of cross-fostering.

Three potentially serious problems associated with use of cross-fostering as an option for eggs produced in captivity are;

i) lack of synchronisation between captive laying
and foster parent laying in the wild population;
ii) sexual imprinting of fostered chicks onto the
parent species; and

iii) dispersal of juveniles fostered to pied and hybrid parents out of the MacKenzie Basin.

The laying period of the focal pair spanned September 18 (1983) to January 28 (1983). Comparatively, wild black stilt pairs lay from mid-September to early December and pied/hybrid stilts slightly later (Pierce 1982). Foster parent availability for eggs produced in captivity then, is most critical at the beginning and end of this period. Final clutches laid in captivity have been especially vulnerable to lack of suitable foster parents and so have been retained to increase captive stocks. Also, January to March in the wild sees the dispersal of juvenile and adult cats and ferrets. This places a high predation pressure on late-nesting stilts (Pierce 1982). Cross-fostering of the final clutch laid in captivity each season has resulted in loss of these eggs or of chicks.

Foster species chosen should be similiar enough in breeding biology and type of social system to the endangered species being managed, to ensure successful hatching and rearing of fostered chicks. But sufficient ethological, ecological and physical differences need to exist to prevent hybrid matings between the two species (Kepler 1978). A choice of foster parent species is not always available however, as exemplified by the management restrictions placed on black stilts.

Introgressive hybridisation between black and pied stilts occurs naturally in the wild, probably owing to a shortage of potential mates (Pierce 1984b). The ability of black stilts to maintain a small population over the last 20-25 years, can be explained by their wintering apart from pieds and their preferential choice of dark plumage mates (Pierce 1984b). Hybridisation of the two species has always been a concern in their management (Veitch 1985), but the productivity of such unions has been reduced by using hybrid pairs to rear black stilt chicks in lieu of their own. In the past three years, 23 chicks have been reared to fledging by two black adults, 10 by one black parent and one other stilt and the remaining 14 by hybrid or pied parents (Veitch 1985). Although removal of hybrid eggs may reduce the incidence of intermediate forms, the practice may also result in fewer potential foster parents in the future and a reduction in black stilt heterozygosity. The decreased availability of darker plumage birds from which to choose a mate may result in black stilts pairing with lighter hybrids/pieds.

Unfortunately, since many endangered species are slow to reach maturity, it often takes several years to know the outcome of cross-fostering in terms of adult sexual response (Cade 1978). With most rare species this time is not generally available since numbers are critically low before intensive manipulation is attempted. Immediate action is then essential to prevent extinction of the species.

Sexual imprinting of birds onto their foster parents is well known in precocial species (Immelman 1972). Only one example of the effect of fostering on recurvirostrid behaviour has been published (Triplet and Sauer 1983). The "natural" adoption of a European avocet chick by pied oystercatchers *Haematopus ostralegus* resulted in this individual acquiring some of its "parents" behavioural patterns. Despite the ability of avocet chicks to forage independently from hatching, the chick studied adapted to being fed by its parents. Most behaviour retained normal avocet patterns however, eg., scratching, preening, pecking, plunging and sieving (Triplet and Sauer 1983). Experiments involving mate preference testing of captive-reared juveniles at Mount Bruce were not possible, because early social experience of these birds was variable. Cross-fostered mallards *Anas platyrhynchos* (Kruijt et. al., 1982) and snow geese *Anser caerulescens* (Cooke and McNally 1975, Owen 1980) have a strong tendency to choose mates with the same plumage type as their foster parents. If foster parents were removed, association preferences of snow geese for birds of parental plumage were reversible. It was more likely however, to be maintained through association with birds of identical plumage to the parent birds. Snow geese also choose mates on the basis of their own and sibling colouration (Cooke and McNally 1975). In addition to social experience as an influence on species recognition and mate selection in precocial species, genetic components also play some role. Results of plumage colour and social experience experiments with flocks of Japanese quail *Coturnix coturnix japonica* led Blohowiak and Siegel (1983) to conclude that "genetic mechanisms, sexual imprinting and subsequent long term social experiences, influence optimisation of mate selection". Sexual imprinting reinforced the genetic mechanisms underlying species recognition and mate choice.

Altricial species such as the zebra finch Poephila guttata (Immelman 1972, Sonnemann and Sjolander 1977), herring gulls Larus argentatus and black-backed gulls Larus fuscus (Harris 1970), exhibit mate preferences for the species which raised them. Immelman found though, that reversal of this sexual preference was possible if zebra finch chicks were transferred to their own parents before their 25th day, or if they were reared with conspecifics. The former approach has recently been utilised by the New Zealand Wildlife Service in the black robin cross-fostering programme, after behavioural modification was evident as a result of robins being reared by Chatham Island tits Petroica macrocephala chathamensis (Merton, pers. comm.).

Colour banding has even been shown to influence conspecific mate preferences (Burley et. al., 1982). Zebra finches exhibited preferences for mates with colour bands coinciding with colours that naturally occur in the beak and plumage of this species.

Harris's (1970) cross-fostering experiments with gulls, revealed not only facilitation of hybridisation between species, but a change in migratory habits as well. Herring gulls are non-migratory in Britain but cross-fostered herring gull chicks acquired the migratory habits of their parents (Harris 1970). Only one of the fourteen black stilts reared by pied or hybrid foster parents in the past four years, has been known to have returned to its natal area and was still alive at three years of age (Veitch 1985). Of the ten chicks reared by one black parent, three (i.e., one yearling, one two-year old and one three-year old bird) have been observed back in the basin. Of 23 reared by both black parents, 11 (48%) reached two years old or were still alive as yearlings (Veitch 1985). Lower return rates of cross-fostered black stilt chicks may result from dispersal of these young out of the basin with pied/hybrid foster parents before winter and their subsequent non-return. This possibility is supported by the observation of one banded juvenile at a North Island lake in March 1985. This chick had been cross-fostered to a light hybrid/dark hybrid pair and had not been seen since banding in early 1981.

Removal of pied or hybrid members of a pair as soon as their fostered black stilt chicks fledge, would be advantageous in decreasing the incidence of dispersal out of the natal area (Veitch 1985). Chicks cross-fostered to black x hybrid parents have been observed attached to groups of black stilt juveniles (Nilsson 1983) or loosely associated with non-breeding pied stilts (Nilsson 1984). Early associations of these juveniles may influence later choice of mates.

Despite its associated problems, cross-fostering of black stilt eggs has so far proven successful in increasing recruitment of juveniles into the wild population. Uncertainties involving mate preferences and post-breeding dispersal behaviour of cross-fostered young have been minimised in recent years by using the darkest plumage birds available for parenting. Imprinting on the foster species may be reversible if post-fledging association with other black juveniles occurs. As these birds do not breed until 2-3 years of age, it will be several years before the effects of this method can be evaluated.

6.2.3 Release as sub-adults

> "Many prerequisites must be met before reintroduction [of an endangered species] should be contemplated. Does the wild habitat have the capacity to absorb the reintroduced animals? Does the surplus stock have the right characteristics for release into available habitat? Can the individuals survive the transition from the support and protection of captive management to the harsh realities of the wild? Only when all these questions can be answered satisfactoraly can reintroduction be embarked upon, and even then only if the resources and finance for doing so are available".
>
> (Brambell 1977)

The establishment of a self-sustaining population as a result of reintroduction of a species back into its original habitat has rarely been achieved in endangered species management (Fyfe 1978). Endangered birds are not the best candidates for successful introduction, as they generally have low reproductive success, highly specialised ecological requirements and solitary social organisations. As many populations are small in numbers, they cannot be released en masse (Fyfe 1978).

Five potential problems in release of sub-adults reared in captivity into the wild population are;

i) dispersal back to their natal area (eg., Mount Bruce) after release;

ii) introduction of disease from captivity into the wild;

iii) inappropriate behavioural characteristics of hand-reared stock (eg., taming, lack of predator avoidance response);

iv) release at the wrong time of the year or at an age which does not ensure the highest survival rates;

v) the carrying capacity of the environment into which captive progeny are released may not be sufficient to accomodate the extra individuals.

Site tenacity of released stock has proven a problem with raptorial species in the past (Fyfe 1978). One solution is to keep birds in captivity at the intended release site for a period before their release. This approach has been used with the eagle owl (Bubo bubo) reintoduction programme and was especially successful when captive birds were rearing young (Fyfe 1978). The principle may be applied to release of captive-reared black stilts and will be elaborated on in later discussion.

Careful screening for infectious diseases in birds prior to release is desirable (Cooper 1977). Disease in the stilt population held at Mount Bruce has not yet been evident, although other species held there have been prone to contagious viral infections. Veterinary examination and a period of quarantine is essential for a disease-free translocation.

Instinctive (innate) behaviour necessary for survival in the wild must be presumed to be present in captive-born stock (Brambell 1972). However, much behaviour is learnt or at least perfected by practise and this cannot always occur in captivity. There is an added risk that captive birds may learn behavioural traits which are disadvantageous to it in the wild eg., habituation or taming.

Eight black stilt yearlings hand-reared at Mount Bruce were liberated into a protective exclosure in the MacKenzie basin in October 1981 and January 1982. Although one of these birds was observed four weeks after release, none survived. Two were killed by harrier hawks and all were very tame (Pierce 1982). After release, they foraged among tall vegetation where predators may be hiding, rather than in the open water where wild stilts foraged. Pierce (1982) recommended strongly that "unless the habitat in captive pens was made to resemble that in the wild more closely, and unless precautions be taken to ensure that birds are predator wary, .. there should be no further releases of captive-reared black stilts".

Tameness of captive reared birds is a problem if such progeny are to be returned to the wild (Kear 1977). Some species (eg., mallard) demonstrate an inherent capability to revert to wild behaviour after captive rearing, especially if slowly liberated by a "gentle release" method (Lee and Kruse 1973). Four hybrid stilts reared in captivity, were released on August 11 1981 at Pauatahanui Reserve, Wellington. These birds also did not survive, even though a gentle release method was used.

Under a more "natural" environment than that in which the previously released stilts were reared, captive chicks reared by parent birds during this study demonstrated antipredator responses similiar to those of wild chicks (i.e., freeze, and run and freeze). These behavioural patterns were initiated as a response to the presence of harrier hawks and Australian magpies and the subsequent alarm calls of parent stilts. The breeding male emitted "mobbing" calls when aerial predators passed overhead and chicks responded to these calls, especially in the first two weeks after hatching. These juveniles however, appeared to habituate to the presence of humans and the "freeze, run and freeze" response toward aerial predators waned toward and after fledging. Change in response type may have been the result of normal ontogeny, although this could not be established without a more thorough comparison with chicks reared in the wild. This type of comparison was attempted during two visits to the wild population. Insufficient sampling time, difficulties in observing chicks and infrequent intrusions of aerial species near black stilt chicks, did not allow more than a comparison of response to human intrusion.

The individuals of the focal pair exhibited some innate behavioural patterns and responses to predators. These included stereotyped species-typical nest-building, copulatory, incubation and chick-rearing behavioural patterns, the removal of egg-shell from within a nest of newly-hatched eggs and "mobbing" calls. Some behavioural patterns described in other recurvirostrids were infrequently observed or were not observed at all in captivity eg., flight toward harriers in a similiar manner to that observed toward magpies and humans. This pattern may be learnt only by experience in the wild. During the long family bond period i.e., six months in captivity (pers.obs) and six to eight months in the wild (Pierce 1982), black stilts probably learn about their environment; sources of food, roosting sites, wintering areas, etc. Wild chicks may also learn predator avoidance through experience, which would not be possible for captive-reared birds until after release. Buitron (1983) suggested that mobbing by parent birds for example, may benefit offspring by teaching them about a particular danger so they will recognise and mob that predator in the future.

The method of release of sub-adults then, should be one in which a gradual acclimatisation to the released environment is allowed. Young fledglings are probably more primed psychologically and physiologically for rapidly acquiring traits that enhance survival (Fyfe 1978). Release of young birds has been successful in mallard liberations (Lee and Kruse 1973). Failure of sub-adult releases of black stilts may have been related to a lack of parental influence on early learning experience and on being retained too long under captive conditions.

In conclusion, release of sub-adult black stilts reared in captivity without parent birds has proven unsuccessful to date. Inappropriate reactions toward predators and taming of these birds were probably the most important reasons for this failure. These difficulties in releasing captive stock may perhaps be overcome to some extent by allowing them to be reared by their parents. Antipredator behaviour of captive chicks reared by the focal pair of this study was similiar to that observed in the wild. It is likely however, that much of predator avoidance and learning about the environment takes place after fledging, via experience or from parent birds (Pierce, pers. comm.). This is especially so, now that trapping around nest-sites is undertaken by Wildlife Service personnel. Young stilts do not encounter many (if any) cats or ferrets until after flying out of the trapping area (Pierce, pers. comm.).

6.2.4 Increasing captive stocks

> "Now that multi-generation propagation is being attained with many orders, the care and biological complexities of long-term management are increasing concern about the differential responses of the captive propagules of various

> species to inbreeding, photoperiod, nutrition, imprinting...
> (Conway 1978)

Propagation of a species from only a few individuals able or willing to breed can result in inbreeding which may be detrimental to genetic variability and ability of offspring to respond to environmental change (Kear 1977). Inbreeding can decrease the number of heterozygous gene loci in a population and therefore increase chances of mutations becoming irreversibly established in a population (Brambell 1977). Small populations in captivity may be prone to failure resulting from these mutations causing problems such as infertility eg., Hawaiian goose (Humpreys 1972, cited in Kear 1977) or may not have any effect eg., Laysean teal (Kear 1977). So the extent of any detrimental effect of inbreeding will depend on the number of potentially lethal genes present in the founder population. Inbreeding is a problem in any small natural population however. To minimise the risks of inbreeding and of natural calamities extinguishing a population, we should aim at establishing as many colonies of as many individuals as we can (Benirschke 1977). Mount Bruce is presently limited by lack of facilities for housing more captive pairs of black stilts. The present aviaries may be too close to house a pair in each, since there was evidence of redirected aggression onto a mate when adjoining aviaries were occupied by other stilts. As has been demonstrated in similiar species, pairs may inhibit reproductive performance of others, if in visual and/or vocal contact.

6.3 Management suggestion

That somewhere in the MacKenzie basin, aviaries be erected for stilts with the aim of establishing one or more captive breeding pairs as close to the "natural" range of black stilts as possible. Five clutches per season may be produced by a pair. Of these clutches, I suggest that the first three or four be cross-fostered to black/dark hybrid pairs and the final clutch left with parent birds to be reared. These juveniles could be released after fledging or when the family party breaks up in the following spring.

6.3.1 Advantages

1) One captive pair are able to produce 2-3 times more eggs per season

than have been found from wild pairs (although actual production in the wild is likely to be higher than that indicated by the number of clutches located). Pairs cannot "disappear" after clutch removal.

2) If successful, wild pairs may eventually be left with their first or second clutch to rear with minimum disturbance, the majority of eggs for cross-fostering coming from captive birds.

3) Releasing juveniles reared by captive blacks in the MacKenzie Basin;
  a) reduces mate preference uncertainties of rearing under pied/hybrid stilts;
  b) reduces the probability of dispersal (of Mount Bruce reared birds back to the North Island or migration out of the basin in winter by juveniles cross-fostered to pied/hybrid stilts)
  c) enables 3-4 juveniles to be reared (on natural and supplementary food) past fledging and possibly over the first critical winter. A cross-fostered clutch may only fledge 1-2 juveniles which then must survive through winter.

4) The facilities for taking eggs and incubating them already exists in the Mackenzie basin. The only financial outlay neccessary to establish captive pairs would be that for land and aviaries. If a year-round worker continued to be employed, it would be possible to maintain captive stilts over winter by supplementary feeding. Possible sites for aviaries may be within the predator exclosures already erected by the Royal Forest and Bird Protection Society (plate 6.1).

5) Currently, juvenile stilts which are hatched and reared from the last clutch laid each season at Mount Bruce must be housed. Because aviary space is limited at present, this has proven to be a problem. This problem is eliminated if captive pairs are housed within the "natural" range of black stilts, because progeny from final clutches could be released.

6) Establishment of a second captive population would ensure against loss of all present stocks from disease and act as an additional source of replacement stock.

PLATE 6.1 Predator-proof exclosure at Micks Lagoon, Waitaki Basin.

6.3.2 Problems

1) Resources; It is possible that aviaries may need to be similiar to the present breeding enclosure at Mount Bruce. This may involve considerable expense and the "lock-up" of resources (i.e., aviaries) in only one or two areas.

2) Location of aviaries; An area which is already utilised by stilts for breeding but which does not attract a large number of potential "neighbouring" birds for captive pairs, would be ideal. There may however be problems locating an area which does not completely freeze over during winter or experience heavy snowfall. Food shortages over winter could be met by supplementary feeding (most of the Mount Bruce black stilts use oxheart mix as a <u>total</u> food supply).

3) Aviary requirements and housing regimes necessary for the formation of pairs still need to be established before successful breeding of further pairs can take place (discussed in section 6.2.1).

4) There is a likelihood that juveniles "learn" much of the winter feeding areas from parents. Release in spring may allow sufficient time however, for captive-reared juveniles to learn how to use the wild habitat and associate with other stilts before winter.

5) Use of present captive stocks for establishment of a second captive population, introduces the risk of disease from parent birds being passed to juveniles and out into the wild population. Veterinary consultation should be sought on this point.

6) A permanent year-round worker within the Mackenzie basin would need to be employed, to feed and monitor captive stilts.

6.4 Captive breeding as a management option for endangered species

Captive breeding does not alone assure protection of a species from extinction. Obviously we need also to provide protection from factors which have led to its decline. An integration of management techniques is neccessary, including continued protection of nest sites and chicks from predators, manipulation of eggs to induce increased productivity and the use of cross-fostering and captive rearing techniques to increase recruitment into the population.

Captive propagation of endangered species is becoming more predictable, more science than art (Conway 1983). Artificial insemination, artificial incubation and supplementary feeding are already important in breeding programmes for wild birds of prey, cranes, pheasants and waterfowl. I suggest on the basis of my observations reported here and on referenced literature, that the potential for use of captive breeding as an option for management of black stilts has yet to be fully exploited. The potential for propagation of other endangered New Zealand species in captivity, should also be examined.

APPENDIX ONE

Taxonomy of the Recurvirostridae

Gruson (1976) lists 14 forms of avocet or stilt and includes 8 of these in the genus *Himantopus*. Seven of these forms are further classified by Gruson, as subspecies of the eighth (*Himantopus himantopus* - the black-winged stilt). However American ornithologists (Coleman 1981) recognise *knudseni*, *mexicanus* and *melanurus* as subspecies of *H. mexicanus*. The New Zealand checklist classifies *novaezealandiae* as a full species and *leucocephalus* as a subspecies of *H. himantopus* (Kinsky 1970).

A further four forms are grouped into the genus *Recurvirosta* (avocets); *americana*, *andina*, *avocetta* and *novaehollandiae* (Gruson 1976). One additional form is designated the only member of its genus; *Cladorhynchus leucocephalus* (banded stilt) and the final form included in this family is *Ibidorhyncha struthersii* (ibisbill). The latter form has been little studied and perhaps fits more closely, at least behaviourally, into the Family Haematopodidae (Pierce, in press)

APPENDIX TWO

Questionnaire sent to institutions holding Recurvirostridae

QUESTIONNAIRE (One species per form)

1. Name of institution: ....
2. Species of stilt/avocet held: ....
3. Number of adults: .... Sex: .... Age: ....
   juveniles ...... Sex: .... Age: ....
4. How many (approximately) additional stilts/avocets have you held in the past five years?
   adults ....
   juveniles ....
5. Have either past or present stocks included breeding pairs? If so, how many pairs and in which years have these pairs successfully bred?

Pair number	Year(s) bred
....	....
....	....
....	....
....	....
....	....

6. Are progeny kept in captivity/released into the wild? .....
   ....
7. Were clutches single or was multiple laying induced? If latter, what is the maximum number of clutches/pair to be laid in one season?:
   ....
   ....
8. How are breeding pairs/surplus stock housed? (Please give brief description of aviaries including approximate dimensions, type of food supply, i.e., artificial and/or natural, proximity to nearest stilts/avocets)
   ....
   ....
   ....
   ....
   ....
   ....

APPENDIX TWO (cont)

9. What method have you used in determining sexes? (e.g., behavioural observation, hormonal faecal analysis, morphometrics, etc.). Were these successful?

....

....

....

....

10. How are pairs formed? i.e., are they arbitrarily decided or given a mate choice?

....

....

....

....

....

11. Are you aware of any behavioural studies/publications on this species in captivity?

....

....

....

....

....

APPENDIX THREE

List of institutions replying to a questionnaire
(by geographical area)

1) Auckland: Auckland Zoological Park, Auckland, New Zealand.
2) Mount Bruce: National Wildlife Centre, Mount Bruce, Wairarapa, New Zealand.
3) Otorohanga : Otorohanga Zoological Society, Otorohanga, New Zealand.
4) Perth: Perth Zoological Gardens, South Perth, Western Australia.
5) Taronga: Zoological Parks Board of New South Wales (Taronga Zoo), Sydney, Australia.
6) Dallas: Dallas Zoo, Dallas, Texas, U.S.A.
7) Los Angeles: Los Angeles Zoo, Los Angeles, California, U.S.A.
8) New York Bronx: New York Zoological Park (Bronx Zoo), New York, U.S.A.
9) Bochum: Tierpark Bochum, Bochum, West Germany.
10) Koln: Aktiengesellschaft Zoologischer Garten, Koln, West Germany.
11) Rheine: Tierpark Rheine, Rheine, West Germany.
12) Wuppertal: Zoologischer Garten Wuppertal, Wuppertal, West Germany.
13) Emmen: Noorder Zoo Emmen, Emmen, Holland.
14) Amsterdam: Stichting Koninklijk Zoologisch Genootshap Natura Artis Magistra, Amsterdam, Holland.
15) Bern: Stadtischer Tierpark Dahlholzli, Bern, Switzerland
16) Budapest: Budapest Fovaros-Allat-Es Novenykertje, Budapest, Hungary.

APPENDIX FOUR

Faecal hormone ratios obtained during sexing of stilts

19 September 1984

Individual (band no.)	Oestrogen/testosterone ratio	Probable sex
2605	nr	nr
2606	0.22	male
2611	0.25	male
2612	2.82	female
5112	4.09	female
5113	0.15	male
5114	nr	nr

11 October 1984

2605	0.008	probable male
2606	0.78	probable female
2607	0.72	probable female
2608	0.37	possible male
2609	0.89	probable female
2610	0.14	probable male
2611	0.03	probable male
2612	0.64	probable female
5108	0.45	unknown
5109	0.15	probable male
5110	0.33	possible male
5112	0.69	probable female
5113	0.16	probable male
5114	0.001	probable male

KEY : nr = no result

APPENDIX FIVE

Morphological measurements of black stilts held at Mount Bruce

i) Bill length - From the tip of the upper mandible to the first feathers in the centre of the forehead.

ii) Tarsus length - From the notch behind the proximal end to the joint between middle toe and front of the tarsus.

iii) Wing - From the front of the carpel joint to the tip of the longest primary feather (wing flattened but feathers not straightened).

iv) Weight - live weight.

Measurements of adult black stilts held at Mount Bruce

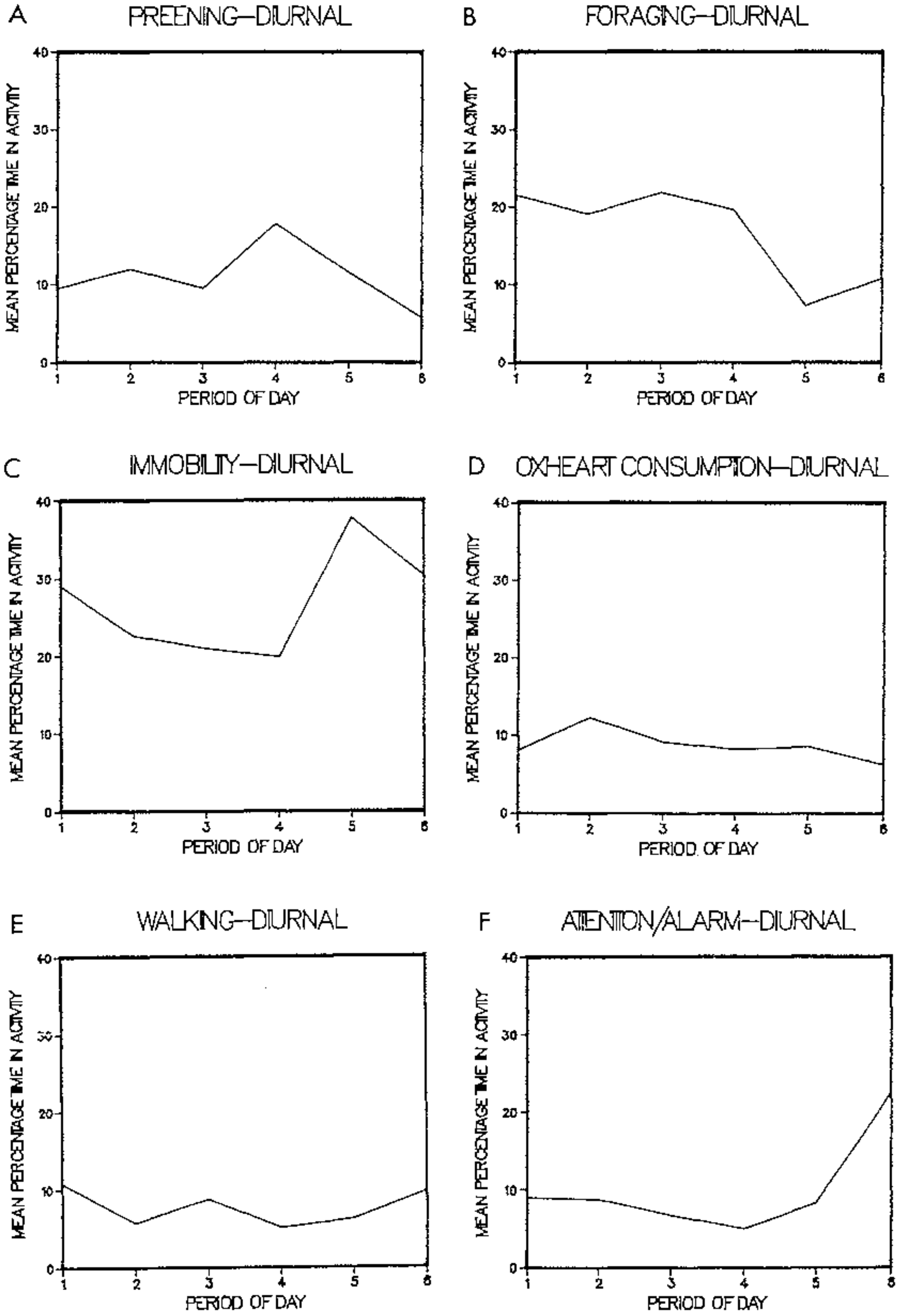
Individual (band number)	Bill length (mm)	Tarsus length (mm)	Wing length (mm)	Weight (g)
2605[1]	69.7	97.0	248	226
2606	68.2	92.4	225	224
2607	70.3	90.3	242	220
2608	69.0	87.3	230	210
2609	70.8	98.6	255	215
2610	-	96.7	257	215
2611[1]	68.0	92.9	245	225
2612[2]	69.3	87.5	244	225
5108	66.7	89.6	237	210
5109	67.1	89.4	245	215
5110	69.7	93.4	245	220
5112	64.0	84.0	240	220
5113	65.6	83.8	238	235
5114	71.9	89.2	240	240

KEY : [1] = known male [2] = known female

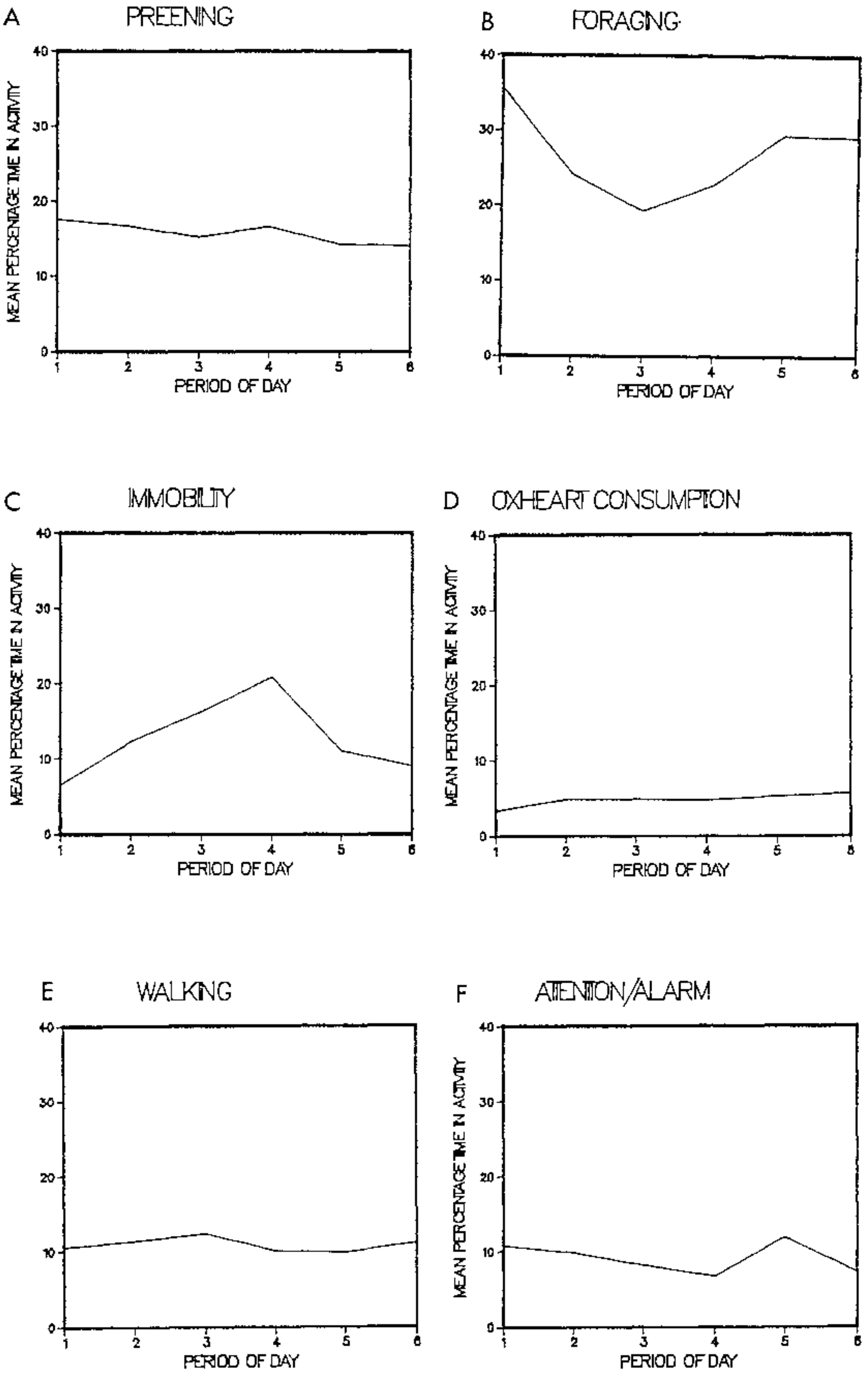
APPENDIX SIX

Diurnal time-budget (combined individuals and stages)

1982-83 SEASON



APPENDIX SIX (CONT.)
1983-84 SEASON



APPENDIX SEVEN

Responses of captive and wild chicks to the presence of predators

TABLE 1. Antipredator behaviour of captive chicks

AGE CLASS 1 (2-34 DAYS)

predator	response*							
	1	2	3	4	5	6	7	N
human	0	7	0	55	2	0	3	67
hawk	0	3	0	0	0	5	0	8
magpie	8	4	3	0	1	2	0	18
other	0	0	0	0	0	0	0	0

AGE CLASS 2 (39-67 DAYS)

human	0	0	0	24	3	0	0	27
hawk	0	5	0	0	15	6	0	26
magpie	0	0	0	6	18	0	0	24
other	0	2	0	0	1	3	0	6

APPENDIX SEVEN (CONT)

Table 2. Antipredator behaviour of wild chicks

AGE CLASS 1 (2-34 DAYS)

predator	response*								
	1	2	3	4	5	6	7	8	N
human	2	11	0	0	0	0	2	0	15
hawk	1	1	0	0	0	0	0	0	2

AGE CLASS 2 (39-67 DAYS)

human	0	0	0	0	3	0	0	1	4

KEY :

1 = freeze;
2 = walk/run & freeze;
3 = remain sitting;
4 = move/remain in open;
5 = stand alert/upright;
6 = stand & tilt head;
7 = run;
8 = freeze then fly.

APPENDIX EIGHT

Individual parameter values for the adult tip call

Individual 2609 - female (n = 13)

VARIABLE	UNITS	MEAN (±1 S.D)	RANGE
A	(msec)	18.0 ± 3.1	15.1 - 22.6
B	(Hz)	491.6 ± 23.0	462.0 - 539.0
C	(Hz)	4560.0 ± 428.9	3850.0 - 5313.0
D	(msec)	582.1 ± 112.3	430.3 - 822.9
E	(msec)	580.9 ± 112.1	430.3 - 822.9

Individual 5108 - unknown sex (n = 9)

VARIABLE	UNITS	MEAN (±1 S.D)	RANGE
A	(msec)	27.6 ± 11.1	15.1 - 45.3
B	(Hz)	654.5 ± 47.1	616.0 - 731.5
C	(Hz)	7374.9 ± 581.0	6314.0 - 7700.0
D	(msec)	503.7 ± 88.9	415.2 - 641.7
E	(msec)	503.7 ± 88.9	415.2 - 641.7

Individual 2607 - female (n = 4)

VARIABLE	UNITS	MEAN (±1 S.D)	RANGE
A	(msec)	50.9 ± 3.77	45.3 - 52.8
B	(Hz)	539.0 ± 0	539.0
C	(Hz)	7700.0 ± 0	7700.0
D	(msec)	414.3 ± 20.0	388.8 - 437.9
E	(msec)	413.9 ± 24.6	388.8 - 437.9

APPENDIX NINE

Individual parameter values for the adult yak call

Individual 12 - wild black (n = 5)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	82.3 ± 6.7	75.5 - 90.6
B	(hz)	585.2 ± 50.2	500.5 - 616.0
C	(hz)	877.8 ± 50.2	808.5 - 924.0
D	(hz)	870.1 ± 51.6	808.5 - 924.0
E	(hz)	885.5 ± 38.5	847.0 - 924.0
F	(msec)	12.0 ± 11.4	0 - 22.6
G	(msec)	971.0 ± 481.0	656.8 - 1525.1
H	(msec)	971.0 ± 481.0	656.8 - 1525.1

Individual 14 - wild black female (n = 14)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	115.9 ± 6.0	105.7 - 124.6
B	(hz)	492.2 ± 34.3	462.0 - 577.5
C	(hz)	778.2 ± 34.3	731.5 - 847.0
D	(hz)	695.7 ± 31.9	654.5 - 731.5
E	(hz)	783.7 ± 40.9	731.5 - 866.2
F	(msec)	1.3 ± 7.7	-15.1 - 18.9
G	(msec)	344.5 ± 297.2	86.8 - 1049.4
H	(msec)	350.3 ± 262.4	86.8 - 1049.4

APPENDIX NINE (CONT.)

Individual 23 - wild black female (n = 8)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	121.3 ± 4.7	113.2 - 128.3
B	(hz)	625.6 ± 39.8	577.5 - 693.0
C	(hz)	875.9 ± 53.4	770.0 - 924.0
D	(hz)	726.7 ± 43.3	654.5 - 770.0
E	(hz)	885.5 ± 35.6	847.0 - 924.0
F	(msec)	3.7 ± 10.6	0 - 30.2
G	(msec)	444.8 ± 209.6	203.8 - 690.8
H	(msec)	444.8 ± 209.6	203.8 - 690.8

APPENDIX TEN

Individual parameter values for the adult eerr call

Individual 15 - wild node F

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	290.0 ± 93.4	158.5 - 407.7
B	(Hz)	628.8 ± 62.9	539.0 - 693.0
C	(Hz)	805.3 ± 30.8	770.0 - 847.0
D	(Hz)	705.8 ± 31.4	654.5 - 731.5
E	(Hz)	840.6 ± 28.9	808.5 - 885.5
F	(msec)	-79.9 ± 41.1	-128.3 - -30.2
G	(msec)	227.1 ± 49.5	162.3 - 302.0
H	(msec)	233.4 ± 45.4	162.3 - 286.9

Individual 16 - wild node F

A	(msec)	318.6 ± 63.7	211.4 - 369.9
B	(Hz)	592.9 ± 34.4	539.0 - 616.0
C	(Hz)	877.8 ± 17.2	847.0 - 885.5
D	(Hz)	700.7 ± 74.0	616.0 - 808.5
E	(Hz)	889.3 ± 25.1	847.0 - 904.7
F	(msec)	-13.6 ± 43.8	-83.0 - 37.7
G	(msec)	445.4 ± 266.9	256.7 - 634.2
H	(msec)	441.7 ± 272.3	249.1 - 634.2

APPENDIX TEN (CONT.)

Individual 17 - wild node F (n = 9)

A	(msec)	322.9 ± 52.5	241.6 - 392.6
B	(Hz)	568.9 ± 46.3	500.5 - 616.0
C	(Hz)	795.7 ± 33.3	731.5 - 847.0
D	(Hz)	654.5 ± 33.3	616.0 - 693.0
E	(Hz)	810.6 ± 31.1	770.0 - 847.0
F	(msec)	-28.1 ± 45.3	-124.0 - 15.1
G	(msec)	366.2 ± 190.6	226.5 - 679.5
H	(msec)	367.2 ± 189.8	226.5 - 679.5

APPENDIX ELEVEN

Individual parameter values for the adult staccato call

Individual 9 (n = 53)

VARIABLE	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	27.8 ± 26.1	7.5 - 173.6
B	(hz)	592.7 ± 95.9	462.0 - 924.0
C	(hz)	3905.0 ± 1386.8	2233.0 - 7700.0
D	(msec)	116.0 ± 110.5	15.1 - 445.4
E	(msec)	115.6 ± 110.6	15.1 - 445.4

Individual 7 (n = 32)

A	(msec)	14.5 ± 4.3	7.5 - 22.5
B	(hz)	593.1 ± 42.4	539.0 - 770.0
C	(hz)	3104.1 ± 666.8	1309.0 - 4389.0
D	(msec)	106.4 ± 114.8	45.3 - 679.5
E	(msec)	106.4 ± 114.8	45.3 - 679.5

Captive male (n = 50)

A	(msec)	16.4 ± 9.1	7.5 - 75.5
B	(hz)	620.7 ± 81.1	539.0 - 924.0
C	(hz)	4036.3 ± 1355.9	2464.0 - 7700.0
D	(msec)	88.0 ± 73.1	37.7 - 468.1
E	(msec)	103.0 ± 130.3	37.7 - 853.0

APPENDIX TWELVE

Individual parameter values for the juvenile chap call

Individual 24 (n = 5)

VARIABLES	UNITS	MEAN (± 1SD)	RANGE
A	(msec)	83.8 ± 1.7	83.0 - 86.8
B	(Hz)	1832.6 ± 58.4	1771.0 - 1886.5
C	(Hz)	2910.6 ± 169.1	2618.0 - 3041.5
D	(Hz)	1740.2 ± 63.3	1694.0 - 1809.5
G	(msec)	973.9 ± 194.9	796.5 - 1162.7
H	(msec)	1033.1 ± 189.7	815.4 - 1162.7

Individual 25 (n = 7)

A	(msec)	63.6 ± 7.9	56.6 - 79.3
B	(Hz)	2436.5 ± 155.1	2156.5 - 2618.0
C	(Hz)	3426.5 ± 38.5	3388.0 - 3465.0
D	(Hz)	2315.5 ± 333.0	2002.0 - 2926.0
G	(msec)	223.9 ± 45.9	147.2 - 286.9
H	(msec)	223.9 ± 45.9	147.2 - 286.9

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