ASPECTS OF THE BIOLOGY OF THE LITTLE SHAG

(Phalacrocorax melanoleucos brevirostris VEILLOT 1817)

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

Craig William Matthews
February 1984

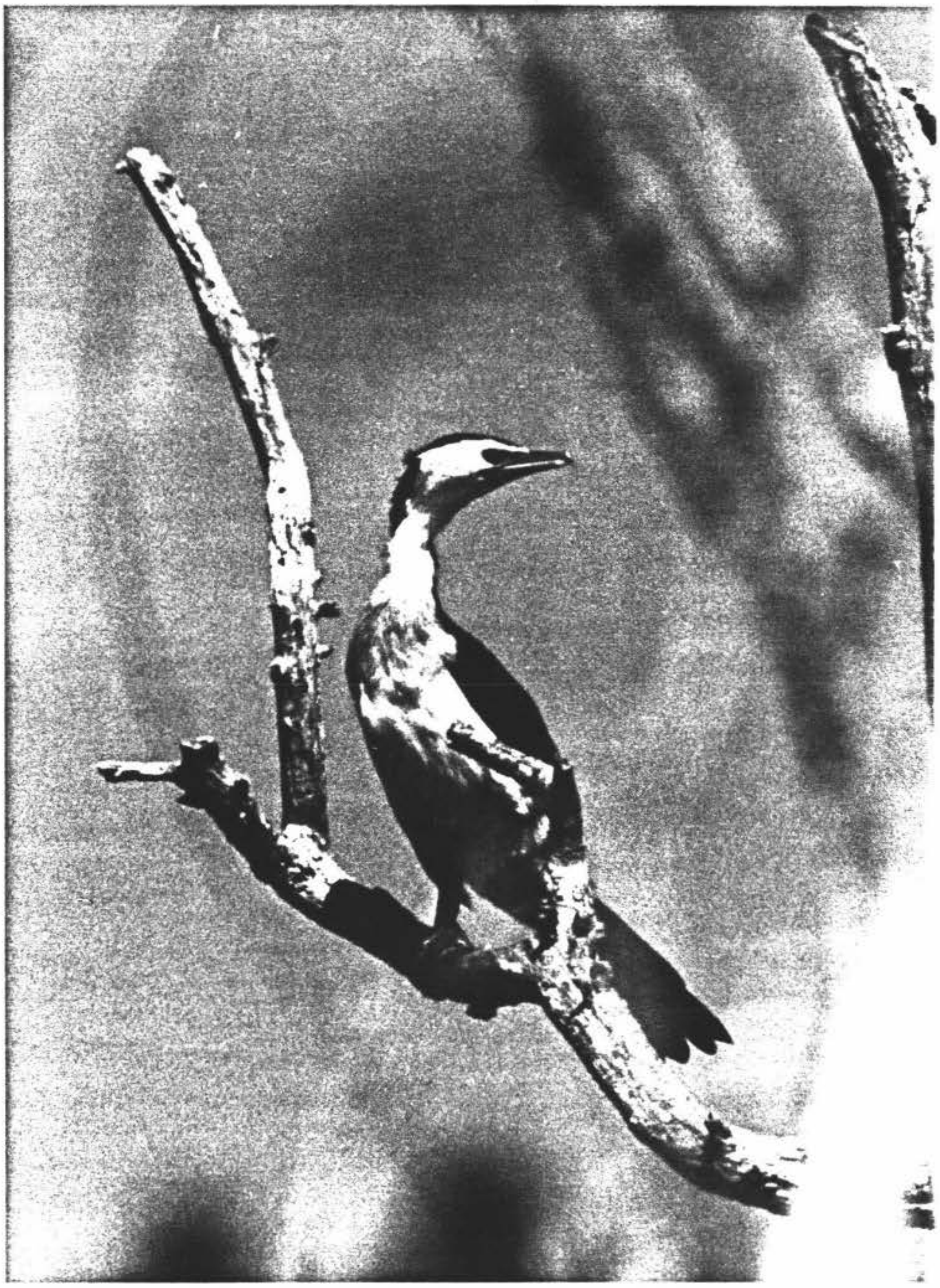


PLATE 1: ADULT LITTLE SHAG

ABSTRACT

Aspects of the biology of the little shag (Phalacrocorax melanoleucos brevirostris Veillot) were examined from December 1980 until April 1983 at Hamilton's and Sexton's Lagoons in lowland Manawatu.

Body measurements and plumage patterns of both sexes are taken from dried specimens. Although females tend to be smaller, the differences are not significant. Plumage patterns, based on the proportion of white, are listed, and possible reasons for plumage differences between New Zealand and Australia discussed.

Postures and behaviour patterns are documented, and related to ordinal and family members. The most distinctive postures and behaviour patterns relate to courtship and sexual activities.

Aspects of breeding ecology are recorded, and comparisons between New Zealand and Australian populations made from records of the respective nest record schemes. Fundamental differences occur, possibly due to the unpredictable fluctuations which seem to characterise the Australian freshwater environment.

Seasonal and daily time budgets are detailed at both lagoons. Rest and self-maintenance activities decrease during breeding, and tend to occur at dawn and evening. The variable relation of movement and reproductive activities is discussed in terms of season, phase of breeding, and time of day.

ACKNOWLEDGEMENTS

Thanks are due to many people, for helping make this thesis possible.

I would firstly like to thank my supervisor Dr. Robin Fordham, for his constructive criticisms and advice at all stages of the thesis.

Valuable statistical advice was given by Mr W.D.Stirling and Dr. Ed Minot, who also gave me invaluable help in computing.

Thanks are also due to Dr. Alison Bimler, who proof-read all chapters and offered valuable editorial comments.

Unrestricted access to study areas was kindly provided by Mr A.Hamilton, Mr M.Voss, and Mr B.Sexton, who all showed keen interest throughout.

The Wildlife Service of the Department of Internal Affairs provided $900.00 towards travelling expenses. Much of the equipment used in the study was provided by the Botany and Zoology Department, Massey University.

Thanks are also due to Mr J.S.Bartle, Curator of Birds at the National Museum, and Mrs S.M.Reed, Associate Ornithologist at the Auckland War Memorial Museum, for allowing me to obtain body measurements and plumage diagrams.

The conveners of the New Zealand and Australian Nest Record schemes, Mr D.Grockett and Mr D.Purchase sent copies of data which has proved invaluable in this thesis.

I have benefited from correspondence with Dr. W.H.Siegfried, Dr. A.J.Williams, and Dr. H.H.Berry, the latter kindly providing reprints of papers which were unavailable in New Zealand.

Mrs Heather Murphy, Mrs Pauline Patchell, and Mr Ronald DeRose provided considerable assistance in practical aspects of thesis presentation, while the Central Photographic Unit of Massey University provided colour photographs. The staff of the Computer Department, Massey University, printed the text and helped me with problems of formating.

I am also grateful for the friendship and help shown by staff and senior students of the Botany and Zoology Department.

And last, but by no means least, many thanks are due to my parents, who have not only actively encouraged me throughout the study, but provided practical support, most notably in the form of a car to travel to and from study areas.

CONTENTS PAGE

LIST OF TABLES

LIST OF PLATES

LIST OF FIGURES

FIGURE PAGE

APPENDICES

TABLE

CHAPTER ONE:
INTRODUCTION.

CHAPTER ONE: INTRODUCTION

1.1:The Order Pelecaniformes

1.1.1:Taxonomy

Van Tets (1976), states that the vernacular names "shag" and "cormorant" are used for all members of the family Phalacrocoracidae, along with appropriate adjectives to distinguish the species. Van Tets (op.cit.) also points out that New Zealanders and fishermen prefer shag, while Australians, North Americans and bird watchers use cormorant. In England, shag and cormorant refer to separate species. In this study, shag will be used, except when referring to recognized common names of a species; e.g. P.auritus, the double-crested cormorant.

The order Pelecaniformes has been recognised as a distinct taxonomic entity since 1805 when Cuvier referred to them as the Totipalmes. Later they were referred to as the Steganopodes (Illiger, 1811; Gadow, 1893; cited in Millener, 1972). The order is an ancient one. According to Swinton (1965), bones from the hind-leg of an ancestral cormorant have been found in Transylvanian late Cretaceous rocks. He further states that Pelecaniform fossils are well represented in early Tertiary deposits. Living Pelecaniformes comprise five families if the Anhingidae are ascribed to the sub-family Anhinginae in the Phalacrocoracidae, as mooted by Sibley (1960), or six families (Wetmore, 1960). This study follows Wetmore's (1960) classification as follows:

- Order Pelecaniformes (Steganopodes)
  - Suborder Phaethontes
    - Family Phaethontidae, tropic birds (3 species)
  - Suborder Pelecani
    - Superfamily Pelecanoidea
      - Family Pelecanidae, pelicans (7 species)
    - Superfamily Suloidea
      - Family Sulidae, gannets and boobies (7 species)
      - Family Phalacrocoracidae, cormorants (29 species)
      - Family Anhingadae, snakebirds or darters (2 species)
  - Suborder Fregatae
    - Family Fregatidae, frigatebirds (5 species)

According to Nelson (1978a), the Sulidae, Phalacrocoracidae, and Anhingidae could be allied in the Superfamily Suloidea, and along with the Pelecanidae could form the Suborder Pelecani. The Fregatidae and Phaethontidae could be placed in the separate suborders, Fregatae and Phaethontes. Anatomical evidence (Lanham, 1947), and egg-white electrophoretic data (Sibley, 1960) indicate, however, that the Fregatidae and Phaethontidae are more closely related to each other, than either is to the Pelecani.

Anatomical comparisons also led Lanham (1947) to conclude that the Anhingidae and Phalacrocoracidae are the most closely related Pelecaniform families, and Sibley (1960), finding that egg-white proteins of anhingas and shags were virtually identical, suggested that anhingas should be treated as a subfamily of the Phalacrocoracidae. However, comparison of social communication patterns between the two groups (Van Tets, 1965) supports Lanham's view.

Within Phalacrocorax, a dichotomy exists between shags with a continental distribution, and shags with a marine-coastal distribution. According to Van Tets (1965), continental shags differ from marine shags in their ability to perch in trees, the inclusion of sticks in their nest material, in the heron-like neck posture during flying, and by having a wing-waving rate roughly half that of marine shags.

Some authors (cited in Van Tets 1965) think that four species of Phalacrocorax should be placed in a separate genus, Halietor: the Pygmy Cormorant (P.pygmaeus), from North Africa and central Europe east to Afghanistan; the Long Tailed Cormorant (P.africanus), from Africa and Madagascar; the Little Cormorant (P.niger), from India South-east to Borneo; and the Little Pied Cormorant (P.melanoleucos), from New Guinea, Australia and New Zealand (Landsborough-Thomson, 1964). All live mainly in lakes and rivers and are distinguished by their small size and relatively long tails. The validity of Halietor is contentious (see Van Tets, 1965 for discussion), but Van Tets (1965) considers that the switching of body postures in the Wing-waving and Gape-bowing displays of P.melanoleucos could be common characteristics of Halietor.

1.1.2:Morphology

The six pelecaniform families may be distinguished by the following morphological characters, adapted from Nelson (1978b),

FAMILY	PHAETH.	PELECA.	SULIDA.	PHALAC.	ANHING.	FREGAT.
Totipalmate Feet	yes	yes	yes	yes	yes	yes
Mandible with hook	no	yes	no	yes	no	yes
External nares	open	shrunk	closed	closed	shrunk	shrunk
Coloured gular	no	yes	yes	yes	yes	yes
Nuptial crests	no	yes	no	yes	yes	no
Neck length	short	long	short	long	long	short
Leg length	v.short	short	short	short	short	v.short
Mod.cervical vert.*	no	yes	yes	yes	yes	yes

* Modified 8th and 9th cervical vertebrae for use in prey capture.

All or most of the family are characterised by; totipalmate feet (web-footed), a coloured gular pouch, short legs and modified cervical vertebrae.

1.1.3:Distribution

Several main concentrations of this cosmopolitan order occur in higher latitudes, probably because fish are plentiful, but in terms of families and species the order is undoubtedly tropical and subtropical in distribution and (probably) origin (Nelson 1978b). Thus all boobies, pelicans, frigatebirds, tropicbirds, and darters, as well as several species of shag breed in the tropics, and two of the three species of gannet migrate there while the third occasionally visits tropical zones (Nelson, 1978b).

1.1.4:Breeding

The order Pelecaniformes includes a range of types, from near solitary nesting species (e.g. Abbott's Booby, <u>Sula abbotti</u>), to strongly colonial forms such as the Guanay Cormorant (<u>P.bougainvillii</u>), in which colonies may comprise several million densely packed pairs. Nest sites vary through the order from ledges, and holes in cliffs and trees, to branches and bushes. Nests vary in size from large to non-existent. According to Nelson (1978b), clutch size is usually three or four in pelicans, three to six in shags and darters, one to four in gannets, and always one in frigatebirds and tropicbirds. However the largest clutch commonly laid is four, which occurs only in species with an extremely rich food source. Brood size appears to be correlated with the frequency with which young are fed, those parents foraging furthest (normally in areas with poor food supply) having the smallest broods. Within the Pelecaniformes there appear to be four main patterns of breeding(from Nelson 1978a):

(1) Strictly annual, strongly seasonal breeders (e.g. gannets). These species live chiefly in the Northern Palearctic and are well adapted to predictable climate and food.

(2) Strictly annual, loosely seasonal breeders(e.g. the majority of the Pelecaniformes). Although breeding annually, the start of laying for these species may vary by weeks or even months between different years. This pattern is marked in species inhabiting high tropical latitudes.

(3) Biennial seasonal breeders. Besides Frigatebirds only Abbott's Booby lays every second year. The chicks grow very slowly, and are fed as free-flying young for up to fourteen months by the parents.

(4) Non-seasonal breeders. Two species of booby and one species of tropicbird have shortened their breeding cycles to less than twelve months. These species live in areas of poor food supply (Galapagos and Ascension Islands), and short breeding cycles may increase the chance of experiencing favourable periods.

1.1.5:Behaviour

Most Pelecaniform birds have a common courtship sequence which serves to establish the nest bond and pair bond for a season or more (Van Tets, 1965). The basic sequence is as follows:

(1) A nest site is selected by the male.

(2) The female selects a male by his advertising display.

(3) The male eventually surrenders the nest site to his mate (usually after appeasement signals by the female), then collects nest material for her.

(4) The female constructs the nest alone, or with the assistance of the male.

(5) Copulation usually occurs when the male returns from collecting nest material. There are no special pre- or post-coital displays in the Pelecaniformes.

(6) The pair bond is strengthened by joint activities, such as nest building, allo-preening (Cullen, 1963), and nest defence.

(7) After pair bond establishment, both birds share nesting duties, e.g. nest guarding, incubation, and caring for nestlings.

Pelecaniform parents help in the thermoregulation of eggs and chicks by shading them when it is hot, and brooding them when it is cold. This is important, as all Pelecaniform birds have nidicolous young, which hatch in a relatively underdeveloped state and stay in the nest some time after hatching and are naked when hatched. The exception is the Phaethontidae, whose chicks have some down at hatching. They also have in common similar method of feeding young, and a similar pre-landing display, which appears to be derived from food begging (Van Tets, 1965).

1.1.6:Feeding

Nelson (1978b) states that all members of the Pelecaniformes are fish eaters, partly or wholy marine, and between them have evolved a wide range of fishing methods. Gannets, boobies and tropicbirds are powerful plunge divers, while pelicans scoop fish from shallow water and even snatch food from surfacing shags. Frigatebirds pursue their food aerially by chasing flying fish, picking food off the sea surface, or stealing from other seabirds. Both the Anhingadae and Phalacrocoracidae dive from the surface, and pursue their prey underwater where the former family stalk and spear their prey, whilst the latter grab. Although large numbers of pelecaniform birds may gather together to feed, only in the Pelecanidae and Phalacrocoracidae do co-operative and communal fishing occur (although not in the little shag).

1.2:The Little Shag:*Phalacrocorax melanoleucos brevirostris*

The O.S.N.Z. checklist (1970), currently recognizes three genera of shags in New Zealand: (i) *Phalacrocorax*, containing four species, characterised by relatively thick bills and black feet, living in marine and freshwater environments; (ii) *Leucocarbo* containing three species of pink-footed shags; and (iii) *Stictocarbo*, a single species with a relatively slender bill. Both *Leucocarbo* and *Stictocarbo* are exclusively marine (Falla *et al*, 1979).

1.2.1:Description

The little shag is approximately 56cm high, the feet are black, the bill is black above and yellowish below, and the iris greyish-brown. It is readily distinguished from the little black shag (*P.sulcirostris*) by having a thicker bill and relatively longer tail (Oliver, 1955; Falla *et al*, 1979).

The adult plumage of the little shag is variable. In New Zealand the most common form is glossy black, with white face, cheek and chin, and white commonly extending to the throat. The other form, identical to the little pied shag of Australia (Falla *et al*, 1979), has entirely white underparts. Oliver (1955) believed these two forms were separate, hybridising species, but Falla (1932) considered the white-throated and little pied forms were conspecific. The little shag is now recognized (O.S.N.Z., 1970) as a dimorphic subspecies of the little pied shag. The first individuals of the little pied shag were collected in Australia by Veillot (1817; cited in Oliver, 1955), and the white-throated form was described from New Zealand specimens by

Gould (1837; cited in Oliver, 1955).

Most immature little shags have dull brownish-black plumage over the body, including the throat, with a yellow bill and face, although immature birds of the little pied morph are often dull smokey-white below. Chicks are pink when first hatched, but rapidly develop browny-black down, with tufts of white (see plate 13) in birds that will assume the little pied form (Falla et al, 1979).

The little shag is the most widespread freshwater shag in New Zealand, found in mountains far inland and along the whole coastline south to Stewart Island. It is recorded as a visitor to most northern off-shore islands, but only rarely to sub-antarctic islands (Falla et al, 1979).

Little shag breeding colonies are mainly in still, sheltered locations, such as lakes, ponds, swamps, estuaries and inlets. Trees are favoured nesting places, but mai-mais (shooter's blinds), sedge (Carex), snags and bushes growing out of the water are also used. Generally, colonies are situated so that nests are directly over water. Because the birds gradually kill their host tree (Gilham, 1960), the colony moves from time to time. The little shag breeds in association with other shags, particularly P.carbo, P.varius and P.sulcirostris, and on Lake Rotoehu, they have nested with Dominican gulls (Larus dominicanus), (C.H.Lusk pers.comm.). Little shags have an extended breeding season, but near Auckland they appear to have a fairly regular breeding cycle with a peak in egg laying in September or early October. The normal clutch size is three or four (Falla et al, 1979).

Aside from calls related to specific displays (described in Chapter 3), the most obvious sounds are low calls made by courting birds. Falla et al, (1979), desribes these as muffled sounds somewhere between a low bark and a coo.

In inland waters food includes eels, native freshwater fish, and larvae of various aquatic insects (Dickinson; 1951, Falla et al, 1979).

1.2.2:Aims of the study

Detailed literature on little shags is scant, the earliest paper of importance being Harley (1946), who described briefly the two male advertising displays (although he referred to them as displays of nesting birds). This information was used by Van Tets (1965), in a review of social communication patterns in the order Pelecaniformes, in which the patterns were considered to be derived from threat and pre-takeoff displays, and nest building. However, as many aspects of the little shags behaviour were not described, the question of whether communication within the species mirrored general trends throughout the Pelecaniformes and Phalacrocoracidae could not be addressed. A complete behavioural desription of the little shag, is therefore an essential first step in assessing its familial and ordinal affinities.

Food items of the little shag were listed by Dickinson (1951) and McNally (1957), while Stonehouse (1967) discussed feeding habits and diving rhythms in several New Zealand shags (including the little shag). The diet and feeding habits of little shags and little black shags in Australia were compared in detail by Miller (1979), who concluded that (i) the little shag is better adapted for shallow-water feeding; (ii) it includes comparatively less fish and more crustacea in its diet; and (iii) seasonal variation in diet is associated with changes in prey availability rather than changes in food preference. Recently, Miller (1980), studied proximate control of reproduction, and considered that in the little shag; (i) daylength was the most likely stimulus for testicular and ovarian maturation; (ii) the timing of regression was variable and possibly affected by declining social stimulation, drop in temperature, and drop in water level; and (iii) laying was completely synchronous within, but slightly staggered between sub-units of a colony, and very different between colonies. Miller′s conclusions can be put into perspective by considering a broader overview of the birds activities; thus, data relating to how little shags apportion their time between different activities in separate seasons, and through the day, are required, particularly as time budget information is lacking for any shag.

This study of the little shag therefore had two principal aims:

(i) To describe fully its characteristic postures and patterns of behaviour.

(ii) To quantify seasonal and diurnal time budgets for adults.

Subsidiary data on breeding, plumage, and bodily measurements were also collected.

1.2.3:Study Areas (Figs.1.1 to 1.3)

1.2.3.1:Hamilton's Lagoon (Fig.1.2 and Plate 2)

Hamilton's Lagoon in Kairanga County (40°26"S x 175°29"E), is an ox-bow lake created by a meander of the Manawatu River (about 20km south-west of Palmerston North, Fig.1.1). It is roughly 600m long, 20 - 30m wide, and 1 - 2m deep. The lagoon is surrounded by pasture and crop-land and is bordered by willow (Salix spp.), macrocarpa (Cupressus macrocarpa), toetoe (Cortaderia toetoe), rushes (Juncus spp.), and an isolated stand of kahikatea (Podocarpus dacrydioides). In the middle of the lagoon are two large clumps of raupo (Typha orientalis).

The following information is from Cowie (1978), unless otherwise stated. Hamilton's lagoon sits atop one of the larger levees of the river flats, built up by flood deposits from local rivers. The soils surrounding the lagoon are silt loams, and are mainly used for dairying, fattening and cropping, with ryegrass (Lolium spp.) and clover (Trifolium spp.) being the commonest pasture species.

The climate is characterised by warm summers and mild winters, a relatively evenly distributed yearly rainfall, and prevailing west to northwest winds (Robertson 1959, cited in Cowie 1978). Average rainfall is 890mm-950mm, the driest month is March, and the wettest, June. Raindays vary from 120-173 per year in different parts of the county. Mean monthly temperature ranges from 8.0 °C in July, to 17.5 °C in February, with an annual mean of 12.6 °C. Large diurnal temperature fluctuations are characteristic of the area. Frosts commonly occur from April to October, with the greatest number occuring in June, July, and August. An average of 64.3 frosts per year are recorded.

Three colony sites were utilised at Hamilton's Lagoon (Fig.1.2):

(i) The mai-mai (Plate 3): This was situated on the southern side of the lagoon, and was surrounded by water. The mai-mai was always the first site to be occupied by breeding birds, possibly because the majority of the previous season's nests remained intact. This site was used during 1980/1981 and the beginning of the 1981/1982 breeding season. A maximum of 11 nests were seen.

(ii) The dead willow: This tree was situated directly opposite the mai-mai and used up to and including the 1980/1981 season, after which the tree rapidly disintegrated and was not used again for nesting. A maximum of 10 nests were seen, all on branches overhanging the water.

(iii) The prone willow (Plate 4): This tree was located on the northern side of the lagoon about 150m south of site 2. Before its use as a colony during the latter part of the 1981/1982 season, it was a favoured roost. A maximum of 13 nests were seen before the tree was blown down during a storm (Plate 5).

1.2.3.2:Sexton's Lagoon (Figs.1.3 and Plate 6)

Sexton's Lagoon is a roughly bow-shaped lagoon 1km from the coast (Fig 1.1), about half way between Himatangi beach and Foxton beach. The lagoon is about 500m long and up to 70m wide. At the southern end a causeway crosses the lagoon, cutting off a quarter of its area. This small portion is rapidly becoming clogged with raupo and rushes. The middle half is open water used heavily by black swans (Cygnus atratus), as well as the little shag. The remaining quarter is almost totally clogged with raupo, except for a few open areas near shooters' mai-mais. Other bird species present include white-faced heron (Ardea novae-hollandiae), mallard duck (Anas platyrhynchos), New Zealand shoveller (A. rhynchotis variegata), and pukeko (Porphyrio porphyrio melanotus).

Sexton's Lagoon is a small dune lake, in sand country described by Cowie et al (1967) as being a complex of dunes, sand plains, and peaty swamps. Unconsolidated dunes and flats of the Younger Dune Complex, which are much subject to wind erosion (Cowie and Smith, 1958), border the coast and extend up to 6.4km inland. Further inland are consolidated dunes and flats of the Older Dune Complex (Cowie and Smith, 1958), from which water seeps to the coast, but because drainage is impeded by the younger dunes, lagoons form at the interface of the two complexes (Cowie and Smith, 1958). The basically sandy soils are used for sheep and cattle farming, forestry, or left in scrub (Cowie et al, 1967).

The climate (Cowie et al, 1967) is basically similar to that at Hamilton's Lagoon. Rainfall is lowest in the Himitangi-Foxton area, and increases from March, the driest month, to July, the wettest. Rainfall decreases till September, increases again during October, and decreases through summer. At Foxton, 7km south of the study area, there is an average of 119 rain-days per year. The prevailing north to northwest winds frequently reach gale force in early spring and summer, but usually decrease in frequency and strength between July and August (Cowie et al, 1967).

At Sexton's Lagoon one colony site was used (Plate 6). This was an almost prone poplar (Populus spp.), one of a grove of several hundred on the northern side of the lagoon. This partially submerged tree had been nested on before, but for the previous five seasons a site at Turnbull's Lagoon had been used (until the lagoon was drained during 1982).

1.2.4:Weather

Meterological data were obtained from the Department of Scientific and Industrial Research (D.S.I.R.), Grasslands Division (see Appendix 1). Climatic variables taken from the period of study were compared with the averages from the previous 30 years.

(1) Wind: For all but three months of the entire study period, the wind flow was greater than the 30 year average. Wind flow at Hamilton's Lagoon was 1.19 times greater than the average; at Sexton's Lagoon 1.46 times greater, with a peak flow of 1.75 times greater than average during November 1982.

(2) Hours of sunlight: During the 21 months spent at Hamilton's Lagoon 12 months had less sun than average (including a continuous eight month stretch from June 1981 to January 1982). At Sexton's Lagoon, six of the seven months had less sun than average.

(3) Average monthly temperature: Two long-term trends were seen; (i) from January to June 1981 temperatures were warmer than average and (ii) temperatures were consistently cooler from August 1982 to April 1983 (cooler temperatures occured during 17 of the 28 months).

(4) Monthly rainfall: Seventeen months of the study period were drier than average (including a four month period from October 1981 to January 1982, and a six month period from June to November 1982).

1.2.5:General Methods

Observations began at Hamilton's Lagoon on 5 January 1981. On 26 November 1981, harriers (<u>Circus approximans</u>), destroyed the last clutch of little shag eggs. Breeding recommenced at a new site on the lagoon, until that site was in turn destroyed by a storm before breeding had ended on 22 January 1982 (Plate 5). Observations continued at Hamilton's Lagoon, but when no shags were present by late September 1982 (in 1981 courtship began on 5 August), observations were started at Sexton's Lagoon (7 October 1982). Field work at Sexton's Lagoon ended on 27 April 1983, when the birds dispersed at the beginning of the duck shooting season.

Observations were made at Hamilton's Lagoon from a caravan and at Sexton's Lagoon from a portable hide. For general behavioural observations a wristwatch, counter, 7x50 and 13x30 binoculars were used. Photographs were taken with a Pentax Spotmatic camera and a Pentax 500mm telephoto lens. A Pentax K1000 camera with Pentax 55mm lens and Tokina 100mm-300mm zoom lens was also used. Observations were made during three periods each week; 1500 hours to dusk (Tuesday), dawn to 1000 hours (Wednesday), and 1000 hours to 1500 hours (Friday). Time budget data were collected by noting the activities of each adult shag at the end of five-minute intervals (scan sampling; Altmann, 1974), throughout the three main observation periods. Results were

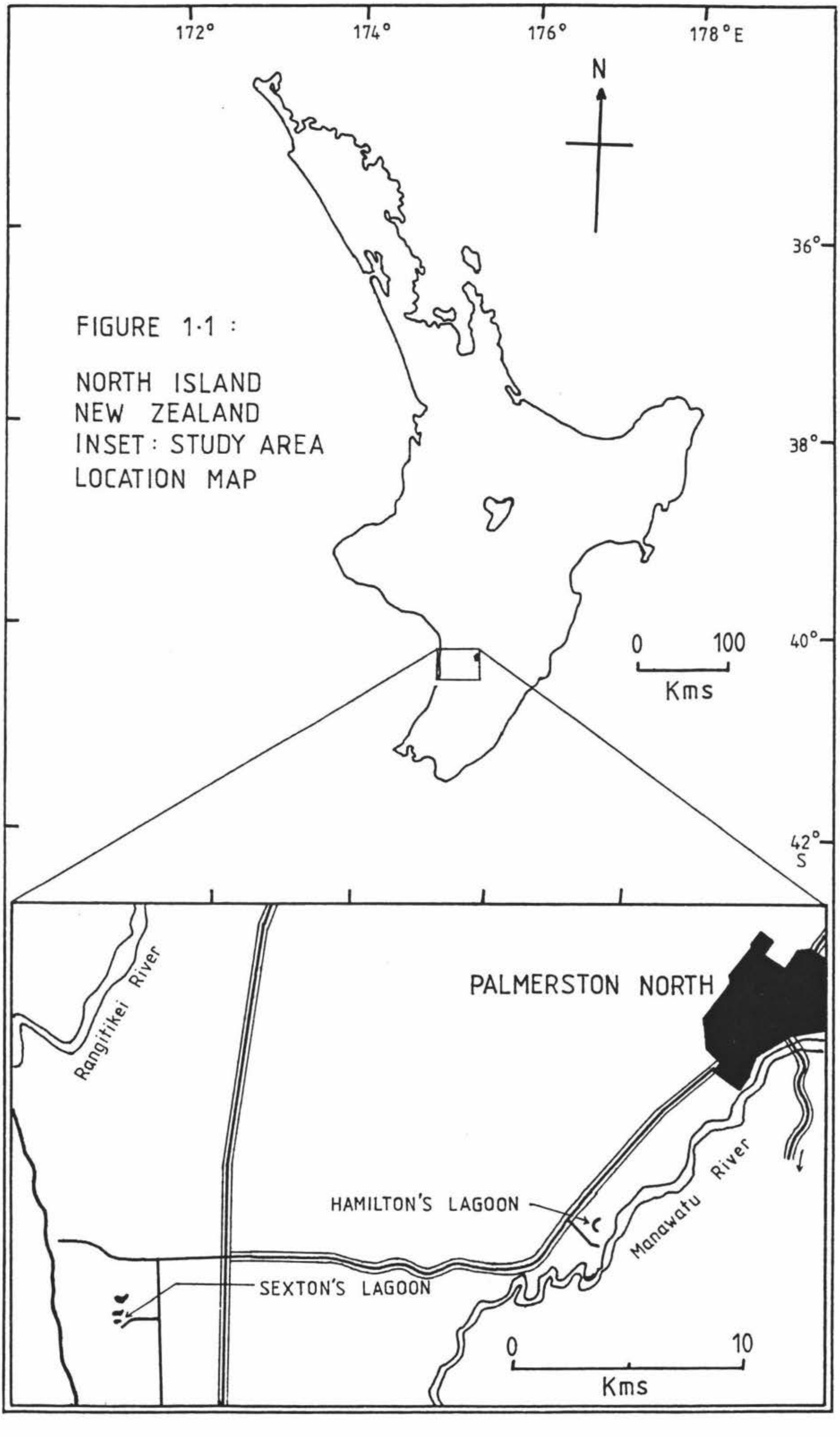


FIGURE 1·1 :

NORTH ISLAND
NEW ZEALAND
INSET : STUDY AREA
LOCATION MAP

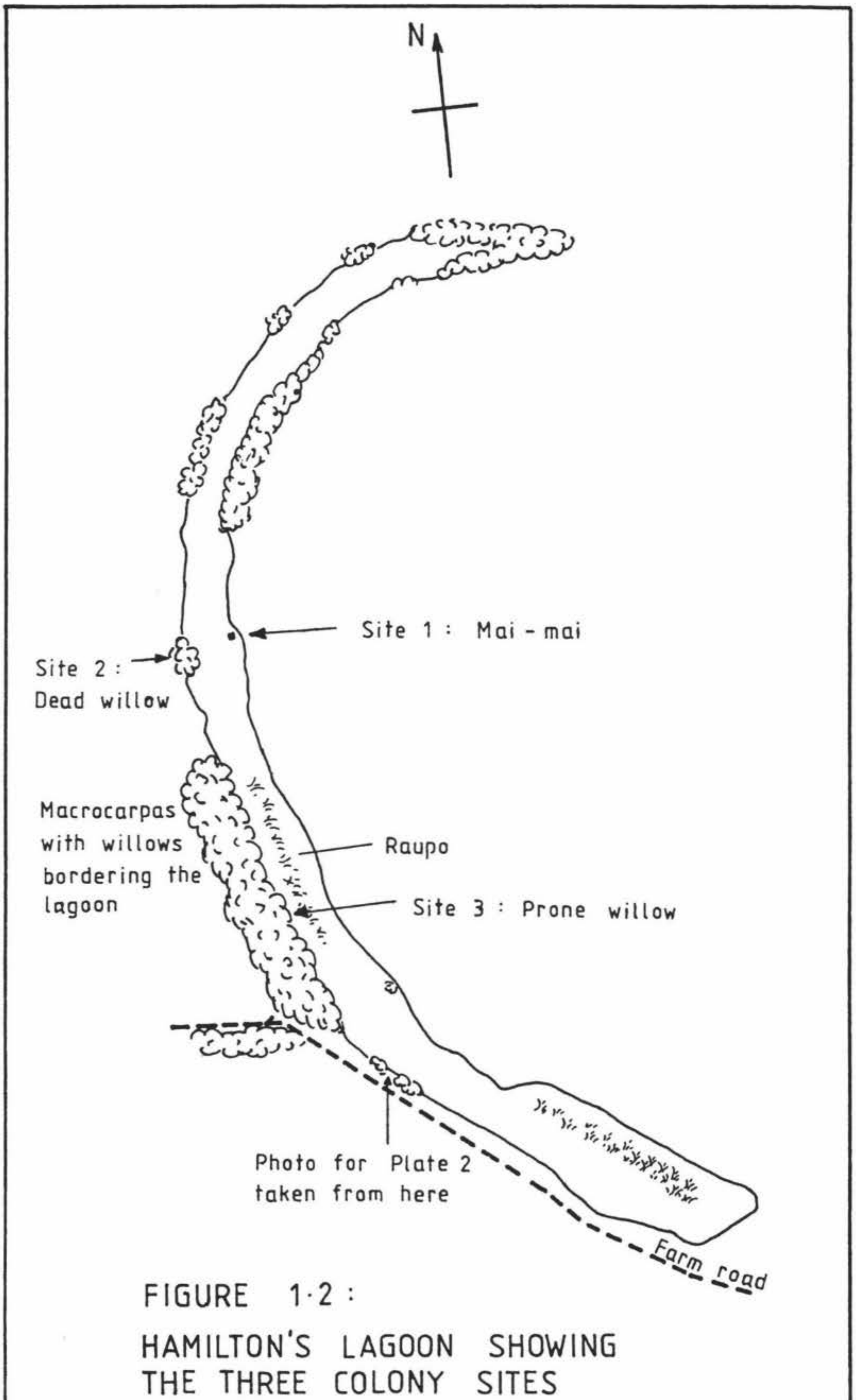


FIGURE 1·2 :

HAMILTON'S LAGOON SHOWING THE THREE COLONY SITES

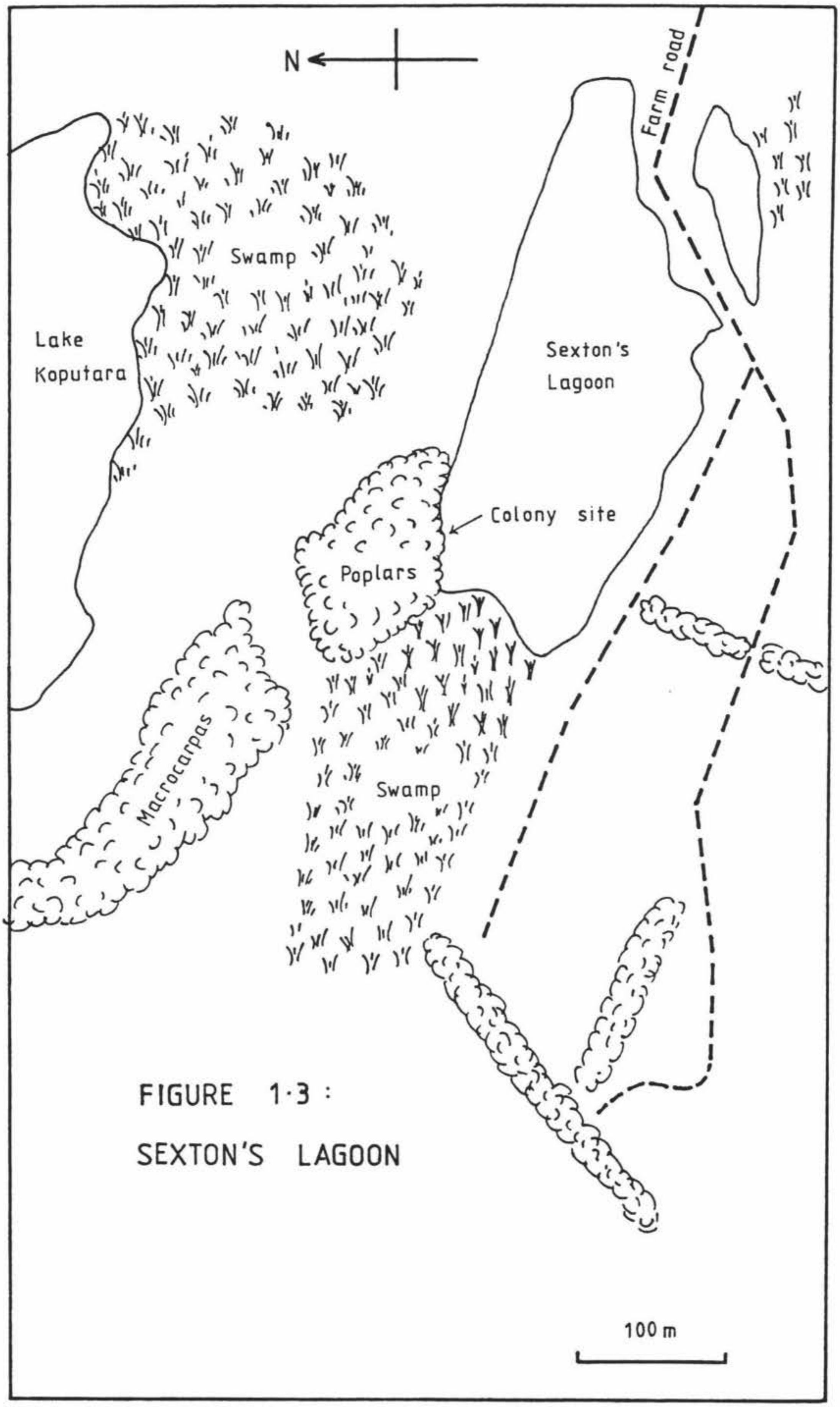


FIGURE 1·3 : SEXTON'S LAGOON

tabulated on a table of 16 activity categories (detailed in Chapter 5). Breeding data were obtained by visiting nests at least once per week using an aluminium dinghy. Nests were identified by painted cards attatched to the nest. A car fender mirror attatched to a broom handle was used to record nest contents above eye level. Plumage diagrams were prepared from 35 labelled adult study skins at the National Museum in Wellington and the Auckland War Memorial Museum, as well as from live adult breeding shags at Hamilton's Lagoon and Sexton's Lagoon and assigned to one of four categories according to the amount of white in the plumage (section 2.2). Measurements of bodily characters (following Gurr, 1947) were taken at both museums using vernier callipers to an accuracy of 0.1mm.

1.2.6 Constraints on the analysis

The performance of a chi-squared test to compare the 81/82 and 82/83 breeding seasons demonstrated that while certain parts of each day were very similar, differences in overall trends meant that each season needed to be treated separately. The observed differences may have been due to (i) the geographical separation of the two study areas, and the different individuals that were studied (ii) the difference in weather conditions between the two seasons (section 1.2.4), and (iii) the incompatibility of the major events that occured at each colony site, i.e. the destruction of the progeny of the Hamilton's Lagoon colony, and the different extent of breeding activities observed at each site.

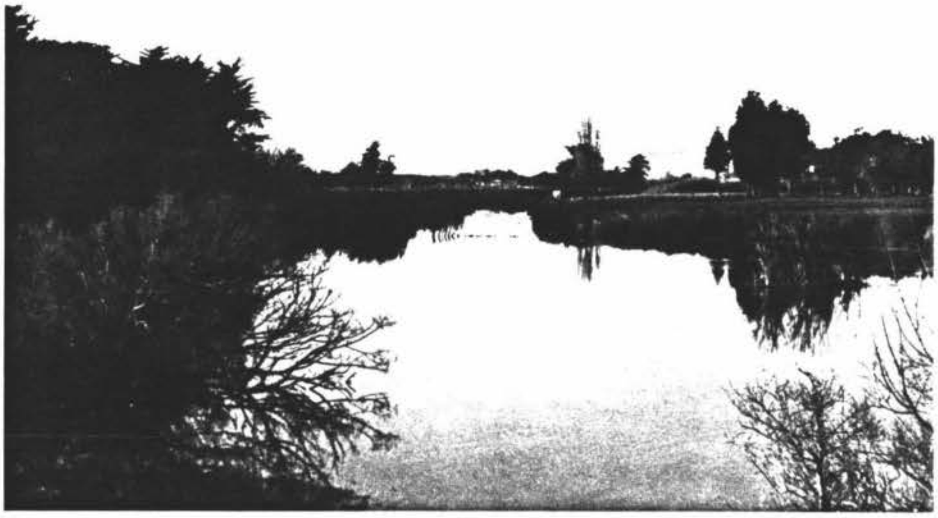


PLATE 2: GENERAL VIEW OF HAMILTON'S LAGOON

PLATE 3: BIRDS NESTING ON THE MAI-MAI

PLATE 4: PART OF THE PRONE WILLOW COLONY

PLATE 5: RESULTS OF THE STORM AT THE PRONE WILLOW

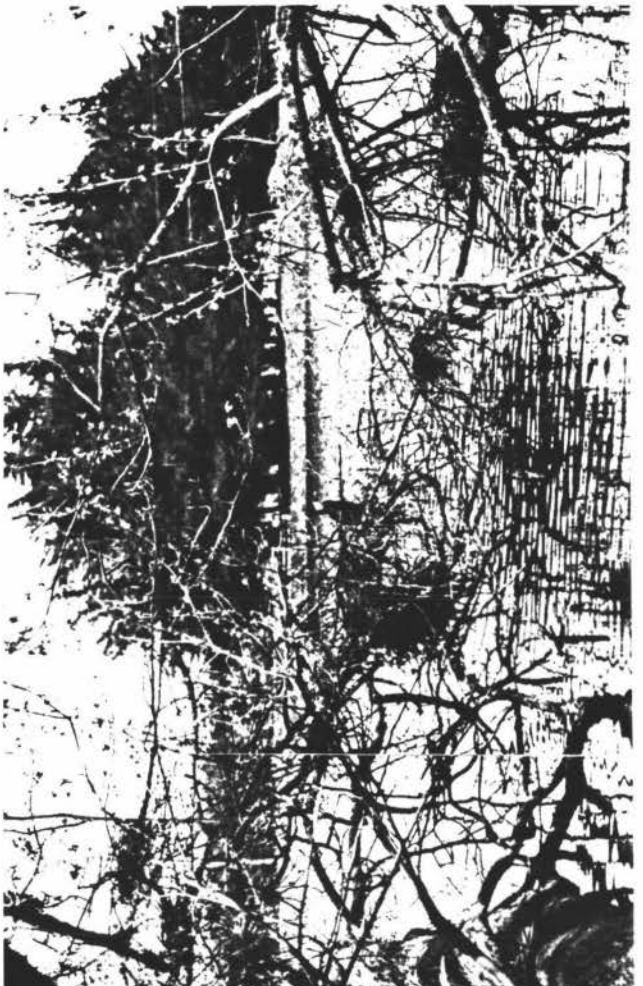


PLATE 6: SEXTON'S LAGOON COLONY

CHAPTER TWO:
BODY MEASUREMENTS AND PLUMAGE PATTERNS

CHAPTER TWO: BODY MEASUREMENTS AND PLUMAGE PATTERNS

2.1: Measurements

Measurements of both sexes were compared using a two-tailed Mann-Whitney U test with 95% confidence limits (Siegel, 1956). Distortion of some of the dried skins prevented the taking of all measurements.

Measurements taken at the National Museum and the Auckland War Memorial Museum are summarised below:

	MALES				FEMALES			
	n	MEAN	S.E	RANGE	n	MEAN	S.E	RANGE
EXPOSED CULMEN	12	30.8	0.43	20.0-33.6	12	30.0	0.78	28.2-32.2
BILL WIDTH	12	9.2	0.09	8.3-10.1	11	9.2	0.97	7.1-12.3
BILL HEIGHT	12	12.9	0.32	10.3-14.3	10	12.1	0.28	11.0-14.0
TARSUS	11	38.9	0.86	33.3-43.7	8	36.4	0.78	32.8-39.5
MIDTOE & CLAW	8	60.0	0.84	55.4-63.3	5	56.5	0.97	54.5-60.0

Results showed that although females did tend to be slightly smaller, there were no significant differences between the sexes in any measurement. Based on the work of Burley (1981), the little shag's apparent sexual monomorphism is not surprising, as Burley (op.cit.) hypothesises that sexual indistinguishability should tend to occur in, (i) populations that breed together in groups and, (ii) monogamous species, both of which apply to the little shag.

2.2: Plumage Patterns

Plumage diagrams were taken from skins at the National Museum and the Auckland War Memorial Museum. Each diagram was assigned to one of the following categories:

(i) Fully Pied: Individuals in which the ventral surface was completely white between the chin and the tail.

(ii) Intermediate A: individuals with more than 50% and less than 100% white on ventral surfaces between the head and the tail.

(iii) Intermediate B: individuals with less than 50% white on ventral surfaces between head and tail.

(iv) White-throated: individuals with white confined to the throat and face.

From a sample of 35 dried skins and live shags, the numbers in each category were: Fully pied: 6, Intermediate A: 5, Intermediate B: 3, White-throated: 21. This data was then analysed using a variant of the binomial theorem (W.D.Stirling. pers.comm.) to give 95% confidence intervals for the percentage of each category in the New Zealand population:

Fully pied: 4.1 to 29.6
Intermediate A: 2.7 to 26.0
Intermediate B: 0.0 to 17.8
White-throated: 43.8 to 76.2

In my sample, the white-throated phase is in a majority by a factor of 7 to 2 over the fully pied phase. This raises the question of what pressures have selected for the lower proportion of white in New Zealand populations, compared with that in Australian ones (where almost all individuals are fully pied).

Simmons (1972), suggested that white ventral areas in some species of shags promote countershading and act as camouflage during hunting. Siegfried <u>et al</u> (1975), further postulated that such shags should feed on relatively active prey, while species with more uniformly dark plumage should feed on relatively sedentary prey. According to this hypothesis therefore, variation in plumage types between New Zealand and Australia could arise if there was a greater proportion of slow moving or sedentary prey in New Zealand waters. Miller (1979), however, showed that in Australia the dark-plumaged little black shag feeds mainly on fish, while the little shag with its white undersurface, feeds mainly on crustacea and aquatic larvae. As most fish move faster than the majority of crustaceans, these observations contradict Siegfried et al's (1975) hypothesis.

Siegfried et al (op.cit.) have further postulated that the generally dark plumage of Phalacrocoracids is receptive to solar radiation, and assists shags in retaining metabolic heat. Because of its size, the little shag may be more suseptible to the heat loss, because of the relatively higher ratio of volume to surface area. Thus the pressures of crypticity and heat retention may act in opposite directions. Interestingly Falla et al (1979), state that the proportion of the fully pied form is highest in the warm north of the North island. Unfortunately, quantitative plumage data from the rest of the country are unavailable, and at least one possible anomaly exists: Kinsky (1969) reported that all little shags on Campbell Island were fully pied, probably because the colony was recently started by Australian immigrants.

Until the heat retention properties of the little shag's plumage are examined, the idea that thermal considerations have influenced plumage change within New Zealand populations remains speculative. Even if the influence of heat retention is found to be important, there is no simple correlation between plumage colour and heat retention. As Walsberg (1983) has pointed out, whether a dark plumage will acquire a larger or a smaller heat load depends on a wide variety of environmental and organismal factors, which may vary between species and be under the behavioural contral of the individual.

CHAPTER THREE:
POSTURES AND BEHAVIOUR PATTERNS

CHAPTER THREE:POSTURES AND BEHAVIOUR PATTERNS

3.1:Introduction

This chapter describes the postures and calls of little shags and documents behavioural responses to their physical and social environment, as a first step towards assessing familial and ordinal affinities. All behavioural descriptions refer to adults, except those in section 3.7.

3.2 Normal and alert

3.2.1:Normal

In the "normal" posture the neck assumes a characteristic 'S' bend, and appears relaxed even when the bird moves its head to scan the surroundings. The angle of the body with the horizontal ranges from 70 to 80 degrees in calm conditions to nearly zero in very strong winds when the tail is also raised or lowered as a conterbalance. As wind speed increases the bird progressively faces into it.

3.2.2:Alert

Alert postures grade from the "alert", characteristic of an undisturbed bird checking its surroundings, to "anxiety head-waving" performed in response to near threat such as an approaching predator. In the alert, the head and straightened neck are moved from side to side with the body stationary. For anxiety head-waving, head, neck and body all move from side to side: the head and neck movements are a high intensity version of the alert movements. Occasionally the posture resembles the "look" and "crouch" phases of take-off (Daanje, 1951), except that the look phase is more exaggerated in the little shag.

3.3:Movement

3.3.1:Walking

On land walking consists of a high stepping waddle typical of pelicans, sulids, anhingas and shags (Van Tets 1965). When walking slowly, the neck is `S' shaped and the wings are held close to the body, while in running birds the outstretched wings and tail are used as a counterbalance.

Perching birds move in a sideways `shuffle' with wings held close to the body, but again when moving quickly, the wings and tail are used for balancing. In hopping from one branch to another, the birds leap with both feet together, frequently opening wings mid-leap. Components of this movement have become ritualised as the "Hop" (section 3.3.4).

3.3.2:Flying

In flight, little shags resemble the form of a cross with the head, neck and tail horizontally extended, and the feet tucked beneath the tail. The general pattern of flight is standard throughout the order, and is characterised by the alternation of several wing beats with a glide (Van Tets, 1965). Van Tets (op.cit.) also states that all Pelecaniforms are capable of soaring, and long lines and `V's of flying birds are seen in many species. In the little shag, the longest glides (about 100m) are seen as a bird approaches the colony and soaring is often seen after disturbances. `V' shaped flight formations are common when groups fly back to the colony for the night. Following a disturbance in the colony the birds group in the air, wheeling and circling high overhead, and later break off in ones and twos to glide back to the colony, often circling once or twice more, before finally landing. Over water the little shag seldom flies more than about 3m above the surface, but over land may fly at a height of at least 20m. This is also seen in the pied shag (Millener, 1972).

3.3.3:Take-off and Landing (Fig.3.1)

My own observations confirm that take-off consists of the three phases previously described by Daanje (1951) and Van Tets (1965): (i) the look (Fig.3.1A), where the head and neck are extended up and forward, the closed bill is pointed in the direction of take-off, and the wings are partially raised. (ii) the crouch (Fig.3.1B), where the body is tensed and lowered, in readiness for (iii) the leap (Fig.3.1C), in which the body and feet are 'erupted' forwards enabling the bird to become airborne. A breeding adult often "Kinks" its throat and partially raises the crest for the first few metres of flight when leaving the colony. This behaviour pattern is identical in appearance to the pre-landing display of the pied shag (Millener 1972). However, unlike the pied shag, take-off is silent in the little shag.

Take-off from land is the same as take-off from an elevated perch except that three or four thrusts of the legs may be needed before the bird reaches flight speed. Water take-offs are similar except that on calm days after fishing, the bird may splash along for as much as 20m before finally becoming airborne. When landing on an elevated perch, a gliding bird approaches from a lower altitude, and rapidly back-strokes the wings just before landing. The feet are splayed to absorb the shock of landing; nevertheless, overbalancing into the water is not uncommon (particularly in the young). When landing on water the shag glides in at a shallow angle, backstrokes the wings and splays the feet, skiing along on its feet before coasting on its belly to a stop.

Landing is typically followed by a "post-landing" display which varies considerably throughout the Phalacrocoracidae (Van Tets, 1965). In the little shag, the bird reaches forward with raised wings, then retracts to the normal (in some cases the alert) posture. The various body components of this display can vary; thus body position grades from being almost imperceptibly forward with slightly raised wings, to nearly horizontal with widespread wings (identical to the crouch of take-off. Head position ranges from being slightly forward with closed bill, to an extended head and neck with open bill (similar to higher levels of threat). According to Van Tets (op.cit.), this display probably functions in individual and species recognition, and may have originated as a composite of recovery after landing; and preparation for flight, fight, or submission. Aspects of landing have become ritualised as the Hop (section 3.3.4).

3.3.4:The Hop

Van Tets (1965) describes this display as an abbreviated symbolic flight which starts with a take-off display (the Pre-hop), and ends with a Post-landing display (the Post-hop, Fig.3.1D). The little shag's Pre-hop display does resemble an abbreviated take-off in which (i) the look is dispensed with; and (ii) the body is only slightly lowered and in the normal position, instead being almost horizontal (as in the crouch of take-off). The wings are partially raised. The Post-hop consists of the bird reaching forward and down, with the beak opening at the forward limit of extension. The throat is kinked (see young kinking throat in plate 10). The bird retracts to the normal posture as the beak shuts and wings lower. Usually the beak is directed forwards, but during early courtship, it is sometimes pointed towards the female, possibly indicating a threat component. The Pre-hop and Post-hop resemble modified take-off and post-landing postures, respectively. The Hop is also seen during copulation (section 3.6.2), nest-relief (section 3.6.6), and presentation of nest material (section 3.6.5). The Hop varies between a short flight from, and back to, the nest site (circle-flying, Van Tets, 1965), down to hopping a few centimetres. The display may serve to attract attention of conspecifics or actual or potential mates (Van Tets, op.cit.).

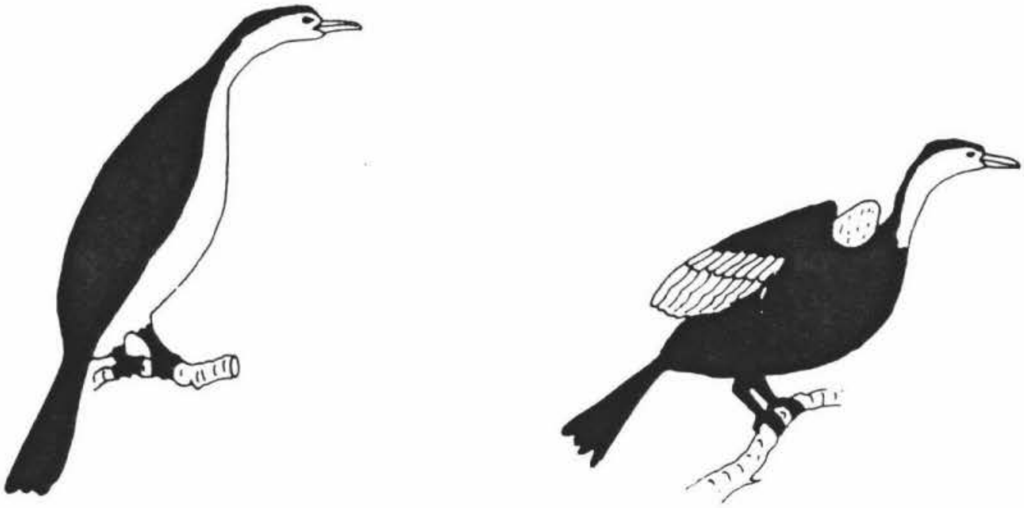
3.3.5:Swimming

When swimming on the surface, head and tail are horizontal, while the neck is in the upright 'S', a position characteristic of all Pelecaniformes (Van Tets, 1965). On the surface, feet are used alternately, but underwater they are paddled simultaneously (Van Tets op.cit.). After first alighting on water, about one third of the body is above water, but within a few minutes back and tail are submerged because the shag's plumage rapidly absorbs water (Rijke, 1967) (Millener, 1972 remarks that the rate of plumage wetting in little shags is greater than in pied shags). During slow and normal swimming the head is held motionless, but at high speeds it is pointed foward and nodded back and forth, as when juveniles swim after parents.

3.4:Maintenance

3.4.1:Stretching

There are two main stretch postures, both of which are not repeated:



A. Look

B. Crouch

C. Take-off

D. Post-hop

FIG. 3.1: TAKE-OFF AND LANDING POSTURES.

(i) The single wing-stretch, in which the body is in the normal posture while one wing is stretched, and the same side of the tail is fanned.

(ii) The double wing-stretch where both wings are opened simultaneously and raised above the horizontal body, head and neck are stretched forward, and the tail is slightly fanned and held more or less erect. According to Millener (1972), both the leg and foot of the pied shag are stretched backward and forward, but I have not observed this in the little shag.

3.4.2:Sleeping and Yawning

When sleeping, the bird stands with folded wings, and the posteriorly twisted head and neck lie down the mid-line of the back, with the beak hidden in the mantle feathers. Millener (1972) reports that pied shags may sleep on one leg, but I have not seen this in little shags.

Yawning birds open the mandibles fully, while the head is angled from horizontal to about 90 degrees. The gular pouch is extended while the head and neck are frequently shaken from side to side. Millener (1972) states that pied shags yawn frequently (no data given), but in 19 months of observations of the little shag, only 6 yawns were seen.

3.4.3:Thermoregulation

Cool temperatures alone have no observable effect on little shags, but if cool temperatures are associated with high winds, the birds often sleek their feathers close to the body. According to Berry (1976), such behaviour minimizes the effects of cold air on the body. During cold and windy days in summer at Sexton's lagoon (i) a greater proportion of birds assumed the sleeping position than on warm days, and (ii) the total attendence at the colony was greater. These observations could suggest that halting energy-demanding activities such as foraging for food in adverse weather conditions, may lessen the individual's energy loss (c.f. Kessel, 1976).

As the ambient temperature rises the bill is opened progressively and the gular region expanded, achieving the greatest area of evaporative cooling (Berry, 1976). Cooling is augmented by fluttering the gular region (Fig.3.2), where intensity and duration are directly varied by temperature, humidity, and wind speed (Berry op.cit.).

3.4.4:Preening

Little shags spend a considerable amount of time preening, the exact proportion depending on the season and time of day. Contour feathers are preened with a repeated nibbling motion while tail and wing feathers are passed through the mandibles, before being replaced in the original position. Oil from the uropygial gland is spread over the wings by the bird's head. As in pied shags (Millener, 1972), preening is most frequent on the breast and wings, while in the little shag is least on the tail and stomach.

3.4.5:Scratching

In common with other shags (Simmons, 1961; Millener, 1972), the little shag brings the foot straight up to the head - the 'direct' form of Simmons (1961). Its neck is arched so that the head is at belly level, the body is in the normal posture and the third claw is used to scratch.

3.4.6:Spread-wing posture

The spread-wing posture of the little shag is similar to that described in other shags. In the little shag, the bird usually shakes head and body, flicks its tail and flaps its wings, apparently to remove excess water. Subsequently the bird either holds both wings outstretched for five minutes and then preens, or else it alternates the spread-wing posture with preening for several minutes.

Four hypotheses have been advanced to explain the functional significance of this posture: (i) Heath (1962) proposed that the posture had some thermoregulatory function, (ii) Rijke (1968) considered it may be used for wing-drying (iii) Rijke (op.cit.) thought the posture may aid in balancing, and (iv) Jones (1978) speculated that the posture has an intraspecific signalling function.

Following physiological experiments performed on the anhinga and double-crested cormorant, Hennemann (1983) concluded that the spread-wing posture served thermoregulatory and wing-drying functions in the anhinga, but only wing-drying in the double-crested cormorant. The possibility that smaller shags such as the little pied shag used the posture for thermoregulation was refuted by Winkler (1983), who found that the little cormorant (Phalacrocorax niger) does not use the spread-wing posture for thermoregulation (he does however acknowledge that due to the complexity of the processes involved, extrapolation to other species or environments is difficult).

3.4.7:Bathing

During bathing, the head and neck are extended, and briefly dipped beneath the surface, causing water to be thrown on the back. The half spread wings are vigorously flapped, propelling the bird for several metres in a straight line or circle. Bathing lasts between three and ten minutes, is usually followed by preening, and is similar to bathing in other shags (Snow, 1963; Millener, 1972).

3.4.8:Drinking

On the one occasion this was observed the open beak was dipped into the water, then the head and neck were tilted upwards. No swallowing motions were seen.

3.4.9:Excretion and Egestion

(i) Cloacal excretion

Crouching slightly, the bird excretes a whitish liquid with considerable force. In all shags young chicks attempt to excrete over the nest rim (Gilham, 1960); consequently surrounding branches develop a conspicuous white coating. According to Gilham (op.cit.), shag faeces are highly acidic and usually kill the tree.

(ii) Regurgitation of food or pellets.

During regurgitation, the head and neck are arched almost straight down, the beak opened wide, while the head is shaken vigorously from side to side. Pellets are formed because certain parts of the diet (heavy bones, otoliths, and chitinous exoskeletons), cannot easily be dissolved in the stomach (Van Dobben, 1952). As in other shags, food is frequently regurgitated in response to disturbance (Millener 1972).

3.5:Agonistic behaviour

According to Snow (1963), all aggressive displays in shags involve pointing the bill at the object of aggression; conversely all those of appeasement involve pointing the bill away from the object of submission.

3.5.1:Threat display (Fig 3.2)

Following Snow (1963) and Millener (1972), threat behaviour is separated into stationary aggression, usually shown by a bird on the nest or nest site when it is unwilling to move, and mobile aggression, exhibited away from the nest.

There is a contiuum of intensity in all forms of aggression, starting at the lowest intensity of stationary aggression, where the extended neck and closed bill are pointed at the object of aggression. At higher intensities, the head and closed bill are jerked rapidly towards the intruder. At the highest intensity the crest is fully raised, tail slightly elevated, and the wings may also be partially raised. The bill is repeatedly thrust towards the intruder, and is widely opened at the forward limit of each thrust. "Nest-quivering" (section 3.6.5), which is often performed after such behaviour, is possibly a "displacement activity" (Lorenz, 1952).

During mobile aggression the wings are held slightly away from the body, or, at the highest intensity, half spread. As the bird advances toward an intruder the partly opened beak is repeatedly thrust foward (similar to the pied shag; Millener, 1972).

3.5.2:Fighting

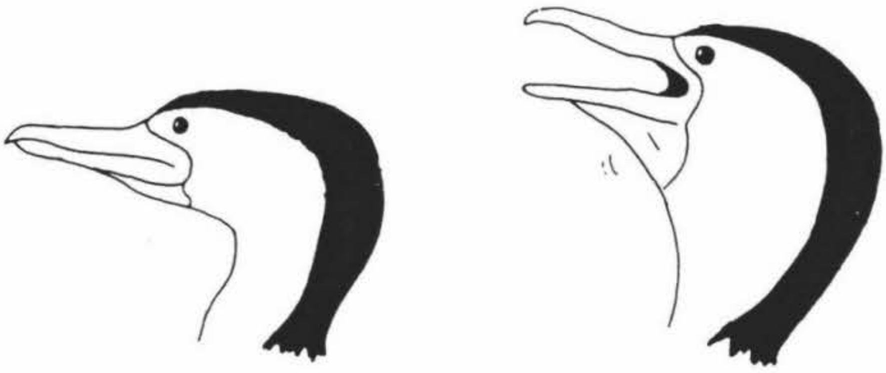
I observed fighting once (21 August 1981), between two shags on a nest site. Both shags had their wings spread, pecked at their opponent's bill and grabbed hold of his wings. During the fight one bird tumbled into the water. According to Van Tets (1965), fighting in the Pelecaniformes normally occurs between members of the same sex. Further, fights are comparatively rare, tending to occur at nest sites where nest or pair bonds have not become firmly established. At Hamilton's Lagoon, a male unsuccessfully tried seven times to claim a nest site immediately adjacent to that of an advertising male. The displaying male expelled the intruder each time, until the newcomer approached the nest site from behind. The intruder occupied the site, both males Nest-indicated (section 3.6.4) to each other, and no further aggression took place. From examples quoted by Van Tets (1965), fighting behaviour appears to be similar throughout the order.

3.5.3:Submissive display (Fig.3.2)

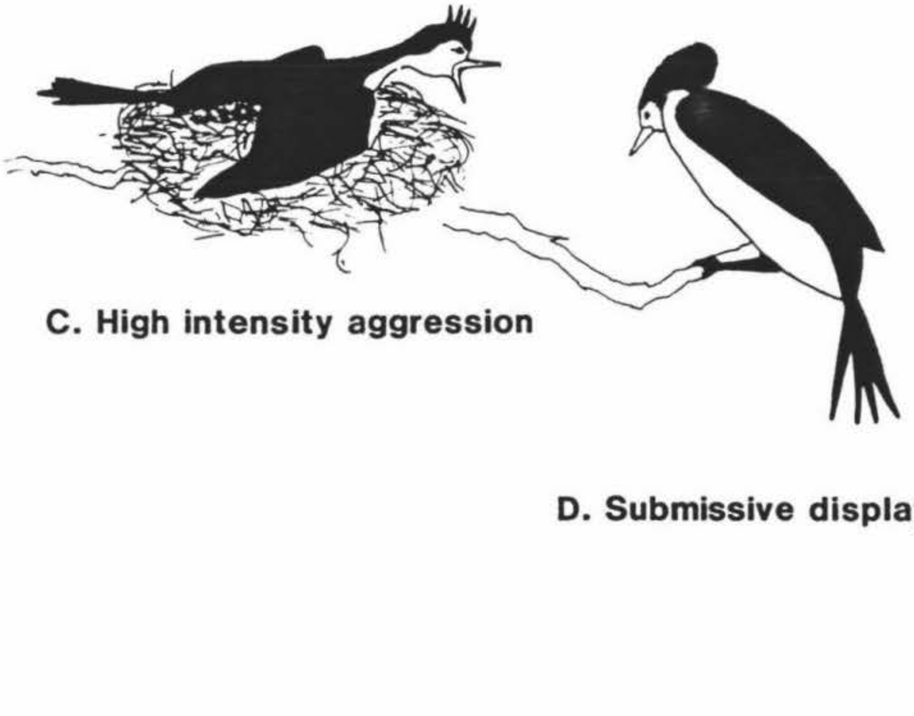
In a submissive bird, the feathers are sleeked, making the bird appear smaller than normal. The head and neck are drooped, and the bill faces away from the aggressor. I have observed submissive behaviour in three situations: (i) as the response of an intruder to a high-intensity stationary threat given by a territory owner, (ii) in certain courtship activities (section.3.10), and (iii) as the response of a juvenile to an older bird which had perched nearby (also seen in juvenile *P.aristotelis*; Snow, 1963).

3.6:Reproduction

Little shag territories formed between late August and early September at Hamilton's and Sexton's Lagoons. Males defend an existing nest or new nest site against other males. The minimum territory size is delimited by the distance an adult can reach with its neck fully extended. Various courtship and pair maintenance behaviours help to form and maintain these territories. Brown's (1975) definition of a territory as being "a fixed area from which intruders are excluded by means of some combination of advertisement threat and attack" is selected as being appropriate for the little shag.



A. Normal head position **B. Maximum gular flutter**



C. High intensity aggression

D. Submissive display

FIG. 3.2: GULAR FLUTTERING, AGGRESSION AND SUBMISSION.

3.6.1:Male Advertising (Fig.3.3)

The two displays used are the "Squat-thrust" (Figs.3.3B & 3.3C) and the "Gape-bow" (Fig.3.3D).

Birds performing the Squat-thrust stand erect with folded wings held slightly away from the body. Squatting to a nearly prone position, the bird quickly thrusts upwards, during which the chest rapidly expands, the wings extend further from the body, the crest is raised and feathers are ruffled (particularly on the side of the head), the tail is slightly elevated, and a two-syllable "uh-aaah" call is given. According to Van Tets (1965), the Squat-thrust is analogous to the "wing-waving" display of many gannets and shags, except that in little shags, wings are only raised once per display. My observations indicate the Squat-thrust also differs in having few movements of the head and neck. Thus, the emphasis of the display is overt body movement, rather than the head movement seen in other family members.

Gape-bowing males stand erect with a closed beak, then the whole body is vigorously stretched forward so the head finishes below feet level (unless it meets an obstruction). The beak is opened at the bottom of the downstroke, and a one syllable call is made. The wings are kept close to the body throughout, and the tail is more or less parallel to the body. Van Tets (1965) considers that Gape-bowing is related to the Gape display of other shags. Gape-bowing is performed more often than the Squat-thrust, and while both displays serve to attract potential mates, the Gape-bow appears to attract females from a greater distance. Both displays feature an open beak, which may indicate an aggressive origin (Van Tets, op.cit.). I believe that body switching (the change from a vertical to a horizontal body positon, and vice-versa) may serve to emphasise the sexual nature of both displays, particularly as body switching is absent from the rest of the bird's behaviour.

3.6.2:Copulation (Fig 3.4A)

Copulation mostly occurs during changeover or presentation of nest material by the male. The male hops or walks sideways to the female, who may Nest-indicate (section 3.6.4) to him. The male mounts on the

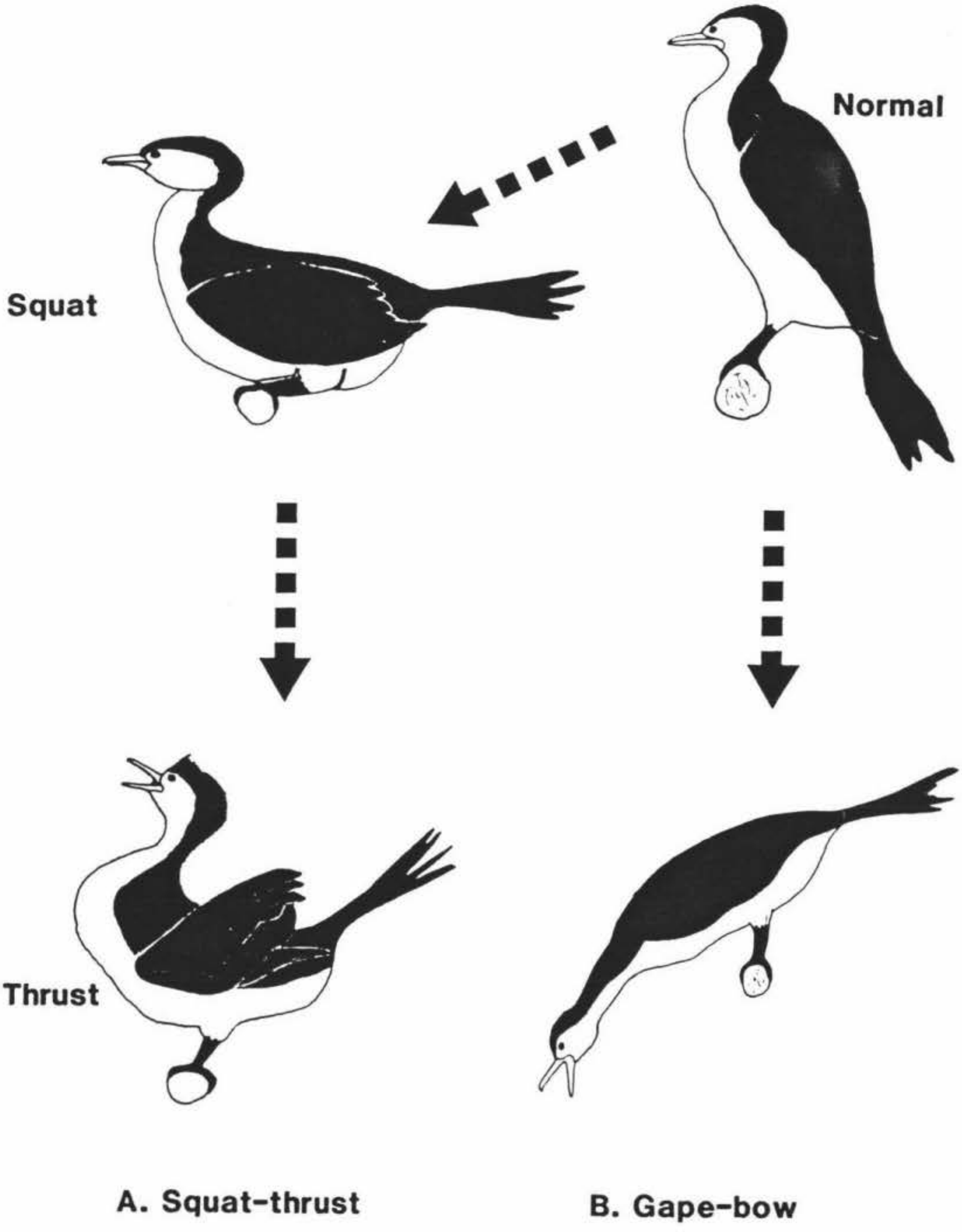


FIG. 3.3: THE MALE ADVERTISING DISPLAYS
(SQUAT-THRUST AND GAPE-BOW).

female's back, and grips her head or neck in his mandibles. The female's head and neck are sometimes curved downward so her bill is lodged in the bottom of the nest, possibly keeping the neck steady, and this may help the male to balance (Snow, 1963). The male then treads on the female's back, lowers his tail, and makes cloacal contact. Snow (op.cit.) and Millener (1972) report that males make a characteristic call, but I have not heard this in little shags. The male Hops off and preening usually occurs, but apparent displacement activities (Lorenz, 1952), such as re-arranging of nest material, may take place. On the basis of sexual identification by sexually specific displays (e.g. male advertising) and individual plumage diagrams, no reverse mountings (Selous, 1927; cited in Millener, 1972) were observed but promiscuous matings (Snow, 1963) apparently occur. Copulation in this bird closely resembles descriptions given for other familial and ordinal members (Snow, 1963; Millener, 1972; Nelson, 1978b).

After courtship and up to the start of egg laying, it is not uncommon to see a paired male advertising, but only while the female is absent. Apparently unpaired females may be attracted, and on at least one occasion, copulatory movements took place (I could not determine if cloacal contact occured). If the mate returns while another female is present, the intruding female is vigorously expelled by the mated female. Apparent promiscuity has been documented in other shags (Harris, 1982), as well as in other species of monogamous birds (see Gladstone, 1979). From the point of view of the male, this promiscuity may act as an insurance against non-reproductive mates, or against the possibility that his genes are not present in the offspring. For females, Gladstone (1979) believes that multiple fathers for offspring may act as a hedge against fluctuating environmental conditions.

3.6.3:Nest building

In common with other members of the order, males collect most, if not all, nest material, while females build the nest (Van Tets, 1965). During the earliest stages of construction, fragile material such as leaves and waterweed are often presented to the female. This material has no structural value, buts its offering may act as a stimulus for copulation or assist in pair formation. When copulation occurs, it

A. Copulation

B. Mutual nest-quivering

FIG. 3.4: COPULATION AND NEST QUIVERING.

appears to stimulate the male to collect more nest material. In one case, a male made 15 collection trips within three-quarters of an hour after copulation.

The sticks which make up the nest base proper are stouter than those which make up the rim and lining. Base sticks are laid criss-cross forming a crude platform (plate 7). Such platforms are easily damaged, and many nests do not proceed beyond this stage. Twigs are then added and intertwined to construct the rim, while the finest twigs make up the lining. The female inserts material with a movement identical to Nest-quivering (section 3.6.5). Nest material reflects what is readily available at the site (at Hamilton's Lagoon willow was the most common nest material; at Sexton's lagoon it was poplar). Items such as string and fabric may also be added to nests. Construction of a complete nest takes three to five days, but material is still added after the chicks hatch. Nests from previous seasons appear to be re-occupied in preference to the construction of new nests, and take less time to prepare. Sometimes, eggs are laid in the crude platforms, but are usually lost unless they become wedged between sticks.

3.6.4:Nest-indicating (after Van Tets, 1965)

There are two variations of Nest-indicating, both resembling a low intensity, silent Gape-bow. In one form the downstroke of the bill ends with the bill prodded into the nest or below the feet, while the other form ends with nest material being re-arranged. The display is usually seen early in the breeding season during changeover or presentation of nest material, thereafter it decreases in frequency. It is occasionally seen as a response to conspecific intruders (and in one case to a black shag, P.carbo). Nest-indicating is regarded as a site-ownership display by Snow (1963) and Van Tets (1965); as re-directed fighting by Berry (1976); and as nest maintenance by Bernstein and Maxson (1982a). In the little shag it could serve the functions of site-ownership, threat, and recognition (Van Tets; cited in Bernstein and Maxson, op.cit.). Displays with multiple functions have also been observed in other shags (Snow, 1963), as well as in gulls (Beer, 1975).

3.6.5:Nest-quivering (after Snow, 1963; see Fig.3.4B)

Nest-quivering is normally performed at the nest site. The standing or sitting bird holds nest material in its beak and quivers its head about 1-2cm from side to side. During early courtship the display is frequently mutual, occuring as the male presents nest material to his mate, in the following sequence: (i) the male arrives with nest material and gives the Greeting call (section 3.6.6), (ii) the male holds one end of the material, the female the other, and together they first quiver upwards, then curve their heads downwards and quiver at nest level, and (iii) the female takes the material, quivers upwards, and places the material in the nest. If no material is being presented, one member of the pair often quivers the tail feathers of the other. During early courtship both birds stand, but later in the season one bird usually sits and quivers, and ultimately the display is entirely dispensed with. Snow (1963) states that Nest-quivering is characteristic of immature birds and can have an aggressive function; but in little shags I have never observed this, although Nest-quivering is somewhat similar in appearance to Nest-indicating. The display's decreasing frequency as the pair bond further develops is suggestive of a possible role in pair formation.

3.6.6:Nest-relief

During early breeding the incoming bird invariably gives the Greeting call (a series of repeated "aark-aark"s), in the last few feet before alighting. This call is restricted to territory owners and can be performed to eggs and chicks as well as to mates. The incoming bird hops to the side of the nest while the sitting bird often Nest-indicates to its mate. Mutual Nest-quivering, and quivering the mate's tail feathers, may also occur before actual changeover takes place. When the sitting bird does not move, the incoming bird gently nudges its mate aside. After changeover, the departing shag hops away and usually preens. Generally it leaves almost immediately afterwards, but one individual stayed for 22 minutes before flying off. Millener (1972) states that male pied shags usually call after gaining possession of the nest, but I have not heard this in little shags. Later in the breeding season, the greeting call and other displays associated with early breeding disappear from the repetoire.

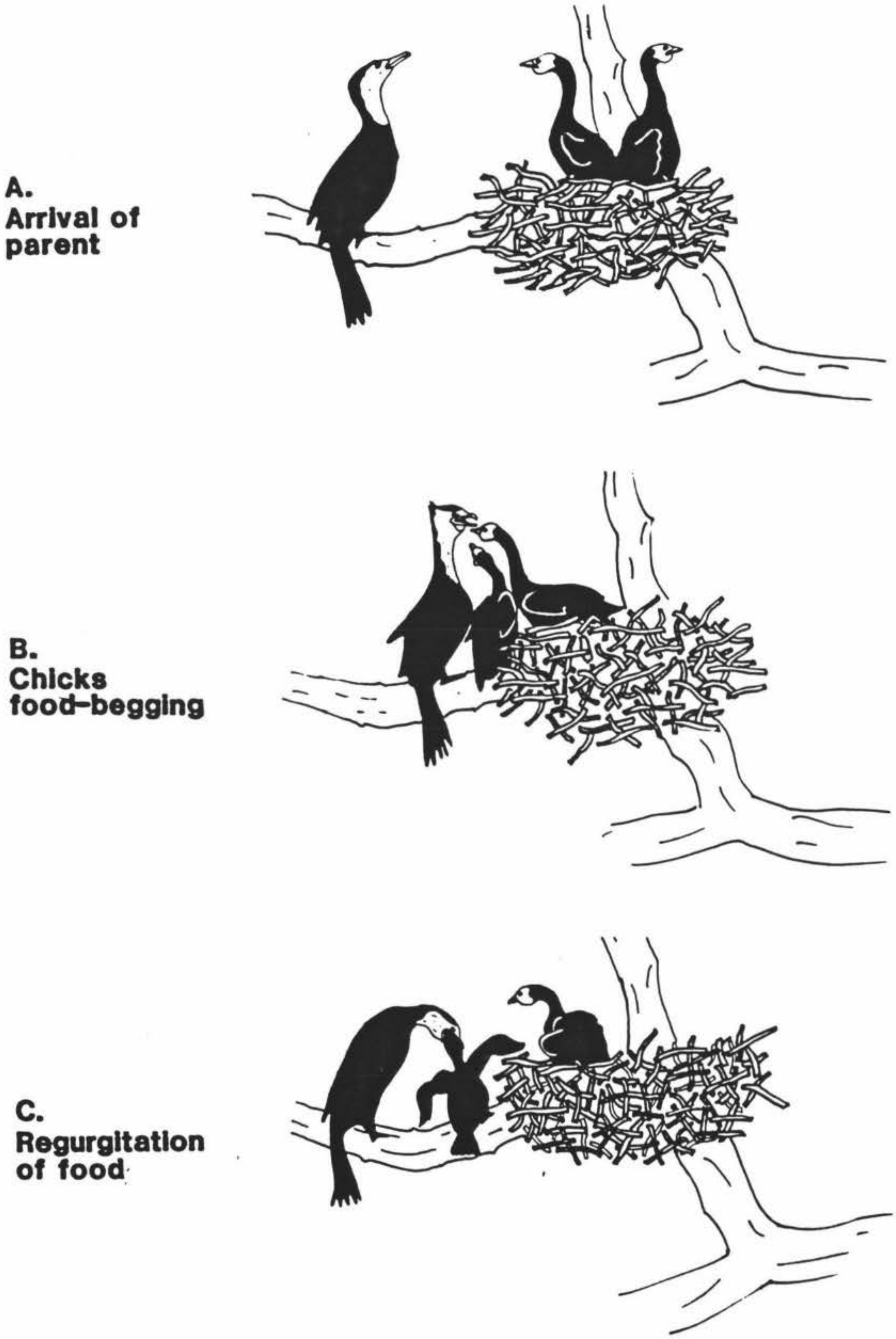
3.7:Behaviour of Young

3.7.1:Food-begging (Fig.3.5)

Naked chicks make uncoordinated begging movements accompanied by the food-begging call (a repetitive, high-pitched "whee-whee"), and as they cannot stand, the parents sit while feeding them. At this stage, little shag chicks are fed about five times daily, and the studies of other workers e.g. Snow (1963), Berry (1976), and Mitchell (1977), indicate that at this stage of the chicks development, food is probably in the form of a semi-liquid paste.

When a parent returns to the nest (Fig.3.5A), older downy chicks start to beg (called "beg-waggling" by Millener, 1972). The chick flaps its wings, while the outstretched head and neck are pointed towards the kinked gular region of the parent (Fig.3.5B). The parent makes swallowing motions, and opens its beak, so that the chick can insert its head into the parent's throat (Fig.3.5C). Chicks are not fed in any particular order, but it is possible that the largest and strongest chicks get most food because they jostle their siblings away. According to some authors (Morrison et al, 1979; Williams and Berger, 1979), this may cause the youngest chicks to starve. Chicks are fed in bouts lasting from 3 to 11 seconds (mean=6.7, n=14), but in a given session each chick does not receive all its food at once. Chicks up to the age of four weeks are always fed on the nest, and after that they move off the nest to meet the incoming parent.

Fledged chicks beg with head, neck and body horizontally extended, while the wings are outstretched and lightly waved, and a high pitched call similar to that of very young chicks is made. Juveniles generally move towards the parents and not vice-versa. If parents are reluctant to feed their young, juveniles will lightly tap the base of the adult's bill with a rapid quivering motion. This eventually stimulates the parent to regurgitate, but sometimes it flys to the water (apparently to gain relief from the chick's begging). Millener (1972) states that juvenile pied shags can be fed on the water, but I have not seen this



A.
Arrival of parent

B.
Chicks food-begging

C.
Regurgitation of food

FIG. 3.5 : FEEDING OF YOUNG.

in little shags. Juveniles are fed two or three times daily and are indiscriminate in their begging. Young juveniles may also beg towards older siblings (the younger often inserts its head into the elder's mouth; also observed by DeLaRonde & Greichus, 1972), towards adults other than their parents, or even towards another species of shag (adult little black shag), but I never saw food regurgitated in these situations.

3.7.2:Responses to disturbance

During the first three days of life, chicks can barely hold their heads up, and offer no resistance to an intruder or make any attempt to escape (Plates 8 and 9). Lack of physical resistance continues for two weeks, except that from about 10 days chicks will stand and peer at an intruder, and cower if a hand approaches them. If handled when covered with down at about 20 days of age, chicks will regurgitate food and defecate. At about this age, chicks peck at an intruder, and hold on to the nest with the feet and beak, making their removal difficult. Chicks immediately become silent and huddle down in the nest if the alarm call is made (a series of low pitched "coos"). One adult initiates the call, but within one or two seconds it spreads throughout the colony. From about 30 days of age, chicks climb out onto surrounding limbs to escape, and, soon after, climb frantically into surrounding branches and even jump into the water in response to a major disturbance. On one occasion at Hamilton's lagoon this behaviour resulted in the death of two chicks who were unable to climb back onto the nest. Flying juveniles (Plate 14) are extremely sensitive to disturbance; generally they show the alert posture at greater intensities than adults in similar situations, and take a longer time returning to the colony if they have been disturbed into flight. In one instance, all adults had returned to the colony within 10 minutes, but the juveniles did not return for at least an hour after being frightened away.

3.7.3:Thermoregulation

Chicks are continuously brooded by a parent for at least 20 days, by which time they have attained a complete covering of down. At

Hamilton's Lagoon, the exposed young could flutter the gular pouch in a coordinated manner by this age. At Sexton's Lagoon, the young were continuously brooded for 32 days and gular fluttering was not observed. No specalised postures or behaviour patterns as seen in cape cormorant chicks (Berry, 1976), were observed.

Young at Hamilton's Lagoon were brooded until at least 20 days of age, while chicks at Sexton's Lagoon were not permanantly exposed until 35 days of age, which may mean that resistance to cold does not develop until then. This difference between the two colonies in successive years in the length may have been due to the greater chill factor caused by higher winds and lower temperatures than normal at Sexton's Lagoon (see section 1.2.4). It is possible that aside from the direct effects of weather, more subtle long term effects may occur. Thus, as parents were unable to forage together at Sexton's Lagoon until the young were 35 days old, chicks may have received less food, and their subsequent development rate could have been effected. The severe weather conditions may also impose a greater energetic stress on the parents, particularly in maintaining of body temperature. Other behavioural responses of young to cold and wind included huddling close together in the bottom of the nest, and shivering. The fact that down and feathers first develop on the back, the most exposed area, and lastly on the upper legs and head, which can be readily covered, may be significant in the chicks developing thermoregulatory ability (compare Plates 11 and 12).

3.7.4:Play

The most common form of play consisted of a chick pulling and tugging at pieces of nest material. On two occasions, two chicks were seen tugging at opposite ends of a twig, and in one instance a swimming chick was seen playing with a piece of flax (similar to play recorded by Snow, 1963 and DeLaRonde and Greichus, 1972). Snow (op.cit.) states that play is seen in chicks older than 40 days; in the little shag it was seen in mobile well developed chicks of at least 40 days of age.

3.7.5:Flying and Fledging

Wing flapping (associated with food begging) starts early in life, and increases in duration and intensity until the chick fledges. At Sexton's Lagoon fledging occured at 63 days of age, but this may be rather late due to possible delaying effects of the bad weather. First flights are made from branch to branch or from branch to water in and around the colony. At 65-70 days of age, 30 second circular flights around the colony are common.

3.8:Interspecific interactions and Grouping

Little shags were often seen perching with black shags and little black shags. Solitary black shags ignored the little shags. If a group of black shags perched together with little shags, individual black shags were more likely to be aggressive. If a black shag threatened, the little shag would almost invariably retreat quickly to another perch. In one case, a black shag and a little shag threatened each other for four and a half minutes before the little shag finally retreated. On another occasion a juvenile was literally plucked out of the air when it flew too close to a perching black shag.

Groups of about 12 of the more aggressive little black shags often roosted at night at Sexton's Lagoon beside the little shags. Whenever this happened, perching little shags would be forced to move by incoming little black shags, and because the colony tree was usually filled to capacity with roosting birds, the displaced little shags moved to a neighbouring tree.

Reactions to the approach of a harrier varied with the season. In autumn and winter, a harrier approaching to within 20m of a group of roosting little shags would cause them to dive in different directions into the water. As the harrier often hesitated in mid-strike when the shags dived, this could indicate possible confusion on the part of the harrier (in contrast I have seen a flying harrier snatch individuals from a compact flotilla of ducklings). During breeding, this behaviour was not shown until the harrier approached within two of metres of the colony, and on one occasion I saw a harrier destroy a clutch of eggs within two metres of other nests that had sitting birds in them. It seems that increased 'flightiness' between breeding seasons is characteristic in little shags, and could benefit individuals by making them less vulnerable to predation. Flightiness during breeding, however, may increase the risk to eggs and chicks of predation and temperature extremes.

Little shags are gregarious, both in and out of breeding. Presence of one or two little shags at a roosting site rapidly attracts other conspecifics to perch. When roosting together, individuals space themselves in excess of one and a half body lengths; any attempt to perch closer normally results in agonistic display. Comparison of roost photographs from different seasons reveals a generally closer perching distance during breeding, but whether this was the result of increased mutual tolerance, or a function of the increased density at breeding roosts (colonies) could not be determined. The advantages to individuals of such groupings are difficult to quantify, but in this shag they could be related to detection and confusion of predators. I have observed that approaching harriers are detected at greater distances by groups (detection evidenced by showing of alert postures), rather than individual little shags (c.f. Kenward, 1978). It is possible that roosts act as information centres for efficient location of patchily distributed food (Ward & Zahavi, 1973; in Krebs, 1974), however as the little shag is a solitary feeder, this is unlikely.

3.9:Discussion

Components of little shag's communication patterns are variably related to behaviour patterns of other ordinal and familial members.

(i) Voice: Specific calls in the little shag relate to: male advertising, Greeting, food-begging and alarm. Interestingly, Van Tets (1965) states that there is no alarm call in the Pelecaniformes; but that many displays have characteristic calls associated with them.

(ii) Bill position: A forward pointing bill is seen in pre-take-off, threat, the Post-landing display, and the Hop. Van Tets (op.cit.) considers the forward pointing bill to be more intimidating than bill positions such as up, down, or sideways. In the little shag, appeasing bill positions are seen in submission, male advertising, Nest-indicating, Nest-quivering, and during changeover and copulation. That some courtship and pair maintenance displays feature both intimidating and appeasing bill positions, may indicate conflicting tendencies within the individual. The wide open bill is common in threat and recognition displays in the order. An open bill is seen in high-intensity threat, the Post-landing display, the Hop, male advertising, and Nest-quivering. The bill displays of many pelecaniforms, but not in the little shag, are enhanced by brilliant colouration of the inside the mouth lining.

(iii) Head and Neck: Almost all head movements of the little shag occur in the median plane (as in the rest of the order; Van Tets, 1965), except in anxiety head-waving, during which exaggerated side to side head movements occur. Small side to side movements occur in Nest-quivering and Nest-indicating. In high-intensity threat, anxiety head-waving and flying, the little shag's neck is arched rather than straight. The little shag lacks the straight-necked recognition display ("pointing") of some cormorants, but nest-indicating replaces this behaviour pattern.

(iv) Body: The switching of body posture in the male advertising display does not occur elsewhere, either in the display repetoire of the little shag, or in the order. The only comparable difference in body posture is in the horizontal body position of birds sitting on the nest, compared with the upright posture of perching birds. This is seen throughout the Phalacrocoracidae (Van Tets, 1965).

(v) Plumage: The median dorsal crest is raised by little shags sitting on the nest (in contrast to normal perching birds who never raise the crest). Van Tets (1965) however, notes that in P.carbo and P.olivaceus, that the raised crest is characteristic of non-sitting birds (no data for other shags given). The crest is also raised by the little shag during high-intensity threat, while the body feathers are ruffled and the crest is raised during the wing-waving display.

(vi) Wings: Backward wing rotation is seen in the "sky-pointing" of sulids, wing-waving of Phalacrocoracids, and the snap-bow of the anhinga (Van Tets 1965). Wing-waving is unique in the little shag in wings are seen in the little shag's threat, chicks' food-begging, spread-wing posture, pre-take-off, and the Post-landing and Post-hop displays (seen in similar contexts throughout the order; Van Tets, op.cit.).

(vii) Tail: Up and down tail movement helps in balance throughout the order (including the little shag) but is not used for display purposes (Van Tets , 1965). The little shag's tail is spread during landing, stretching and the spread-wing posture. Van Tets (op.cit.) considers that tail spreading is not a constant feature of pelecaniform displays. The tail is raised by little shags sitting on the nest, during the double-wing stretch, and by the female during copulation. Lowering of the male's tail during copulation occurs throughout the order.

(viii) Feet: Aside from the alternate treading on the females back by the male just prior to copulation (also seen in other family members: Millener, 1972; Berry, 1976), the feet are not used for display purposes in this family (feet are used by some sulids; Nelson 1978b).

3.10:Conclusions

In essence, the most distinctive behaviour patterns in the little shag are the male advertising displays, and as one of the major functions of courtship is species and sex recognition (T.R.Halliday; chapter 7, Krebs & Davies, 1978), this is perhaps not surprising. Recognition is enhanced by distinctive vocalisations and fairly species-specific recognition displays (the Hop and Post-landing displays). The least variation throughout the order occurs in mechanical activities such as maintenance and locomotion. As no behavioural literature is available on other micro-cormorants, assessment of phylogeny based on behavioural homologies is not possible (Van Tets, op.cit. considers that body switching may be characteristic of a genus Halietor). Van Tets (op.cit.) has divided the genus Phalacrocorax into marine and continental shags (see section 1.1.1) thus: in determining phylogeny, it may be significant that the little shag resembles continental shags by its ability to perch in trees and the inclusion of sticks in the nest material, while resembling marine shags in arching its neck before take-off and flying with its neck stretched forward like a crane.

PLATE 7: INITIAL NEST PLATFORM

PLATE 8: HALF-DAY OLD CHICK

PLATE 9: ONE TO FOUR-DAY OLD CHICKS

PLATE 10: FIVE TO TEN-DAY OLD CHICK

PLATE 11: TWO-WEEK OLD CHICK

PLATE 12: ONE-MONTH OLD CHICKS

PLATE 13: SEVEN WEEK OLD CHICK

PLATE 14: FULLY FLEDGED JUVENILE

CHAPTER FOUR:
ECOLOGY

CHAPTER FOUR: ECOLOGY

4.1:Introduction

Aspects of the little shag's breeding ecology were studied at Hamilton's and Sexton's Lagoons. Ecological comparisons between New Zealand and Australia were facilitated by analysis of data from the nest record schemes of both countries. Other methods are described in section 1.2.5.

4.2:Coloniality in the little shag

A wide range of nest-sites are utilised by the little shag, so that lack of suitable nest sites was probably not the main factor bringing about the development of the colonial habit in this species (as is the case in most seabirds; Nelson, 1980). As the little shag has no communal defence against predators it is unlikely that decreased chances of predation favoured the creation of coloniality. I believe that unpredictable food reserves have selected for coloniality. In Australian freshwater lakes, Miller (1979) demonstrated the unpredictable nature of the little shag's food supply and in 1980 documented sudden abandonment of chicks and eggs, partly because of decreasing food. Also, Horn (1968) has shown mathematically that a centrally located colony is the most energetically efficient way of collecting unpredictably located food. Limited food resources could also be the ultimate limit to colony size in the little shag. From as few as six (O.S.N.Z. nest records) up to some several hundred pairs (Buller, 1888) have been recorded nesting together, with the most common number being about 30 (O.S.N.Z. loc.cit.). It would be useful to determine whether large food reserves are correlated with large colony size, in the same way that colonies of 100 million guanay cormorants are associated with vast localised food resources (Nelson, 1980).

4.3:Breeding Seasons in New Zealand and Australia

New Zealand and Australian nest record schemes were examined for differences between the two countries in the production of eggs and young.

4.3.1:Results

(i) Egg Production on a monthly basis (Fig.4.1A)

In New Zealand, eggs have been recorded from August to the end of February, 90% of egg production occurring between the start of October and the end of December. The New Zealand breeding season is characterised by a single main peak in egg production in December (52.3% of total egg production). In Australia, eggs have been recorded from August to May. There are two peaks in egg production; November (24.6%) and February (8.3%).

(ii) Young production on a monthly basis (Fig.4.1B)

Young are recorded in New Zealand from the end of October to late February. Monthly numbers of young closely follow egg production trends (96.8% of young are produced during October to December, 61.3% in December). In Australia, young are recorded from August to the end of February and in May. The two unequal peaks of egg production have become identical in terms of the production of young (25.0% in November and February). As the presence of young in May comes from one site on one occasion, I believe this result is best considered to be an anomaly, possibly due to re-nesting or unseasonal and localised environmental conditions (see Llewellyn, 1983).

4.3.2:Discussion

Work by Miller (1980) and Llewellyn (1983) indicate that in Australia, the little pied shag is very much an opportunistic breeder; the initiation of breeding is to a large extent determined by localised factors, in particular, a rise in water level leading to a build up of food (Llewellyn, op. cit.). This probably explains Miller's (1980) observation that, while egg-laying tends to be fairly synchronous within colonies, it is very different between colonies. The unpredictability of Australia's environmental conditions is also shown by the sudden abandonment of eggs and chicks at the end of the little pied shag's breeding season (Miller, 1980), which has not been recorded in New Zealand. The more stable water levels within New Zealand suggest that other factors may be responsible for initiation of breeding within New Zealand (Miller, op.cit., documents photoperiod and air temperature as being contributory factors in the initiation of breeding in Australia). Initiation of breeding in New Zealand caused by a combination of photoperiod and air temperature could account for

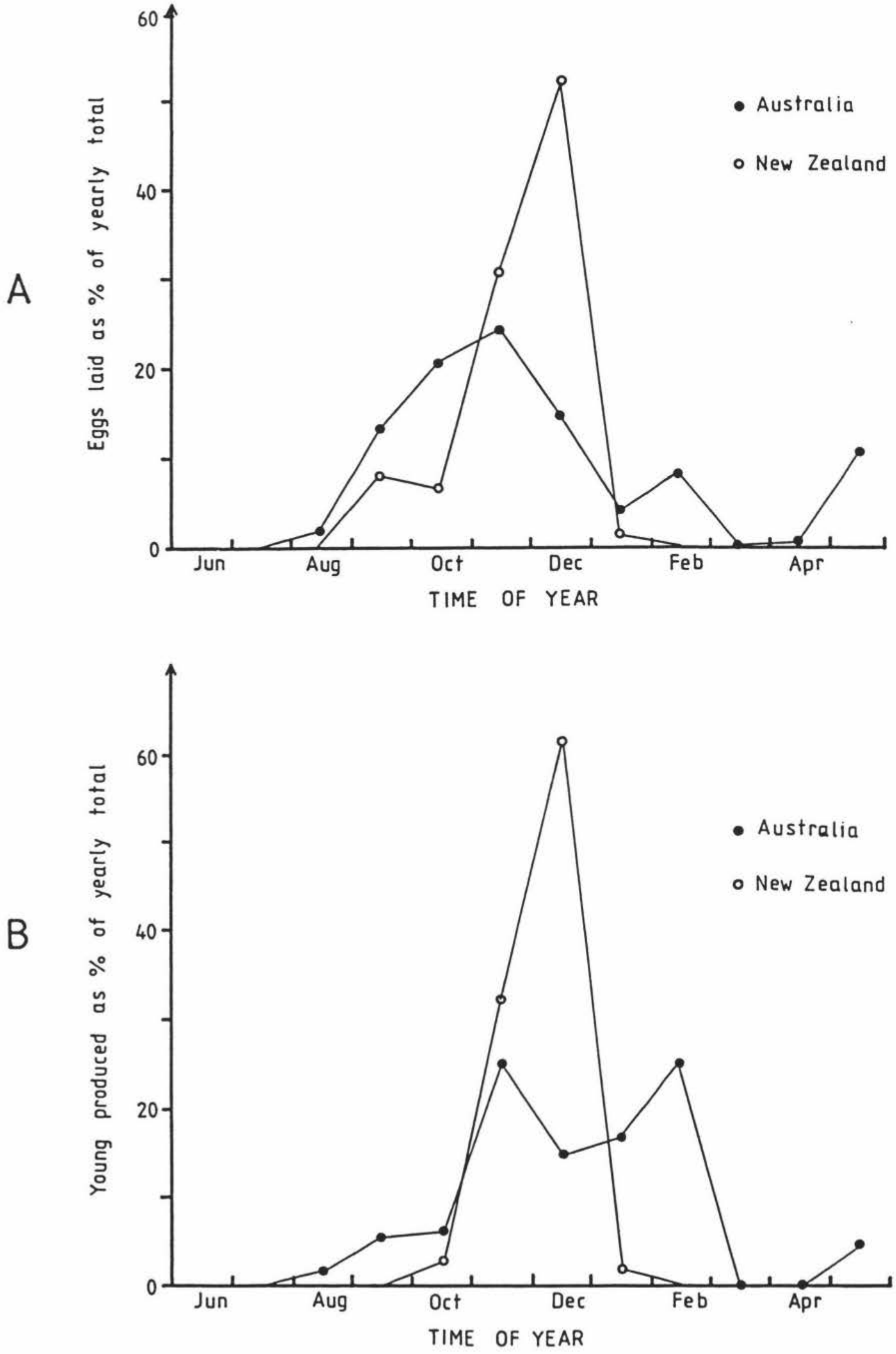


FIGURE 4.1: DISTRIBUTION OF EGGS (A) AND YOUNG (B) PRODUCED PER MONTH IN AUSTRALIA AND NEW ZEALAND

the differences in laying and production of young in the two countries. That November and February in Australia have become equivalent in terms of young production indicates a higher mortality during the November peak in egg production. Reasons for this are difficult to quantify, but could be related to predation levels or a greater environmental unpredictability earlier in the season. As is discussed in the next section, environmental unpredictability has also influenced clutch size between the two countries.

4.4:Clutch and Brood size in New Zealand and Australia

4.4.1:Results

Average clutch and brood sizes were determined from New Zealand and Australian nest record schemes. Clutch size was also determined from Hamilton's and Sexton's Lagoons, and brood size from Sexton's Lagoon. In the table (below), my results are not combined with those of the nest record scheme. Clutch and brood sizes are as follows:

	N	CLUTCH SIZE	S.E	N	BROOD SIZE	S.E
HAMILTON'S LAGOON	9	2.89	0.30	-	-	-
SEXTON'S LAGOON	23	2.43	0.23	10	2.80	0.29
NEW ZEALAND	123	2.78	0.25	90	2.71	0.06
AUSTRALIA	241	3.53	0.10	96	2.80	0.56

These results were analysed by t and d - tests to determine the degree of relationship between them. It was found that:

(1) Clutch size was significantly different between Australia and New Zealand ($p<0.001$).

(2) Brood size was not significantly different between New Zealand and Australia.

(3) Clutch size at Hamilton's Lagoon was not significantly different to results from the New Zealand nest record scheme.

(4) Clutch size at Sexton's Lagoon was significantly greater than size recorded at Hamilton's Lagoon and the New Zealand nest record scheme ($p<0.001$). Brood size at Sexton's Lagoon also exceeded the New Zealand mean ($p<0.001$).

4.4.2:Discussion

Various hypotheses have been put forward to account for clutch size variation within and between species (for review see Klomp, 1970). For the little shag, Miller (1979) has presented data relating water level to the unpredictability of the little pied shag's food supply , while Miller (1980) and Llewellyn (1983) have stated that water levels are at least partially responsible for both initiation and termination of breeding. The evidence for the little pied shag seems to support the view of Rickleffs (1977) that in an environment with unpredictable food, clutch size is related to the level of food resources available in the best season. This results in some young starving in most years, but in good years, large numbers of young are produced. I believe this explains the larger clutch size of the little pied shag in Australia. Further, if chicks are starved in accordance with their age (selective starvation of the youngest chicks has been recorded in other shags, e.g. Morrison et al, 1979; Williams & Burger, 1979), nestlings in excess of the maximum number that can be reared in any particular year can be starved with little effect on the survivors. O'Connor (1978; cited in Williams & Burger, 1979) states that in species in which breeding success is effected by food supply, hatching should be asynchronous; an adaptation which is characteristic of the little shag as well as other family members. Brood reduction may not be the only factor operating in these circumstances. In shags where the fate of each egg of known position in the laying sequence has been followed until the end of the egg period (Snow, 1960; Williams & Burger, 1979), it was found that mortality was mainly restricted to the last-laid egg of a clutch. Unfortunately, no comparable data exist for the little shag.

The significantly lower clutch size at Sexton's Lagoon is reflected in the fact that 26.0% of clutches contain one egg (as compared to 8.7% and 13.0% in Australia and New Zealand respectively). Possible contributing factors to this are:

(1) Timing: as most of the results from Sexton's Lagoon were taken from the latter part of breeding, a similar effect to that described by Snow (1960) might have occurred i.e. the breeding success of established breeders decreases as the season advances, as it does in inexperienced breeders.

(2) Age of breeders: Snow (op.cit.) also states that as the breeding season proceeds, a higher proportion of inexperienced breeders nest, resulting in a lower breeding success. A similar phenomenon may have been in evidence at Sexton's Lagoon.

(3) Site quality: As most of the one egg clutches seemed to come from peripheral sites (no concrete data available), this may have increased the chances at such sites of predation. This has been recorded by a number of workers e.g. Snow (1960), Coulson (1968 and 1971) and Potts (1980). Brood size at Sexton's Lagoon is larger than that of the New Zealand nest record data, probably because five of the six broods of three young were laid during the breeding peak (when clutch size would be expected to be larger).

4.5:Mortality

4.5.1:Mortality of young

Little shag eggs and chicks suffered mortality caused by several agents.

(1) Predation: The most significant example of this was the destruction of all clutches at the mai-mai (Hamilton's Lagoon) by a harrier. At Sexton's Lagoon, a ferret (Mustela putorius) was seen 10m from the colony, while ferret tracks were seen at the base of the tree. Gulls have been cited as potential predators of the eggs and young of shags by a number of workers e.g. Snow (1960), Coulson (1968), but while Dominican gulls were often seen flying over the colonies, no individual approached the nests. Possibly the difficulties of landing in trees make gulls unlikely predators in this situation. Dominican gulls have, however, been recorded as predators on mai-mai colonies of little shags on Lake Rotoehu (C.H.Lusk, pers.comm.). In view of the potential dangers of predation, it is perhaps surprising that little shags do not exhibit any anti-predator behaviour. Based on work by Siegal-Causey and Hunt (1981), I consider that the little shag depends on the position of nests for predator deterrence. These authors describe the

effects of predation on nests of the cliff-face nesting pelagic cormorant (P.pelagicus), and the cliff-top nesting double-crested cormorant. The latter species utilises a vigorous anti-predator defence behaviour, while the former does not exhibit such behaviour and depends on the inaccessability of its nest sites as an anti-predator deterrence. While eggs and young chicks are vulnerable to predation, adults are probably not (for reasons see section 3.8).

(2) Starvation: starvation of whole broods occurs in the little pied shag in Australia, when broods are abandoned by parents at the end of the breeding season (Miller 1980, cites decreasing food caused by a lowering of water levels as the reason for this). Because sudden desertion of broods has not been recorded in New Zealand, I cannot assertain if such starvation occurs in the little shag. Starvation of the youngest chick in a brood because of sibling competition has been recorded by a number of shag workers e.g. Snow (1960), Williams and Burger (1979), but no quantitative data exist for little shags.

(3) Egg infertility: A number of eggs failed to hatch at the expected time. Unfortunately, they all disappeared within one or two days of discovery, so it was not possible to determine if these eggs were infertile. Drent et al (1964) found egg infertility of between 9% and 28% during studies of the pelagic and double-crested cormorants, while Morrison et al (1979) found that 38.9% of olivaceous cormorant (P.olivaceous) eggs failed to hatch.

(4) Human interference: The one definite example of this is recorded in section 4.7.(below). Kury and Gochfield (1975) have recorded that human interference in colonies of coastal shags exposes the young to predation.

4.5.2:Total mortality of young

At Sexton's Lagoon, I found that 37.3% (n=67) failed to hatch. Drent et al (op.cit.) documented egg mortality rates of between 37% and 50%. Of the chicks that did hatch at Sexton's Lagoon, 45.2% died within a week. It was not possible to obtain an accurate figure for the proportion of young that fledged, as chicks left the nest and moved around the colony some time before fledging.

4.5.3:Adult mortality

Because the breeding season is the most physiologically demanding period for an adult, it would be logical to expect a greater mortality during and after breeding. O.S.N.Z. recovery data from 66 little shags showed: 18(27.3%) of recoveries took place in summer, 20 (30.3%) in autumn, 15 (22.7%) in winter, and 13 (19.7%) in spring. A chi-squared test revealed no significant difference in seasonal mortality on the basis of these results. Similar seasonal results to these were found in the Dominican gull (Fordham, 1970).

4.6:Incubation Period

Because of predation by harriers and storms, I was unable to complete measurement of the incubation period at Hamilton's Lagoon. During twice-weekly visits to the colony at Sexton's Lagoon, I was able to determine the incubation period of three clutches, where five eggs hatched out of a total of eight (one egg failed to hatch; the other two disappeared). The average incubation period was 27.4 days (range=26-28 days). Two of the five chicks died after hatching, while the others vanished at about ten days of age. Although this is a small sample results from other workers show similar incubation periods for other family members. For example Millener (1972) documents an average incubation period of 28.8 days (range=25-33 days) in the pied shag, Mitchell (1977) documents 28 days (range=26-30) in the double-crested cormorant, and Morrison et al (1979) states that the olivaceous cormorant has an average incubation period of 24.6 days (range=23-26). A similar consistency in incubation is recorded within the Sulidae, where all have incubation periods between 42 and 46 days (Nelson, 1978a).

4.7:Banding and dispersal

In an attempt to gain some idea of dispersal patterns within New Zealand, twelve chicks from the mai-mai at Hamilton's Lagoon were banded during visits in late 1980 and early 1981. During one banding visit two chicks jumped into the water and died because they could not climb back into the nest. As parents were disturbed into flight during my visits, I also feared that vacated clutches or broods would become vulnerable to exposure or predation. Consequently, banding was not continued in subsequent seasons. No recoveries of the birds which I banded have been made, but it is possible that dispersal from the natal colony may be similar to that of the little pied shag in Australia. Llewellyn (1983) found that fledglings rapidly dispersed away from their natal area in the first 10 months of their independence, then returned. After this, their dispersal was very erratic, although greater dispersal took place from environmentally unpredictable inland areas, than from the more stable coastal areas. The lack of such violent extremes within New Zealand may indicate a generally conservative pattern of dispersal in the little shag (although this species does have the potential to travel long distances; one banded little pied shag was recovered 2900km away from its natal colony; Llewellyn, op.cit.).

4.8:Miscellaneous observations

4.8.1:Diving times

The diving times of three little shags were timed, as they dived for food in an ornamental lake. I reasoned that the smooth bottom of the lake would not obstruct the diving birds. The mean diving time was 14.8 ±0.3s (n=11, range=12.1-15.5). Stonehouse (1967) records a mean duration of 16 secs for little shags diving in the sea.

4.9:Conclusions

(1) In terms of their breeding ecology, the little pied shag of Australia and little shag of New Zealand show fundamental differences. This is in large part due to the environmental unpredictability that characterises much of the Australian freshwater environment. These environmental fluctuations lead to:

(A) A longer breeding season in Australia characterised by two peaks in breeding activity. The Australian trends refect localised responses to environmental changes (particularly changes in water levels), that do not occur in New Zealand to the same extent (where more predictable factors influencing initiation of breeding result in a normally-distributed spread of laying within a shorter time span).

(B) A significantly larger clutch size in Australia than New Zealand (3.53 as opposed to 2.78), while there is no significant difference in brood size. The greater egg mortality in Australia reflects a "boom or bust" response of the little pied shag to its environment.

(2) At Sexton's Lagoon, 37.3% of eggs failed to hatch, while 45.2% of chicks died within a few days of hatching.

(3) Incubation period was found to be 27.4 days, a figure closely matching incubation periods for other family members.

CHAPTER FIVE:
TIME BUDGETS

CHAPTER FIVE:TIME BUDGETS FOR THE LITTLE SHAG

5.1:Introduction

For effective self maintenance and reproduction, a little shag must perform a variety of activities, each requiring an expenditure of time. By recording how much time is taken up by each activity, a time budget can be constucted. The primary aim of this chapter is to assess the way in which little shags apportion their time between different activities throughout the year, and during different times of the day. Methods for the collection of time budget data are described in section 1.2.5. For ease of analysis, related behaviours (described in Chapter 3) were clumped together to form; (i) rest; made up of normal perching and sleeping, (ii) maintenance; made up of preening, scratching and wing-drying, (iii) breeding activities; made up of courtship, copulation, nest building, sit-on-nest, brooding and feeding of young, (iv) Movement; made up of flying, swimming and hopping. Sit-on-nest refers to paired adults sitting on empty nests while brooding refers to adults sitting on eggs or chicks. Birds sitting on nests or brooding were recorded as such, irrespective of other activities they may have been engaged in e.g. if an individual was simultaneously brooding and preening, the activity was recorded as brooding. Wherever practical, days were divided into seven two-hourly periods. During non-breeding at Hamilton′s and Sexton′s Lagoons, the day was divided into five periods: dawn, morning, noon, afternoon and evening. These divisions make observations at different times of the non-breeding season more comparable. A computer generated analysis of variance (ANOVA) was used to determine the significance of daily trends.

5.2:Seasonal trends in major activities

5.2.1:Results (Table 5.1)

(A) Rest (Fig.5.1)

Breeding observations began at Hamilton′s Lagoon in August 1981 and

TABLE 5.1: MONTHLY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN MAJOR ACTIVITY CATEGORIES AT HAMILTON'S AND SEXTON'S LAGOONS

YEAR	MONTH	N	REST	MAINTENANCE	MOVEMENT	PAIR FORMATION & MAINTENANCE	SIT-ON-NEST	CARE OF YOUNG
1981	A	1015	45.0	34.5	9.3	11.2	-	-
	S	1112	40.5	31.4	12.6	2.5	12.9	-
	O	4113	48.1	27.2	7.6	5.1	12.0	-
	N	4663	40.7	25.8	3.8	2.1	13.9	13.7
	D	6295	22.3	20.7	2.0	2.1	22.7	30.2
1982	J	6777	18.4	21.4	1.1	0.8	20.5	37.8
	A	1055	59.2	28.6	12.2	-	-	-
	M	558	67.5	25.3	7.2	-	-	-
	J-S	172	76.2	11.6	12.2	-	-	-
	O	5720	23.9	5.3	3.1	1.2	25.4	41.1
	N	11573	39.1	13.2	4.4	3.0	6.7	33.6
	D	6118	32.7	17.3	3.8	1.7	0.2	44.3
1983	J	3858	61.6	36.8	1.6	-	-	-
	F	255	70.2	28.6	1.2	-	-	-
	M-A	403	67.3	32.2	0.5	-	-	-

ended in January 1982. The frequency of resting birds dropped from 45.0% in August to 18.3% in January. After breeding, resting increased until it occupied 76.2% in June-August 1982. During the three months of breeding observations at Sexton's Lagoon, resting varied between 23.8% in October, 38.1% in November and 32.2% in December. Rest rose to 70.1% in February 1983, before tailing off to 66.3% in March; the final month in which data could be collected before the colony was deserted for autumn.

(B) Maintenance (Fig.5.1)

At Hamilton's Lagoon, the frequency of maintenance activities was similar to rest through to April 1982, after which maintenance decreased relative to rest and declined to an absolute low during June-September (11.5%). At Sexton's Lagoon the frequencies of maintenance and rest were also fairly similar, and for maintenance, a low of 5.3% was seen in October.

(C) Breeding activities

At Hamilton's Lagoon 10%-20% of adults were engaged in breeding activities before eggs were laid. After laying, breeding activities occupied 50%-60% of the time. At Sexton's Lagoon breeding related activities decreased from 67.7% in October to 43.3% in November, after which a slight rise took place in December (46.2%). The frequency of (i) courtship and pair formation, (ii) sitting on nests, and (iii) care of the young, as proportions of total activity and total breeding activities are shown in Figs. 5.2 and 5.3 respectively. Figure 5.2 shows that;

(1) From August 1981 to January 1982, a general decline in courtship and pair formation occurred at Hamilton's Lagoon, but a consistent trend was not obvious at Sexton's Lagoon.

(2) The percentage of birds sitting on the nest at Hamilton's Lagoon varied widely, with a peak occurring in December 1981 (22.7%). At Sexton's Lagoon however, a rapid decrease took place in the last months of breeding (from 25.4% in October to 0.2% in December).

(3) At the mai-mai, a maximum of 13.7% of birds were engaged in care of the young during November 1981. At the prone willow, care of the young was 30.2% in December, rising to 37.8% in January when breeding was terminated. At Sexton's Lagoon, care of the young fell in frequency from October to November, then rose slightly to 43.4% in December.

Figure 5.3 indicates that:

(1) All breeding activities were concerned with courtship and pair formation during the first two months of breeding at Hamilton's Lagoon. Afterwards, courtship and pair formation decreased in frequency as more birds were engaged in sit-on-nest and care of young. At Sexton's Lagoon a slight peak in pair formation occurred in November.

(2) In both breeding seasons, a progressive and steady decrease in sit-on-nest was mirrored by a rise in care of the young. During December 1981 and January 1982, the proportion of sit-on-nest did not decrease at the same rate as at Sexton's Lagoon.

(D) Movement (Fig. 5.1)

Observations of seasonal trends at the prone willow and Sexton's Lagoon were made difficult by obstructing foliage. During the first four months at Hamilton's Lagoon observations were unrestricted by foliage, and as breeding progressed, flying and swimming decreased. At Sexton's Lagoon, more flying was seen during breeding, an opposite situation to Hamilton's Lagoon.

5.2.2:Discussion

The data presented here do not constitute a total time budget for the little shag. Construction of a total time budget would involve observation of birds at their feeding areas, and as the shags feed opportunistically over a wide area, this was not possible. Comparison between the three colony sites was made difficult by the predation of all clutches at the mai-mai, destruction of the prone willow colony by storm, and the late start to breeding at Sexton's Lagoon.

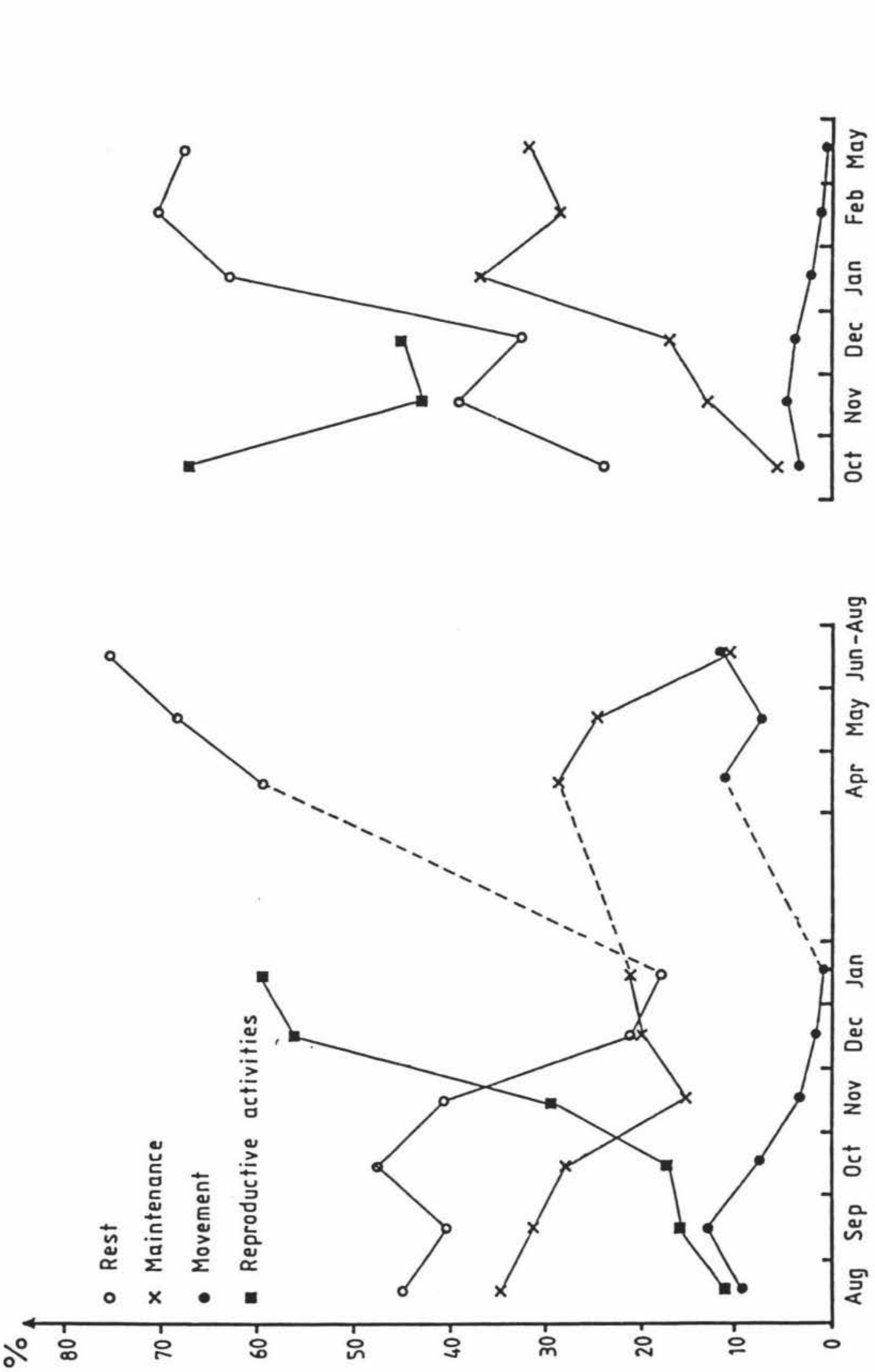


FIGURE 5.1 THE PROPORTION OF ADULTS ENGAGED IN MAJOR ACTIVITY CATEGORIES AT HAMILTON'S LAGOON (AUG 1981 - SEP 1982) AND SEXTON'S LAGOON (OCT 1982 - APR 1983)

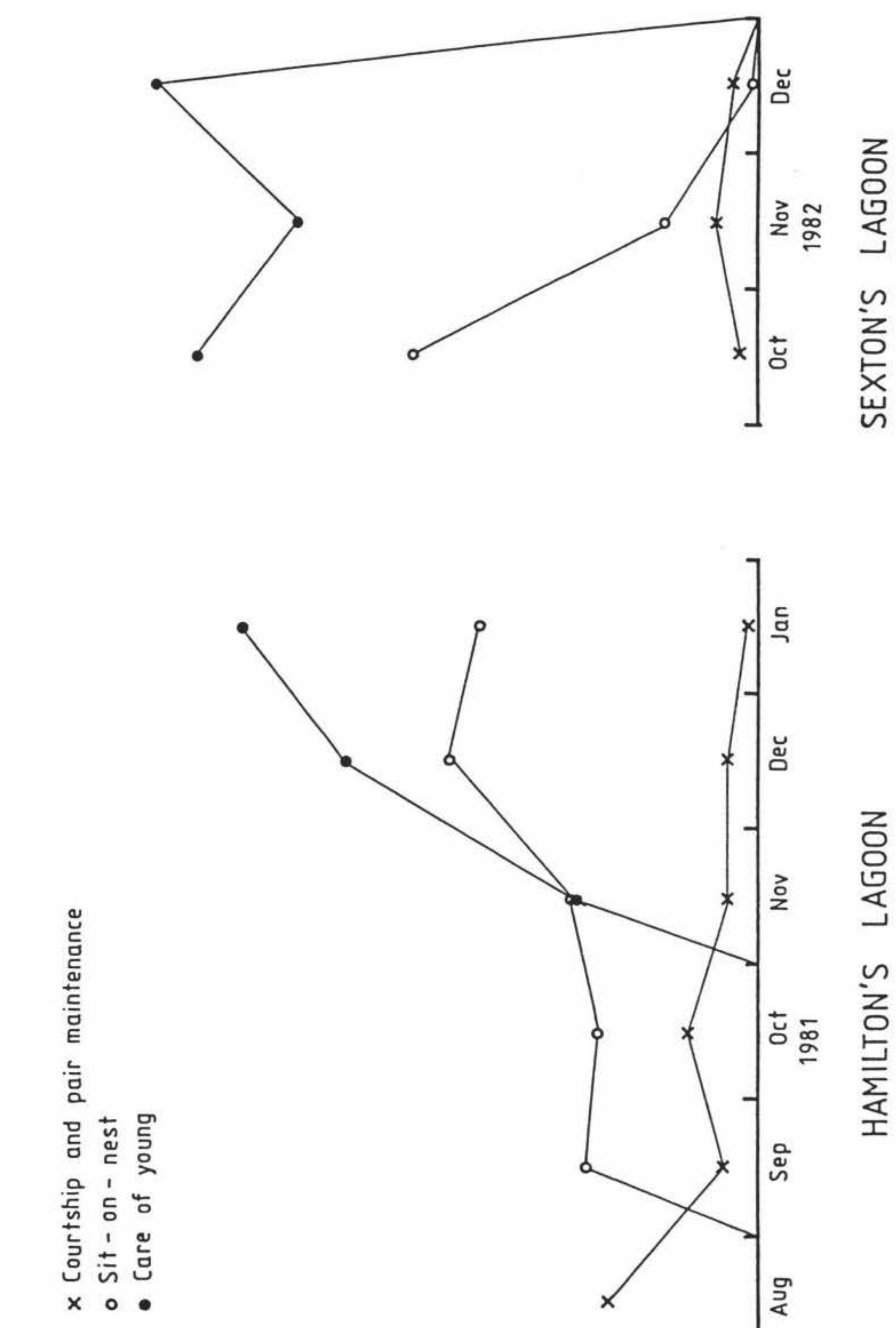
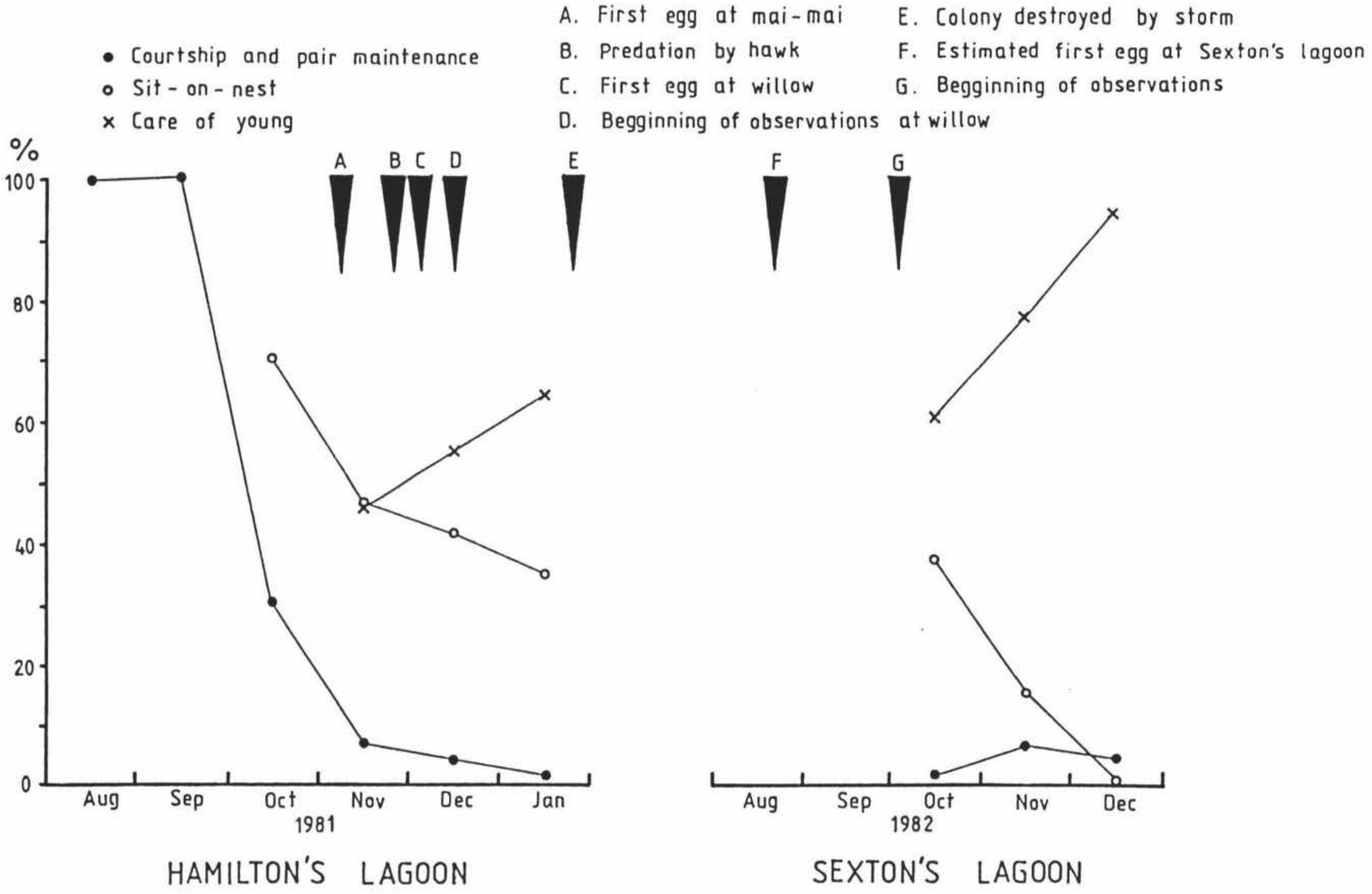


FIGURE 5.2: THE PROPORTION OF THE ADULT POPULATION ENGAGED IN BREEDING-RELATED ACTIVITIES AT HAMILTON'S AND SEXTON'S LAGOONS

FIGURE 5.3: THE CONTRIBUTION OF THREE BREEDING-ACTIVITY-CATEGORIES TO THE TOTAL REPRODUCTIVE TIME-ACTIVITY BUDGET AT HAMILTON'S AND SEXTON'S LAGOONS



The lower incidence of rest during breeding reflects the increased time spent by adults in breeding activities, especially in care of the young.

Similar trends for maintenance and rest were seen during both breeding seasons, and the non-breeding season at Sexton's Lagoon. However, maintenance decreased relative to rest during winter observations at Hamilton's Lagoon. As observations during non-breeding at Sexton's Lagoon took place in relatively warm weather, the absence of a similar trend in these categories may indicate a trade-off between activity and non-activity in unfavourable environmental conditions (seen in shorebirds; Evans, 1976). It would be useful to measure the amount of time spent feeding in warm and cold parts of the non-breeding season.

The increase in reproductive activity after laying is self explanatory; what is interesting is the slight secondary peak in breeding during December 1982. Secondary peaks have also been recorded in Australian populations of the Little shag (Miller, 1980) and is consistent with other ecological observations (chapter 4).

At the mai-mai, the frequency of birds sitting on the nest had already begun to decline from a maximum when breeding came to an abrupt halt. Later at the prone willow, a similar although shorter breeding cycle seemed to take place (this could have been caused by the onset of unfavourable weather conditions in relation to food supply; as described by Miller, 1980). At Sexton's Lagoon however, a much more consistent decrease occurred as breeding ended (see Figs. 5.2 and 5.3). Because breeding was uninterrupted at Sexton's Lagoon, I have assumed that this site represents a normal end to breeding. In comparison, the rate of decrease in frequency of sitting birds at the prone willow (Hamilton's Lagoon), was not as steep as at Sexton's Lagoon. I consider this is because re-nesting by pairs from the mai-mai occurred in addition to initial nesting by new birds. Unfortunately, only one re-nesting pair could be positively identified, but this habit occurs in other shags (Millener, 1972). Figure 5.3 also shows that changes in the frequency of birds sitting on the nest are reciprocal to frequency changes in care of the young. In spite of the disparity of events at Hamilton's and Sexton's Lagoons, figure 5.3

still shows a strong continuity in trends.

The high frequency of movement during the initial stages of breeding at Hamilton's Lagoon was due to nest material trips made by the male (as mentioned in 3.6.3, males have been recorded making as many as 15 trips in 45 minutes). The obstructing foliage at Sexton's Lagoon resulted in an apparently lower incidence of movement. The increased flying during breeding at Sexton's Lagoon was derived from trips for nest material and food for the young.

5.3:Daily trends in total numbers and activities during breeding

5.3.1:Daily trends in total numbers

During the pre-egg and egg phases at the mai-mai (Hamilton's Lagoon), numbers of birds present were low at dawn and evening while at the prone willow (Hamilton's Lagoon) and at Sexton's Lagoon, numbers were high at same times. This difference was due to the absence of all birds at night during the pre-egg phase, and the absence of non-breeders during the egg phase at the mai-mai. At all other sites, breeders and non-breeders roosted together at night.

At the prone willow and Sexton's Lagoon, morning numbers were less than evening numbers. The rapid departure of birds accounted for the low morning figure, in contrast to the steady build up in numbers which took place during the afternoon.

Low numbers occurred in all three egg phases from mid-morning to mid-afternoon, although slight midday peaks were seen in three of the egg phase months. For the most part, I saw very few birds feeding at Hamilton's and Sexton's Lagoons; thus I believe that absence of feeding birds was responsible for the general low in numbers around midday. In support of this Van Dobben (1952) states that P.carbo shows morning and afternoon foraging periods, coupled with a rest during the middle of the day. If some birds feed comparatively close to the colony, they may return to the colony to rest, accounting for the midday peak sometimes seen.

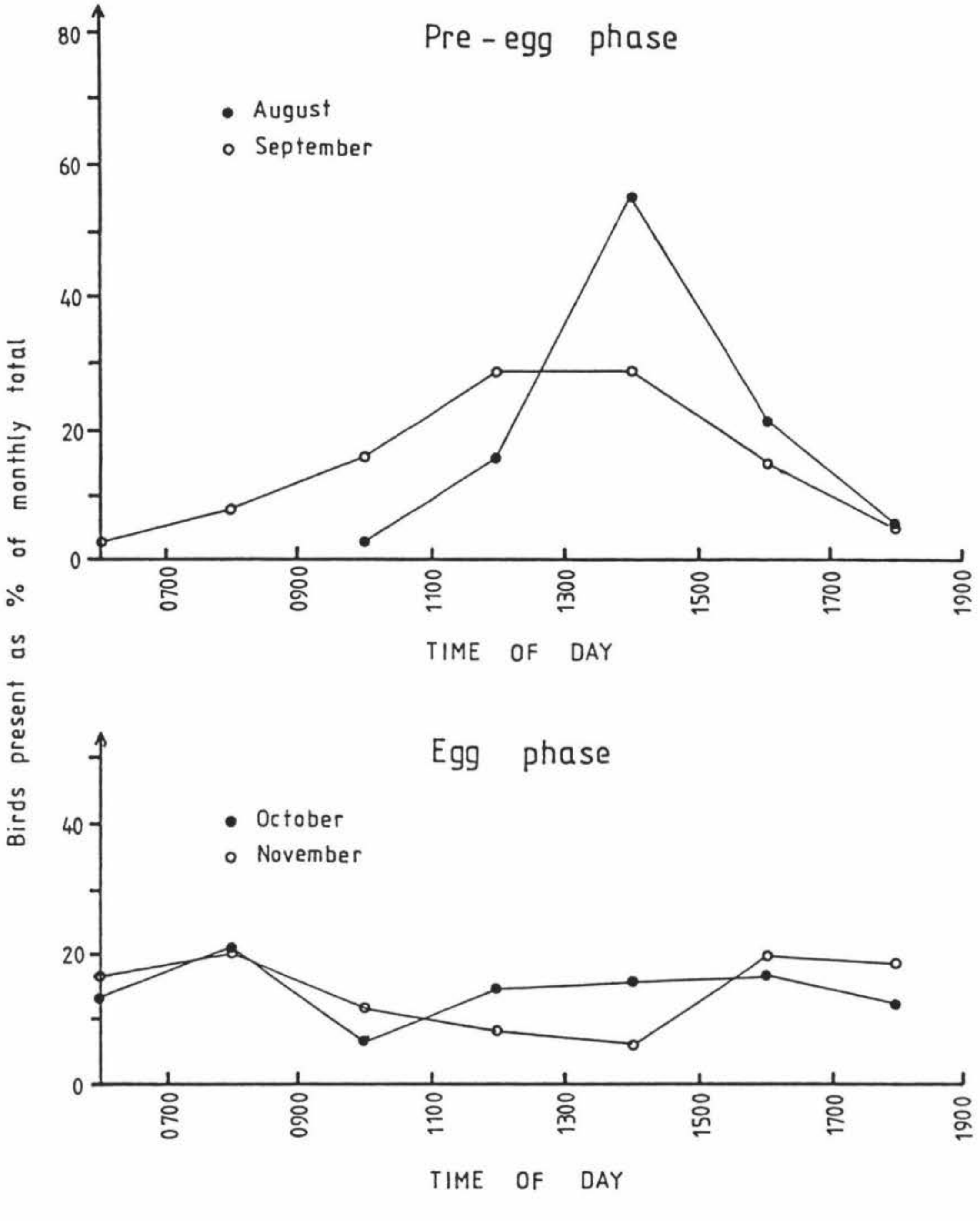


FIGURE 5.4A: BIRDS PRESENT AT DIFFERENT TIMES OF THE DAY AS A PERCENTAGE OF TOTAL MONTHLY NUMBERS AT THE MAI-MAI (HAMILTON'S LAGOON)

5.3.2:Daily trends in activities (Appendix 2)

Although some of the events during the pre-egg phase at the mai-mai were biologically interesting, the small sample size precluded any statistically significant trends being revealed by ANOVA. This also occurred during the egg phase at the mai-mai. The large standard errors of activities at the mai-mai also reflect the small sample size (Appendix 3).

(A) Rest (Fig. 5.6)

Resting in the pre-egg phase was most frequent from 0700-0900 hours, and least around midday. A secondary peak occurred in the afternoon, followed by a rapid decline as evening set in. During the egg-phase at the mai-mai, resting was infrequent around midday and most common in the afternoon. Daily trends for rest during this phase were not significant. Daily trends at the prone willow at Hamilton's Lagoon and at Sexton's Lagoon were similar. On average, resting was most frequent during dawn and evening. Significant quadratic trends ($p<0.001$) reflect the dawn and evening peaks while the significant linear trends ($p<0.001$) reflect the stable frequency of rest during the rest of the day. Similar trends were seen at the prone willow, although the results were not statistically significant. Not surprisingly, sleep was mostly observed at dawn and evening, both at Hamilton's and Sexton's Lagoons. Sleep occurred more often during the day at Sexton's Lagoon, and included a slight midday peak.

(B) Maintenance (Fig. 5.7)

At Hamilton's Lagoon, maintenance during the pre-egg phase was proportionately higher during the afternoon and less during the morning than in the egg phase. An increase to a midday peak, followed by a slight fall off occurred during the egg phase at the mai-mai. Maintenance trends at the prone willow closely resembled trends for rest during this period; with a dawn, midday, and evening peak. At Sexton's Lagoon maintenance was fairly steady throughout the day, except for an evening peak. In view of similar trends in rest and maintenance observed at the prone willow and Sexton's Lagoon, it is not surprising that maintenance at these two sites showed similar statistically significant quadratic and linear trends (all at $p<0.001$).

(C) Reproductive activities (Fig. 5.8)

Sit-on-nest and care of the young are independent of time of day, and are not discussed here. Considerable variation occurred in courtship and pair formation throughout the phases of breeding. During the pre-egg phase a distinctive midday peak took place. The second egg phase at Hamilton's Lagoon was characterised by an early morning peak, followed by a rapid drop, after which a continuous and gradual rise took place throughout the day until another fall at evening. At Sexton's Lagoon, a similar level of courtship occurred in the morning, leading to a slight midday rise. A gradual decline set in during the rest of the day. Quadratic daily trends ($p<0.001$) in courtship and pair formation occurred at the prone willow and Sexton's Lagoon, but because the patterns at each site were opposite, I can determine no biological significance for this result. In terms of individual behaviours; nest building at Hamilton's and Sextons's Lagoon followed similar trends (see Fig. 5.10). At both sites, an early morning and mid-afternoon peak, with a midday and evening low, occurred. A slight drop was seen from 0600-0700 hours followed by a slight rise at 0800 hours. Not enough chicks were present at Hamilton's Lagoon to analyse daily trends for the feeding of young. Evidence from Sexton's Lagoon (Fig 5.11) suggests that the majority of feeding of young took place in the morning until 1100 hours, and between 1700-1900 hours.

(D) Movement (Fig. 5.9)

Trends in movement as a whole tended to be variable, but flying from the colony peaked at dawn. This is supported by significant quadratic trends ($p<0.001$) seen at Sexton's Lagoon. Similar non-significant trends were seen at the prone willow.

5.3.3:Discussion

The decrease in evening rest seen at the mai-mai is attributable to the absence of non-breeders at this time. As a consequence, a relatively high proportion of birds were sitting on nests, giving the appearance of decreased rest. The peak in rest during 0700-0900 hours may be significant, because this period immediately precedes the peak in pair formation. The midday low at the mai-mai is due to a general absence of birds not sitting on eggs or young. However, this explanation does not apply to the midday lows seen during January and October 1982, when large numbers of birds were present. Because these two months are breeding peaks, it is possible that increased demands on parents may cause the absence of a midday peak. The increased sleeping during the day seen at Sexton's Lagoon is probably a result of unfavourable weather conditions (see also section 3.4.3).

The midday peak in courtship and pair formation during August 1981 is largely the result of one day's observation, and as courtship was not seen with such frequency on any subsequent occasion, this peak is probably anomalous (possibly influenced by the day's unseasonally warm and sunny weather).

The peak in nestbuilding at 0600 hours may indicate that this category occurred in the morning before foraging. Birds which have returned to the colony from feeding may have accounted for the afternoon peak.

The morning and evening peaks in feeding of the young may reflect thermoregulatory needs of the young. The last feed during the day would sustain the chicks through the night, while the early morning feed comes at a time of low food reserves in the chick and cool morning temperatures.

The high frequency of early morning flying is due to the rapid departure "en-masse" of foraging birds. Birds arrive back at the colony for the night in the last one or two hours before sunset, accounting for the secondary peak in flying seen at this time.

5.4:Daily trends in numbers and activities outside of breeding (Fig.5.11)

5.4.1:Results

(A) Numbers (Fig.5.5)

At Hamilton's Lagoon, total numbers at the colony increased from about an hour after sunrise until about 1400 hours, after which numbers decreased. To my knowledge, little shags did not roost at Hamilton's Lagoon outside from breeding (birds were seen flying north of the lagoon as evening approached, but no roosting site could be found). At Sexton's Lagoon, a steady increase in numbers occurred throughout the day, except for a slight afternoon drop. Birds roosted at night at Sexton's Lagoon until late January 1983. For the remaining three months of observation, numbers showed a steady increase throughout the day, until one or two hours before sunset, when the birds departed.

The early morning low in numbers at Hamilton's and Sexton's Lagoons is due to the absence of feeding birds, while a lack of night roosting birds lowered early morning numbers at Hamilton's Lagoon even further. Foraging birds and individuals leaving for the night roost would account for the decrease in numbers during the afternoon at Hamilton's Lagoon. Lack of night roosting at Sexton's Lagoon after late January is difficult to explain, but may be related to seasonal shifts in feeding areas (Bartholomew, 1943 states that seasonal changes in feeding areas is the main factor causing shift of roosting sites in the double-crested cormorant). The timing of this shift (one month after the end of breeding) could also indicate a gradual waning of the breeding drive, making the colony site less "socially attractive".

(B) Activities (Fig.5.12)

Because of differences in the ease of observation, unequal periods of observation (April to September at Hamilton's Lagoon, January to late April at Sexton's Lagoon), and the fact that 85.4% of non-breeding results came from one month (the only non-breeding month to have birds roosting at the colony overnight), direct comparison of the two seasons was not possible. Trends in major activities at Hamilton's Lagoon were; (i) lows in rest occurred during the morning (57.6%) and as evening approached (59.6%), with the greatest amount of rest taking place in the afternoon (77.1%), (ii) maintenance was lowest in the afternoon (10.6%) and highest in the evening (34.0%) while, (iii)

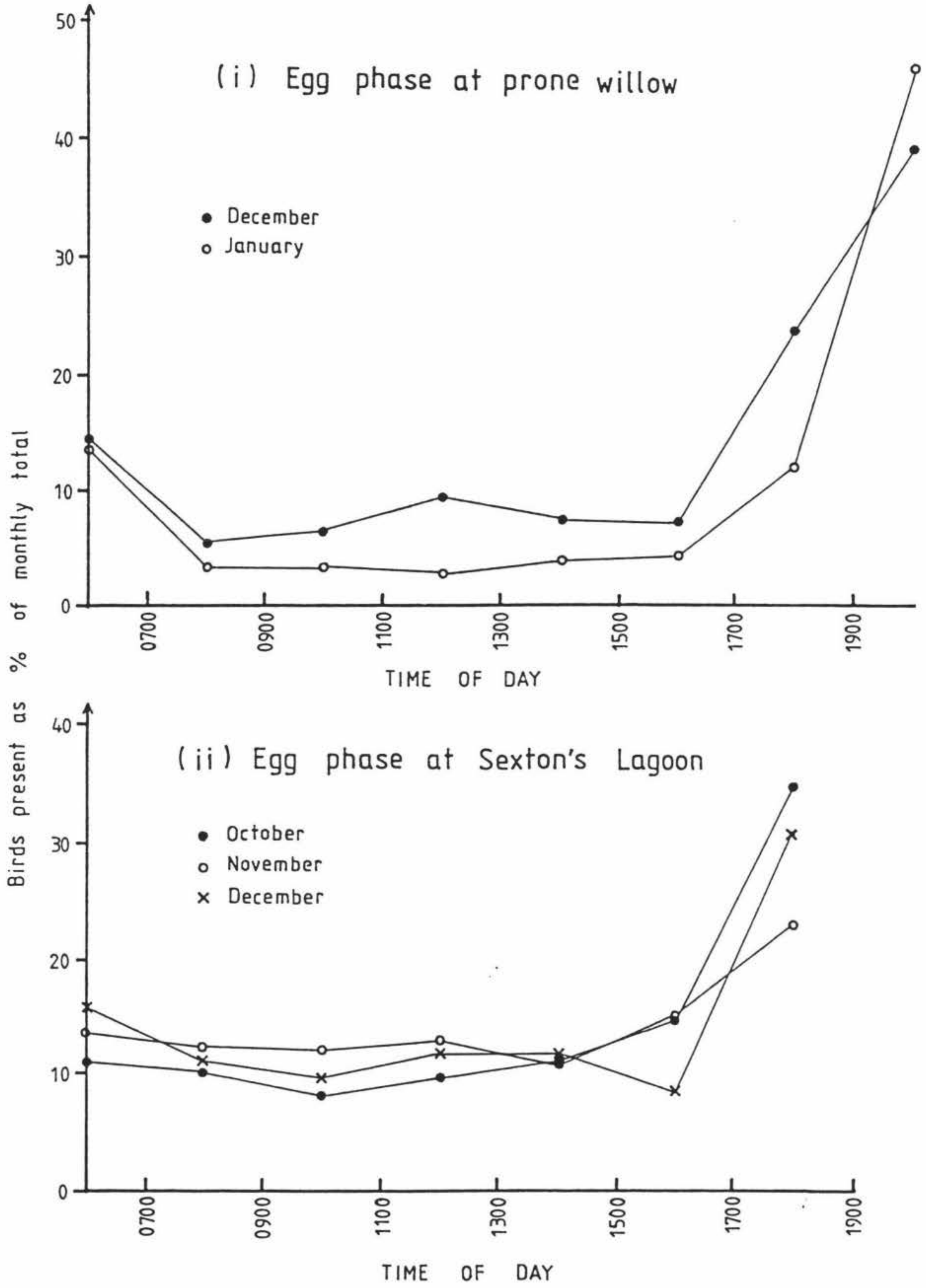


FIGURE 5.4B: BIRDS PRESENT AT DIFFERENT TIMES OF THE DAY AS A PERCENTAGE OF TOTAL MONTHLY NUMBERS DURING THE EGG PHASE AT THE PRONE WILLOW AT HAMILTON'S LAGOON (i) AND DURING THE EGG PHASE AT SEXTON'S LAGOON (ii)

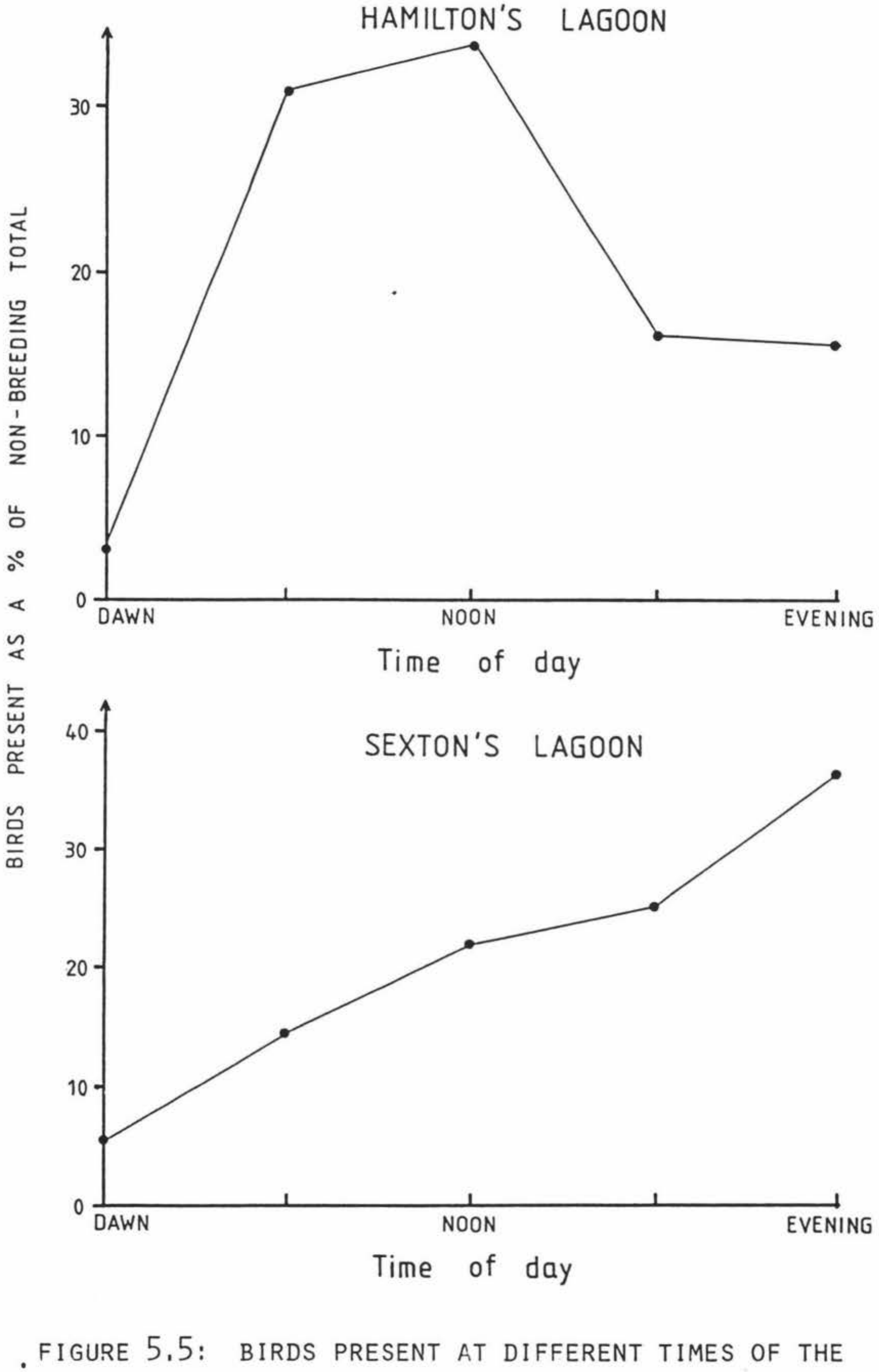
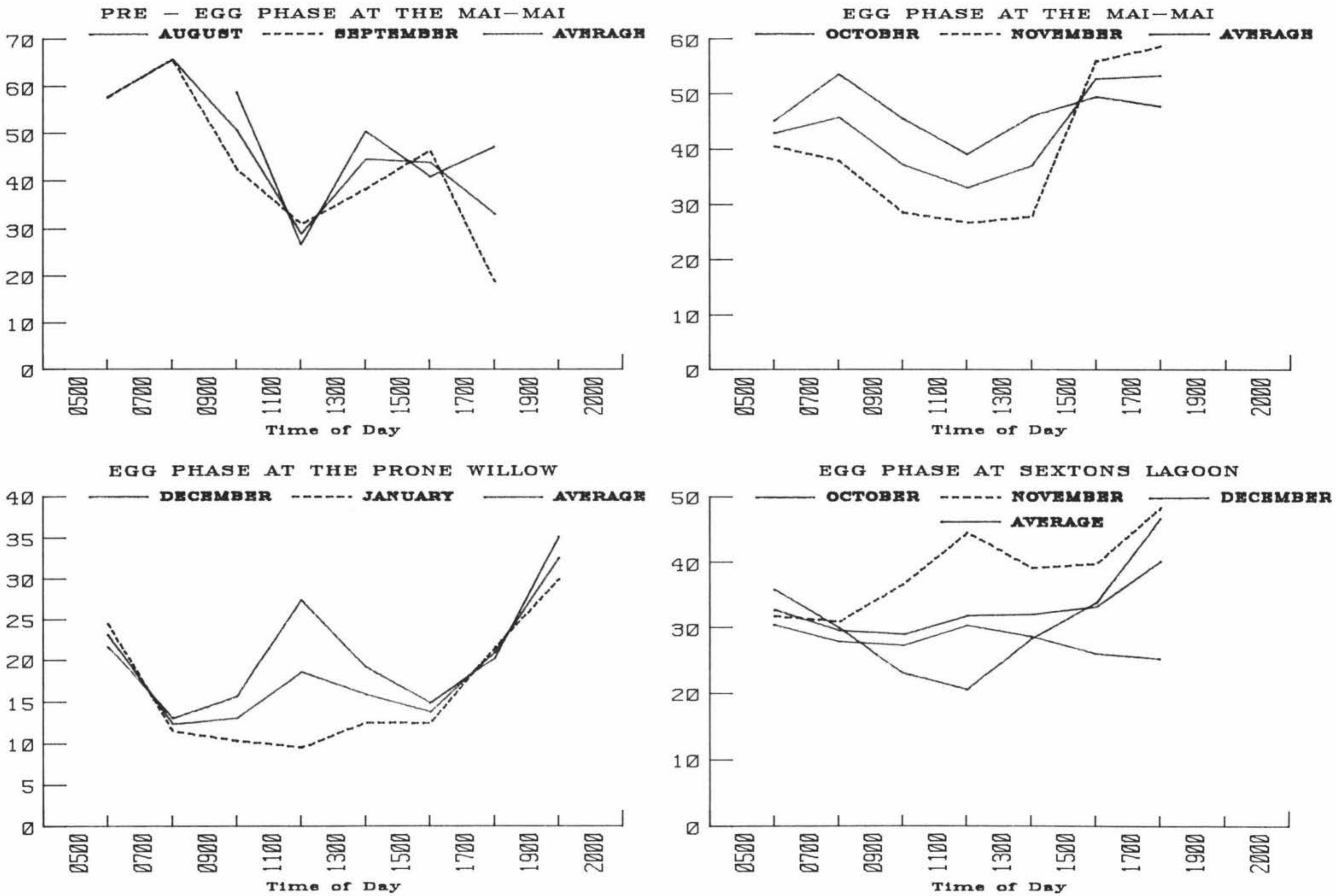


FIGURE 5.5: BIRDS PRESENT AT DIFFERENT TIMES OF THE DAY AS A PERCENTAGE OF TOTAL NUMBERS AT HAMILTON'S AND SEXTON'S LAGOONS DURING THE NON-BREEDING SEASON



PRE – EGG PHASE AT THE MAI–MAI

EGG PHASE AT THE MAI–MAI

EGG PHASE AT THE PRONE WILLOW

EGG PHASE AT SEXTONS LAGOON

IGURE 5.6 DAILY TRENDS IN PERCENTAGE OF RESTING BIRDS DURING DIFFERENT PHASES OF BREEDING

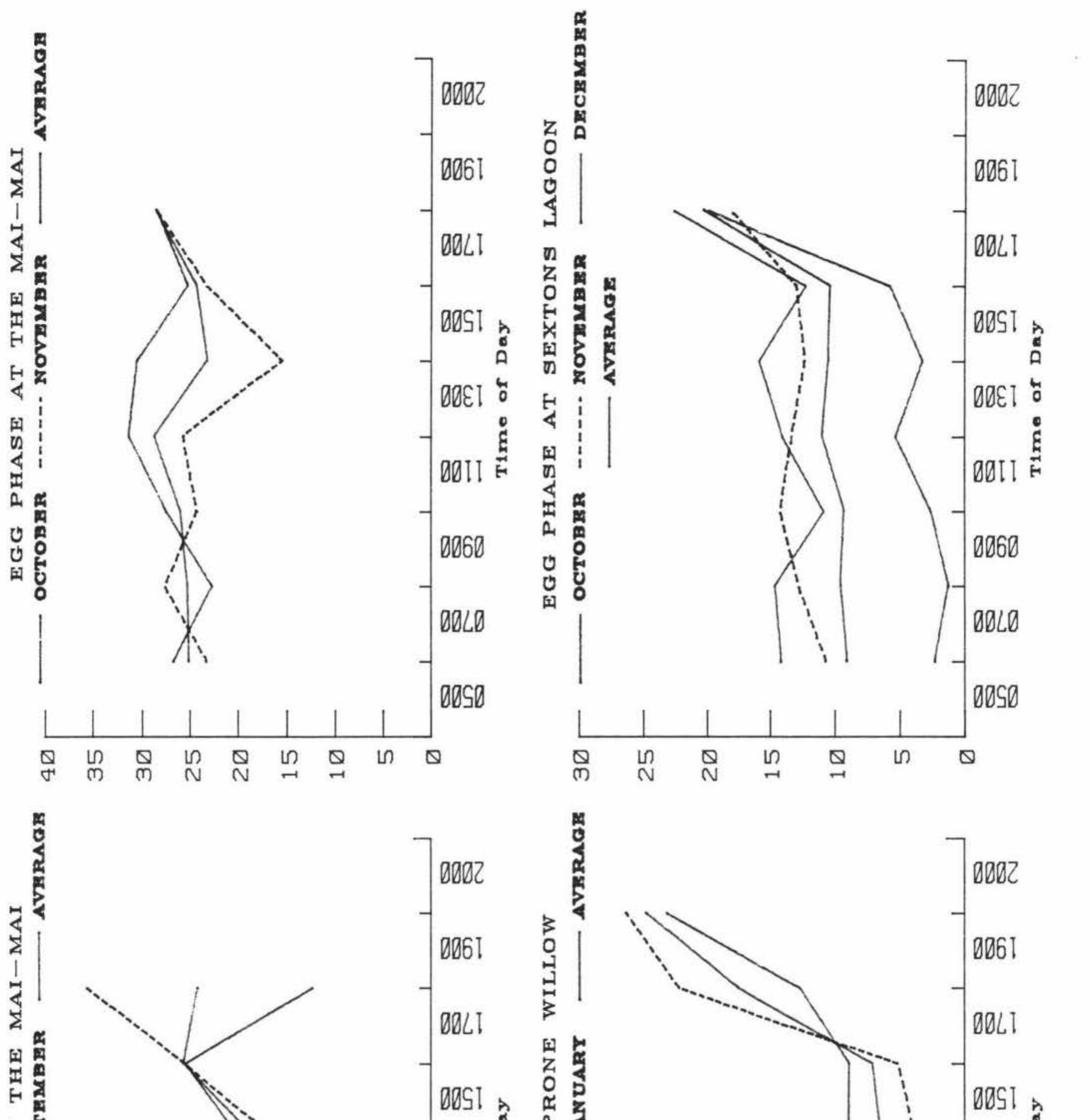


FIGURE 5.7 DAILY TRENDS IN PERCENTAGE OF MAINTENANCE DURING DIFFERENT PHASES OF BREEDING

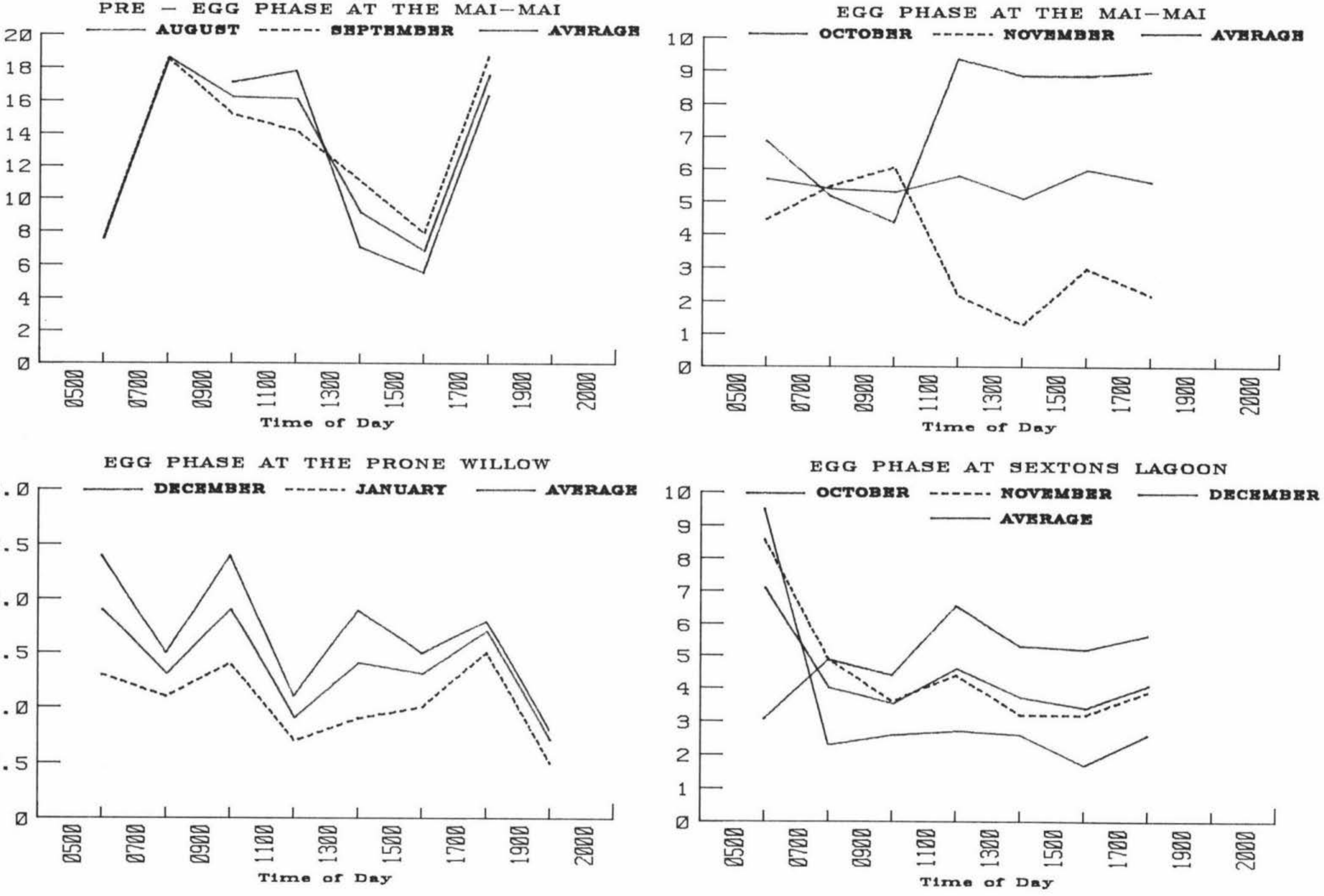


FIGURE 5.8 DAILY TRENDS IN PERCENTAGE OF MOVEMENT DURING DIFFERENT PHASES OF BREEDING

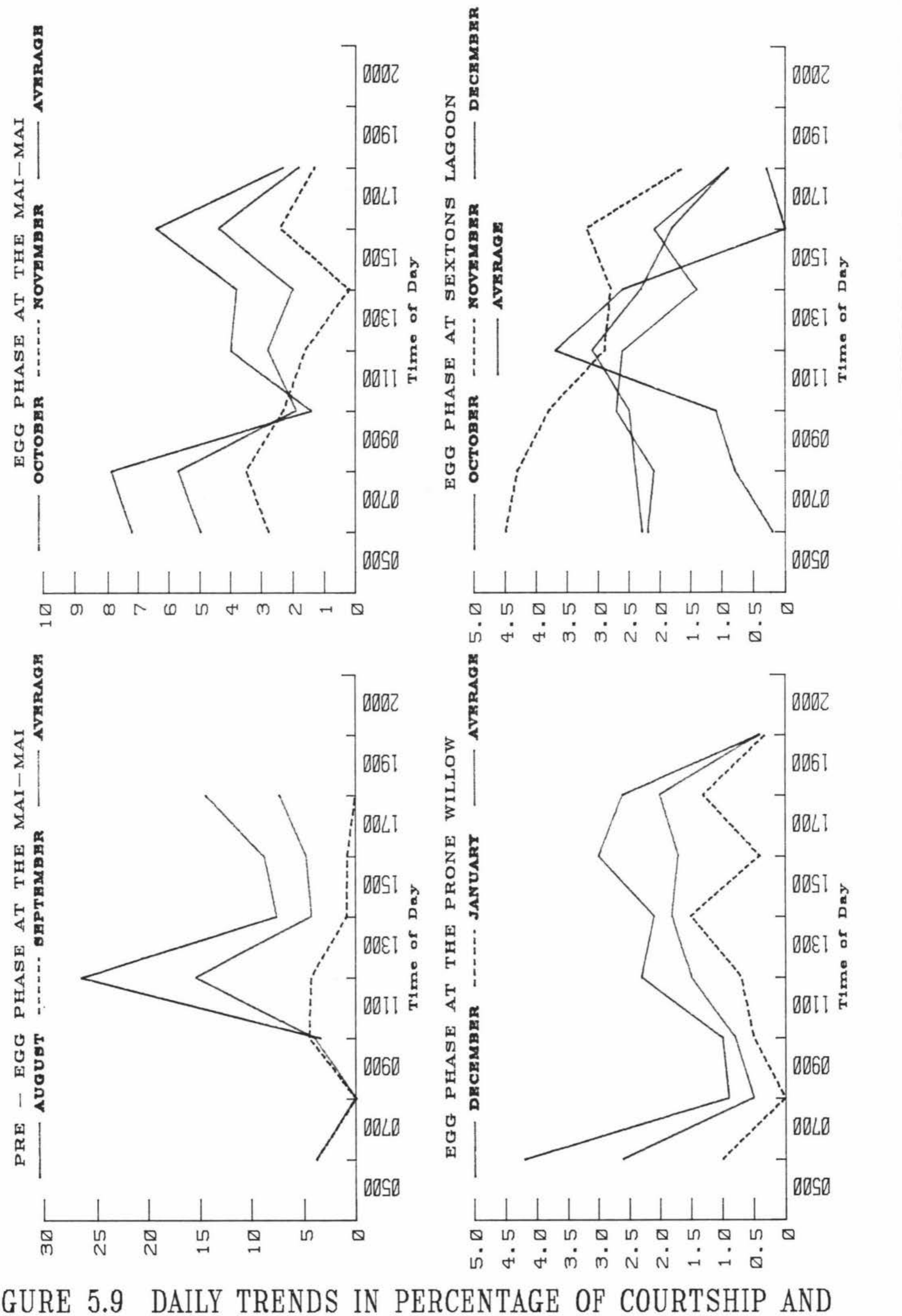


FIGURE 5.9 DAILY TRENDS IN PERCENTAGE OF COURTSHIP AND PAIR FORMATION DURING DIFFERENT PHASES OF BREEDING

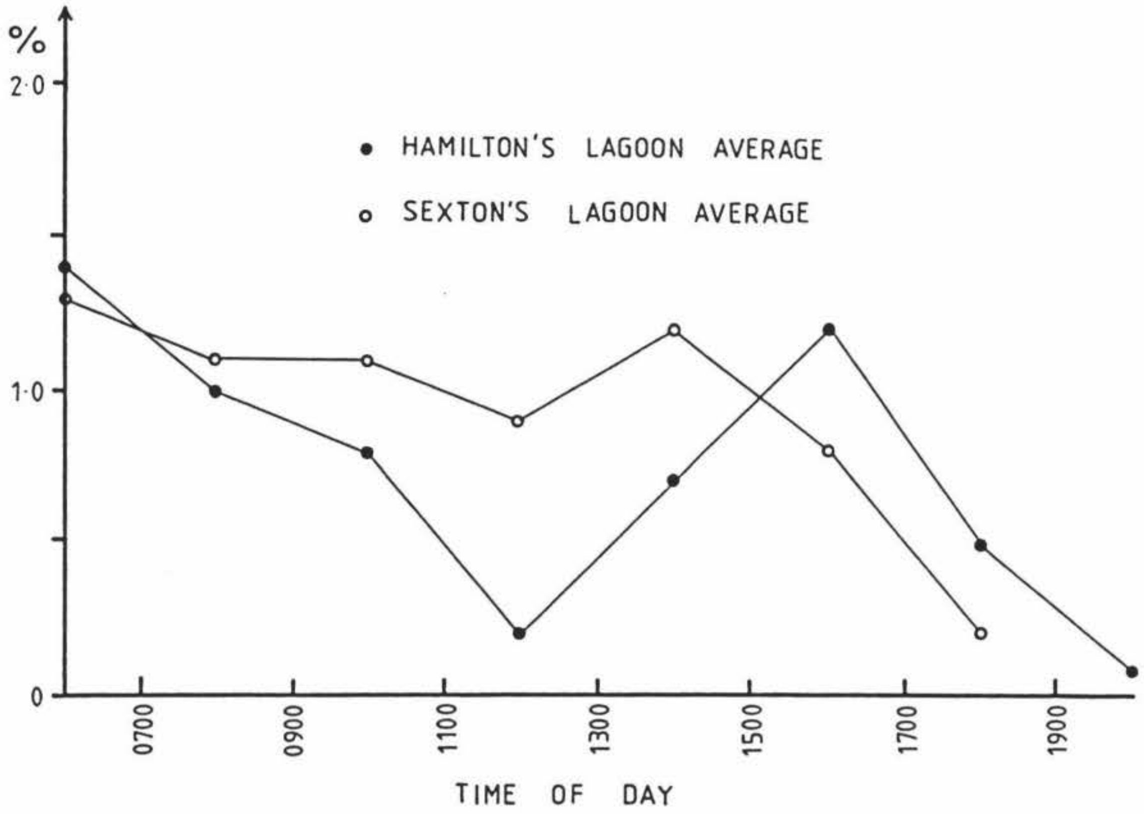


FIGURE 5.10: MEAN NUMBER OF BIRDS ENGAGED IN NEST BUILDING DURING THE DAY AT HAMILTON'S AND SEXTON'S LAGOON

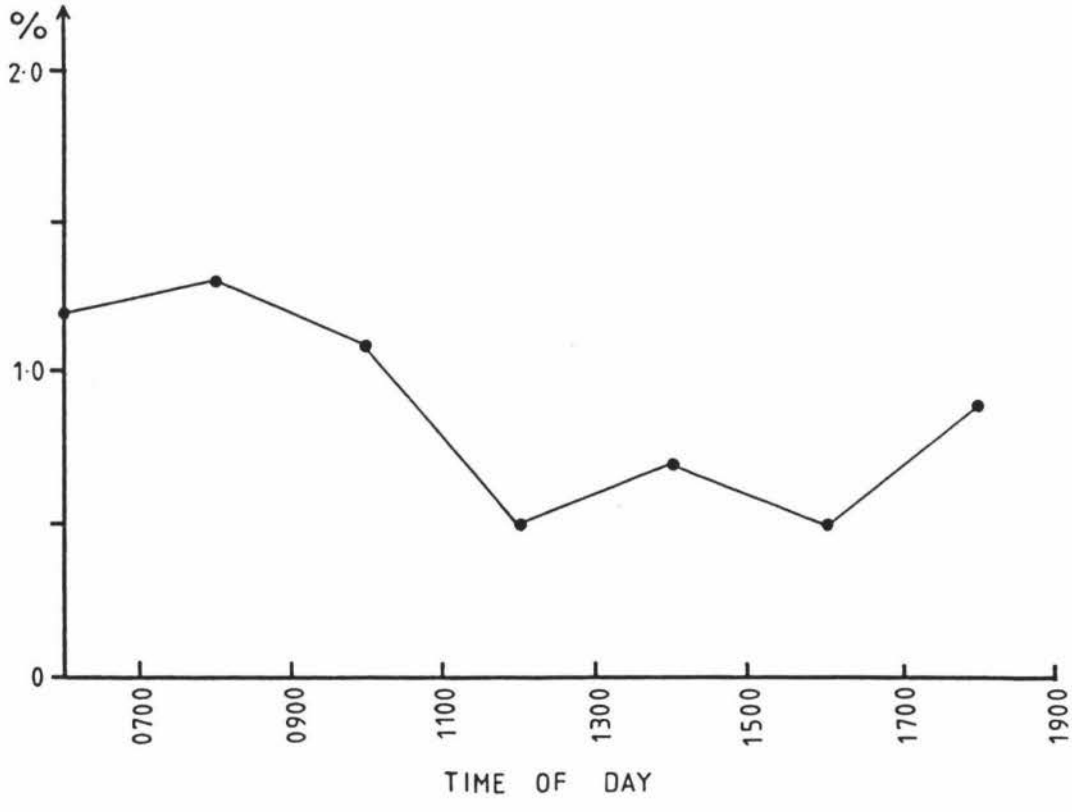


FIGURE 5.11: MEAN NUMBER OF ADULTS ENGAGED IN FEEDING YOUNG DURING THE DAY AT SEXTON'S LAGOON

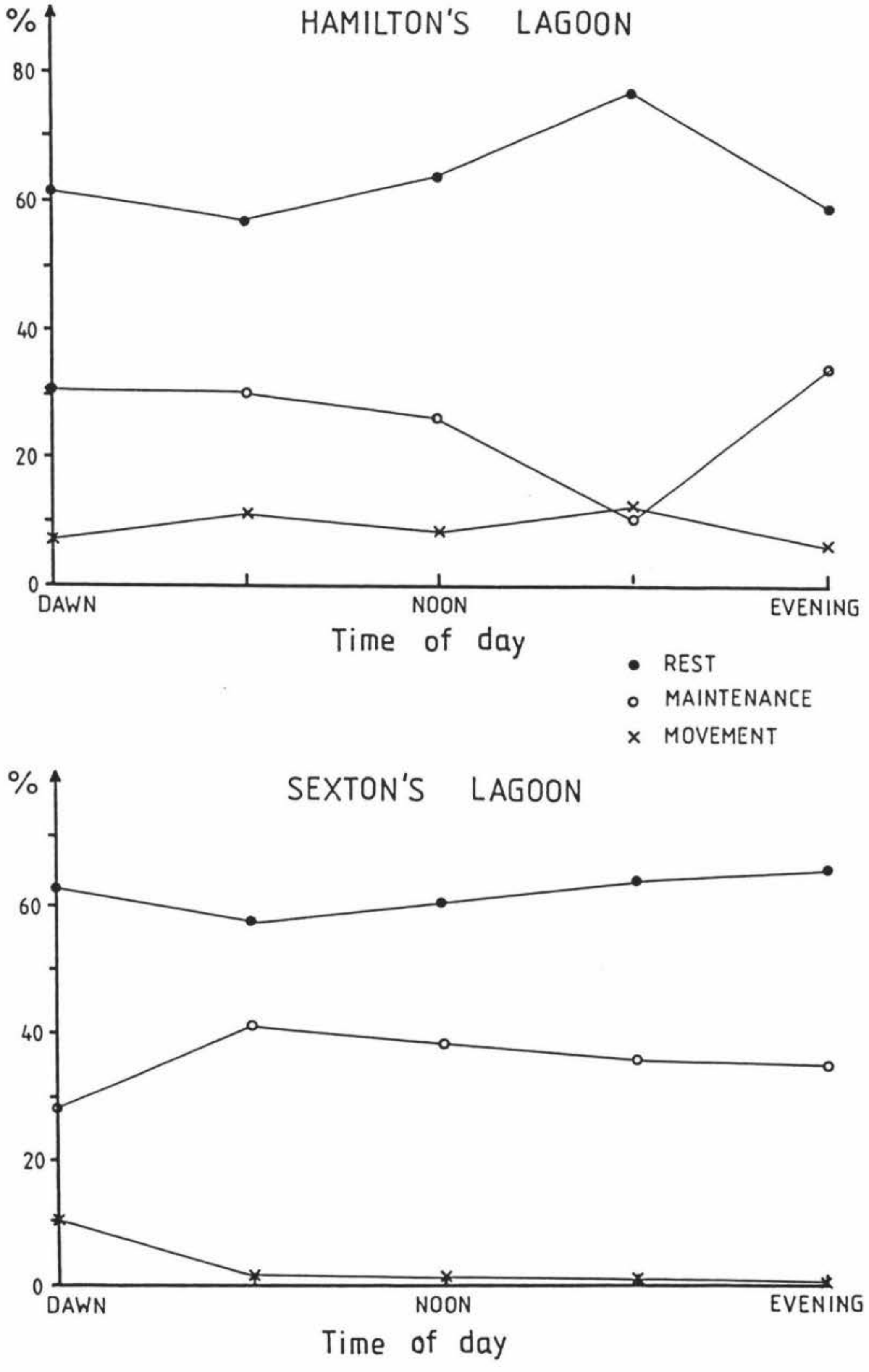


FIGURE 5.12: DAILY TRENDS IN PROPORTION OF THE POPULATION ENGAGED IN MAJOR ACTIVITY CATEGORIES DURING THE NON-BREEDING SEASON AT HAMILTON'S AND SEXTON'S LAGOONS

movement was lowest at dawn and evening (7.5% and 6.4% respectively) and highest in the morning and afternoon (11.6% and 12.3% respectively). At Sexton's Lagoon, (i) rest was lowest in the morning (57.2%), after which it increased at a steady rate through to an evening peak (65.3%), (ii) maintenance was lowest at dawn (27.7%), increased to a peak during the morning (40.9%) and gradually decreased through to the evening (34.1%), (iii) a peak in movement was seen at dawn (10.0%) and decreased thereafter to a low of 0.6% as evening approached.

5.4.2:Discussion

Overall trends in rest and maintenance at Sexton's Lagoon tended to be steadier during non-breeding than breeding. I believe this could reflect more time being available throughout the day as a result of the end of breeding activities. The high dawn frequency of movement at Sexton's Lagoon was due to the same rapid early morning departure that occurred during breeding. The dawn and evening lows in movement at Hamilton's Lagoon were due to the absence of birds at these times. The apparent increase in movement at Hamilton's Lagoon was due to the lack of obstructing foliage. Afternoon and evening trends in rest and maintenance at Hamilton's Lagoon did not show the same steady trends that occurred at Sexton's Lagoon. This could result because Hamilton's Lagoon was not used as an overnight roost. The increase of rest could indicate a hiatus in activity between the last feed of the day, and departure for the night roost.

5.5:Conclusions

(1) Rest decreases in frequency as breeding proceeds, and peaks after the end of breeding (seen at Sexton's Lagoon). Rest peaks again immediately before the physiologically demanding period of breeding (seen at Hamilton's Lagoon).

(2) Maintenance also decreases in frequency as breeding proceeds. Maintenance peaks in the month immediately after the end of breeding and is low just before the start of the following breeding season.

(3) During breeding, rest and maintenance tend to peak at dawn and evening. Rest is sometimes seen at midday, but not during the months of peak breeding activity.

(4) As a rule, sleep occurs during early morning and as night approaches. However, at Sexton's Lagoon (particularly in November and December 1982), sleep occurs throughout the day, possibly indicating a compromise between energy gain and loss in unfavourable weather conditions, where the energetic costs of foraging are considerably raised.

(5) Thermal considerations may mean that young are fed, (i) in the morning, when cool temperatures coupled with lack of food during the night make chicks vulnerable to heat loss and, (ii) as evening approaches, to fortify the young for the night ahead.

(6) Because reproductive demands are not placed on parents during the non-breeding season, rest and maintenance tend not to peak at dawn and evening, as is the case during breeding. Results from the non-breeding season at Hamilton's Lagoon, however, may indicate that frequency changes in rest and maintenance result from the imminent departure of little shags to their night roost.

CHAPTER SIX:
SUMMARY

CHAPTER SIX:SUMMARY

Chapter 1:INTRODUCTION

The biology of the Order Pelecaniformes was discussed, followed by a brief description of the little shag. Main aims and study areas were described, as well as weather patterns, and general methods of the study.

Chapter 2:BODY MEASUREMENTS AND PLUMAGE PATTERNS

Body measurements taken from dried skins indicated that females tended to be smaller, although the results were not significant. The white-throated plumage phase (individuals with white confined to throat and face) accounted for 60% of individuals, while only 12% of individuals were of the fully pied phase (individuals with a totally white ventral surface). Almost all Australian individuals are fully pied. The causes of this difference could not be identified, although it appears likely that differences in prey between the two countries have not been a factor.

Chapter 3:POSTURES AND BEHAVIOUR PATTERNS

Postures and behaviour patterns of the little shag were described and related to that of ordinal and familial members. The little shag has two distinctive and unique features of its male-advertising courtship displays: (i) a switching of the body from the vertical to the horizontal planes in both male advertising displays and (ii) the wings are raised only once per display in the squat-thrust display of male advertising. The rest of the behavioural repertoire is similar to other ordinal and familial members, particularly self-maintenance activities. There is however an alarm call in this species, contrary to Van Tets (1965) statement that there is no such call throughout the order. I suggest that the differences in male advertising displays could be important in assessing the validity of Halietor; a separate genus proposed by some authors for the so called micro-cormorants (including the little shag).

Chapter 4:ECOLOGY

Breeding ecology was studied at Hamilton's and Sexton's Lagoons, although results from the former were severely effected by harrier predation and storms. Ecological comparisons were also made on the basis of data fron New Zealand and Australian nest record schemes.

The breeding season in Australia occurred over a longer period than in New Zealand, and had a bimodal pattern of egg and young production. As well as breeding taking place in a shorter time, a normally-distributed pattern of egg and young production was seen in New Zealand. The clutch size in Australian populations (3.53) was significantly larger than clutch size than in New Zealand (2.78), but brood size is not significantly different. Both results may reflect large unpredictable variations (particularly in food supply because of changing water levels) that occur in Australian freshwater environments.

Thirty-seven percent of eggs failed to hatch and 45.2% of chicks died within a few days at Sexton's Lagoon. The single most significant mortality factor was predation. Attention was drawn to the lack of an active anti-predator defence in the little shag, but rather to the relative inaccessability of the nests.

More dead adults were recovered in summer and autumn (during, and after breeding) than in winter and spring. However, the trends were not significant.

An average incubation period of 27.4 days was recorded, consistent with trends in other family members.

Chapter 5:TIME BUDGETS FOR THE LITTLE SHAG

Time budget data were collected from August 1981 to the end of April 1984. A total time budget could not be constructed because the adults could not be followed to their feeding areas. Because of the difficulties in reconciling major events at Hamilton's Lagoon (harrier predation and storms) with events at Sexton's Lagoon, results from the mai-mai and the prone willow were treated separately, as were results from Sexton's Lagoon.

(1) The proportion of rest and maintenance was greater outside of breeding, and progressively decreased from the beginning to the peak of breeding.

(2) A high frequency of movement was observed in the first two months at Hamilton's Lagoon, because males were collecting nest material.

(3) Courtship, pair formation, and the number of birds sitting on empty nests or eggs decreased as breeding proceeded while care of the young increased.

(4) Rest and maintenance were commonest at dawn and evening, but were comparatively low and constant throughout the rest of the day. However, at the mai-mai, relative lows in these catgories occurred at dawn and evening, as the mai-mai was not used as a night roost by the non-breeding portion of the population.

Sleep was concentrated at dawn and evening, but was also relatively more common at Sexton's Lagoon during the day than at Hamilton's Lagoon, possibly because of unfavourable weather conditions at Sexton's Lagoon.

(5) Movement as a whole tended to be rather erratic, but flying tended to be concentrated at dawn due to the rapid departure of birds leaving for the first foraging trip of the day.

(6) Courtship and pair formation at the mai-mai were erratic and no significant daily trends resulted. At the prone willow and Sexton's Lagoon, significant daily trends occurred, but are difficult to compare as the quadratic trends at the prone willow showed high points at dawn and evening and a low near midday, while Sexton's Lagoon showed the inverse. The significance of this is unclear.

(7) Nest building peaked during the early morning and afternoon. The high frequency of nest-building at 0600 hours may mean that trips for nest material occur before the day's first foraging.

(8) At Sexton's Lagoon feeding of the young was commonest during the early morning and early evening. Feeding of young shags has not been recorded at night, and cool morning temperatures may mean that the early morning feed is important in sustaining the chick through the day.

Comparisons between non-breeding periods at Hamilton's Lagoon and Sexton's Lagoon were difficult to make, because birds did not roost overnight at Hamilton's Lagoon, but did so at Sexton's Lagoon for a period corresponding to 85.4% of the data collected for the non-breeding period. Reasons for this are unclear, but may be related to seasonal shifts in feeding areas or a decrease in breeding motivation as breeding ends.

Rest and maintenance during non-breeding did not show the morning and evening peaks that were characteristic of these trends during breeding. As no time was taken up with breeding activities, time was available throughout the day for rest and maintenance. This resulted in generally linear trends throughout the day for activity categories. At Hamilton's Lagoon there was a high in rest and a low in maintenance during the afternoon, which may reflect a rest subsequent to feeding, and just prior to departure to the night roost.

Movement during non-breeding was relatively static throughout the day, except for a dawn peak in flying at Sexton's Lagoon, due to the rapid departure of birds to forage.

APPENDIX 1

WEATHER PATTERNS DURING STUDY PERIOD COMPARED WITH 30 YEAR AVERAGE

	WIND		SUN		TEMP		RAIN	
	STUDY	30YR	STUDY	30YR	STUDY	30YR	STUDY	30YR
JAN 81	328	267	219	207	19.0	17.6	155	74
FEB	364	257	171	185	18.7	18.0	68	58
MAR	239	240	144	166	18.9	16.8	58	72
APR	315	222	149	136	15.7	14.0	43	72
MAY	218	213	138	109	11.1	11.2	135	96
JUN	210	203	53	91	10.3	8.8	121	88
JUL	230	200	89	106	8.6	8.1	109	97
AUG	229	222	90	117	8.4	9.2	57	85
SEP	417	260	101	129	10.6	10.9	98	76
OCT	349	272	134	159	12.2	12.5	43	82
NOV	301	282	159	173	14.6	14.4	35	75
DEC	322	271	161	190	12.8	16.2	93	100
JAN 82	387	267	193	207	17.5	17.6	70	74
FEB	305	257	196	185	18.7	18.0	69	58
MAR	214	240	180	166	16.5	16.8	81	72
APR	243	222	174	136	12.9	14.0	14	72
MAY	278	213	124	109	11.0	11.2	104	96
JUN	177	203	85	91	8.2	8.8	64	88
JUL	262	200	130	106	8.6	8.1	63	97
AUG	290	222	119	117	9.0	9.2	52	85
SEP	290	260	117	129	9.9	10.9	48	76
OCT	361	272	135	159	11.1	12.5	80	82
NOV	494	282	122	173	15.1	14.4	60	75
DEC	396	271	166	190	14.4	16.2	160	100
JAN 83	464	267	210	207	15.6	17.6	59	74
FEB	299	257	184	185	16.8	18.0	29	58
MAR	371	240	142	166	16.1	16.8	49	72
APR	268	222	108	136	13.4	14.0	87	72

WIND = Total wind flow/month (km).
SUN = Total hours of sunshine/month.
TEMP = Mean monthly temperature (^{o}c).
RAIN = Mean rainfall/month (mm).
30YR = Mean for 30 years from 1950 - 1980 (D.S.I.R. Palm North.

TABLE 2A: DAILY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT HAMILTON'S LAGOON DURING AUGUST & SEPTEMBER 1981

AUGUST 1981

	0600-0700	0700-0900	0900-1100	1000-1300	1300-1500	1500-1700	1700-1900
Norm	-	-	58.8	26.6	50.4	40.9	47.3
Sleep	-	-	-	-	-	-	-
REST	-	-	58.8	26.6	50.4	40.9	47.3
Preen	-	-	17.2	21.6	31.3	40.5	21.8
Scratch	-	-	-	1.2	0.2	3.3	-
Wing Dry	-	-	3.4	4.9	3.4	0.9	-
MAINTENANCE	-	-	20.6	27.7	34.9	44.7	21.8
Fly	-	-	10.3	6.8	3.7	2.3	9.1
Swim	-	-	6.9	9.9	3.2	3.3	5.5
Hop	-	-	-	1.2	0.2	-	1.8
MOVEMENT	-	-	17.2	17.9	7.1	5.6	16.4
Court	-	-	3.4	25.4	6.9	7.9	14.5
Copulate	-	-	-	1.2	0.7	0.9	-
Nest-build	-	-	-	1.2	-	-	-
PAIR FORMATION & MAINTENANCE	-	-	3.4	26.5	7.6	8.8	14.5

SEPTEMBER 1981

	0600-0700	0700-0900	0900-1100	1000-1300	1300-1500	1500-1700	1700-1900
Norm	57.9	65.7	42.4	30.9	38.3	46.4	18.7
Sleep	-	-	-	-	-	-	-
REST	57.9	65.7	42.4	30.9	38.3	46.4	18.7
Preen	26.9	8.6	25.9	31.0	26.8	44.1	56.2
Scratch	-	-	-	1.0	0.9	-	-
Wing Dry	3.8	7.1	0.6	2.0	0.9	0.8	6.3
MAINTENANCE	30.7	15.7	26.5	34.0	28.6	44.9	62.5
Fly	3.8	1.4	5.7	4.7	4.4	6.3	6.3
Swim	3.8	14.3	9.5	9.2	6.7	0.8	12.5
Hop	-	2.9	-	0.3		0.8	-
MOVEMENT	7.6	18.6	15.2	14.2	11.1	7.9	18.8
Court	3.8	-	1.3	1.3	-	0.8	-
Copulate	-	-	1.9	2.3	0.9	-	-
Nest-build	-	-	1.3	0.7	-	-	-
PAIR FORMATION & MAINTENANCE	3.8	-	4.5	4.3	0.9	0.8	-
SIT ON	-	-	11.4	16.6	21.1	-	-

TABLE 2B: DAILY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT HAMILTON'S LAGOON DURING OCTOBER & NOVEMBER 1981

OCTOBER 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
Norm	43.5	53.6	44.3	38.9	46.2	49.6	47.8
Sleep	1.9	0.1	1.4	0.2	–	–	–
REST	45.4	53.7	45.7	39.1	46.2	49.6	47.8
Preen	24.8	22.6	24.7	28.6	29.2	21.5	25.5
Scratch	1.5	0.1	2.0	2.0	0.5	1.1	1.1
Wing Dry	0.6	0.1	1.0	1.0	1.0	2.8	2.1
MAINTENANCE	26.9	22.8	22.7	31.6	30.7	25.4	28.7
Fly	4.0	1.6	0.7	2.8	2.3	2.9	1.9
Swim	2.1	2.9	3.4	5.9	6.1	5.1	6.5
Hop	0.8	0.7	0.3	0.7	0.5	0.9	0.6
MOVEMENT	6.9	5.2	4.4	9.4	8.9	8.9	9.0
Court	5.8	6.0	0.7	2.1	1.5	3.7	1.5
Copulate	0.8	1.2	–	1.6	0.3	0.9	0.4
Nest-build	0.6	0.7	0.7	0.3	2.0	1.8	0.4
PAIR FORMATION & MAINTENANCE	7.2	7.9	1.4	4.0	3.8	6.4	2.3
SIT ON	13.6	10.4	20.8	15.9	10.4	9.7	12.2

NOVEMBER 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
Norm	39.1	37.6	28.4	26.8	27.9	40.1	34.8
Sleep	1.5	0.4	0.2	–	–	15.9	20.9
REST	40.6	38.0	28.6	26.8	27.9	56.0	58.7
Preen	21.9	25.4	22.0	24.1	14.9	22.8	28.6
Scratch	0.6	1.1	1.1	0.8	0.7	0.3	0.1
Wing Dry	0.9	1.3	1.4	1.0	–	0.3	–
MAINTENANCE	23.4	27.8	24.4	25.9	15.6	23.4	28.7
Fly	1.9	3.0	2.1	0.4	0.2	1.6	1.5
Swim	1.9	1.8	3.8	1.2	1.1	1.1	0.4
Hop	0.7	0.7	0.2	0.6	–	0.3	0.3
MOVEMENT	4.5	5.5	6.1	2.2	1.3	3.0	2.2
Court	0.6	0.6	0.3	–	–	0.3	–
Copulate	0.3	0.4	0.3	1.0	–	0.8	0.6
Nest-build	1.9	2.5	1.7	0.6	0.2	1.3	0.7
PAIR FORMATION & MAINTENANCE	2.8	3.5	2.3	1.6	0.2	2.4	1.3
SIT ON	16.9	16.6	18.4	7.9	14.3	12.2	8.7
CARE OF YOUNG	11.8	8.6	20.1	35.6	40.7	3.1	3.4

TABLE 2C: DAILY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT HAMILTON'S LAGOON (DECEMBER 1982)

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900	1900-2000
Norm	19.3	13.1	15.7	27.4	19.1	14.9	20.2	30.5
Sleep	2.4	-	-	-	-	-	0.1	4.7
REST	21.7	13.1	15.7	27.4	19.1	14.9	20.3	35.2
Preen	13.3	18.6	10.3	20.8	14.2	13.9	19.8	37.4
Scratch	0.3	0.5	0.6	0.9	0.5	1.0	1.1	1.3
Wing Dry	0.1	0.2	0.5	0.3	0.3	-	0.4	0.1
MAINTENANCE	13.7	19.3	11.4	22.0	15.0	14.9	21.3	38.8
Fly	1.7	1.3	2.1	0.6	1.2	1.3	1.4	0.7
Swim	-	-	-	-	-	-	-	-
Hop	0.7	0.2	0.3	0.5	0.7	0.2	0.4	0.1
MOVEMENT	2.4	1.5	2.4	1.1	1.9	1.5	1.8	0.8
Court	1.0	0.3	0.3	0.8	1.0	1.0	1.6	0.3
Copulate	0.5	-	-	0.9	0.6	0.5	0.5	-
Nest-build	2.7	0.6	0.7	0.6	0.5	1.5	0.5	0.1
PAIR FORMATION & MAINTENANCE	4.2	0.9	1.0	2.3	2.1	3.0	2.6	0.4
SIT ON	23.2	32.4	35.1	26.1	39.3	26.5	19.6	9.9
CARE OF YOUNG	34.9	42.8	34.4	21.1	22.6	39.2	33.4	15.5

TABLE 2D: DAILY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT HAMILTON'S LAGOON (JANAURY 1982)

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900	1900-2000
Norm	20.6	11.3	10.3	9.5	12.5	12.4	21.3	21.9
Sleep	3.9	0.2	-	-	-	-	0.3	8.1
REST	24.5	11.5	10.3	9.5	12.5	12.4	21.6	30.0
Preen	20.3	4.3	5.5	3.9	5.8	8.1	35.6	41.1
Scratch	0.6	1.2	0.5	0.6	0.3	0.4	1.2	2.8
Wing Dry	0.5	-	-	-	0.3	0.1	0.4	0.1
MAINTENANCE	21.4	5.5	6.0	4.5	6.4	8.6	37.2	44.0
Fly	0.9	0.6	1.4	0.5	0.9	1.0	1.3	0.5
Swim	-	-	-	-	-	-	-	-
Hop	0.4	0.5	-	0.2	-	-	0.2	-
MOVEMENT	1.3	1.1	1.4	0.7	0.9	1.0	1.5	0.5
Court	0.7	-	0.5	0.7	0.9	0.1	1.2	0.3
Copulate	-	-	-	-	0.3	-	-	-
Nest-build	0.3	-	-	-	0.3	0.3	0.1	-
PAIR FORMATION & MAINTENANCE	1.0	-	0.5	0.7	1.5	0.4	1.3	0.3
SIT ON	18.6	29.7	28.2	28.4	25.3	27.4	14.1	9.4
CARE OF YOUNG	33.2	52.2	53.6	56.2	53.4	50.2	24.3	15.8

TABLE 2E: DAILY TRENDS IN THE PERCENTAGES OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT SEXTON'S LAGOON (OCTOBER 1982)

	0600-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
Norm	6.8	3.9	8.8	20.6	28.5	13.5	36.6
Sleep	29.1	26.1	14.2	-	-	20.5	10.2
REST	35.9	30.0	23.0	20.6	28.5	34.0	46.8
Preen	0.7	1.1	1.6	3.3	2.3	3.5	18.4
Scratch	1.0	0.1	0.7	1.4	0.3	0.7	0.6
Wing Dry	0.7	0.1	0.4	0.7	0.7	1.7	1.1
MAINTENANCE	2.4	1.3	2.7	5.4	3.3	5.9	20.1
Fly	0.7	1.6	2.1	2.3	0.9	0.7	2.0
Swim	2.2	2.6	1.2	4.1	4.1	4.1	3.5
Hop	0.2	0.7	1.1	0.2	0.3	0.4	0.2
MOVEMENT	3.1	4.9	4.4	6.6	5.3	5.2	5.7
Court	0.2	0.8	1.0	3.2	0.5	-	0.2
Copulate	-	-	-	-	-	-	-
Nest-build	-	-	0.1	0.5	2.1	-	0.1
PAIR FORMATION & MAINTENANCE	0.2	0.8	1.1	3.7	2.6	-	0.3
SIT ON	23.1	21.5	23.7	22.3	20.8	18.4	11.1
Brood	33.7	40.7	44.4	41.4	39.5	36.1	25.2
Feed Young	1.6	0.8	0.5	-	-	0.4	0.8
CARE OF YOUNG	35.3	41.5	44.9	41.4	39.5	36.5	26.0

TABLE 2F: DAILY TRENDS IN THE PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT SEXTON'S LAGOON (NOVEMBER 1982)

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
Norm	29.4	30.9	35.5	41.6	37.9	37.9	43.0
Sleep	2.5	0.1	1.2	3.0	1.3	2.0	5.4
REST	31.9	31.0	36.7	44.6	39.2	39.9	48.4
Preen	9.3	11.7	13.2	12.1	11.8	11.9	17.3
Scratch	0.9	0.5	0.7	0.8	0.3	0.8	0.9
Wing Dry	0.6	0.7	0.4	0.5	0.3	0.4	0.1
MAINTENANCE	10.8	12.9	14.3	13.4	12.4	13.1	18.3
Fly	7.8	3.2	2.4	3.4	2.3	2.5	3.0
Swim	0.2	0.8	0.6	0.6	0.3	0.3	0.8
Hop	0.6	0.9	0.6	0.4	0.6	0.4	0.1
MOVEMENT	8.6	4.9	3.6	4.4	3.2	3.2	3.9
Court	1.8	1.9	2.1	1.8	2.0	1.8	1.3
Copulate	0.1	-	0.1	-	-	-	-
Nest-build	2.6	2.4	1.6	1.1	0.8	1.4	0.3
PAIR FORMATION & MAINTENANCE	4.5	4.3	3.8	2.9	2.8	3.2	1.6
SIT ON	6.7	5.6	6.2	7.0	13.4	7.2	5.3
Brood	36.4	39.8	34.5	26.8	28.3	32.8	21.4
Feed Young	1.1	1.5	0.9	0.9	0.7	0.6	1.1
CARE OF YOUNG	37.5	41.3	35.4	27.7	29.0	33.4	22.5

TABLE 2G: PERCENTAGE OF ADULTS ENGAGED IN VARIOUS ACTIVITIES AT SEXTON'S LAGOON (DECEMBER 1982)

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
Norm	24.2	23.6	25.2	25.5	27.3	25.0	32.1
Sleep	6.3	4.3	2.1	4.9	1.4	1.0	13.2
REST	30.5	27.9	27.3	30.4	28.7	26.0	25.3
Preen	12.9	12.8	9.2	11.7	13.4	11.0	20.3
Scratch	0.7	1.0	0.9	1.4	1.4	0.8	1.5
Wing Dry	0.6	0.9	0.8	1.0	1.1	0.5	0.9
MAINTENANCE	14.2	14.7	10.9	14.1	15.9	12.3	22.7
Fly	7.6	2.0	2.1	2.3	1.7	1.4	2.4
Swim	-	-	-	-	-	-	-
Hop	1.9	0.3	0.5	0.4	0.8	0.3	0.2
MOVEMENT	9.5	2.3	2.6	2.7	2.6	1.7	2.6
Court	0.8	1.1	1.2	1.4	0.6	1.0	0.5
Copulate	-	-	-	-	-	-	-
Nest-build	1.4	1.0	1.5	1.2	0.8	1.1	0.4
PAIR FORMATION & MAINTENANCE	2.2	2.1	2.7	2.6	1.4	2.1	0.9
SIT ON	-	-	-	-	-	-	-
Brood	42.7	51.4	54.5	49.5	50.2	57.3	27.7
Feed Young	0.9	1.6	2.0	0.7	1.3	0.6	0.8
CARE OF YOUNG	43.6	53.0	56.5	50.2	51.5	57.9	28.5

TABLE 2H: DAILY TRENDS IN ACTIVITY PERCENTAGES DURING NON-BREEDING AT HAMILTON'S AND SEXTON'S LAGOONS

HAMILTON'S LAGOON

	DAWN	MORNING	NOON	AFTERNOON	EVENING
REST	61.8	57.6	64.2	77.1	59.6
MAINTENANCE	30.9	30.8	26.9	10.6	34.0
MOVEMENT	7.3	11.6	8.9	12.3	6.4

SEXTON'S LAGOON

REST	62.3	57.2	60.3	63.5	65.3
MAINTENANCE	27.7	40.9	38.0	35.5	34.1
MOVEMENT	1.0	1.9	1.7	1.0	0.6

APPENDIX 3

TABLE 3A: COMPUTER GENERATE STANDARD ERRORS FOR DAILY ACTIVITY CATEGORIES DURING THE PRE-EGG PHASE AT THE MAI-MAI (HAMILTON'S LAGOON)

AUGUST 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
REST	*	*	*	0.0	3.5	7.0	6.3
MAINTENANCE	*	*	*	0.0	12.5	4.0	2.4
COURTSHIP & PAIR FORMATION	*	*	*	0.0	6.4	2.1	7.6
MOVEMENT	*	*	*	0.0	2.7	0.9	1.1

SEPTEMBER 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
REST	*	0.0	0.0	19.4	5.4	4.1	0.0
MAINTENANCE	*	0.0	0.0	0.6	4.9	8.6	0.0
COURTSHIP & PAIR FORMATION	*	0.0	0.0	1.0	1.2	2.6	0.0
MOVEMENT	*	0.0	0.0	6.4	1.9	16.0	0.0

* - No data available

0.0 - Only one sample available

TABLE 3B: COMPUTER GENERATED STANDARD ERRORS FOR DAILY ACTIVITY CATEGORIES DURING THE EGG-PHASE AT THE MAI-MAI (HAMILTON'S LAGOON)

OCTOBER 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900
REST	0.7	8.4	11.2	5.0	3.6	2.4	4.4
MAINTENANCE	3.6	8.5	5.5	2.2	0.9	2.3	1.0
COURTSHIP & PAIR FORMATION	3.4	3.2	2.0	1.3	0.5	1.7	1.3
MOVEMENT	0.8	3.7	0.9	1.3	0.7	1.3	3.1

NOVEMBER 1981

REST	10.1	4.4	4.9	9.9	13.0	5.0	23.1
MAINTENANCE	11.2	1.9	3.5	10.7	11.0	11.2	12.2
COURTSHIP & PAIR FORMATION	1.7	1.6	1.3	0.5	0.5	0.9	0.8
MOVEMENT	0.6	0.7	0.6	2.3	0.9	1.6	2.1

TABLE 3C: COMPUTER GENERATED STANDARD ERRORS FOR DAILY ACTIVITY CATEGORIES DURING THE EGG PHASE AT THE PRONE WILLOW (HAMILTON'S LAGOON)

DECEMBER 1981

	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900	1900-2000
REST	3.3	3.0	1.4	5.3	6.4	0.1	0.3	2.0
MAINTENANCE	1.2	4.1	3.6	0.6	0.5	2.0	4.5	2.3
COURTSHIP & PAIR FORMATION	1.3	0.9	0.6	0.4	1.2	1.2	1.8	0.4
MOVEMENT	0.2	0.5	0.8	1.4	0.2	0.2	0.6	0.2

JANUARY 1982

REST	10.8	11.8	14.3	7.6	9.4	11.1	12.3	4.8
MAINTENANCE	7.5	3.8	1.7	2.5	2.6	2.2	6.6	3.2
COURTSHIP & PAIR FORMATION	0.4	0.4	0.4	0.0+	1.0	0.2	0.6	0.3
MOVEMENT	0.1	0.2	0.2	0.4	0.6	0.2	0.4	0.2

+ In this case 0.0 indicates that no courtship was observed at this time.

TABLE 3D: COMPUTER GENERATED STANDARD ERRORS FOR DAILY ACTIVITY CATEGORIES DURING THE EGG PHASE AT SEXTON'S LAGOON

OCTOBER 1982

TIME	0500-0700	0700-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900	1900-2000
REST	*	1.6	1.3	0.6	5.2	0.5	6.5	0.0
MAINTENANCE	*	0.7	0.4	0.7	1.5	1.1	1.4	0.0
COURTSHIP & PAIR FORMATION	*	0.5	0.6	0.1	1.3	0.8	0.1	0.0
MOVEMENT	*	0.4	0.3	1.0	0.4	0.1	0.7	0.0

NOVEMBER 1982

REST	6.5	5.2	7.5	5.8	5.5	5.1	3.5	3.4
MAINTENANCE	2.2	2.5	3.1	1.7	1.9	1.5	1.7	2.0
COURTSHIP & PAIR FORMATION	2.3	2.2	1.4	1.4	0.7	1.7	0.7	0.8
MOVEMENT	1.1	1.1	0.4	0.9	0.3	0.6	0.9	1.4

DECEMBER 1982

REST	4.3	8.7	5.2	4.6	2.1	2.5	3.0	2.1
MAINTENANCE	1.9	4.8	3.2	2.8	2.2	2.3	4.0	2.9
COURTSHIP & PAIR FORMATION	0.7	0.5	0.3	0.4	0.3	0.5	0.8	0.3
MOVEMENT	2.3	0.7	0.8	0.2	0.5	0.5	0.4	0.4

* - No data available

0.0 - Only one sample

LITERATURE CITED

Altmann, A. (1974). Observational study of behaviour: sampling methods. BEHAVIOUR, 49, 227-267.

Bartholomew, G.A. (1943). The daily movements of cormorants in San Francisco Bay. THE CONDOR, 45, 3-18.

Bernstein, N.P. & S.J.Maxson. (1982). Behaviour of the antarctic blue-eyed shag. NOTORNIS, 29, 197-207.

Beer, C.G. (1975). Multiple functions and gull displays. Pages 16-55 in FUNCTION AND EVOLUTION IN BEHAVIOUR (Edited by G.P.Baerends, C.G.Beer & A.Manning). Clarendon Press Oxford.

Berry, H.H. (1975). Physiological and behavioural ecology of the cape cormorant. MADOQUA, 9, 5-55.

Brown, J.L. (1975). THE EVOLUTION OF BEHAVIOUR. W.W.Norton & Co.Inc. New York.

Buller, W.L. (1888). A HISTORY OF THE BIRDS OF NEW ZEALAND. Edited by E.G.Turbott. Whitcomb & Tombs Christchurch.

Burley, N. (1981). The evolution of sexual indistinguishability. Pgs 121-138 in NATURAL SELECTION AND SOCIAL BEHAVIOUR. Edited by R.D.Alexander and D.W.Tinkle. Blackwell Scientific Oxford.

Coulson, J.C. (1968). Differences in the quality of birds nesting in the centre and edges of a colony. NATURE, 217, 478-479.

- (1971). Competition for breeding sites causing segregation and reduction in young production in colonial animals. Pages 257-268 in PROCEEDINGS OF THE ADVANCED STUDY INSTITUTE ON DYNAMICS OF NUMBERS IN POPULATIONS. Oosterbeek.

Cowie, J.D. (1978). Soils and agriculture of Kairanga County, North Island, New Zealand. SOIL BUREAU BULLETIN 33, N.Z.D.S.I.R.

Cowie, J.D., P.Fitzgerald & W.Owers. (1967). Soils of the Manawatu sand country. SOIL BUREAU BULLETIN 29. N.Z.D.S.I.R.

Cowie, J.D. & B.A.J. Smith. (1958). Soils and agriculture of Oroua Downs, Taikorea , and Glen Oroua districts, Manawatu County. SOIL BUREAU BULLETIN 16. N.Z.D.S.I.R.

Cullen, J.M. (1963). Allo-, auto-, and heteropreening. IBIS, 105, 121.

Daanje, A. (1951). On locomotory movements in birds and the intention movements which derive from them. BEHAVIOUR, 3, 48-98.

DeLaRonde, G.G. & Y.A.Greichus. (1972). Care and behaviour of penned double crested cormorants. THE AUK, 89, 644-650.

Dickinson, P. (1951). Stomach contents of New Zealand inland shags. AUSTRALIAN JOURNAL OF MARINE AND FRESHWATER RESEARCH, 2, 245-251.

Drent, R.H., G.F.Van Tets, F.Tampa & K.Vermeer. (1964). The breeding birds of Mandarte Island, British Columbia. CANADIAN FIELD NATURALIST, 78, 208-263.

Evans, P.R. (1976). Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution and movements in the non-breeding season. ARDEA, 64, 117-139.

Falla, R.A. (1932). New Zealand cormorants in the collection of the Auckland Museum, with notes on field observations. AUCKLAND INSTITUTE AND MUSEUM RECORDS, 1, 139-155.

Falla, R.A., R.B.Sibson & E.G.Turbott. (1979). A NEW GUIDE TO THE BIRDS OF NEW ZEALAND. Collins. Auckland.

Fordham, R.A. (1970). Mortality and population change of Dominican gulls in Wellington, New Zealand. JOURNAL OF ANIMAL ECOLOGY, 39, 13-27.

Gilham, M.E. (1960). Vegetation of New Zealand shag colonies. TRANSACTIONS OF THE NEW ZEALAND ROYAL SOCIETY, 88, 363-380.

Gladstone, D.E. (1979). Promiscuity in monogamous colonial birds. THE AMERICAN NATURALIST, 114, 545-557.

Gurr, L. (1947). Measurements of birds. NEW ZEALAND BIRD NOTES, 2, 57-61.

Harley, K.L.S. (1946). Display and nesting of the little pied cormorant at Brisbane botanical gardens. EMU, 45, 298-300.

Harris, M.P. (1982). Promiscuity in the shag as shown by time-lapse photography. BIRD-STUDY, 29, 149-154.

Heath, J.E. (1962). Temperature fluctuation in the turkey vulture. THE CONDOR, 64, 234-235.

Hennemann, W.W. (1983). Environmental influences on the energetics and behaviour of the anhinga and double-crested cormorant. PHYSIOLOGICAL ZOOLOGY, 56, 201-206.

Horn, H.S. (1968). The adaptive significance of colonial nesting in the Brewer's Blackbird. ECOLOGY, 49, 682-694.

Jones, P.J. (1978). A possible function of the 'wing-drying' posture in the reed cormorant, Phalacrocorax africanus. IBIS, 120, 540-542.

Kenward, R.E. (1978). Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. JOURNAL OF ANIMAL ECOLOGY, 47, 449-460.

Kessel, B. (1976). Winter activity patterns of black-capped chickadees in interior Alaska. WILSON BULLETIN, 88, 36-61.

Kinsky, F.C. (1969). New and rare birds on Campbell Island. NOTORNIS, 16, 25-236.

Klomp, H. (1970). The determination of clutch size in birds. ARDEA, 58, 1-124.

Krebs, J.R. (1974). Colonial nesting and social feeding strategies for exploiting food resources in the great blue heron Ardea herodias. BEHAVIOUR, 51, 99-131.

Krebs, J.R. & N.B.Davies. (1978). BEHAVIOURAL ECOLOGY, AN EVOLUTIONARY APPROACH. Sinauer Associates Inc. Sunderland, U.S.A.

Kury, C.H. & M.Gochfield (1975). Human interference and gull predation in cormorant colonies. BIOLOGICAL CONSERVATION, 8, 23-25.

Landsborough Thomson, A. (1964). A NEW DICTIONARY OF BIRDS. T.Nelson & Sons Ltd. London.

Lanham, U.N. (1947). Notes on the phylogeny of the Pelecaniformes. THE AUK, 64, 65-70.

Llewellyn, L.C. (1983). Movements of cormorants in South-Eastern Australia and the influence of floods on breeding. AUSTRALIAN WILDLIFE RESEARCH, 10, 149-167.

Lorenz, K. (1952). KING SOLOMON'S RING. Methuen. London.

McNally, J. (1957). The feeding habits of cormorants in Victoria. VICTORIA FISH AND WILDLIFE DEPARTMENT, FISH CONTRIBUTION NUMBER 6.

Millener, P.R. (1972). The biology of the New Zealand pied cormorant P.varius varius. Unpublished M:Sc thesis in Zoology. University of Auckland.

Miller, B. (1979). Ecology of the little black cormorant, Phalacrocorax sulcirostris, and little pied cormorant, Phalacrocorax melanoleucos, in inland New South Wales. 1: Food and feeding habits. AUSTRALIAN WILDLIFE RESEARCH, 6, 79-95.

- (1980). Ecology of the little black cormorant, Phalacrocorax sulcirostris, and little pied cormorant, Phalacrocorax melanoleucos, in inland New South Wales. 2: Proximate control of reproduction. AUSTRALIAN WILDLIFE RESEARCH, 7, 85-101.

Mitchell, R.M. (1977). Breeding biology of the double-crested cormorant on Utah Lake. THE GREAT BASIN NATURALIST, 37, 1-23.

Morrison, M.L., E.Shanley & R.D.Slack. (1979). Breeding biology and age specific mortality of olivaceous cormorants. THE SOUTHWESTERN NATURALIST, 24, 259-266.

Nelson, J.B. (1978a). THE SULIDAE; GANNETS AND BOOBIES. Aberdeen University studies series no.154. Oxford University Press Oxford.

-(1978b). THE GANNET. T. & A.D.Poyser ltd. Berkhamstead. England.

-(1980). SEABIRDS; THEIR BIOLOGY AND ECOLOGY. Hamlyn, London, New York, Sydney.

Oliver, W.R.B. (1955) . NEW ZEALAND BIRDS. A.H. & A.W.Reed Ltd Wellington.

Ornithological Society of New Zealand (O.S.N.Z.) (1970). ANNOTATED CHECKLIST OF THE BIRDS OF NEW ZEALAND. A.H. & A.W.Reed Ltd Wellington.

Potts, G.R. (1969). The influence of eruptive movements, age, population size, and other factors in the survival of the shag. JOURNAL OF ANIMAL ECOLOGY, 38 , 53-102.

- (1980). Population dynamics and breeding success of the shag on the Farne Islands. JOURNAL OF ANIMAL ECOLOGY, 49, 465-484.

Rickleffs, R.E. (1977). A note on the evolution of clutch size in altricial birds. Pgs 193-214 in EVOLUTIONARY ECOLOGY (Edited by B.Stonehouse and C.Perrins) Macmillan Press London.

Rijke, A.M. (1968). The water repellency of the feather structure of cormorants. JOURNAL OF EXPERIMENTAL BIOLOGY, 48, 185-189.

Ross, K. (1976). Notes on the behaviour of captive great cormorants. THE WILSON BULLETIN, 88, 143-145.

Serventy, D.L., V.Serventy & J.Warham. (1971). THE HANDBOOK OF AUSTRALIAN SEABIRDS. A.H. & A.W.Reed Sydney

Sibley, C.G. (1960). The electrophoretic patterns of avian egg-white proteins as taxonomic characters. IBIS, 102, 215-274.

Siegal-Causey, D. & G.F.Hunt (1981). Colonial defense behaviour in double-crested and pelagic cormorants. THE AUK, 98, 522-531.

Siegel, S. (1956). NONPARAMETRIC STATISTICS FOR THE BEHAVIOURAL SCIENCES. McGraw-Hill Kogakusha Ltd.

Siegfried, W.R.A., A.J.Williams, P.G.H.Frost, & J.B.Kinahan. (1976). Plumage and ecology of cormorants. ZOOLOGICA AFRICANA, 10, 183-192.

Simmons, K.E.L. (1961). Problems of head scratching in birds. IBIS, 103A, 37-49.

- (1972). Adaptiveness of various plumage types in birds. BRITISH BIRDS, 65, 465-479.

Snow, B.K. (1960). The breeding biology of the shag on the island of Lundy, Bristol Channel. IBIS, 102, 554-575.

- (1963). The behaviour of the shag. BRITISH BIRDS, 56, 77-103, 164-186.

Stonehouse, B. (1967). Feeding behaviour and diving rhythms of some New Zealand shags. IBIS, 109, 600-605.

Swinton, W.E. (1965). FOSSIL BIRDS. British Museum (Natural History). London.

Van Dobben, W.H. (1952). The food of cormorants in the Netherlands. ARDEA, 40, 1-63.

Van Tets, G.F. (1965). A comparitive study of some social communication patterns in the Pelecaniformes. ORNITHOLOGICAL MONOGRAPHS, 2, 1-88.

- (1976). The origin of shags and cormorants, Phalacrocoracidae. Pages 121-124 in PROCEEDINGS OF THE XVI INTERNATIONAL ORNITHOLOGICAL CONGRESS. Australian Academy of Science Canberra.

Walsberg, G.A. (1983). Coat colour and solar heat gain in animals. BIOSCIENCE, 33, 88-92.

Wetmore, A. (1960). A classification for the birds of the world. SMITHSONIAN MISCELLANEOUS COLLECTION, 39, 1-37.

Williams, A.J. & A.E.Berger. (1979). Aspects of the breeding biology of the imperial cormorant Phalacrocorax atriceps at Marion Island. LE GERFAUT, 69, 407-423.

Winkler, H. (1983). Das flugelspreitverhalten der mohrensharbe Phalacrocorax niger. JOURNAL FUR ORNOTHOLOGIE 124, 177-186.