

KINGSFORD, Richard Tennant
Ph.D. May 1987

R. B. 15b.

The University of Sydney

Copyright in relation to this thesis*

Under the Copyright Act 1968 (several provisions of which are referred to below), this thesis must be used only under the normal conditions of scholarly fair dealing for the purposes of research, criticism or review. In particular no results or conclusions should be extracted from it, nor should it be copied or closely paraphrased in whole or in part without the written consent of the author. Proper written acknowledgement should be made for any assistance obtained from this thesis.

Under Section 35(2) of the Copyright Act 1968 the 'author of a literary, dramatic, musical or artistic work is the owner of any copyright subsisting in the work'. By virtue of Section 32(1) copyright 'subsists in an original literary, dramatic, musical or artistic work that is unpublished' and of which the author was an Australian citizen, an Australian protected person or a person resident in Australia.

The Act, by Section 36(1) provides: 'Subject to this Act, the copyright in a literary, dramatic, musical or artistic work is infringed by a person who, not being the owner of the copyright and without the licence of the owner of the copyright, does in Australia, or authorises the doing in Australia of, any act comprised in the copyright'.

Section 31(1)(a)(i) provides that copyright includes the exclusive right to 'reproduce the work in a material form'. Thus, copyright is infringed by a person who, not being the owner of the copyright and without the licence of the owner of the copyright, reproduces or authorises the reproduction of a work, or of more than a reasonable part of the work, in a material form, unless the reproduction is a 'fair dealing' with the work 'for the purpose of research or study' as further defined in Sections 40 and 41 of the Act.

Keith Jennings
Registrar

*'Thesis' includes 'treatise', 'dissertation' and other similar productions.

4. 15b

Reproductive biology and habitat use
of the
Maned Duck Chenonetta jubata (Latham)

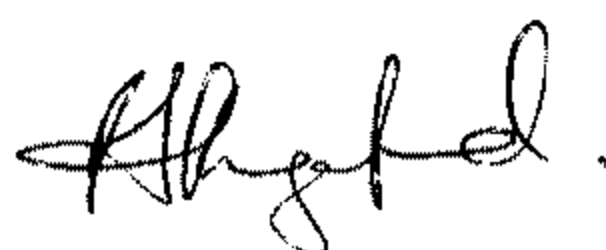
by Richard Kingsford

A thesis submitted in fulfillment of
the requirements for the degree of
Doctor of Philosophy

School of Biological Sciences, University of Sydney

April 1986

The work contained in this thesis is the result of my own investigation, except where otherwise acknowledged.

A handwritten signature in cursive script, appearing to read 'R. Kingsford'.

Richard Kingsford

ABSTRACT

The Maned Duck Chenonetta jubata is an important anatid species in rural New South Wales. The specific aims of this study were to investigate habitat use and reproductive biology of the Maned Duck on the Southern Tablelands of N.S.W. The study also provides basic information on the ecology of Maned Ducks.

Both adults and ducklings had a principally vegetarian diet. The composition of the diet closely reflected the abundances of the various surrounding plant species. Insects were rarely included in the diet but when they were, it was often intentional. There was no evidence that females selected invertebrates to offset higher nutritional demands during breeding, instead, these seem to be overcome by grazing more intensely. During drought, Maned Ducks fed on the wheat and oat grain which were given to livestock.

Like the diet, the activity patterns of this species were similar to other grazing anatids, with ducks spending little time on the water. Grazing and loafing on land were the principal activities. Bathing, mating and picking insects off the water were exclusively aquatic activities. A comparison of activity patterns on four dams indicated that there were diurnal patterns for some activities, but the principal activity, grazing, tended to occur throughout the day. Although, there was some evidence that Maned Ducks grazed at night, most nocturnal activity appeared to be loafing. All activities on land were performed close to the water. This was apparently due to aerial predation. Two observations supported this. Ducks, in grazing flocks, performed a frequent behaviour, where individuals "dashed" to the water, usually in response to the alarm calls of other bird species. Furthermore, grazing Maned Ducks frequently performed vigilant behaviour.

Most farm dams appeared to fit the requirements of this species, as there were few habitat characteristics correlated to duck-use. However, dams which were small and covered by vegetation were not used. There were also some weak trends in habitat use. During the breeding seasons of 1981

and 1983, some ducks used those dams closest to potential nesting cavities. In the drought year of 1982, the distribution of Maned Ducks on farm dams was strongly correlated to the only available food source, which was wheat grain.

Breeding occurred between the end of July and the end of November, showing there was considerable variability in its timing and extent. In the climatically normal years of 1981 and 1983, breeding seasons were similar. However, in 1982, only a few ducks bred and those that did, bred later. Duckling mortality showed a similar pattern of interannual variation, with higher duckling mortality in 1982 than in other years.

Changes in flock size showed a seasonal pattern in 1981 and 1983. Birds moved in pairs during the breeding season and amalgamated into larger flocks towards the end of the year. In 1982, flock size was large throughout the year which was probably because of the harsh climatic conditions. Analysis of the structure of such flocks showed that these flocks consisted of pairs of birds which moved independently among flocks. An extended period of parental care past fledging suggested that flocks which formed towards the end of the year, after breeding, contain some family groups.

Both males and females play an active role in parental care. The male begins by guarding the female when she is building up energy reserves for breeding. During early brood care the female is principally concerned with feeding, apparently taking little active part in parental care. The male continues his guarding role throughout the brood care period while the female starts playing a more active role in parental care after the first two weeks. Sharing of parental responsibilities is reflected in a long term pair bond. While the mating system differed from that of many Anatini, I found that the displays of Maned Ducks were similar in complexity to those of the two Aix species, A. sponsa and A. galericulata.

Many of the characteristics which have set this species apart amongst the Cairinini are probably the result of convergent adaptation. There is good evidence that this species is more closely related to the two Aix species than has been previously thought.

Acknowledgements

I wish to thank my supervisor, Associate Professor Peter Sale, for his support and encouragement during this study. In addition, his constructive criticisms of drafts of this thesis were much appreciated.

Many others made valuable contributions throughout this study. My thanks go to Sue Briggs, whose initial support, and enthusiasm for this study were particularly helpful. Without this, my study would have had an even more shaky start. The provision of aluminium bird bands by the Australian Bird Banding Scheme and the efficiency with which this was done, were also appreciated. I would like to thank Jeff, Jess and Charlie Prell of "Gundowringa" for allowing me to shoot on their property and also for being so hospitable. Thanks also go to both Michael Johnson and Charles Bradbury for giving me free rein on their farms. Charles and his father also kindly let me use farming equipment and material. I am very grateful to my family and the many friends who frequently endured hours of cold-laden misery during banding. Often, apart from the help that they gave, their enthusiasm was a particularly refreshing tonic. To Bill Stern go thanks for preparing and repairing electrical equipment and, on many occasions, providing much needed light relief.

I am especially indebted to Dr Rich Bradley and Dr Stuart Cairns for their painstaking criticisms on drafts of this thesis. I am also grateful for the helpful criticisms of Dr Peter Fullagar (my co-supervisor). Dr Stuart Cairns, Associate Professor Robinson and David Bradley gave freely of their statistical knowledge and guided me through, what often seemed, an impenetrable fog of complexity. My sincere thanks go to them.

Thanks must go to my late grandmother, Cecily Kingsford, for nurturing in me, an appreciation and love of birds which was one of the driving forces behind this study. My parents, Margaret and David Kingsford, were also integral to the successful completion of this study. Apart from providing financial assistance and the use of their farm and facilities, they gave me invaluable help, advice and encouragement.

Finally, I am indebted to my wife Rosie for enduring much of the cost of this study. She helped with the preparation of this manuscript and did most of the figures. Her support, patience and encouragement were invaluable.

The study was partly supported by funds from the University of Sydney Research Grant fund.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1 GENERAL INTRODUCTION.....	1
CHAPTER 2 STUDY SITES.....	5
CHAPTER 3 FOOD HABITS	
Introduction.....	7
Methods.....	8
Results.....	13
Discussion.....	17
CHAPTER 4 ACTIVITY PATTERNS	
Introduction.....	24
Methods	
Sampling methods.....	25
Data analysis.....	28
Results	
Diurnal activities.....	31
Nocturnal patterns.....	36
Vegetation.....	36
Discussion.....	37
CHAPTER 5 HABITAT ASSOCIATIONS	
Introduction.....	44
Methods	
Survey methods.....	45
Choice of variables.....	46
Nest site characteristics.....	47
Data analysis.....	47

Results

Characteristics of farm dams.....	52
Abundance of Maned Ducks on farm dams.....	53
Distribution of Maned Ducks.....	55
Nesting habitat.....	58
Discussion.....	60

CHAPTER 6 REPRODUCTIVE SUCCESS

Introduction.....	66
-------------------	----

Methods

Timing of breeding.....	67
Duckling survival and production.....	68
Brood size variation.....	70

Results

Timing of breeding.....	71
Variation in brood size.....	72
Brood movement.....	72
Duckling survival.....	73
Duckling production.....	75
Discussion.....	77

CHAPTER 7 FLOCK STRUCTURE

Introduction.....	83
-------------------	----

Methods

Trapping.....	85
Data analysis.....	87

Results

Behaviour synchrony and cohesion in flocks.....	90
Flock structure.....	91
Flock size.....	92
Sex ratios.....	93
Population dynamics.....	93
Discussion.....	95

CHAPTER 8 MATING SYSTEM

Introduction.....	102
Methods	
Displays.....	104
Pair bond duration.....	104
Parental care.....	104
Results	
Displays.....	108
Pair bond duration.....	114
Parental care.....	114
Discussion.....	119

CHAPTER 9 FINAL DISCUSSION..... 128

REFERENCES..... 136

APPENDICES

Appendix 1 Comfort behaviours.....	148
Appendix 2 ANOVA Tables-Activity patterns.....	149
Appendix 3 ANOVA Tables-Maned Duck numbers.....	153
Appendix 4 Flock structure-number of observations.....	155
Appendix 5 ANOVA Tables-Parental care.....	156
Appendix 6 Moults and Plumages.....	159



Three Maned Ducks Chenonetta jubata; two males and one female.

CHAPTER 1GENERAL INTRODUCTION

The Maned Duck Chenonetta jubata is the only species in this genus of the perching ducks (Tribe Cairinini) and is endemic to Australia. Most of the previously known information on this species is contained in Frith's (1967) classic book on Australian waterfowl. Subsequent research has been included in a second edition (Frith 1982). A comparison of the sections on the Maned Duck in the two editions, reveals the limited extent of the knowledge on this species and the lack of research in the intervening years. Apart from some additional data on clutch size and the omission of just over four paragraphs in the second edition, the two sections are identical. (Throughout this thesis, the later edition is cited although the information contained, essentially duplicates that in the earlier edition.)

The few detailed studies on this species have concentrated on its feeding habits (Frith 1957a), particularly as these have affected rice growing (Kinghorn 1932; Frith 1957b). Some banding studies have also provided information on dispersal and mortality (Frith 1959b; Norman 1971). Hence, Cowan's (1973) comment that the detailed ecology, physiology and behaviour of Australian waterfowl is largely unknown, is still relevant for this species and there is clearly a need for more basic information.

Some evidence exists that this species has recently increased in number (Briggs et al. 1985b) and extended its distribution (Frith 1982, p 35; Blakers et al. 1984). This increase in numbers is well illustrated using data gathered from hunter kills on opening day of the duck shooting season at Barrenbox Swamp, in south-eastern N.S.W. (Braithwaite & Norman 1974, 1976, 1977, 1981; Norman et al. 1984; Briggs unpublished data). From 1972-1974, Maned Ducks were ranked as the fifth most important game species. In 1975, they ranked fourth and from 1976-1981 and 1984, they were the third most important species. There was no

shooting season in 1983, due to drought conditions, but in 1982, they ranked as the second most important species, challenging Frith's (1963) claim that the two most important waterfowl species in South-eastern Australia, were the Pacific Black Duck Anas superciliosa and the Grey Teal A. gibberifrons. Such data may be biased, particularly as ranking is dependent on populations of other species. However, a thorough examination of the data showed that these were probably real changes in the Maned Duck population, for this area.

With the general decline of wild ducks in Australia (Frith 1982, p 36), it is particularly encouraging to find a species which appears to be increasing in numbers. Increases in other waterfowl species have generally been attributed to a reduction in the amount of shooting (Owen & Thomas 1979; Frith 1982, p 140). Frith (1982, p 35) said that the introduction of improved pastures and grain crops, combined with the creation of farm dams, had allowed Maned Ducks to extend their range. Others have also noted the positive impact of farm dams on some Australian waterfowl (Lavery 1966a, 1971, 1974; Braithwaite 1980). However, data on the reproductive potential and habitat suitability on such waterfowl habitat, are only available from North American studies (Bue et al. 1964; Dwyer 1970; Lokemoen 1973; Ruwaldt et al. 1979; Mack & Flake 1980; Hudson 1983).

The present study into the relationship between Maned Ducks and dams at one site, begins with a particularly relevant anecdote. Mr Charles Bradbury, an early landholder on my main study site, was once a duck-shooter. During the 1930s, while shooting Pacific Black Duck, A. superciliosa, the then most abundant resident duck species, he saw "a strange grey duck" for the first time. This, he later identified as a Maned Duck. This appears to be the first record of this species in the area. Apparently, Maned Ducks have not always been resident on this site. Dams were coincidentally also a relatively recent additions to the countryside.

The relationships of the Maned Duck to the other Anatidae is also particularly interesting. Delacour and Mayr (1945) described it as an aberrant anatid and were the first to include the Maned Duck in the Tribe Cairinini (perching ducks). Before this, it was thought to be related to

the shelducks (Tadornini), because of its grazing lifestyle and goose-like body form. Two common names, which were previously used (R.A.O.U. 1978), reflect these two perspectives. Its association with water near wooded areas (Frith 1982, p 262) and its perching capabilities, probably earned it the name of the Australian Wood Duck (North 1913), while its resemblance to the shelducks resulted in it being called the Maned Goose. It is now generally agreed that this species is one of the Cairinini (Delacour 1964; Johnsgard 1965; Frith 1982). Within the Cairinini, a number of workers have noted that Maned Ducks share some characteristics with the two species in the Aix genera, the American Wood Duck A. sponsa and the Mandarin Duck A. galericulata (Delacour & Mayr 1945; Johnsgard 1960a, 1965; Delacour 1964). Nevertheless, there is still some doubt about its closest relative (Frith 1982, p 282; Serventy et al. 1985).

The taxonomy of the Anatidae has mainly been built on adult body shape, duckling downy plumage, wing speculum colour and pattern, tracheal anatomy and some behavioural characters (McKinney 1978). Comparative behaviour has been a particularly fruitful avenue of investigation into the systematics of this group (Lorenz 1941, 1953; Johnsgard 1965). In particular, the occurrence of some distinctive displays have provided useful taxonomic characters. However, in such approaches, the emphasis has been on similarities, with the sources and significance of differences attracting less attention (McKinney 1975). Some workers attempted to incorporate observations on the social systems of the different anatid species into a phylogenetic framework (Johnsgard 1962; Kear 1970). This has proved to be difficult.

The view that displays were merely "conventions" which promoted species isolation (Sibley 1957; Johnsgard 1963) combined with the problems of incorporating the social system of a species into a phylogenetic framework have made it difficult to understand the behaviour patterns of various waterfowl species. The break-through came when it was discovered that environmental factors were important determinants of behaviour patterns in birds (Cullen 1957; Crook 1964). Some display repertoires were better explained by considering the ecology of the species (McKinney 1970; McKinney et al. 1978), as were the structures of animal social systems (Orians 1969; Emlen & Oring 1977; Krebs & Davies 1981).

Following this new way of thinking, McKinney (1973) advocated a new approach to the investigation of behaviour patterns in waterfowl. In particular, he considered it important when examining the behaviour patterns of a species, to consider these in the context of feeding habits, activity patterns, and social systems. This has meant that the taxonomist has had to adopt a wider viewpoint in an effort to differentiate those characteristics which might be "plastic" in terms of natural selection, from the more taxonomically reliable or "conservative" characteristics. Conversely, some of the problems which confront the ecologist cannot be resolved without a thorough understanding of an animal's behaviour (McKinney 1973).

The principal objectives of this study were to investigate habitat utilisation and reproductive biology of the Maned Duck. To investigate habitat use, I focused on feeding habits (chapter 3), activity patterns (chapter 4) and habitat associations (chapter 5). A proper understanding of an animal's diet can reveal much about its ecological demands. This can be improved by finding out how much time an animal devotes to various activities. I also aimed to use the activity patterns of Maned Ducks, to determine what parts of the habitat were important. Finally, I attempted to use the presence of Maned Ducks on each dam to identify whether there were particular characteristics of a dam which made it suitable to Maned Ducks. Apart from the investigation into reproductive success (chapter 6), the study of reproductive biology followed a behavioural line. I examined the flock structure during the breeding season (chapter 7) and the displays and mating system of this species (chapter 8).

Besides providing worthwhile information on the general ecology of this species, the identification of which ecological factors were possibly important to Maned Ducks gave me a particularly good ethoecological basis for a discussion of the taxonomic relationships of this species. I also used the available literature on this species and the two Aix species to compare similarities and differences (chapter 9), since insights into adaptations come mainly from comparative study (McKinney 1973).

CHAPTER 2STUDY SITES

I used two sites for this study. Both were on the Southern Tablelands of N.S.W. (Fig. 1) which is part of the Eastern Uplands of the continent (Mabbutt 1970). This area is geologically characterised by basalt caps on the ranges. Most of this study took place with the Maned Duck population on Site A ($34^{\circ}18' \text{ S } 149^{\circ}42' \text{ E}$) which is at an altitude of 610m (Fig.1). To avoid disruption to this population, I shot Maned Ducks for diet analysis at site B ($34^{\circ}34' \text{ S } 149^{\circ}34' \text{ E}$) which is over 60km from site A (Fig. 1). Although the following describes site A, climate and vegetation are similar as the two sites are relatively close to each other.

Climate in this part of Australia can be classified as subhumid mesothermal (Thornwaite 1931). The monthly rainfall pattern (over 80 years) from site A, shows that a similar amount of rain falls each month (Fig. 2a). Nevertheless, there are clearly defined seasons, with short daylengths and low temperatures in the winter (June-August; see Fig. 2b). Winter temperatures can be as low as -7°C , with some winter precipitation falling as snow each year. Summer temperatures may reach 37°C .

There are three properties on site A (Fig 3), all principally run for livestock production. Bubalalah and Tanjenong adjoin, while Grathawai is separated from these two by a distance of 10kms. This area was first claimed by white settlers in the 1850s, when the Bradbury family arrived on Grathawai and the North family on the other two properties. Agricultural development soon followed with tree clearing in the 1900s. However, not all areas were completely cleared and large stands of eucalypts still remain over some of the site, characterising it as low open-forest (Specht 1970). These tend to be confined to the less fertile soils. Other areas have been substantially cleared (Fig. 4) although a few scattered large trees remain.

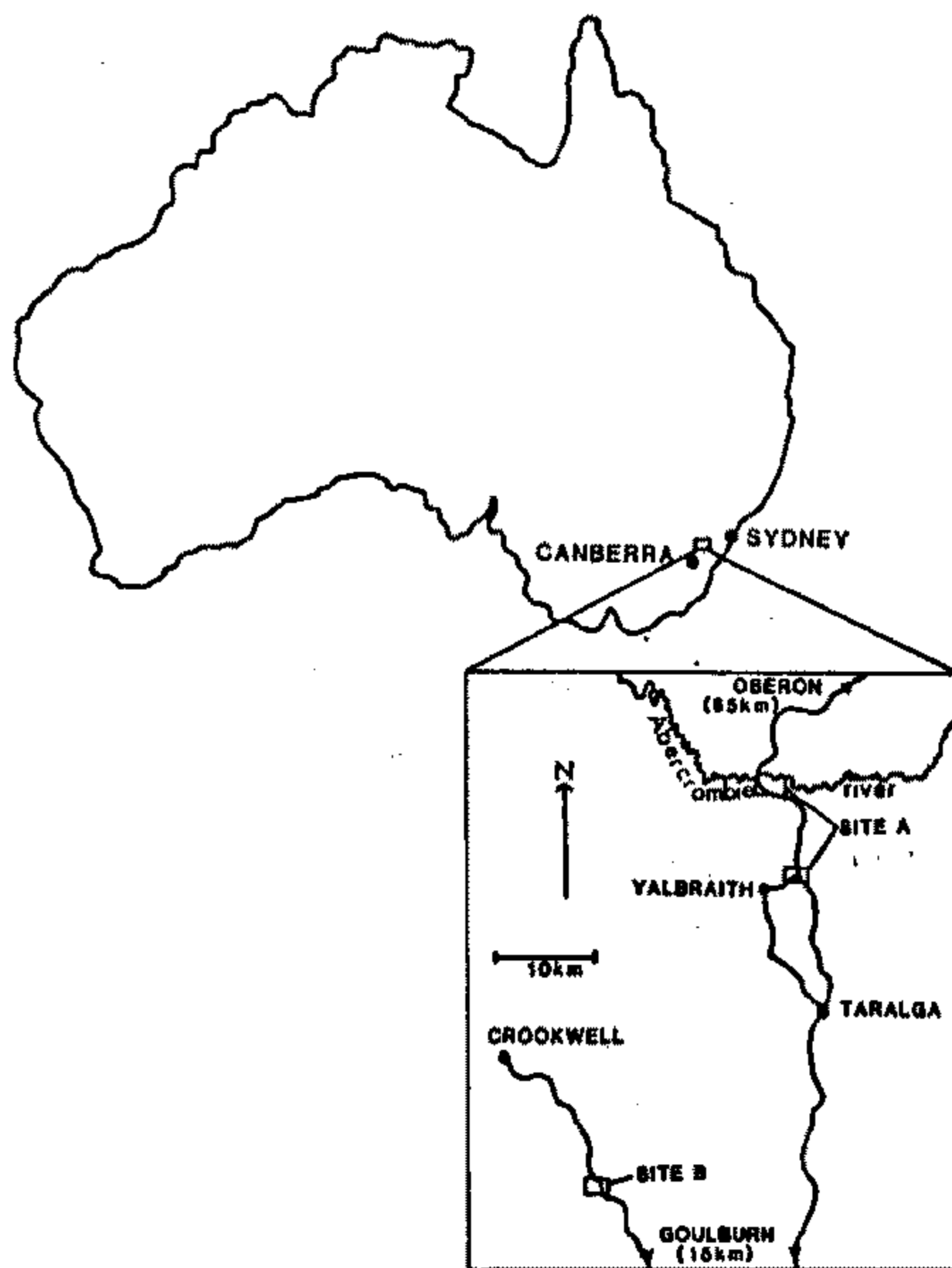


Figure 1. Location of the study sites.

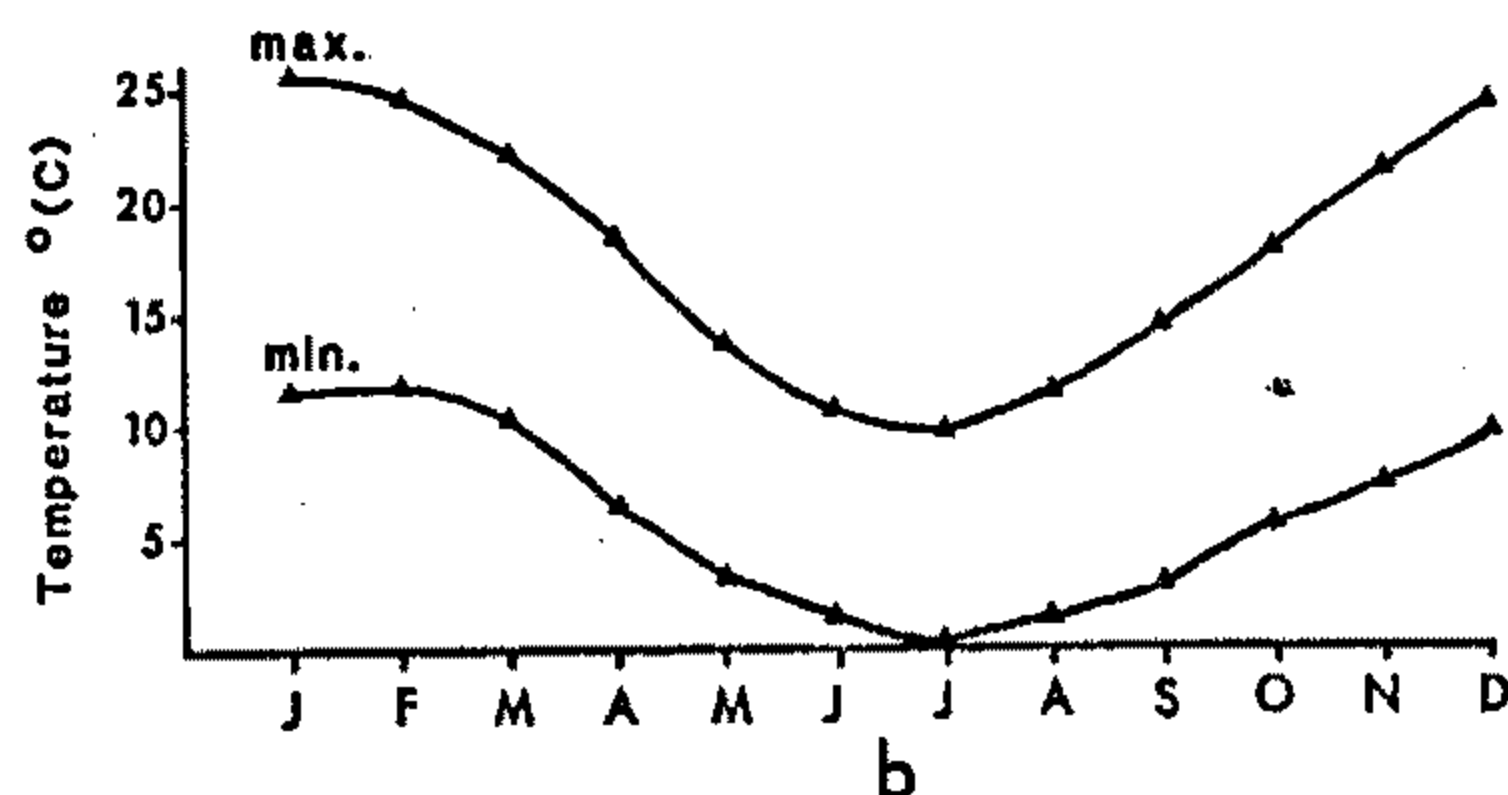
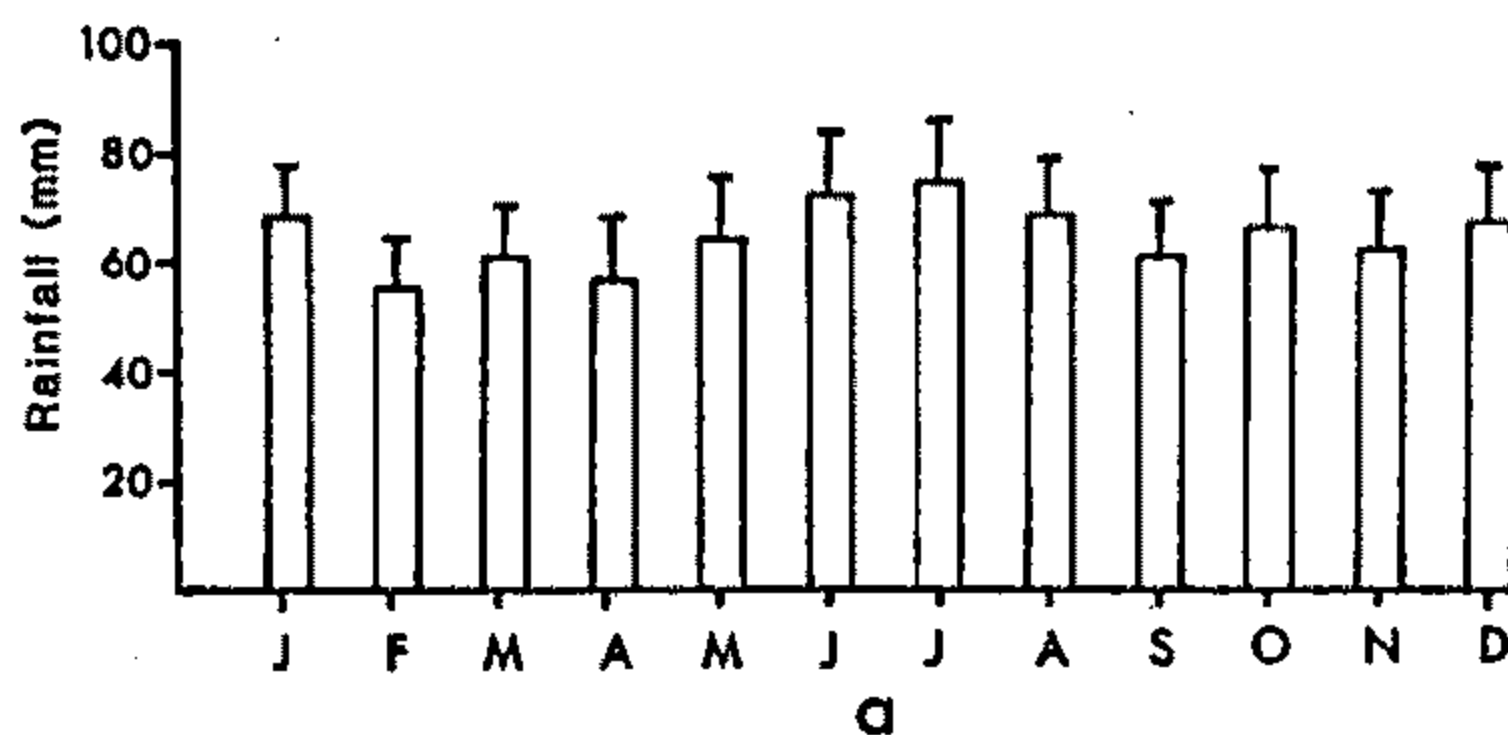


Figure 2. Mean monthly rainfall and temperature (Minimum and Maximum) for study site A. Rainfall data collected over an 80 year (1900-1980) period on site A, given with 95% confidence limits. Temperature data collected at the Taralga Post Office over 10 years (1970-1980).

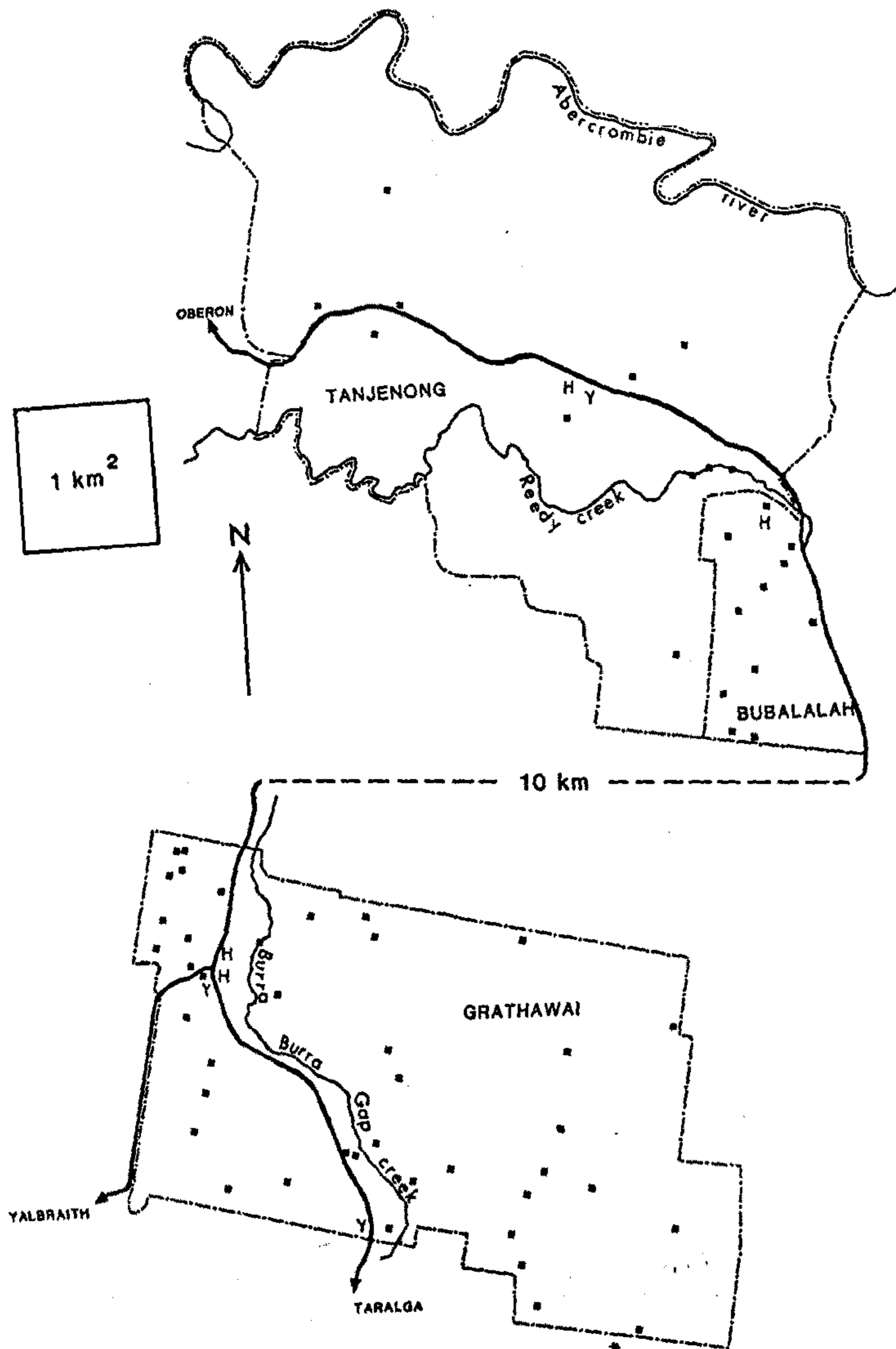


Figure 3. Detailed map of study site A. The three properties are separated by boundaries (marked as-----). Tanjenong and Bubalalah adjoin while Grathawai is 10 km south by road. Farm dams are marked as small solid squares. "H" signifies a farm house and "Y" cattle or sheep yards.



b

Figure 4. Examples of dams on the site. a- there are five farm dams in this photograph. These are marked by the earthen walls of the dams. b is an example of a typical dam.

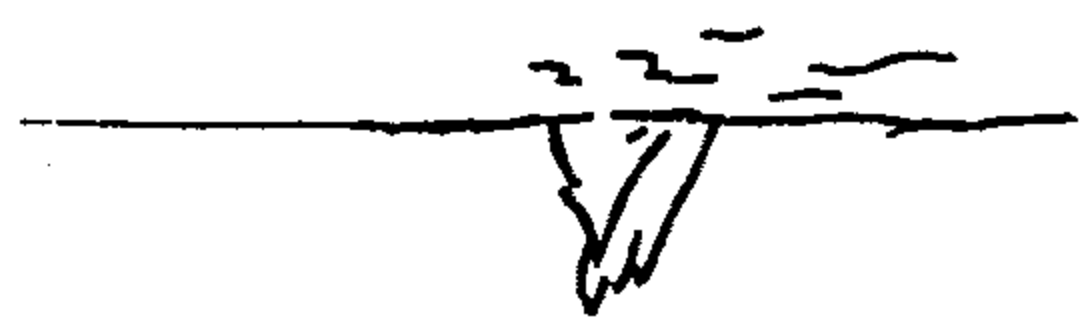
Clearing was followed by pasture improvement in the 1950s. This mainly involved planting the Mediterranean annual, subterranean clover Trifolium subterraneum. This species is particularly important in putting nitrogen into soils and also overcame nutrient deficiencies, throughout Australia (Donald 1970). Like many areas similarly settled, the natural vegetation has since been seriously affected by grazing and cultivation (Doing 1972). Much of the pasture on this site is made up of various exotic plant species, which have either been planted or have invaded the area.

Better water conservation was essential for the livestock, which came with pasture improvement. In many areas of Australia, the ubiquitous farm dam probably fulfilled this requirement. There are a number of different types of dam throughout Australia (Timms 1980), depending on which design is most efficient at retaining water, in particular areas. All dams on this site are gully dams (Fig. 4) where a simple dam wall is constructed across a gully blocking the subsequent passage of water. Their placement largely depends on the distribution of gullies and the priorities of the property. On this site, the first dams were established in the early 1930s (see chapter 5). These have increased in the intervening years until, in 1983, there were 66 dams on the site.

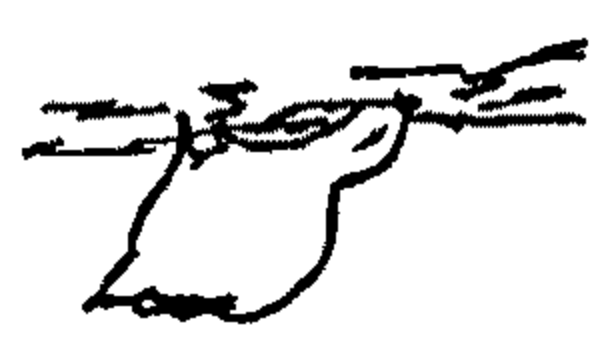
CHAPTER 3FOOD HABITSIntroduction

Dietary studies on the Maned Duck have shown that this species is principally vegetarian and feeds by grazing on young green herbage (Frith 1957b, 1959c; Lavery 1971). Frith (1982, p 16) describes the food of the Maned Duck as entirely vegetable but invertebrates have been found in the diet (Frith 1957b, 1959c; Lavery 1971). This presence could be the result of accidental ingestion if the duck is truly herbivorous, or may be an intentional component of the diet. The fact that Maned Ducks have also been reported to pick insects off the water surface (Briggs 1983), supports the latter hypothesis. Some Anatinae, considered primarily vegetarian have been shown to feed on invertebrates while breeding (Swanson & Nelson 1970; Krapu 1974; Landers et al. 1977; Drobney & Fredrickson 1979). Notably, females have a higher proportion of invertebrates in their diet just before and during laying (Drobney & Fredrickson 1979). This is believed to overcome the increased protein demand since plant foods are lower in protein (Krapu & Swanson 1975). It is possible that Maned Ducks exhibit a similar dietary shift.

Although Frith (1959c) sampled ducks throughout the year, no attempt has been previously made to directly investigate the diet of Maned Ducks during breeding. The present study was designed primarily to describe the types of foods eaten by adult Maned Ducks during breeding and ducklings on farm dams. More specifically, I wished to investigate the importance of invertebrates in the diet, particularly in relation to female reproductive status. Dietary habits were compared for 1981 and 1982. In 1982, poor rainfall resulted in an environment that was almost devoid of green herbage. It was quite obvious that Maned Ducks could not feed on their usual food items and I felt it was an ideal opportunity to investigate the diet of this species during drought conditions. I also wanted to find out if Maned Ducks feed selectively. According to Frith (1957b), based on a qualitative assessment of the dominant vegetation, there is no selectivity.



UPENDING



DABBING



SURFACE PICKING



GRAZING

Figure 5. Feeding behaviours and dabbling of Manded Ducks.

Methods

I employed a two-pronged approach to this study of feeding habits, using behavioural observations and the contents of oesophagi. Quantitative behavioural observations were collected in 1982 over thirty-nine days between July and September at site A using instantaneous sampling methods detailed in chapter 4.

Analysis was complicated by having, both different flock sizes and variable observation stints. To overcome the first problem and confine analysis to feeding behaviours, percentages were used for each period. I also used a mean percentage, for a particular flock, to overcome the latter difficulty. I used three categories to describe feeding behaviour (Fig. 5).

1) Grazing -birds systematically crop the vegetation. It was difficult to differentiate between ducks actually pecking or moving between vegetation clumps so grazing described all this.

2) Dabbling -the head is dipped below the surface and a feeding action takes place. An attempt was made to assess the importance of dabbling by collecting four one litre scoop samples from the edge of a dam soon after dabbling had occurred. These were taken from four positions randomly chosen around the perimeter of the dam. Samples were later sorted for potential food items.

3) Surface picking -active pursuit of invertebrates on the water surface. This was only recorded when the actual prey was seen.

Additional ad libitum observations of adults and ducklings were collected during the breeding seasons of 1981, 1982, and 1983. Data for ducklings are presented in the form of observation-days. These were variable observation periods, for a particular day, on which duckling feeding behaviour was recorded. Only two behavioural categories were used; insect feeding and grazing. Inevitable bias is likely to be encountered where such methods are used and results probably favour the rarer event (Altmann 1974); in this case, invertebrate feeding.

Oesophageal contents were collected at site B in 1981 and 1982. I shot forty Manded Ducks between July and October 1981 and, in 1982, prompted by the quite different environmental conditions, experienced by the whole district that year (see chapter 6), I shot another ten ducks. The following description refers to ducks that were shot during the breeding season of 1981. The breeding season in the south, for this species, is between September and October (Frith 1982). I assumed this marked brood appearance. So, based on an incubation period of 28 days (Frith 1982), I began sampling in July, approximately one month earlier than the time ducks would be expected to first start laying. I hoped that this would also allow for any regional or climatic uncertainty in the start of the breeding season.

At first, I tried to shoot ten ducks, five of each sex, in the first week of each month. This, I hoped would enable me to correlate dietary composition with sampling month, as an indirect measure of reproductive status. However, monthly individual breeding status was highly variable. Drobney and Fredrickson (1979) advocated the analysis of samples on a physiological basis to overcome the problems of long breeding seasons, so monthly samples were amalgamated and analysis was based upon an individual's reproductive status.

After locating a flock on a particular dam, I observed the ducks feeding for ten minutes before collection, following methods developed by Swanson and Bartonek (1970). Ducks were then stalked using the dam wall as a screen. After shooting, I weighed each duck and transferred the contents of the oesophagus and proventriculus immediately into 70% ethanol to limit post-mortem digestion (Swanson & Bartonek 1970). Although the proventriculus produces results, which are intermediate between the gizzard and oesophagus, in terms of differential digestion, (Swanson & Bartonek 1970), it often contained readily identifiable plant material and was therefore included in the analysis. Gizzard contents were not used because of bias associated with differential digestion (Swanson & Bartonek 1970; Briggs et al. 1985a). It would also have taken too long to identify plant fragments.

I assessed the reproductive status of females in 1981 using a

combination of methods developed by Krapu (1974), and Braithwaite and Frith (1969). Females with ovaries weighing less than 3 grams with no follicular development were judged not to have initiated laying, while those with ovaries weighing a minimum of 3 grams and showing some follicular development were considered to be pre-laying. Laying females had one or more ruptured follicles. The oviduct of these "laying" females was also greatly enlarged. No females in a post-laying stage were sampled. This is perhaps the consequence of sampling over a small area. Few ducks remained that would have reached this stage.

After gut contents were collected, I measured potential food abundance for each duck shot between July and September (n=30). Johnson (1980) advocates the use of the term "abundance" instead of availability to avoid subjective judgement of what is actually accessible to an animal. Ducks shot in October were not assessed because preliminary analysis had indicated that there was little selectivity occurring. Percentage cover was used as an estimate of abundance using a 1m² quadrat with 100 points (regular spacing). To reduce subjectivity, this was thrown over my shoulder so that it landed no further than 10m from where the duck was shot. I used intersection of quadrat strings to produce scores for each plant item present. In cases where determination of which plant was under the point was doubtful, the string was pushed down until it lay directly on the vegetation. Four quadrats were used to estimate abundance for each duck shot which gave an average percentage cover for the vegetation present. Two groups of plant species proved, at the time, to be difficult to classify and so were only identified to family. These were the grasses (Poaceae) and legumes (Leguminosae). Other plants were usually identified to species level, although thistle species (Asteraceae) were grouped. I built up a plant reference collection and identified plants using Lamp and Collet (1976), Leigh and Mulham (1965), Burbidge (1966) and Hunter (1970). Invertebrates were identified using C.S.I.R.O (1970). I did not assess abundance for some food items. Oats grain (seed from cultivated Oats Avena sativa) was never found while invertebrate taxa were usually flying, so abundance would have been difficult to measure.

Oesophageal contents were sorted in the laboratory and as with abundance measurements, Poaceae and Leguminosae were grouped because of

the difficulties associated with classifying small pieces in various immature stages of growth. I also picked out four samples of twenty legume pieces and separated each for drying. These corresponded to an estimate of the food consumed for twenty pecks (mean=0.047g). As ducks grazed by pecking it is likely that each piece corresponded to a peck (this may be an underestimate as small pieces, not included are likely to be the result of pecking plants close to the focal one). Food items were then dried for 48 hours at 50-55°C and samples weighed to the nearest 0.1mg.

Most investigations of waterfowl food habits use a volumetric treatment of food items (Frith 1957b, 1959c; Lavery 1971; Hocutt & Dimnick 1971; Goodrick 1979; Norman & Mumford 1982). I chose dry weight analysis for this predominantly vegetative material, because it overcomes the problem of variable water content of food items (Sugden 1973). It also probably has more direct nutritional interpretation (Reinecke & Owen 1980). Despite the intuitive attractiveness of using volumetric measurements, there is little evidence that feeding is directly determined by volume. Anatidae are capable of considerable gut expansion to accomodate different sized food items (Paulus 1982) and the fact that they will gorge on grain (Swanson et al. 1974), is evidence that the relationship between volume and feeding may be tenuous. The obvious fact that gut analysis only uses contents from one feeding period further distances the relationship. Such criticisms can equally be directed to dry weight analysis. There are inevitable problems associated with any method. Braithwaite (1966) recognised that a another problem with food analysis is the bias produced by harder foods such as seeds. Unfortunately such a problem is likely to be magnified using dry weight analysis, as harder foods will be more resistant to drying. In 1981, only two ducks contained seed (oats grain), so this bias may not be important to analysis that year. However, domination of the diet by oats grain in 1982, would bias samples and this should be considered when comparisons are made against other food items. Unavoidable nutrient leaching by preservatives may also have occurred, although this was likely to be a constant factor over all samples.

I have presented food habits data using methods developed by

Swanson et al. (1974) which reduce certain biases and facilitate comparison with other studies. Three measurements are used. a) Aggregate dry weight equals the total dry weight of a particular food item, in the sample of all birds, divided by the total dry weight of all food items in the sample. This measure may give disproportionate weight to a few ducks which contain much more food than others (Swanson et al. 1974) and the volumetric equivalent has usually been used in dietary studies of Australian waterfowl. b) The aggregate percentage equals the proportion of a particular food item in a particular bird, averaged over all birds. This is the best unbiased estimate (Swanson et al. 1974; Landers et al 1977). c) Frequency of occurrence, the last measure, is the number of birds containing a particular food item divided by the number of birds in the sample. This method typically overestimates the importance of rare foods and should be used in association with other methods. It is important because it shows the whole range of items. All are presented for completeness.

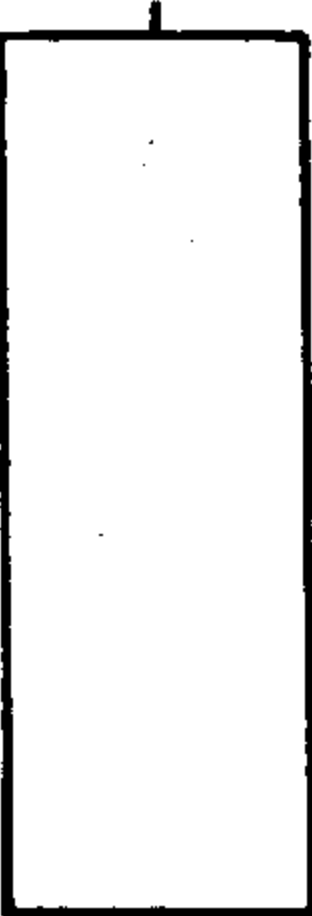
Paired Student t-tests were used to test hypotheses that certain food items are found in greater proportions in the diet than in the environment. Percentage dry weight for each food item in an oesophagus was calculated. This value was then compared to the average abundance measurement for this item, derived from the four quadrats (also percentages) taken at the site where the duck was shot. Where an item was neither recorded in the oesophagus nor in abundance measurements, then that duck was not included in that particular analysis. Data were transformed using the angular transformation ($\arcsin$) to normalise percentage data (Zar 1974).

One factor unbalanced analysis of variance was used to compare the proportion of Poaceae eaten by ducks from four reproductive categories. These were females a) not reproductively active (n=3), b) prelaying (n=5), c) laying (n=3), and d) all males (n=15). Leguminosae were not analysed because of dependence on Poaceae, which is inevitable where two items dominate the diet.

OBSERVATION DAYS

200-

Grazing Invertebrate feeding



% PERCENTAGE

20 -

40 -

60 -

80 -

100 -

Grazing Surface picking Dabbling

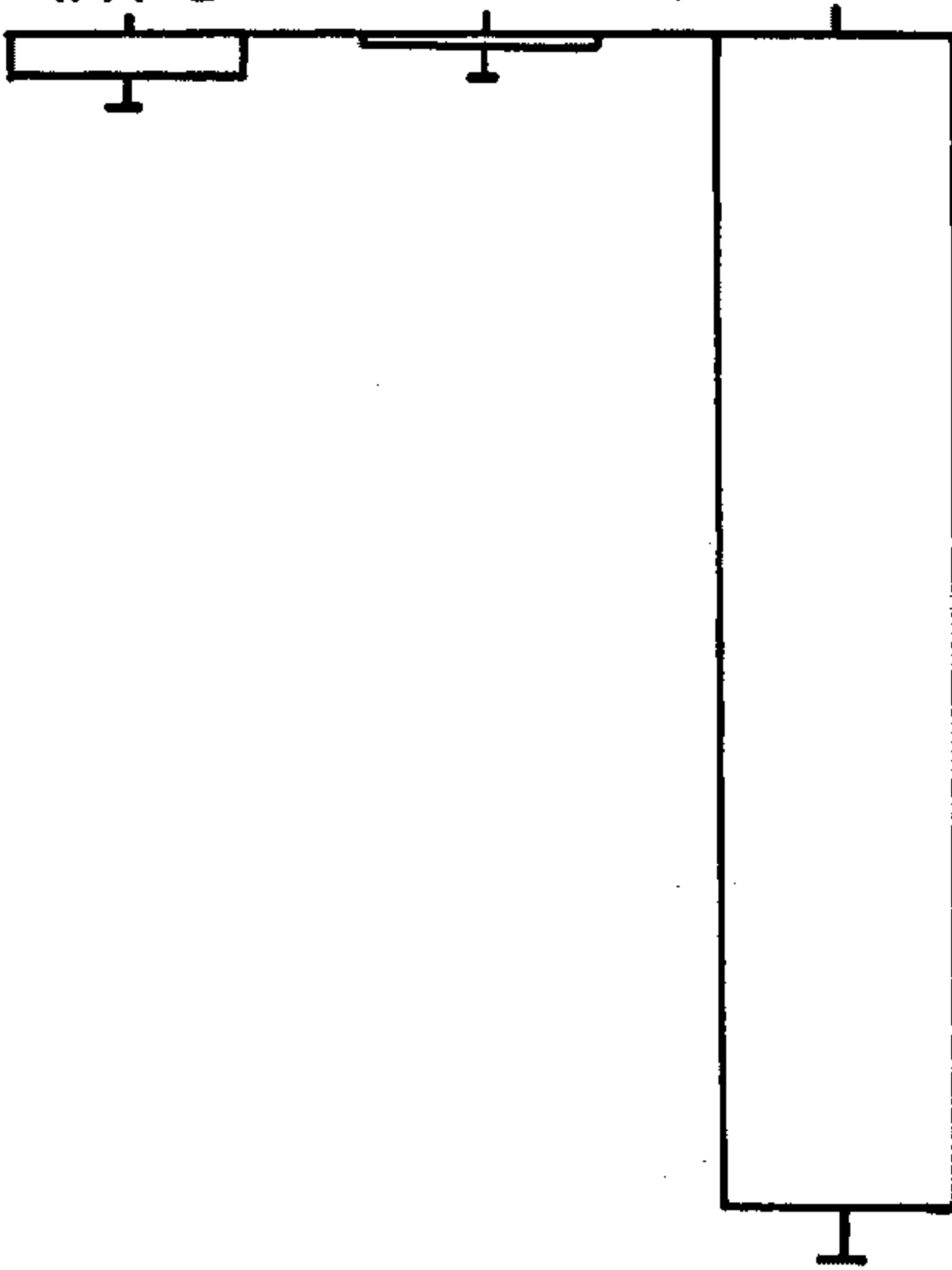


Figure 6. Percentage frequency of Handed Duck feeding behaviours, from observations in 1982 over 39 days (n=17,710 feeding behaviours). Means given with 95% confidence limits.

Figure 7. Results of ad libitum observations on duckling feeding behaviour (n=244 observation days).

Results

Maned Ducks are predominantly grazers (98% of the feeding behaviour) (Fig. 6). Other behaviours were rare, although at least a few ducks were seen dabbling sometime during an observation period.

Dabbling Maned Ducks, typically, remain in one position at the edge of the dam and take some of the substrate in their bills (Fig. 5). This is then followed by rapid bill movements just under the water, which perhaps function to sift the mud away from the harder grit and sand. The four scoop samples taken from the edge of the dam, were predominantly sand and mud with only two dragonfly larvae (Odonata). No attempt was made to measure the proportions of sand and mud.

Surface picking (Fig. 5) was the least frequent feeding behaviour consistently observed, and occurred usually when flying ants (Hymenoptera) and midges (Diptera) were emerging. Invariably some fell in and struggled on the surface of the water which usually induced the whole flock to take to the dam and feed on them. Ducks would swim from one to another invertebrate and, with the bill just submerged, perform two or three rapid opening and shutting movements of the bill before swallowing. Quantitative behavioural observations ceased in early November 1982 although ad libitum observations continued. Towards the end of this time there was very little green herbage anywhere and it was apparent that ducks were actively searching for terrestrial insects using a fast stabbing action as they moved in the area surrounding the dam. Some of this feeding behaviour may have been categorised as grazing in my earlier observations. I did not observe this behaviour again during the period of study (1981-1984) indicating that this may be a temporary response not merely seasonal.

Upending (Fig. 5) was observed only once. A duck, swimming in the shallows submerged the anterior half of its body as it fed on Juncus sp. (spiny rush). This was lying in the shallows after it had been broken down by cattle.

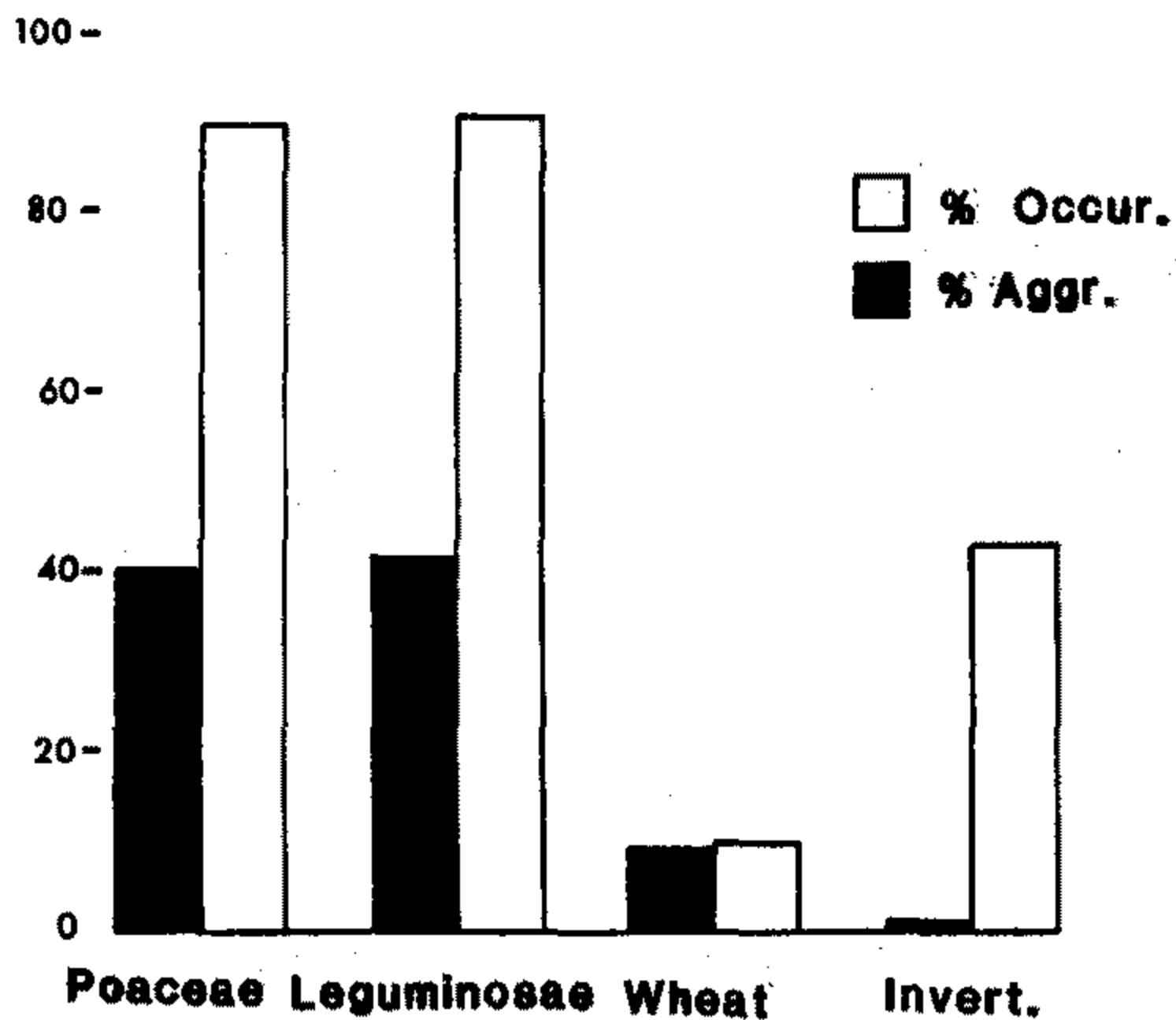


Figure 8. Main food items found in the oesophagi of Maned Ducks collected in 1981 (n=31) measured as i) Aggregate percent (proportion of the particular food item in a each duck averaged over all ducks) and ii) Percent occurrence (number of ducks containing a particular food item divided by the number ducks in the sample).

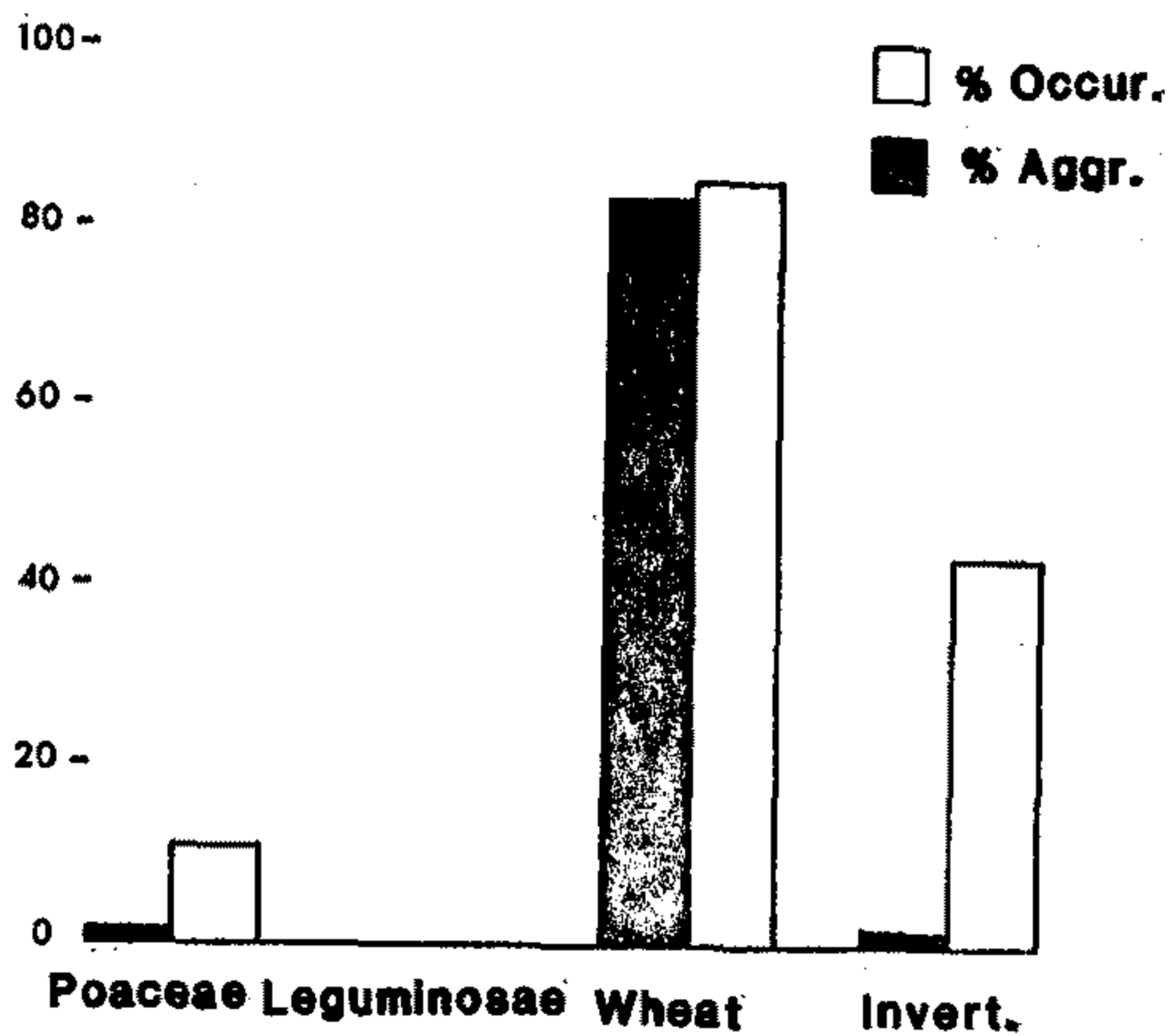


Figure 9. Main food items found in oesophagi of Maned Ducks collected in 1982 (n=10) measured as i) Aggregate percent and ii) Percent occurrence.

Ducklings also usually grazed and were seen catching invertebrates on only four occasions (Fig. 7). These were usually picked off aquatic vegetation or from the surface of the dam. This behaviour was not age related. One brood was seen grazing as soon as it had left the nest hole.

Nine birds with fewer than five items were excluded from oesophageal diet analysis. Figure 8 shows the importance of green herbage to Maned Duck in 1981. Food was dominated by legumes and grass species (Table I). Grass species found in the study site at this time were; Phalaris tuberosa, Hordeum sp. (barley grass), Lolium perreneum (rye), Dactylis glomerata (cocksfoot), Poa annua (snow), Arrhenatherum elatius (oat) and Bromus sp. (brome) while legumes were dominated by Trifolium subterraneum (subterraneum clover) with some Trifolium repens (white clover) and various Medicago sp. (medics). Poaceae and Leguminosae both occurred in over ninety percent of the ducks, and together, accounted for over 80% of the food eaten, as measured by aggregate % (Table I). A number of other plant species occurred in varying quantities in the oesophagi with some more common species such as Montia fontana and Cerastium fontanum found in only small amounts (Table I). At no stage was any senescent vegetative material found in oesophagi. Cultivated oats Avena sativa in the form of grain, produced aggregate % and aggregate dry weight measurements that were quite different. Two ducks had large quantities of grain in their oesophagi and this caused disparity between the two types of measurements which were otherwise comparable. This demonstrates the importance of using aggregate percentage measurements. Invertebrates were only found in very small quantities in 1981 although they did occur in over 43% of all ducks (Fig. 8; Table I). They accounted for less than 0.05 % of the total food as measured by aggregate %. All were terrestrial and were predominantly dipterans (Family Sciariidae) and some collembolans, although two large beetles (Coleoptera) gave a greater aggregate % measurement. However % occurrence measurements show that many more dipterans were found in the oesophagi.

In 1982 only ten ducks were shot but despite the small sample size there were important dietary differences between the two years. Food was totally dominated by oats in 1982, with other herbage, specifically Poaceae and Leguminosae appearing rarely and only found as senescent

Table I. Oesophageal contents of Handed Duck shot in the breeding season of 1981 (n=31) and 1982 (n=10). Items measured as aggregate percentage, aggregate dry weight and percentage occurrence. Order follows Burbridge (1966)

Food Item.	Aggr. %	Aggr. Dry weight	% Occur.
PLANT	1981	1982	1981 1982
Poaceae	39.8	0.2	29.5 0.1
Avena sativa (grain)	8.7	85.5	39.5 99.4
Leguminosae	40.1	0	26.6 0
Rumex acetosella	2.9	4.9	0.3 0.1
Montia fontana	2.1	0	1.0 0
Cerastium fontanum	0.6	0	0.4 0
Capsella bursa-pastoris	0.2	0	0.1 0
Cressula albertina	0.3	0	0.2 0
Plantago lanceolata	0.1	0	0.1 0
Arctotheca calandula	2.9	0	1.2 0
Taraxacum officinale	0.4	0	0.3 0
Hedysarum sp.	0.6	6.6	0.1 0.1
Cotula australis	0.3	0	0.2 0
Isotria medeolae	0.8	0	0.3 0
Rodolphe sp.	0.1	0	0.1 0
Salix sp.	0	0.9	0 0.2
Total	99.9	98.1	99.9 99.6
INVERTEBRATES			
O. Diptera	0.009	0.003	0.013 0
O. Collembola	0.004	0	0.002 0
O. Coleoptera	0.015	1.950	0.021 0.050
O. Heteroptera	0.001	0	0.001 0
O. Psocoptera	0.001	0	0.001 0
Total	0.03	1.953	0.038 0.050

material (Table I; Fig. 9). Some hardier plants, Rumex sp. and Plantago sp., were also found. Suprisingly, there was even one example of a duck which had eaten the leaf from a Salix sp. (Willow tree). As well, the diversity of plant food also decreased, in comparison to 1981. Invertebrates were mainly coleopterans although some dipteran aquatic larvae and one aquatic beetle (F. Hydrophilidae) were consumed.

Food items in the oesophagi were compared to abundance measurements in 1981 and there was little evidence that particular food items were selected (Fig. 10). Three food items were found in significantly greater proportion in the environment (Table II). Neither thistles nor Malva sp. were ever found in the oesophagi of ducks, although both occurred in abundance measurements (Fig. 10). Cerastium fontanum occurred in significantly greater proportion in the environment. Other items showed no significant difference between abundance and occurrence in the oesophagus (Fig. 10). A negative mean in Table II indicates a greater abundance in the habitat for a particular species. Some plant species, Crassula sieberina, Plantago lanceolata and Cotula australis had positive means and it is possible that a larger sample may detect selection for these.

Three two way nested analyses of variance (months by ducks) were performed on abundance measurements (percentage cover) using quadrats as replicates. Poaceae, Leguminosae and the remainder of plant species were all considered seperately. Variability was considerable, with the two factors accounting for only 0.39, 0.42 and 0.59 (factor sum of squares/total sum of squares) for the three respective analyses. The factor of ducks was significant in all analyses ($p < .05$). This simply shows that there was a difference between the vegetation on dams where ducks were shot.

Unfortunately, I did not quantitatively assess the abundance of either invertebrates or oat grain. However, there were many slow flying dipterans (Family Sciaridae) amongst the vegetation in 1981. Oats grain was used to a limited extent as supplemental food for sheep in 1981, but in the following year, drought relief measures resulted in extensive sheep feeding with oat grain. It was more abundant in 1982.

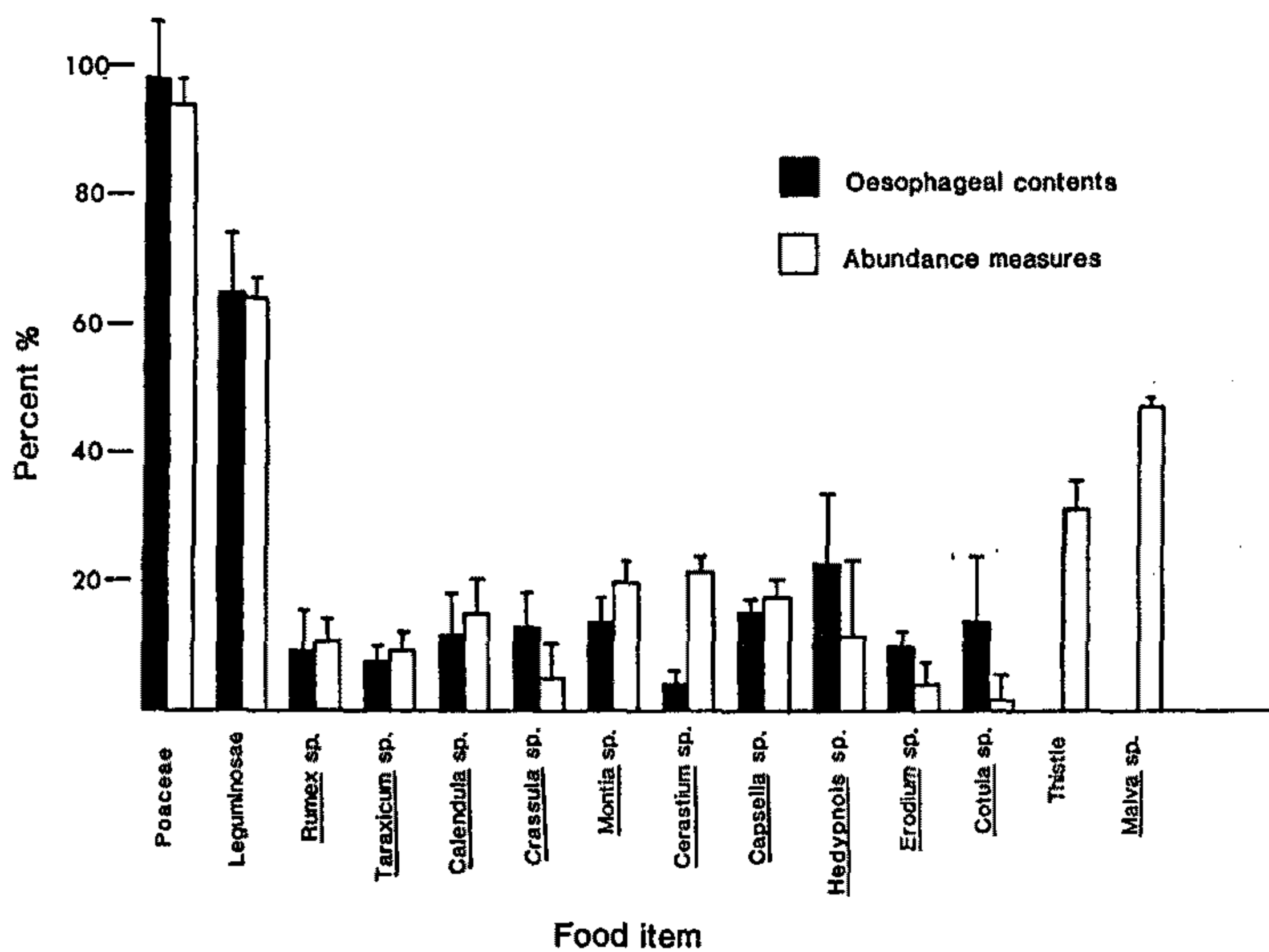


Figure 10. Mean percentage dry weight for each food item in oesophagi of Maned Ducks shot between July and September 1981 (n=26). This is compared to mean abundance where the duck was shot. Data transformed by arcsin and given with 95% confidence limits, after arcsin transformation.

Table II. Diets of Maned Ducks compared to food abundance. Results of paired Student's t-test for plant food items, mean= % oesophagus - % abundance. Data transformed using angular transformation (***-significant $p < 0.001$)

Food Item	N	Mean	T value	significance
Poaceae	26	1.83	0.38	ns
Leguminosae	26	0.64	0.15	ns
<u>Montia fontana</u>	21	-3.81	1.62	ns
<u>Cerastium fontanum</u>	20	-9.08	4.17	***
<u>Arctotheca calendula</u>	18	-2.45	0.65	ns
<u>Capsella bursa-pastoris</u>	15	-3.42	0.94	ns
<u>Taraxicum officinale</u>	12	-0.66	0.27	ns
Thistle	10	-15.78	6.65	***
<u>Rumex acetosella</u>	6	-1.17	0.23	ns
<u>Erodium sp.</u>	5	2.70	0.92	ns
<u>Plantago lanceolata</u>	4	4.21	0.40	ns
<u>Crassula sieberinia</u>	4	4.17	0.79	ns
<u>Malva sp.</u>	3	-18.90	39.68	***
<u>Cotula australis</u>	3	4.98	0.80	ns

There was no evidence that dietary differences were related to reproductive status ($p > 0.05$). Ducks in any particular reproductive category fed equally on grass. Males ate the same food as reproductively active females. Laying females weighed an average of 940 g ($n=6$, others were included which did not have sufficient food contents for analysis). I found so few invertebrates in oesophagi that analysis against reproductive condition was precluded.

Discussion

These results are similar to those of other workers. Both behavioural observations and oesophageal contents show that Maned Duck predominantly graze during the breeding season. However, other feeding actions were observed. Weller (1964a) lists upending and dabbling as feeding actions in this species, but gives no indication of their relative importance. On only one occasion was upending observed during many hours of observation and its rarity probably precludes it from being considered an important feeding behaviour on farm dams. A higher incidence may conceivably be found in a different habitat.

The categorisation of dabbling as a true feeding behaviour may be misleading because so few potential food items were found in scoop samples which were predominantly grit and sand. It is also unlikely that the invertebrates found would have been available to the duck because duck dabbling and scoop sampling differ considerably in the way that the substrate is sampled. Scoop sampling is more likely to catch mobile invertebrates (Order Odonata), as it is probably a faster action. (The possibility exists for small protozoa to be ingested by this method but these are unlikely to be important.) Since it is known that Anatinae consume large quantities of sand and grit which aid digestion and provide minerals (Weller 1964a), I think that dabbling behaviour in this species, probably serves such a function. Further support for this theory, is provided by the fact that sand was always found in the gizzards of ducks which were shot.

The food composition is similar to that found by other studies (Frith 1957b, 1959c; Lavery 1971). Unlike some Australian studies of waterfowl food habits, where methodology may be criticised, those on the Maned Duck can be used for a general comparison because these studies have usually used contents from the upper digestive tract. Frith (1959c) states that contents of the proventriculus and gizzard are used, but it is unclear if this included oesophageal contents. Obviously different methods of analysis preclude direct comparisons. However, as in other studies, plant matter dominated the diet during the breeding season of

1981 (Fig. 8). All plants in this study were terrestrial and this compares favourably with the small proportion of aquatic plants found by Lavery (1971). However, Frith (1959c) found 41% of the food, although vegetable, was aquatic. Poaceae were particularly important in all studies although legumes did not form as large a proportion of the diet in the other studies.

Frith (1982) proposed that Maned Ducks feed principally on green herbage. I similarly found no senescent vegetative material in the oesophagi of ducks collected in 1981 despite the fact that it is present in pastures throughout the year (Langlands & Holmes 1978). In 1982, however, grasses found in oesophagi were all senescent. This is probably attributable to availability. There was no green herbage because of the harsh climatic conditions experienced this year. In fact oat grain dominated the diet (Fig. 9). Other waterfowl species also feed on waste grain (Goodrick 1979; Fredrick & Klaas 1982). In 1982, oat grain was probably the most important food item and could possibly have been essential to the maintenance of Maned Ducks when environmental conditions deteriorated.

Invertebrates have rarely been found in all studies. Frith (1959c) found invertebrates in only two of the months, that were sampled and used to form an annual distribution of the food consumed (overall mean=0.7%). Lavery (1971) found even fewer (0.1-0.6%). Invertebrates made up less than 1% of the diet in the present study during 1981 and these were Sciaridae and collembolans, both small detritus feeders which were found in large numbers amongst the vegetation. Their appearance in the diet is more likely to be the result of accidental ingestion. In 1982, the presence of a few terrestrial beetles and dipterans in the diet (Table I), as well as observations of ducks searching for terrestrial invertebrates in the latter months of 1982, preclude such an explanation. There could be a greater dependence on animal food when there is little green herbage. Further, although Maned Ducks rarely performed the feeding behaviour surface picking during this study, this does show that invertebrates are intentionally eaten. When surface picking occurred it would often take precedence over grazing, as in the case of emerging flying ants. However, at no time did I see Maned Ducks catching faster moving invertebrates

(Order Orthoptera) which were abundant in 1982. So, perhaps Maned Ducks are limited to those invertebrates which are either slow moving or incapacitated.

No food items appeared to be selected (Fig. 10). However, after data collection, there were a number of methodological problems which could have biased results.

i) Abundance was only assessed within a radius of 10m from where each duck was shot. Oesophageal contents would undoubtedly contain food from other parts of the dam because Maned Ducks move quickly when grazing.

ii) The time of day that ducks were shot may be important. Ducks shot early in the day had few items in the oesophagus so that percentage conversion may result in a bias towards these items. Ideally comparison should be between ducks with relatively "full" oesophagi.

iii) There was no guarantee that ducks had been on a particular dam before I arrived, so oesophagi could conceivably contain food from elsewhere.

iv) Abundance measurements were heterogeneous for any one site.

v) There is a dependence problem in the analysis caused by using data related by percentages.

The fine tuning required to demonstrate if selection existed, was also hampered by problems related to assessing food abundance. This may be a general problem, as too often, food availability is presented without confidence limits (Hobbs & Bowden 1982). Perhaps a more experimental approach with observations of the actual search paths of each duck is required. I have seen Maned Ducks moving to patches of clover to feed, ignoring grasses, and this, combined with the reputation that Maned Ducks have as pests in agriculture (Kinghorne 1932; Frith 1957b; Briggs 1977), probably indicates that selection for certain food items, may sometimes occur. It may be that selection occurs at a more gross scale, so that the mere presence of Maned Ducks on a particular dam is an indication that selection has already taken place. A test for selection at the individual pasture site would then be superfluous. However at this level, these results support Frith's (1957b) hypothesis that Maned Ducks only feed according to the abundance of various food items. Further support for this hypothesis comes from simple theoretical models, which assume equal

value for food items. They predict that grazing predators should evolve a generalist feeding strategy and a broad diet since selection only increases search time (Nudds 1980) except when food is abundant.

I also found no differences in diet related to reproductive status. The fact that dietary differences occur between sexes of many North American waterfowl during breeding may not necessarily be the result of selection. It may simply reflect differing food availability to the sexes. In some species, males feed less than reproductively active females (Siegfried 1974b; Dwyer 1975; Reinecke & Owen 1980), so there may be behavioural constraints on the availability of some food items to a particular sex. This could possibly result in fewer invertebrates in the food of males. Certainly, the additional protein content of invertebrates may be necessary to some waterfowl, however the implication that selection processes are involved may be unwarranted. Seasonal abundance of invertebrates may account for the increased numbers found in the oesophagi of females. Unfortunately, little attempt is usually made to measure the abundance of food items in the field.

In this study, although I shot few females in laying condition, there was no indication that females selected invertebrates to offset the increased protein demand at this time. Although sample sizes were small, behavioural observations, which monitored many females known to be reproductively active, showed similar results. Reinecke and Owen (1980) also found that there was no difference in the food eaten by male and female black duck Anas rubripes. It is possible that dietary differences, in these cases, could be reflected in the quantity of food eaten rather than type differences.

In Maned Ducks, dietary protein for breeding females which is essential to egg laying, must come from plant foods in this species. Insufficient data are available to answer the question of whether or not there is enough protein in the plant food at the time of laying. However, some arguments can be advanced in its favour. Agricultural practices over the last century have resulted in more nutritious pastures in Australia with native pasture species, which are lower in the production of domestic grazing animals (Arnold 1964), being replaced by higher yielding

introduced pastures (Semple 1970; Lazenby & Swain 1973). More importantly, nitrogen fixing legumes have increased the productive capacity of pastures and provided much greater protein (Donald 1941; Lazenby & Swain 1973). Shapter (1935) calculated the average crude protein content of some pasture legumes (Medicago denticulata, Trifolium subterraneum, T. fragiferum and T. repens) to be 23.68% of the total dry weight at maturity. With the possible exception of T. fragiferum, all species occur on site B. Beck (1952) found similar protein contents for legumes. Grasses have even less protein (6% of dry weight, Shapter 1935). Drobney (1980) calculated that the American Wood Duck Aix sponsa, a closely related species, relying on exogenous sources for protein, had to meet a maximum daily requirement of 5.1g when laying, with other non protein requirements being met by fat reserves. On this basis, a rough estimate of the protein load on laying Maned Duck may be calculated. The average weight of A. sponsa during laying, January-March, was approximately 608g (Landers et al. 1977). Maned Duck laying females weighed 940g. Therefore, a relative maximum protein requirement for Maned Duck, adjusted for weight, could be 7.9g. However, birds do not have a 100% conversion efficiency for dietary protein. Scott et al (1976) found laying chickens could only utilise 55% of their dietary protein. An ingestion rate is required before calculation of the amount of feeding time. Although I have no data for peck rates of laying females, I found that females with young had peck rates of 1.6 pecks/sec (see chapter 8). Combining this with the estimate that 20 pecks of legume weighed 0.047g, meant that a laying Maned Duck would need to feed uninterrupted for at least 3.6 hours to meet the maximum protein demand. Of course grazing involves much more than just pecking. Ducks must walk between patches of vegetation, search for food, as well as perform various vigilant behaviours. So, time is likely to be increased to perhaps as much as five hours actual feeding time. If a laying female is reliant on a grass diet then she needs to feed for fourteen hours. As most pastures are a mixture of the two plant groups, one would expect a daily feeding time somewhere between these two estimates. Since this is the maximum daily requirement, the amount of time needed to feed may be reduced at other times during reproduction.

I think this exercise serves to demonstrate two things if allowances

are made for unknown variables. It appears to be possible, on energetic grounds, for Maned Duck during laying to meet protein demands by grazing. However, this may only be accomplished through intensive grazing on the part of the female. At such times it may be advantageous for the female to adopt some sort of selectionist policy for more nutritious food items. As well as this the quality of the diet may be important. Krapu & Swanson (1975) found Pintails Anas crecca fed on wheat, failed to breed. In 1982, with the preponderance of oats grain in the diet, the nutritional quality of the diet may not have been sufficient to support breeding.

Duckling diet is similar to that of adults, being predominantly vegetarian. Frith (1982) maintained that early duckling diet is principally concentrated on invertebrates, later altering to a vegetarian diet as the duckling gets older, as in A. sponsa (Hocutt & Dimnick 1971). This study provides contrary evidence. I found no age-related differences. Newly hatched ducklings were usually observed grazing on vegetation and seldom seen feeding on invertebrates (Fig. 7). Moreover, such ad libitum sampling probably further biases the results in favour of the invertebrate feeding. Perhaps Frith's (1982) observations of duckling diet were taken in a habitat where many invertebrates were present. Alternatively, observations of ducklings soon after hatching, are likely to may seasonally coincide with a greater abundance of invertebrates. This may contrast observations on the diet of older ducklings which could be made when invertebrates are not so common. Such a criticism may be directed to other reported dietary shifts (Hocutt & Dimnick 1971).

Some conclusions about the food habits of Maned Ducks can be made from this study. This duck's feeding behaviour is like many generalist herbivores, in that the results of analysis of food habits produces long lists of food items which reflect habitat and seasonal differences. Plant foods are sufficiently nutritious to meet breeding demands although this may not be the case when environmental conditions deteriorate. Invertebrates are a component of the diet but are not utilised in sufficient quantity to be deemed essential to breeding. In contrast to the diet of the closely related species, Aix sponsa, which feeds on aquatic vegetation and invertebrates (Coulter 1957; Landers et al. 1977, Drobney & Fredrickson 1979), the Maned Duck fed almost exclusively on

terrestrial plants in this study. Diet and feeding activity appears to be more similar to that of various species of geese (Marriot 1970; Owen 1971; Harwood 1977; Ydenberg & Prins 1981). Differences between the results of this study and other published observations on Maned Ducks (Frith 1957b, 1959c; Lavery 1971) probably simply reflect habitat differences. Aquatic plants are rarely found around the dams in my study site which possibly results in an accentuated grazing habit in this sort of environment.

All feeding behaviours probably involve the same actions with only the prey item being different. Maned Ducks are probably constrained by morphological adaptations to a grazing existence. They have hind limbs particularly suited to walking and a bill that is "goose-like", being short and thick with serrations suitable for cropping vegetation. Common feeding behaviours of other waterfowl, diving, upending and dabbling are not important in this species' feeding repertoire.

CHAPTER 4ACTIVITY PATTERNSIntroduction

The cyclical nature of many biological processes is well known (Colquhoun 1971) and is often manifested in the daily activity patterns of animals. Most perform activities at certain times of the day (Nielsen 1984), with many species resting in the middle of the day and feeding in the morning and evening (Altmann 1959; Verbeck 1964; Morton 1967; Clough & Hassam 1970). Some studies on waterfowl have shown that activity patterns can be a useful way of identifying what ecological factors are important to a species (Siegfried 1974b; Tamisier 1974, 1976; Bruggers & Jackson 1977; Skead 1977; Norman et al. 1979; Quinlan & Baldassarre 1984). Other studies used the activity patterns of different waterfowl species to understand the reproductive demands on males and females (Dwyer 1975; Miller 1976; Gilmer et al. 1977; Asplund 1981). However, although I collected data while ducks were reproductively active, I made no attempt to correlate activities to breeding condition during this particular part of the project (dealt with in chapter 8).

Norman et al. (1979), in one of the few studies on the activity budgets of Australian waterfowl, examined the relationship between diurnal activities and types of habitat for three species of Anatini. Following such an approach, my primary aim was to use the activities of Maned Ducks to monitor their use of habitat. This was intriguing since the farm dam, which is the principal habitat for this species in this area, is a comparatively simple ecosystem with little biological diversity (Timms 1980).

I also attempted to investigate the variability of diurnal activity patterns between and among dams. In many accounts of activity patterns little attention is paid to variability in the timing of activities. Instead, the data are usually presented in the form of overall percentages. Moreover, few studies have collected data on activity patterns from more than one habitat, so reported patterns may be an artifact of local habitat conditions.

Methods

In 1982, I observed the activity patterns of Maned Ducks for 170 hours between June and November on site A. Before starting, I chose four dams for my observations; B.1, T.1, G.31, and G.33 (the letter identifies the property) based on two criteria. I had to be able to approach them relatively easily without disturbing the ducks and the dams had to have with high Maned Duck usage in 1981. After selection of the study dams, I built a hide from old packing cases. The design was simple (Fig. 11) with enough room in each for a chair and a small amount of equipment. A small hinged door at the back provided access while three slits (8x20cms) cut in front and sides, fitted with a small hinged door, permitted full view of the dam. To avoid detection, only one slit was ever open. A corrugated iron roof nailed to the top of each hide protected them from the rain while four star pickets secured the hide to the dam wall, preventing it from being blown over in high winds. Finally, concealment wings (sides of packing cases) nailed to each hide reduced the chance of detection.

I placed star pickets along eight radiating lines equally spaced around the dam, at 5m, 10m, 20m, 40m, 60m and 80m from the dam. These enabled me to judge how far from the dam Maned Ducks performed their various activities.

Sampling methods

I tried to standardise sampling effort between sites, but irregular visits by ducks to these dams precluded a systematic sampling regime. Two further factors contributed to the variable pattern of observations (Fig. 12). Some sessions were prematurely ended when I was detected, while in others, ducks flew from the dam for little apparent reason.

I have defined an observation period as the time spent watching a flock on a particular dam on a particular day (Fig. 12). These usually started just before daybreak. After arriving at an observation dam, I established whether or not Maned ducks were present, and their position in

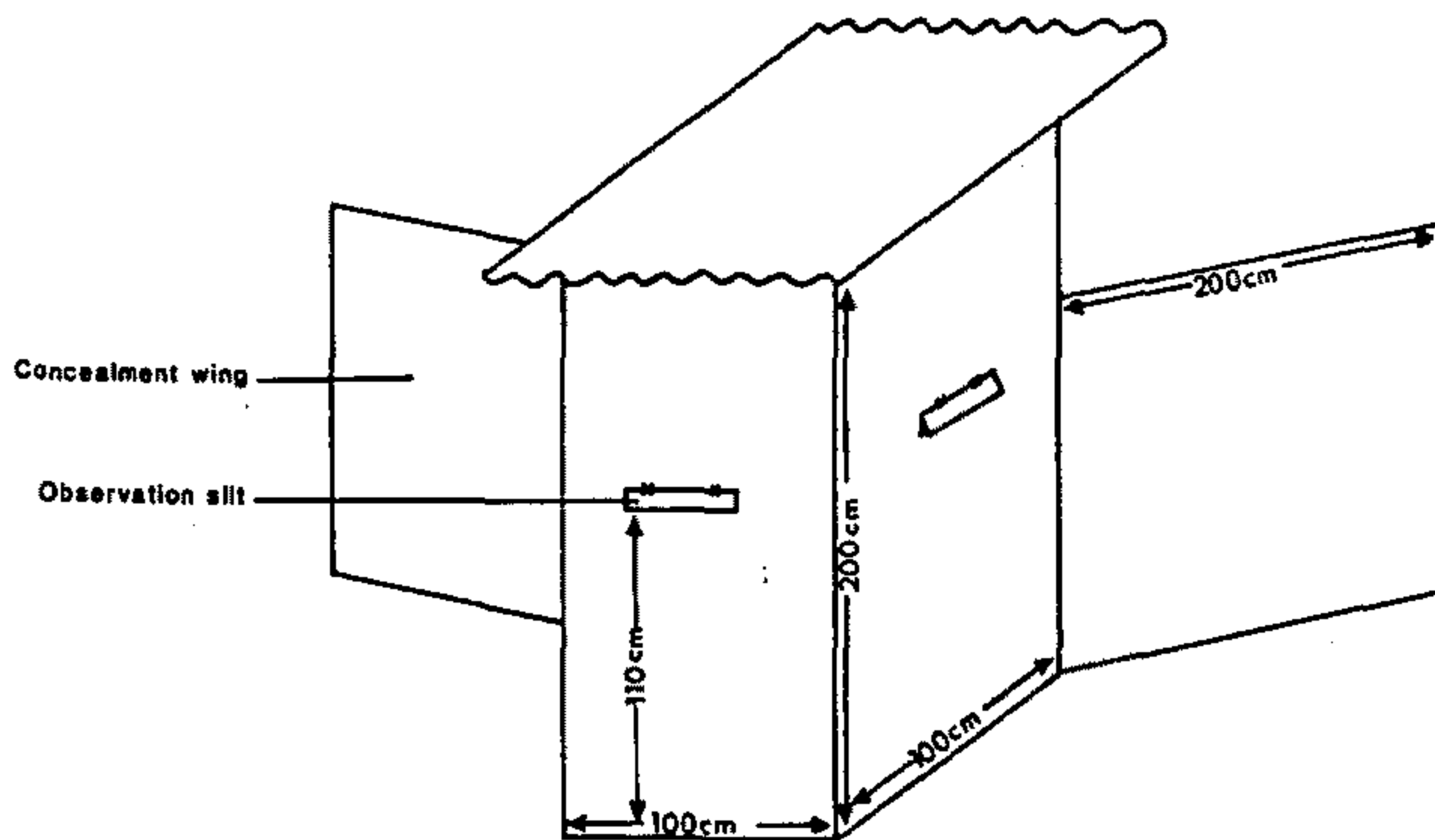


Figure 11. Design of hides, built from wooden packing cases.

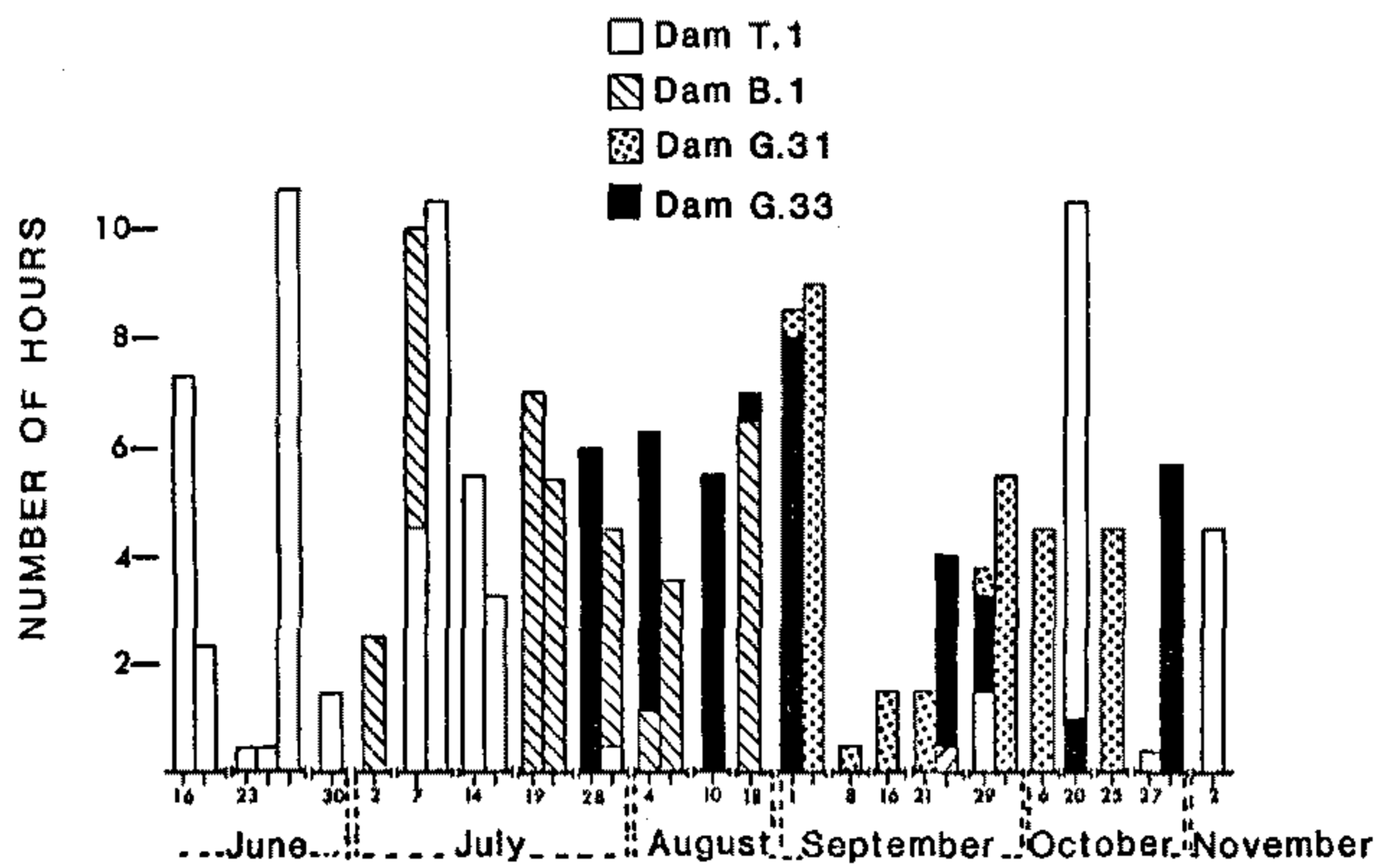


Figure 12. Distribution of observations on the activity patterns of the Maned Duck in 1982. Samples collected between June and November, on four dams.

relation to the approach route. Sometimes, I had to wait until the ducks moved to a better position.

Once in a hide, I used instantaneous sampling to estimate the amount of time ducks spent performing various activities. With this method, activities are treated as states and not behavioural events (Altmann 1974), so that duration of particular behaviours is not measured. Problems may arise where activities are not recorded "instantaneously" because it may take some time to see and record the behaviour of all individuals. Behaviours of individuals recorded early, could then determine the activities of individuals recorded later in the sample. To avoid this, sampling time should be as short as possible. Altmann (1974) found that frequently workers fail to indicate how much time is actually spent sampling instantaneously. I estimated that it took five seconds to sample flocks of between twenty and thirty and less for smaller flocks. This was considerably less than rates reported by Altmann (1974). This meant that there was little chance of any earlier recorded behaviours influencing later ones. Flock synchrony simplified the recording of behaviours considerably. It was possible to record the behaviour of up to thirty individuals at a time by concentrating on those few that were performing a different activity. The activity of the rest could simply be calculated through subtraction. On two occasions, when flock size exceeded thirty, the sampling routine was no longer manageable and had to be abandoned and I moved to another dam. Most of my observations were diurnal but on two moonlit nights, when there was sufficient light to use my binoculars, I also observed activities of Maned Ducks. I collected quantitative data on only one of these nights and although the same methods were used, I could not distinguish between loafing and comfort activities.

Sampling sessions spanned half an hour which allowed the other half of the hour to observe displays. I wrote down the activity of each duck every two minutes when sampling. This gave a certain amount of independence to sample points as well as providing a large data set. I prepared data sheets with each activity marked against distance from the dam. Every two minutes, I completed a data table with the number of ducks engaged in a particular activity and where each was in relation to the

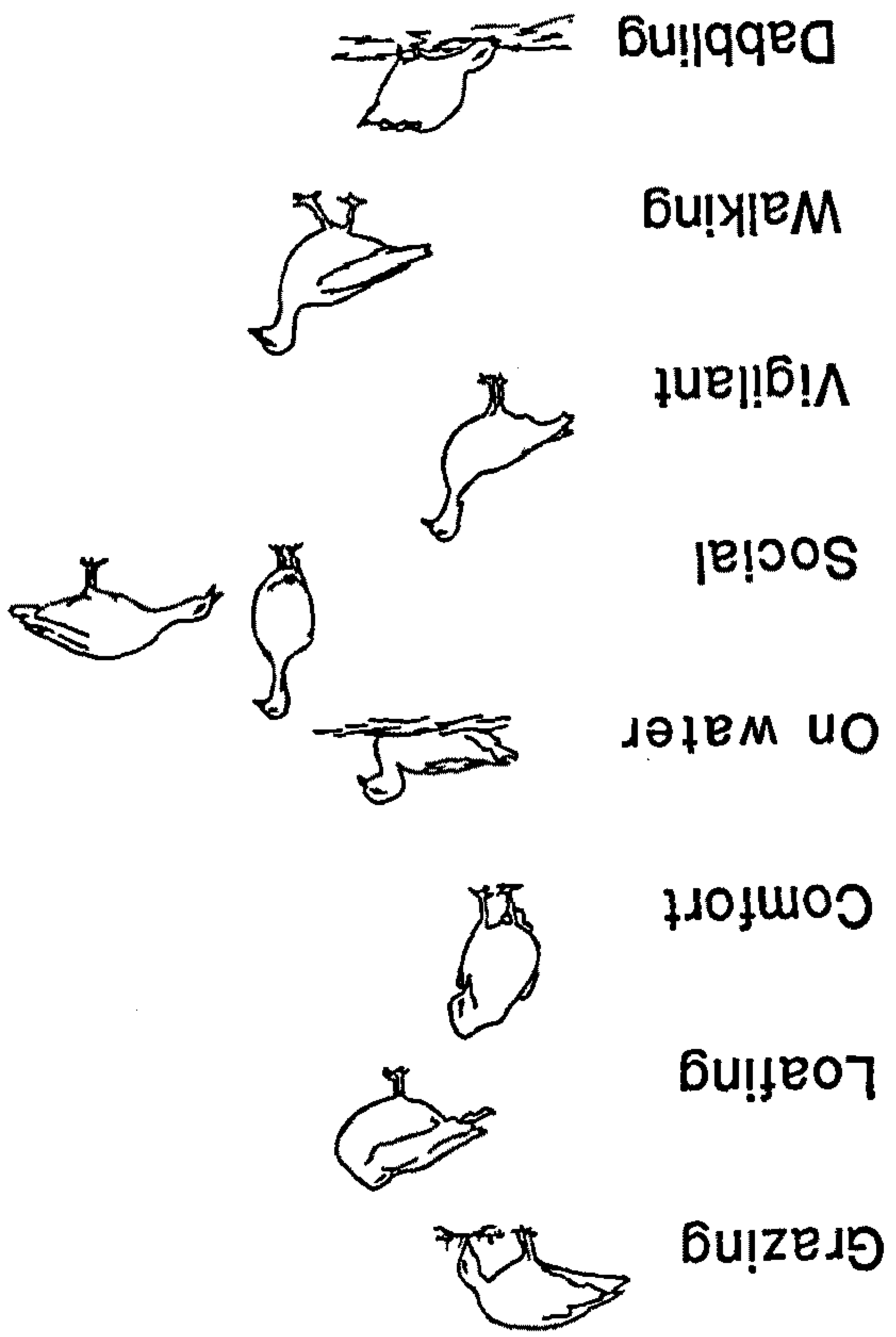


Figure 13. Categories of behaviour patterns used.

dam.

I separated activities into those occurring on land and those occurring on water. I did not differentiate activities performed on the water but further separated those on land. Of the terrestrial activities, grazing and dabbling (perhaps not truly terrestrial) have already been described. Other activities were (see Fig. 13);

i) Loafing.

Resting or sleeping Anatidae are commonly referred to as loafing (Miller 1976; Bruggers & Jackson 1977; Norman et al. 1979). Maned Ducks adopt a number of positions when loafing on land. They stand, on either one or two legs, with their heads resting back on their shoulders or turned around and bill tucked behind the wing (Fig. 13). Frequently, eye closure accompanies these positions. Sometimes ducks fold up their legs and just sit on the ground. Flocks of more than ten loafing ducks, usually have all permutations of this activity.

ii) Comfort.

The comfort activities of Anatidae have already been thoroughly described by McKinney (1965a) and most occurred in this species (Appendix 1). This category incorporated any maintenance activity (preening) and also scratching behaviour, presumably to relieve irritation. I may have inadvertently misclassified some displays derived from comfort movements (McKinney 1965a) in this category.

iii) Social.

Social activities incorporate a diverse range of different displays and of these, only preflight displays were not included (see chapter 7). Performance of these, inevitably resulted in immediate departure of my study animals. With any agonistic behaviour, all participants were included.

iv) Walking.

This category only included Maned Ducks that were moving from point to point, not ducks walking as they grazed.

v) Vigilance.

I admitted only Maned Ducks adopting the Extreme head up posture (Fig. 13) into this category. The other vigilant posture, Head up (see chapter 8) was difficult to identify when there were a number of birds in a flock.

To assess vegetation composition at different distances from each dam, I used a percentage cover measure (detailed in chapter 3). Plants were placed in three groups, Poaceae, Leguminosae and other plants. Although, I identified individual species in the latter group, I combined them for analyses. Species composition was similar to that of site B (Fig. 10). As well as the vegetation, I also estimated the amount of bareground. To determine the placement of a quadrat from the dam, I used a combination of two random numbers. The first decided the position around the perimeter of the dam and hence the direction. From this point, the second determined, within each distance interval, how far I paced directly away from the dam. This resulted in four replicate percentage cover scores for each of the intervals 0m-5m, 5m-10m, 20m-40m, 40m-60m, 60m-80m and >80m from the edge of each observation dam.

Data analysis.

I examined the effects of the three factors, observation dam (DAM), time of day (TIME) and distance from the dam (DIST) on the different activities by treating each activity separately and using fixed three factor analyses of variance. The last factor was not applicable for ducks that were on water or dabbling (at the edge of the dam) so the appropriate fixed two factor analyses of variance were used for these activities. I used the ANOVA and NPAR programs within the Statistical Packages for the Social Sciences (SPSS) to analyse data with unequal replication (Nie et al. 1975).

Time was included as a factor by dividing each day into five time intervals and adjusting for seasonal differences in daylength by calculating the number of daylight hours from sunrise to sunset times for each observation day. Samples were then placed in the appropriate time

Table III. Range of start and finish times for corresponding time intervals used in the analysis of activity patterns of Handed Ducks, in 1982. Eastern Australian standard time used

DATE RANGE		T1.1	T1.2	T1.3	T1.4	T1.5
16/6/82	START: 6.58am	8.58am	10.58am	12.58pm	2.58pm	
	FINISH: 8.57am	10.57am	12.57pm	2.57pm	4.57pm	
2/11/82	START: 6.03am	8.42am	11.21am	3.00pm	4.39pm	
	FINISH: 8.41am	11.20am	1.59pm	4.38pm	7.07pm	

INTERVALS

interval. This method provided a satisfactory adjustment for the problem of increasing daylength. Hence, spring days had longer time intervals than those in winter (Table III). When a sample spanned two time intervals, it was included in the interval where the majority of two minute observations fell.

I have already described the levels for the last factor, distance from the dam. Some distances were precluded from particular analyses. Ducks cannot graze on the water's edge (0m), so this level was omitted. Other intervals were straightforward. However, although I collected data for intervals >80m in most analyses I have amalgamated these further intervals as activities were so seldom observed at these distances from the dam.

I treated each half hour of instantaneous observations as a single sample. The principal reason for doing this was that it reduced the dependence of observations. This was applicable not only on an interactivity basis but also between distances. Ducks loafing at 10 metres from the dam obviously could not also be grazing at 30 metres. It also reduces dependence among two minute observations since the time between observation samples, may not be enough for activities to be independent. Ducks that are grazing at a certain time are likely to still be grazing two minutes later.

Half hour samples consisted of 16 instantaneous scans, taken every two minutes. Each scan included the number of ducks engaged in each activity at that time. The 16 scans were totalled, for each activity and distance from the dam, and converted to a percentage of all observations for that half hour to overcome possible flock effects. Otherwise, the largest flocks would influence the analyses substantially, simply because they would contribute more to the overall number of observations (based on individuals). In a species that forms a flock it is also unlikely that individuals act independently.

I transformed all data by the angular transformation ($\arcsin$) following conversion to percentages (Zar 1974) and analysed each activity separately to further reduce dependency. Results of analyses of variance

for each of the activities are presented in Appendix 2. I used Student Neuman Keuls (SNK) tests to compare means. These were appropriately modified to deal with unequal group sizes (Steel & Torrie 1960).

Results

A) DIURNAL ACTIVITIES

a) Individual categories

I will present each category separately and look at the relative influence of the three factors, observation dam (DAM), distance from the dam (DIST) and time of day (TIME), on each activity.

i) Grazing

Two of the three factors measured affected this activity significantly. Both DIST and DAM were significant main effects (Table 2-A, Appendix 2). However, the significant interactive effects of the two ($F_{15,996}=18.24$, $p<0.001$) subsumed these. Figure 14 is a histogram showing all the possible means for the combination of these two factors. Ducks grazed more in four of the intervals. These were 10-20 metres and 20-40 metres from dam T.1 and 0-5 metres and 5-10 metres from dam B.1. They spent 70% of their grazing time on dam T.1, between 10 and 40 metres and 81% of grazing time, on dam B.1, less than 10 metres from the dam. Although grazing did not occur with a similar intensity on the other two dams, there were detectable differences with distance from water. On dam G.31, ducks grazed more between 20 and 40 metres from the dam than they did within five metres of the dam. On the fourth dam, G.33, few ducks grazed beyond 20 metres (9%). Apart from dam B.1, few ducks grazed in the 0-5 metre interval and ducks, with the exception of those on dam G.31, seldom grazed at distances greater than 40 metres from the dam. It must be remembered that not only does interval size vary, but also that the area available to grazing increases proportionally to the square of the distance from the dam. Hence, there is disparity in the area covered by each interval. The interval 40-60m covers a larger area than 20-40m. Nevertheless, the location of most intense grazing activity varied with the dam. TIME did not affect grazing activity significantly ($F_{4,996}=1.974$, $p>0.05$).

Ducks usually graze in a series of bouts of variable length. These

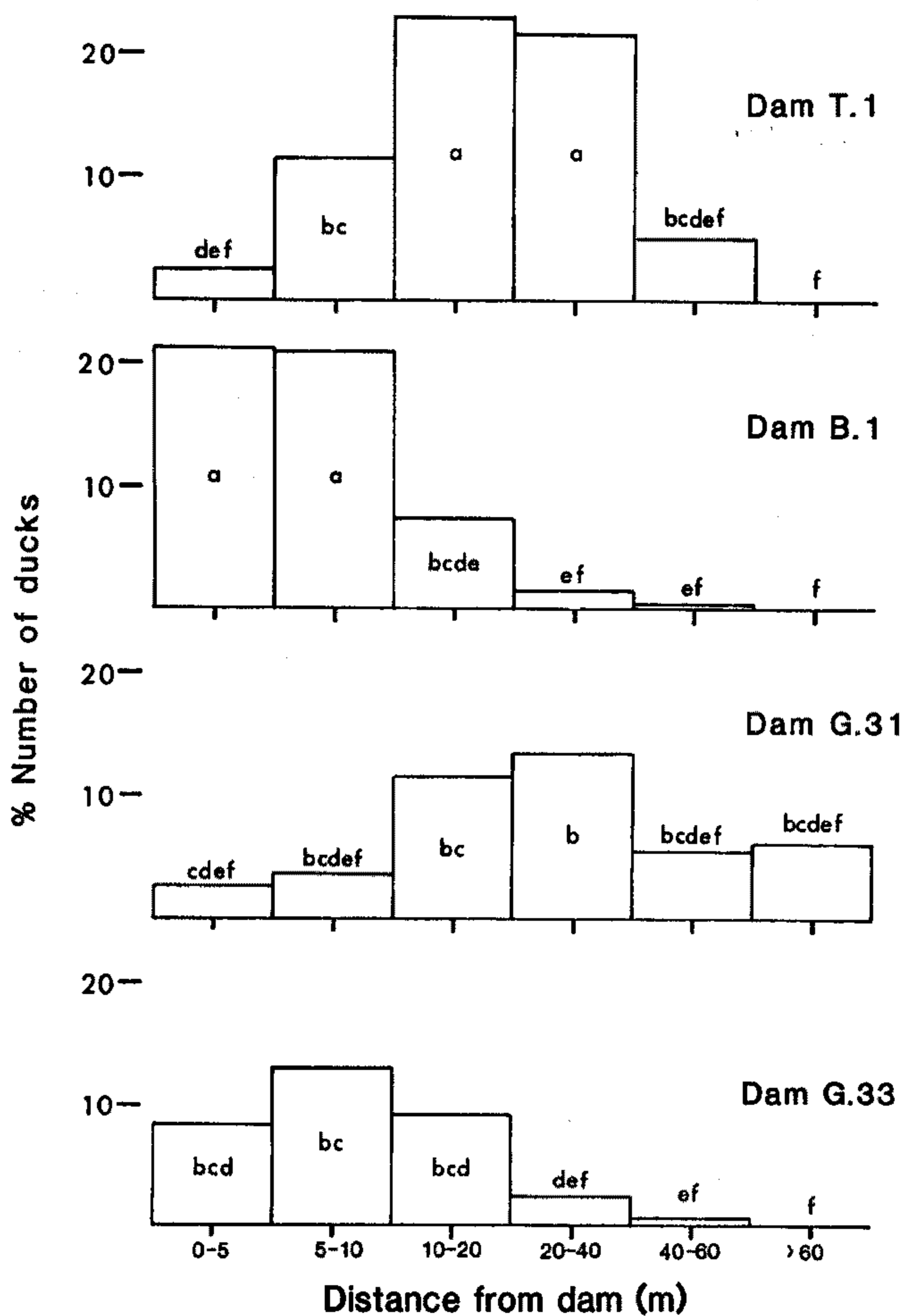


Figure 14. Summary of mean differences in a significant dam x distance interaction for grazing activity. Dams are T.1, B.1, G.31 and G.33. Numbers shown are the mean percentage number of ducks grazing for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

TABLE IV. Frequency of stimuli and responses of Maned Duck "dash" behaviour over a day. Alarm calls by Noisy miner Manorina melanoccephala, Australian Magpie-Lark Grallina cyanoleuca, Australian Magpie Gymnorhina tibicen, Galah Cacatus roseicapillus and Eastern Rosella Platycercus eximius. "Different" stimuli were the call of the Australian Raven Corvus coronoides and a motorcycle

BEHAVIOUR	STIMULUS		
	ALARM CALL	UNKNOWN	DIFFERENT
dash 5m	8	3	-
dash 10m	5	1	1
dash to water	2	-	1
flight to water	2	2	-
Total 25			

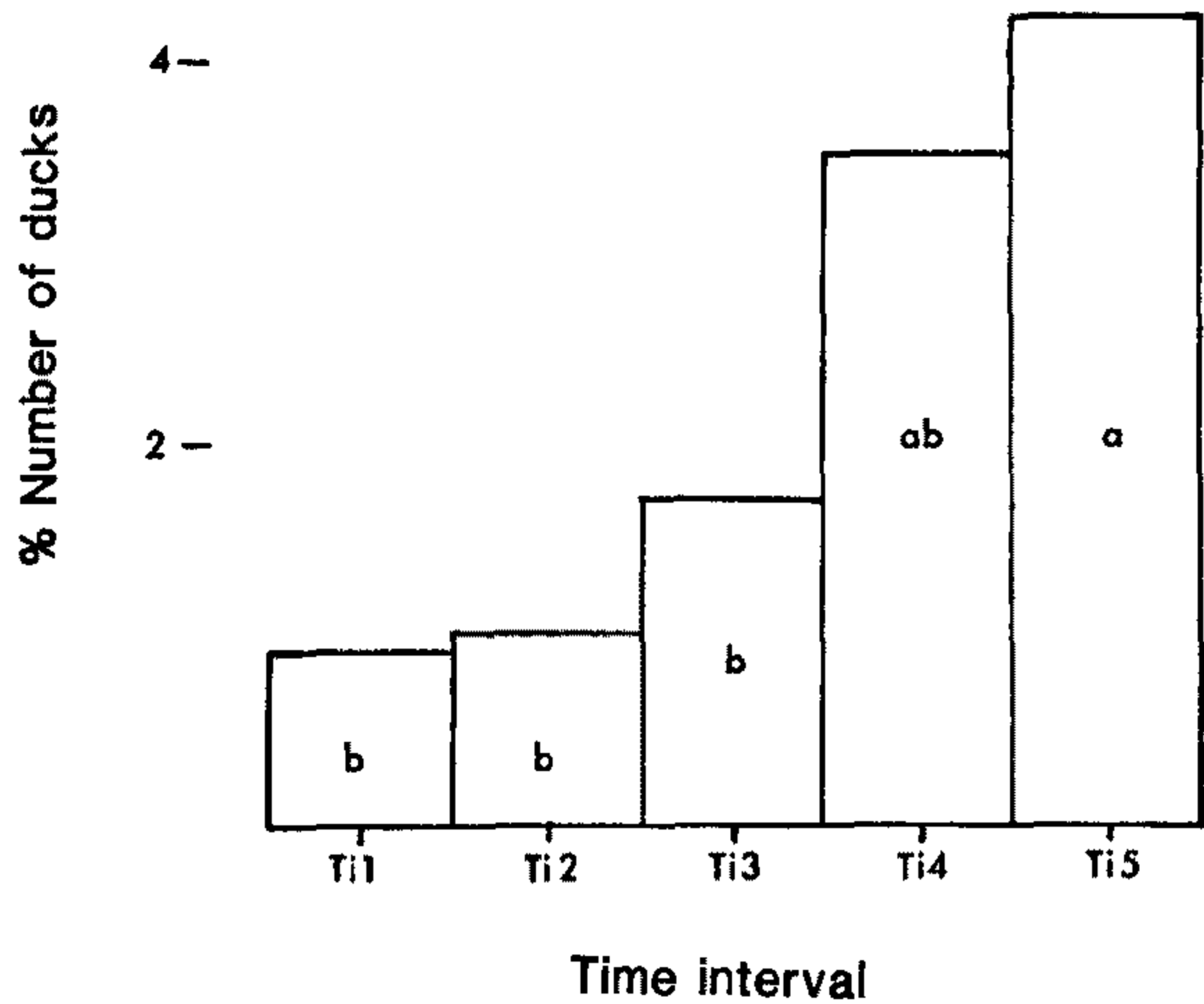


Figure 15. Summary of mean differences in the significant time effect on dabbling. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks dabbling for a half-hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p<0.05$).

can last up to forty-five minutes but are more often 10-15 minutes. Periods of loafing and comfort activity usually punctuate these bouts. While watching flock behaviour, I soon noticed that many of grazing bouts were stopped when the ducks "dashed" back to the dam. They would raise their heads to the "extreme head up" vigilance posture before either running or flying in the direction of the water. I monitored the incidence of this behaviour, over a day, on dam T.1 and categorised it into four types based upon the level of response (Table IV). Alarm calls by other species of birds nearly always stimulated this "dash" behaviour. However, other bird calls produced no reaction. An Australian Raven Corvus coronoides and motorcycle also stimulated this behaviour (different). A road, passing close to this dam, carried between ten and twenty cars a day but these usually had no effect on duck behaviour apart from an occasional vigilance posture.

ii) Dabbling

TIME had a significant effect on dabbling activity ($F_{3,166}=4.02$, $p<0.05$). Ducks dabbled most frequently late in the day (Fig. 15), which was similar on all dams ($F_{3,166}=2.57$, $p>0.05$).

iii) Loafing

Maned Ducks usually loafed close to the dam. Results of three factor analysis of variance, produced two significant first order interactions. The factor DIST was common to both. Comparison of means for these first order interactions are presented in Figures 16 and 17. Results of the significant DAM x DIST interaction ($F_{12,830}=8.98$, $p<0.001$) are presented in Figure 16. Maned Ducks loafed most of all in the 0-5 metre interval on dam G.31, the 5-10 metre interval on dam B.1 and the 10-20 metre interval on G.33. Apart from on dam G.33, ducks spent a similar amount of time loafing at the waters edge (0 m), on all dams (Fig. 16). On all dams, there was a clear drop in the amount of loafing activity at distances greater than 20 metres from the dam, beyond which little to no loafing took place. Overall, Maned Ducks did 96% of their loafing at a distance less than 20 metres from the dam's edge. Without dam G.33, this is reduced even further to 10 metres. On this dam, ducks invariably loafed on a particular slope (10m-20m) which overlooked the dam.

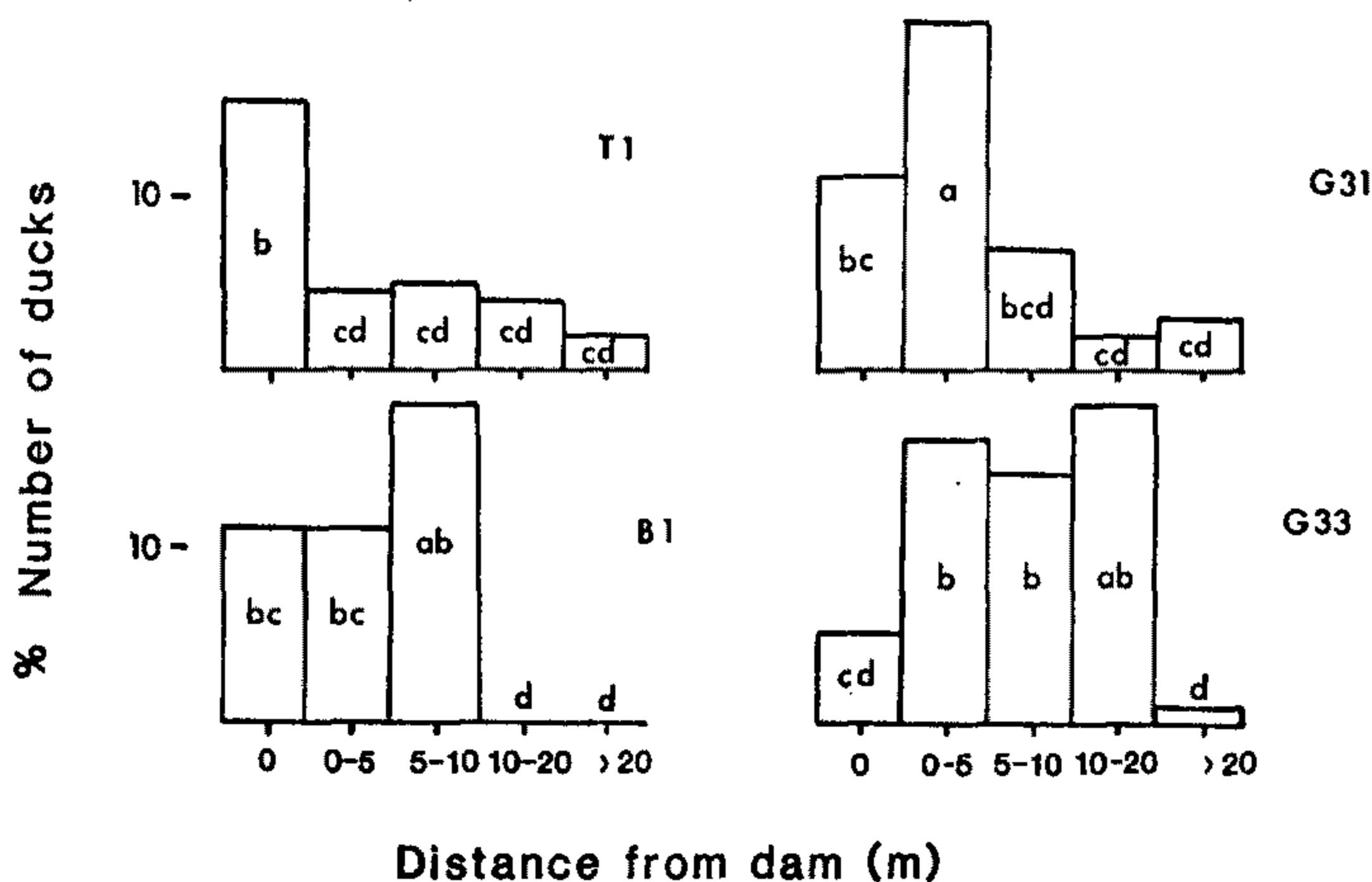


Figure 16. Summary of mean differences in a significant dam x distance interaction for loafing activity. Dams are T.1, B.1, G.31 and G.33. Numbers shown are the mean percentage number of ducks loafing for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

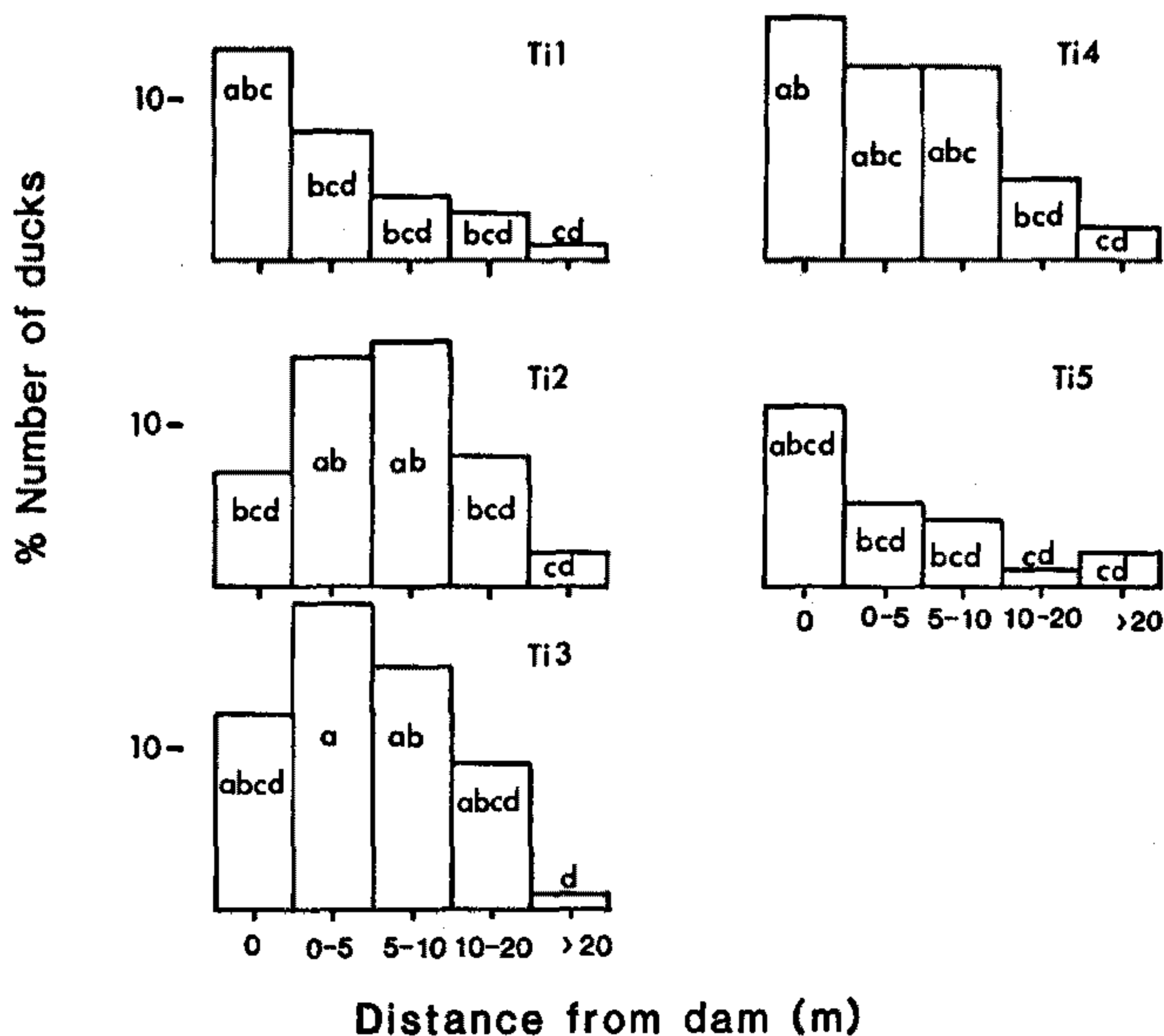


Figure 17. Summary of mean differences in a significant time x distance interaction for loafing activity. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks loafing for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

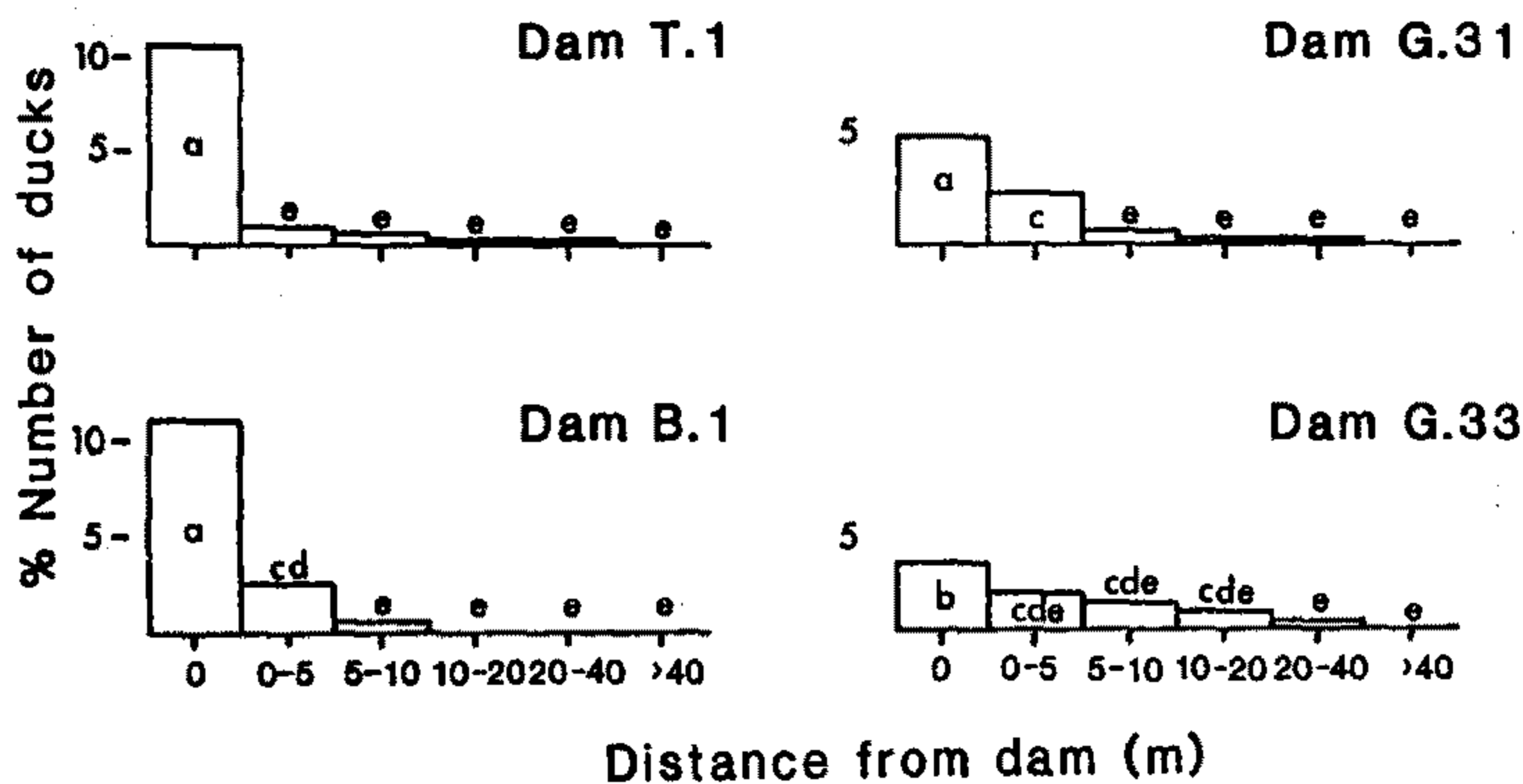


Figure 18. Summary of mean differences in a significant dam x distance interaction for comfort activity. Dams are T.1, B.1, G.31 and G.33. Numbers shown are the mean percentage number of ducks performing comfort activities for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

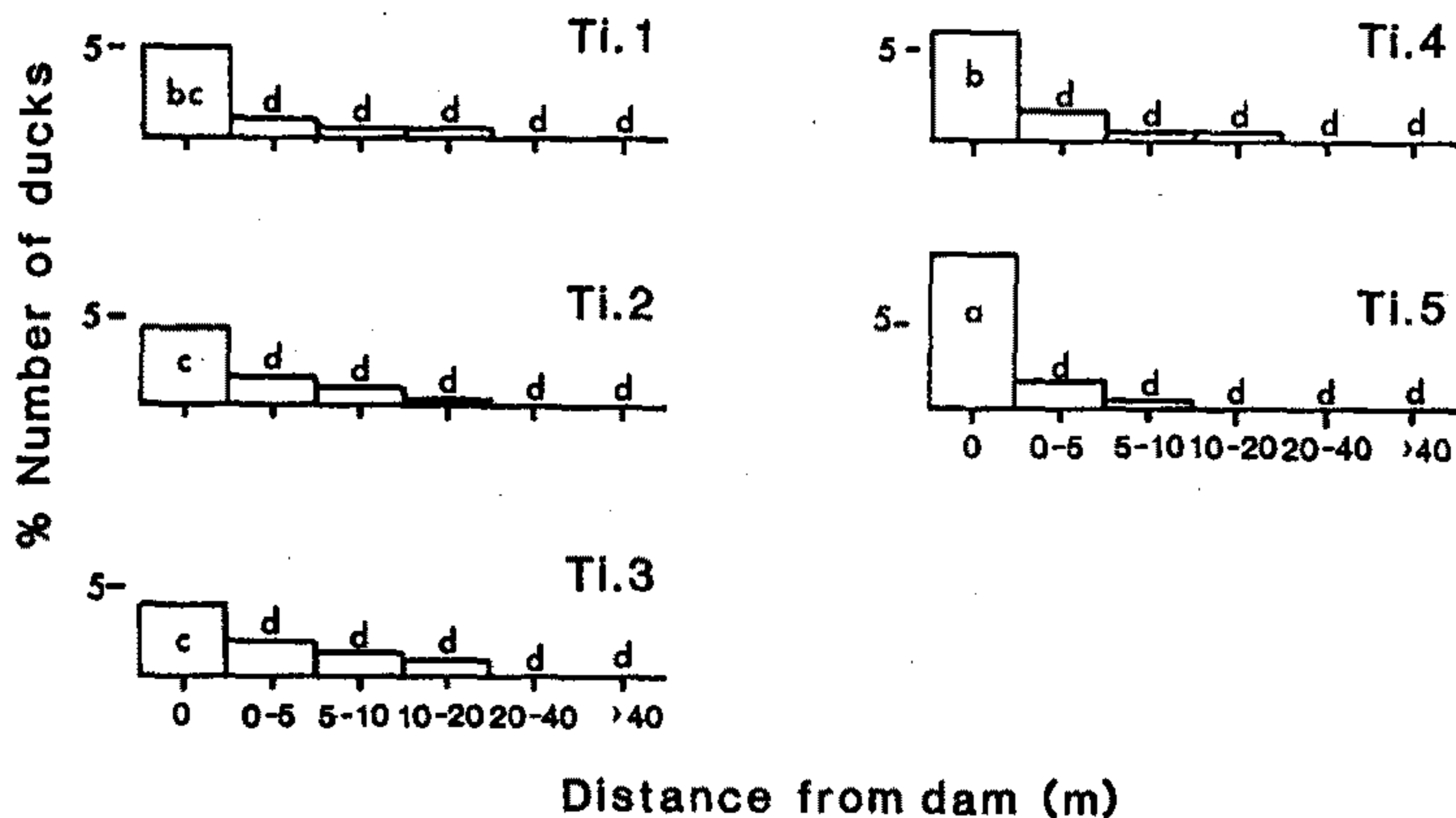


Figure 19. Summary of mean differences in a significant time x distance interaction for comfort activity. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks doing some sort of comfort activity for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

The second first order interaction (TIME x DIST) ($F_{16,830}=1.68$, $p<0.05$) meant that ducks loafed at certain distances depending on the time of day. SNK tests for differences in means did not show clear differences (Fig. 17). Possibly, ducks loafed more at the water's edge (0 m) at the beginning (Ti.1) and end (Ti.4 and Ti.5) of the day. During the middle of the day, Ti.3, ducks appeared to loaf in the intervals 0-5 and 5-10 metres from the dam. There may also be an overall decrease in the frequency of loafing at Ti.1 and Ti.5, as the means for these times, tended to be grouped lower over all distances.

iv) Comfort

Two significant first order interactions were detected. Figure 18 presents all means for the highly significant DAM x DIST interaction ($F_{15,996}=3.12$, $p<0.001$). Most ducks performed comfort activities on the edge of the dam. This was consistent for three of the dams, T.1, B.1 and G.31 ($p<0.05$). However, on dam G.33, ducks performed comfort activities more frequently at distances further from the dam, up to 20 metres away, which I have already considered. Grouping over all dams, ducks spent 87% of their comfort behaviour less than 5 metres from the edge of the dam. Near the edge of the dam, Maned Ducks usually preened while further from the dam, when grazing, comfort activities usually amounted to occasional scratching.

The second significant first order interaction was TIME x DIST ($F_{20,996}=3.55$, $p<0.001$). Figure 19 summarises comparisons of all means. At beginning (Ti.1) and the end of the day (Ti.4 & Ti.5), ducks were more likely to be engaged in comfort activities near the water's edge. Ducks performed most comfort activities late in the day (Ti.5), which was associated with increased bathing activity on the water in the evening. These inevitably ended with a number of ducks preening on the water's edge.

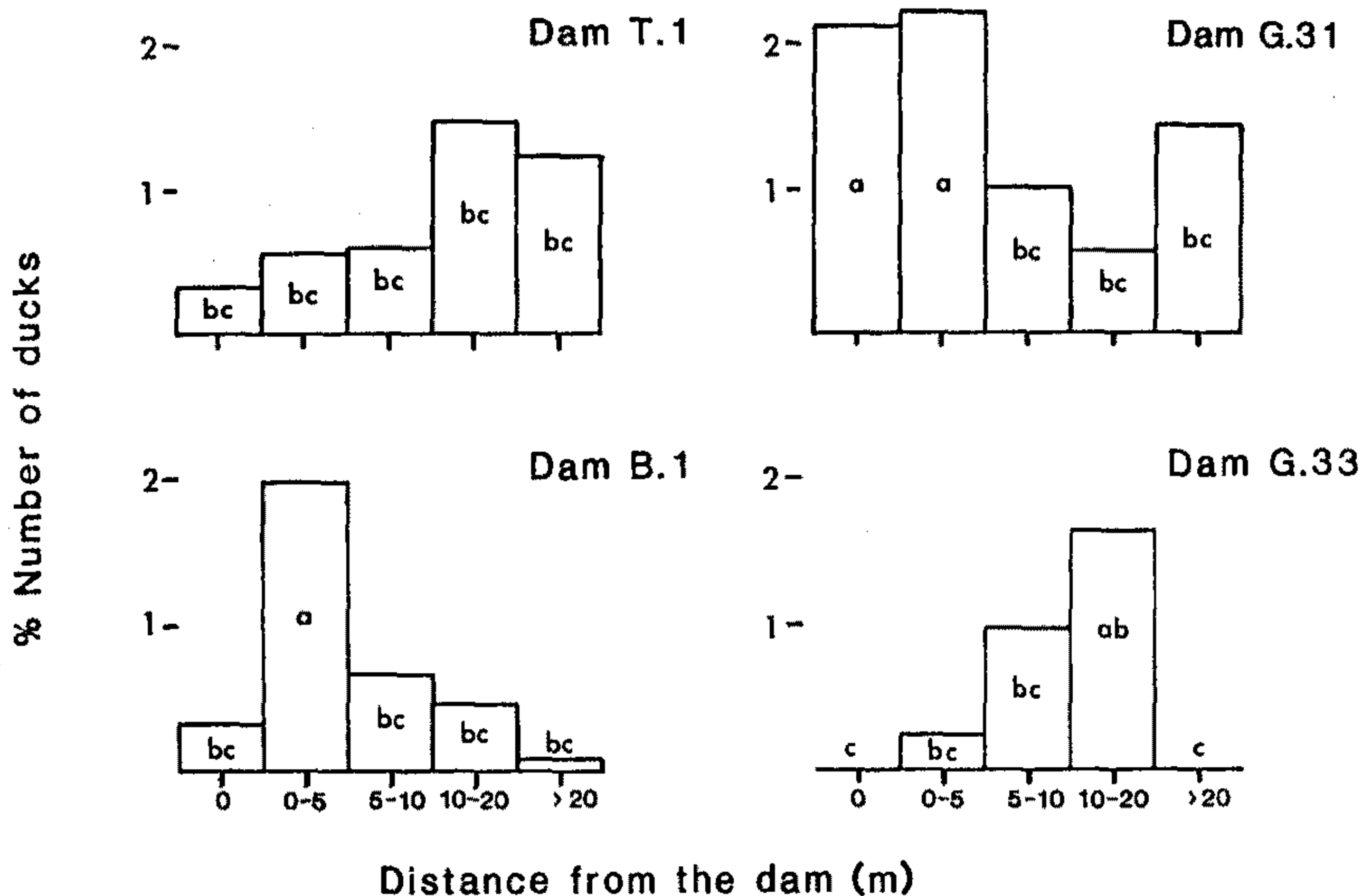


Figure 20. Summary of mean differences in a significant dam x distance interaction for social activity. Dams are T.1, B.1, G.31 and G.33. Numbers shown are the mean percentage number of ducks doing social activities for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Newman Keuls tests, $p < 0.05$).

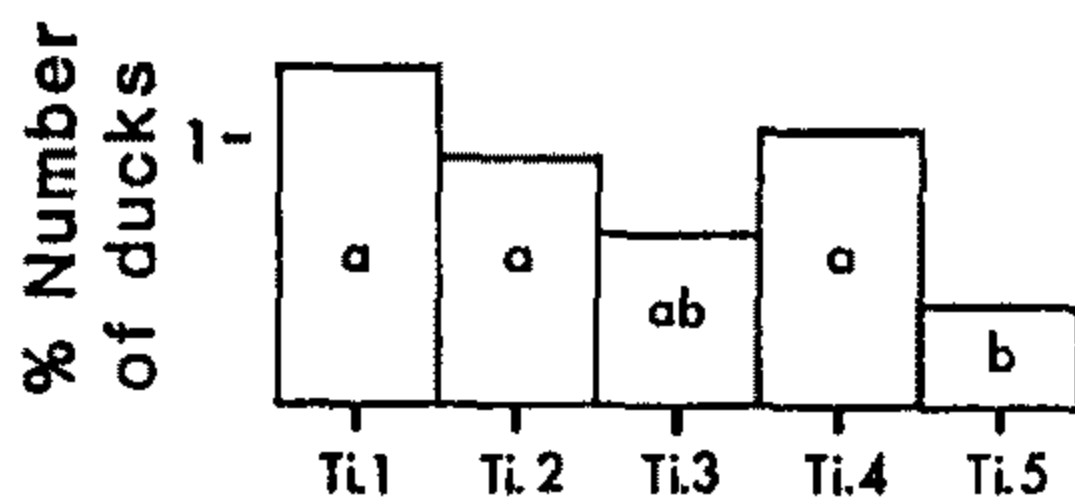


Figure 21. Summary of mean differences for the significant time effect on social activity. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks doing social activities for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Newman Keuls tests, $p < 0.05$).

v) Social

This activity incorporates many independent behaviours which occur on land, so that results of analysis should be interpreted in relation to some of these behaviours. One first order interaction was significant, dams x distance ($F_{12,830}=4.24$, $p<0.001$). The distribution of social activities on land probably closely correlates grazing (Fig. 14). Most social behaviour on land appeared to be agonistic (see chapter 8) and usually occurred when a particular duck got too close to another while grazing. For example, on dam B.1 ducks grazed principally in the 0-5 metre interval (Fig. 14) and there was a similar increase in the social activity in this interval for this particular dam (Fig. 20). Time intervals, the factor not included in this interaction was a significant main effect ($F_{4,830}=3.09$, $p<0.05$). Comparison of means showed that ducks spent more time engaged in social activity early in the day, than later (Fig. 21). Further interpretations are difficult to make.

vi) Walking

Figure 22 shows the comparison of means for the one significant first order interaction (DAM x DIST, $F_{12,830}=2.04$, $p<0.05$) resulting from a three factor analysis of variance (Appendix 2). Ducks walked more often in the 0-5 metre interval over all dams. On dam T.1, this was the 0-10 metre interval. The amount of walking activity did not differ significantly among other distance zones. Time of the day affected the performance of this activity ($F_{4,830}=2.57$, $p<0.05$; Fig. 23). Ducks walked more at the beginning of the day (Ti.1) than in the middle (Ti.3) which could correlate with any increased grazing activity at this time.

vii) Vigilance

Results of analysis showed there was a significant 2nd order interaction for this activity (DAM x DIST x TIME, $F_{60,996}=1.55$, $p<0.05$). This means that the effect of a particular factor was dependent on the combination of the other two factors. It is of interest that only one first order interaction was significant (DAM x DIST, $F_{15,996}=4.85$, $p<0.001$). Possibly, these two factors are more important in the

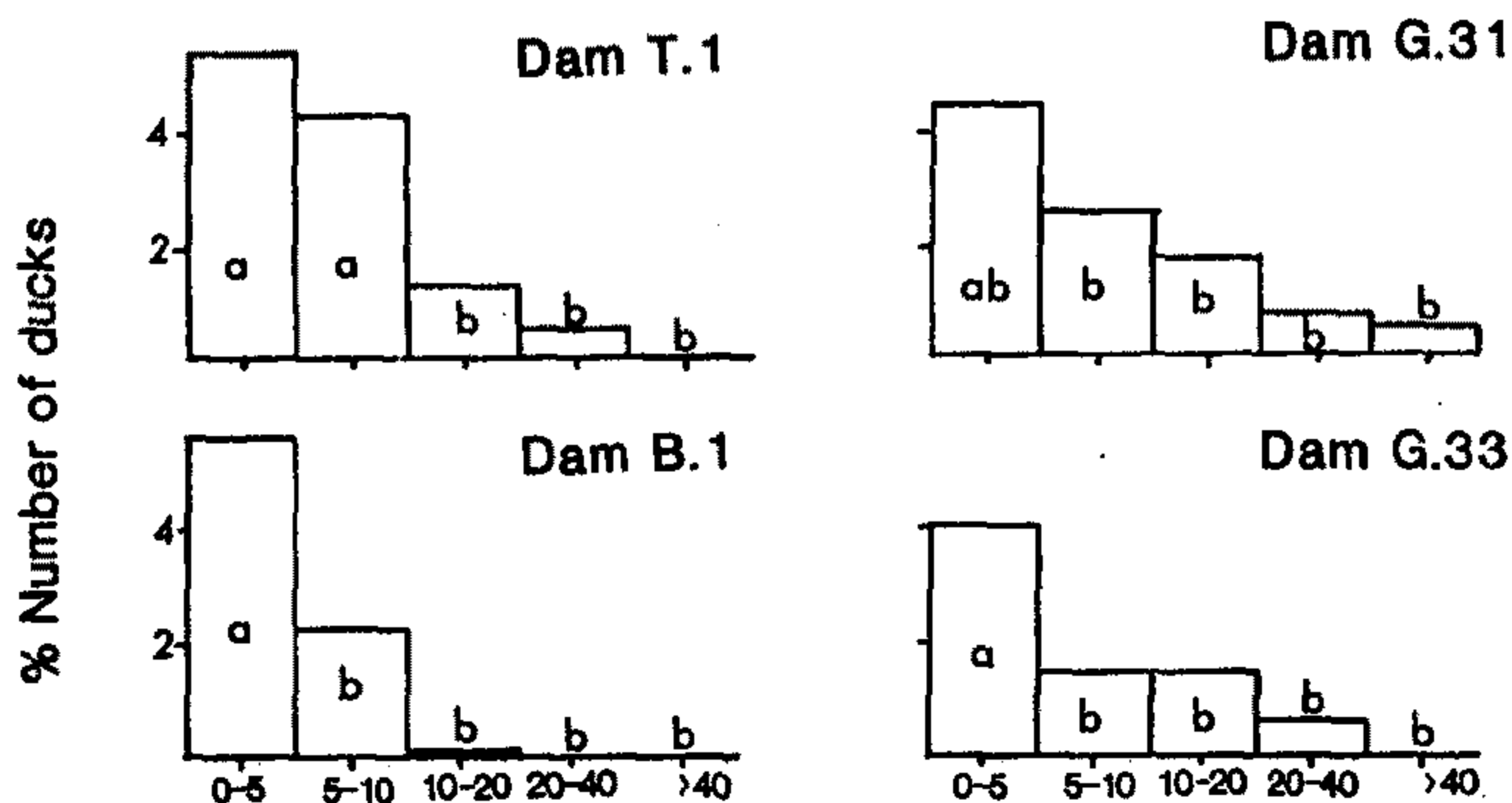


Figure 22. Summary of mean differences in a significant dam x distance interaction for walking activity. Dams are T.1, B.1, G.31 and G.33. Numbers shown are the mean percentage number of ducks walking for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

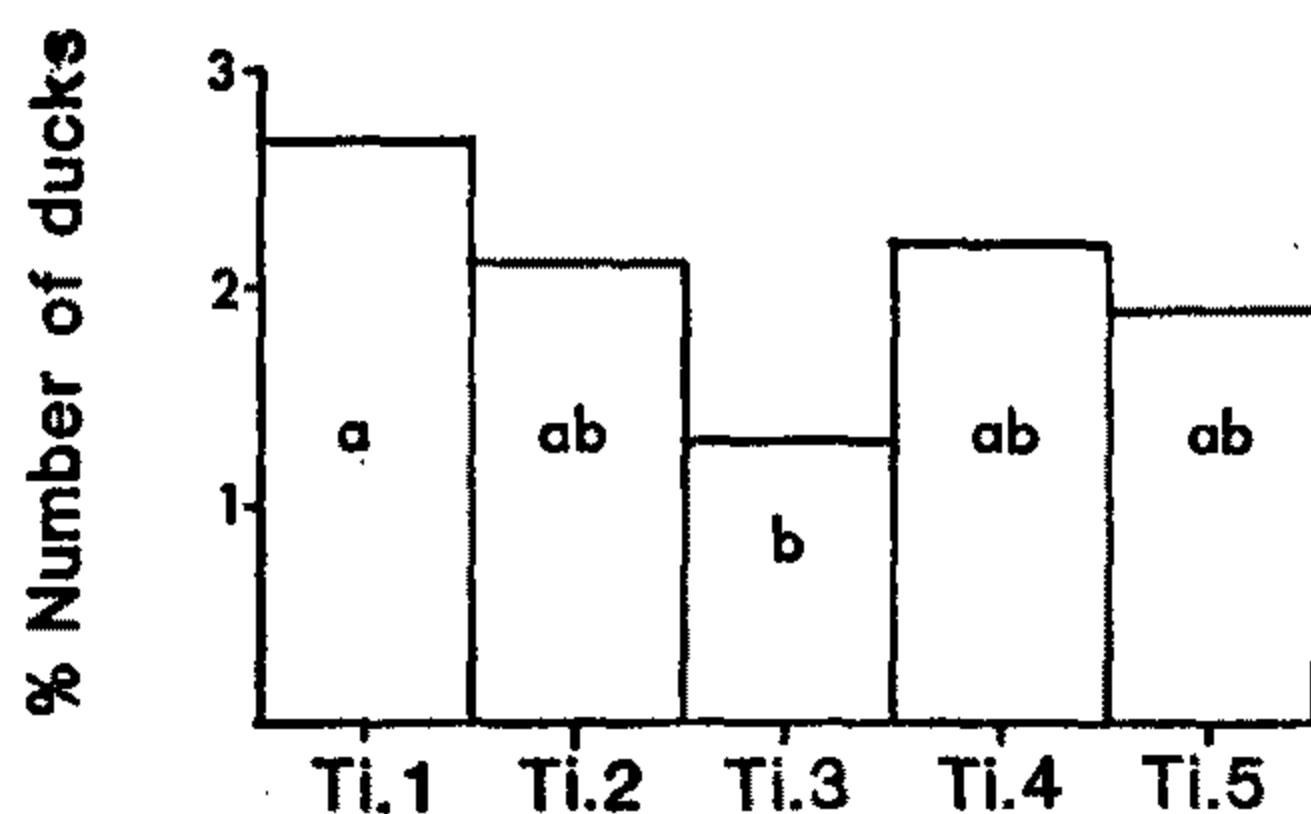


Figure 23. Summary of mean differences in the significant time effect on walking. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks walking for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

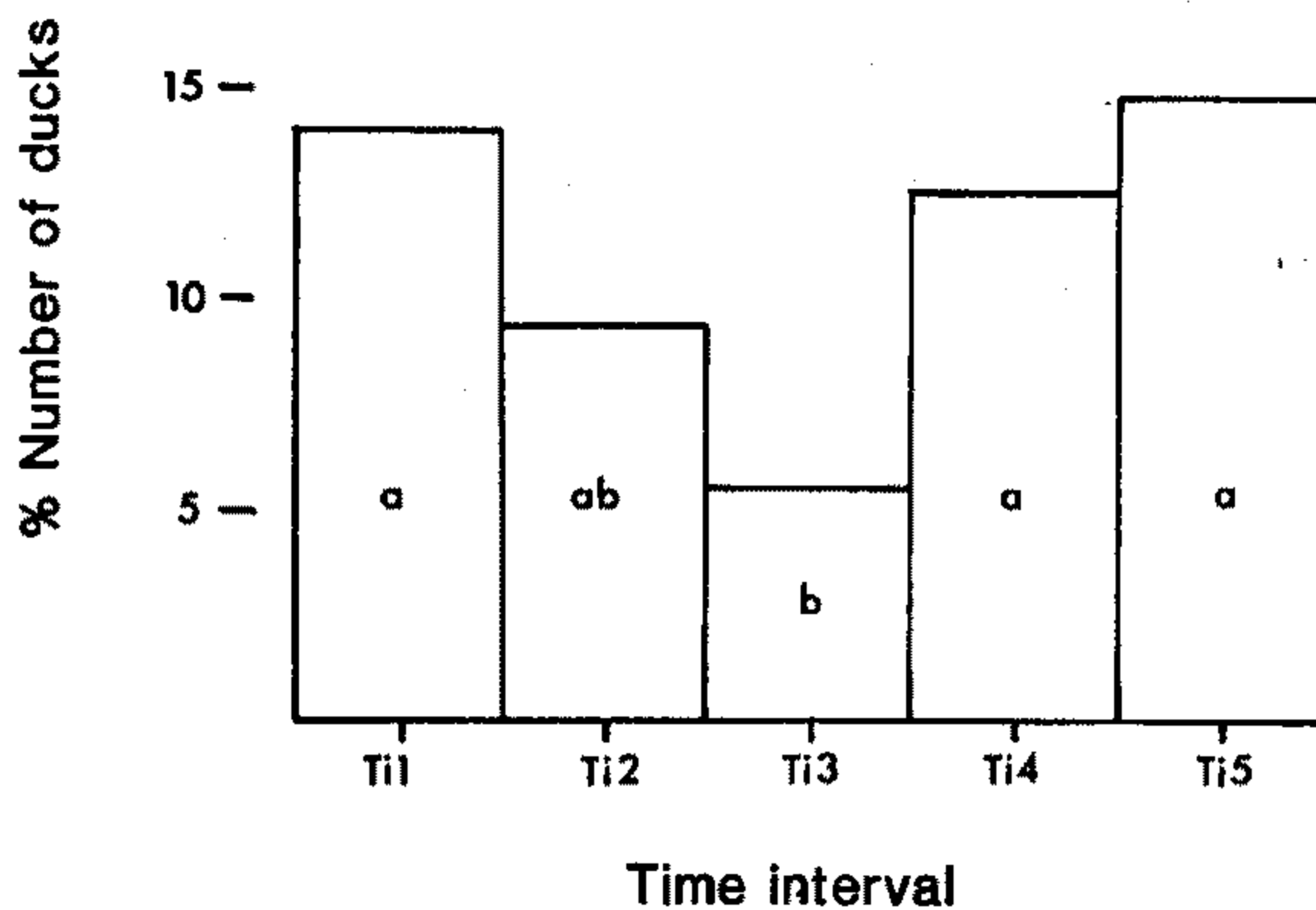


Figure 24. Summary of mean differences for the significant time effect for ducks on water. Time intervals are Ti.1-Ti.5. Numbers shown are the mean percentage number of ducks on water for a half hour period (arcsin transformed). Letters in histograms group means. If the letters differ between categories then there is a significant difference between those two means (results of Student Neuman Keuls tests, $p < 0.05$).

interpretation of the results.

viii) On water

When moving on the water, ducks swam from one side of the dam to the other or from the middle to the side of the dam. Sometimes, after dashing, Maned Ducks remained stationary on the water, in a vigilant posture. On water also included a number of other activities. Bathing and other comfort movements occurred but I rarely saw Maned Ducks loafing on water. Some displays were also performed on water (see chapter 8). As well, Maned Ducks occasionally fed on insects (surface picking; chapter 3). There was no significant interactive effect produced by the two relevant factors, TIME and DAM (Appendix 2). Observation dam was not a significant factor ($F_{3,166}=0.448$, $p>0.05$) but ducks did spend more time on the water at certain times of the day ($F_{4,166}=4.76$, $p<0.001$). Comparison of means showed that ducks spent less time on water in the middle of the day (T1.3) than late in the day (T1.5) (Fig. 24). Other comparisons of means were not significant. However, the overall variability was not explained by these two factors ($p>0.05$; Table 2-H, Appendix 2) which was perhaps attributable to the large number of times that ducks landed on the water after "dash" behaviour. This was likely to be independent of time and observation dam.

b) Comparison of diurnal activities.

Although distance from the dam was the most important factor overall, it was not common to all activities. To compare the various activities, I averaged data over all dams, distances and time intervals for each activity (Fig. 25).

Grazing and loafing dominated the diurnal behaviour of Maned Ducks, together accounting for 62% of the activities (Fig. 25). Ducks grazed (33%) slightly more than they loafed (29%). Very little behaviour occurred on the water (7%). This was exceeded by vigilance behaviour (9%) which tended to be more important when ducks were grazing. Despite the fact that Maned Ducks form flocks, social activities took up little of the behaviour (4%).

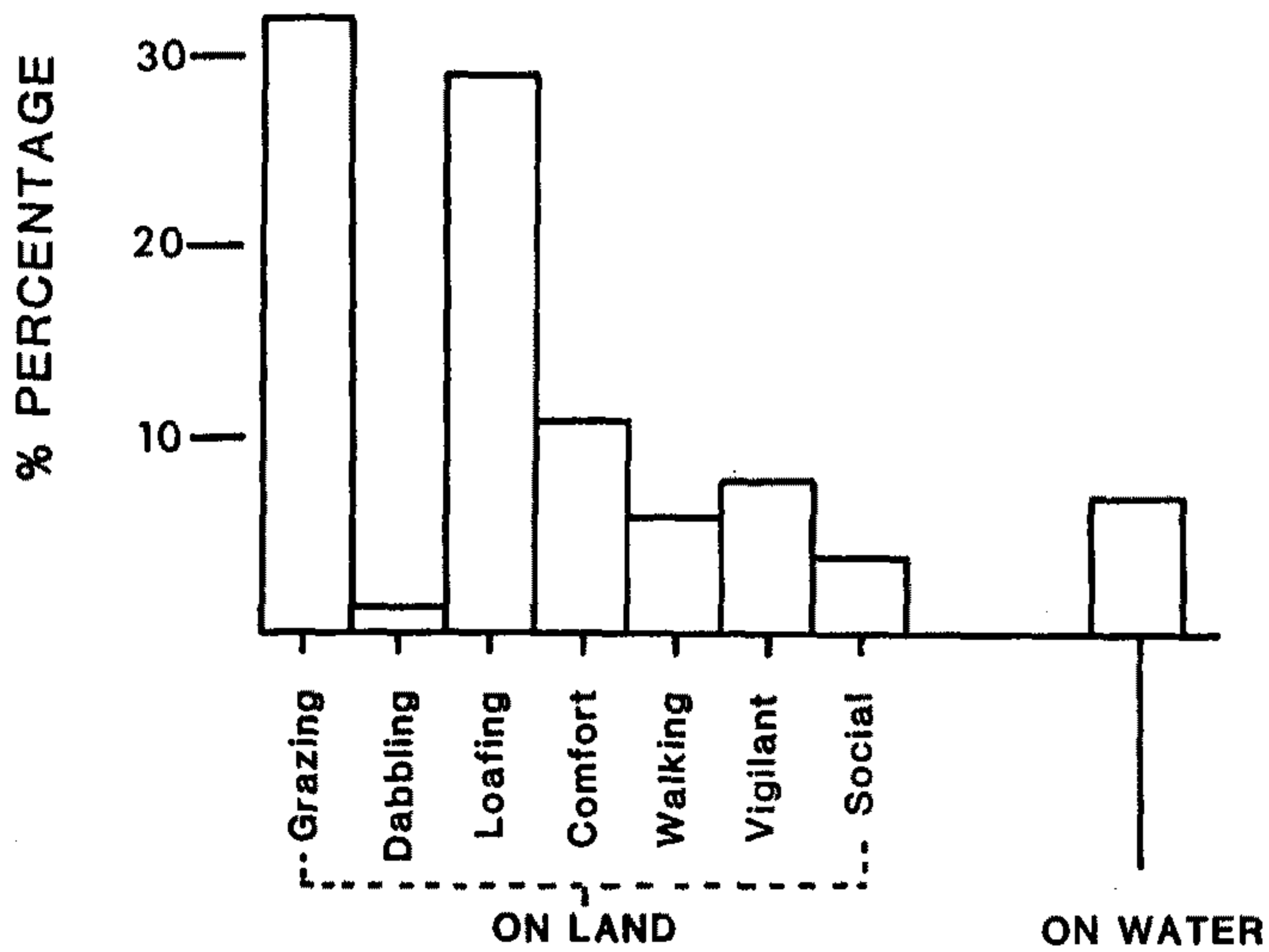


Figure 25. Diurnal comparison of activities, averaged over all dams and distances from the dam. Mean percentage number of ducks doing each activity for a half hour period.

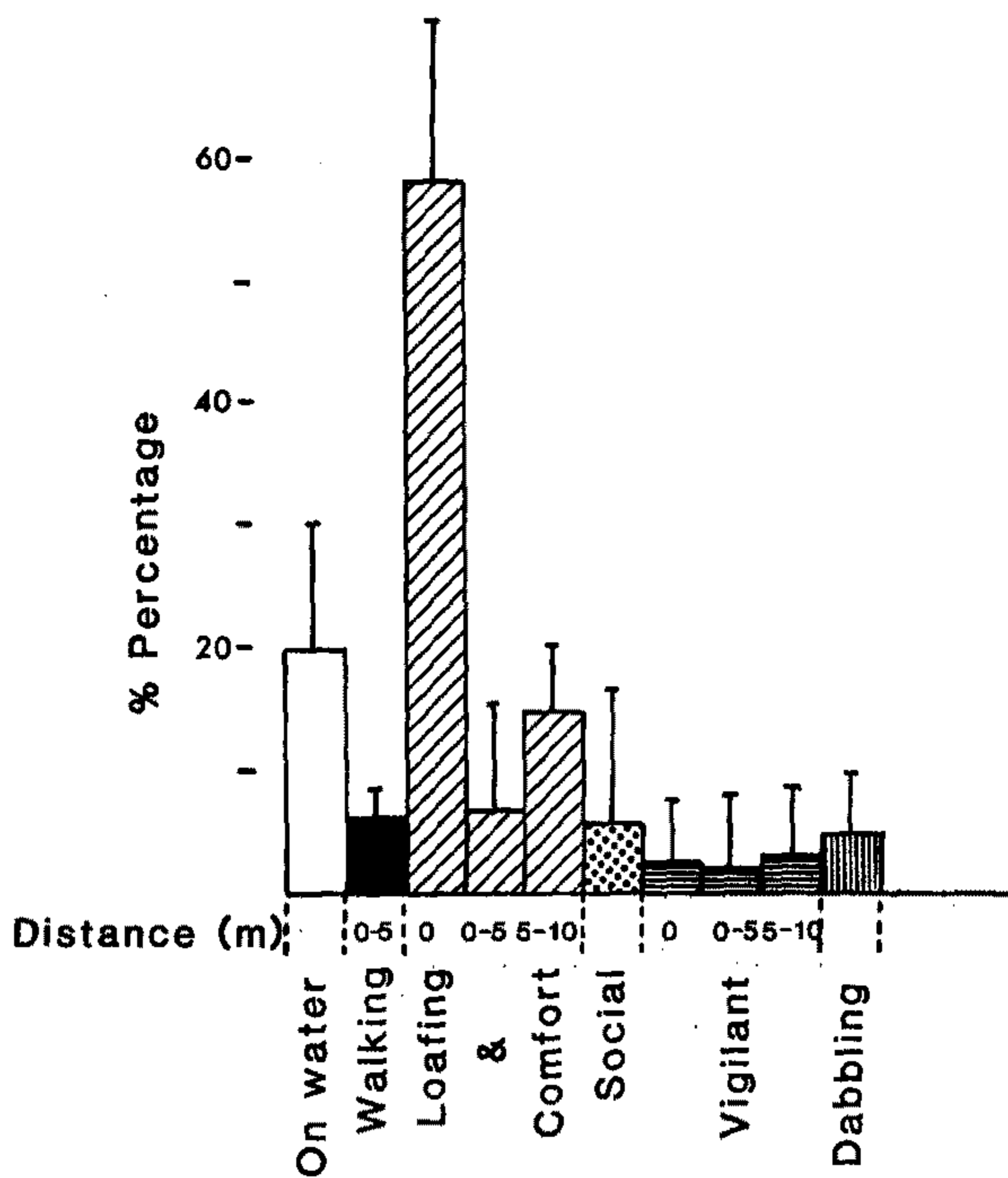


Figure 26. Nocturnal behaviours of the Maned Ducks over one moonlit night. Activities, comfort and loafing, treated together. Mean percentage number of ducks performing a particular activity for a half hour interval with 95% confidence intervals (arcsin transformed) (n=5; half-hour intervals).

TABLE V. Summary of Kruskal Wallis tests for vegetational differences at different distances from a particular dam. Four replicates for each distance. The numbers 1,2,3,4,5, and 6 correspond to respective distance intervals from the dam, 0-5m, 5-10m, 10-20m, 20-40m, 40-60m. (* significant at p<0.05). Means are compared by Student Newman Keuls' tests with underlined numbers indicating significant groupings (p<0.05)

DAM COMPONENT MEASURED CORRECTED CHI-SQUARE SIGNIFICANCE MEAN COMPARISON

(ascending order)

T.1	Poaceae	19.8	*	<u>1 2 4 6 3 5</u>	
	Leguminosae	18.6	*	<u>1 2 3 4 5 6</u>	
	Other plants	8.4	ns		
	Bare ground	19.4	*	<u>5 6 4 3 2 1</u>	
B.1	Poaceae	16.0	*	<u>1 2 3 6 5 4</u>	
	Leguminosae	3.5	ns		
	Other plants	8.6	ns		
	Bare ground	18.5	*	<u>6 5 4 3 1 2</u>	
G.31	Poaceae	16.3	*	<u>1 2 6 3 4 5</u>	
	Leguminosae	14.6	*	<u>1 3 4 5 2 6</u>	
	Other plants	7.4	ns		
	Bare ground	12.9	*	<u>3 2 6 5 4 1</u>	
G.33	Poaceae	13.5	*	<u>1 6 5 2 4 3</u>	
	Leguminosae	12.7	*	<u>1 2 3 4 5 6</u>	
	Other plants	5.9	ns		
	Bare ground	12.86	*	<u>5 3 4 2 6 1</u>	

B) NOCTURNAL PATTERNS

Figure 26 compares the frequency of various nocturnal activities over five hours. A combination of loafing and comfort was the most frequent activity. This occurred predominantly at the water's edge. Ducks did not graze during this observation period although I did see them grazing on the second night. I have also heard large flocks of Maned Ducks vocalising at night some distance from the dam as large flocks do while grazing during the day.

C) VEGETATION

I compared the amount of particular vegetation types found at different distances on each of the observation dams. Variance heterogeneity, even after transformation for percentage data ($\arcsin$), made analysis by a non-parametric method more appropriate. I used Kruskal-Wallis one-way rank tests and SNK tests (Zar 1974) to compare vegetation types at each distance and dam (Table V). On T.1, there was more grass (>10m) and clover (>20m) further from the dam and although not significant there appeared to be more bare ground closer to the dam (ascending means). Only grass varied with distance on B.1 while there was little grass and clover within 5m of G.31 which was covered by bare ground. Similarly, dam G.33 had more bare ground close to the dam with grass and clover found elsewhere. Other plants were distributed evenly over most distance intervals.

Discussion

I chose to look at the effects of three factors; observation dam, time of the day and distance from the dam, on the performance of various diurnal activities of the Maned Duck. Their effects on activities varied. There were some strong dam differences. Maned Ducks grazed more on dams T.1 and B.1 and accordingly, they loafed less on these dams and more on G.31 and G.33. Since these were the two main activities, a reduction in one usually resulted in more of the other. However, this result may be due to the sampling distribution. Much of the data collected for dams T.1 and B.1 were in the winter (Fig. 12), when comparatively lower temperatures prevailed. With colder temperatures, birds need more energy (Kendeigh 1970) and they spend more time feeding (Verner 1965). Nevertheless, if real differences exist, grazing could be correlated to pasture improvement. Both dams, G.31 and G.33 are surrounded by largely unimproved pastures. In contrast, the other two dams have few trees and a higher quality pasture of exotic grasses and legumes. Maned Ducks could graze more on these dams to build up their reserves for reproduction.

Ducks also grazed differently on each dam, particularly in the intervals close to each dam. On dam B.1, ducks grazed much closer to the water. This dam was only used for watering by sheep and had a lot of clover in the 0-5m interval which had not been trampled by cattle, a common condition of the other dams (Table V). Interestingly, although there were few other vegetational differences on this dam (Table V), grass further from the dam was coarse and senescent which may account for this grazing pattern since Maned Ducks seem to prefer green herbage (chapter 3). This was also illustrated on dam G.31, where ducks sometimes grazed at a particular spot rich in clover, some distance from the dam (>60m) (Fig. 14). They would walk quickly out to this patch, ignoring the poorer quality native pastures, along the way. Similar preference behaviour was also observed on dam T.1 when it was being filled by piped water from a creek. There was new pasture growth where the water left the pipe and ran (30m) into the dam. While this lasted, Maned Ducks concentrated their grazing activity here. The higher protein content of

new growth (Rockwood 1974, Milton 1979) may explain this preference.

Some activities were more common at certain times of the day. As in other Anatinae (Skead 1977), I found that Maned Ducks spent more time on the water at the beginning and end of the day (Fig. 24). In the evenings, this was probably because most individuals in a flock bathed towards dusk and then followed this with a period of intense preening (Fig. 19). However, the reason why Maned Ducks spent more time on the water early in the day, was not so clear. There appeared to be more agonistic behaviour on water in the morning which was probably also reflected in the increased social activity on land (Fig. 21). Since much nocturnal activity was possibly spent loafing or performing comfort activity at the edge of the dam (Fig. 26), this increased agonistic activity early in the day may function in the establishment of a flock hierarchy, which appears to exist, even in loosely knit pigeon flocks (Murton et al. 1966). Ducks also tended to dabble more towards the end of the day (Fig. 15) which may be because they need to supplement the grit in their gizzards (chapter 3) after a day of feeding.

Like other Anatidae (Owen 1972; Ebbinge et al. 1975; Bruggers & Jackson 1977; Norman et al. 1979), loafing activity of Maned Ducks was more prevalent in the middle of the day (Fig. 17), but there was no indication that Maned Ducks grazed more at any stage during the day. This contrasts the behaviour of other grazing Anatidae which have an increased period of feeding activity early and late in the day (Owen 1972; Ebbinge et al. 1975; Owen & Thomas 1979). Patterns in the grazing activity of Maned Ducks may also be confounded by the effects of comparatively short feeding bouts which may function to give the birds time to digest.

Many grazing anatids spend much of the day feeding (Owen 1972, Ebbinge et al. 1975, Harwood 1977, Owen & Thomas 1979). However, I did not find that this was true for Maned Ducks. Patterns reported independently by Burton and Hudson (1978) and Fredrick and Klaas (1982) for the Snow Geese Anser caerulescens were much closer to those obtained for this species. It is particularly interesting that Fredrick and Klaas (1982) observed two quite different feeding strategies in Snow

Geese, depending on whether the geese fed on hunted areas or refuge areas. This indicates that, besides possible seasonal differences in grazing patterns, there may also be habitat differences. Nevertheless, it also importantly shows, that the grazing pattern of the Maned Duck lies within the bounds of patterns observed in some grazing anatids.

Apart from diurnal grazing, I was able to confirm Frith's (1982) observations that Maned Ducks graze at night. However, this may not be a regular nocturnal activity. Ebbinge et al. (1975) found that Barnacle Geese Branta leucopsis switched from a diurnal to nocturnal grazing pattern when the moon was full. Unfortunately, I was only able to observe nocturnal activities of Maned Ducks when the moon was full. There was some further evidence that grazing at night was not a regular habit. Loafing and comfort activity close to the edge of the dam, dominated activities on the first night and, in addition, whenever I made observations after sunset or before daybreak, Maned Ducks were almost always loafing on the edge of the dam. As well as providing some evidence that this may be an important nocturnal activity, this also contrasted observations of loafing later in the day, when ducks loafed further from the dam (Fig. 17). Increased vulnerability to predators at night, may be the reason for this relationship. I saw no evidence for traditional evening roosting areas, as in other Cairinini (Parr et al. 1979). I also found no evidence for any regular nocturnal feeding forays of Maned Ducks, reported by Frith (1982). However, Maned Ducks did feed on waste grain near a grain silo which was 200m from the dam on one of the observation nights. Possibly, the nocturnal feeding behaviour observed by Frith is more prevalent where there are food sources separated from the central camps.

All activities performed by Maned Ducks showed patterns related to distance from the dam. With the activities social, walking and vigilant, this distance effect was probably because the duck happened to be in these intervals when grazing. However, ducks spent 92% of their grazing activity less than 40m from a dam (Fig. 14). Such a pattern of behaviour was intriguing as I had expected ducks would graze far from the dam.

A number of explanations could be invoked for this pattern. The most

obvious is that Maned Ducks are found where preferred food items are. There was little gross difference in vegetation composition in relation to distance from the dam (Table V). There was some initial effect close to the dam (0-5m) where little vegetation grew. This was due mainly to cattle watering and trampling the area. Not surprisingly, this is the area where most of the ducks were recorded walking (Fig. 22). Vegetation differences could be important in explaining much of the variability in grazing close to the dam but did not satisfactorily explain the clear drop off in use at a certain distance from the dam.

Another more likely explanation is that Maned Ducks obtain sufficient food close to the dam. The theoretical amount of area available to ducks as they graze away from the dam, increases proportionally to the square of the distance from the dam. So, there is a considerable amount of pasture within forty metres of the dam. However, ducks do not graze over the whole available area and, when grazing, often move off directly away from the dam. Further evidence that this was not the explanation, came from observations in 1982. There was little herbage anywhere later this year (chapter 3) and food appeared to be short except possibly where ducks fed on wheat grain (chapter 5). Nevertheless, Maned Ducks usually remained "constrained" by habitat limits.

A clue to a more likely possible explanation of this habitat use comes from the behaviour of Maned Ducks. They frequently look up (vigilant postures) while grazing, and natural history accounts of the Maned Duck remark on this duck's wariness (Byrne 1974). Frith (1982) says of the Maned Duck that it is an "...extremely shy and wary bird will have seen the observer first; accordingly it is nearly always seen flying silently or frozen into an alarm posture". This frequent vigilance behaviour (Fig. 25) probably enables Maned Ducks to detect approaching predators like other bird species which flock (Inglis & Isaacson 1978; Lazurus 1978; Caraco 1979; Barnard 1980; Bertram 1980; Metcalfe 1984).

Furthermore, the alarm calls of avian species produced an anti-predator behaviour, an escape response called dashing (Table IV). These calls nearly always preceded the appearance of an avian predator, of which, there were a number resident on the study site (Brown Goshawk

Accipiter fasciatus, Peregrine Falcon Falco peregrinus, Brown Falcon Falco berigora, Little Eagle Hieraaetus morphnoides and Wedgetailed Eagle Aquila audax). Other smaller resident avian predators were not considered because they were probably incapable of preying on the larger Maned Ducks. However, those listed are all probably predators of Maned Ducks. Observations of predator attacks are notoriously rare but I caught three Peregrine Falcons and one Brown Goshawk in traps after they had fed on Maned Ducks and I also saw a Wedge-tailed Eagle prey on a juvenal Maned Duck seizing it, as it grazed. Besides these, I twice saw a Brown Goshawk unsuccessfully attack Maned Ducks. Both times, the ducks flew to the middle of the dam, once diving, like other Anatinae in response to avian predators (Norman et al 1979). On the second occasion, after attacking, the goshawk remained on the dam wall for nearly ten minutes with the Maned Ducks remaining vigilant in the middle of the dam. Ten minutes after the goshawk left, they swam to the shore. Most of these aerial predators probably need to attack ducks either in the air (Rudebeck 1951) or on the ground and would be incapable of plucking ducks off the water.

These observations suggest that water acts as a refuge for Maned Ducks from aerial predators. Since these ducks are comparatively slow flyers (Frith 1982), the best strategy could be to get to the safety of the water as soon as possible. Tamisier (1976) found that a Pintail Anas acuta, when pursued by a Peregrine Falcon dropped to the water presumably to escape. Moreover, unlike geese, they may be more vulnerable to predation because of their small size. Although, Maned Ducks have some behaviours which are exclusively restricted to water, such as bathing and mating, much of the time that I recorded birds on the water, was after they had "dashed" there. "Dashes" included under "unknown" in Table IV were possibly because ducks had just responded to the presence of a predator and were in a state of increased awareness. Maned Ducks appeared to be more vigilant following the passage of an avian predator and possibly more prone to performing escape behaviour with little motivation. Such a strategy may be adaptive as the predator is still likely to be in the vicinity.

The role that each farm dam plays as a refuge from predators, is further supported by the spatial distribution of comfort and loafing

activities. Ducks performed both close to the edge of all dams, except G.33 (Figs 16, 17, 18 & 19). On this dam, ducks loafed on a particular slope 10-20m from the dam, which may have given them a better vantage point, from which to detect predators. Other Anatinae also tend to loaf and perform comfort activities in the water (Skead 1977). It seems sensible for animals to perform those activities not related to feeding in the safety of cover (Caraco 1979). During loafing or comfort bouts, Maned Ducks seemed to perform less Extreme head up behaviour, so proximity to the safety of water could be an advantage which offsets the reduced chance of predator detection. Owen and Thomas (1979) found that wigeon Anas penelope grazed closer to pools of water. Perhaps such behaviour reflects a similar vulnerability to aerial predators, rather than the suggested reason, that they need to drink often. Gillespie (1985) also found that anatids were more likely to damage those barley crops closest to water. However, in another study which looked at this interaction, Owen (1971) found that distance to safety was not an important determinant of grazing activity in White-fronted Geese Anser a. albifrons. Since farm operations were the disturbance factor considered, the geese could have become habituated, in the same way that Maned Ducks tolerated the passage of cars, perhaps rendering this an inappropriate measure of safety.

Terrestrial predators of Maned Ducks are probably red foxes, feral cats and man. I found some evidence that foxes preyed on Maned Ducks during banding and brood care (chapters 7 & 8). Twice, when I saw contact, ducks responded by simply moving away by about 10m. This may be the same sort of phenomenon reported for the lion, where the predator does not attempt capture if the prey are aware of its presence (Elliot et al. 1977) and as a consequence, prey do not exhibit true anti-predator behaviour. On the third occasion, at night, a fox pursued some ducks, which moved into the water to escape. Since fox attacks may have higher success rates on dark nights (Kruuk 1964), there may be an interesting interaction between nocturnal activities of Maned Ducks and predation pressure.

The activity patterns of the Maned Duck appear to be more similar to grazing Anatidae (Owen 1972, Ebbs et al. 1975, Harwood 1977, Burton & Hudson 1978; Owen & Thomas 1979; Fredrick & Klaas 1982) than those of

ducks more closely related, like the American Wood Duck Aix sponsa (Parr et al 1979)(Fig. 25). More time is spent grazing than in the diurnal feeding of other Anatinae (Siegfried 1974b; Norman et al. 1979), which may be related to the inefficiencies of a grazing habit. Some grazing geese seem unable to digest cellulose (Marriot & Forbes 1970) and so rely on a continuous flow of food (Sibley 1981) to obtain sufficient nutrients which may also be true of Maned Ducks.

With the increased amount of time spent grazing, little time is spent on the water. However, some behaviours necessitate that the link with the aquatic environment be maintained. Maned Ducks mate and bathe on the water. From this study there is a further, perhaps equally important factor. Maned Ducks require close proximity to water to escape predation. Like other Anatidae (Tamisier 1974, 1976), predation probably plays an important role in determining the spatial distribution of activity patterns in this species.

CHAPTER 5HABITAT ASSOCIATIONSIntroduction

There is some evidence that the range (Blakers et al. 1984) and number (Briggs et al. 1985b; chapter 1) of Maned Ducks have increased. The introduction and proliferation in farm dams have apparently made some positive contribution to this (Lavery 1966b; Braithwaite 1980; Frith 1982). Before the introduction of farm dams, Maned Ducks were probably confined to the timbered fringes of rivers or any naturally occurring areas of water (Gould 1865; North 1913; Frith 1959b, 1959c, 1982). A preliminary survey over this site indicated that not all farm dams were equally used by Maned Ducks. Frith (1957a) observed that flocks traditionally used a part of a river bank which was not obviously different to other areas. He suggested that there might be a combination of reasons for a particular area being attractive (Frith 1982, p 264). The large number of dams on the site seemed to provide a good opportunity for investigating such questions of habitat suitability using multivariate statistics. These have proved useful for hypothesis generation about bird-habitat relationships (Karr 1980; Capen 1981; Grier 1984).

Habitat selection or preference in birds is thought to operate through behavioural mechanisms which result from the summation of various proximate cues (Hilden 1965). Quantitative methods have revealed the complexity of this process (Karr 1980). A number of studies have purported to show relationships between waterfowl populations and habitat structure (Weller & Fredrickson 1973; Lokemoen 1973; Ringelman et al. 1982; Kaminski & Prince 1984), but the implication that ducks actually select in some of these, may be unjustified, since few studies have gone beyond a correlational approach (Wiens 1976; Karr 1980).

In this study, my primary objective was to determine which variables, reflecting habitat structure on farm dams, were closely related to the distribution of flying Maned Ducks and Maned Duck broods. Annual and seasonal (breeding and after breeding) habitat associations were compared and nest site characteristics assessed.

Methods

A) Survey methods

Counts of Maned Ducks for each dam, provided a measure of habitat use, and in conjunction with various physical variables for that dam, could be used to determine what habitat characteristics might be important. Similarly, counts of broods provided a measure of the suitability of brood rearing habitat.

Long term studies are usually required to adequately describe habitat use and overcome some of the methodological problems associated with its detection (Kikkawa 1968; Wiens 1983). To meet this requirement, I surveyed the dams on site A over a four month period (Sept-Dec), for the years 1981-1983. Ducks on a dam were easily counted throughout surveys because dams were so open (Fig. 4). Surveys often took the most part of the day, during which, I counted every Maned Duck on the site, recording on which dam they were. Surveys began when the first broods appeared during the annual breeding season (see chapter 6) and continued every four days until the end of December. However, due to the fact that breeding activity was erratic in 1982, this survey period was extended until the 10th of January 1983.

These survey methods may have produced two biases which would affect measures of habitat use. Conceivably, ducks could be counted twice since they sometimes flushed off a dam when I approached. This was unlikely to be important as I was usually able to see where they had flown and not include them again. The other bias was possibly more serious and demanded some attention. It was possible that dam use by Maned Ducks was related to the diurnal cycle. Regular surveys which visited a dam at the same time each day could then be biased. To offset this, I used four survey routes. However, these were not mutually exclusive since dams could usually be approached from only two directions. There was, however, some evidence that movement of Maned Ducks did not follow any regular pattern over the period of a day. Results of a Kolmogorov-Smirnov goodness-of-fit test (Zar 1974), on data collected during activity patterns showed that

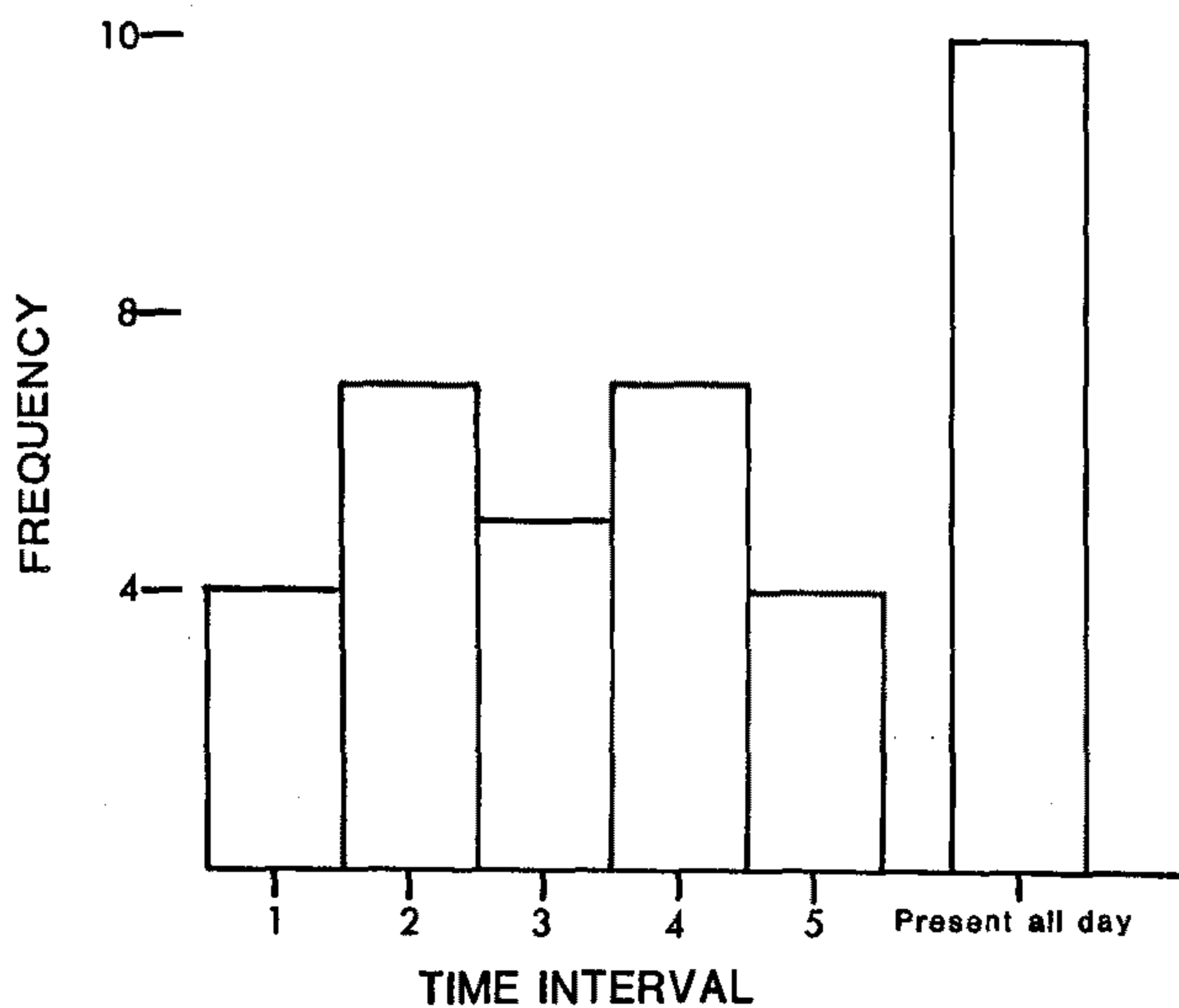


Figure 27. Frequency with which Maned Ducks left dams throughout the day (n=27). Time intervals are as calculated in Chapter 4. Last category is the frequency which Maned Ducks remained on a particular dam for the full day.

ducks did not leave dams at any particular time of the day (chi square=0.052, $p>0.05$, $n=27$). In fact, many flocks stayed on one of the four dams for the full day (Fig. 27).

B) Choice of variables

Partridge (1978) defines habitat to mean all the physical and biotic factors which make up the place in which an animal lives. Measurement of all the factors is obviously not possible. Some thought should be given to both the choice and the number of variables to be included which can have considerable bearing on results, particularly where multivariate statistical techniques are used (James 1971). I based variable choice on two criteria; they should have some plausible relationship to the behaviour of Maned Ducks (i.e. the variable was organism defined (Wiens 1976; Karr 1980; Taylor et al. 1984) and also, between years variation of variables was insignificant compared to the variation between dams. I used eleven variables measured for each of the 64 dams, to describe habitat structure.

These variables were; the amount of surface vegetation (COVER), age of dam (AGE), area, depth, composition of the surrounding vegetation (three variables; GRASS, CLOVER, TUSsock), visibility from duck height (VISIBIL), location, surrounding tree density (TREES) and the number of tree holes close to the dam (HOLES). I also included a dichotomous variable in 1982. This was WHEAT which identified those dams close to areas (<150m) where livestock were being hand-fed with wheat grain. It was not relevant in the other two years.

Methods for measuring seven of these variables, need to be described. Most dams were triangular or circular in shape so random measurements of the base/height and diameter gave area approximations. Depth was a mean of five random depth measurements made along a line strung across each dam. Using methods detailed in chapter 4, I calculated mean percentage cover for the amounts of grass (other than tussock), clover and tussock (Tuss). The bareground component reduced interdependence of variables which was important to later analysis. Some annual variation in the composition of surrounding vegetation was possible, although there was

considerable stability in the types of plants that made up particular pastures. To obtain measures of the visibility from duck height, I measured the distance from ground to eye level of ten Maned Ducks (mean=30.5cm $\pm$ 0.45 S.E.). These were held in the Extreme head up posture (see chapter 8) during banding (chapter 7). The calculated visibility measure was the mean of 16 measurements from this height. There were four measures taken from each quadrant. I randomly chose a position in each quadrant and from here, measures were taken; across, away from, and in either direction along the tangent to, the dam. I set an upper limit of 200m for each reading, so that the mean would not be influenced by large readings. Location signified whether or not dams were in a deep gully, flat open area or between the two. Objectivity was possible because the first two categories could be distinguished easily. Tree density, I measured on aerial photographs as the area within 400m of a dam covered by trees. In the field, I searched within the same area for the number of potential nesting holes (see next section).

C) Nest site characteristics

Maned Ducks are obligate hole nesters but finding nests was difficult because ducks often nested some distance from the dam. Watching the flight of incubating pairs after they had fed on a dam (see chapter 8), proved fruitless because they were soon lost amongst the trees. One way of assessing nest site density, was to inspect all potential cavities around a dam. A hole was deemed "potential" if the diameter exceeded 9 cm since this was the cavity size through which the smallest female Maned Duck could fit (girth measured while banding; n=10). Since breeding females tended to be large, the 12 cm hole for the largest female was probably more realistic. For each hole, I measured the diameter, depth, height above ground and distance to the nearest water. Trees were identified from their leaves and fruits (Brooker & Kleinig 1983). Methods for tree climbing followed those detailed in Perry (1978).

D) Data analysis

1) Abundance on Properties

I compared numbers of Maned ducks on the three properties, Grathawai,

Tanjenong and Bubalalah, during the months September-December, 1981-1983, using two factor analyses of variance (Zar 1974) following transformation of the data by $\log(x+1)$ to overcome heteroscedasticity of variances (Zar 1974). Separate one-way analyses of variance, for each measured variable, were also used to compare dams across the three properties.

2) Distribution

a) Multivariate analysis

I used Principal Component Analysis (P.C.A.) to describe dams into types, base on a reduced set of the selected variables. P.C.A. is a useful analytical technique for determining dependence when no prior patterns are suggested (Blackith & Reyment 1971). It reduces the dimensionality of the initial suite of variables by calculating newly transformed functions (components) which are orthogonal linear functions of the original variables (Kendall 1957). Geometrically, the first principal component comes from the highest eigenvalue (largest variance explained) and forms the first axis, with the next axis coming from that linear function which explains the next highest amount of variance and so on.

I also used multiple linear regression analyses, to find out how good the selected variables were at explaining the distribution of, both broods and fledged Maned Ducks. In this analysis, a linear model is formed which explains the variability of a dependent variable Y in terms of a number of independent variables, X_i s (Sokal & Rohlf 1981). The relative importance of each individual variable can also be determined. This overcomes cross correlational problems associated with those studies which employ simple correlation analysis (e.g. Godin & Joyner 1982). The general form for the multiple linear regression equation is;

$$Y = b_0 + b_1X_1 + b_2X_2 + \dots + b_iX_i$$

where b_0 is the Y intercept and b_i the partial regression coefficients. Standard partial regression coefficients (beta) provide a

further means for comparison of relative contributions made by variables. Tables X and XI give other parameters used to assess generated models.

Interpretation may be difficult if the regressor variables are correlated (multicollinearity) and could result in partial regression coefficients which are unreliable estimators of the true value (Kim & Kohout 1975; Green 1978). However, this does not render analysis invalid (Mead 1971). One solution is to first carry out a P.C.A. of the original variables to produce independent orthogonal components. These are then used in a multiple regression (Langlands & Sanson 1976; Short et al. 1983). This approach has two drawbacks. It is dependent on the interpretability of the components and the greatest danger is that some variable that is particularly important in the prediction of the dependent variable could be lost because it has little correlation with the original set of independent variables. For these reasons, I decided not to use this method. However, to reduce multicollinearity, I left depth out of regression analyses as it was reasonably highly correlated with Area ($r^2=0.547$) and of the two variables, it had less relevance to the ecology of the Maned Duck.

Violation of some assumptions may affect multiple linear regression procedures. The sample must be randomly drawn. I have mentioned possible biases in survey methods. The array of Y's for a given combination of X's should follow the normal distribution. Since I used a relatively large sample size, this assumption could perhaps be relaxed (Kim & Kohout 1975). Additionally, the regression of Y and X's must be linear and all the Y arrays must be homogeneous. For linearity, I examined scattergrams of duck-use against each variable. Direct examination of residual output through SPSS New Regression (Hull & Nie 1981) provides a means for checking if there are violations of the last two assumptions.

The first dependent variable in analyses was duck-use (a measure of the presence of fledged Maned Ducks). For duck-use, I excluded adults with broods. Furthermore, to make all survey days comparable, duck counts on dams in a given year were converted to a percentage of each survey day. This was because the primary objective of the study was an evaluation of habitat associations and the effects of large daily emigrations and

immigrations of Manded Ducks needed to be reduced. In addition, since habitat relations may vary through the breeding season (Whitmore 1979), I analysed the data for two periods. Period 1 corresponded to the breeding season (beginning of surveys up to when the last brood began to be incubated). Period 2 (after breeding) represented the remainder of the year. Annual variation in the length of the breeding seasons meant that a different number of survey days were included each year (Tables X & XI).

With such multivariate statistical techniques, some attempt should be made to crossvalidate the models produced (Green 1978; Sokal & Rohlf 1981). This permits an assessment of the validity of the generated models. I therefore, subdivided both parts of the survey period (breeding and after breeding) into two further separate samples of equal survey days. Since there are possibly time effects, I took consecutive survey days and randomly assigned them to the two samples.

Duck-use, the first dependent variable tested, was the summed values for each dam across all survey days in each sample. I divided data on habitat use, into four samples each year: two subsamples of data from breeding periods, and two subsamples of data from periods after breeding. Multiple regression analysis was then performed on each sample.

The second dependent variable tested was brood-use. This was a count of the number of days that each brood stayed on a particular dam and gave a dependent variable in "brood-days". This was then square root transformed to improve normality (Sokal & Rohlf 1981). However, before doing the regression analysis, I included a further variable, (Hatch). This took care of broods which were on a dam simply because adults nested there. Only broods which were found when ducklings were 2-3 days old scored for this variable. Since broods are led to the nearest water following hatching (Frith 1982), I assumed that nest sites were closest to these particular dams.

I used the SPSS stepwise multiple regression program, NEW REGRESSION, for these analyses (Hull & Nie 1981). This takes the variable which makes the greatest reduction in the residual variation of the dependent variable and includes it first. It is a better technique than forward or backward

methods, as it allows for variables already included to be deleted (Green 1978).

Maned Ducks were not present on a few dams each year. To find out which variables might distinguish these dams from dams which were used, I applied two group discriminant function analysis (Green 1978). Here, the selected variables form a single function which best discriminates between the two groups. I used the stepwise Wilks' method which extracts the single best discriminating variable at each step from those remaining, significantly improving Wilks' lambda (Klecka 1975). As in stepwise multiple regression, this procedure allows for subsequent removal of variables if their power of discrimination is reduced after addition of variables in later steps.

3) Breeding

a) Nest Holes

Inspected holes were categorised into those used by Maned Ducks, other birds, mammals, those with indeterminate occupancy and those not used by vertebrates. I used unbalanced one-way analyses of variance to compare diameter, depth, height above ground and distance to water. Data were transformed ($\log x+1$) to correct for heterogeneity of variances (Zar 1974).

b) Brood Production

To examine the importance of tree cavity density on dams to brood production, I regressed the number of broods hatched on each dam (earlier defined) against the number of Holes for that dam. Both variables were transformed by $(x+0.5)^{1/2}$ to improve normality (Zar 1974).

TABLE VI. Descriptive statistics of eleven variables measured on each of 64 dams. The qualitative variable (Gully) was ranked 0-3

	MEAN	MEDIAN	MAX	MIN	STDEV
PERCOV(%)	6.5	0	70	0	17.4
AGE(yrs)	11.5	11.0	48	1	9.6
AREA(m ²)	329	218	2290	40	348
DEPTH(cm)	110.0	120.0	253.0	15.0	53.8
GRASS(%)	61.5	63.0	95	20	18.7
CLOVER(%)	21.9	18.0	67.0	0	17.8
TUSS(%)	5.7	0	50.0	0	12.1
VISIBIL(m)	64	62	148	26	21.4
TREES(x10m ⁴)	9.9	6.5	33.5	0	9.5
HOLES	2.30	0	18	0	4.0

LOCATION 0 1 2 26 27 11

TABLE VII. Correlation matrix for ten dam variables (** significance at p<0.01) n=64

	PERCOV	AGE	AREA	DEPTH	GRASS	CLOVER	TUSS	VISIBIL	TREES	HOLES
AGE	-0.105									
AREA	0.033	-0.071								
DEPTH	-0.204	-0.267	0.547**							
GRASS	0.056	-0.136	-0.063	0.095						
CLOVER	-0.063	0.088	-0.158	-0.327**	-0.578**					
TUSS	0.096	-0.104	0.060	0.109	-0.088	-0.359				
VISIBIL	-0.137	0.024	0.203	0.211	0.241	-0.075	-0.287			
TREES	0.099	-0.092	0.070	-0.006	-0.085	-0.224	0.395**	-0.381**		
HOLES	-0.029	-0.121	0.139	0.136	0.000	-0.101	0.060	-0.160	0.088**	

Results

A. Characteristics of farm dams

Table VI shows descriptive statistics for the 11 variables measured on all dams in the study site. The cumulative age distribution of dams is presented in Figure 28 as well as when Maned Ducks were first reported in this area (chapter 1).

Interrelationships between the variables can be illustrated using correlations (Table VII). Correlation coefficients greater than 0.320 are significant at $p < 0.01$ (62 df). Clover and grass were negatively correlated so that dams tended to have either clover or grass surrounding them and dams with a large surface area tended to have the greater average depth. Although Holes and Trees had a significant correlation, this was not as high as expected. This was the result of clearing practices, during which most of the smaller trees are usually knocked down leaving a few mature trees which are the ones with cavities.

To categorise dams, variables were combined using Principal Component Analysis (P.C.A). Location was left out because qualitative variables weaken this type of analysis (Jeffers 1982). Bartlett's sphericity test showed that the overall correlation matrix was significant (chi-square $_{45} = 136.31$, $p < 0.001$), justifying the use of P.C.A. (Green 1978). This extracted four independent orthogonal components, which had been rotated to make them conceptually simpler (Table VIII). There were others, but only those components whose eigenvectors exceeded unity were retained (i.e. accounted for more than 10% of the variability). In total, the four accounted for 65.8% of the variance. The loadings relate the variables to these components (Table VIII) and represent amount of correlation each of the measured variables has with the particular component. Comrey (1973) considered that loadings lower than 0.45 were fair to poor contributors for orthogonal interpretation. Following this criterion, I looked at only those loadings above this level.

Three variables, Tussock, Tree density and Holes had high positive

TABLE VIII. Results of Principal Component Analysis after Varimax-Rotation, giving factor loadings of each of 10 dam variables measured on the sixty-four dam in the study site

	Component			
	I	II	III	IV
PERCOV	0.05	-0.16	0.03	0.83
AGE	0.09	-0.35	-0.12	-0.47
AREA	0.03	0.84	-0.07	0.05
DEPTH	0.02	0.86	0.17	-0.08
GRASS	-0.16	-0.07	0.92	0.05
CLOVER	-0.28	-0.21	-0.82	-0.09
TUSS	0.62	0.12	0.07	-0.29
VISIBIL	-0.65	0.32	0.29	-0.16
TREES	0.84	0.02	0.03	-0.02
HOLES	0.59	0.15	0.21	-0.31
Eigenvalues	1.98	1.65	1.69	1.14
Variance explained	20.0%	16.9%	17.3%	11.6%
Cumulative variance	20.0%	36.9%	54.2%	65.8%

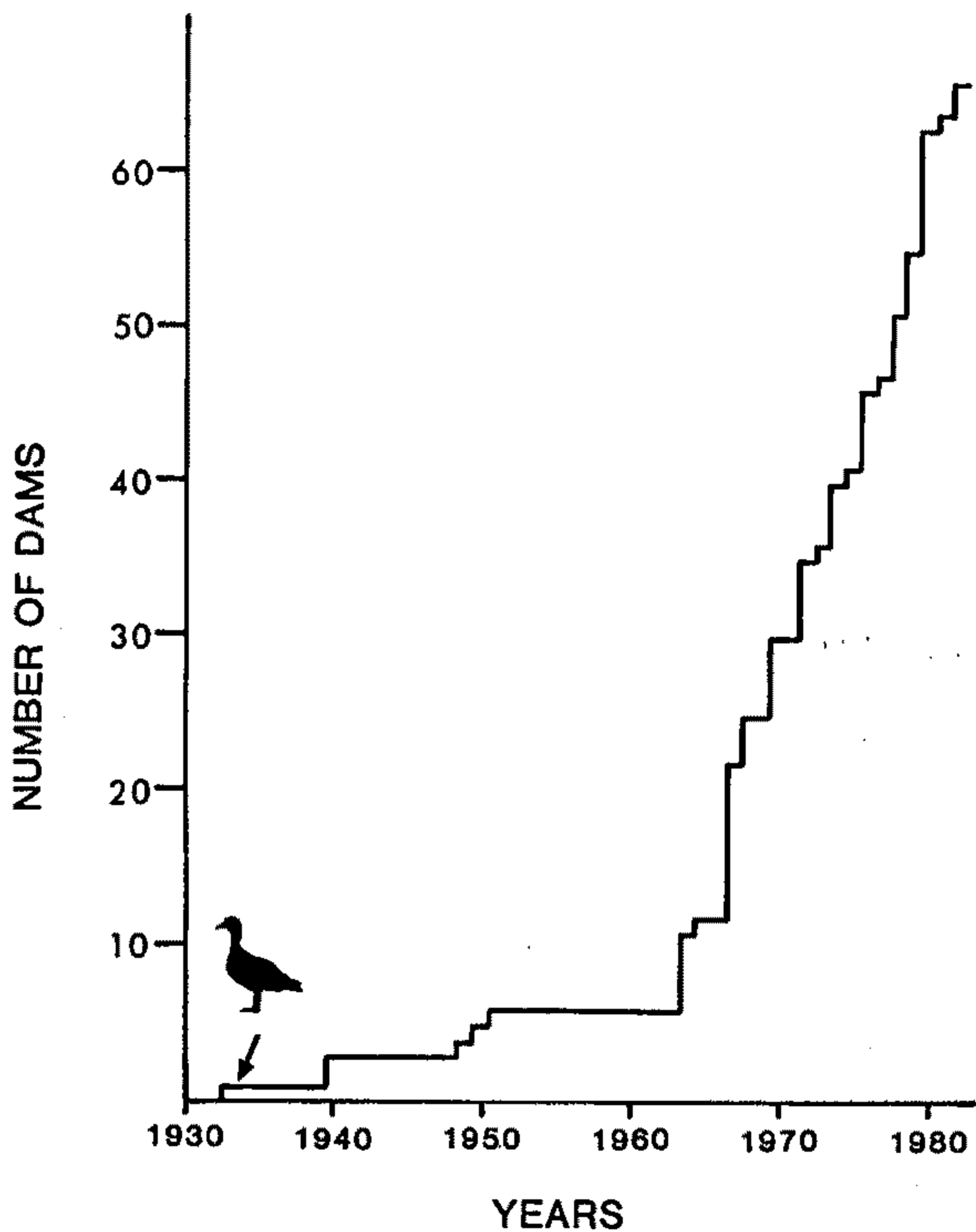


Figure 28. Age at which dams were put in, as a cumulative total. The Maned Duck shows when the first anecdotal sighting of the species occurred in this area.

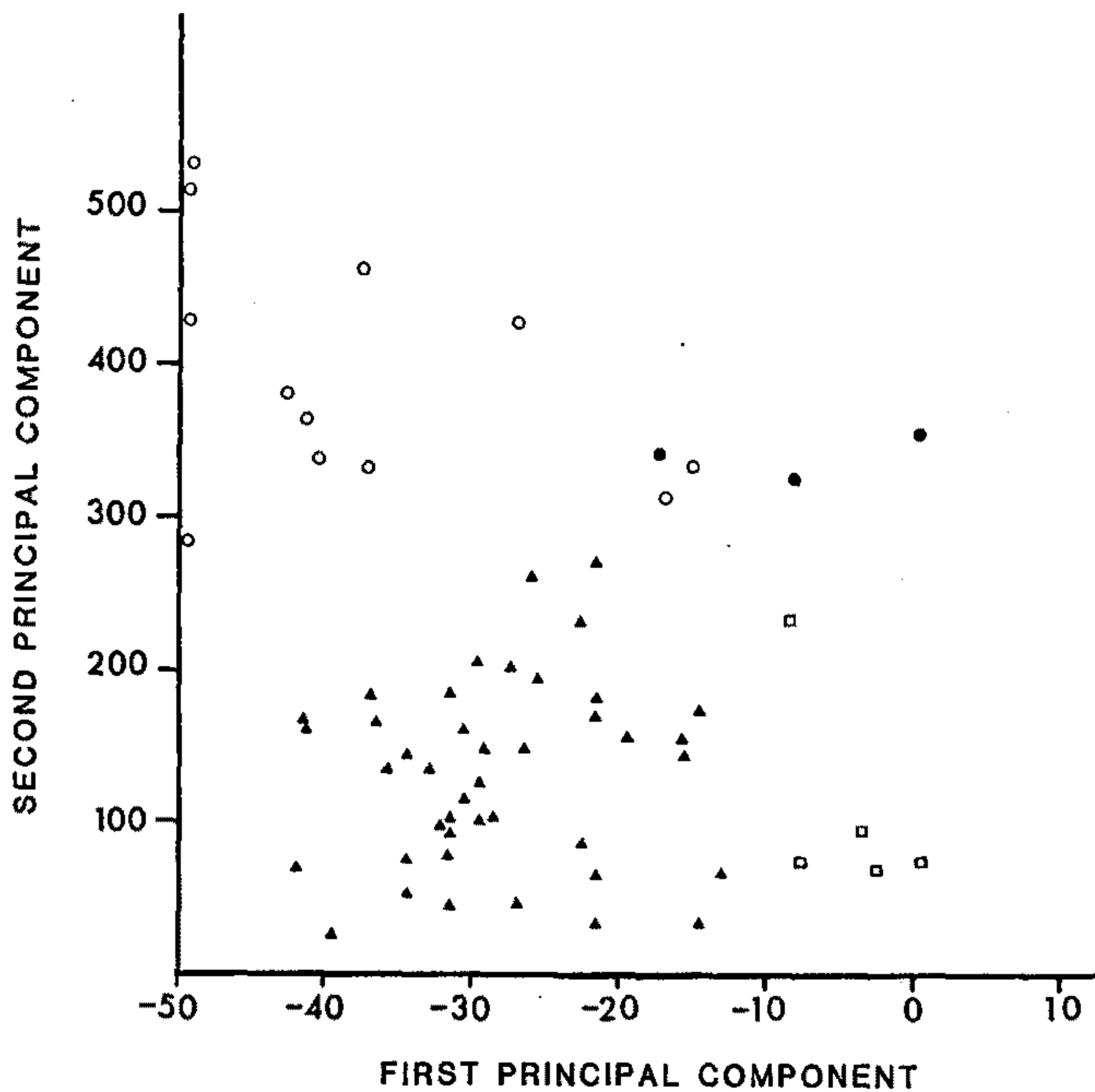


Figure 29. Positions of the 64 dams in the reduced space of the first two principal components (after rotation). Open circles are large dams, open squares woodland dams, closed circles large woodland dams and closed triangles are those dams which could not be determined.

loadings on the first component, while Visibility loaded quite highly in a negative direction. This component categorises dams in woodland areas. Here, little clearing had occurred and few exotic pastures established (high tussock loading). The average visibility from duck height was also restricted on woodland dams because of the tall coarse tussock grass (seldom grazed low by livestock) and the large number of surrounding trees. The second component could be considered as one of size. It had high loadings on area and depth. Surprisingly, it only accounted for 16.9% of the variability and reflects the fact that dams tended to be the same size. I took these first two components and calculated component scores for each dam and graphed these (Fig. 29). Dams found in woodland areas and large dams ($>430\text{m}^2$) are featured. However, these components together do not account for a large amount of the variability. Most dams remained clumped together.

Grass and clover loaded highly on the third component although in opposite directions. This could be interpreted as reflecting the vegetation structure of the dam surrounds. The fourth component proved more difficult to interpret. The amount of surface vegetation is the dominant variable but there is also a small negative loading on age. This categorised recently established dams with a large amount of surface vegetation.

B. Abundance of Maned Ducks on farm dams

There were three properties on site A (see chapter 2). Two of these, Tanjenong and Bubalalah were adjacent. Property size and the number of dams present each year, are given in Table IX.

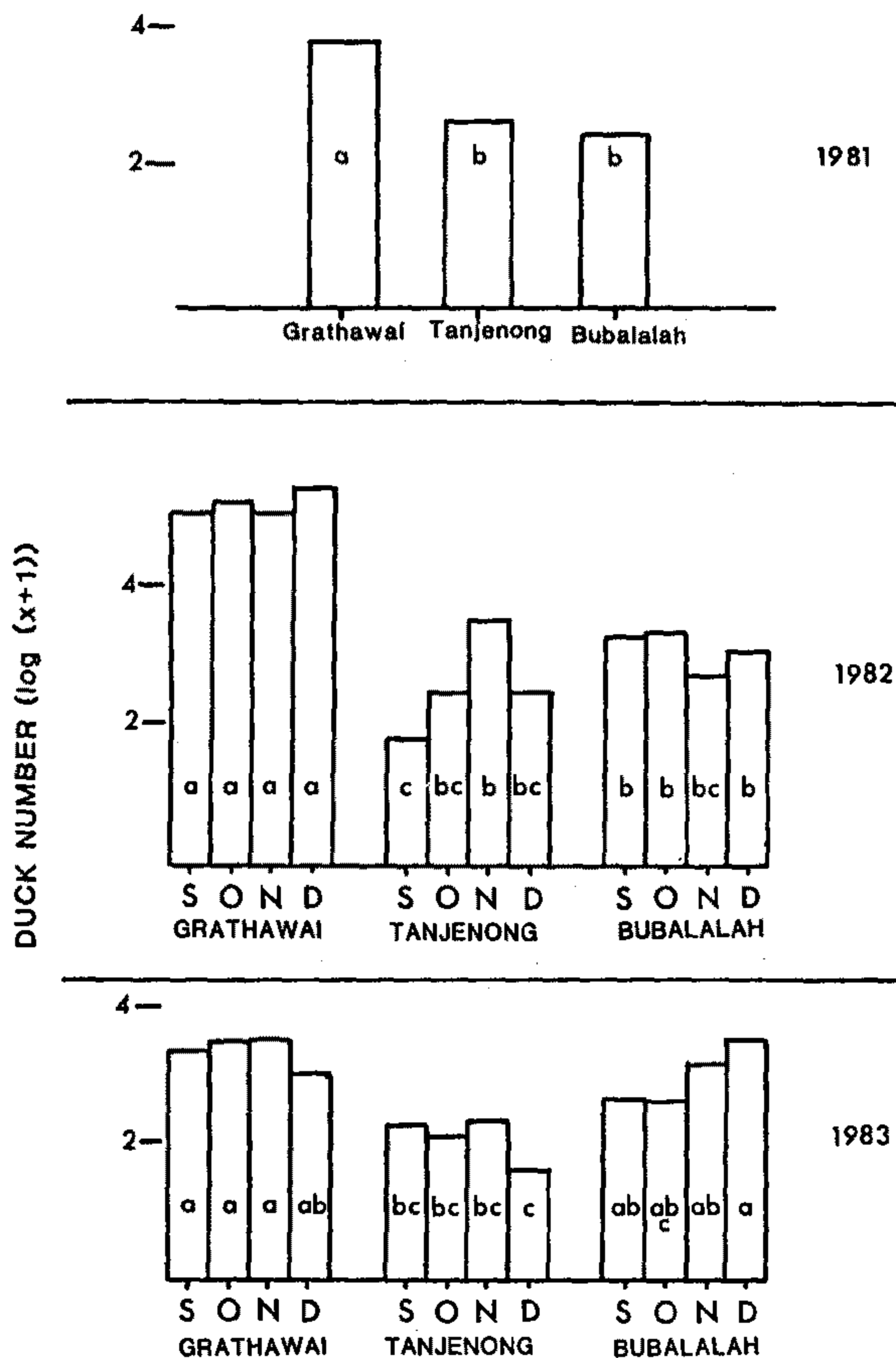


Figure 30. Results of three separate (1981-1983) analyses of variance (Months x Properties) for each of the three years. In 1981, only the main effect was significant ($F_{2,66}=24.3$, $p<0.001$) while in 1982 and 1983, there were significant first order interactions ($F_{6,99}=14.6$, $p<0.05$) and ($F_{6,93}=2.3$, $p<0.05$) respectively. Letters in histograms group means for which there was no significant difference for any one year ($p>0.05$) using Student Neuman Keul's tests.

TABLE IX. Comparison of the three properties on study site A

PROPERTY	AREA (ha)	%Agr Development	No. of DAMS		
			1981	1982	1983
Grathawai	1100	80	40	34	42
Tanjenong	1200	40	10	7	10
Bubalalah	200	100	14	13	14

Grathawai, although not the largest property, had the most dams. A large percentage of this property has also been sown to improved pastures. In contrast, Tanjenong is slightly bigger but has few dams and comparatively little agricultural development. Bubalalah, which is the smallest in area, has a similar number of dams to Tanjenong. Different numbers of dams were the result of two more dams being established in 1983, while some dried up in 1982.

I compared dam types on the three properties. One-way analyses of variance, for each of the selected variables, showed no differences between the dams on the three properties for any of the variables measured. Although dam types were similar on the three properties, the numbers of Maned Ducks found on each, were different.

In 1981, there was no interactive effect (Table 3-A, Appendix 3) and numbers did not change over the four month period September-December ($F_{3,66} = 1.704$, $p > 0.05$). However, there was a highly significant property effect ($F_{2,66} = 24.29$, $p < 0.001$). There were more ducks on Grathawai than on either Tanjenong or Bubalalah (Fig. 30). Numbers on the latter two properties' dams were similar.

The results in 1982 were not as clear cut (Table 3-B, Appendix 3). They were complicated by the fact that there was a significant interaction term ($F_{6,99} = 2.49$, $p < 0.05$). Nevertheless, numbers of Maned Ducks on Grathawai exceeded those found on the other two properties (Fig. 30). Results of Student Newman Keul's (SNK) tests also showed no consistent

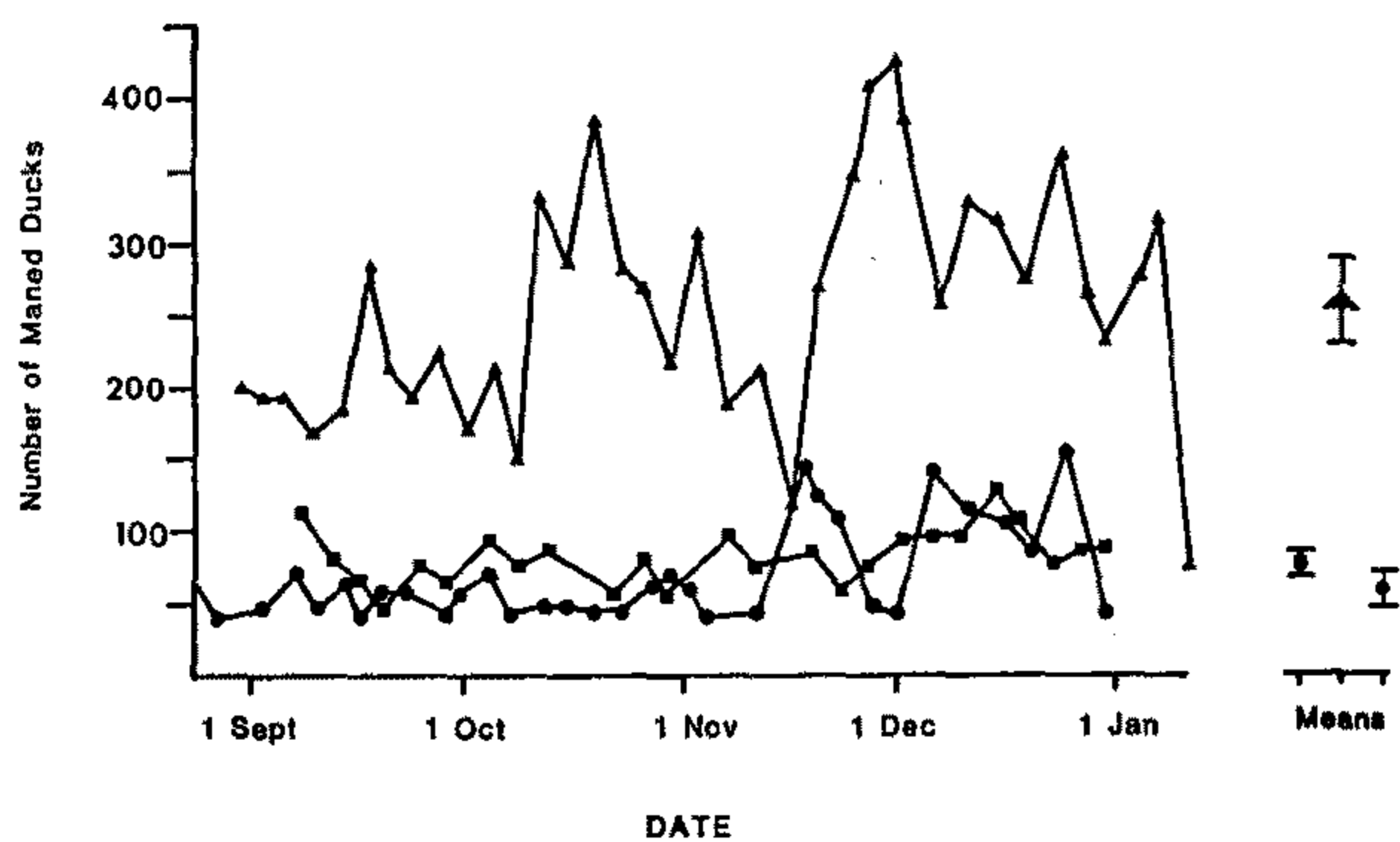


Figure 31. Survey counts of Manded Ducks for 1981-1983. Means and 95% confidence limits also given for each year.

differences between the other two properties although September numbers on Tanjenong were below nearly all those of Bubalalah. As with the previous analysis, there was a significant interactive term in the 1983 analysis ($F_{6,93} = 2.26, p < 0.05$; Table 3-C, Appendix 3). Maned Duck numbers differed according to the month and property. Grathawai no longer held an unassailable position with the greatest number of ducks (Fig. 30). Bubalalah had as many Maned Ducks in December as Grathawai. This was because, for some time, there was a large flock camped on dam B.16 which may have reflected flock social dynamics after breeding more than habitat selection. Numbers on Tanjenong tended to be lower than those on the other properties.

Apart from property differences, there was also considerable annual variation in total numbers of Maned Ducks (Fig. 31). Population counts were variable, with similar numbers in 1981 and 1983 but significantly more ducks counted in 1982.

C) Distribution of Maned Ducks

Results of stepwise multiple linear regression used to examine relationships between the distribution of Maned Ducks and the ten variables are presented in Table X and XI. Analysis of each pair of subsamples has yielded similar results with the same independent variables usually being included and accounting for a similar proportion of the variance. This is good evidence for the validity of the analyses used and gives confidence concerning the generality with which conclusions can be drawn.

1) Breeding Season

Final linear models accounted for different amounts of variation ranging from 11.7% in sample 2 (S2) of 1983 to 38.7% in S2 of 1982 (Table X). All multiple correlation coefficients were positive, reflecting the association of independent variables with the dependent variable. Apart from the variable Gully, all other variables were related

TABLE X. Results of stepwise multiple linear regression of duck use, during the breeding seasons of 1981, 1982 and 1983 on 64 dams, using the eleven selected variables and Wheat in 1982. Coefficients of multiple correlation (R) and standardised regression (beta) are presented for those variables which explained a significant amount of the variation. These are listed according to their order of addition to relevant models. (*-p<0.05; **-p<0.01; ***-p<0.001). n is the number of sample days included in a particular regression analysis

BREEDING SEASON.

YEAR					Inor in				
(n)	SAMP	VARIABLE	R	R ²	adj R ²	var. expl.	Beta	t-val.	sig.
1981	S1	Holes	0.326	0.106	0.092	0.106	0.364	3.07	**
(6)		Visibil	0.403	0.163	0.135	0.056	0.241	2.03	*
	S2	Visibil	0.349	0.122	0.108	0.122	0.402	3.53	***
		Holes	0.478	0.229	0.203	0.106	0.331	2.90	**
1982	S1	Wheat	0.562	0.316	0.302	0.316	0.562	4.90	***
(15)									
	S2	Wheat	0.593	0.352	0.339	0.352	0.642	5.85	***
		Gully	0.640	0.410	0.387	0.058	-0.246	-2.24	*
1983	S1	Visibil	0.330	0.109	0.095	0.109	0.385	3.50	***
(10)		Holes	0.501	0.251	0.227	0.142	0.380	3.45	***
	S2	Visibil	0.361	0.130	0.117	0.130	0.361	3.10	**

positively to duck-use. In the breeding season of any one year, the same variables were included in the particular linear model for the two samples. However, the order of inclusion for Holes (numbers of potential nest holes around a dam) and Visibility (average distance that one could see from duck height) was reversed in S2 1981. The contribution of Visibility differed between the two samples but parameters for Holes were similar. In 1983, the S1 model also included these two variables but the S2 one did not add Holes. Nevertheless, Holes did have the next highest partial correlation with duck-use and would have been the next variable included in the equation.

Four models included Visibility. Three of these also had Holes as an important regressor variable. Comparison of contributions made by variables can be achieved by looking at the standardised regression coefficients (beta). These show that the relationship with Visibility just exceeded that with Holes in most models where both were included, the exception being S1 1981 (Table X).

Drought feeding of livestock feeding near dams (Wheat) in the breeding season of 1982, accounted for more of the variation than did any of the variables included for other years. This variable was the one most related to duck-use. In S2 1982, Gully was included and related to duck-use in a negative direction.

2) After breeding

Five of the original variables explained a significant amount of the variation, namely Visibility, Area, Grass, Wheat and Holes (Table XI). Apart from Holes in S1 1982, all were positively related to duck-use.

Area (surface area of dams) was the most frequently included variable, and occurred in all models, except S2 1982. The positive relationship between Area and duck-use was the highest in S1 1982. Another variable included more than once was Visibility (S1 1981 and S2 1982). This accounted for a similar amount of the variation for the two periods. As in the breeding season, Wheat was related to duck-use in

TABLE XI. Results of stepwise multiple linear regression of duck use, after breeding in 1981, 1982 and 1983 on 64 dams, using the eleven selected variables and Wheat in 1982. Coefficients of multiple correlation (R) and standardised regression (beta) are presented for those variables which explained a significant amount of the variation. These are listed according to their order of addition to relevant models. (*-p<0.05; **-p<0.01; ***-p<0.001). n is the number of sample days included in a particular regression analysis

AFTER BREEDING.									
YEAR					Incor in				
(n)	SAMP	VARIABLE	R	R ²	adj R ²	var. expl.	Beta	t-val.	sig.
1981	S1	Visibill	0.328	0.107	0.093	0.107	0.276	2.317	*
(7)		Area	0.411	0.169	0.142	0.062	0.253	2.129	*
	S2	Area	0.436	0.190	0.177	0.190	0.451	4.05	***
		Grass	0.497	0.247	0.222	0.057	0.240	2.15	*
1982	S1	Area	0.522	0.272	0.258	0.272	0.497	4.76	***
(4)		Wheat	0.639	0.408	0.385	0.136	0.391	3.76	***
		Holes	0.687	0.471	0.440	0.035	-0.254	-2.45	*
	S2	Visibill	0.382	0.146	0.130	0.146	0.346	2.76	**
		Wheat	0.464	0.215	0.184	0.069	0.266	2.12	*
1983	S1	No variables included.							
(7)									
	S2	Area	0.441	0.195	0.182	0.195	0.441	3.93	***

1982. The final two variables, Grass and Holes, were included as the last variables in the respective equations of S2 1981 and S1 1982. Both accounted for little variation although it is interesting that Holes was negatively related to duck-use.

3) Comparison of multiple regression models

I graphed partial regression coefficients and associated 95% confidence intervals for variables included more than once over all models (Fig. 32). Regression coefficients for Holes although similar ($p > 0.05$) during the breeding season, were different from the one after breeding in 1982 ($p < 0.05$). Where Visibility was included in models, it did not differ significantly. However, Wheat had a much stronger relationship during the breeding season of 1982 than after breeding ($p < 0.05$), although this may be attributable to the small number of survey days included in this sample. Area, which was only relevant after breeding made a similar contribution to the models, it was included in.

4) Dams not used

No ducks were recorded on nine of the dams in 1981, nine in 1982 and ten in 1983. Discriminant functions had poor discrimination power, given by the high Wilk's lambda (varies between 0 for high discrimination and 1 for low discrimination) and the low amount of variation explained (squared canonical correlation coefficient). However, some variables were significant as discriminators. Percentage surface of the dam covered by vegetation (Percov) was the most important variable, operating in a negative direction, in all the discriminant functions (Table XII). This translated into a positive weighting (Fisher's linear discriminant classification) of those dams not used (0) and a negative weighting in dams used in group 1. Maned Ducks tended not to be found on those dams with a lot of surface vegetation. The other variable included, in all functions, was Trees (density of trees around dams). In 1981, Maned Ducks tended to be found on smaller dams with fewer trees. The case was the same in 1982 although the presence of wheat was an important

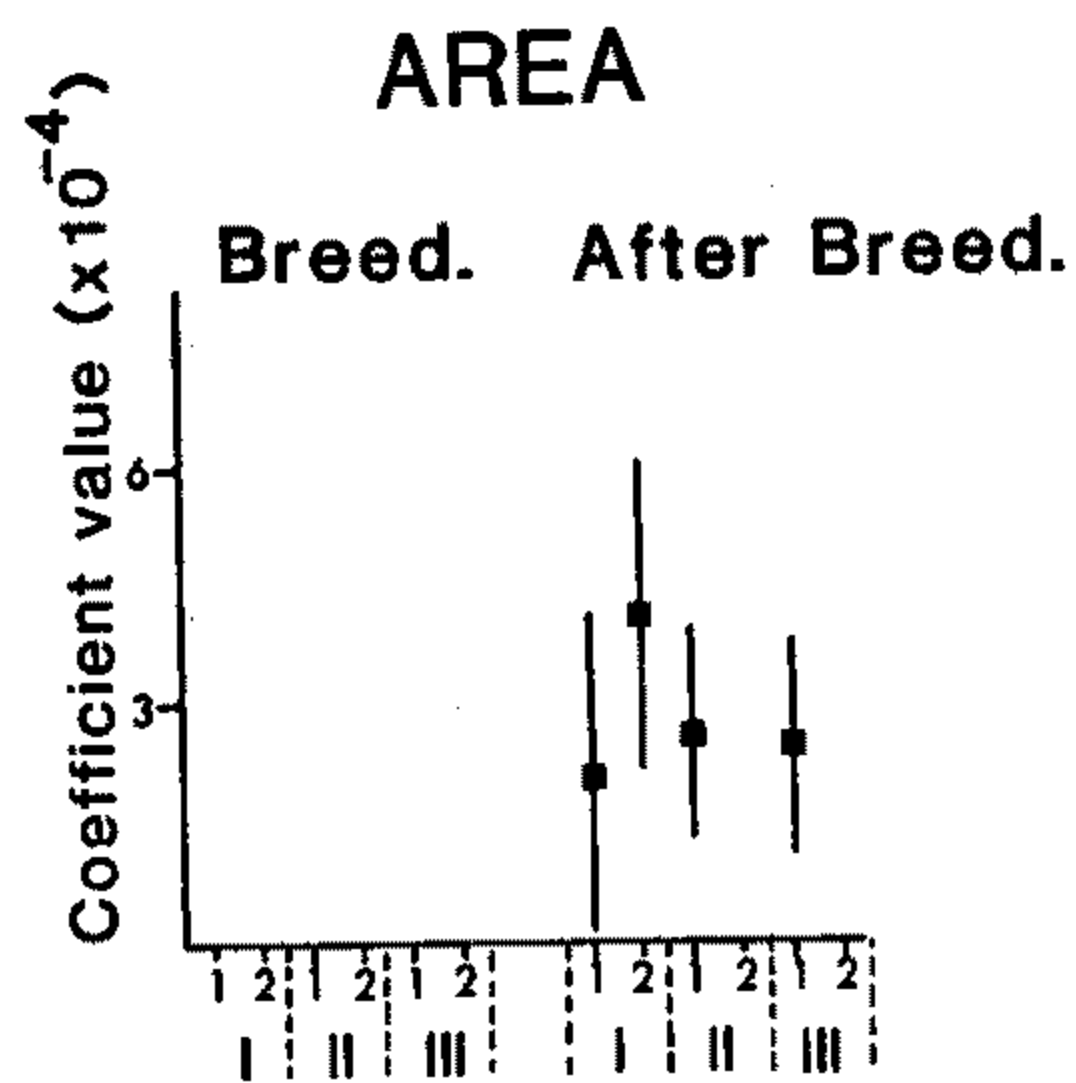
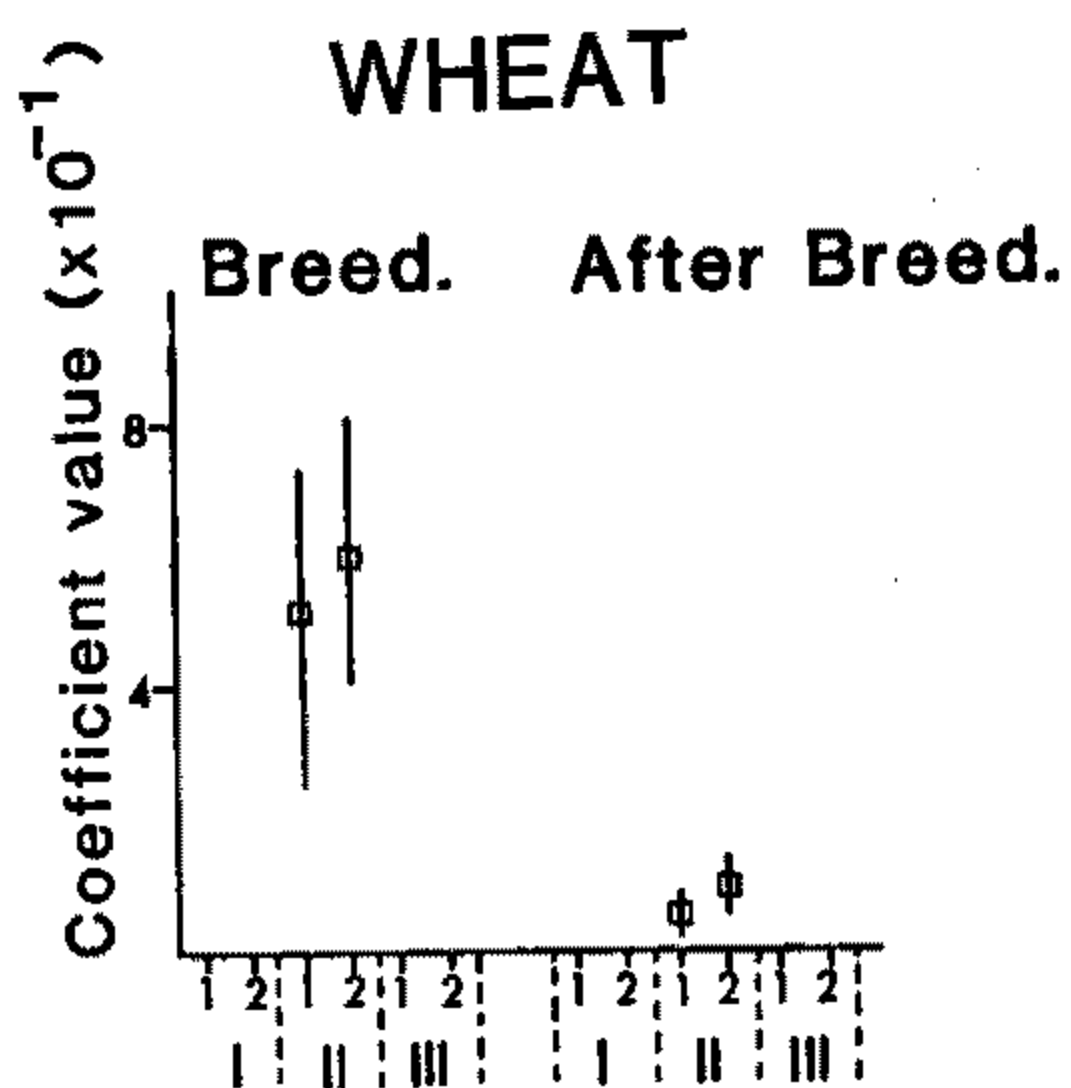
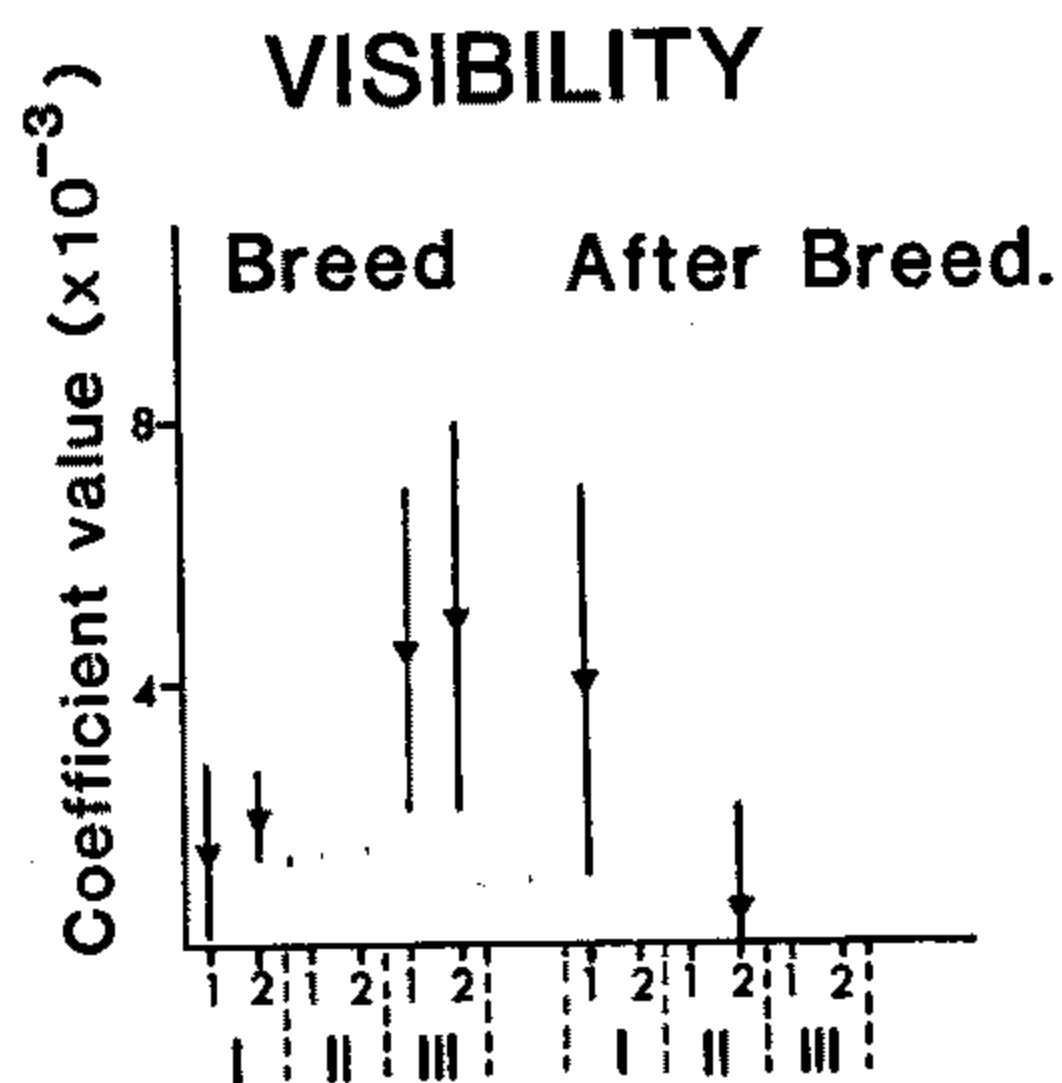
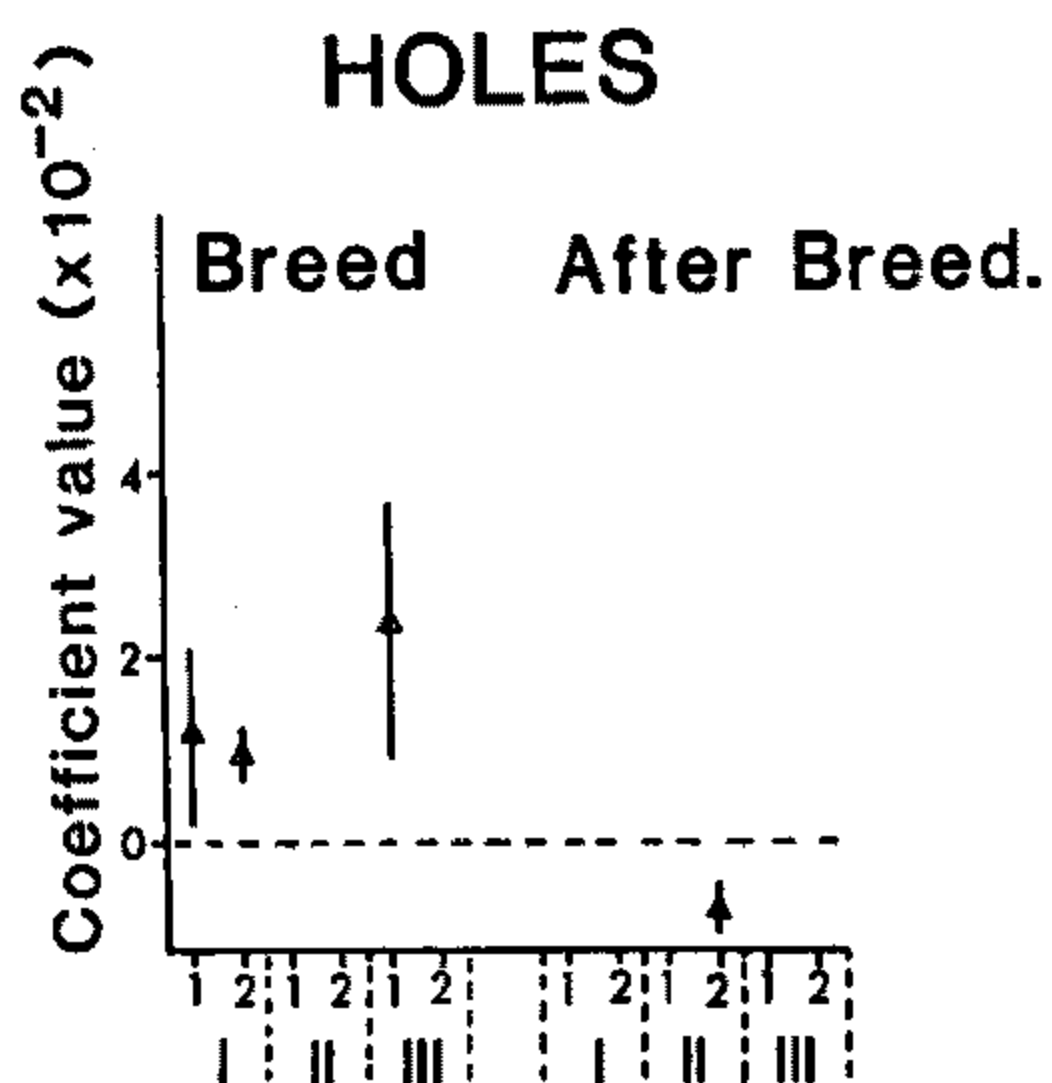


Figure 32. Regression coefficients (with 95% confidence intervals) compared for variables included more than once in stepwise multiple regression analyses. Duck-use was the dependent variable analysed during breeding and after breeding. 1 and 2 designate the sample number. I, II, and III represent the respective years 1981, 1982 and 1983.

Table XII. Results of stepwise discriminant function analysis using Wilk's method for two group discrimination; dams where Maned Ducks were recorded at least once (1) and dams where no Maned Ducks were found (0), for a particular year. CC^2 is the canonical correlation coefficient. Significant variables are listed in order of addition to the three discriminant functions

YEAR	CC^2	WILK'S LAMBDA	VARIABLE	STANDARDISED CANNON. DISCRIM. FUNCTION	FISHER'S LINEAR DISCRIM. FUNCT.	
				COEFFICIENTS	0	1
1981	0.25	0.755	Percov	-0.752	0.075	-0.002
			Area	0.459	0.001	0.030
			Tree	0.667	0.005	0.103
1982	0.26	0.737	Percov	-0.787	0.053	-0.004
			Area	0.351	0.003	0.006
			Tree	0.494	0.059	0.121
			Wheat	0.532	0.473	2.317
1983	0.23	0.77	Percov	-0.871	0.072	-0.006
			Age	0.604	0.233	0.141
			Tree	0.604	0.023	0.096

discriminator.

5) Traditional dam use

Those ten dams with the most Maned Ducks (summed over all survey days) for each year were ranked and are presented in Figure 33, for each year. At one stage during the three years, 22 out of the 64 dams could be ranked in the top ten dams used. Only one of these, G.33, was included in the top ten dams each year. Six registered in two of the years while the majority, fifteen, appeared only once. Those that were important in more than one year showed no consistency in their rankings.

D) Nesting Habitat

1) Hole characteristics

I climbed 74 trees and inspected 95 holes (Table XIII). Eucalyptus dalrympleana and E. bridgesiana were the dominant tree species. Few trees had holes. Most trees with holes were Mountain gums E.dalrympleana, although I found holes in other eucalypt species, E. pauciflora, E. rossi, E. tereticornis, E. mannifera, E. viminalis, and E. polyanthemus. Those trees with holes were usually the larger ones. Other common eucalypt species with no cavities were E. macrorhyncha, E. fastigata, and E. bridgesiana. Of the 95 holes inspected only nine holes proved to be used by nesting Maned Ducks. Many (39) had never been used by birds or mammals. These tended to be shallower ($F_{4,94}=28.0$, $p<0.001$) than Maned Ducks' nests and usually contained leaves and dead branches. Others seemed to be used but it wasn't possible to say any more about them. There was usually little debris on the floor of the cavity. Three Sugar Gliders Petaurus breviceps four Greater Gliders Petauroides volans and three Brush-tailed Possums Trichosurus vulpecula were the mammalian occupants of ten of the holes. I found sign that only a few birds used the holes; Australian Kestrel Falco cenchroides Sulphur-crested Cockatoo Cacatua galerita and a Spotted Pardalote Pardalotus punctatus.

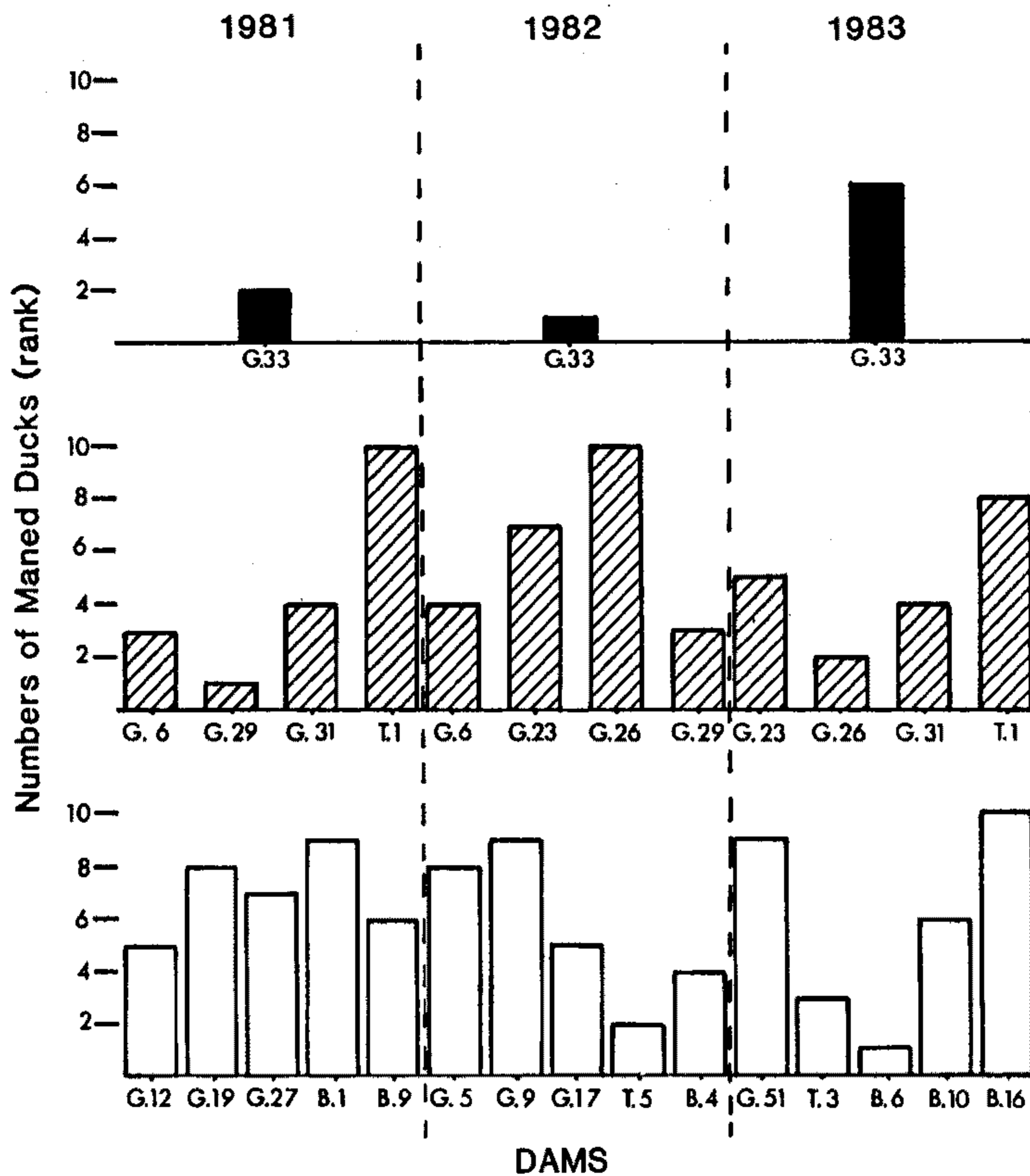


Figure 33. Ten dams with the highest recorded number of Maned Ducks for each year. Dams are ranked according to total numbers each year. Letters refer to individual dams on the three properties, Grathawai, Bubalalah and Tanjenong. Solid bars-dam ranked each year, hatched bars-dams ranked twice in three years and open bars-dams ranked once in the three years.

Table XIII. Mean measurements for holes inspected on trees (n=95). Results given for analyses of variance to compare four of the categories (other bird species not included)

Manned Ducks				Mammals determined used			
Other				Not			
				Not			
Diameter (cm)	17.6	15.6	19.1	14.7	16.5	ns	
Depth (cm)	126.2	77.0	87.0	88.4	31.4	0.001	
Height above ground (m)	6.6	8.6	7.9	8.0	7.4	ns	
Distance to water (m)	85.6	83.0	88.0	120.0	110.0	ns	
Number found.				33	39		

TABLE XIV. Results of stepwise multiple regression of brood use (square root transformed), during 1981, 1982 and 1983 on 64 dams, using the 11 selected variables, Hatch and Wheat in 1982. Coefficients of multiple correlation (R) and standardised regression (beta) are presented for those variables which explained a significant amount of the variation. These are listed according to their order of addition to relevant models. (*-p<0.05; **-p<0.01; ***-p<0.001)

YEAR	VARIABLE	R	R ²	adj R ²	var. exp.	Beta	t-val.	sig.
1981	Holes	0.648	0.420	0.411	0.420	0.633	6.76	***
	Tummock	0.683	0.468	0.449	0.047	0.216	2.31	*
	Hatch	0.773	0.597	0.589	0.597	0.605	5.86	***
1982	Holes	0.806	0.649	0.635	0.052	0.283	2.74	**
	Hatch	0.678	0.460	0.451	0.460	0.470	5.34	**
	Area	0.807	0.651	0.640	0.191	0.444	6.08	***
1983	Holes	0.825	0.681	0.666	0.031	0.212	2.44	*
	Hatch	0.678	0.460	0.451	0.460	0.470	5.34	**
	Area	0.807	0.651	0.640	0.191	0.444	6.08	***

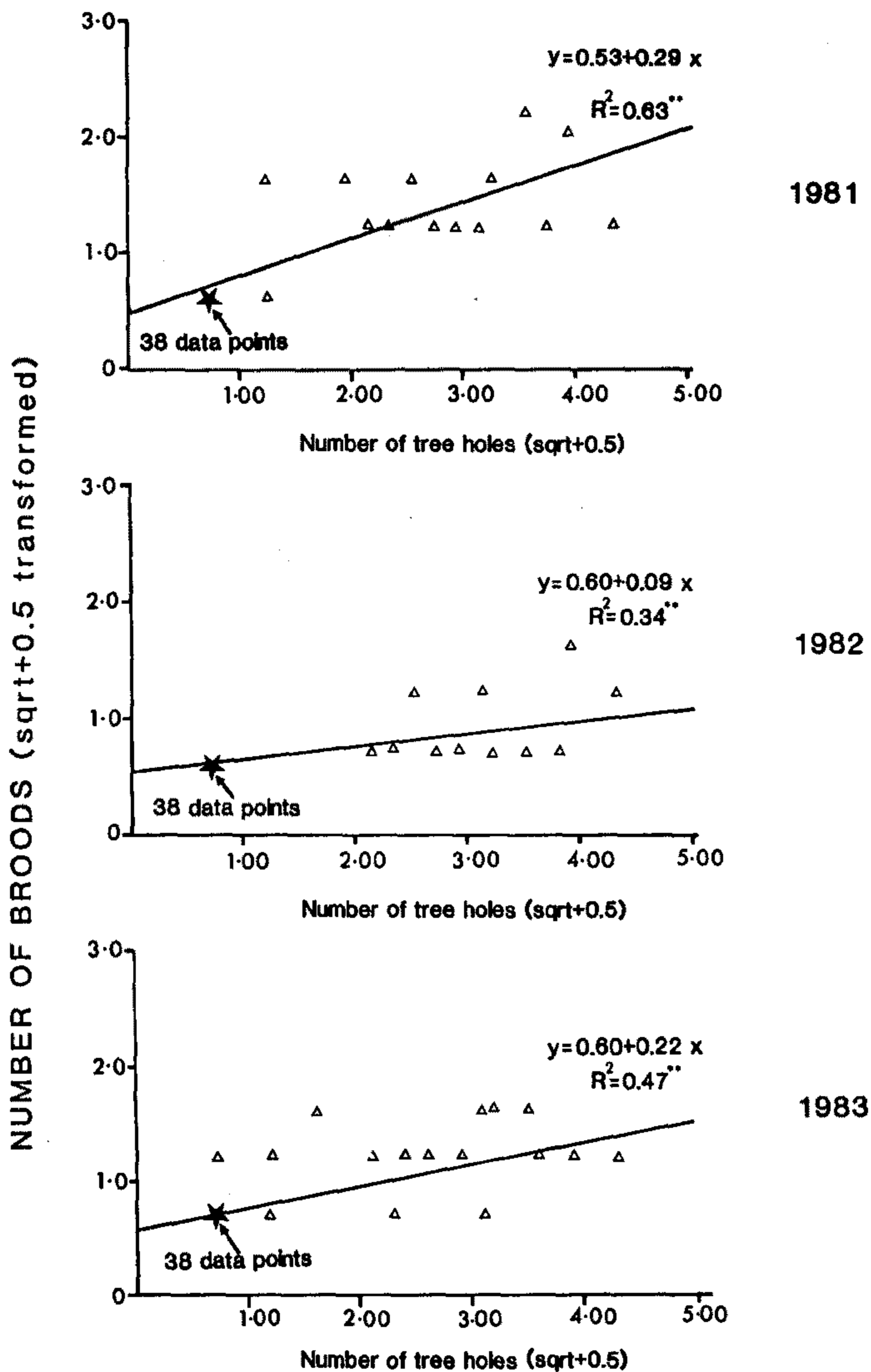
Incr in

2) Brood Production

There were more broods produced on those dams which had a higher number of holes (Fig. 34). However, analysis of covariance showed this was not a consistent relationship in the three years (1981-1983) ($F_{0.05(1),2,188}=256.7$, $p<0.001$). SNK tests showed that all slopes for regression equations were different ($p<0.05$). This meant that the density of holes, although important to production, was not a constant predictor of the number of broods produced.

3) Brood Use

Table XIV presents results of stepwise multiple regression models. The three models accounted for 46.7%, 64.9% and 68.1% of the variation in the three separate years. The multiple correlation coefficient was positive for all models. Four of the selected variables were significantly related to brood use. Holes was included in all three linear models with its contribution being most in 1981. The variable which dominated the latter two models was Hatch (dams where broods were hatched). This explained 59.7% and 46.0% of the variation in 1982 and 1983. The other two variables to be included were Tussock in the 1981 model and Area in 1983. Tussock accounted for only a little of the variation (4.7%) but Area accounted for 19.1% in the relevant model.



Results of three (1981-1983) regression analyses, with number of broods as the dependent variables and number of holes on dams as the independent variable.

Discussion

Historically, farm dams are a new waterfowl habitat, first appearing in 1933 on this study site. This probably coincided (chapter 1) with the arrival of the first Maned Ducks (Fig. 28). The majority of dams (89%) have been established since 1960. Presumably, before 1933, the only wetlands, besides the Abercrombie river which was not surveyed, were two small perennial creeks which run through the separate property areas (chapter 2). In 98 surveys of the area, I saw Maned Ducks using one of the creeks on only three occasions. These were on consecutive survey days after there had been considerable rain causing this creek to flood. This had resulted in some inundated areas along it, comparable in size to a small dam. In terms of relative use, Maned Ducks were on these creeks for only 0.07% of survey time. For the rest of the time, Maned Ducks used the numerous dams in the area.

Numbers of Maned Ducks on the three properties also reflected this close association, with differences in numbers on the three properties largely attributable to variation in the number of dams (Table IX). Apart from one month, Grathawai had more Maned Ducks in the three years 1981-1983, than the other two properties (Fig. 30). Moreover, Tanjenong and Bubalalah, with almost equal numbers of dams, had similar numbers of Maned Ducks in all years, apart from late in 1983. There were slightly fewer ducks on Tanjenong, which may have reflected differences in agricultural development (Table IX).

In 1982, total numbers of Maned Ducks seemed to contradict this trend, since 20% of the dams dried up (Table IX) and yet the population increased (Fig. 31). This year (1982) was climatically exceptional. Drought conditions prevailed and this resulted in little natural food (chapter 3) for Maned Ducks to be found anywhere. On many properties, livestock had to be fed wheat or oat grain. Maned Ducks, typically, congregated in large numbers on dams close to where wheat was fed to sheep. As a result, the strongest correlation between the distribution of Maned Ducks and any of the selected variables was the location of wheat feeding in 1982 (Tables X & XI). After livestock had eaten, Maned Ducks

fed on the grain left on the ground. Not all properties employed these drought relief measures, so that the increase in numbers in this year was possibly due to an influx of birds from other areas. Some dabbling ducks (Anatini) will concentrate in times of drought (Kaminski and Prince 1984). Although it has been suggested that Maned Ducks leave a district in times of drought (Rowley 1975) or when local conditions deteriorate (Norman 1971, Frith 1982), it appears that the existence of a food supply (wheat) in times of drought may be a more important determinant of local movement. This influx of birds may also have been due to habitat loss caused by drought in the more arid parts of Australia.

Apart from the relationship with wheat, much of the variability in the distribution of Maned Ducks was unexplained by the selected variables. Social factors, principally the formation of flocks, probably contributed most to this variability, overriding any habitat differences. Disturbance probably also added to the variability. Maned Ducks sometimes remained on a dam for two weeks if they were not disturbed, while on others, in the presence of frequent farming operations, they stayed only temporarily. I saw one flock, about to land on a dam, swerve away to another because there was a large flock of sheep around it. Nevertheless, some variables accounted for significant amounts of the variation in the dependent variable, duck-use.

Apart from 1982, habitat associations during the breeding season were different to those after breeding. In the breeding seasons of 1981 and 1983, climatic conditions were similar and the same two variables, Holes and Visibility were positively related to duck-use. P.C.A. showed that these variables described different types of dam (Table VIII). Both loaded highly on the first principal component but in opposite directions. Survey data showed that Maned Ducks used both dam types at the same time rather than using them at different times in the survey period. On dams with high visibility there was little tussock grass, few trees, and livestock kept the pastures grazed low so that one could see far at duck height. These dams were also usually sown to exotic pasture species. Maned Ducks could have either used these dams because they had more nutritious pastures (Donald 1941) or because they were so open that it allowed greater breadth for surveillance. I saw ducks seeking out areas

of pasture and this, combined with results from activity patterns (chapter 4), provide some evidence that both interpretations might be relevant. Without experimentation or better assessment of food availability (chapter 3), the relative contribution of these two factors to Maned Duck distribution is difficult to determine.

Other Maned Ducks associated with those dams where Holes (Number of tree holes around a dam) was high. As obligate hole nesters, nest searching and feeding during the incubation period probably both contributed to this positive relationship. As well, weight for this relationship, may come from the establishment of a home range prior to nesting as in A. sponsa (Gilmer et al. 1978). The failure of this variable to register in 1982 (Table X) was probably because so few Maned Ducks bred this year (see chapter 6) and those which did, would have accounted for little of the variability. There was variability in the reproductive condition of individuals (chapters 3 & 6) during the breeding season and these two population responses could be related to the reproductive state of individuals. Visibility may be associated with those individuals not breeding. Further evidence for this comes from the inclusion of Visibility in "after breeding" models and the negative relationship of Holes, at this time (Table XI).

Like the hole nesting A. sponsa (Gilmer et al. 1978; McComb & Noble 1981), Maned Ducks probably nested close to water. On dams where there were no tree cavities within 400m, I found no newly hatched broods. Observations on a dam installed in 1983 provide further evidence. This dam was established between 400m and 1km from a dam that had not produced broods the previous two years. The new dam was also sited close to (<50m) a number of mature eucalypts with potential cavities. In the breeding season of 1983, there was considerable nesting activity and three broods produced on this dam. In contrast, I saw no nesting activity the two previous years on the old dam which was within 1km of the same cavities. However, Frith (1982) notes that Maned Ducks do nest up to a 1 km or more from water. Possibly, this is a rare event, with Maned Ducks preferring to nest close to the dam if nest sites are available. There may be selection pressures which force Maned Ducks to nest close to water. Females could incur higher energetic cost by flying far, to and from the nest site when

incubating, while duckling mortality may be an ultimate factor determining proximity of the nest site, since it may be directly related to the amount of overland travel (Ball et al. 1975). More work needs to be done, but if such a relationship does exist, then either the installation of dams close to nest holes may increase the availability of cavities or perhaps the use of nest sites may allow populations to be established where they previously did not exist.

Not only was the proximity of potential cavities probably important but also the number of holes. Dams with more cavities had more broods hatched on them in all three years (Fig. 34). The linear relationship between the two was weak because Holes was not a measure of cavity occupancy by Maned Ducks. Cavities also occupied few of the trees within 400m² of a dam. Trees with holes were larger and probably older, since cavity development in eucalypts occurs when trees are well over fifty years old (McIlroy 1978; Ambrose 1982). Many of the holes, I suspected, were not used, while others were used by various species of mammals and birds (Table XIII). Maned Ducks' nests were in deeper holes than those cavities not used, otherwise I found no significant differences. The possibility of some competition for cavities from other bird species and arboreal mammals may occur and could lend itself to experimental manipulation using nest boxes. Methodological problems make interpretation of this nest site data difficult. I identified few cavities where Maned Ducks had nested. This was, in part, due to the fact that I searched for tree holes after the breeding season to avoid disturbing the breeding population and so I was reliant on indirect signs of occupancy. Better description of nest characteristics could be achieved through the use of radio telemetry (Dwyer 1972) or cavity inspection at the relevant time of the year.

Brood use of dams is largely dependent on the location of the nest site since it was most related to Holes and Hatch. My inexperience in the detection of broods may have biased brood-use in 1981, resulting in Hatch not being related to brood-use in that year. This has implications for other studies where reported habitat associations with broods occur (Lokemoen 1973; Mack & Flake 1980; Godin & Joyner 1982). Brood-use may be more correlated to better nesting conditions (Shearer 1960; Dwyer 1970)

than to any of the measure physical variables. In this study, broods occasionally moved to other woodland dams and this could have been reflected by the the inclusion of Holes and Tussock, after adjustment for Hatch. On these dams, there was more cover for predator avoidance (see chapter 8) and less disturbance (farming operations). I noticed that those broods on particularly open dams, with little vegetation around them, usually stayed only temporarily.

Area was related to brood use in 1983. Predator avoidance has been invoked to explain similar results in other waterfowl studies (Evans & Black 1956; Lokemoen 1973; Godin & Joyner 1982). However, it may not be a particularly important variable for this species, as it only registered once in the three year analyses. Maned Ducks probably rely on alternative methods of predator avoidance (see chapter 8).

After breeding, Maned Ducks usually collect in large flocks (Frith 1982; chapter 7). The number and types of variable included in linear models at this time were less uniform than in the breeding season (Table XI). However there was some consistency. The most frequently included variable was Area. Maned Ducks were found on larger dams after the breeding season. With larger flock sizes (Frith 1982; chapter 7), more Maned Ducks would perhaps need a larger surface area of water either to escape predation (chapter 4) or for bathing activity.

Although most of the dams were used at some stage during the survey period some were used more frequently. Frith (1982) claimed that Maned Ducks have traditional "camp" sites which they use each year. I found little evidence for any tradition. The most frequently used dams differed each year, with only one dam being included every year (Fig. 33). Most dams were important in only one of the years. Maned Ducks usually stayed camped on a dam for no more than two weeks.

A few of the dams were not used at all. These tended to be small and have a lot of surface vegetation (Table XIV). The importance of vegetation cover as a possible deterrent to duck-use, was emphasized by observations on two dams which changed over the two years. One dam, established in 1981, was used by a pair that year, but in 1982 and 1983,

it was overgrown with surface vegetation and no Maned Ducks have been seen on it since. Another dam, B.16, was small and overgrown. The dam was enlarged in 1982 and it dominated counts of Maned Ducks on Bubalalah (Fig. 30). On dams covered by vegetation, Maned Ducks would presumably find it difficult to land or swim. Disturbance may also be an important factor, since one dam close to sheepyards and a "T" junction in the road only once had Maned Ducks.

Like other grazing anatids (Heitmeyer & Vohs 1984; Summers 1985), Maned Ducks distribution was most highly correlated to variables away from water, confirming the view that water simply functions as a "focal point" (Frith 1959c; Braithwaite 1975) for bathing or predator escape (chapter 4). Which habitat characteristics are important was dependent on breeding requirements and possibly food availability. The latter is probably an important determinant of Maned Duck distribution when conditions deteriorate. However, the considerable amount of unexplained variation in Maned Duck distribution and variability between associations of some years indicates that most dams, with a few exceptions, satisfy the ecological requirements of Maned Ducks. Since the complexity of cues for habitat selection may develop at an individual level (Partridge 1978), the use of radio telemetry on a few individuals could lead to a much better understanding of habitat relationships, particularly as it relates to the known reproductive state of individuals. The variability found in this study also emphasizes the shortcomings of short term local survey counts for waterfowl as a way of determining habitat preferences.

CHAPTER 6REPRODUCTIVE SUCCESSIntroduction

In the southern areas of the continent, where rainfall is regular, Maned Ducks breed during the spring (Braithwaite 1976a; Frith 1982). However, there is considerable variability in the timing of breeding elsewhere in Australia. This probably prompted Frith (1982) to say that breeding in this species is largely controlled by rainfall and Braithwaite (1976a) to suggest that the species showed characteristics of truly facultative breeding. As yet, however, there has been no detailed investigation of breeding in this species. To date, most of our knowledge of breeding cycles in Australian waterfowl has been inferred from histological examination of testes. There are some exceptions (Riggert 1977; Braithwaite 1982). Whilst such data probably give a good indication of the "breeding season", only egg laying or brood appearance are true measures of breeding activity.

For many Australian waterfowl, the timing of breeding is known but recruitment levels into the adult population are not. With the increasing importance of Maned Ducks as a game species (see chapter 1), knowledge of reproductive output is essential. The information will allow us to assess whether there will be a sustainable yield and aid in planning shooting seasons. The aim of this part of the project was to determine annual variation in the timing of breeding, variations in brood size as a measure of clutch size, and an annual assessment of duckling survival and production. The study extended over two climatically normal years and one drought year, which enabled me to measure the effects of climate on reproductive success.

Methods

Data for the timing of breeding, duckling survival and duckling production were collected during regular surveys (see chapter 5). These were frequent (every four days) to obtain precise measures of each reproductive parameter.

Timing of breeding

The breeding season for a bird species can be defined as the mean date on which females lay the first egg of their clutch (Perrins & Birkhead 1983). Although I observed the behaviour of some incubating Maned Ducks (see chapter 8), I found too few active nests (chapter 5) to consider this aspect of the breeding cycle in detail. However, it was possible to determine when broods hatched, because Maned Ducks lead their young from the nest site to water as soon as the ducklings hatch (Frith 1982). During this study, I found most broods within four days of hatching. Any old broods found for the first time, which were older than four days, were aged (Appendix 6) and their hatch dates determined. Backdating hatching dates by an incubation period of 28 days (Frith 1982), gave a good approximation of when incubation began. Actual timing of breeding season would predate this by the number of eggs in each clutch, since Anatinae generally lay one egg a day (Weller 1964b; Breckenridge 1956; Bruggers 1979). I did not attempt to perform this further step because there was no measure of egg loss for each brood but, in any event, such added precision was unlikely to affect the timing reported here as I used two week intervals.

Little is known about the precise timing of breeding in this species, so the strategy used to determine the beginning of regular brood surveys was to wait until the first brood was sighted. In 1981, this was on 8 September. Subsequent surveys this year, produced only one older brood, confirming that this was about the best time to begin surveys. Following this, I started surveys at the beginning of September in 1982, but the early appearance of broods in 1983 meant an earlier start to surveying.

Daily rainfall data were collected throughout the study on Grathawai. This property was separated from the other two properties but apart from occasional summer storms, rainfall patterns tended to be similar. Temperature measures for this period came from data collected at the Taralga Post Office which is 16km from the site. Temperatures for the latter half of 1983 had to be supplemented with Goulburn records because no records were kept at Taralga. In addition to these environmental variables, I used the GROWEST (=GROWth ESTimation) model to estimate weekly plant growth on the site (Fitzpatrick & Nix 1970; Nix 1982). Since Maned Ducks feed primarily on pasture plants (chapter 3), this gave me a method for examining the possible effects of food supply on breeding in this species. The model was particularly suitable because it was developed for use in comparative analysis of temperate and tropical pasture species of Australia, which were predominant on this site.

The GROWEST model has functions which transform the dynamic non-linear responses of plants, to major environmental factors, into dimensionless indices which range between 0 and 1 (Nix 1982). It produces four indices on a weekly basis: light, moisture, temperature and growth. The last is formed from the product of the first three. Invariable input parameters are for plant type, optimum temperature, soil type, initial soil water and maximum store water. In addition, variable weekly parameters included are rainfall, radiation and temperature. Weekly radiation and temperature measures came from the available data base (Nix 1982). Although there may be some annual variation in these two parameters, it is probably negligible compared to seasonal variation (see Fig. 35). Rainfall, however, is far more variable and I used daily measures for the three years, 1981-1983.

Duckling survival and production

The main problem with the analysis of survival estimates for reproduction, is countering potential biases. Measuring survival simply as the percentage of the observed number of eggs or offspring which ultimately hatch or reach a certain stage of development, can lead to overestimation of offspring survival (Mayfield 1975; Miller &

Johnson 1978; Klett & Johnson 1982). Bias stems primarily from the problem that afflicts most studies of such survival. This is, that not all nests or broods are found at the beginning of their development. Survival is then higher because older developed broods or nests are more likely to reach final development simply because they have progressed so far already.

To overcome this, Mayfield (1961, 1975) put forward a simple method which, although considered appropriate (Miller & Johnson 1978; Johnson 1979; Klett & Johnson 1982) has not been widely used (Hensler & Nichols 1981). Those studies which have used the technique have been primarily concerned with egg to hatching survival. However, it can also be used to calculate the survival of nestlings (Mayfield 1975) and Ringelman & Longcore (1982) successfully adopted the method to analyse survival rates of juvenile Black Ducks Anas rubripes.

Mayfield's method works on the basis of days at risk (sensu. Johnson 1979). It copes with broods found some time after they have hatched and broods whose end is not known. The currency is duckling-days, where each day that a duckling survives, scores one duckling-day. For example, a brood of six ducklings first seen on 1 October and subsequently observed with only five ducklings on 5 October would yield 22 duckling-days of risk for that period (5 ducklings x 4 days) + (1 ducklings x 2 days). Five of the ducklings survived the four days while one was lost somewhere between visits.

From the total risk in duckling-days and number of ducklings lost in broods, a daily mortality may be calculated which is a probability.

$$\text{Daily mortality: } p = \frac{\text{No. of ducklings lost}}{\text{Total No. of duckling-days}}$$

The daily survival rate is then (1-p) and if the number of days to fledging is known (57 days, Appendix 6), a probability for survival to fledging may be calculated.

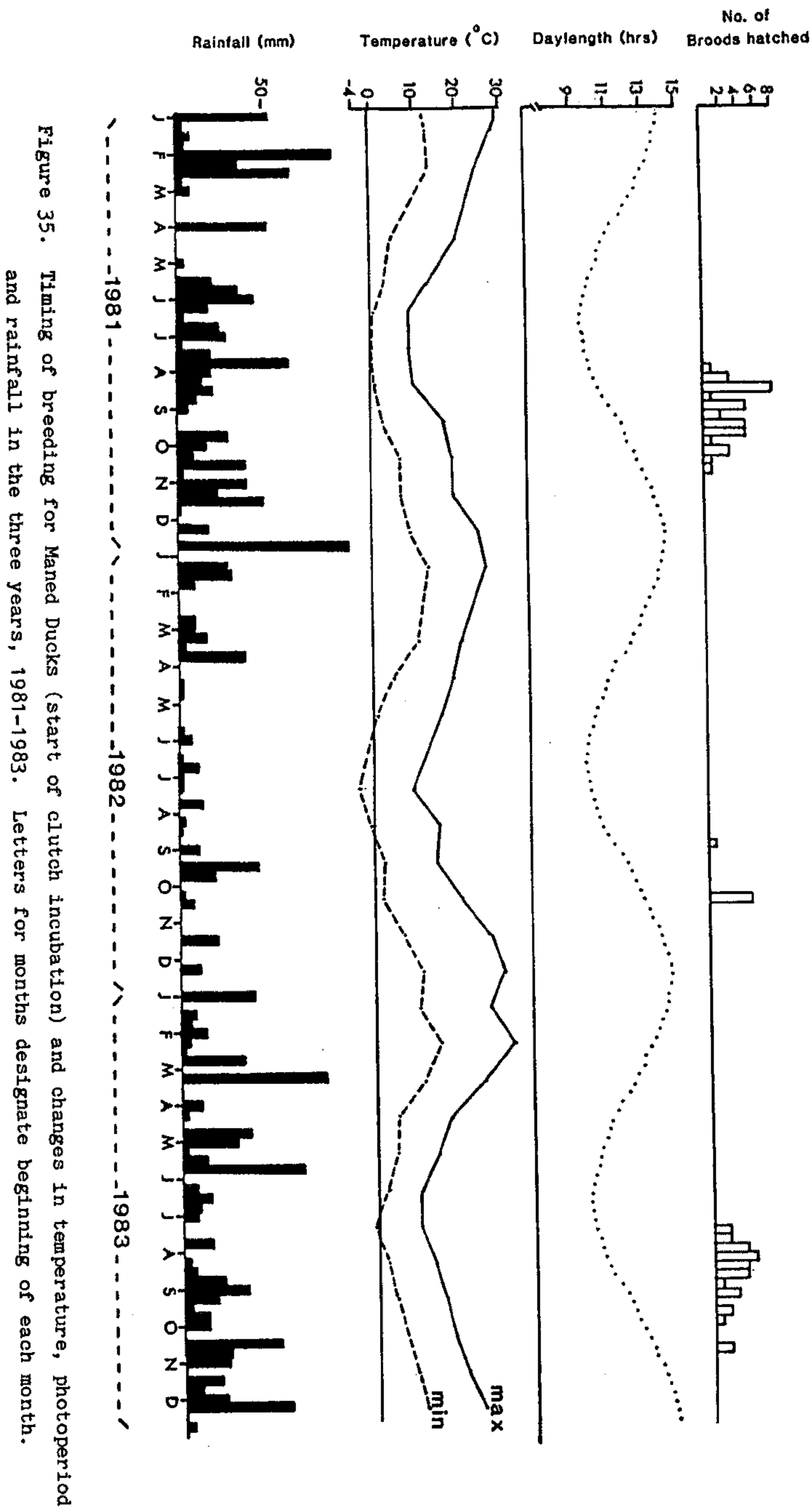
$$\text{Survival to fledging} = (1-p)^{57}$$

Further versatility for the model came when Johnson (1979) provided a method for estimating variance for mortality rates.

Brood size variation

I used fixed effect two-way analysis of variance to investigate annual and seasonal changes in brood size. Only data for the comparable years of 1981 and 1983 were used because sample sizes in 1982 were too small. Since I was primarily interested in clutch size variation, I used only brood sizes of ducklings aged less than one week old. Most of these were found soon after they had hatched. Both breeding seasons were then split up into early, mid and late stages for the different seasonal categories and analysis performed. This may have been a better measure of clutch size than one based on the number of eggs because of the difficulty in finding nests of this species. In contrast, all broods should be found.

I left two broods out of this analysis. With brood sizes of 16 and 19, they had six more ducklings than the next largest brood. As a result, I considered them to be the product of dump nesting (intraspecific nest parasitism). This is a widespread phenomenon in waterfowl (Weller 1959; Yom-Tov 1980) and can often result in particularly large clutch sizes (Jones & Leopold 1967; Clawson et al. 1979). The inclusion of these two broods in the analysis may have hidden brood size patterns for individual females.



Results

Timing of breeding

Breeding each year coincided with increasing photoperiod (daylength) and temperature (Fig. 35). However, the timing of breeding differed between years. The earliest start to breeding was in 1983, when incubation of the first broods started in the third week of July (Fig. 35). It happened two weeks later in 1981, but in 1982 began over a month later, at the beginning of September. The length of the breeding season was also different. The longest was in 1983, spanning more than three months contrasting that of 1982, which only lasted just over a month (Table XV). One could expect to find Maned Ducks starting incubation any time between the end of July and beginning of November on this site (Fig. 35).

Hatch dates for the three years were significantly different ($F_{2,66}=14.96$, $p<0.001$). Although breeding was earlier in 1983 compared to 1981, the longer breeding season in 1983 meant that there was no significant difference between mean hatch dates for these two years (Table XV). However, hatch dates for 1982 were significantly later than either of these two years.

Brood hatching tended to coincide with the spring period of pasture growth (Fig. 36). To some extent this was determined by rainfall. However, the annual rainfall pattern was variable, tending to fall throughout the year (Fig. 35). The amount of rainfall was similar in 1981 and 1983 but there was considerably less in 1982 (Table XVI). Contrasting this annual variability, there was a predictable pattern to pasture growth. A period of very little growth, during the winter months, dominated. However, the seasonal and annual variation in this pattern was interesting. There was often good growth during the summer months (December-February), but compared to spring growth, it tended to be more variable (Fig. 36). Autumn (March-May) growth was also variable, showing some good growth but sometimes dropping suddenly. Growth patterns in 1981 and 1983 were different to those of 1982. The period of spring growth in

TABLE XV. Hatching dates (means and standard errors) and length of breeding for the years, 1981-1983. N is the number of different broods on the site at some stage during their development

YEAR	Mean	S.E.(days)	N	Hatching date	Length of breeding
1981	7 October	3.6	33		69
1982	18 November	5.1	6		43
1983	21 September	5.1	30		101

TABLE XVI. Annual comparison of rainfall and total growth index (from model GROWEST)

YEAR	TOTAL RAINFALL(mm)	NO. OF RAIN DAYS	TOTAL GROWTH INDEX
1981	964.7	108	13.7
1982	330.2	55	6.4
1983	776.8	111	11.1

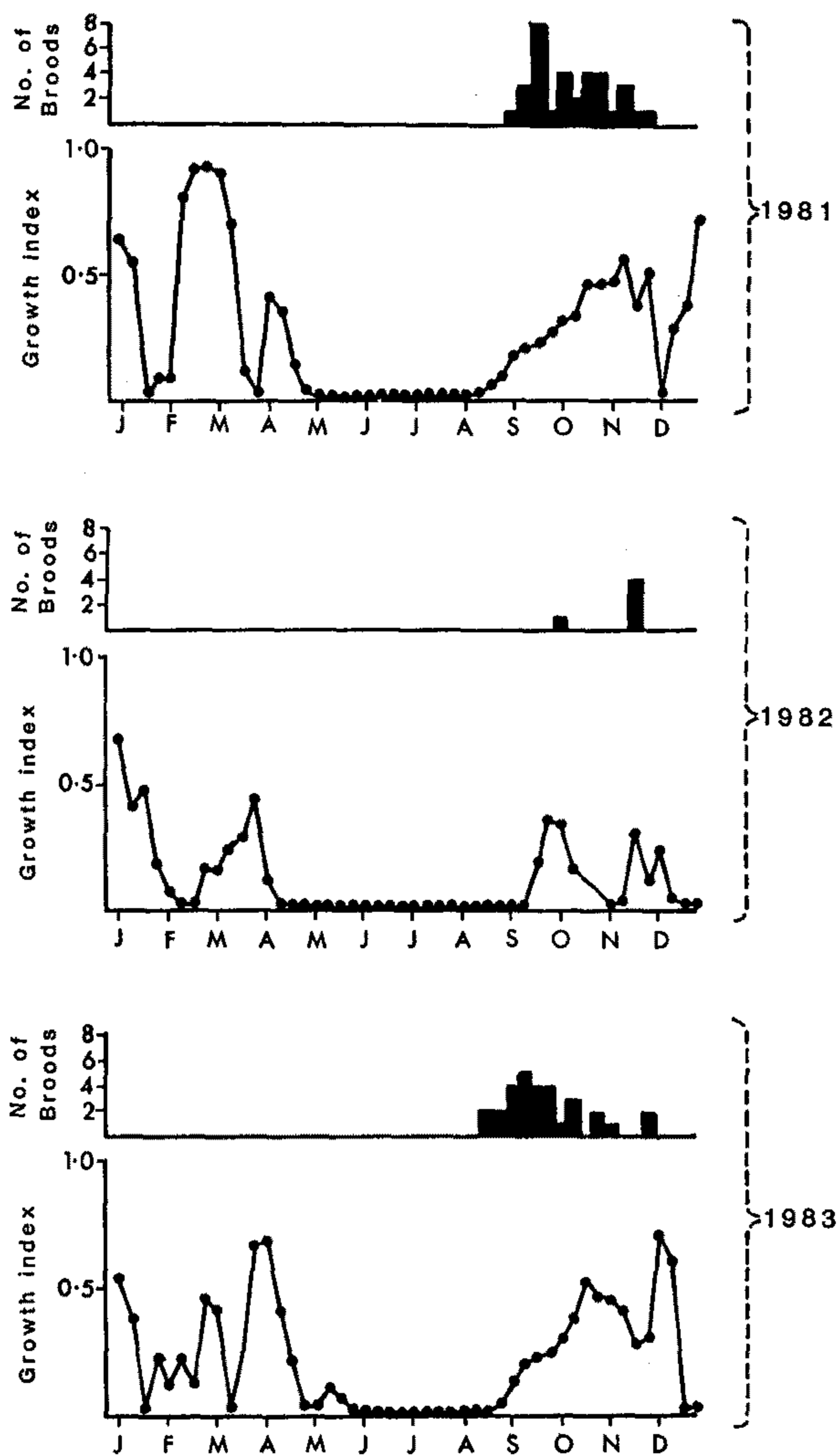


Figure 36. Relationship between brood hatching and the annual cycle of pasture growth, generated using the model GROWEST for this site in the three years, 1981-1983.

TABLE XVII. Two-way analysis of variance of brood sizes, for ducklings less than 7 days old, testing for the effects of stage of breeding (Early, Mid, Late) and Year (1981, 1982, 1983). The year 1982 was not included because there were too few broods (*-p<0.05; **p<0.01)

SOURCE OF VARIATION	DF	MEAN SQUARE	F	SIGNIF
YEARS	1	35.50	6.34	*
STAGES	2	38.37	6.85	**
YEARS x STAGES	2	5.44	0.97	ns
EXPLAINED	5	24.58	4.39	**
RESIDUAL	41	5.60		

TABLE XVIII. Differences between category means in the two-way analysis of variance on brood sizes at hatching. Lines joining categories means that there is no significant difference at p<0.05 (Student Newman-Keuls test). Mean brood size in 1982, at hatching, was 6.0 (n=5)

VARIABLE	N	MEAN BROOD SIZE
a) Year		
1981	24	5.04
1983	23	6.78
b) Stage		
Early	18	7.17
Mid	15	6.07
Late	14	4.07

1982, was neither as high nor as sustained as in the other two years (Fig. 36) and the total growth indices for 1982 were only about half those for the other two years (Table XVI). Actual pasture growth, this year, was likely to be less than indicated because the model does not account for livestock grazing pressures, which were particularly severe. In most paddocks, there was no vegetational cover, so response to rain was probably not as immediate as in other years.

On this site, breeding was between mid July and late October, but I also saw two broods in the district, during the autumn (March-May) of 1981. Evidence for some autumn breeding also comes from trapping between June and August of 1981 and 1984. I trapped a few individuals which were in juvenal plumage. Since this plumage probably only lasts for three months (Appendix 6), these ducks would have hatched in the autumn.

Variation in brood size

There were significant seasonal and annual differences in brood sizes at hatching (Table XVII). Brood sizes were smaller in 1981 and broods hatched later in the season were significantly smaller than those hatched early or during mid breeding season (Table XVIII). Although there was no difference between early and mid season brood sizes, there was some indication of a seasonal decline. Larger sample sizes may have resulted in significant differences between these stages.

Brood movement

There was considerable evidence of brood movement. Broods could often not be found on subsequent visits to a dam where they had been previously recorded. This meant either one of three things, total brood mortality, brood movement or problems with brood detection. The latter probably contributed in 1981, since I was able to monitor individual broods for much longer in 1983 ($t_{61}=5.11$, $p<0.001$). Monitoring a particular brood in 1981 averaged 12.5 days compared to 38.2 days in 1983. Small sample size in 1982 precluded this year from the analysis. However,

I was also able to monitor individual broods for longer this year (mean=23.2 days). In the latter two years, I was better at not stimulating the vigilant behaviour of parents with broods. This was unlikely to be the reason in the latter two years because broods which could not be found were left undisturbed on the previous visit.

The best evidence for movement came from six broods with marked parents, which moved between dams on the study site. Movements for these were about 1 km (mean $0.93 \pm$ S.E. km). The greatest distance travelled was 1.4 kms. Movements occurred throughout the brood care period although there was some evidence that broods tended to move more while ducklings were young. Not all broods moved. In 1983, 36% of broods remained on the same dam until fledged.

Duckling survival

Survival estimates for ducklings came from 72 broods produced over the three years of this study (Table XIX). Differences in the total risk (duckling days) could be attributed to the already mentioned inexperience in brood monitoring during 1981, while in 1982, it was due to the small number of broods produced. However, these factors did not affect estimates of survival using Mayfield's method. There were significant annual differences in daily survival of ducklings (Table XIX). Ducklings hatched in 1981 and 1983 had comparable probabilities of daily survival. However, duckling survival in both years differed significantly from that in 1982. For this year, there was only about a 16% chance that a duckling would survive to the fledging stage.

These survival rates may be affected if assumptions of the Mayfield model are violated. An inherent assumption in the method is that individual brood identification is possible. This problem is not usually pointed out, probably because the method has mostly been applied where subjects are static, nests or passerine nestlings. However, brood mobility in precocial species, like Maned Ducks, makes this more of an obstacle. High proportions of marked breeding birds helped in this study. There were 62%, 83% and 63% of broods with at least one parent banded for

TABLE XIX. Annual differences in duckling survival of Manded Ducks using Mayfield's method. See text for calculation of exposure, daily survival and survival to fledging. Number of broods is the total number of different broods which were seen on the study site at some stage in their development

YEAR	TOTAL RISK	TOTAL LOSSES	NO. OF BROODS	DAILY SURVIVAL	SURVIVAL TO FLEDGING
	(duckling-days)			(95% confidence limits)	(95% confidence limits)
1981	2349.0	5	33	0.9978 (0.9959-0.9997)	0.8862 (0.7912-0.9830)
1982	509.5	16	6	0.9686 (0.9531-0.9840)	0.1624 (0.0647-0.4000)
1983	8069.0	29	30	0.9964 (0.9950-0.9977)	0.8142 (0.7515-0.8770)

Table XX. Number of broods arriving for the first time on the site compared to the number of broods leaving the site in 1981 and 1983, according to age category (*-indicates a significant difference using the Binomial test (Zar 1974, p 287)

YEAR	AGE CATEGORY (days)							
	4-7	8-14	15-21	22-28	29-35	36-42	43-49	50-57
1981	No. entering	2*	4	2	4	1	0	0
	No. leaving	11*	5	2	2	4	2	0
1983	No. entering	3	3	3	2	0	0	0
	No. leaving	3	1	0	1	3	0	0

the respective years, 1981-1983. In addition, broods were spread out over many of the dams and, apart from 1981, brood movement was not too widespread so broods could usually be identified according to their location. A rapid growth rate for ducklings (Appendix 6) and an often constant brood size also reduced the possibility of making the wrong identification.

There are three other assumptions associated with Mayfield's method. If a loss occurs between visits, ducklings are assumed to have survived for half the intervening period. Mortality is also assumed to be constant over the fledging period (Klett & Johnson 1982). Finally, all ducklings are assumed to be subject to the same mortality. The condition that mortality is constant throughout the fledging period was not met (Fig. 37). A total of 60 ducklings were recorded lost during the three years. Combining the three years, showed that there was a tendency for higher mortality during the early part of the brood care period (Fig. 37). Mortality declined with increasing age of the ducklings, and no ducklings were recorded lost in the 10 days prior to fledging. Survival estimates could have been biased high because of this variability. However, mortality rates were not large, so this was unlikely to be important. Inadequate samples of ducklings within each age class precluded calculation of mortality rates for different stages, which is some remedy (Mayfield 1975; Johnson 1979; Klett & Johnson 1982). Losses were also assumed to occur midway between visits. Johnson (1979) considered that this assumption held if visits averaged less than 15 days and there was less than moderate mortality. This study met both these requirements. The final assumption is that survival estimates are independent of the ducklings within broods. Following Ringelman and Longcore (1982), I used contingency table analysis (2x19, 2x6 and 2x27 for the respective years 1981, 1982, 1983) to compare the expected brood size at last sighting with the observed brood size at last sighting. The expected brood size was the product of the relevant survival estimate over time and the original brood size. Where there is dependency, one would expect significant deviations. In all three years, analyses were not significant ($p > 0.05$ for respective chi-squares; 0.38, 4.12, 3.68). There was little violation of assumptions to the model, so survival estimates are unlikely to be unduly biased.

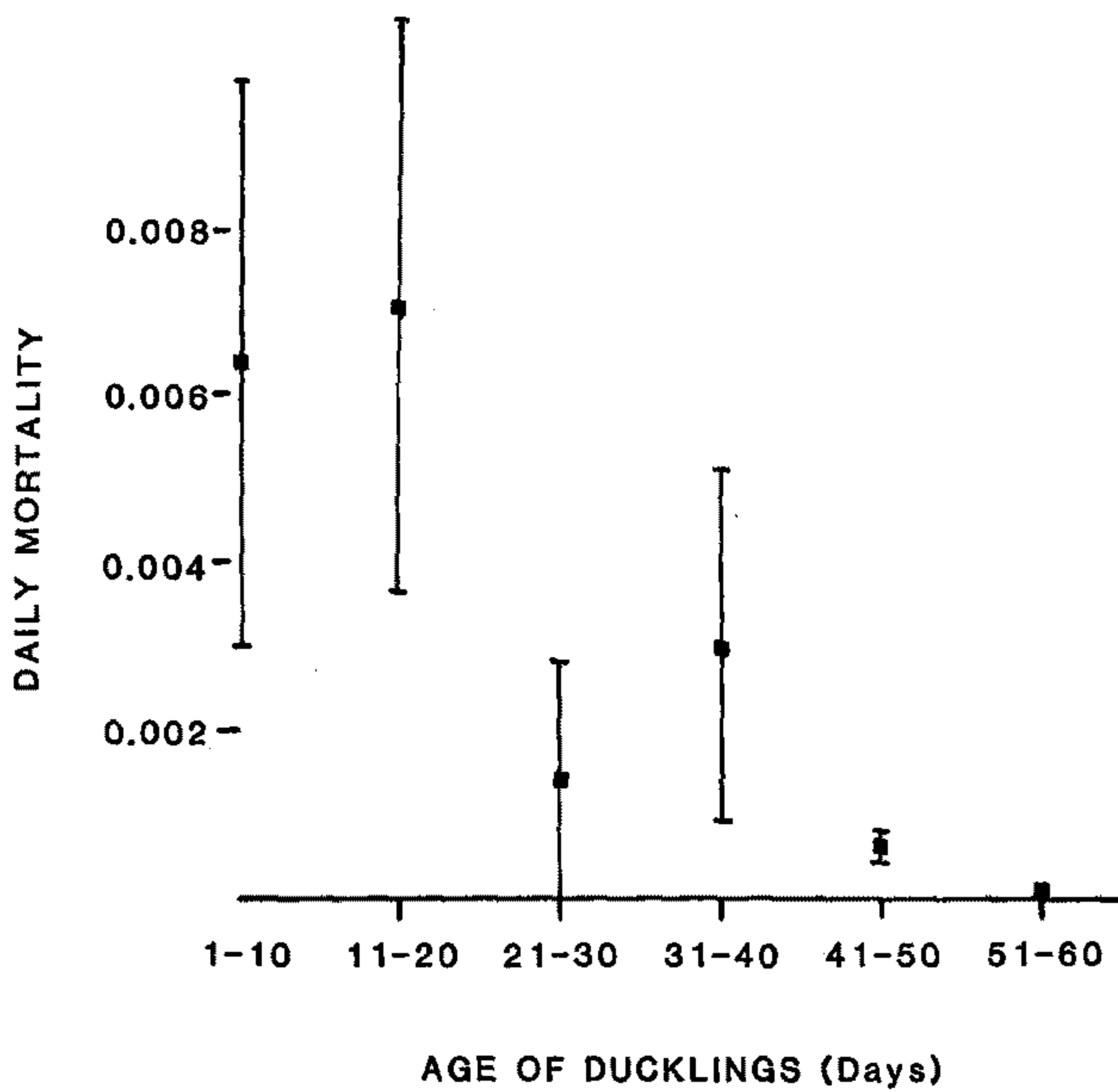


Figure 37. Changes in daily duckling mortality with age ($\pm$ 95% confidence limits). Mortality calculated using Mayfield's method for estimating reproductive success. Data pooled for all three years.

TABLE XXI. Annual differences in the duckling production of Handed Ducks. Only broods aged less than one week were considered. These were assumed to have been produced on the site. Older broods may have moved into the site from dams outside. Number of ducklings hatched was the number of brood multiplied by mean clutch size for that particular year. Number of ducklings produced, was the product of number of ducklings in a particular year and the survival rate

PROPORTION OF	NO.	NO. OF	ESTIMATED NO. OF
YEAR BREEDING ADULTS	OF BROODS	DUCKLINGS HATCHED	DUCKLINGS FLEDGED

1981	0.33	23	116	103
1982	0.03	5	30	5
1983	0.63	24	163	133

TABLE XXII. Reproductive output of the three properties compared. See Table XXI for definition of production

PROPERTY	AREA(ha)	No. of dams	NO. of broods produced	Mean NO. of broods/10 dams for 1981 and 1983
----------	----------	-------------	------------------------	--

GRATHAVAI	1100	40	15	4	15	3.8
TAMJENONG	1200	10	5	0	5	5.0
BUBALALAH	200	14	3	1	4	2.5
						Mean=3.8

My estimates of duckling survival ignore the possibility of total brood mortality. This could result in overestimates of duckling survival, since duckling mortality could go undetected. Such total brood loss may have occurred on some occasions when broods disappeared. In this study, this mortality could only be detected if adults were banded and subsequently seen without their broods, which happened only once. One way of gauging the extent of total brood loss, is to compare the number of new broods arriving on the site for each age category, against the number of broods which left the site in that age bracket (Table XX). More broods leaving would suggest brood loss. For this analysis, the first age group was shortened, to exclude broods that had just hatched. There was only one significant difference. This was during the first stage of brood care in 1981 (Table XX). There were more broods which left the site than arrived, perhaps indicating some total loss of young broods this year. These analyses indicate that there was little evidence for total brood mortality. Nevertheless, estimates of duckling mortality should be probably be considered as minimum estimates.

Duckling Production

Duckling production was high in 1981 and 1983, but low in 1982 (Table XXI). All indices reflected this trend. In 1982, there were few broods produced and this combined with a higher mortality this year, meant that only an estimated five ducklings fledged. There were also higher ratios of breeding to non-breeding ducks in 1981 and 1983, compared to 1982 (Table XXI). Differences between 1981 and 1983 were attributable to a higher number of Maned Ducks on the site in 1981. A higher brood size at hatching in 1983 also meant that there were more ducklings produced this year.

There was a predictable difference in the production of the three properties, for all three years. Grathawai produced more broods each year than either of the other two properties (Table XXII). This trend was more related to the number of dams on each of the properties than to differences in area. There were a few more broods produced on Tanjenong than Bubalalah except in 1982. This translated into a lower production to

dam ratio for Bubalalah for the two years, 1981 and 1983. Although more broods were produced on Grathawai, Tanjenong had the highest production to dam ratio of 5. The whole site had a production potential of 3.8 broods for every 10 dams.

Discussion

During the non-drought years of 1981 and 1983, Maned Ducks bred from late winter to early spring (mid July to early September)(Fig. 35). This timing was earlier than Frith's (1982) observations for similar districts, of a September-October breeding. However, Frith did not define "breeding" and could well have meant this to be the time when broods first appeared. Average hatching dates for this study (Table XV), apart from the extraordinary year of 1982, agreed more closely with Frith's observations.

Lack (1968) suggested that two factors determine the date of breeding in birds, namely food resources for the offspring and the female's capacity for egg production. Ducklings, like adult Maned Ducks, are predominantly grazers (chapter 3) and in all three years hatched during the period of spring growth (Fig. 36). This was not the only period of growth during the year but there was some evidence that plant growth was more sustained during the spring compared to other times of the year. High rainfall during summer could result in high growth indices but these did not last long because of high temperatures. It seems likely then, that ducklings are produced at the optimum time of year in relation to food, which appears to be true for most Australian waterfowl (Frith 1959d; Braithwaite & Frith 1969; Lavery 1970a,b; Braithwaite 1982). This provides some evidence that duckling survival may be an important ultimate factor determining the timing of breeding.

With ducklings hatching at this time of the year, females must prepare for breeding during mid to late winter (July-August) when there is minimal plant growth (Fig. 36). It has been argued, that under such conditions, birds need some proximate stimulus which predicts the time breeding will be most successful (Perrins & Birkhead 1983). Frith's (1982) statement that rainfall "initiates" breeding in this species, suggests that he considered rainfall to be this factor. However, during this study, the timing of breeding did not clearly coincide with any particular rainfall pattern (Fig. 35). There was insufficient evidence to conclude that rainfall was the proximate factor initiating breeding.

Whilst environmental changes, such as water level, are thought to be important determinants of breeding in some Australian waterfowl (Frith 1959d), photoperiod has been implicated in the timing of breeding in the Pacific Black Duck Anas superciliosa (Braithwaite & Frith 1969; Braithwaite 1976b). The influence of photoperiod on the breeding of birds is well documented (Lofts & Murton 1968; Farner & Lewis 1971; Murton & Westwood 1977). However, Ward (1972) questioned the prominence given to this factor, arguing that many of the experiments conducted did not necessarily exclude the possibility of food being the most important proximate factor. If food was not limited during experiments, birds provided with a longer photoperiod could feed for longer. This, combined with the observation that most of these photoperiodic responses have only been demonstrated on males (Meier & Macgregor 1972), does not exclude the possibility that nutritional aspects for the female may be the most important determinant of breeding. Nutrition has been concluded to be the most important factor in some bird species (Harris 1969; Payne 1969; Ashmole 1971; Jones & Ward 1976). Furthermore, some studies have shown that the date of laying for some bird species can be substantially advanced with supplementary feeding (Drent & Daan 1980; Ewald & Rohwer 1982). For Maned Ducks, increasing photoperiod during late winter could mean that females can build up the necessary body reserves for a breeding season ultimately determined by duckling survival. Even though there was minimal plant growth during 1981 and 1983, there was food available to Maned Ducks during the winter, on which females could have built up nutrient levels sufficient for breeding.

Such a nutritional hypothesis explains variation in the timing and extent of breeding seasons each year. It could be argued that breeding was delayed in 1982 because females found it difficult to obtain sufficient nutrients to breed. There was very little natural food (chapter 3) and the main constituent of the diet, wheat grain, may not have provided sufficient nutrition for breeding females. Krapu and Swanson (1975) found that wheat, as a dietary staple for Pintails Anas acuta, was inadequate for breeding. The relatively few Maned Ducks which bred this year (Table XXI), and the brief breeding season (Table XV), provide further support for such an assessment. Poor breeding in 1982 could not be attributed to insufficient nest sites since these

were the same for all three years. In addition, although some dams dried up and others lost water this year, this was also unlikely to be important because Maned Ducks will produce ducklings on small dams (chapter 5). The reduction in number of dams could not explain the large drop in breeding activity. Very poor rainfall in 1982 was the most likely cause. It was not clear why ducks bred both earlier and longer and had larger clutch sizes in 1983 compared to 1981 but this may have also been related to food resources.

Little is known of the proximate factors which might control the termination of breeding (Farner 1967; Immelman 1971) but, again food may be important. Jones and Ward (1976) suggested that, in the Red-billed Quelea Quelea quelea, if the nutritional plane was high for females after breeding, they may continue to breed. Although wild anatids are usually single brooded (Weller 1964b), the American Wood Duck Aix sponsa can produce more than one brood in a season (Drobney 1982; Fredrickson & Hansen 1983). Some Maned Ducks did apparently breed in the autumn. Perhaps, some pairs are able to build up nutrient levels, following breeding, to the point where they can breed again. Conceivably, double brooding occurs. Observations of breeding in captive Maned Ducks, where food is probably not limited, provides further support. Maned Ducks are apparently capable of producing as many as three broods in a season (Delacour 1964; Rutger & Norris 1970). There is even one account of a female which layed five clutches in a single season (in Kear & Murton 1976).

Braithwaite (1976a) suggested the Maned Duck shows characteristics of true facultative control of breeding. However, the nutritional hypothesis which I have presented is simpler and adequately explains continental variability in the timing of breeding. Whilst rainfall is undoubtedly important, particularly for the subsequent growth of potential food for this species, it does not satisfactorily explain the timing of breeding for areas, such as this site, where there is rainfall throughout the year. It would be interesting to monitor the lag time between rainfall and breeding in Maned Ducks in dry parts of the continent, where rainfall is probably the sole determinant of plant growth.

Clutch size is also an important determinant of reproductive success. I used brood sizes as soon after hatching as possible, to measure variation in this parameter. Frith (1982) found that clutch size averaged 10.4 eggs ($n=32$). This was higher than average brood sizes (Table XVIII), soon after hatching for all three years of this study and could imply that there is substantial mortality between the egg and hatching stage. Leopold (1951) found that as many as 33% of ducklings were lost moving from the nest site to water in the American Wood Duck *Aix sponsa*, which has similar nesting habits to this species. This may account for some of the discrepancy. However, direct comparisons should not be made since data on clutch size, such as that collected by Frith, may be biased. Apart from the difficulties in locating an unbiased sample of nests, seasonal, annual, latitudinal variation is likely. Larger clutch sizes may be overrepresented if nest searching took place early in the breeding season, since clutches produced later tend to be smaller for many groups of birds (Klomp 1970; von Haartman 1971). Such bias did not afflict this study which continued until breeding ceased. Without knowing when and where Frith gathered his data, this data can probably not be used in comparisons. It is interesting that Masters and Milhinch (1974) found that brood sizes near Perth ranged from 8-11, so either there is considerable variation or these estimates are also biased. Further work in different parts of Australia using unbiased methods may shed some light on such differences.

Like other Anatinae (Toft et al. 1984), brood size for Maned Ducks at hatching, showed a seasonal decline in 1981 and 1983 (Tables XVII & XVIII). Clutch sizes of many waterfowl similarly decline (Martz 1967; Johnsgard 1973; Batt & Prince 1979; Ely & Raveling 1984) and this has been attributed variously to, young anatids producing fewer eggs than more experienced adults (Grice & Roger 1965; Finney & Cooke 1978; Krapu & Doty 1979; Rockwell 1983; Dow & Fredga 1984), ducks reneesting (Batt & Prince 1979; Krapu 1981) and adverse environmental conditions (Ryder 1970; Ankney & MacInnes 1978). However, Toft et al. (1984) concluded that seasonal decline in brood size was independent of these sources of variation and proposed an evolutionary explanation based on Lack's (1948, 1954) hypothesis for clutch size. Toft et al. (1984) concluded, after a thorough examination of brood size variation in five

species of Anatinae, that there were consistent changes in certain conditions during the breeding season so that the optimum clutch size also changed with the season. Combining this with evidence that such parameters as clutch size have genetic bases (Noordwijk et al. 1980), they suggested that those females breeding later or earlier in the season always do so. This may also explain seasonal variation in the brood size of Maned Duck broods found during this study.

Besides timing of breeding and clutch sizes, duckling survival is an important determinant of reproductive success. One potential problem with estimates of survival was total brood mortality. This occurs in a number of waterfowl species (Reed 1975; Newton 1977; Talent 1980; Zicus 1981b) and in some species, affects about 20% of broods (Eltringham 1974; Ringelman & Longcore 1982). Apart from one age category (4-7 days, 1981), comparison of emigration against immigration for different age classes showed no difference (Table XX), which indicated that brood loss was not significant. Problems early in the study with parental vigilance may have caused the one significant result, rather than total brood loss. I disturbed more broods that year than in either of the other two years, and this may have pushed broods off the study site. Nevertheless, although not statistically detectable, total brood mortality may be important and if known could lower estimated survival rates.

Ducklings had a much better chance of survival in 1981 and 1983 compared to 1982 (Table XIX). There are two possible reasons for this which may have acted in concert. Predation pressure may have been higher in 1982 as there were fewer broods, and food was also short that year, so ducklings may have died of starvation. In all three years, most mortality occurred when ducklings were less than two weeks old (Fig. 37). This is also found in other waterfowl species (Reed 1975; Newton 1977; Zicus 1981b; Talent et al. 1982). Potentially, there may have been more predators on this age class. Besides the predators of adults (chapter 4), Kookaburras, Ravens, White-faced Herons and Australian Kestrels would probably be able to prey on downy ducklings. Older ducklings are probably too large.

Brood movement, not yet documented in this species, could contribute

to mortality. Ball et al. (1975), monitoring Mallard Anas platyrhynchos broods, suggested that duckling mortality in this species was directly related to the amount of overland travel. There were too few identified broods which moved to determine if this was true, but two broods seemed to sustain heavier losses after travelling.

Low survival rates, combined with poor breeding in 1982, meant that fewer ducklings were produced this year compared with the other two years (Table XXI). However, even in drought years, some breeding occurs. Production estimates also confirmed the importance of farm dams to this species. There was a direct relationship between the number of broods produced and the number of farm dams (Table XXII). It is interesting that Tanjenong had the highest production to dam ratio. This was probably because more of the dams on this property, had surrounding nest holes. This seems to be a reasonable indicator of breeding potential (chapter 5).

There are a number of parameters which determine reproductive success for a species. Breeding in this species seems to be similar to many other Australian waterfowl. The ducklings for this site, seem to be produced when conditions are best, during the spring. However, the extent and timing of breeding is affected by climatic conditions. In drought years breeding may be delayed and severely restricted. Duckling mortality in such years is also high. In normal years, there is particularly high survival for ducklings. Most mortality occurs when the offspring are young.

In addition to providing some measure of reproductive output for this species, this study also showed that Maned Ducks are capable of breeding successfully on farm dams. This has important implications for assessing how the creation of this habitat might have benefited the status of this species.

CHAPTER 7FLOCK STRUCTUREIntroduction

Maned Ducks are nearly always found in flocks. Sometimes these can number more than 2000 ducks but are more frequently less than 100 birds (Frith 1982, p 264). Some of the variation in flock size seems to be attributable to seasonal changes. Frith (1982) observed that flocks disperse during the breeding season and afterwards ducks congregate on larger bodies of water, their numbers swelled by recruited juvenals.

Flocks of Maned Ducks are supposed to be more stable than those of most other Australian ducks but little is known about their flock behaviour (Frith 1982, p 265). Frith contended that flocks are composed of family groups and reported that groups of Maned Ducks stay together for years. Such long term associations would have important implications for social behaviour. This may also prove interesting from a comparative point of view, since some geese (Anserinae) and shelducks (Tadornini) have close family ties which may persist for some time, (Boyd 1953; Raveling 1969b, 1979a; Summers 1983), while brood mates of some Anatinae exhibit little association during migratory and midwinter flights (Martinson & Hawkins 1968).

Besides the individual composition of flocks, the sex ratio of the population may also be influenced by the social behaviour of a species. Generally, waterfowl populations are skewed in favour of males (Aldrich 1973); this being variously attributed to differential mortality (Bellrose et al 1961; Aldrich 1973) and different patterns of movement between the sexes (Johnsgard & Buss 1956; Alford & Bolen 1977; Nichols & Haramis 1980). Little is known about changes in the sex ratio of Maned Ducks, although during 11 days of banding in southern inland N.S.W., Briggs et al. (1983) trapped significantly more males than females. However, such data are prone to bias.

The objectives of this part of the study were to quantitatively examine seasonal and annual variation in the flock size of Maned Ducks, to investigate flock behaviour and determine the composition and stability of a number of flocks. For this work, I studied the behaviour of individually colour banded ducks. In addition, counts of males and females were collected during banding and the surveys of 1981, 1982 and 1983, to investigate changes in sex ratios.

Methods

Data for the analysis of flock structure, flock size and population dynamics came from banded individuals, observations on activity patterns (see chapter 4), surveys (see chapter 5) and some ad libitum observations of flocks.

Trapping

I trapped Maned Ducks with wheat baited funnel traps (McNally & Falconer 1953) between the 29 April 1981 and the 19 February 1984. Most trapping was done before the breeding season each year (Fig. 38). The trapping success closely reflected trapping effort which was determined by logistical constraints. I captured a total of 1244 Maned Ducks, 873 of these being first captures, while the rest were recaptures. Initially, I used only a single trap based on dam G.9 and drove Maned Ducks from other dams. Later, I used seven traps which I moved among the dams, to wherever a flock was camped. Five of these traps were simpler than the original design with only the funnel remaining the same. They comprised a length of 1m wide chicken mesh (diameter 6 cms) wrapped around four star pickets with two further lengths of this mesh providing a roof to the trap. I used fencing tie-wire to knit the various parts together, while rocks secured the trap to the ground. These traps cost less and took considerably less time to make. Since the mesh was doubled, it provided better protection from aerial predators which sometimes attacked trapped Maned Ducks through the mesh.

I put traps within 10m of the edge of a dam. Droppings of Maned Ducks usually marked the best spot. If any cattle were present, a small barbed-wire fence was necessary around the trap, to ensure its continued existence. Once trapping started, I cleared ducks out of the traps once a day. This was because Maned Ducks were easily disturbed and a greater clearing frequency would have probably reduced trapping success. I found late afternoon to evening was the best time, for if ducks were left in traps overnight, they were likely to be killed by foxes. This predation was higher than any by birds of prey, during the day. Trapping success

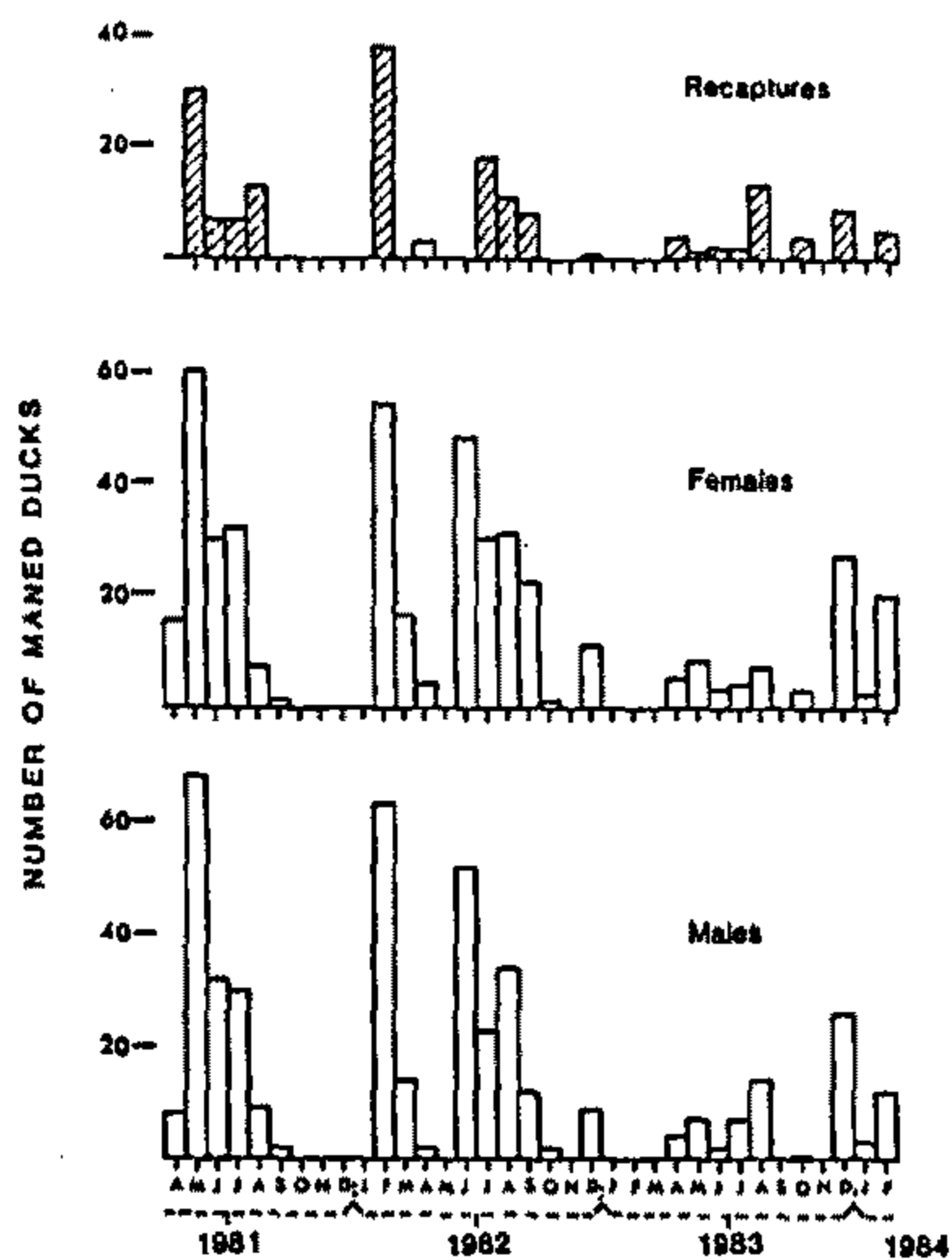


Figure 38. Numbers of male and female Maned Ducks trapped per month during this study. Included are birds trapped for the first time and recaptures (hatched).

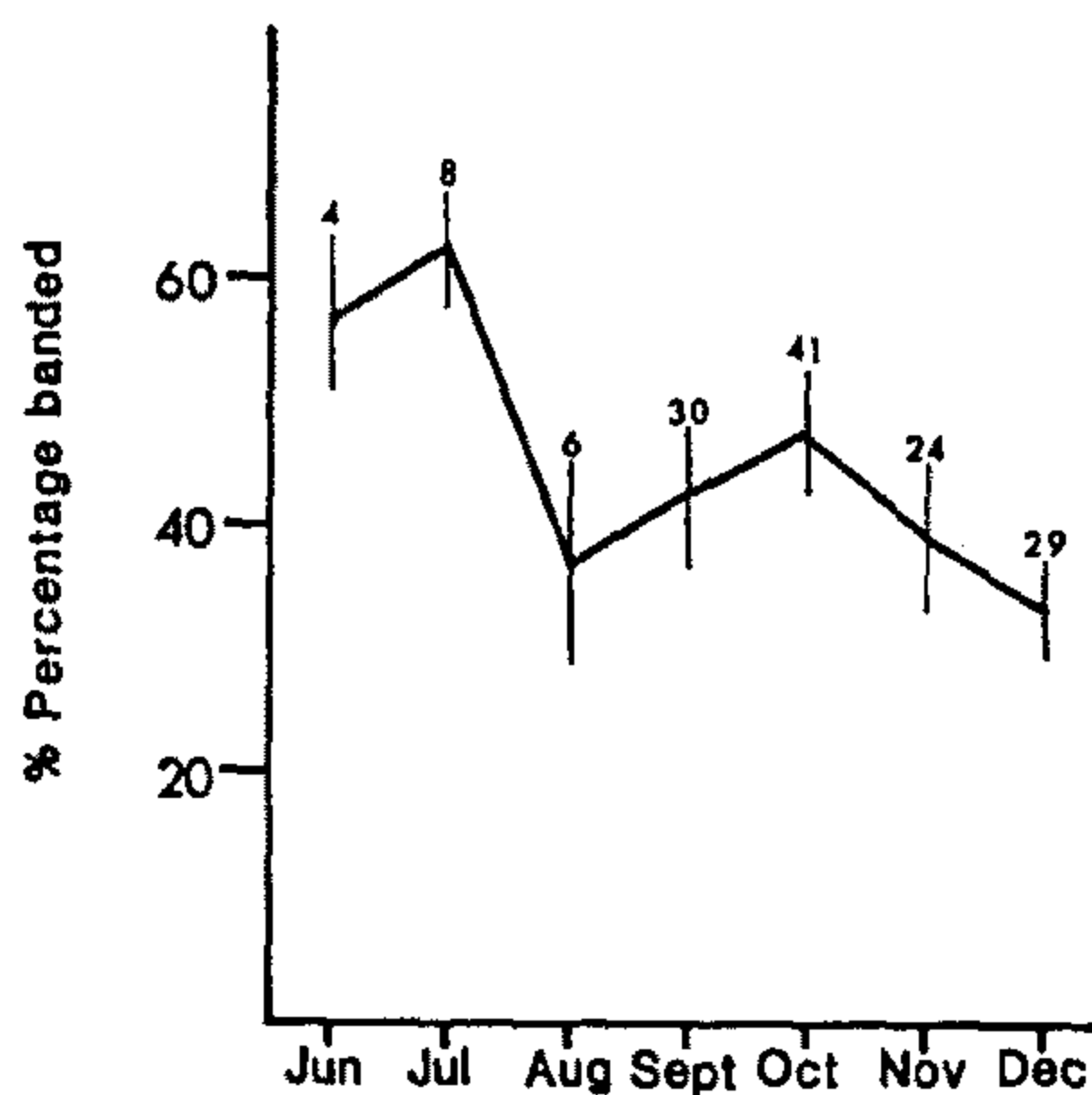


Figure 39. Proportion of the Maned Duck population which was banded (mean $\pm$ S.E.) during the latter half of 1982. Number of flocks given for each month.

ranged from 0-15 Maned Ducks per trap per day and was predominantly dependent on the presence of ducks on the dam and flock size. During 1982, however, success seemed to be higher, probably because there was so little available natural food (chapter 3) and Maned Ducks had also probably picked up the search image for wheat grain (chapter 5).

I put all trapped ducks into a sack and then took body measurements for each duck. In addition, I also attempted to age them by cloacal examination (Hochbaum 1942). Ageing proved to be difficult because the bursa of Fabricius and the occluded membrane across the oviduct (signs of immaturity) were difficult to find. This concurs with observations made by Hochbaum (1942) and Taber (1971). Only the presence or absence of a sheathed phallus (King 1981) was used successfully to determine age. However, since I twice found that males had this at about three months old, it was probably no more useful than the presence of juvenal plumage (Appendix 6).

Each Maned Duck was colour banded using celluloid leg bands which were sealed with acetone to prevent them from unravelling. Initially, I put three bands to a leg. However, this injured the legs of a few individuals. Following this, I used no more than two leg bands per leg. Six colours (black, blue, white, green, red, orange) provided a pool from which I could generate individual colour combinations. As well as these celluloid bands, I put one aluminium band (10mm diam.; 9mm wide), provided by the Australian Bird-Banding Scheme, on each duck. Some of these bands were anodised black and red, and since these three coloured aluminium bands were easily distinguished from celluloid bands, I was also able to alternate on which leg I put them. This further increased the number of banding combinations.

Identifying colour bands sometimes proved difficult. Sunlight bleached some of the orange bands over a long period, making them difficult to distinguish from white bands. As well, celluloid bands would occasionally be either lost, or two would get caught up inside each other. However, these problems only affected the identification of a few birds as I was often able to renew coloured bands when ducks were recaptured. After banding all ducks in a trap, I released them together to ensure that any social structure which existed, was maintained. This may not have

been essential, as Raveling (1969b) found family groups of Canada Geese Branta canadensis reunited if they were not captured together or did not fly off together after they had been processed. This sometimes happened with pairs of Maned Ducks. However, released Maned Ducks usually flew off as a small flock, often to the next dam.

In any study where animals are trapped for marking, some consideration should be given to whether trapping might be biased. The high proportion of banded birds in the population in 1982 (Fig. 39) and also the high percentage of marked breeding birds (chapter 6) provide some evidence that the ducks trapped were representative of the population.

Data analysis

Flock Structure

I defined a flock as a number of Maned Ducks found together on a particular dam. Flocks often remained together throughout the day (chapter 5). To collect data on flock structure, I tried to identify all banded individuals in most flocks I encountered, using a pair of binoculars (7x50 magnification). However, resolution of colour bands was only possible at distances 25m or less from the duck. In addition to hides, wooden screens (1m x 1.5m) with observation slits cut into them were put on many of the dam walls and enabled me to approach ducks. To determine if flock structure was stable, I used data collected from 138 flocks collected between the 6 June 1982 and the 10 January 1983. This period was chosen because a substantial proportion of the population was banded (Fig. 39). Banded ducks seen only once or any flocks in which there was only one banded bird were omitted from the analysis. These contributed little to an understanding of flock structure. Over this period, this left 135 different banded individuals, which I identified within these flocks.

I used cluster analysis to examine flock structure in this data set. Cluster methods provide an informative way of assessing structure in large data sets. They are a group of statistical techniques which group those attributes or objects which are most similar (Romesburg 1984), usually

pictorially in the form of a dendrogram. My problem was one of object analysis (individual ducks; 135 identified) or Q-analysis (Romesburg 1984). Similarity can be defined by various measures and in this analysis, the similarity measure was calculated for every pair of banded ducks in the data set and reflected how often they were found together. To investigate flock structure over time, I defined my similarity coefficient to be a measure of how often "duck k" was found in the same flock as "duck j". A high similarity indicated that they were nearly always found together. Where flock structure is stable over time, one would expect that a number of individuals would have a high similarity and thus be clustered together. The choice of an appropriate similarity measure was the first objective. This was calculated between every duck in the data set, producing a 135 x 135 similarity matrix. The Jaccard similarity coefficient (Sokal & Sneath 1963) seemed the most simple and applicable. Calculation of the Jaccard similarity coefficient is based on a two-way table of the presence and absence of two Maned Ducks in a flock (Fig. 40a). If two ducks are always found together in any flock then they will have a similarity of one, since there will be no mismatches ("b", "c"). My choice of similarity coefficient was also governed by the decision not to include those times when neither bird was seen in a particular flock ("d"). I thought it inappropriate to attach too much importance to these observations (see Sneath & Sokal (1973) for a discussion of this problem). This similarity coefficient is also directly dependent on the number of observations. Figure 40b shows how this similarity measure drops off rapidly as the number of mismatches increases, unless the number of matches also increases. The interpretation of the dendrogram, following cluster analysis, should be done with due regard to how many observations there are for a particular individual. These are listed in Appendix 4.

The second objective was to choose a method of clustering. I used the Single Linkage clustering method (Romesburg 1984). This is probably the simplest hierarchical method. Clusters are formed between those ducks with the highest similarity. If a cluster already has more than one duck, then for the next step, the highest similarity to the duck to be included, is taken from one of those ducks already in the cluster. This continues until all ducks have been clustered into one group. This procedure sometimes results in chaining (Sneath & Sokal 1973), which may hide detail

		Duck k	
		Presence	Absence
Duck j	Presence	a	b
	Absence	c	d

Similarity coefficient $C_{jk} = \frac{a}{a+b+c}$ $0 \leq C_{jk} \leq 1$

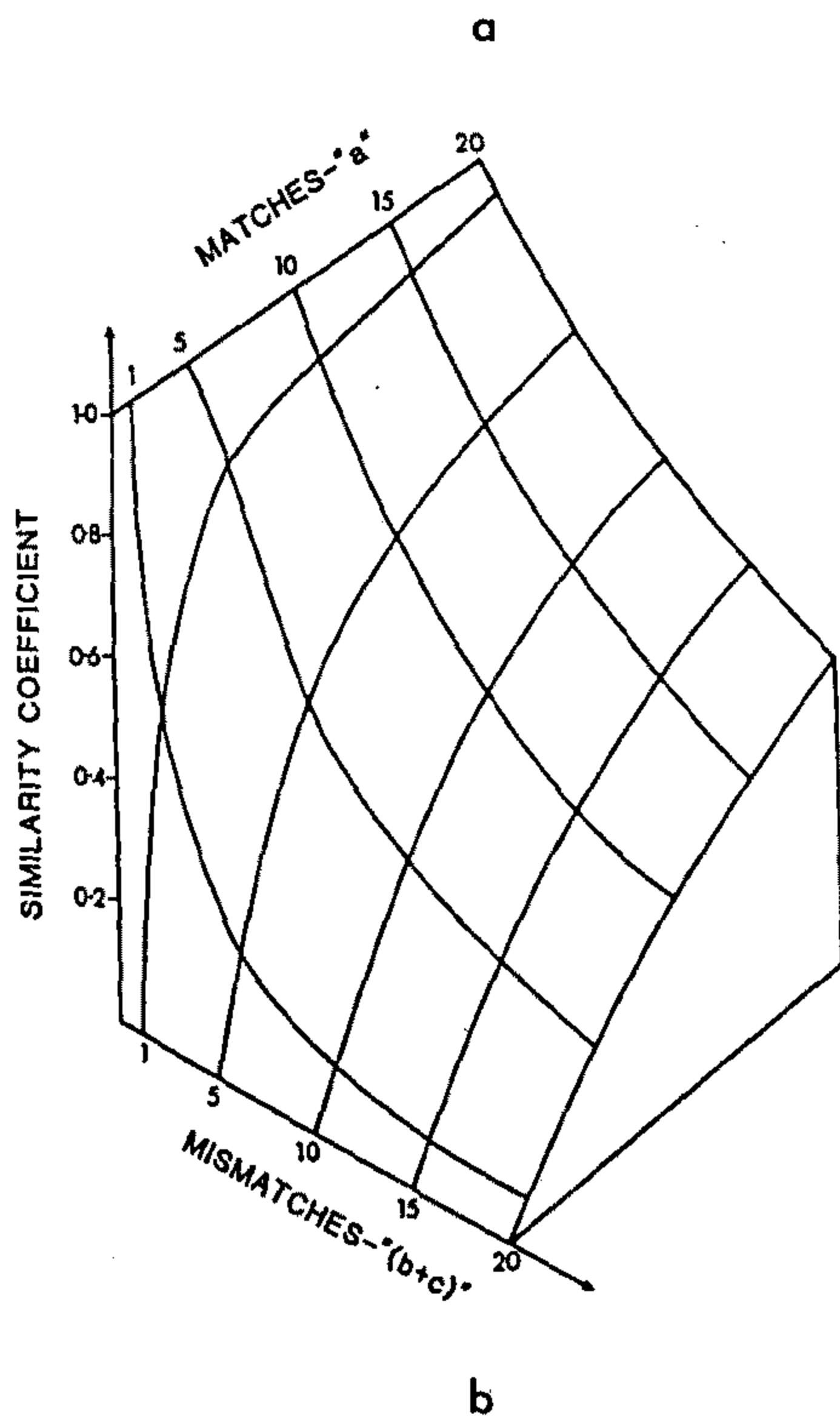


Figure 40. a. The two-by-two table giving the number of matches "a" (i.e. number of times both ducks were in a flock together) and mismatches "b" (number of times duck j present in a flock but not duck k), "c" and "d". From this, the Jaccard Similarity coefficient C_{jk} is calculated. b. Three dimensional representation of this similarity coefficient in response to the number of matches and mismatches.

about clusters. However, in its favour, it is a simple method to apply and understand (Morgan et al. 1976). I used the Genstat statistical computer program described by Alvey et al. (1982), to do the analysis on a Cyber 825.

Behaviour synchrony

I used data collected on activity rhythms, to find out how much intra-flock synchrony there was for each of the different activities (chapter 4). The measure of synchrony used was the proportion of individuals in the flock performing each behaviour at a particular instantaneous scan (every two minutes). I omitted observations on pairs of Maned Ducks because I was primarily interested in the behaviour of larger flocks. Most of these flocks had more than ten birds. To reduce dependency both on other behaviours and on the preceding scan, I randomly selected only one proportion measure per activity, for each half hour period. One-way analysis of variance (Zar 1974) was used to test flock synchrony between behaviours, after data were arcsine transformed to improve normality (Zar 1974).

Sex ratios

I used the chi-square test with correction for continuity (Zar 1974), to determine if there were any significant departures from a 1:1 sex ratio. This was done separately for those Maned Ducks captured for the first time, for recaptures and for survey counts. For trapped Maned Ducks, I treated months as separate samples and calculated a chi-square for each. I then did a test for heterogeneity (Zar 1974) on these samples. This is applicable where there are a number of replicated goodness-of-fit tests (Zar 1974). If the samples are homogeneous then the data may be pooled and subsequently tested. For the survey periods of 1981-1983, I grouped data into months and performed a similar analysis to that used on frequencies of trapped birds, with survey counts on a particular day being treated as samples.

Results

Behaviour synchrony and cohesion in flocks

Synchrony, as measured by the proportion of a flock performing a particular activity, differed significantly according to the activity ($F_{7,554}=27.9$, $p<0.001$). Flocks were most synchronous during grazing, with over 50% of the flock, on average, grazing (Fig. 41). Often, the whole flock would graze but this synchrony was lowered by pairs which behaved independently, particularly during the breeding season. Two other types of behaviour also tended to lower synchrony for grazing. These were individuals walking from the dam to start a grazing bout and others within a grazing flock performing comfort and vigilant activities. Loafing activity also exhibited a degree of synchrony but the proportion of the flock simultaneously performing other activities tended to be low.

Flocks of Maned Ducks were also cohesive when grazing and loafing. Individuals would usually graze close to each other, separated by a distance of 5-10 duck lengths. Large flocks (>30) would sometimes split into two subgroups which foraged in different areas around the dam. However, within these, there was similar cohesion. When ducks loafed, they would often be even closer together. However, during comfort or dabbling activities, Maned Ducks were often some distance apart, around the edge of a dam. Cohesion was also noticeable when a flock flew from a dam. Although ducks usually maintained a compact formation, subgroups would sometimes split from a large flock and fly in different directions. Pre-flight displays probably ensure this cohesion by guaranteeing a synchronous take-off (Lorenz 1941). Pre-flight displays only seem to occur when a flock flies between dams, not when it either flew back to the dam after grazing or when suddenly disturbed. Johnsgard (1965) observed that Maned Ducks perform rapid chin lifting as a pre-flight display, but chin-flicks probably better describe the display. These predominate but other displays include Both-wings-stretch, Wing-and-leg-stretch, Wing-flap, Body-shake and Head-pumping on land. Once an individual starts chin-flicking, this usually stimulates other members of the flock to perform preflight displays. This continues until such a time, as there is

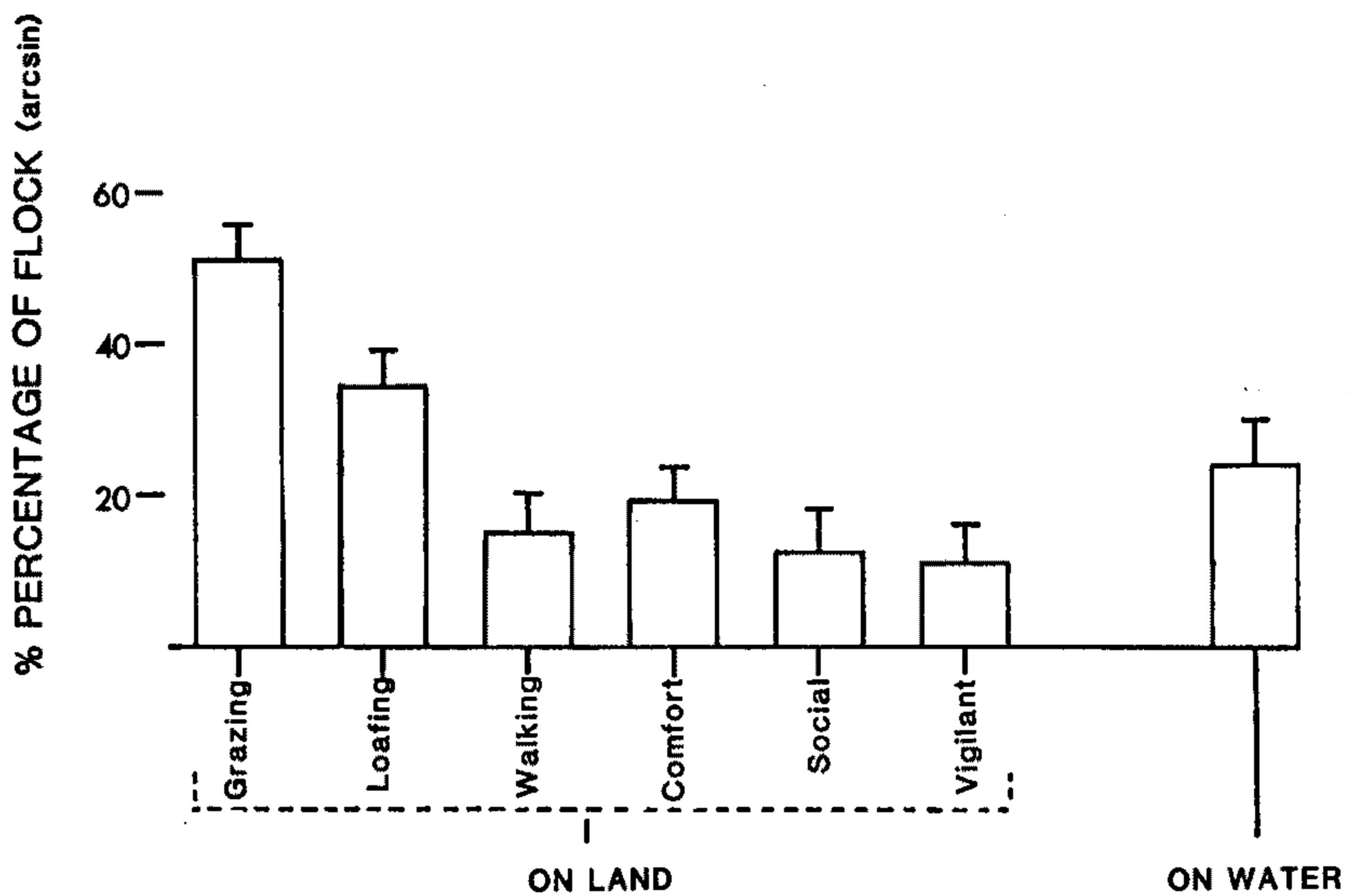


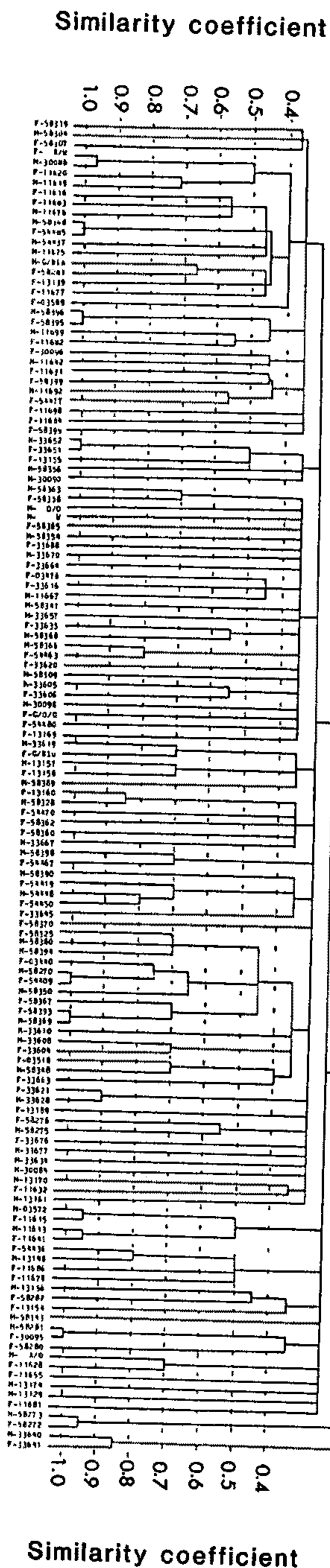
Figure 41. Flock synchrony, for each behaviour, measured as the percentage of the flock (mean $\pm$ 95% confidence limits) doing an activity. There was a significant difference between behaviours ($F_{7,554} = 27.9$, $p < 0.001$).

a large proportion of the flock chin-flicking and one duck takes off. Usually, this duck is closely followed by the entire flock. Sometimes, ducks also vocalise before flying with increasing intensity until flight. If there are subgroups in a large flock, sometimes only one of these will fly off. Pairs will also often separate themselves from the main feeding flock and fly off. I saw other pre-flight displays but these seemed to be exclusively involved with nest searching (see chapter 8).

Flock Structure

The cluster analysis for flock structure revealed some interesting results. Distinct clusters of two Maned Ducks were predominant (Fig. 42). Lines tended to link only two ducks at the higher similarities showing their, close association. As the similarity measure decreased, so more ducks are joined together (i.e. larger clusters formed). However, this is largely due to the hierarchical nature of the analysis. There were six clusters of two ducks with a similarity measure of one. This meant that the two ducks were always found together. At similarities >0.75 , there are 16 clusters, all of which consist of only two ducks. It is not until 0.75 similarity is reached, that there is a cluster of three ducks (58270, 54409, and 03440). However, since the similarity measure is also largely dependent on the number of observations, there must be some doubt as to whether this really reflected a true social grouping. The similarity for these three ducks was based on only three, three and four observations respectively (Appendix 4). Over 48% of all Maned Ducks included in this analysis clustered as members of pairs above a similarity of 0.55. Closer inspection of all two duck clusters, shows that without exception, all involved male and female birds. In most cases, my records confirmed that these were paired birds (chapter 8). Some clusters of known paired ducks had relatively low similarity (eg. R/O-11628). This could be attributed to female absence at the time of surveying because she was incubating. Since cluster methods were used, some attempt should be made to assess the validity of this result (Romesburg 1984). It would seem that the overall similarity in clustering of a number of birds as pairs, would provide the necessary validity. It may be said that Maned Duck flocks seem to be composed of pairs which move independently between

Figure 42. Dendrogram for flock structure, formed after Single Linkage clustering on the flock associations of 135 banded Maned Ducks in 1982. Similarity levels given are calculated from the Jaccard similarity measure ($0 \leq C_{ij} \leq 1$). Individual Maned Ducks are identified by their sex (M or F) and the number of their aluminium band, supplied by the Australian Bird-Banding Scheme. Those whose band numbers could not be identified, are represented by the colour combinations of their celluloid colour bands.



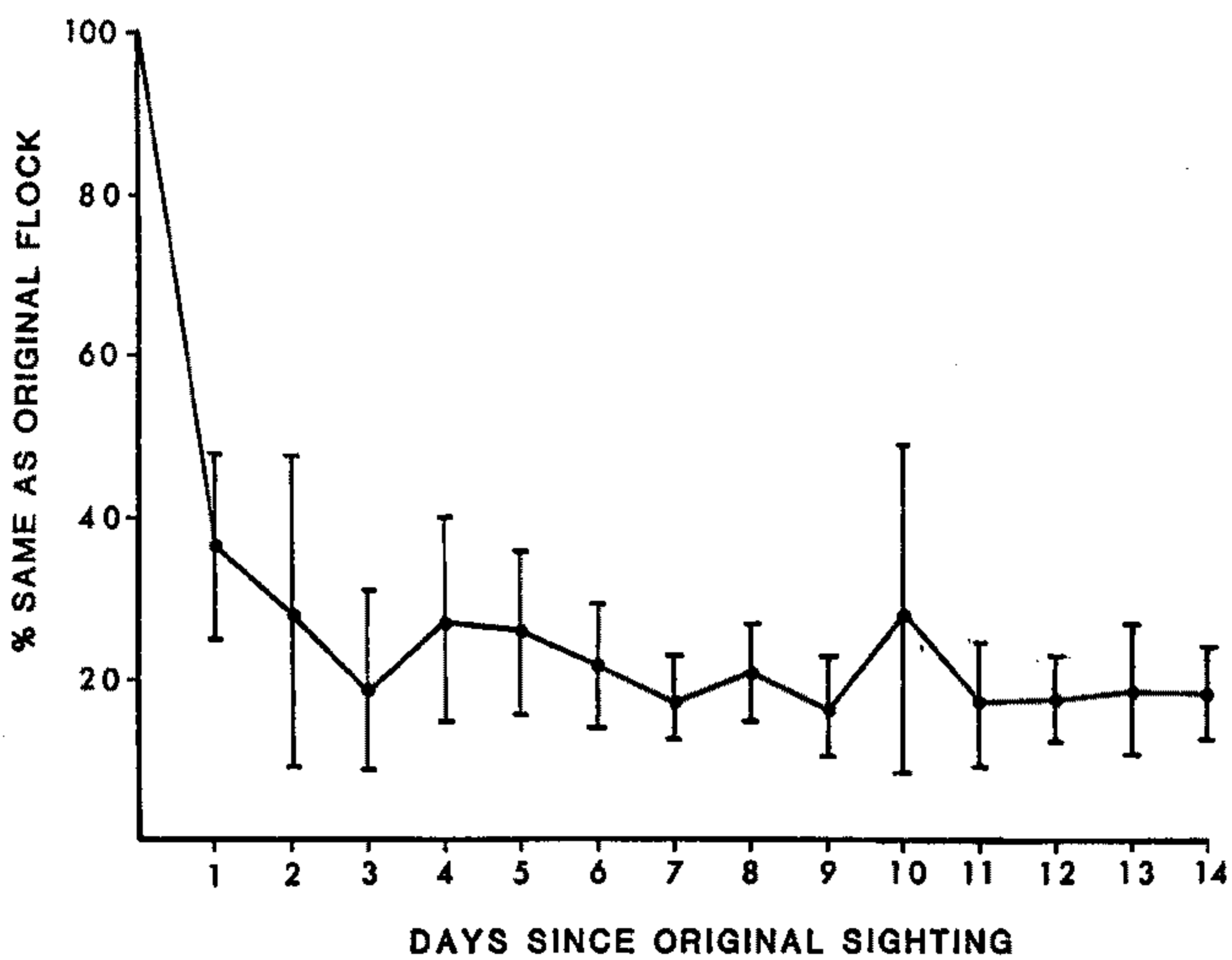


Figure 43. Changes in the composition of particular flocks over time. Flocks were defined as the same, over time, if they had one Maned Duck in common and were on the same dam. Percentage of the flock which remained the same (mean $\pm$ S.E.), was the number of banded ducks which were the same in the two flocks divided by the total number of banded individuals.

flocks, and flock structure beyond this is unstable.

The unstable flock structure was also apparent for those flocks whose composition I was able to monitor over time. Any two flocks were considered to be the same, over time, if they were on the same dam and had at least one marked individual in common. I arbitrarily had a cut off point at two weeks and calculated how many of the original flock remained the same for periods of 1-14 days. This measure was the number of banded ducks which were the same in the two flocks, divided by the total number of banded individuals in the two flocks, which was then converted to a percentage. On average, only about 38% of a flock remained the same a day later (Fig. 43). Although this was marginally higher than other later days, there was essentially little difference. On average, about 20% of the flock was the same if it was measured 2-14 days later. Percentage levels any lower were probably precluded because flock sizes were small, and in many cases a level of 20% meant that only one duck was the same.

Flock size

In 1981 and 1983, mean flock size was low at the beginning of the survey period (September) but tended to increase later in the year (Fig. 44). During September and October, flocks of two or three were the norm, whereas later in the year flocks averaged about 20 ducks. Consequently, there were fewer flocks later in the year and flock size was also more variable. This was due to some pairs still moving around independently. In 1982, there was no real pattern. Flock numbers remained relatively high throughout the survey period, September-December, tending to be much higher than the other two years. In 1982, I recorded the highest flock size of 153 on one dam. Associated with changes in flock size, were trends in dam use in 1981 and 1983. Most dams on the study site had a pair of Maned Ducks camped on them in September of 1981 and 1983 but the number of dams decreased in a significant linear fashion towards the end of each year (Fig. 45). There was no such pattern in 1982. In that year, the number of dams used by Maned Ducks varied throughout the year, remaining high even in December.

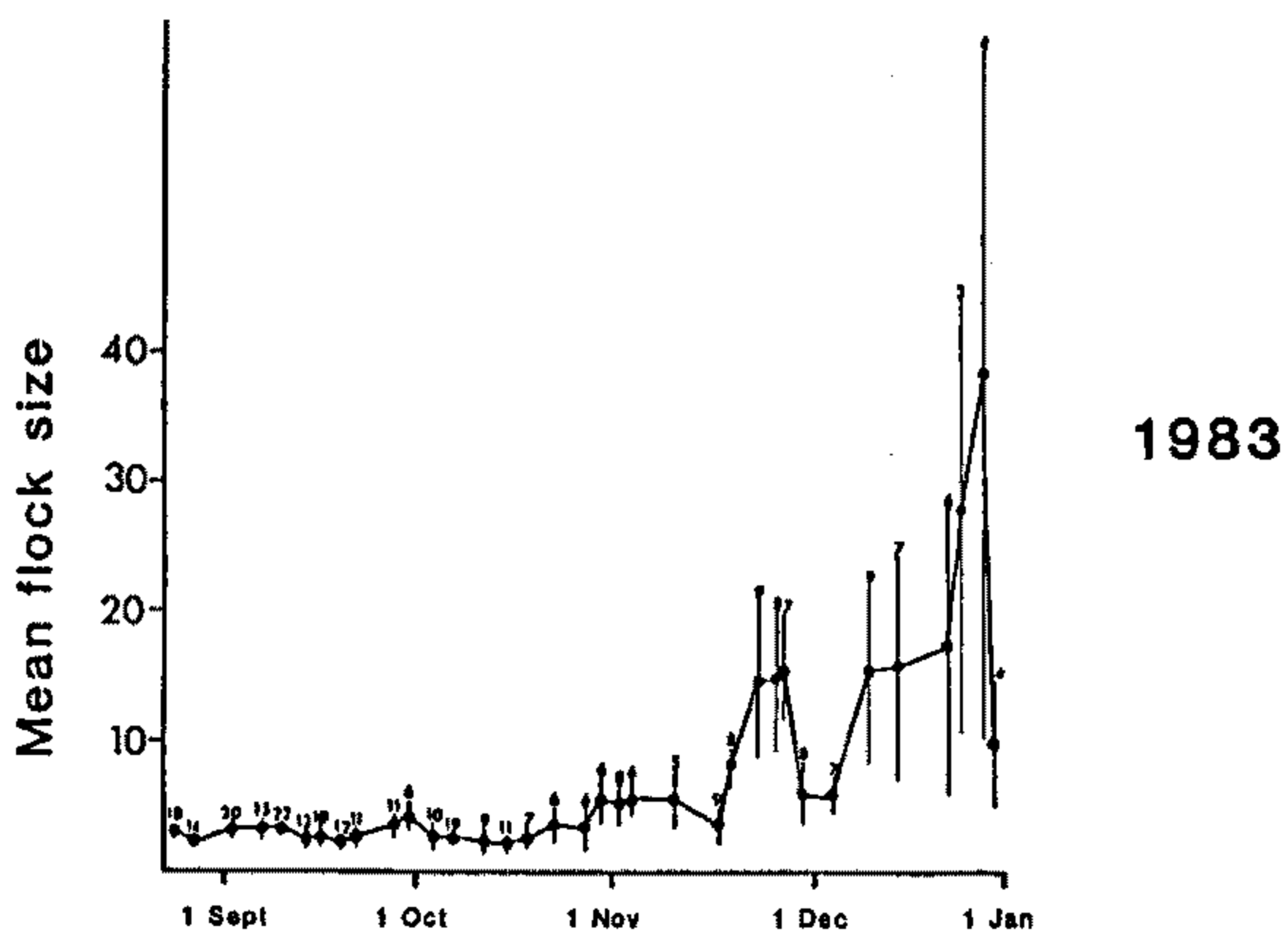
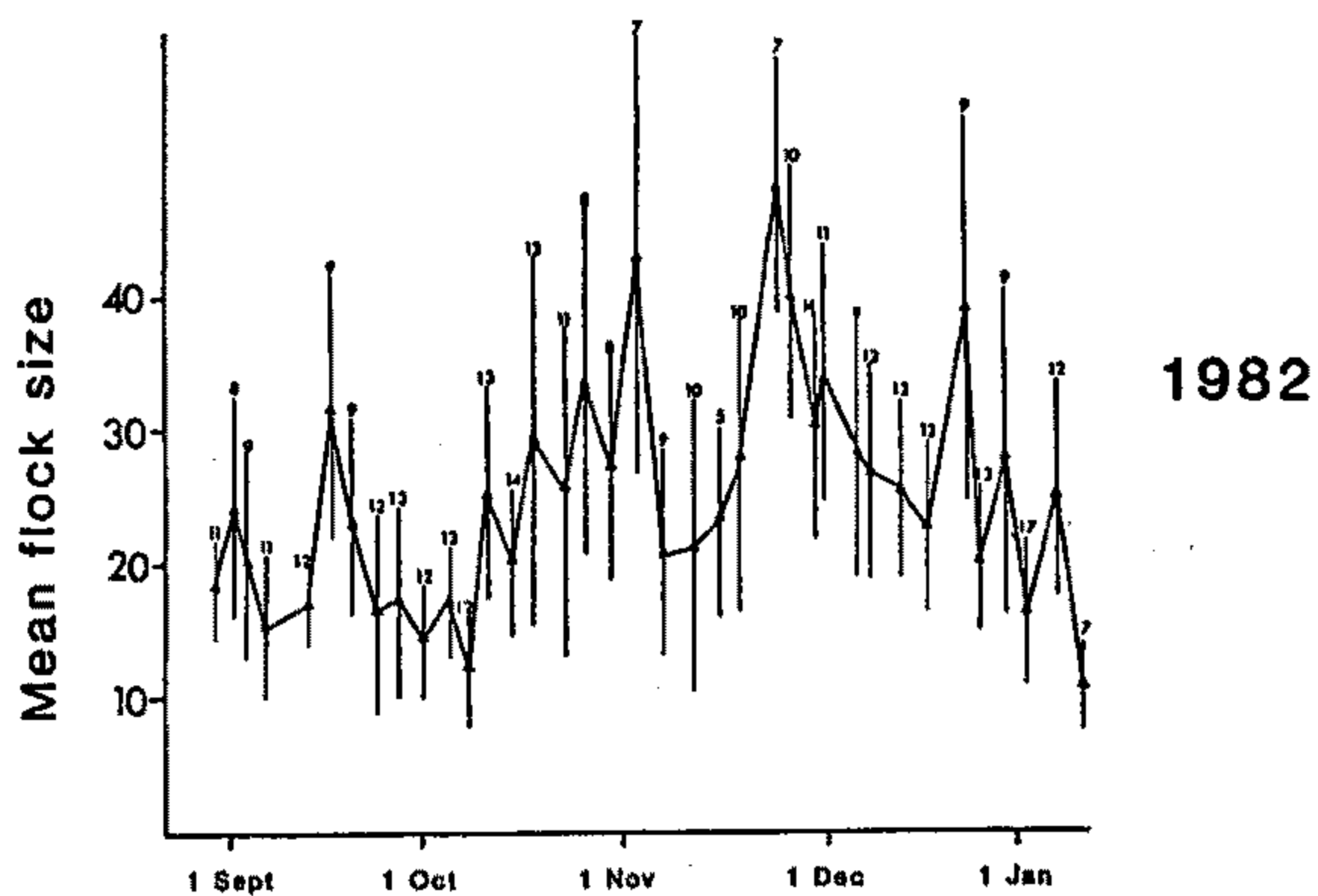
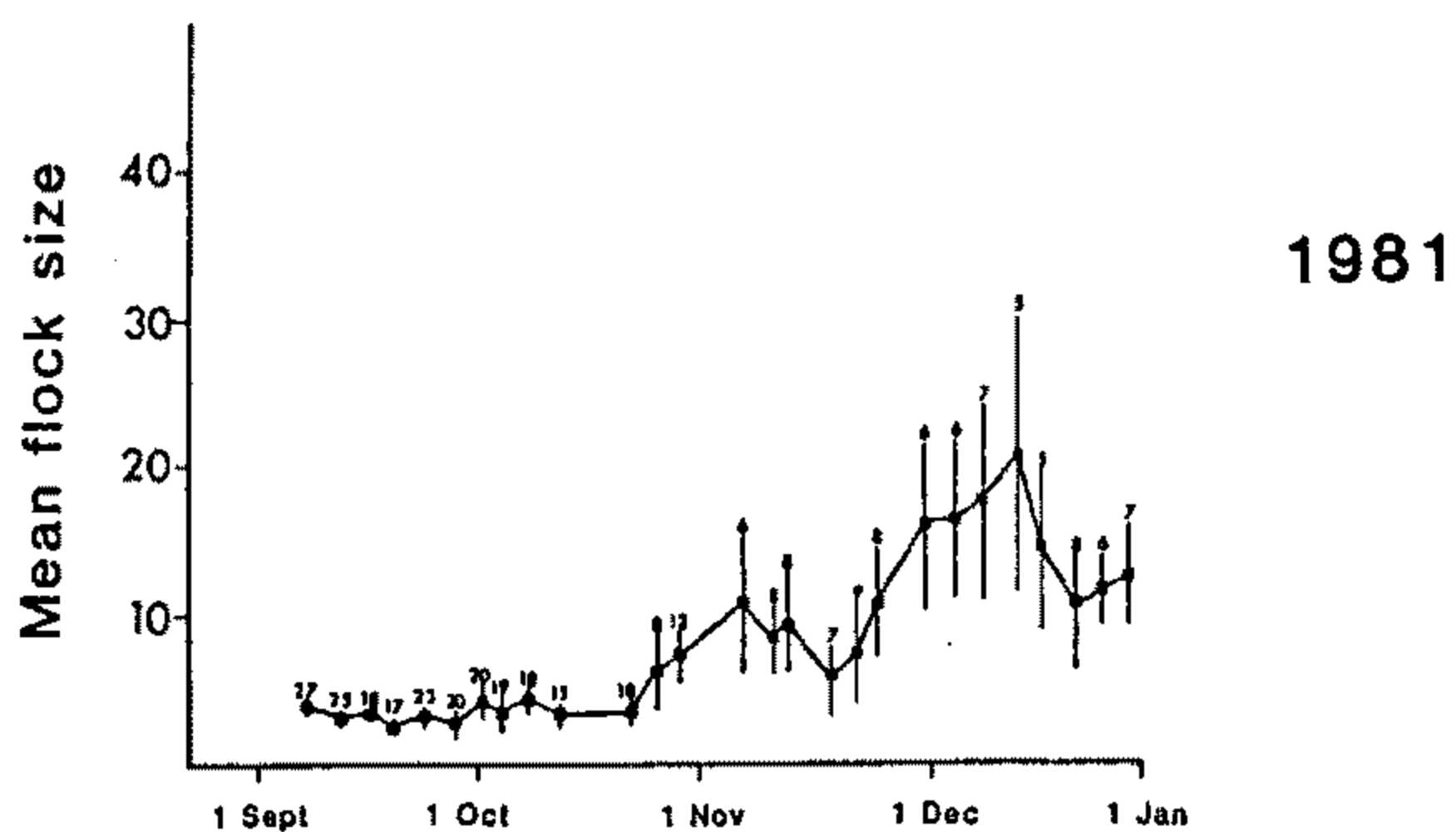


Figure 44. Mean flock size between September and December, 1981-1983. Points are survey days (Bar length=S.E., n=sample size).

% Dams occupied (arcsin)

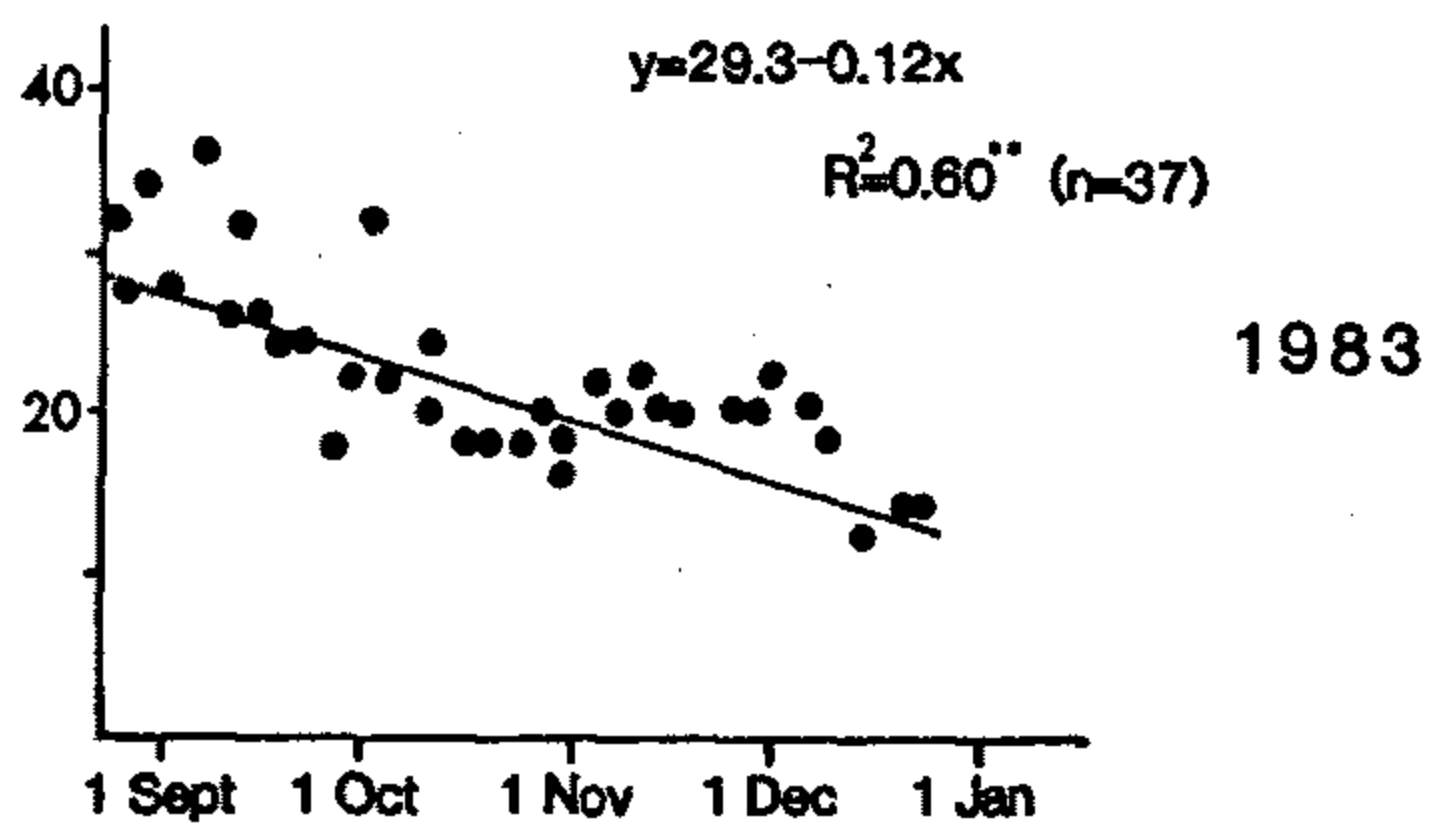
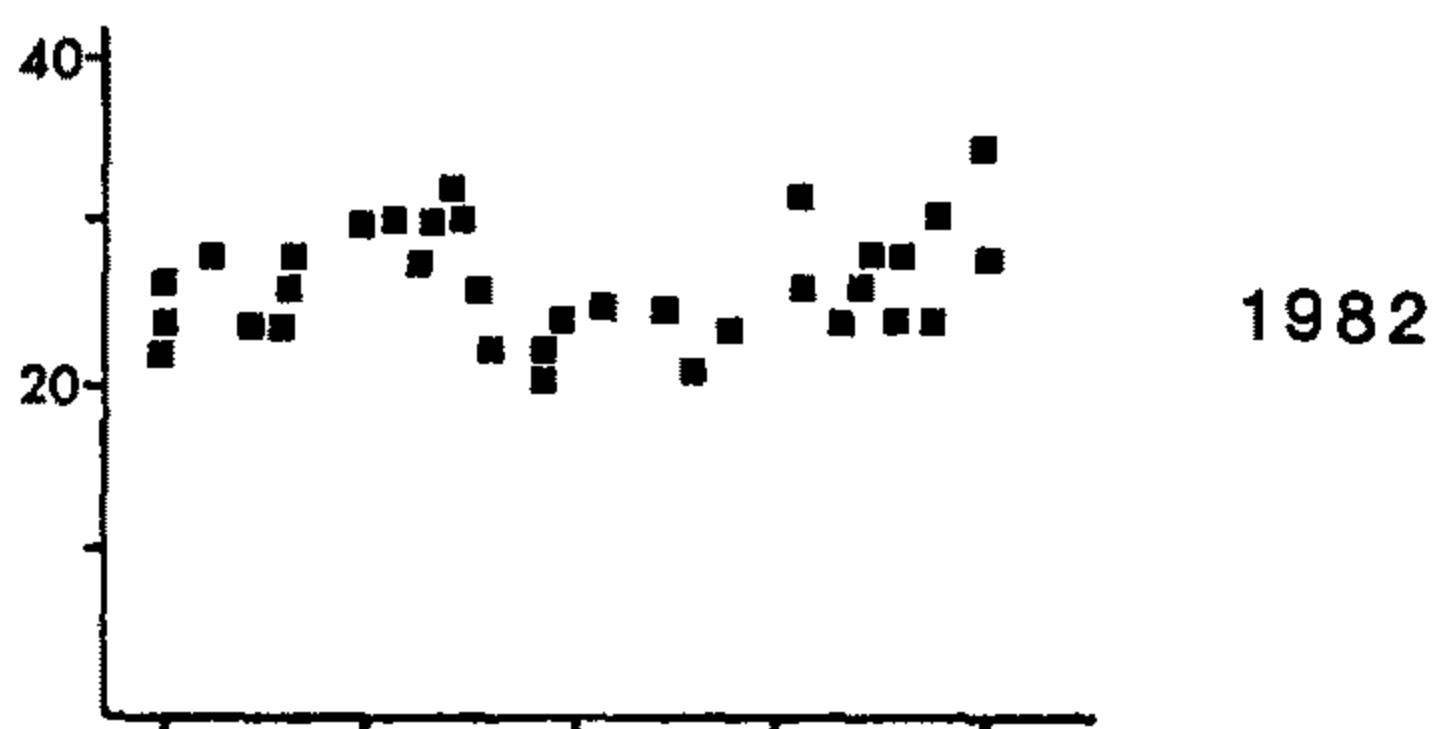
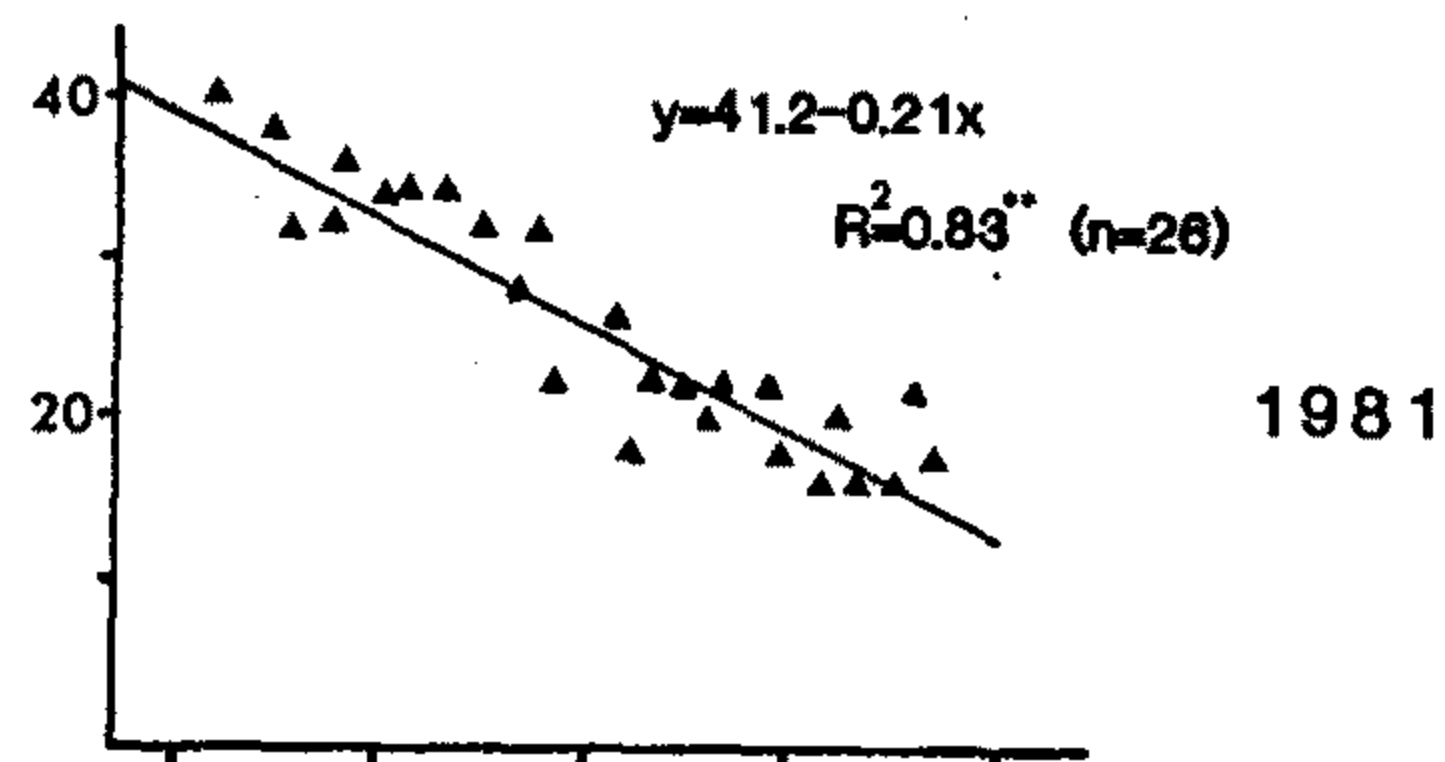


Figure 45. Percentage number of dams on the study site with Maned Ducks on them between September and December of 1981-1983. Points are survey days. Significant linear regression equations were fitted to the data of 1981 and 1983.

Table XXIII. Goodness of fit tests (chi-square) for a 1:1 ratio of males to females from trapping and survey data. Tests are conducted on pooled samples already tested for heterogeneity. All samples were from homogeneous populations. For trapping, samples where observed frequency of both males was below five have been omitted, reducing n. All significant differences favour males. (*-p<0.05; **-p<0.01; ***-p<0.001)

TRAPPING

	<u>n</u>	<u>Chi-square</u>	<u>sig</u>
First capture	837	0.01	ns
Recaptures	206	0.39	ns

SURVEYS

	1981			1982			1983		
	<u>n</u>	<u>Chi-square</u>	<u>sig</u>	<u>n</u>	<u>Chi-square</u>	<u>sig</u>	<u>n</u>	<u>Chi-square</u>	<u>sig</u>
SEPTEMBER	324	14.69	***	111	0.01	ns	174	18.82	***
OCTOBER	294	8.17	**	592	0.49	ns	187	4.19	*
NOVEMBER	158	0.01	ns	404	2.08	ns	155	6.61	**
DECEMBER	178	0.05	ns	428	0.68	ns	22	0.05	ns

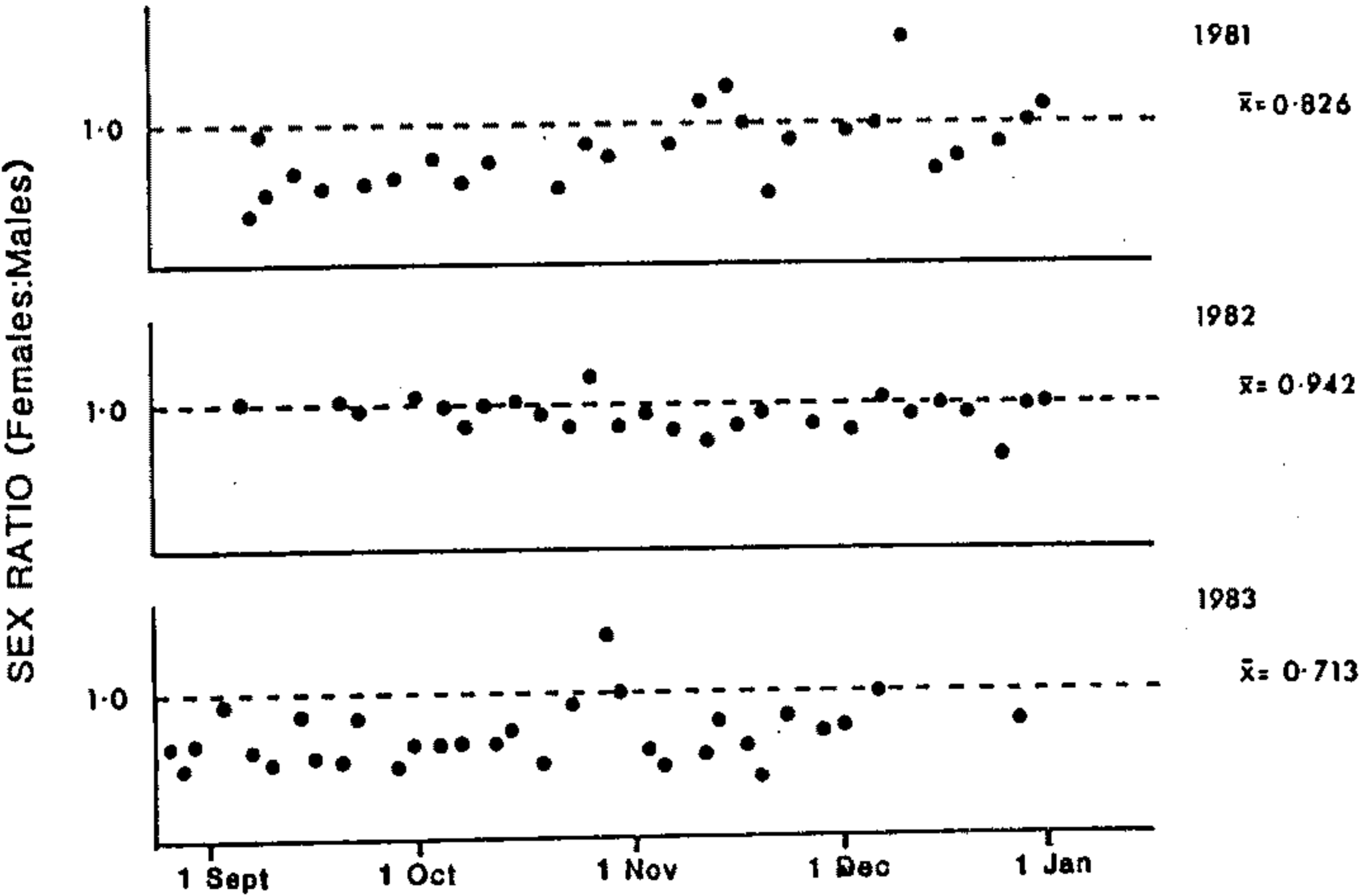


Figure 46. Trends in sex ratio (females:males) for the three years 1981-1983 between September and December.

Sex ratios

There were no significant departures from a 1:1 sex ratio for trapped Maned Ducks (Table XXIII). However, there were some significant deviations for population counts collected from surveys (Table XXIII). These departures occurred in September and October of 1981 and September, October and November of 1983. All favoured males. The two most highly significant results were both in September. However, in 1982, there were no significant departures from a 1:1 ratio. Figure 46 shows these trends in sex ratios between September and December for the three years.

Population dynamics

Throughout this study, I kept records for 406 Maned Ducks which I either trapped or sighted after they were banded (i.e. ducks not seen again after banding were not included). These records included the date and the dam on which the duck was identified, whether the individual was paired and if it had ducklings. The collection of data on population dynamics was not structured although I did attempt to locate and identify every banded individual during survey periods. This was done once every four days. Outside these times, trappings and sightings were opportunistic. I collected 260 trapping records (recaptures) and 575 sighting records. These are a measure of sampling effort as I have not included any duplicated records (i.e. times when more than one duck was identified on a dam, on a particular day), since these would not be a measure of sampling effort.

These records form the basis of the following treatment of population behaviour. I have not included any banded Maned Ducks with ducklings as these are restricted in their movements (chapter 6). The majority of both males (58%) and females (61%) were never sighted or trapped after banding (Fig. 47). Most of the others were seen less than four times. However, there were some individuals on which I have up to 40 records and this number of ducks would have been slightly increased if ducks with broods were also included. There seemed to be little difference between the sampled male and female population.

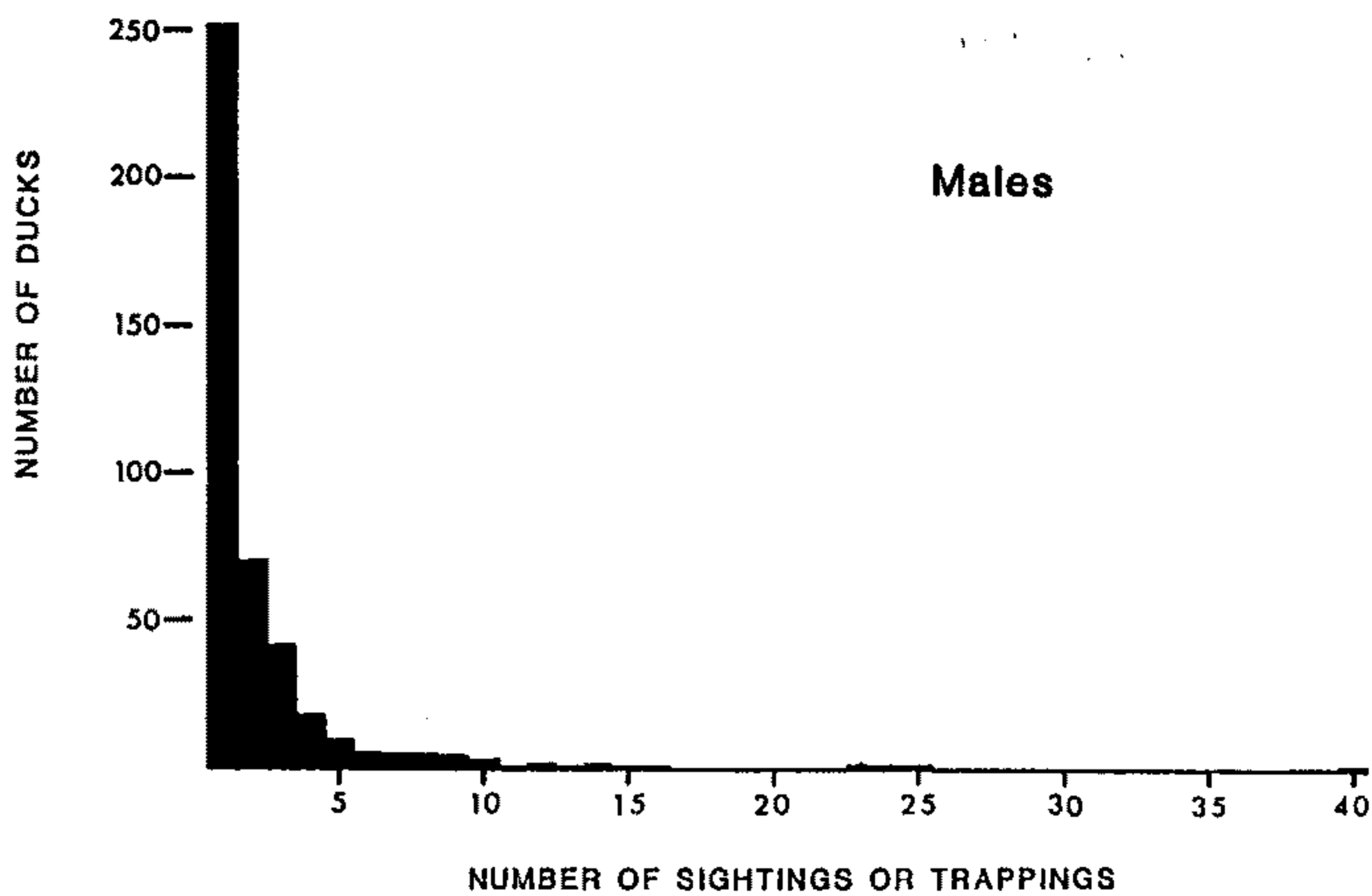
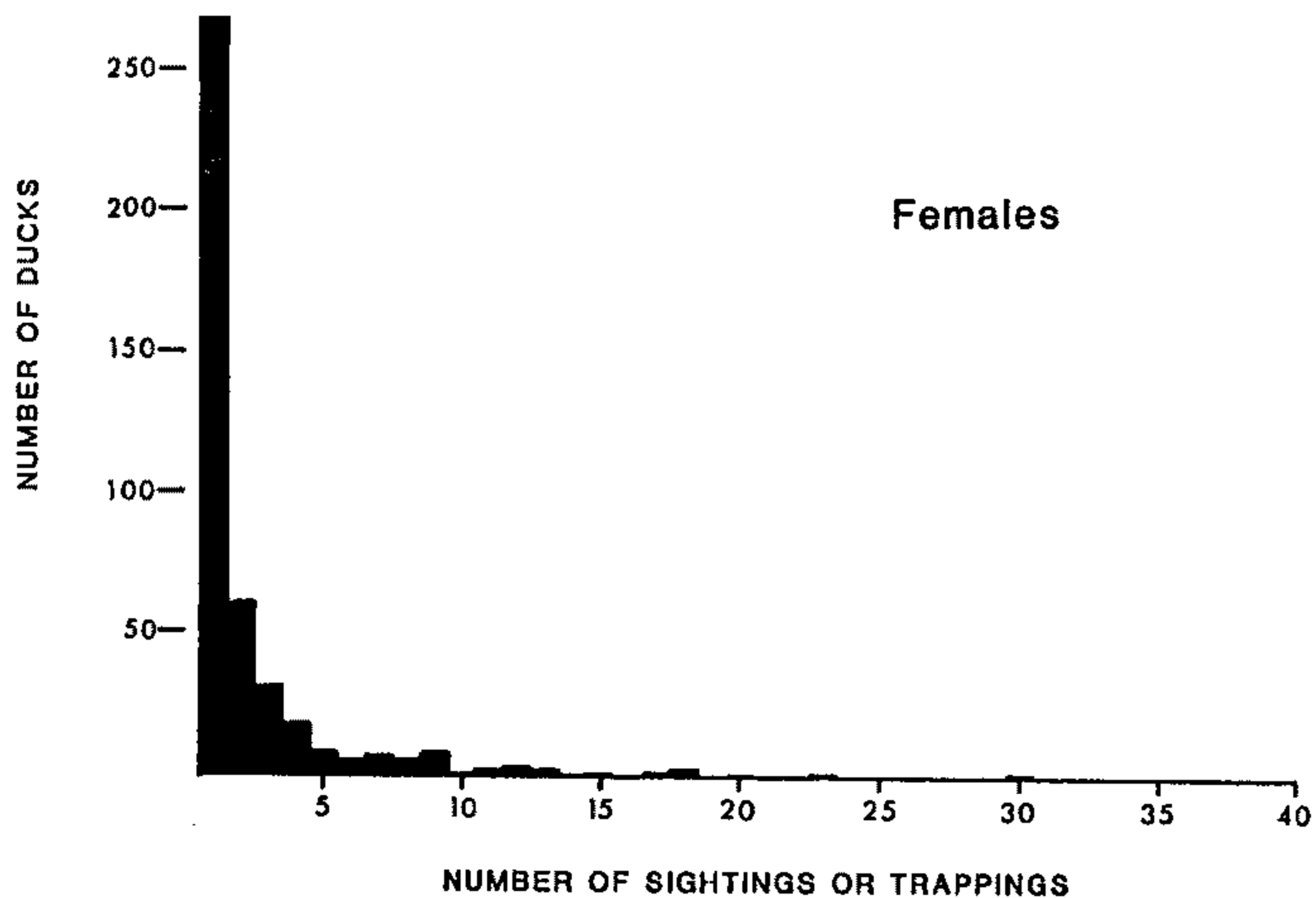


Figure 47. Number of records for male and female Maned Ducks which were banded. One record signifies that the duck was not seen or trapped after being banded, while two records indicates that the individual was subsequently sighted or trapped.

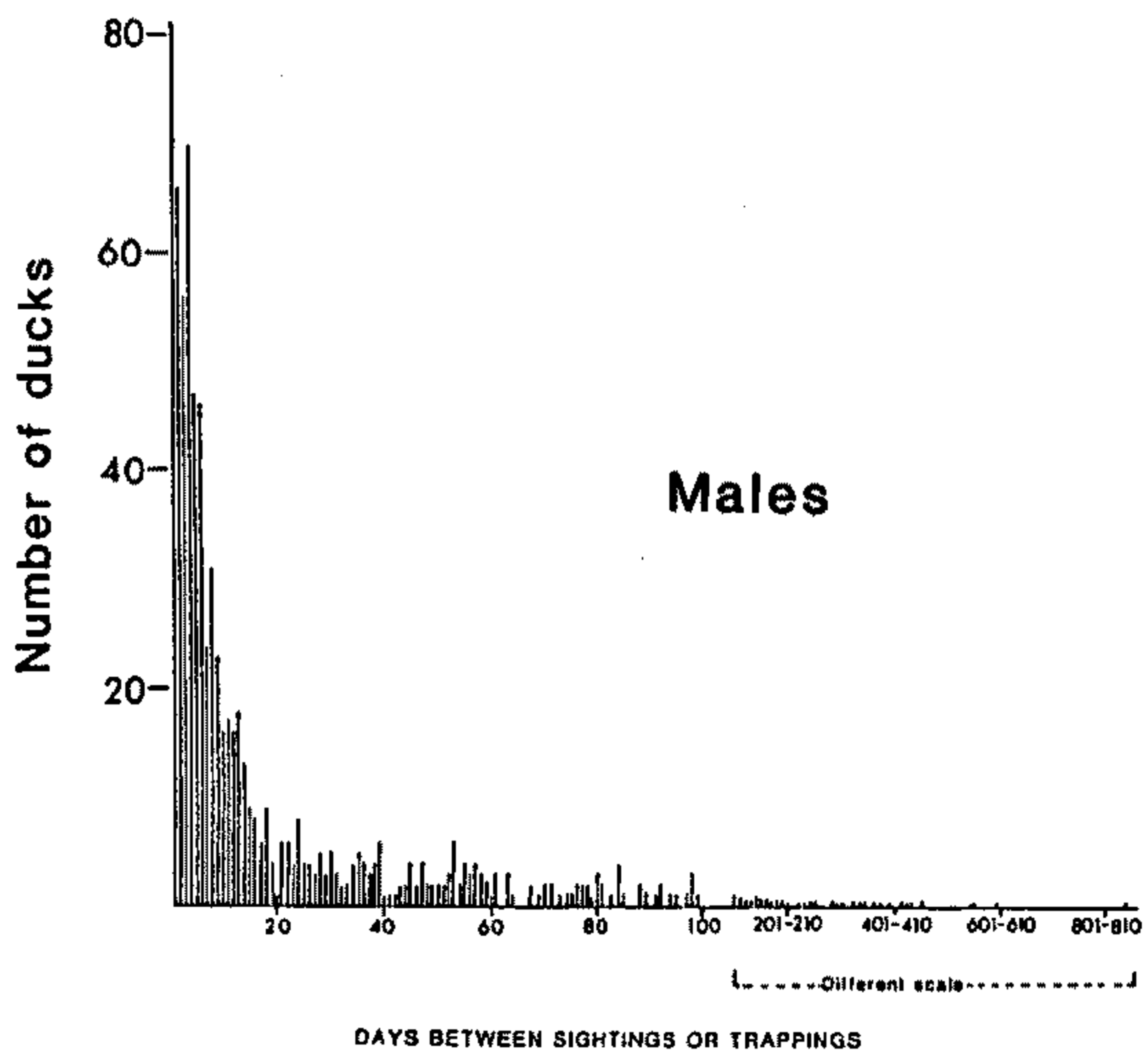
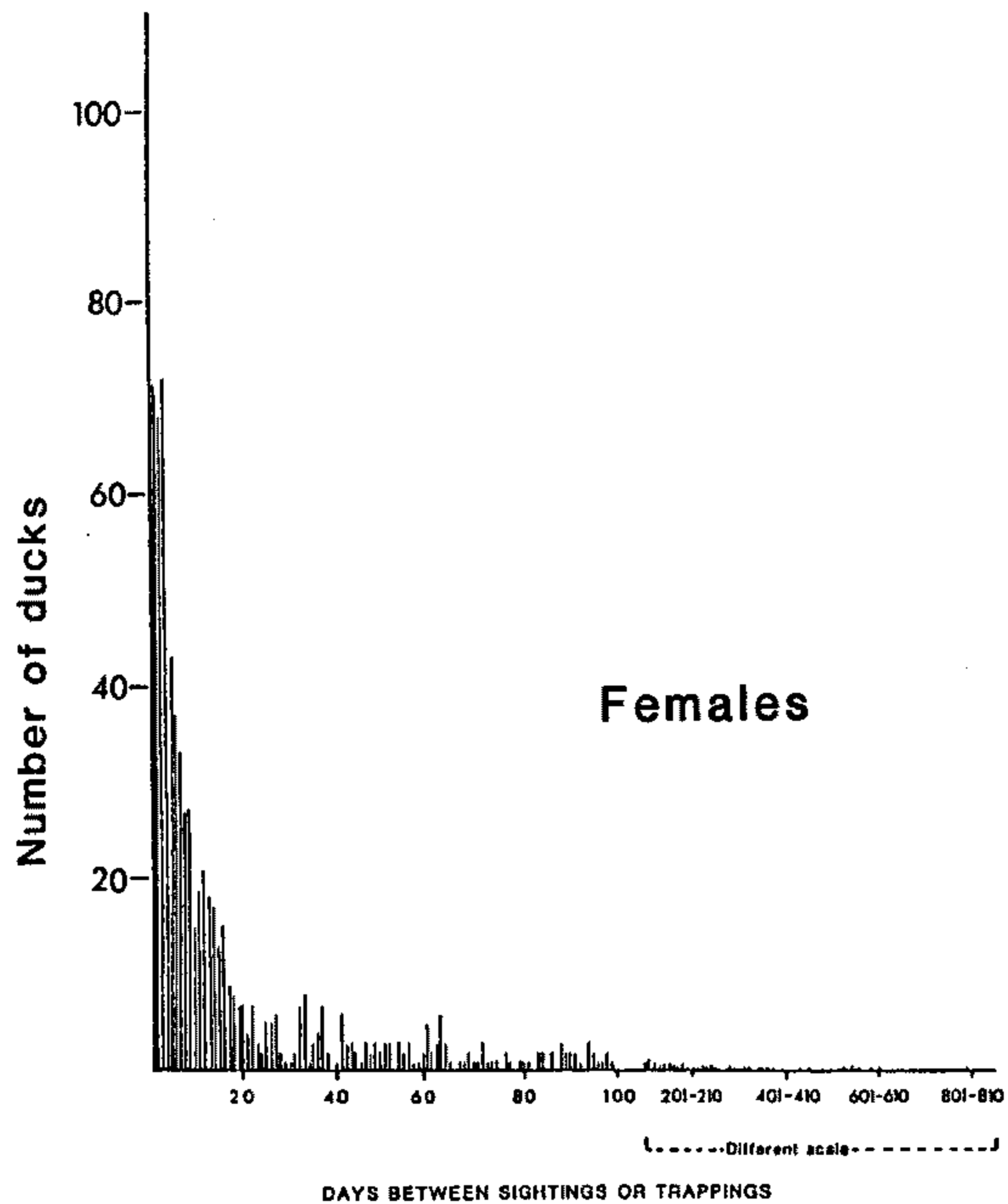


Figure 48. Days between sightings or trappings for those male and female Manded Ducks which were either sighted or trapped again after being banded. This measure is the number of days which separated any two records.

From these records, I also calculated the number of days between records for all ducks. This was a measure of the probability of seeing a duck on the study site, once it had been seen or trapped. There was a good chance that if a Maned Duck was going to be seen again on the study site then it would be seen within ten days (Fig. 48). There is a rapid decline after this for both males and females. Nevertheless, it is interesting that some individuals returned to the study site over 800 days later.

I made no attempt to calculate mortality indices or distribution maps from band returns, as only three bands were returned to me, a recovery rate of 0.3%. One was from the study site, while another was within 30km and the last came from Ararat in Victoria, a distance of 760kms from the site.

Discussion

In 1981 and 1983, there were seasonal changes in the flock size of Maned Ducks similar to those reported by Frith (1982, p 264). Flock sizes were small during the breeding season and then increased later in the year, after breeding (Fig. 44). Although, I did not survey before September, flock size was high at the beginning of the year until the first pairs were sighted on their own, in late May and early June. These changes more closely matched Frith's (1957a) earlier observations of an autumn to winter break up, than that of a spring dispersal (Frith 1982, p 264). By spring, when surveys started, flock size was already low, implying that flocks had already broken up. Since there was little monthly variation in the total numbers of Maned Ducks during the survey period (chapter 5), the reduction in flock size in 1981 and 1983, meant that more of the dams were being used (Fig. 45). Frith (1957b) observed, that during the breeding season every piece of water would ultimately have its one or two pairs of Maned Ducks camped on it. However, I found that a maximum of only about 30% of the dams on the study site had Maned Ducks on them in these two years (Fig. 45). Although surveys did not begin with the breeding season, a similar pattern was apparent earlier. Differences between Frith's observations and those from this study were possibly due to higher populations or fewer potential habitats on his sites. Maned Ducks probably disperse so that they can search for suitable nest sites, since there was some indication that they were more likely to be found on those dams with nest holes nearby (chapter 5).

Comparing changes in flock sizes between the three years, provides further evidence for a correlation between social structure and breeding. Small flock sizes were prevalent only in the breeding seasons of 1981 and 1983 (Fig. 44). Both years were climatically normal. The extensive breeding which occurred in these years was probably an indirect result of this (chapter 6). In contrast, there was little rain and little breeding in 1982. Also most flocks were large (Fig. 44). The few pairs on their own that year, were consistent with the limited breeding (chapter 6). Some autumn breeding in the two normal years (chapter 6), would also explain the existence of a few pairs on their own at the end of the year.

There was some evidence to suggest that flock size was also directly dependent on the reproductive condition of individuals. In the breeding season of 1981, I shot Maned Ducks from a number of different sized flocks. Birds shot as pairs tended to be in full breeding condition, while those in larger flocks had small gonads. This is indicative of reproductive inactivity in seasonally breeding birds (Lofts & Murton 1973). Moreover, the behaviour of pairs on their own also usually showed that they were reproductively active. Females fed a lot, while males tended to be more vigilant (chapter 8). If flock break-up is related to reproductive demands, then perhaps pair independence is important to nest searching, copulation and ultimately the successful rearing of offspring.

During the breeding seasons of 1981 and 1983 when flocks were small, the sex ratio of the population appeared skewed in favour of males (Table XXIII). However, I attributed this to no more than a sampling bias. Incubating females would have been missed in survey counts. This was a likely explanation for a number of reasons. The most significant deviations were in September of the two years, when breeding was probably at its height and females were more likely to be incubating, relative to the rest of the survey period. As well, there were no significant deviations for either, other months of these survey periods when there was no breeding, or for ratios of trapped birds. Furthermore, in 1982, when there was very little breeding, there was no significant departure from a 1:1 sex ratio during the survey period (Table XXIII). It may be concluded that male and female Maned Ducks have neither different movement strategies after breeding nor differential mortality during the breeding season. Both of these have been used to explain a preponderance of males in the populations of a number of other anatids (Johnsgard & Buss 1956; Aldrich 1973; Alford & Bolen 1977). Rather, the problems highlighted by Bellrose et al. (1961) in obtaining a truly representative measure of the sex ratio, seem to be reinforced.

Flock sizes were larger after the breeding seasons of 1981 and 1983 (Fig. 44) and throughout the survey period of 1982, when little breeding occurred. Social organisation, outside the breeding season, can take a variety of forms in birds (Pulliam & Millikan 1982). Much can probably be

learnt about the function of such behaviour by first examining flock stability and behaviour. This initial step is probably often ignored, leaving studies open to possible criticism that hypothesised functions might be confounded by social factors.

I used cluster analysis methods to investigate flock structure. Zicus (1981a) attempted to use such methods in a similar study of Canada Geese Branta canadensis, but found that results were inconsistent with those empirically apparent. Without further information, reasons for this cannot be determined but the simplicity of the methods and direct relationship to the data would seem to cast some doubt on this assertion. Morgan et al. (1976) successfully used these techniques to show group structure in chimpanzees. Data collected from flocks in 1982, strongly indicated that there was little flock stability in this species. Manded Ducks seem to move between flocks as pairs (Fig. 42). Most marked birds were clustered as two bird groups. Any clusters of three ducks could be attributed to either few observations or low similarity and were unlikely to reflect any true social association. Observations of the movement patterns of individuals in a flock, strengthened this. Although flocks were cohesive, birds tended to move as pairs within the flock. Flocks monitored over time showed similar instability in composition. Flock composition seemed to be unstable even over the period of a single day, with only about 38% of the flock remaining the same (Fig. 43). However, the proportion of the flock remaining the same, seemed to stabilise at about 20%. This was because occasionally a few individuals would sometimes stay on a particular dam for some time. Further evidence for this "camping" behaviour comes from days between sightings (Fig. 48). These tended to be concentrated to a few days. If an individual was to be seen or trapped again then it was likely to be within the next few days, usually on the same dam. Occasionally flocks were flushed, but this was unlikely to make any major contribution to the patterns observed because data which was consistently gathered on flock structure, was from those dams which could be approached without disturbing the flock.

Limited data on movement patterns also provided further evidence for instability in flock composition. There were some individuals which stayed on the study site for some time, others which returned to the study

site after an apparent absence of some time, while most stayed for a relatively short time (Figs 47 & 48). For some, I collected a number of records (Fig. 47) which indicates that even over a small area, there are some Maned Ducks which may be described as "local" in their movements, compared to other Australian waterfowl. This supports evidence from other banding studies (Frith 1959b; Norman 1971). Two further observations support this. A female, banded as a juvenal, bred on the site two years later and a pair bred in successive years on the site. Observations of a few individuals which apparently came back through the study site, provides some tentative evidence for the existence of a home range. I have not considered mortality in this interpretation but undoubtedly this also substantially influences apparent movement patterns.

I stopped conducting surveys at the end of December, so there is no data on flock composition after all the ducklings had fledged (see chapter 6). However, it was evident that the large flock sizes at the end of the survey periods of 1981 and 1983, had family groups in them, which supports Frith's (1982, p 265) observations. An extended period of parental care, beyond fledging (chapter 8), was probably the reason. However, these flocks were not only made up of family groups. This was evidenced by the fact that the ratio of juvenals (with a distinctive plumage) to adults was not high in these flocks implying that there were other adults. Flocks of Canada Geese Branta canadensis, appear to behave similarly and there is considerable stability beyond the family group (Craven and Rush 1983). Frith (1982, p 265) considered that stability in the flock structure continued, based on evidence of groups of Maned Ducks found together year after year and groups shot together in different locality, far from where they were banded. Unfortunately, he does not mention the size of these groups. If they were pairs then this would be entirely consistent with the evidence presented here, since I found there was pair stability in flocks, which can extend for some time (chapter 8). This study does not offer any evidence for how long the family group stay together since flocks were not monitored past December and none of the progeny were marked. To resolve such a question, members of a family group need to be marked and followed. However, based on the absence of any stability later in the year beyond that of paired birds, it seems likely that the family group breaks up early in the year. Occasional

observations of groups of juvenals on their own, provide some further support for this. Perhaps, this happens when parents go off to moult their wing feathers. There was some evidence that this moult occurred after breeding, on bodies of water larger than those on this study site (Appendix 6). Parents would then need to travel to such areas. Juvenals would not need to accompany their parents since first year birds probably retain their juvenal wing until the following year (Palmer 1972, p.93). I would suggest that family groups in this species are probably less stable than in the geese and shelducks, largely because these birds probably mature faster, and perhaps breed in their first year.

In summary, there was little evidence for any compositional continuity in flocks of Maned Ducks. There were also few social interactions amongst individuals within the flock (chapter 4), which is similar to the White-fronted Geese Anser albifrons (Boyd 1953). Those that did occur tended to be agonistic (see chapter 8) which further emphasizes the loose associations of individuals which make up flocks. However, flocks of more than two birds tended to be both remarkably synchronous in their behaviour (Fig. 41) and cohesive, particularly while grazing. Well developed pre-flight displays probably also ensure that cohesion is retained when Maned Ducks fly. This cohesion was probably what Frith (1957b, 1982, p 265) referred to as "closely knit" and "compact", in his descriptions of Maned Duck flocks. However, compositional changes do occur. Changes in flock structure were sometimes achieved when subgroups separated from the main flock and flew away. In addition, when a big flock is disturbed individuals often separate, on the wing. It is possible that further changes in flock structure also occur at night.

The absence of any real stability in flocks of Maned Ducks begs the question that has been asked of many bird species, why are flocks formed? For some animals aggregation may simply be due to greater resource patchiness (Wiens 1976). In 1982, there was a patchy distribution of food. The only real food source was the wheat grain which was fed to sheep on near certain dams, as a drought relief measure. Maned Ducks tended to use these dams more (chapter 5) and it was likely that higher flock sizes this year, were partly due to this patchy food distribution.

This observation may have implications for reported high concentrations of Maned Ducks within habitat types (Frith 1982). These may also result from food concentration, although differences in flock size between habitat types may be related to the size of the wetland (chapter 5).

In a more normal year, Frith (1957a) may have implied a similar interpretation when he observed that larger flocks were found on the decreasing number of areas of green growth during the summer, after breeding. It might be expected that if flocking was simply related to such a food concentration, then when the distribution of food was relatively homogeneous, flock size would not increase. Vegetational differences between dams in 1981 and 1983 were minimal and yet flock size was large, which suggests that flock formation in this species is not simply related to resource patchiness. Furthermore, although Maned Ducks were concentrated on a few dams on the study site (Fig. 45), flocks often moved and camped on another similar dam. Variability in habitat association at the time amply demonstrated this (chapter 5). If food concentration was the most important factor, then a stronger habitat association might be expected.

Apart from simple short term concentration of food, two factors have been implicated in the formation of animal groups. These are the needs to forage efficiently and to avoid predation (Rubenstein 1978; Pulliam & Millikan 1983). There has been some argument about the relative importance of the two in the formation of bird flocks (Murton 1971; Lazurus 1972), but it is likely that the tendency to group has evolved a number of times (Grier 1984). Hence, both factors may be important with their relative contributions difficult to separate.

In some bird species, where food is patchy, individuals may benefit from flock formation through social learning (Crook 1965; Ward 1965; Lack 1968; Murton 1971; Krebs et al. 1972). Even though grass and legume species often grew in patches, Maned Ducks usually grazed uniformly over an area, so this was unlikely to be an important factor promoting flock formation. Nevertheless, observations of Maned Ducks moving to a particular patch of clover on dam G.31 (chapter 4) suggests it may register some influence on flock formation. However, this advantage

appears to be minimal.

In some waders, which also form flocks, where there is apparently little to be gained through communal feeding, predation has been considered to be important to flock formation (Goss-Custard 1970). Three reasons suggest that predation may be important to the flock formation of Maned Ducks. First, individuals spend some time of the day performing vigilance behaviour. I have presented some evidence that these postures primarily function in the detection of predators, rather than food location (see chapter 8). Second, there was a well developed predator escape response (chapter 4) and finally, it was noticeable that cohesion was most prominent when Maned Ducks were grazing or loafing away from the dam. However, I noticed no increased cohesion with distance, so the latter observation could equally be an indication of the importance of food.

There are a number of advantages which may reduce the risk of predation on individuals in flocks (detailed in Lazurus 1972). I will only consider the advantages of early warning, since others are largely theoretical. Individuals in larger flocks may detect predators sooner (Powell 1974; Siegfried & Underhill 1975). Besides this, birds in larger flocks also often increase their food intake by decreasing the amount of time spent in vigilant behaviour (Siegfried & Underhill 1975; Lazurus 1978; Caraco et al. 1980). Similar advantages may promote flocking in Maned Ducks. The existence of two apparently different strategies of social structure, one for breeding and the other outside the breeding season, offers some interesting avenues for a cost/benefit comparison of the two.

Maned Ducks probably form compact flocks to offset risks of predation. After breeding these are composed of family groups. However, unstable flock structure later in the year suggests that social structure, after breeding in this species, is probably somewhere between the complete absence of association amongst brood mates of some Anatinae and the strong family ties of some geese. The stability of family groups is probably dependent initially on the degree of parental care and then on the age at which offspring first breed.

CHAPTER 8MATING SYSTEMIntroduction

Most bird species are monogamous (Lack 1968; Orians 1969). Such a mating system is likely to be counterselected in males because they invest little in gamete production compared to females (Wickler & Seibt 1983). The necessity for biparental care has probably been the most important factor redressing this imbalance in many birds, producing monogamous mating strategies. A theoretical framework for investigating mating systems in terms of the parental investments of the sexes (Trivers 1972), has been valuable to the understanding and analysis of mating strategies. Trivers (1972) defined parental investment as "...any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". This definition has undergone some modification so that more attention is focused on future strategies and not past investment (Dawkins & Carlisle 1976, Maynard Smith 1977; Carlisle 1985).

One prediction is that birds with precocial offspring, like Anatidae, would tend to be polygynous as so little parental care is needed (Orians 1969; Emlen & Oring 1977). However, this pattern is not widespread (Orians 1969), which may be because parental care of such offspring carries a cost (Lazurus & Inglis 1978; Walters 1982). Indeed, most Anatidae are monogamous. However, there is an interesting difference between the monogamy of the Anserinae and that of the Anatinae. Most geese and swans tend to have long pair bonds and biparental care, compared to most ducks, which are usually only monogamous for a breeding season and where only the female cares for the offspring (Weller 1964b; Johnsgard 1965; Kear 1970). Kear (1970) considered that biparental care and long pair bonds were a primitive condition in Anatidae while Maynard Smith (1977) suggested that differences between Anserinae and

Anatinae may be due to the duck's reduced exposure to predation, having concealed nest sites and injury feigning behaviour. Hence, offspring would require less parental care than the Anserinae, which generally live in an open habitat and do not feign injury. Such an ecological approach was successfully used by McKinney (1975) to explain differences in the mating systems of the Shoveler Anas clypeata and the Pintail A. acuta. Similarly, Siegfried (1974a) found the mating strategies of some Southern African Anatini could be explained by examining ecological effects. Generally, mating systems are more determined by ecological factors than the phylogeny of a particular species (Orlans 1969; Emlen & Oring 1977; Krebs & Davies 1981).

The Maned Duck is a true Anatinae but it has many ecological characteristics of the Anserinae (chapters 3 & 4). Study of the mating system of this duck may provide some insight into differences in the mating systems of Anatidae. Kear (1970) listed this species as having a long pair bond, however this was based on captive individuals and deserved further investigation. The objectives of my study were to determine the mating system of this species; compare male and female roles in parental care; measure the behavioural cost of parental care, in relation to brood age and brood size; and document the displays which establish and maintain the pair bond. Although Johnsgard (1965) describes some displays of the Maned Duck, they are generally poorly documented (Frith 1982).

Methods

Displays

Descriptions of Maned Duck displays come from field observations. I have defined displays as behavioural patterns or postures ritualised for signal function (Moynihan 1955). Whilst I acknowledge the limitations of such a definition (Beer 1977), it adequately suited the purposes of this study by making a functional distinction between these behaviours and other daily activities (chapter 4). I also filmed copulatory sequences using a reel to reel Sony A.V.C. 3420 video camera with a 200-110mm zoom lens. Some copulatory displays were drawn from these. With two exceptions, I used names of displays established by Lorenz (1941, 1953), Johnsgard (1965) and McKinney (1965a, 1970).

Pair bond duration

I defined paired Maned Ducks as a male and female duck who maintained close proximity and engaged in pair maintenance displays. Trappings or sightings (chapter 7) of ducks together, provided data for pair bond tenure, which was the difference between the earliest and latest recorded observation of a pair together. This represents a minimum estimate and is open-ended. I included only pairs which were together for more than a month (arbitrarily picked) because many pairs remained in the area for a shorter time and would have contributed little to an understanding of pair bond duration. These were not real biological entities representing possible first attempts because neither of the paired birds were seen again separately.

Parental behaviour

During surveys in 1983, I recorded the parental behaviour of Maned Ducks using ten minute focal samples (Altmann 1974). Behaviour was recorded whenever I came across a brood and although not random, survey procedures (chapter 5) limited bias. At each sample session, I counted

and aged the ducklings (Appendix 6) in a brood. To test the behavioural cost of parental care, I similarly monitored the behaviour of paired Maned Ducks without broods. For five of these pairs, I was able to determine their reproductive status by back-dating from the day they subsequently produced broods. All five were either incubating or two weeks prior to incubation and so I have grouped them as "incubating".

For all focal samples, I used a portable event recorder which transcribed signals from a keyboard to a tape recorder every 1/5 second. Eight numeric keys provided a convenient means for partitioning behaviours. I assigned combinations of the keys to six easily distinguishable activities or postures; "Extreme head up", "Head up" (these two, after Lazurus and Inglis (1978)), "grazing", "loafing", "comfort" and the agonistic "rush" display (described in results). Of these, I have already described loafing and comfort activities (chapter 4). Figure 49 illustrates all postures and some activities for ducks with broods. In Extreme head up, Maned Ducks stretch their necks upwards to the fullest extent. This has the effect of slightly raising the axis of the body anteriorly. In contrast, in Head up, the axis of the body remains parallel to the ground and the neck is not fully stretched. I also included as Head up, any pauses in feeding behaviour when the head was raised more than 5cm off the ground. These two postures probably reflect degrees of vigilance, since in the presence of predators, all ducks adopted Extreme head up, while Head up tended to be more common when there were no predators. Grazing Maned Ducks actually pecked or held their heads at vegetation level. Since I was able to concentrate on individuals, this allowed a stricter definition of grazing and vigilant activity than that used in chapter 3.

I collected 126 ten minute focal samples, each of which had 3000 integers separately representing the combination of both male and female behaviours at any one time. Eight of these were for single parent broods and were treated separately. Following storage of focal samples as sequential computer files, I wrote a BASIC program that calculated the total amount of time engaged in each behaviour and the mean bout length for each activity or posture, for the ten minute interval. Behaviour often rapidly oscillated between postures and grazing activity during a



a



b



c



d



e

Figure 49. Postures and some activities performed by Maned Ducks during parental care. (a)-Male Extreme head up (background), female grazing (foreground). (b)-Male (left) and female (right) in Head up. (c)-Male Rush (left), female swimming (right). (d)-Male and Female Extreme head up, ducklings not in the picture (e)-Male (right) in Extreme head up, female (left) in Head up.

sample session so I was also able to calculate a mean duration for each behaviour.

I was interested to see how parental behaviour was related to a number of variables. The design for the analysis of variance tested the effects of duckling age (AGE), number of ducklings in the brood (NO) and the sex of the parent (SEX) on the three behaviours, Extreme head up, Head up and grazing (BEHAV) of parents. I included only these behaviours in the analysis since they dominated all sessions. I used a four factor design with repeated measures on two of the factors (SEX and BEHAV) (Winer 1971). The design is schematically presented in Appendix 5 (Table 5-A). Repeated measures analysis is appropriate when the subjects (ten minute observation sessions on broods) are observed under each of the treatments (SEX and BEHAV). Under such circumstances, observations will be dependent rather than independent (Winer 1971). This type of design, although suffering some loss of power, is often handled more efficiently through multivariate statistical techniques (Winer 1971; Hull & Nie 1981). The SPSS MANOVA program offers such a facility (Hull & Nie 1981). Data are treated as a multidimensional response vector with each response variable representing a unique combination of the two repeated measures.

I performed two analyses on parental behaviour utilising this design. The first investigated variation in the total amount of time which was devoted to particular behaviours, in response to the factors over a ten minute interval. The second, was an analysis of how the different factors were related to the mean bout length of behaviours. This analysis provided a means of seeing how any differences in total time spent, were realised in bout durations. In this latter analysis, the first and last bouts were not included, as they had no respective beginning or end. Degrees of freedom were reduced since sometimes not all three behaviours would occur in a ten minute sample. A duration of zero for those that are absent is not relevant, so I omitted these sample sessions from the analysis. (Repeated measures procedures are not applicable when there are missing values.)

These analyses assume homogeneity of variances for groups (Winer 1971). For total amount of time spent, Cochran's tests for homogeneity

of variances for factor combinations showed that variances differed. However, plots of means against variances and standard deviations did not exhibit any regular abnormalities, so I proceeded with the analysis. For mean bout length, a transformation of $\log(x+1)$ was necessary. The second assumption that the covariance matrix be positive definite (Hull & Nie 1981), was satisfied in both analyses.

Following focal sampling of parents, I used instantaneous scan sampling (Altmann 1974) to record the position of both parents relative to the brood, for five minutes, every 30 seconds. The spatial cohesion of the brood made this possible. I also recorded which parent was on higher ground at the same time. I analysed these data using the binomial test (Zar 1974) and separated samples according to whether the family group was loafing or grazing. Each 30 second scan was likely to be independent for grazing but this was unlikely for loafing and I treated each five minute interval as one sample.

I also collected data on peck rates for ducklings, parents and paired birds without broods. Using a stopwatch, I timed how long it took for ducks to peck 20 times. This usually meant stopping and starting the stopwatch, as the duck frequently raised its head while grazing. These data were analysed using an unbalanced one factor analysis of variance (Zar 1974).

Results

Displays

Table XXIV is a summary of some of the displays which mark various stages of courtship behaviour in Maned Ducks. Some behaviour patterns have been accorded display status, based on the homology of anatid displays, although it was not obvious that they were ritualised for signal function.

a) Pair formation

I occasionally saw groups of up to six Maned Duck males around a female, usually with their heads resting back on their scapulars which made the breast push out. They can maintain this posture while they walk or swim and it probably corresponds to the breast swelling described by Frith (1982). From such a posture, the male usually soon performs a Display Shake (described by Johnsgard 1965). The Display Shake is one of the most elaborate displays in this species but is not always performed in a "social" context. Occasionally a single male out of the flock did a Display Shake. Johnsgard (1965) also intimated that a second more complex display existed, similar to the Double Display Shake of the Mandarin Duck Aix galericulata. Although not as frequently performed as the Display Shake, Maned Ducks do perform a Double Display Shake which, as suggested by Johnsgard, differs from the Display Shake by having an extra component. First, from where the head and neck rest back on the scapulars, the bill is dipped into the water and then pulled rapidly back until the head again rests in the male's scapulars. Following this initial movement, the male performs a movement similar in its entirety, to the Display Shake. The second part of the Double Display Shake is accompanied by a deep rumbling call which seems to be similar to Lorenz's (1941, 1953) description of the noise made by A. galericulata during the Double Display Shake. Usually only males practice these displays, but twice I saw female Maned Ducks perform the Display Shake. Once, after a pair had mated, both performed the display, while on the second occasion, two females performed the

ck. Terminology derived from Lorenz (1953),
 displays marked with *, observations were
 ritualised. "M" and "F" indicate which

behaviours are performed by males and females

<u>PAIR FORMATION</u>		<u>PAIR MAINTENANCE</u>		<u>COPULATORY</u>	
				<u>PRECOPULATORY</u>	<u>POSTCOPULATORY</u>
Inciting (F)		Inciting (F)		Drinking (M, F)	Head-down-tail-up (M)
Preen-behind-wing (M, F)		Rush (M, F)		Head pump (M, F)	Tail wag (F)
Display Shake (M, F)		Burp (M)		Head dip (M, F)	Bathing (M, F)
Double Display Shake (M)		Nibble preen (M, F)		Neck dip (M, F)	Wing flap (M, F)
Wing flap (M, F)		Preen-behind-wing (M, F)		Turning-back-of-head (M)	Nod swim (M)
Turning-back-of-head (M)		Drinking (M, F)		Turn-to-face (M)	*Nibble preen (F)
Jump flight (M)		*Wing raise (F)			Crash diving (M, F)
		*Mutual preening (M)			
		*Breast touching (M, F)			
		*Open bill threat (M, F)			

Display Shake on land near two males who had their heads resting in their scapulars.

Both males and females perform a Preen-behind-wing display which occurs in many Anatinae during pair formation (Johnsgard 1960b; McKinney 1965a). Other probable attention-getting displays (McKinney 1975) were Wing-flap, the male Burp display (Johnsgard 1965) and the Jump flight (Table XXIV). Twice, I saw the Jump flight, which has been described for other Anatidae (Lebret 1958; Johnsgard 1965; McKinney 1970). It was performed by the male. When the male landed beside the female, she usually incited while the male swam away with a Turning-back-of-head display. Once, the female performed a display which I have called Wing-raise. In this display, which I have only seen twice, the tail is pushed up almost to right angles to the normal body orientation while the wings are slightly raised. The head is held erect.

The most characteristic female display is Inciting. This display is unmistakable. Johnsgard (1965) described it as frequent aggressive pointing by a female over her shoulder towards an opponent, accompanied by nasal "wonk" notes. However, I did not notice the chin-lifting by the female which Johnsgard described. This may be attributed to some inexperience in the detection of such subtle displays.

Pair maintenance

Since the formation of a pair bond is probably gradual (Johnsgard 1965), there is likely to be some overlap between those displays categorised as pair formation and pair maintenance (Table XXIV). The defence of an area around a pair seems to be an essential part of pair maintenance. There are two displays which effect this. Inciting behaviour by the female away from the preferred male, at an opponent, is particularly important and is the most commonly observed display in this species. Opponents may be either males or females and the intensity of the display seems to vary according to their proximity. In addition, females' inciting behaviour during early courtship, did not seem as intense. The second display, Rush is an agonistic display which both

males and females perform on land or water. On land, it strikingly resembles the threat displays of the Anserinae. During a Rush, a Maned Duck will move quickly towards a conspecific, with the head held low, neck bent and the bill often open. If the pursued individual is caught, the attacker pecks the opponent's rump and tail region. However, in Maned Ducks, as with many Cairinini (Hillgarth & Kear 1982), serious fighting is rare. When it does occur, two ducks stand facing each other and peck at each other's head and neck. Often, the encounter ends when the mate of one of the contestants also attacks, causing the outnumbered duck to retreat. Agonistic encounters were usually brief although I did see one male direct Rushes at another male for at least half an hour, chasing it throughout a flock.

Other displays which a pair perform, often in the absence of other ducks, probably also function in the maintenance of the pair bond. Breast-touching, mutual preening, vocal signals and greeting sequences probably all serve this purpose. Mutual preening, which functions either as a pair formation or maintenance display (McKinney 1965a), was rare. I only saw it twice. Once, a female nibbled the chin of her male during a copulatory sequence and the second occasion, a male pecked at the chin and chest of his mate and at one point, made as if to pick something off the ground. Breast-touching was probably more common and seemed to occur when birds were disturbed. Twice, I saw a male direct an Open Bill threat towards his female mate. This resembled that described for Anas sparsa (McKinney et al. 1978) and may be part of a greeting display. Vocal signals also seem to be important in the maintenance of contact. Whenever a pair became separated, both would call until they reunited. However, more observations are needed to establish whether these some of these rarer behaviour patterns are really displays.

Copulatory behaviour

No full account exists for the copulatory behaviour of Maned Ducks, although Johnsgard (1965) presented some brief observations on captive individuals. The performance of a copulatory sequence was often predictable. Paired Maned Ducks usually leave the main feeding flock and

walk quickly to the water, with either bird leading. When they enter the water, the male swims in front of the female, Turning-back-of-head (Fig. 50a). Sometimes, both perform a drink display (the bill does not actually touch the water). My observations of other precopulatory behaviour generally concur with those of Johnsgard (1965). After a drink display, the male assumes the Erect posture, characteristic of a copulatory sequence and different to the normal swimming posture (Fig. 13). The male then performs Head pump followed by Head and neck dip or occasionally Head dip. Whilst doing these displays he maintains a lateral orientation to the Erect female (Fig. 50b). Head pumping also sometimes occurs on land but I am unsure of its function.

Johnsgard (1965) recorded Maned Ducks doing Bill dip but I have no record of this. During some precopulatory displays the female was actively doing Head pumps and sometimes Head and Neck dip. These seemed to be more prevalent in long precopulatory sequences, which may be an indication that the pair bond, in these birds, was not fully established. Just before mounting, the male increases the frequency of Head pumping and then Turns-to-face the female who usually adopts a prone position (Fig. 50c). Both sexes seem capable of initiating copulation. One female adopted the prone posture but her mate did not tread and I have also seen males trying to mount an Erect female.

There was considerable variability in copulatory sequences. In some, copulation happened quickly while in others, mating did not take place. Twice, during long sequences, I saw Head and neck dip where the anterior portion of the body was also submerged, while the feet paddled the surface. This was indistinguishable to the upending of a feeding Maned Duck (chapter 3) and lends credence to the view that this display originated from feeding behaviour (Johnsgard 1962; Kear 1970). Long precopulatory sequences or those that started close to the flock often attracted other males which inevitably terminated the sequence. Sometimes, these males would Head and Neck dip, before the pair swam away.

When mating did occur, the male mounted the prone female (Fig. 50d), and grasped the back of her head with his bill. Actual contact was brief and was immediately followed by various post-copulatory displays (Table XXIV). Johnsgard (1965) described one specific male post-

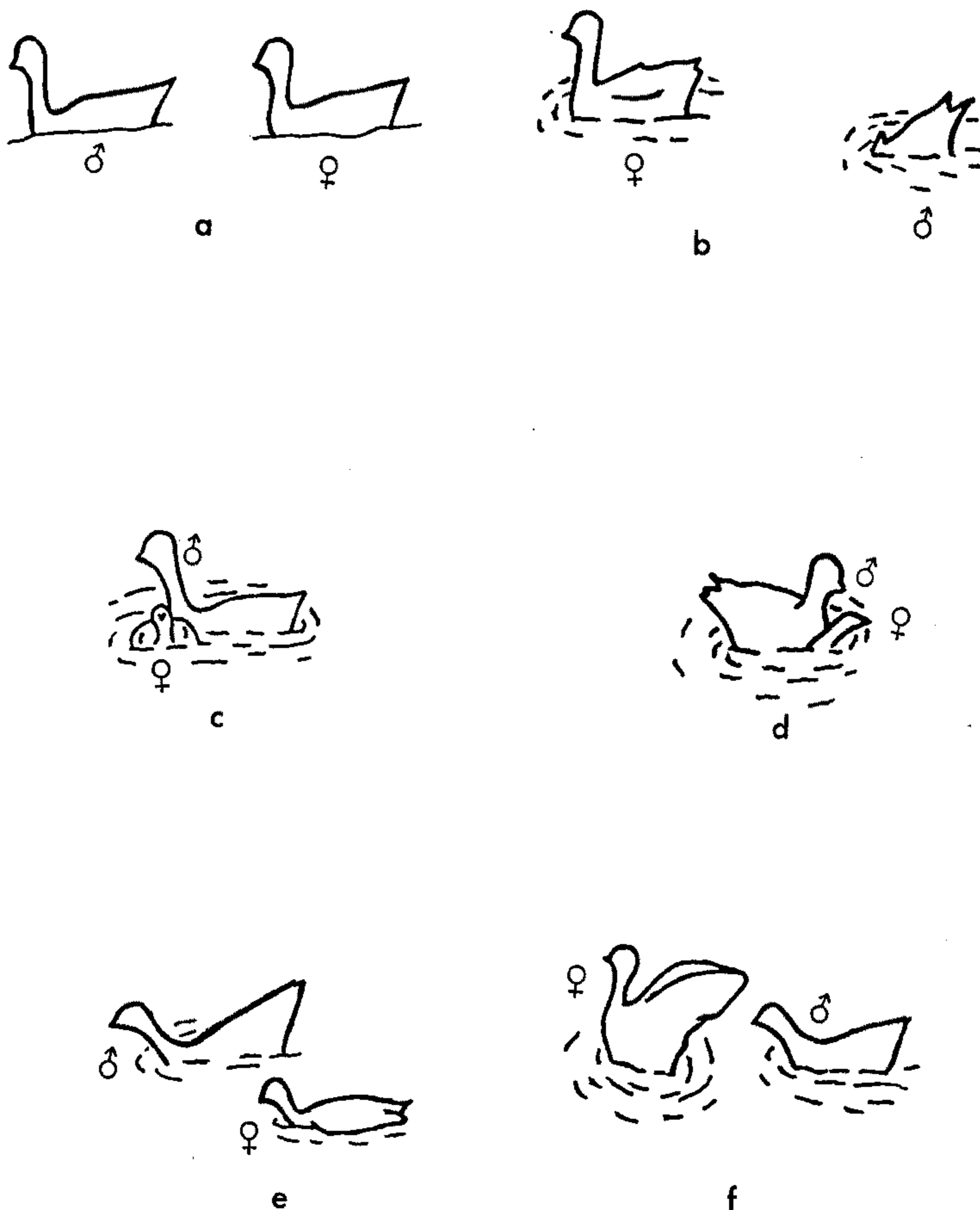


Figure 50. Some Maned Duck displays in a copulatory sequence. (a)-male in Erect posture, Turning-back-of-head while female has not yet fully adopted Erect posture. (b)-female in Erect posture, male Head and neck dipping while laterally oriented to female. (c)-male Turn-to-face, female in prone position. (d)-copulation. (e)-postcopulatory, female bathing while male performs Head-down-tail-up. (f)-female wing flap, male still Head-down-tail-up while swimming around female.

copulatory display of the male (Fig. 50e) which I called Head-down-tail-up. During this display the male, exhibiting the black under tail coverts (Johnsgard 1965), maintains a lateral body orientation to the female as he swims around her. This display wanes and is replaced by a Nod swim display. Johnsgard (1962) observed that males Turn-to-face the female but I did not see this. Males, then, Turn-back-of-head and either bathe or swim to the shore, where they preen. Following copulation, females perform a tail-wag and then bathe. Often this was followed by at least one wing flap and accompanying tail wag (Fig. 50f). I have also seen crash-diving by both birds during post-copulatory sequences, which, although recorded in other *Anas* species (McKinney et al. 1978), does not seem to have been described for any Cairinini. Once, it occurred in the middle of precopulatory behaviour but it was not followed by successful copulation. Possibly, it still serves as anti-predator behaviour in this context.

A pair usually copulated only once, before resuming loafing or grazing activity. However, I saw one pair mate three times over a period of fifteen minutes. Mating behaviour was not restricted to the breeding season, as I saw Maned Ducks mating throughout the year. This suggests that copulation may also play a role in pair maintenance, as in other species (McKinney et al. 1978). I once saw forced copulation of a female (sensu. McKinney et al. 1983).

Nesting

Maned Ducks usually only perched in trees when they were nest searching, which often occurred in the morning. I did see one male parent perched in a tree and also, in 1982, a flock of 30 birds in trees. The latter, I interpreted as anomalous behaviour, resulting from unusually high flock numbers this year (see chapter 7). A few ducks in this flock performed flight intention movements associated with nest searching and these may have stimulated the rest of the flock to fly up to the trees.

Twice, when I saw Maned Ducks leave a dam to nest search, they performed preflight behaviour which was different to the normal Chin-

flicks (see chapter 7). There were neck craning and aiming head movements similar to those described for other Cairinini (Lorenz 1941, 1953; Johnsgard 1962; Delacour 1964). These continued to occur as the pair went from tree to tree during a bout of nest searching. Both ducks inspected cavities by craning their necks inside. Although Frith (1982) reported that no sound is made during nest searching, I found that the female is at her most vocal at this time, making a staccato "took" call. This is an unmistakable sign that Maned Ducks are looking for a nest site, and seems to be a feature of nest selection in many Anatinae (McKinney 1975). The call of the female usually intensifies as she prepares to fly to another tree.

As Frith (1982) observed, the male remains on the nearest dam, while the female is incubating. I saw no evidence to support observations by Rowley (1975) and Frith (1982) that this area was defended from other males. If other conspecifics were near, the male simply separated himself from them and usually loafed on the edge of the dam or grazed away from other Maned Ducks. When I approached lone males whose mates were incubating, they usually did not leave the dam immediately and when they eventually did, they often flew around the dam until I left. If males did not leave they would often adopt a prone position with their legs folded underneath and their neck and head stretched out flat along the ground in front. Males would even do this if the female was present. When a brood is similarly approached, both the male and female will sometimes adopt the same position near the ducklings. This observation suggests that this behaviour, performed by the male while the female is incubating, functions as an anti-predator strategy ensuring that the male is on the dam when the female returns from incubating. Females would return from the nest site, calling as they flew through the trees that surrounded a dam. The male usually replies with a Burp display call. A type of greeting display sequence seems to follow, which on the few occasions observed, involves a combination of drinking, Head pumping displays and once, the Wing Raise display by a female on land. I also saw a male perform an Open bill threat away from his mate, despite the fact that there were no other Maned Ducks on the dam. After feeding, both the male and female perform preflight chin flicks (chapter 7) before flying silently back to the nest site. The male peels off close to the nest and flies back to the dam,

Table XXV. Pair bond tenure in Manded Ducks. Only pairs seen together for more than four weeks are presented (see methods for reasoning). Durations are the difference between initial and final sightings and are the total amount of time a particular pair was seen together, not a measure of bond duration. Initial sighting was when the particular pair seen behaving as a pair. Band numbers listed as supplied by the Australian Bird Banding Authority (prefix 100). Ducks whose bands could not be identified are signified by their coloured band combinations. *Identified pairs where one of the pair was subsequently sighted alone

Band No. Initial sighting Final sighting Duration (months)

03430-03465	16/09/81	27/12/81	3.4
03518-03575	20/09/82	14/10/83	12.8
03572-11615	29/07/82	19/12/82	4.8
11619-11620*	16/06/82	4/08/82	1.7
11628-R/O	23/09/82	5/06/83	8.6
11660-11661*	20/09/83	6/12/83	2.6
11698-11695	19/06/82	18/08/82	2.0
13157-13158	24/07/82	18/05/83	9.9
13160-58328	25/07/82	4/06/83	10.5
13198-54457	29/10/81	21/06/82	7.8
30088-O/R/G	2/03/82	25/6/83	16.0
33605-33606	12/08/82	3/11/82	2.8
54419-54422*	23/08/81	12/10/81	1.7
54440-54442	14/08/81	6/12/81	3.8
54448-54450*	10/08/81	6/09/82	13.1
33619-B/R	7/07/82	5/11/83	16.2
33640-33641	23/08/82	3/06/83	9.5
33824-33828	18/05/83	13/10/83	4.9
33849-33850	25/08/83	4/10/83	1.3
38856-38857	14/08/83	7/10/83	1.8
54409-58270	19/07/82	14/09/82	1.9
54467-58398	17/07/82	12/10/83	15.1
54475-54474	25/09/81	26/11/81	2.1
58272-58273	6/07/82	19/12/82	5.5
58276-58277	24/07/82	30/09/83	14.4
11682-11699	9/06/82	4/12/82	5.9
11686-11689*	10/06/82	11/12/82	6.1
58335-58363	21/06/82	3/11/82	4.5
58395-58396	16/07/82	27/11/82	4.5

while the female (on the one occasion observed) perched on a branch near the nest and briefly preened before resuming incubation. Possibly Frith's (1982) observation of silent nest selection, contrary to my observations (see earlier section), were made as the female returned with her mate to the nest site.

Pair bond duration

Table XXV presents data for those Maned Ducks paired for more than a month. Most of these were ducks recorded together for less than 5 months (56%). However, since this data was dependent on seeing the birds in the area, these apparent short durations were likely to be an artifact of Maned Duck movement (chapter 7) rather than a reflection of real patterns in pair bond duration. There was no evidence that the pairbond was broken for any of birds paired for less than five months. A number of ducks remained paired for more than a year (22%), with one of these pairs, 54467-58398, producing broods in consecutive years. Some of these were probably paired before observations began as they had band numbers in sequence or close together (Table XXV), signifying that they were trapped together. I could only be sure that a divorce had occurred for one pair, 11619-11620 (Table XXV). After seeing the birds together and paired for nearly two months, I subsequently saw both in separate flocks. In other break ups (marked * in Table XXV), only one of the birds in the pair was seen and so the reason for the separation could not be determined.

Parental care

Most of my observations on parental care began after the broods had left the nest hole and taken up residence on a dam. However, I once saw a brood leaving their nest hole. Both parents called continuously from beneath the hole while the ducklings dropped out of the tree from the nest hole, one by one. This took about 45 minutes. After each one had fallen, both parents rushed towards the duckling, but I could not see what the function of this behaviour was.

As precocial offspring, ducklings forage independently and parental care mostly takes the form of vigilant behaviour, which probably functions to detect predators. Before I became accustomed to the behaviour of broods, I frequently stumbled across them and I saw Maned Duck parents employ various anti-predator strategies in response to my presence. These seemed to be related to how far away I was, when first detected. At distances of 50-500m, parents would lead the ducklings away from the dam into surrounding vegetative cover. The peculiar nystagmic walk of Cairinini (Lorenz 1941, 1953) (the nod of the head does not take place with every step but with every second step) was pronounced, giving the impression that it may be a display, serving to further alert the offspring. In addition, the bodies of the parents and ducklings were held low to the ground, in a crouch-like posture. Both male and female continually vocalised as they led their young. Both parents led broods with equal frequency (binomial test (Zar 1974), $p > 0.05$, $n=7$) which implies that ducklings imprint on both parents. This behaviour pattern continues even after offspring are fledged, although the young may not follow.

The family group often froze and huddled close together if I was detected at about 50m. I was never close enough to see how this was achieved but alarm calls were probably important (Weidmann 1956). All members of the group would adopt the posture described earlier for the male with an incubating female. If I approached too closely, then ducklings scattered with both male and female feigning wing injury. Apart from the effect of my presence, I once saw a family group run to the dam and swim to the middle when a fox suddenly appeared. Other potential or "perceived" predators of ducklings (White-faced Heron Ardea novaehollandiae, Kookaburra Dacelo gigas, Magpie Gymnorhina tibicens, Sulphur-crested cockatoo Cacatua galerita, Galah Cacatua roseicapilla and the Australian Raven Corvus coronoides) were usually vigorously attacked by either parent. Even an over inquisitive lamb, twice, bore the full brunt of a male attack. Parents also Rushed conspecifics which approached the brood. Both males and females performed this agonistic display with similar intensity (paired t-test, $t_{22} = -0.4$, $p > 0.05$). The importance of this behaviour pattern was demonstrated to me when a duckling was attacked by a female Maned Duck which had no young.

Table XXVI. Three factor analysis of variance with repeated measures on sex of the paired Manded Duck (SEX) and the behaviours; extreme-head-up, head-up and grazing (BEHAV) and grouped over age of the ducklings (AGE). Age groupings were adults with no ducklings (0), "incubating" adults, and adults with ducklings aged (2-5); (6-15); (16-22); (23-28); (29-34); (35-42); (43-68) days old. The criterion measured was the amount of time spent by ducks in each behaviour over a ten minute sample. (*-p<0.05, **-p<0.01, ***-p<0.001)

BETWEEN BROODS			
AGE	DF	MS	F
BROODS WITHIN GROUPS	8	246682.68	1.86 ***
	109	132538.18	
WITHIN BROODS			
SEX	1	81841.90	ns
AGE by SEX	8	158645.11	ns
SEX by BROODS WITHIN GROUPS	109	95035.24	
Error DF			
BEHAV	2	108	6.15 **
AGE by BEHAV	16	216	3.41 ***
SEX by BEHAV			
	2	108	32.23 ***
AGE by SEX by BEHAV	16	216	3.73 ***

Analysis of the effects of duckling age (AGE) and the number of ducklings (NO) in broods, on the three behaviours (Extreme head up, Head up and grazing) of male and female parents, revealed interesting results. Four factor analysis of variance with repeated measures, showed that the number of ducklings (NO) was not important to the amount of time spent performing each of these behaviours (Appendix 5, Table 5-B). Both the age of the ducklings (AGE) and the sex of the parent (SEX) were significantly related to the time spent performing each behaviour. To further investigate the importance of AGE and SEX on these behaviours, I left out the factor NO, and subdivided brood age into seven categories (Table XXVI). I also included two further groups in the analysis, which were not relevant to the previous analysis. These were Maned Ducks of indeterminate reproductive state with no young ("0") and birds that were known to be either incubating or be just prior to nesting, called "incubating". Age groupings of ducklings followed logically from here (Table XXVI).

There was a significant "between broods" Age effect ($F_{8,109}=1.86$, $p<0.001$). Parents with broods aged 35-42 days spent significantly more time performing the three behaviours than parents with broods aged 2-5 days (Fig. 51). Parents of ducklings aged in the latter group, seem to spend less time performing these three behaviours than all other age groups. Comfort and loafing activities occupied more of the behaviour of parents in this 2-5 day age group (Fig. 52). However, interest lay principally in the "within broods" variation. Males and females spent a similar total amount of time performing the three behaviours Extreme Head up, Head up and Grazing ($F_{1,109}=0.86$, $p>0.05$). The main effect of BEHAV and the first order AGE by BEHAV interaction, were both significant (Table XXVI). However, along with the significant first order SEX by BEHAV interaction, these were all subsumed by the highly significant second order interaction, AGE by SEX by BEHAV ($F_{16,216}=3.73$, $p<0.001$). In other words, the amount of time spent by paired Maned Ducks performing each of the three behaviours varied significantly according to the sex of the parent and the age of the ducklings. Partitioning the degrees of freedom and performing a polynomial contrast (Hull & Nie 1981), showed that most of this was attributable to a linear trend.

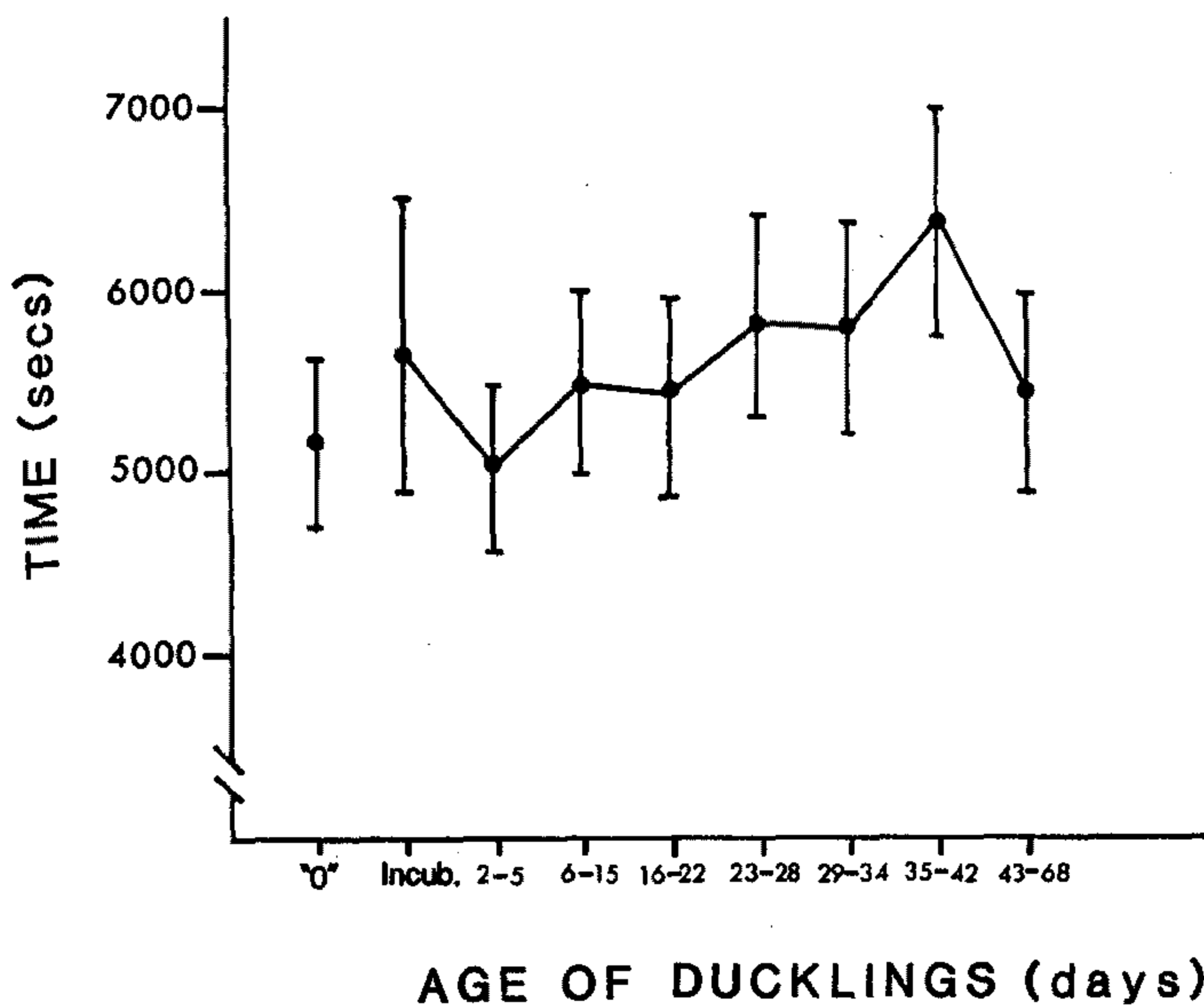


Figure 51. Summary of the significant age effect between broods ($F_{8,109}=1.86$, $p<0.001$) summed over the three behaviours Extreme head up, Head up and grazing. Means ($\pm$ 95% confidence limits calculated from the residual).

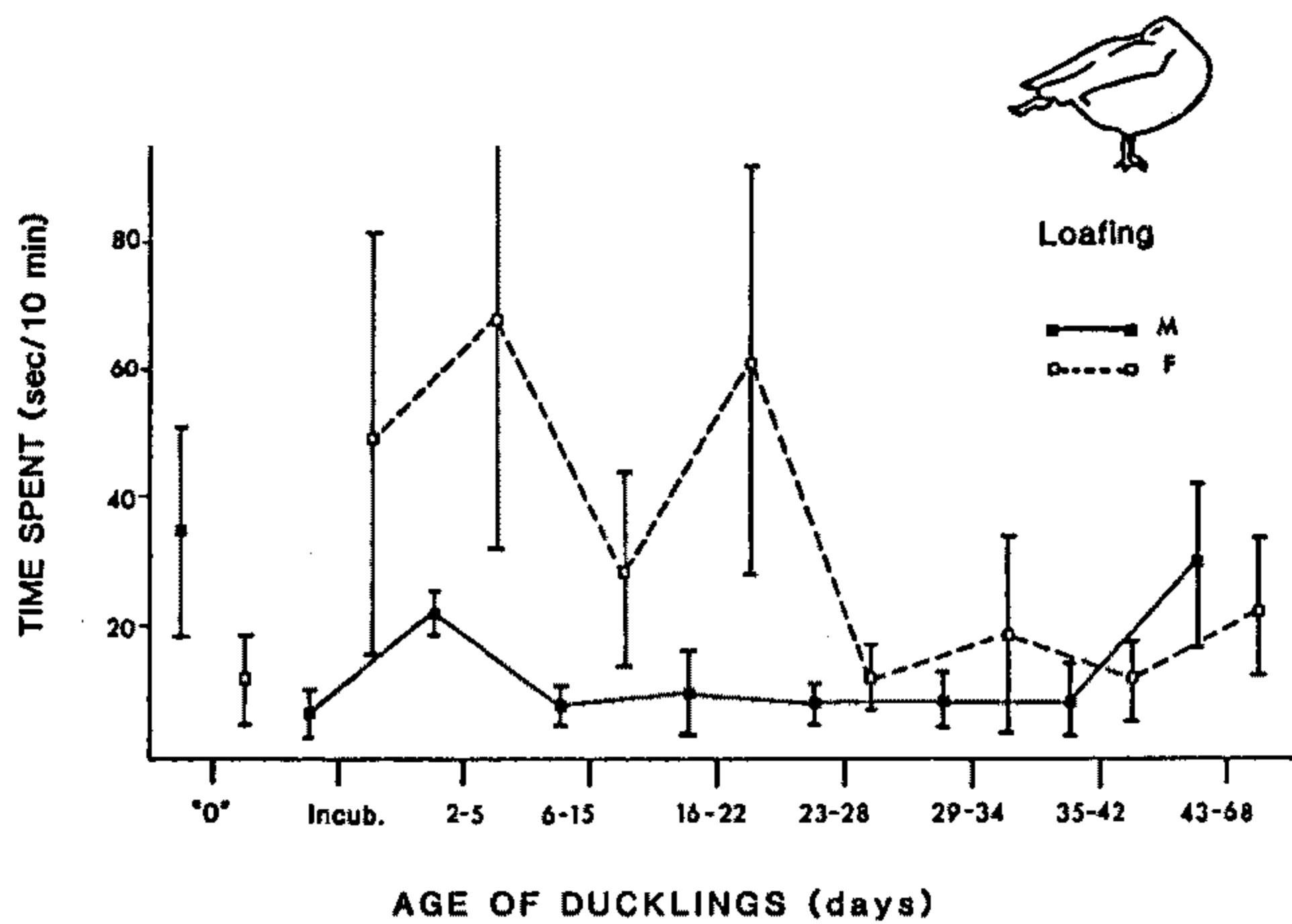
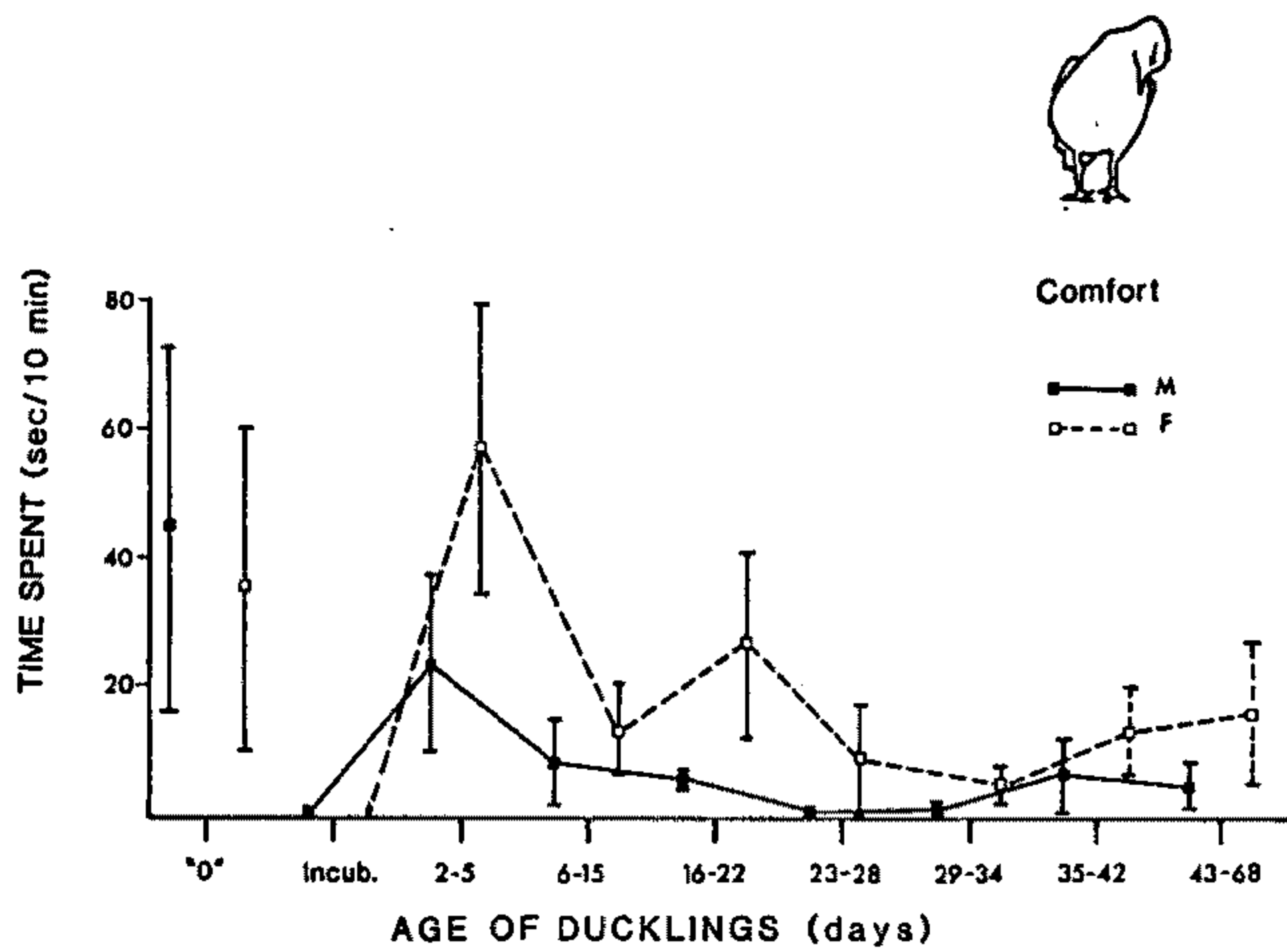


Figure 52. Mean ($\pm$ S.E.) time spent by Maned Ducks performing comfort and loafing activities in relation to brood age. Males-closed squares, females open squares.

Figure 53 summarises results of this interaction. The greatest difference in the behaviour of the sexes exists between Extreme head up and grazing. Extreme head up is highest for males with incubating females and this apparently decreases linearly until the last age category. Extreme head up was significantly higher in males with broods aged up to 34 days old and those with "incubating" females, compared to males in group (0). Past this duckling age, there was no difference between Extreme head up in males with broods and those in group 0. It was not until broods were at least 16 days old that the Extreme head up of female parents matched that of the male. This was due both to an increase in Extreme head up of females and a decrease in male Extreme head up. Female Extreme head up tended to be lower than that of the males throughout the brood care period. Female Extreme head up never exceeded that of males in the "incubating" group or early brood care. There was a drop off in this behaviour for both male and female, towards the end of brood care period. "Incubating" females seldom performed Extreme head up. Nearly all 95% confidence intervals overlap for Head up, although parents with broods over 29 days performed more of this behaviour than "incubating" females. There was also perhaps a linear increase in the amount of Head up performed as the age of ducklings increased. Extreme head up is probably replaced by Head up late in the brood care period. Males in group "0" performed more Head up than other groups.

Corresponding to these changes in Extreme head up, "incubating" females spent much more of their time grazing than their partners. This continued into early brood care. It was not until ducklings reached 6-15 days old, that the time female parents spent grazing decreased to the point where there was no significant difference between the two sexes. Nevertheless, throughout the brood care period females tended to graze more than males.

Two males lost their mates early in the brood care period and both successfully reared their broods. They were not included in analyses but I calculated means for the samples obtained (Fig. 53). For the (16-22) age group, Extreme head up for the single parent male broods lay outside the 95% confidence interval for paired males with broods of this age group (Fig. 53). Furthermore, although there was no significant difference

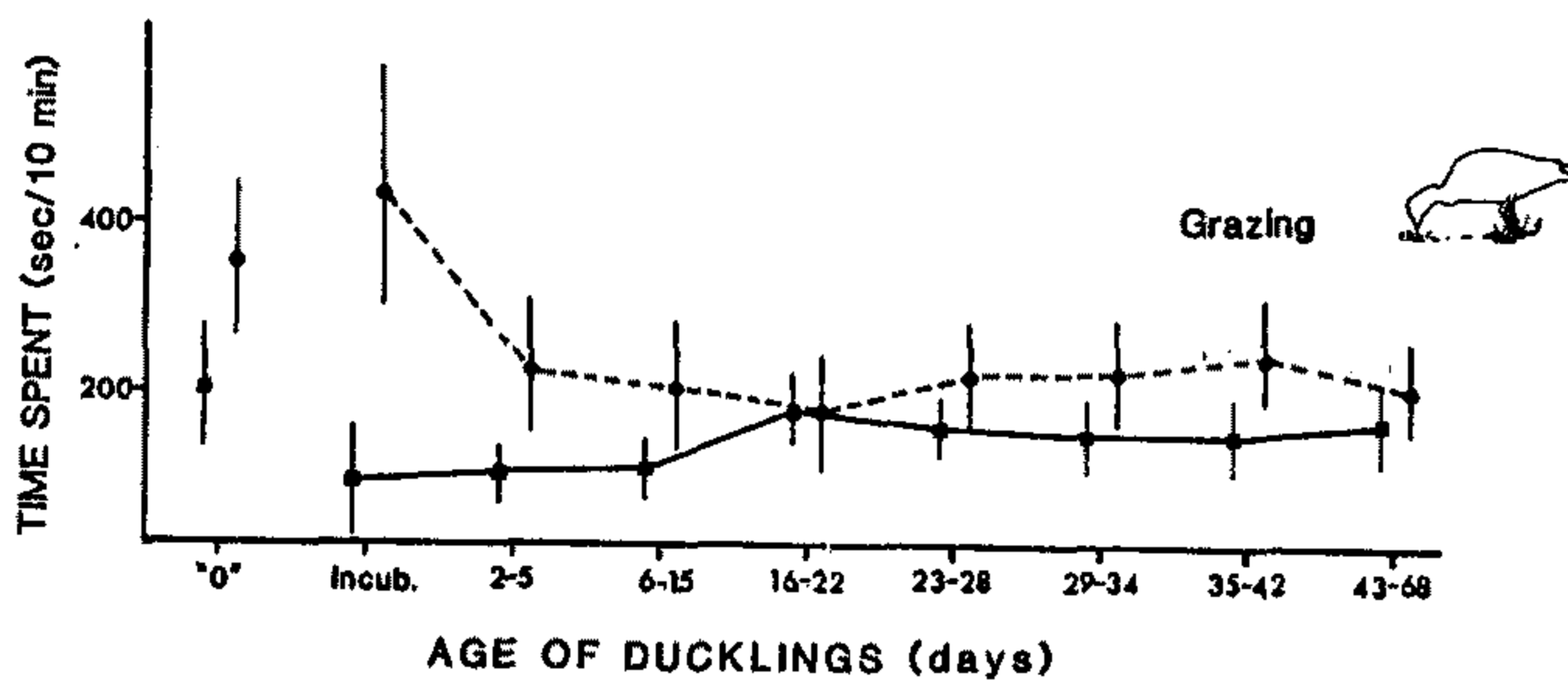
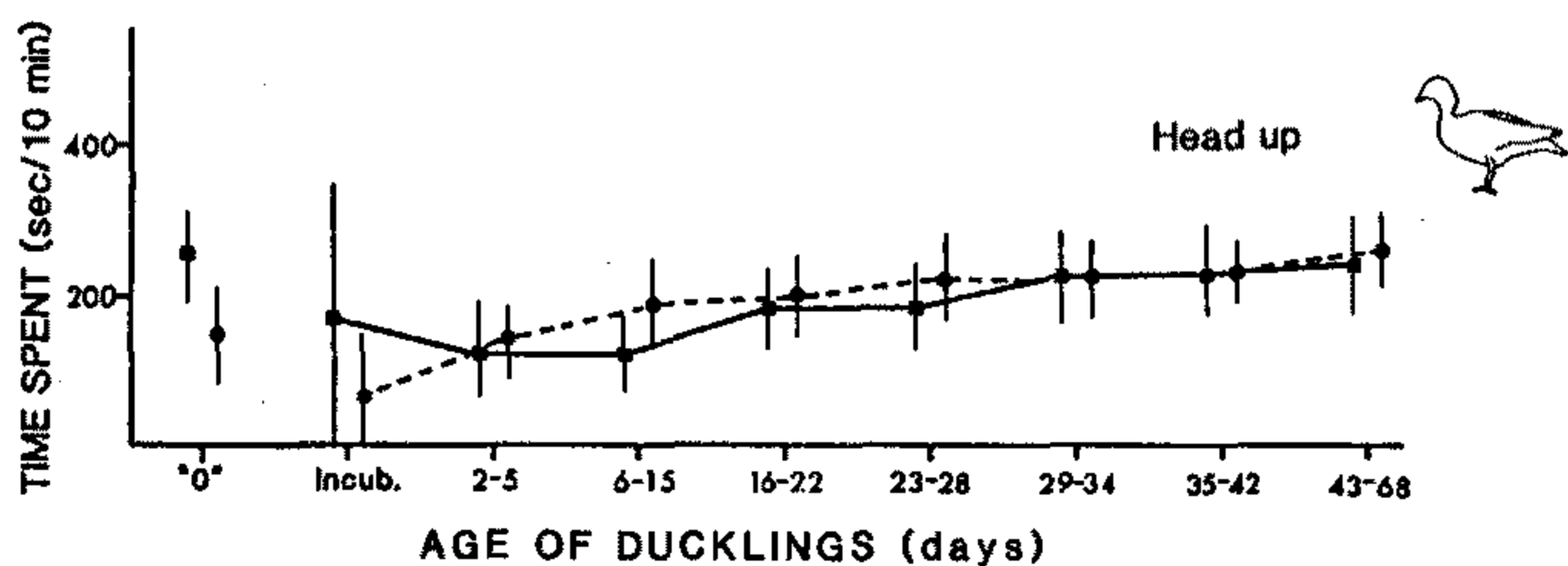
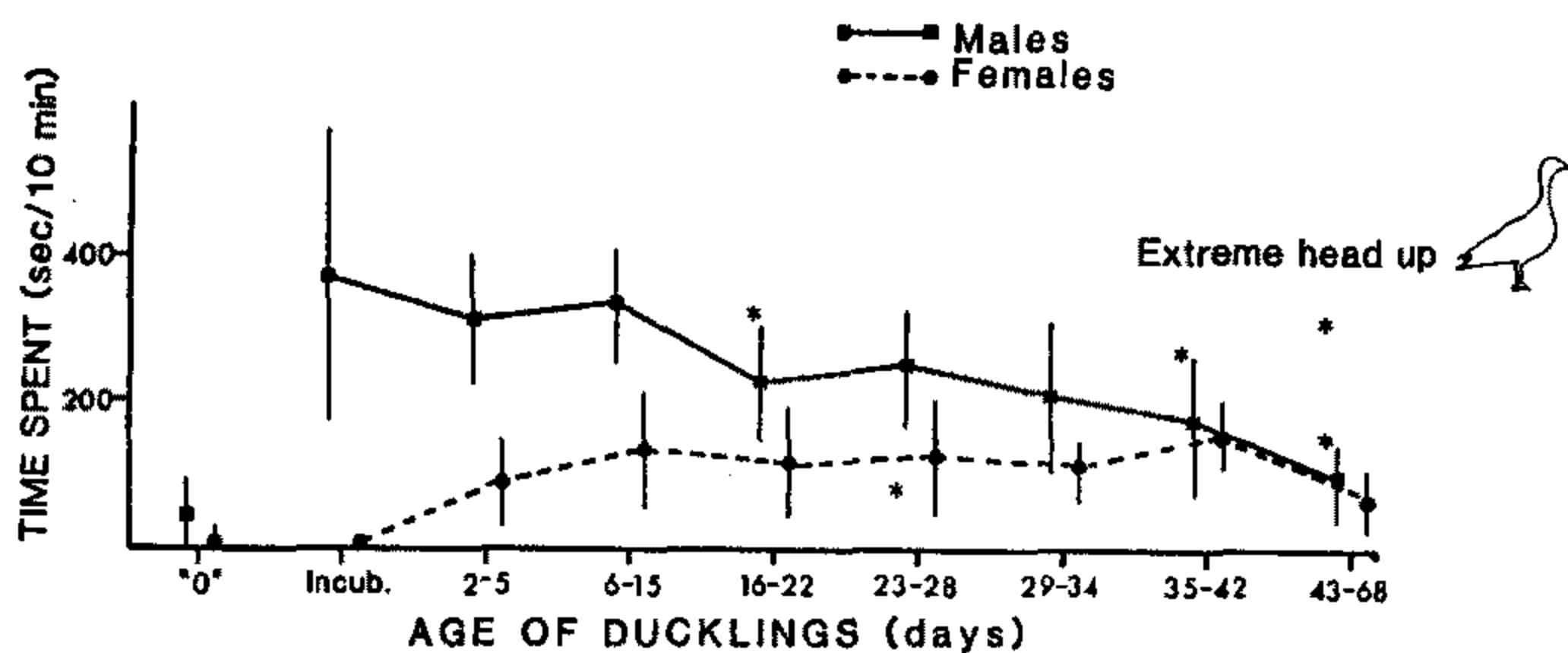


Figure 53. Variation, with brood age, of the time Maned Ducks spent doing the three behaviours Extreme head up, Head up and grazing (Mean $\pm$ 95% confidence intervals). Summary of the significant second order interaction, AGE by SEX by BEHAV ($F_{16,216}=3.73$, $p<0.001$). Males-closed squares, females closed circles. Also included are the single points * which mark values for single parent male broods.

Table XXVII. Three factor analysis of variance with repeated measures on the two factors; sex of the parent (SEX) and the behaviour; extreme-head-up, head-up and grazing (BEHAV) and grouped over age of the ducklings (AGE). Age groupings were: (0-no ducklings) and ducklings aged (2-10), (11-20), (21-28), (29-37), (38-63) days. The criterion measure was the mean bout length for the behaviours; extreme head up, head up and grazing within a ten minute focal sample. Data transformed by $\log(x+1)$ to overcome heterogeneity of variances. (p<0.05, **p<0.01, ***p<0.001)

BETWEEN BROODS				
AGE	DF	MS	F	SIGNIF
BROODS WITHIN GROUPS	5	0.50	1.21	ns
WITHIN BROODS				
SEX	1	0.11	1.52	ns
AGE by SEX	5	0.03	0.49	ns
SEX by BROODS WITHIN GRPS	81	0.07		
BEHAV				
DF	Error DF	F	SIGNIF	
2	80	12.21	***	
10	160	1.61	ns	
SEX by BEHAV				
2	80	11.98	***	
10	160	0.76	NS	
AGE by SEX by BEHAV				

between the two in Extreme head up, for the 23-28 day age group, Head up was significantly higher for single males. In addition, in all subsequent age categories, mean Extreme head up for single male parent broods was towards the top end of the confidence limits.

Despite the large standard errors for comfort and loafing activities, some patterns emerge (Fig. 52). During early brood care, females seem to spend more time loafing and performing comfort activity, than they do later. Contrasting this, males seemed to spend less time overall in both behaviours and did not vary this with age of the brood. Some of the recorded loafing activity for females was when they brooded ducklings, early in the brood care period.

Separate analysis examined how mean bout duration for the different factors was related to the four factors. Neither number in brood nor age of brood were important factors determining mean bout duration (Appendix 5, Table 5-C & Table XXVII). However, mean bout duration of the behaviours was different and varied according to the sex of the paired bird ($F_{2,80}=11.98$, $p<0.001$). Mean duration of female Extreme head up, Head up and grazing did not differ (Fig. 54), but males spent significantly longer periods in Extreme head up than either males or females performing Head up and grazing. Head up in males was also significantly longer than grazing, in males. Although males seemed to spend less time grazing than females, this was offset to some extent, by a faster pecking rate ($F_{4,93}=14.91$, $p<0.001$; see Fig. 55).

There were also differences between the positions of the two parents in relation to the brood. It was not always possible for one of the birds to be on a higher piece of ground. However, where height differences existed, males were higher for all five minute loafing samples ($n=21$). While grazing, this relationship continued. The male was usually higher ($Z=3.00$, $n=109$, $p<0.01$). For proximity to the brood, the relationship was reversed. Where a comparison could be made, females were always nearer to the brood while loafing ($n=21$). With grazing, the spatial relationship was maintained. Where there was one duck closer to the brood, then this was likely to be the female ($Z=56.0$, $n=227$, $p<0.001$).

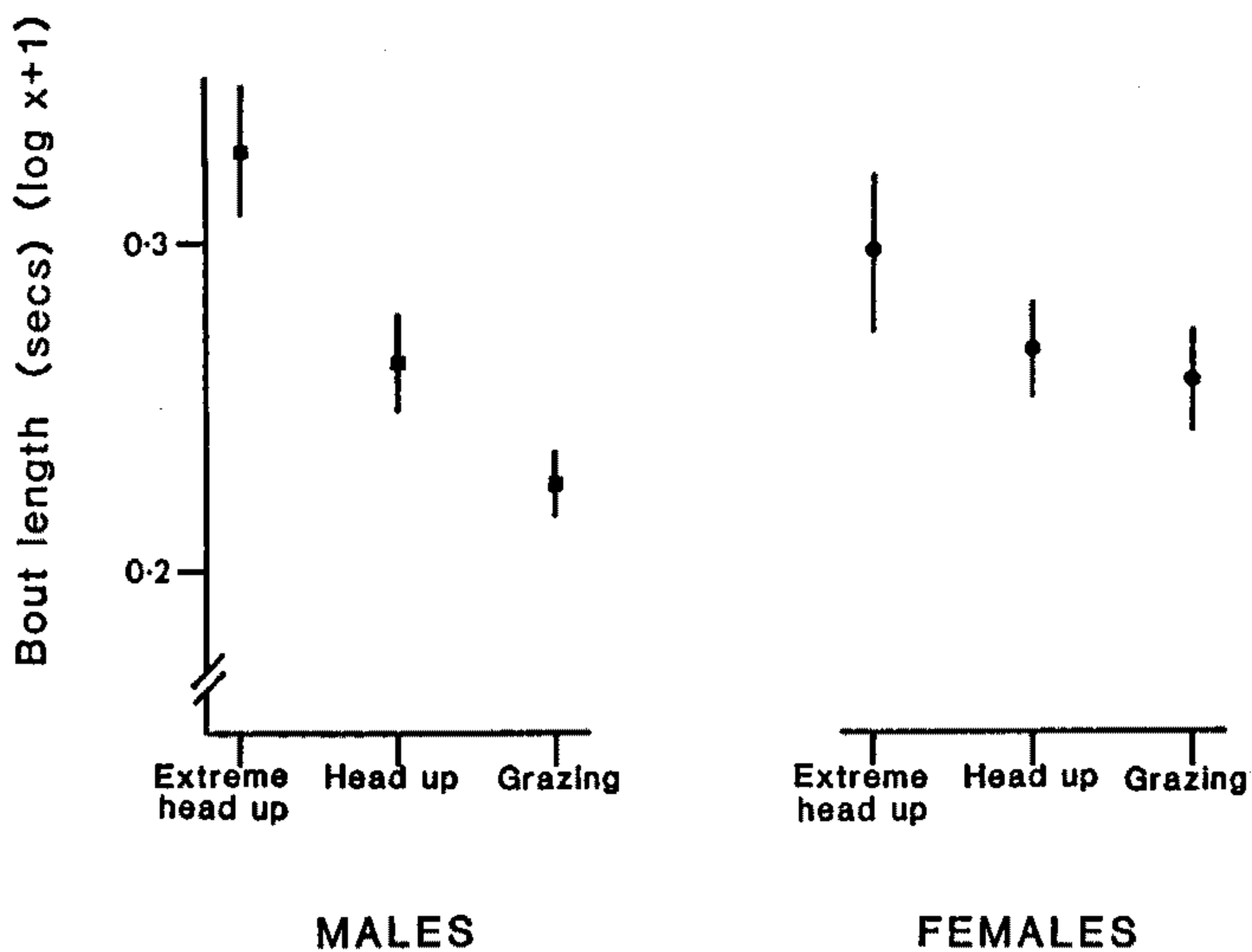


Figure 54. Variation of bout duration for the three behaviours according to the sex of paired Maned Ducks (Means $\pm$ 95% confidence limits). Summary of the first order (SEX by BEHAV) interaction for mean bout duration ($F_{2,80}=11.98$, $p<0.001$), transformed by $\log(x+1)$. Males-closed squares, females closed circles.

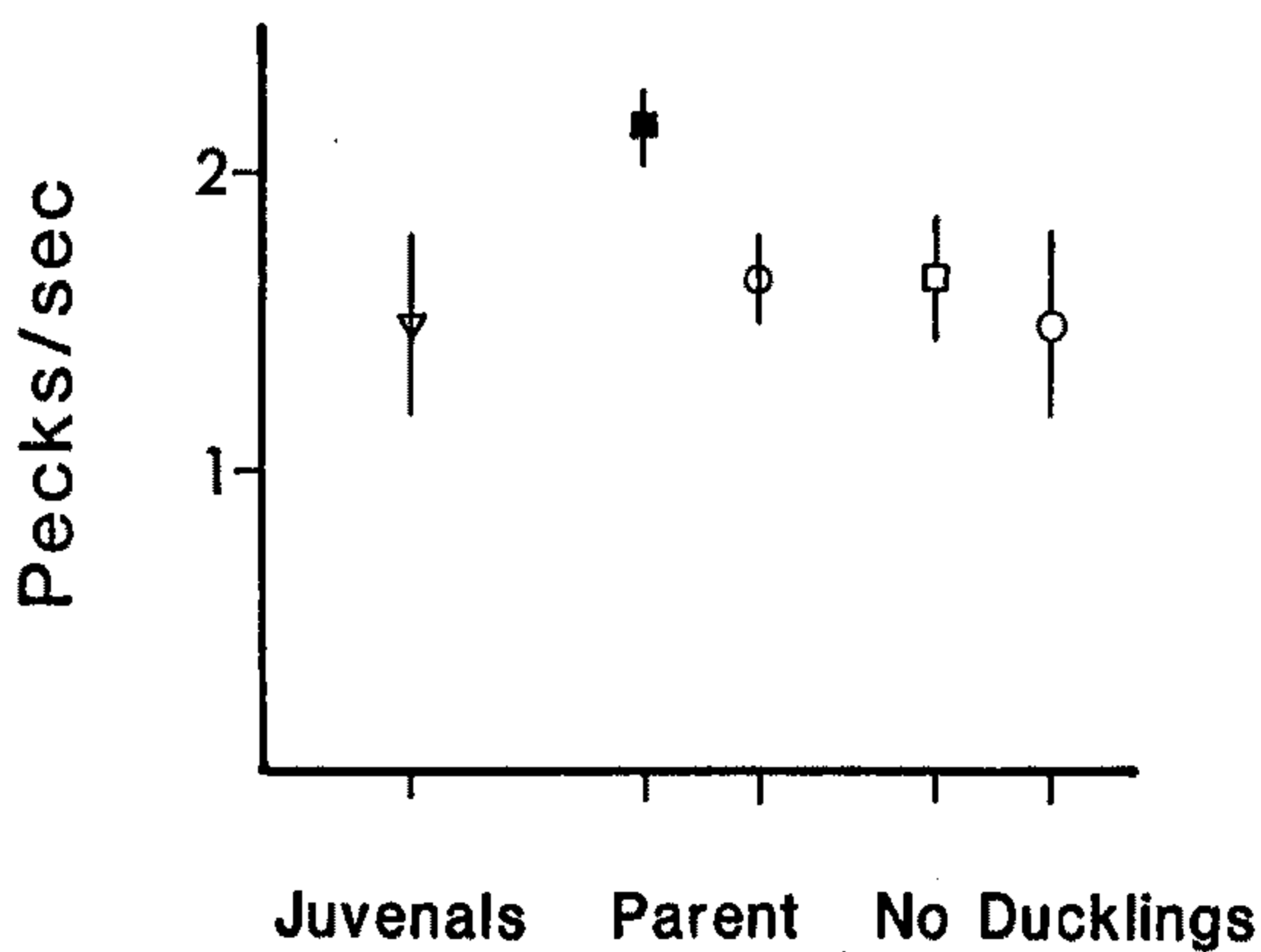


Figure 55. Mean peck rates ($\pm$ 95% confidence limits) for five groups of Maned Ducks.

Discussion

Pair bond

The continual association and the synchrony of activities between paired Maned Ducks, suggests that males mate with a single female in this species, a requirement of monogamy (Brown 1975; Wickler & Seibt 1983; Grier 1984). There is also ample evidence that this is an extended monogamy with pairs being together for more than one breeding season (Table XXV). Pairs may separate if moult migrations exist, as do some shelducks (Patterson et al. 1974), but data from pair associations throughout the year and flock instability (chapter 7), suggest that the pair probably remain together throughout the year. Brown (1975) distinguishes this type of mating system as perennial monogamy, which contrasts the serially monogamous Aix species, where the male deserts the female each breeding season (Kear 1970; Armbruster 1982; Gilmer et al. 1978). There was however, some variability in pair bond duration. Most of this was due to the mobility of the birds and, where only a single individual of an established pair was subsequently sighted, mortality may have been the cause (Table XXV). The one divorce (pair 11619-11620) supports the view that this may be more prevalent in young birds (Coulson & Thomas 1983), since both these birds hatched the previous breeding season.

In such a monogamous mating system as displayed by the Maned Duck, Trivers (1972) argued that a mixed mating strategy including some male adultery might exist. There is some evidence that males in a number of birds exhibit this (McKinney et al. 1984). This seems to be rare in this species which is probably due to the male contributing much to support his mate's breeding effort (McKinney et al. 1983).

Displays

My observations on Maned Duck displays suggest that they are more complex in this species, than has previously been thought (Delacour &

Mayr 1945; Frith 1982). Although usage of relative terms such as "simple" or "complex" is dangerous, particularly where experience is with only one species, a comparison with the two Aix species shows that all three species have a similar display complexity. This concurs with the general observation made by Johnsgard (1965), that the dimorphic Cairinini have more complex displays. Postcopulatory displays seem to be well developed in this species. There is some disagreement about how these may function in the mating system. Johnsgard (1962) suggests that in the Cairinini, the development of special male postcopulatory displays is correlated with short term pair bonds, so they function to ensure pair formation. However, equally they may draw attention to the performer and should be well developed in Anatidae with long pair bonds (McKinney 1975). The long term pair bond of Maned Ducks supports the latter hypothesis.

Besides complexity, the displays of Maned Ducks are similar to those of the two Aix species described by Lorenz (1941, 1953), Johnsgard (1965), Korschegen and Fredrickson (1976), Bruggers and Jackson (1981) and Armbruster (1984). There is a striking resemblance between the Display Shake of the three species and also a remarkable affinity between the Double Display Shake of Maned Ducks and that of the Mandarin Duck Aix galericulata. However, there are differences between the courtship displays of Maned Ducks and those of Aix sponsa and A. galericulata, but this variation does not seem to exceed that found between the two Aix species.

In a perennially monogamous species, pair formation could be expected to involve selection by both sexes, since both have as much to lose. Traditionally, in Anatidae, it is thought that the female selects her mate (Johnsgard 1962). This view has probably arisen from observations of groups of displaying males, an obvious female preference display (inciting), short term pair bonds and on the theoretical grounds of differential investment in the gametes (Parker et al. 1972). Although female competition has been reported in some Anatinae (Heinroth 1911; Johnsgard 1965; Siegfried 1979), it has probably been overlooked as important in the sexual processes. A contributing factor may be the presence of a more subtle male preference display, Turning-back-of-head. As with some Anas species (McKinney 1970), observations of female Maned

Ducks performing Display Shakes, displays usually confined to males, may be indicative of some female competition for males. Nevertheless the occurrence of courtship parties, also prevalent in other Anatinae (Lorenz 1941, 1953; Williams 1983; Johnsgard 1965; Armbruster 1982), where a number of males display around a single female, suggests that female selection may be more important. Under such circumstances, females may be using indirect criteria for assessing a male's worth as a breeding partner (McKinney 1975) or more specifically, the male's ability to provide parental care (Trivers 1972). Inciting behaviour, usually considered exclusively sexual in function (McKinney 1970), is thought to be particularly important to mate selection by females (Johnsgard 1960b).

Inciting is particularly prominent in this species. Johnsgard (1965) likened its form to that of the Brazilian Teal Amazonetta brasiliensis, where there is a direct threatening movement towards the opponent, while Delacour and Mayr (1945) remarked on its similarity with that of Aix. There is an aggressive component in this display to the point where it could be seen as being a true agonistic display, perhaps adapted to maintain separation of birds in grazing flocks. The most frequent context for this display is when Maned Ducks are grazing. If another duck approaches the pair, the female usually incites. This inciting is directed towards either sex, often causing the opponent to retreat. The aggressive intention is often clearly seen, when inciting females sometimes develop this into an Open bill threat and occasionally, a Rush. Furthermore, like the Cinnamon Teal Anas cyanoptera (McKinney 1970), females incite when other Maned Ducks approach the brood. In similar circumstances, males with broods will also occasionally perform inciting-like movements, an observation also made by Lorenz (1941, 1953) for the male A. sponsa. To some extent, Johnsgard (1965) is misleading in his presentation of this behaviour, by implying an exclusively sexual function. Accompanying the inciting female, in the illustration in Johnsgard (1965), is a male which is in the posture from which the Display Shake would be performed.

This confusion about the function of this display, combined with the traditional view that female Anatinae, when performing this display, incite the male to attack competitors (Johnsgard 1962; Weller 1964b), has

probably led to the misleading interpretation of breeding behaviour in this species. Frith (1982) suggested that male Maned Ducks are incited to pursue a particular female but my observations on courtship behaviour make such an interpretation implausible. Inciting females are those that are usually paired and this behaviour has the opposite effect, often making males flee.

Parental care

Both Maned Duck parents provide parental care. Besides accompanying the ducklings throughout the brood care period, they were both likely to initiate anti-predator strategies and attack duckling predators. Such behaviour was probably more dependent on which parent first detected danger and would be adaptive to the survival of the brood.

Of the behaviours common to all Maned Ducks, parents did more agonistic Rush displays than non-parent adults. Lazurus and Inglis (1978) suggested that this type of agonistic parental care functioned to reduce competition for food in Pink-footed geese Anser brachyrhynchus. However, my observations on Maned Ducks suggested that the protection of the ducklings from other Maned Ducks, may be equally important. There were also differences in the amount of time spent doing the behaviours, Extreme head up, Head up and grazing. As these dominated much of the behaviour of Maned Ducks, a reduction in one would result in a corresponding increase in either one or both the other two.

A number of workers have probably equated the equivalent of Extreme head up and Head up with vigilance or alert behaviour in other Anatidae, either for predators or conspecifics (Dwyer 1975, Bruggers & Jackson 1977; Inglis 1977; Asplund 1981). However, Lazurus and Inglis (1978) addressed the possibility that this type of behaviour may be important in obtaining food information in Pink-footed geese. Some discussion of the function of such behaviour in Maned Ducks is necessary before interpreting any observed patterns. Three observations indicate that Extreme head up may primarily function to detect predators. First, males when accompanying their mate during incubation, spend considerable time in Extreme head up.

If this was to obtain food information, then it might be expected that he would direct the female to good food patches. There was never any evidence of this. He often remained behind her, possibly out of her sight and followed while she fed. Second, when food is short, as in 1982 (Chapter 3), one might expect an increase in Extreme head up if it was concerned with getting food information but no such trend was apparent. Finally, the frequent performance of such behaviour in the presence of predators also strongly suggests that Extreme head up probably functions primarily in predator detection. Head up, however, may serve a dual purpose. It incorporated two postures, one during grazing where the head is not fully lifted above the body and that illustrated in Figure 49. Of the postures that made up Head up, the former may be important for finding food.

Extreme head up in male Maned Ducks was highest during incubation, being appreciably higher than Extreme head up in females (Fig. 53). Similar results have been found for a number of other Anatinae during the breeding season (Dwyer 1975; Bruggers & Jackson 1977; Asplund 1981). However, whether or not this is because females increase their feeding activity or whether there is a real increase in male vigilant activity, is usually not clear. In Maned Ducks, there appears to be a real increase in male vigilance compared to paired males of indeterminate reproductive state (group "0") (Fig. 53). In some Anatidae vigilance behaviour at this time, has been correlated to increased territoriality, allowing the female access to vital food resources (Dwyer 1975; Inglis 1977; Asplund 1981). Despite accounts of territoriality in Maned Ducks (Rowley 1975; Frith 1982), I found little evidence for it. Male Maned Ducks did not defend either feeding areas or dams. This is not an unexpected result since feeding areas are probably not defensible and it is questionable whether dams would be considered as resource. Only once, did I see a lone male chase off a pair which had landed on the dam in a three-bird flight (sensu. McKinney 1965b). I can only guess that perhaps the male had an incubating or laying female and so tried to ensure there was no chance of her being fertilised. The male Lesser Snow Goose Anser caerulescens caerulescens apparently guards his mate at such a time (Minneau & Cooke 1979). The rarity of such behaviour, in this species, suggests that if there is such an agonistic period, then it is brief. Such observations

further suggest that vigilant behaviour is primarily for the detection of predators.

Most variation in the three most common behaviours was in Extreme head up and grazing (Fig. 53); an increase in one being reflected in a decrease in the other. Changes were dependent on the sex of the duck and the age of the brood (Fig. 53). This variation may best be interpreted by considering the energetic demands on breeding females and treating brood age as a continuum from "incubating" to the end of brood care. Female birds may lay a clutch which more than equals her total weight (Lack 1968) and in female Anseriformes, this may necessitate an increase in daily energy intake by as much as 50-70% (King 1973). Female Maned Ducks may need to spend considerable lengths of time feeding (chapter 3) especially when the inefficiencies of a grazing habit are considered (Sibley 1981). I found that female grazing was highest when females were incubating (Fig. 53). At such a time, female Anatinae may spend considerable time on the nest (McKinney 1965b; Bruggers 1979; Miller 1976). Maned Ducks females seem to be no exception and confine their feeding to a few bouts during the day. To compensate for the reduction in time spent on the feeding area, females probably need to feed more intensely. One incubating female fed for the full ten minutes sample, not raising her head once. Equally focused, the accompanying male was in Extreme head up for this period which seems to be the pattern for male behaviour during incubation (Fig. 53).

A high incidence of this vigilant behaviour may increase the probability of detecting a predator. This seems to be the reason put forward to account for negative correlations between vigilant behaviour and increases in flock size in a number of birds (Powell 1974; Lazurus 1978; Caraco 1979). Members of the flock benefit from the predator detection behaviour of other birds in the flock (Pulliam 1973; Dimond & Lazurus 1974; Metcalfe 1984) and so reduce their own vigilance. Female Maned Ducks are primarily concerned with feeding when incubating and high male Extreme head up may compensate for the little time spent by the female in this behaviour. Perhaps with such complementary activities, the probability of predator detection is maintained at a high level. However, detection of a predator is not necessarily only dependent on how

much time is spent in vigilant behaviour but also on the length of interscan intervals (Hart & Lendrem 1984). If a Maned Duck spends long periods of time not watching for predators, then its chance of detecting a predator will be less than a duck which spends the same time not watching, but does it in short bursts. Males show the role they play in vigilance by spending less time in between scans (ie. when grazing) than females (Fig. 54). So, there was probably a greater chance that males would detect predators. High overall Extreme head up in males was also reflected in longer Extreme head up bouts. The whole posture of vigilant behaviour beginning with Head up through to Extreme head up is one of increasing the height of the duck. During Extreme head up, the impression is that the whole body is strained to its maximum height. The observation that males spend much more time on higher ground than females suggests that an increase in height may be an important part of vigilant behaviour. Conceivably, an extension in height may increase the area which can be surveyed and hence the effectiveness of predator detection. Lebeda and Ratti (1983) commonly saw male Canada Geese Branta canadensis in trees and contended that these offered loafing sites. However, this behaviour may be an important part of parental care, associated with the need to increase height.

The pattern of high male Extreme head up and high female grazing, during incubation, continued into early brood care (Fig. 53). Female Maned Ducks spent relatively little time in Extreme head up which was probably one of the most important parental care behaviours. This may be because incubation places a considerable energetic burden on the female. Krapu (1981) found that female Mallard Anas platyrhynchos, lost, on average, 25% of their weight during incubation. High female feeding in Maned Ducks during early brood care may be a compensatory mechanism by which females recover energy lost during incubation. The female also seems to spend more time doing comfort and loafing early in brood care than either males or paired females without young in group "0" (Fig. 52). Some of this loafing behaviour was attributable to females brooding their young, particularly early in brood care, serving to protect the ducklings from the cold or rain (Kear 1970). The rest may be because females also need longer periods of rest to reduce energy costs.

Female Maned Ducks start to spend more time in Extreme head up later in brood care which may correlate with an improvement in her condition, resulting from the additional time spent for feeding. Male Extreme head up also starts to drop off with brood age, although I do not know whether this was a response to increased female Extreme head up or to age of the ducklings. Towards the end of brood care, parental care in the form of Extreme head up begins to drop off for both parents (Fig. 53), as theoretically predicted by parent-offspring conflict (Trivers 1974). It was noticeable that duckling Extreme head up and Head up increased with age and so there may have been less need for parental Extreme head up. There is perhaps a point where high parental Extreme head up no longer enhances the chance of predator detection which is probably after the young have fledged since the family group continues to stay together after fledging.

Although brood age seemed to be an important determinant of parental behaviour, brood size did not affect the total time spent, by either Maned Ducks parent, in the three main behaviours Extreme head up, Head up and grazing. This suggests that clutch size is not limited by parental behaviour and supports the hypothesis that the important determinant is the female's ability to form eggs (Ryder 1970; Inglis 1977; Lazurus & Inglis 1978; Raveling 1979b). The female's ability to incubate a certain number of eggs has also been put forward as a determinant of clutch size in birds which do not feed their young (Lack 1968; Maynard Smith 1977). However, the possible existence of dump nesting in this species (chapter 6) and other Anatidae (Weller 1959), indicates that females can probably successfully incubate more eggs than they normally lay. Lazurus and Inglis (1978) present a succinct argument on why the absence of a brood size effect provides further evidence that Extreme head up and Head up behaviours in Pink-footed Geese function as vigilant behaviours. If this behaviour functioned, either to monitor the young or obtain food information, then it would be expected to increase with brood size, since these are shared parental behaviours.

According to parental investment theory a bird should desert its mate if one parent is as effective as two and the chance of remating is good (Trivers 1972; Maynard Smith 1977). Maned Ducks have an extended breeding

system and even if a male is not able to form a new pair bond he could possibly force copulations. The question then, is probably one of whether or not one parent is sufficient for parental care in this species. In three broods a parent was lost, two females and a male. One of the females was killed by a fox but I did not know whether the absence of the other two was due to mortality. However, I observed all three single parent broods for over three weeks, so it was unlikely that it was due simply to a temporary absence. There was no significant reduction in the reproductive success of the three single parent broods but behavioural observations suggested that the two males may have been more vigilant than their counterparts in similarly aged two parent broods (Fig. 53). Hence, there may be an additional parental cost if a partner is lost. The high incidence of vigilant behaviour in Maned Ducks during incubation and parental care, as well as the presence of a number of residential predators (chapter 4), suggest that predation pressure may be high. The mortality of some parents tends also to indicate this. It is likely, particularly when ducklings are young, that the absence of parental care would lead to high mortality since ducklings of this age are seldom vigilant and there were a number of birds, besides raptores, which could have preyed on them. Biparental care may be the product of either high parent mortality and/or high duckling mortality due to predation.

Conclusion

Maned Ducks seem to have a similar display repertoire to the two Aix species, but quite a different mating strategy. The presence of the male Maned Ducks appears to be important during incubation and early brood care since it allows the female to regain some of the costs of reproduction by feeding intensely while the male is vigilant for predators. In later parental care, he may increase his individual fitness by further contributing to parental care. Following brood care, there may be advantages to be had from the maintenance of the pair bond. Mate retention in birds has been shown to result in increased clutch size and hatching success in the following year, reviewed by Rowley (1983). Parental behaviours and an extended pair bond strongly resemble strategies employed by geese (Inglis 1977; Lazurus & Inglis 1978) and imply that ecological pressures have been important in shaping the mating system of the Maned Duck.

CHAPTER 9FINAL DISCUSSION

A grazing lifestyle and the associated characteristics of body structure were probably the features which led workers to include the Maned Duck in the Tadornini (shelducks). Now it is generally accepted that Maned Ducks are perching ducks (Cairinini) and, within this tribe, are closely related to the two Aix species, A. sponsa and A. galericulata (Mayr 1945; Delacour 1964; Delacour & Mayr 1945; Johnsgard 1960a, 1965; Todd 1979). Nevertheless, striking similarities with the Tadornini (Johnsgard 1960a) and the recent grouping of the species with the Tadornini by Kear and Murton (1976), suggest that there may still be some question about its affinities.

Besides the features which are common to most Cairinini (see Delacour 1964), there are a number of reported characteristics which indicate that Maned Ducks are similar to the two Aix species (Table XXVIII). This study has shown that other similarities exist. Maned Ducks have a definite eclipse plumage (Appendix 6), not previously acknowledged (Delacour 1964; Johnsgard 1965). Moreover, the displays of this species are much more like those of Aix species than has previously been thought (chapter 8). One unexpected finding was the performance of "aiming head movements", as a preflight display, during nest searching (chapter 8). This type of behaviour is the common preflight behaviour amongst the Cairinini (Delacour & Mayr 1945) including the Aix species (Lorenz 1941, 1953; Johnsgard 1965). Displays associated with the formation and maintenance of the pair bond in Maned Ducks, are also similar to those described in the literature for the Mandarin and American Wood Duck (chapter 8).

Johnsgard (1965) ventured that if behavioural characteristics were to be used to assess relationships, they must be species constant and distinctive but recognisable to homologous characteristics in other species. At least two displays of the Maned Duck fit this category.

These are the Display Shake (described by Johnsgard (1965)) and the Double Display Shake (chapter 8). The former has also been described for both Aix species (Lorenz 1941, 1953; Johnsgard 1965) but the latter only for the Mandarin Duck (Lorenz 1941, 1953; Johnsgard 1965). Lorenz (1941, 1953) described the latter behaviour in the Mandarin Duck as a Double-grunt-whistle, believing it and the former Display Shake to be intermediate forms of the distinctive Grunt-whistle of the Anatini. McKinney (1975) suggested that this Grunt-whistle display was so distinctive, that it could confidently be used as a taxonomic character because it was unlikely to have evolved more than once. The Display Shakes of Maned Ducks and the two Aix species seem particularly like each other, however, there are undoubtedly differences which may be apparent to workers more familiar with Aix displays. Nevertheless, there appears to be sufficient similarity between the three species, particularly in this display, to leave little doubt in my mind as to the affinity of the Maned Duck.

While these similarities are not immediately apparent to the casual observer, differences are obvious (Table XXVIII). These have doubtless contributed to the confusion about this species' relationships to other Anatidae. However, most can be related to its mode of life. In diet and activity budgets, habits of this species more closely resemble those of some Anserinae or Tadornini than the Aix species (chapters 3 & 4). Morphological differences, like the reported long neck and legs (Delacour 1964) are also likely to be adaptations to a grazing lifestyle. Perhaps even the larger body size of Maned Ducks (Todd 1979) is the result of this.

Differences between the social systems are particularly interesting. To some extent, Maned Ducks have been categorised apart from the two Aix species because the male provides parental care and Maned Ducks have long term pair bonds (Hillgarth & Kear 1982). However, I have argued that such adaptations are likely to be a direct result of their more terrestrial lifestyle (chapter 8). Predation is possibly a more important selective pressure determining the behaviour of a grazing anatid than for those anatid which are more aquatic. The existence of an anti-predator strategy (chapter 4) and vigilant postures, which mirror those of some geese

Table XXVIII. Summary of the similarities and differences between the Maned Duck Chenonetta jubata and the two Aix species, the Mandarin Duck A. galericulata and American Wood Duck A. sponsa. Characteristics mentioned where there has been a specific comparison made in the literature between the two genera. Other features marked with * are those differences or similarities determined from this study.

SIMILARITIES

Bill (Delacour & Mayr 1945)
Male tracheal bulla (Johnsgard 1961b)
Female plumage pattern (Delacour 1964; Johnsgard 1965)
Downy young (Delacour & Mayr 1945; Johnsgard 1965)
Female decrescendo call (Lorenz 1941, 1953)
Hybridised with A. sponsa (Johnsgard 1965)
Displays (Delacour 1945; Delacour & Mayr 1945;
Johnsgard, 1961a, 1965)
*Preflight displays during nest selection
*Eclipse plumage
*Pair formation and maintenance displays

- Terrestrial habit (Johnsgard 1965)
- Wing pattern and colouration (Johnsgard 1965)
- Preflight display (Johnsgard (1965)
- Distribution-~~Aix~~ temperate; C. jubata subtropical
- *Feeding habits
- *Activity patterns
- *Pair bond duration

(Inglis 1977; Lazurus 1978; Lazurus & Inglis 1978) and function to detect predators (chapter 8), provides further support. The social organisation of this species is also similar to that of geese species. Maned Ducks form flocks which are cohesive and compact when grazing and yet composition over time is dynamic (chapter 7). Pairs of Maned Ducks apparently move together between flocks, but independently of other individuals within these flocks. The mating system of Maned Ducks reflects this structure with a long term pair bond and an active role for the male in parental care. Far from such a mating system being primitive (Kear 1970), it appears to have evolved independently in a number of different anatids, principally the geese and shelducks. It is particularly interesting that most of these anatids have a grazing lifestyle.

Some of the differences in displays may also reflect the ecology of this species. McKinney (1975) has argued that displays are not merely conventions operating as species isolating mechanisms, as has been thought (Sibley 1957; Johnsgard 1963), but are signals which have probably been shaped by many selection pressures. There was insufficient information from this study to suggest what the function of many of the displays of the Maned Duck might be, or to pursue a detailed comparison between the display repertoires of the two Aix species and C. jubata. Nevertheless, some differences between displays should be mentioned. The normal preflight Chin flick displays of Maned Ducks (chapter 7) are different to other Anatinae (Johnsgard 1965), but similar to the head shakes and preflight display of some geese (Heinroth 1911; Raveling 1969a). It is possible that this is another example of convergence. Many geese form compact feeding flocks and such a method of communication may be more efficient than the normal aiming head movement of the Cairinini. The final example is Inciting behaviour. This appears to have more of an aggressive component than the Inciting behaviour of the Aix species. It seems to be a true agonistic display (chapter 8) and may be important for the maintenance of individual distance in compact grazing flocks.

An almost insurmountable problem for any study which aims to investigate the relationships of a species, is trying to identify which biological characteristics of a species are plastic and which are more

conservative in the face of natural selection. The comparative approach to such a problem is often fruitful. Cullen (1957) studied the Kittiwake Rissa tridactyla and, by comparing it to other closely related species, showed that many of the adaptations of this species were related to its cliff nesting habit. Following a similar method, I have tried to demonstrate that many of the characteristics of the Maned Duck probably follow directly from its grazing habit.

Mayr (1976) commented that the taxonomic status of many bird genera was only tentatively assigned because little was known about the species in these genera and he noted that some southern regions such as Australia are rich in aberrant taxa and it would simplify avian systematics if many of these could be associated with related taxa of the northern land masses. Such a case could be made for this species. As I have already suggested, many of the behaviour patterns of Mandarin Ducks and American Wood Ducks of the Aix genera are shared by the Maned Duck. I would argue that many of the behavioural and morphological features which have set this species apart from the Aix species (Table XXVIII) and even the Cairinini, are in fact plastic characteristics which cloud the nature of its relationships. The possibly more conservative behaviour patterns (displays) may be a far more reliable indication of its affinities. There may be sufficient justification for including Maned Ducks in the same genus as the two Aix species. It is noteworthy that Delacour and Mayr (1945) included the Mandarin and American Wood Duck in the same genus on the basis of the great similarity between the females of both species. The female Maned Duck is also similar to both Aix females (Table XXVIII). The fact that the two Aix species are temperate as opposed to the subtropical Maned Ducks, does not in itself seem to constitute a large enough difference.

In summary, Maned Ducks have the social organisation, mating system, feeding habits, and activity patterns which resemble those of many geese (Anserinae) and shelducks (Tadornini). Nevertheless, they have a number of morphological and behavioural features which indicate their true relationships. This highlights the problems of trying to incorporate social systems and ecological characteristics into a phylogenetic framework. More attention may need to be paid to groups like the geese

which have long been recognised, as separate from other groups of Anatidae, partly because of their long term pair bonds and distinctive body characteristics, features possessed by the Maned Duck.

The ecology of this species revolves around a grazing habit. Maned Ducks occasionally feed on insects but are mainly grazers (chapter 3). Even during the breeding season, when the female probably requires additional protein for breeding, she obtains this by grazing (chapters 3 & 8). The diet of Maned Ducks reflects the composition of the surrounding pastures (chapter 3) and, as a result, is probably similar to the diet of the livestock which graze these same areas. Except during droughts, most grazing properties probably have vegetation over their whole area, which meets the food requirements of this species. However, the key to habitat acceptability is the presence of the farm dam. Maned Ducks restricted their movements to a relatively small area surrounding the dam with there being a consistent tendency for all terrestrial activities to occur near the water (chapter 4). In fact, I seldom saw Maned Ducks further than 100m from any dam throughout this study. Even when grazing, Maned Ducks did not move far from the water. While the necessity to drink and bathe may have been important, the main reason seemed to be related to aerial predation. During the course of a day, flocks would frequently perform escape responses by "dashing" to the dam (chapter 4). So, although an acceptable food source extended far beyond the dam, predation seemed to restrict the usable food supply to a relatively small area around the dam. This means that the establishment of a dam would, in effect, make available food supplies which were previously not available.

Results from the analysis of habitat associations (chapter 5) support this argument. Few of the habitat characteristics that were measured significantly explained the distribution of Maned Ducks although there were some exceptions. When food was short in 1982, Maned Ducks used those dams where wheat grain was being fed to livestock, as a drought relief measure (chapter 5). Dam area and visibility were also significantly related to the distribution of Maned Ducks. Nevertheless, most dams, apart from those which were small and covered by vegetation, were occupied by this species. This suggests that every time a farm dam is dug, new

Maned Duck habitat is formed, like the two dams constructed in 1982 which were occupied by Maned Ducks almost as soon as they had water in them.

During the breeding season, an animal may have habitat requirements which are different (Whitmore 1979). As obligatory hole nesters, Maned Ducks showed this since they bred on those dams which had potential nest sites nearby (chapter 5). This means that the establishment of dams close to trees containing cavities, probably increases the reproductive potential of an area.

In summary, dams importantly provide an area of water for Maned Ducks to bathe, drink, mate and escape from predators (chapter 4) and, while satisfying these requirements, make available pastures for feeding (chapter 3) and nest sites for breeding (chapter 5) that may otherwise be inaccessible to the birds. The only part of the lifecycle which did not appear to occur on the farm dam was moulting of the wing feathers (Appendix 6). Perhaps birds require larger bodies of water. Although farm dams are sometimes not considered as wetlands (Goodrick 1970), they seem to make a valuable contribution to at least one species of Australian waterfowl and should be considered during discussions of the interaction between habitat type and waterfowl populations of Australia. As new dams are constructed, each opening up new pastures and some new nest sites, the population may be increased. This species may become more important both as a game species and also perhaps as a pest species as it is known to do some damage to rice crops (Kinghorn 1932; Frith 1957b).

As grazing anatids, Maned Ducks appear to owe much of their success to the fact that they are independent of the complex freshwater communities that are often necessary resources for other Anatinae. They may also have profited indirectly from agricultural practices which develop nutritious pastures for livestock (chapter 3). While the dam establishes the habitat, the availability of nutritious pastures may be more important to ensuring that females are able to breed. Drought feeding of livestock with wheat grain is probably also important to Maned Ducks when there is little natural food available (chapters 3 & 5).

Farm dams may have had a large impact on populations of Maned Ducks

in Australia. Both Braithwaite (1980) and Frith (1982, p 35) intimated that farm dams positively affected the status of this species. This study has gone further by providing data to support their statements, and by also tackling the question of how this has been achieved. There are two reasons to suspect that Maned Ducks were absent from my study site (A) prior to the construction of farm dams. Maned Ducks were found exclusively on or near dams, apart from three occasions during flooding (chapter 5) and there is also good anecdotal evidence indicating that there were no Maned Ducks before dams were established on the site in the 1930's (chapters 1 & 5). The site now consistently supports a population of about 60 Maned Ducks (chapter 5).

Further evidence comes from a comparison between the three properties studied during this project. Both the number of flying Maned Ducks and the number of broods hatched each year were more related to the number of dams than to any other characteristic of the properties (chapters 5 & 6). The property, Grathawai, with the most dams, consistently (over the three years) had a much larger population of flying Maned Ducks, irrespective of area (chapter 5). It also produced more broods than either of the other properties (chapter 6). Counts of flying Maned Ducks and broods on the other two properties indicated that these supported similar population sizes. These two properties were different in size (chapter 5), but had a similar number of dams. These results are unlikely to be due to other intrinsic characteristics of the properties, although this possibility cannot completely be discounted.

Estimates for the number of farm dams in Australia, are from about 139,000 (Braithwaite 1980) to over 400,000 (Timms 1980). Maned Ducks bred on this site even during the drought year of 1982. However, breeding was severely restricted and those ducklings hatched suffered higher mortality than in other years. However, I calculated that during a non-drought year, just under four broods hatched for every ten dams on this site (chapter 6). Taking into account duckling mortality (chapter 6), this meant that about 15 ducklings reached the fledging stage for every ten dams. Combining such estimates with the number of dams in Australia, gives some indication of what contribution dams could make to populations of Maned Ducks. Obviously, a number of factors such as climatic

conditions, density of nest sites, density of dams and abundance of possible competitors (e.g. Grass-whistle Duck in Queensland; Lavery 1966a,b), vary over the continent, and each could exert a different influence. Nevertheless, the impact of farm dams on the status of the Maned Duck has probably been considerable.

REFERENCES

- Aldrich, J.W. (1973) Disparate sex ratios in waterfowl. In "Breeding biology of birds", pp 482-489, Ed. Farner, D.S., National Academy of Sciences, Washington, D.C.
- Alford, J.R. and Bolen, E.G. (1977) Influence of winter temperatures on Pintail sex ratios in Texas. Southwest Nat. 21:554-556.
- Altmann, J. (1974) Observational study of behaviour sampling methods. Behaviour 49:227-265.
- Altmann, S.A. (1959) Field observations on a howling monkey society. J. Mammal 40:317-330.
- Alvey, N., Galwey, N. and Lane, P. (1982) An introduction to Genstat. Academic Press.
- Ambrose, G.J. (1979) Mammals and birds of the Wallaby Creek Catchment, Victoria, with special reference to species using tree-holes. Victorian Nat. 96:8-10.
- Ankney, C.D. and MacInnes, C. (1978) Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459-471.
- Armbruster, J.S. (1982) Wood duck displays and pairing chronology. Auk 99:116-123.
- Arnold, G.W. (1964) Factors within plant associations affecting the behaviour and performance of grazing animals. In "Grazing in terrestrial and marine environments". Fourth symposium of the British Ecological Society, Oxford.
- Ashmole, N.P. (1971) Sea bird ecology and the marine environment. In "Avian Biology Vol I", pp 223-286. Eds Farner, D.S. and King, J.R., New York and London, Academic Press.
- Asplund, C. (1981) Time budgets of breeding mallard in northern Sweden. Wildfowl 32:55-64.
- Ball, I.J., Gilmer, D.S., Cowardin, L.M. and Riechmann, J.H. (1975) Survival of wood duck and mallard broods in north-central Minnesota. J. Wildl. Manage. 39:776-780.
- Barnard, C.J. (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus*). Anim. Behav. 28:295-309.
- Batt, B.D.J. and Prince, H.H. (1979) Laying dates, clutch size and egg weight of captive Mallards. Condor 81:35-41.
- Beard, E.B. (1964) Duck brood behavior at the Sney National Wildlife Refuge. J. Wildl. Manage. 28:492-521.
- Beck, A.B. (1952) The composition of the Dwalganup strain of Subterranean clover. J. Dept. Agr. W. Aust. 1:257-259.
- Bear, C.G. (1977) What is a display? Amer. Zool. 17:155-165.
- Belrose, F.C., Scott, T.G., Hawkins, A.S. and Low, J.B. (1961) Sex ratios and age ratios in North American ducks. Ill. Nat. Hist. Surv. Bull. 27:391-474.
- Bertram, B.C.R. (1980) Vigilance and group size in ostriches. Anim. Behav. 28:278-286.
- Blackith, R.E. and Reyment, R.A. (1971) Multivariate Morphometrics. Academic Press, London and New York.
- Blakers, M., Davies, S.J.J.F. and Reilly, P.N. (1984) The Atlas of Australian Birds. Royal Ornithologists Union, Melbourne University Press.
- Boyd, H. (1953) On encounters between wild White-fronted geese in winter flocks. Behaviour 5:85-129.
- Braithwaite, L.W. (1966) Ecology of the Black Swan. Master's thesis. University of Sydney.
- Braithwaite, L.W. (1975) Managing waterfowl in Australia. Proc. Ecol. Soc. Aust. 8:107-128.
- Braithwaite, L.W. (1976a) Breeding seasons of waterfowl in Australia. Proc. 16th Int. Ornith. Congr. pp235-247.
- Braithwaite, L.W. (1976b) Environment and timing of reproduction and flightlessness in two species of Australian ducks. Proc. 16th Int. Ornith. Congr. pp489-500.
- Braithwaite, L.W. (1980) Waterfowl resources and their management. In "An ecological basis for water resource management". Williams, W.D., (Ed.), A.N.U. Press, Canberra.
- Braithwaite, L.W. (1982) Ecological studies of the black swan IV. The timing and success of breeding on two nearby lakes on the Southern Tablelands of New South Wales. Aust. Wildl. Res. 9:261-275.
- Braithwaite, L.W. and Frith, H.J. (1969) Waterfowl in an inland swamp in New South Wales. III Breeding. C.S.I.R.O. Wildl. Res. 14:65-109.
- Braithwaite, L.W. and Norman, F.I. (1974) The 1972 open season on waterfowl in south-eastern Australia. CSIRO Div. Wildl. Res. Tech. Pap. No. 29.
- Braithwaite, L.W. and Norman, F.I. (1976) The 1973 and 1974 open seasons on waterfowl in south-eastern Australia. CSIRO Div. Wildl. Res. Tech. Memo. No. 11.

- Braithwaite, L.W. and Norman, F.I. (1977) The 1975 and 1976 open seasons on waterfowl in south-eastern Australia. CSIRO Div. Wildl. Res. Tech. Memo. No. 13.
- Braithwaite, L.W. and Norman, F.I. (1981) The 1977 and 1978 open seasons on waterfowl in south-eastern Australia. CSIRO Div. Wildl. Res. Tech. Memo. No. 15.
- Breckenridge, W.J. (1956) Nesting study of wood ducks. J. Wildl. Manage. 20:16-21.
- Briggs, S.V. (1977) Ducks and irrigated rice crops for the 1976/1977 season in southern New South Wales. Wildlife Management in Australia. Proceedings, Field and Game Federation of Australia, La Trobe University, Melbourne.
- Briggs, S.V. (1983) Ducks, Geese and Swan. Family : Anatidae. In Parks and Wildlife-Wetlands. Ed Haigh, C. National Parks and Wildlife Service.
- Briggs, S.V., Brown, B.K., Maher, M.T., Brickhill, J.G. and Kingsford, R.T. (1983) Mortality of maned duck and grey teal during the 1982 open season at Barrenbox Swamp, N.S.W. Aust. Wildl. Res. 10:537-543.
- Briggs, S.V., Maher, M.T., Davey, C.C. (1985a) Bias in food habits of Australian waterfowl. Aust. Wildl. Res. 12:507-514.
- Briggs, S.V., Maher, M.T., Palmer, R.P. (1985b) Hunter activity and waterfowl harvests in New South Wales, 1977-82. Aust. Wildl. Res. 12:515-522.
- Brooker, M.I.H. and Kleinig, D.A. (1983) Field Guide to Eucalypts in South-Eastern Australia. Inkata Press, Melbourne.
- Brown, J.L. (1975) The Evolution of Behaviour. W.W. Norton and Co. New York.
- Bruggers, R.L. (1979) Nesting patterns of captive mandarin ducks. Wildfowl 30:45-54.
- Bruggers, R.L. and Jackson, W.B. (1977) Time budget of mandarin ducks under semi-natural conditions. Wildfowl 28:87-93.
- Bruggers, R. and Jackson, W.B. (1981) Age related differences on reproductive behaviour of male mandarin duck. Bird Study 28:107-114.
- Bue, I.G., Uhlig, H.G. and Smith, J.D. (1964) Stock ponds and dugouts pp 391-398. In "Waterfowl tomorrow", Ed Linduska, J.P. U.S. Government Printing Office, Washington, D.C.
- Burbidge, N.T. (1966) Australian Grasses. Vol I. Angus and Robertson.
- Burton, B.A. and Hudson, R.J. (1978) Activity budgets of lesser Snow Geese wintering on the Fraser River estuary, British Columbia. Wildfowl 29:111-117.
- Byrne, J. (1974) Duck hunting in Australia and New Zealand. A.H. Reed and A.W. Reed, Wellington, Sydney, London.
- Capen, D.E. (1981) The use of multivariate statistics in studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87. 249pp.
- Caraco, T. (1979) Time budgeting and group size; a theory. Ecology 60:611-617.
- Caraco, T., Martindale, S. and Pulliam, H.R. (1980) Avian flocking in the presence of a predator. Nature 285:400-401.
- Carlisle, T.R. (1985) Parental response to brood size in a cichlid fish. Anim. Behav. 33:234-238.
- Clawson, R.L., Haartman, G.W. and Fredrickson, L.H. (1979) Dump nesting in a Missouri Wood Duck population. J. Wildl. Manage. 43:347-355.
- Clough, G. and Hassam, A.G. (1970) A quantitative study of the daily activity of the warthog in the Queen Elizabeth National Park, Uganda. E. Afr. Wildl. J. 8:19-24.
- Colquhoun, W.P. (1971) Biological rhythms and human performance. Academic Press, London and New York.
- Comrey, A.D. (1973) A First Course in Factor Analysis. Academic Press, New York.
- Coulson, J.C. and Thomas, C.S. (1983) Mate choice in the Kittiwake Gull. In "Mate Choice". pp 361-376, Ed Bateson, P., Cambridge University Press, Cambridge.
- Coulter, M.W. (1957) Food of wood ducks in Maine. J. Wildl. Manage. 21:235-236.
- Cowan, I.M. (1973) The conservation of Australian waterfowl. A.F.A.C. Special Publication No. 2, Australian Government Publishing Service Canberra.
- Craven, S.R. and Rusch, D.H. (1983) Winter distribution and affinities of Canada geese marked on Hudson and James Bays. J. Wildl. Manage. 47:307-319.

- Crook, J.H. (1964) The evolution of social organization and visual communication in the weaver birds (Ploceinae). Behaviour Suppl. 10:1-178.
- Crook, J.H. (1965) The adaptive significance of avian social organisation. Synp. Zool. Soc. London 14:181-218.
- CSIRO. (1970) The Insects of Australia. Melbourne University Press, Melbourne.
- Cullen, E. (1957) Adaptations in the kittiwake to cliff nesting. Ibis 99:275-302.
- Dawkins, R. and Carlisle, T.R. (1976) Parental investment, male desertion and a fallacy. Nature 262:131-133.
- Delacour, J. (1945) The display of the Manded Goose. Wilson Bull. 57:129.
- Delacour, J. (1964) The Waterfowl of the World. Vol III. Published Country Life Ltd.
- Delacour, J. and Mayr, E. (1945) The family Anatidae. Wilson Bull. 57: 3-55.
- Dimond, S. and Lazurus, J. (1974) The problem of vigilance in animal life. Brain, Behav. Evol. 9:60-79.
- Doing, H. (1972) Botanical composition of pasture and weed communities in the Southern Tablelands Region, South-Eastern Australia. C.S.I.R.O. Div. Plant Indust. Tech. Paper 30.
- Donald, C.M. (1941) The nutritive value of pastures and pasture research. Six lectures delivered at the University of Sydney, 1941. The University of Sydney.
- Donald, C.M. (1970) The Pastures of Southern Australia. In "The Australian Environment", Ed. Leeper, G.W. fourth edition, CSIRO, Australia, Melbourne University Press.
- Dow, H. and Fredga, S. (1984) Factors affecting reproductive output of the Goldeneye Duck *Eucephala clangula*. J. Anim. Ecol. 53:679-692.
- Drent, R.H. and Daan, S. (1980) The prudent parent:energetic adjustment in avian breeding. Ardea 68:225-252.
- Drobney, R.D. (1980) Reproductive bioenergetics of wood ducks. Auk 97: 480-490.
- Drobney, R.D. (1982) Body weight and composition changes and adaptation for breeding in wood ducks. Condor 84:300-305.
- Drobney, R.D. and Fredrickson, L.H. (1979) Food selection by wood ducks in relation to breeding status. J. Wildl. Manage. 43:355-363.
- Dwyer, T.J. (1970) Waterfowl breeding habitat in agricultural and nonagricultural land in Manitoba. J. Wildl. Manage. 34:130-136.
- Dwyer, T.J. (1972) An adjustable radio package for ducks. Bird Banding 43:282-284.
- Dwyer, T.J. (1975) Time budget of breeding Gadwalls. Wilson Bull. 87:335-343.
- Ebbinge, B., Canters, K. and Drent, R.H. (1975) Foraging routines and estimated daily food intake of barnacle geese wintering in the northern Netherlands. Wildfowl 26:5-19.
- Elliot, J.P., McTaggart Cowan, I. and Holling, C.S. (1977) Prey capture by the African lion. Can. J. Zool. 55:1811-1828.
- Eltringham, S.K. (1974) The survival of broods of the Egyptian Goose in Uganda. Wildfowl 25:41-48.
- Ely, C.R. and Raveling, D.G. (1984) Breeding biology of Pacific White-Fronted Geese. J. Wildl. Manage. 48:823-837.
- Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.
- Evans, C.D. and Black, K.E. (1956) Duck production studies on the prairie potholes of South Dakota. U.S. Fish Wildl. Serv. Soc. Sci. Rep. Wildl. 32: 59pp.
- Ewald, P.W. and Rohwer, S. (1982) Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in Red-Winged Blackbirds *Agelaius phoeniceus*. J. Anim. Ecol. 51:429-450.
- Farner, D.S. (1967) The control of avian reproduction cycles. Proc. 14th Int. Ornith. Congr. 107-133.
- Farner, D.S. and Lewis, R.A. (1971) Photoperiodism and reproductive cycles in birds. In "Photophysiology Vol VI" pp325-370. Ed. Giese, A.C. New York: Academic Press.
- Finney, G. and Cooke, F. (1978) Reproductive habits in the Snow Goose:the influence of female age. Condor 80:147-158.

- Fitzpatrick, E.A. and Nix, H.A. (1970) The climatic factor in Australian grassland ecology. In "Australian Grasslands". pp3-26. Ed Milton Moore, R. Australian National University Press, Canberra.
- Fredrick, R.B. and Klaas, E.E. (1982) Resource use and behaviour of migrating snow geese (Anser caerulescens). J. Wildl. Manage. 46:601-614.
- Fredrickson, L.H. and Hansen, J.L. (1983) Second broods in wood ducks. J. Wildl. Manage. 47:320-326.
- Frith, H.J. (1957a) Breeding and movements of wild ducks in inland New South Wales. C.S.I.R.O. Wildl. Res. 2:19-31.
- Frith, H.J. (1957b) Wild ducks and the rice industry in New South Wales. C.S.I.R.O Wildl. Res. 2:32-50.
- Frith, H.J. (1959a) The ecology of wild ducks in inland New South Wales. I. Waterfowl habitats. C.S.I.R.O. Wildl. Res. 4:97-107.
- Frith, H.J. (1959b) The ecology of wild ducks in inland New South Wales. II. Movements. C.S.I.R.O. Wildl. Res. 4:97-107.
- Frith, H.J. (1959c) The ecology of wild ducks in inland New South Wales. III Food habits. C.S.I.R.O Wildl. Res. 4:156-181.
- Frith, H.J. (1959d) The ecology of wild ducks in inland New South Wales. IV. Breeding. C.S.I.R.O. Wildl. Res. 4:156-181.
- Frith, H.J. (1963) Movements and mortality rates of the Black Duck and Grey Teal in South-eastern Australia. C.S.I.R.O. Wildl. Res. 8:119-131.
- Frith, H.J. (1967) Waterfowl in Australia. 1st edition, Angus and Robertson. Sydney.
- Frith, H.J. (1982) Waterfowl in Australia. 2nd edition, Angus and Robertson. Sydney.
- Gillespie, G.D. (1985) Feeding behaviour and impact of ducks on ripening barley crops grown in Otago, New Zealand. J. Appl. Ecol. 22:347-356.
- Gilmer, D., Ball, I.J., Cowardin, L.M., Mathisen, J.E. and Riechmann, J.H. (1978) Natural cavities used by wood ducks in North-Central Minnesota. J. Wildl. Manage. 42:288-298.
- Gilmer, D.S. Kirby, R.E., Ball, I.J. and Reichmann, J.H. (1977) Post-breeding activities of mallards and wood ducks in north-central Minnesota. J. Wildl. Manage. 41:345-359.
- Godin, P.R. Joyner, D.E. (1982) Pond ecology and its influence on Mallard use in Ontario, Canada. Wildfowl 32:28-34.
- Goodrick, G. (1970) A survey of wetlands of coastal New South Wales. C.S.I.R.O. Div. Wildl. Res. Tech. Memo No. 5.
- Goodrick, G.N. (1979) Food of the Black Duck Anas superciliosa and Grey Teal Anas gibberifrons in coastal New South Wales. Aust. Wildl. Res. 6:319-324.
- Goss-Custard, J.D. (1970) Feeding dispersion in some overwintering wading birds. In "Social Behaviour in Birds and Mammals", Ed. Crook, J.H. pp. 1-35. Academic Press, London.
- Gould, J. (1865) Handbook to the birds of Australia. Vol II. 627pp 2 vols. Pub. by author, London.
- Green, P.E. (1978) Analyzing multivariate data. The Dryden Press, Hinsdale, Illinois.
- Grice, D. and Rogers, J.P. (1965) The wood-duck in Massachusetts. Final Report Project Number W-19-12, Massachusetts Division of Fish and Game.
- Grier, J.N. (1984) Biology of animal behaviour. St Louis:Times Mirror/Mosby College.
- Haartman, L. Von. (1971) Population dynamics. In "Avian biology Vol I". Eds Farner, D.S. and King, J.R. pp 392-459. Academic Press, New York.
- Harris, M.P. (1969) Food as a factor controlling the breeding of Puffinus lherminieri. Ibis 111:139-156.
- Hart, A. and Lendrem, D.H. (1984) Vigilance and scanning patterns in birds. Anim. Behav. 32:1216-1224.
- Harwood, J. (1977) Summer feeding ecology of lesser snow geese. J. Wildl. Manage. 41:48-55.
- Heinroth, O. (1911) Beitrage zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Proc. V. Inter. Ornith. Congr., Berlin, 1910, pp 598-702.

- Heitmeyer, M.E. and Vohs, Jr, P.A. (1984) Distribution and habitat use of waterfowl wintering in Oklahoma. *J. Wildl. Manage.* 48:51-63.
- Hensler, G.L. and Nichols, J.D. (1981) The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.* 93:42-53.
- Hilden, O. (1965) Habitat selection in birds. A review. *Annales Zoologici Fennici* 2:53-75.
- Hillgarth, N. Kear, J. (1982) Diseases of perching ducks in captivity. *Wildfowl* 32:156-162.
- Hobbs, N.T. and Bowden, D.C. (1982) Confidence intervals on food preference indices. *J. Wildl. Manage.* 46:505-507.
- Hochbaum, H.A. (1942) Sex and age determinism of waterfowl by cloacal examination. *Trans. Seventh N. American Wildl. Conf.* 7:299-307.
- Hocutt, G.E. and Dimnick, R. (1971) Summer food habits of juvenile wood duck in East Tennessee. *J. Wildl. Manage.* 35:286-292.
- Hudson, M.S. (1983) Waterfowl production on three age-classes of stock ponds in Montana. *J. Wildl. Manage.* 47:112-117.
- Hull, C.H. and Nie, N.H. (1981) SPSS update 7-9 New procedures and facilities for releases 7-9. McGraw-Hill Book Company.
- Hunter, P.J.P. (1970) Hunter's guide to grasses, clovers and weeds: a useful and informative guide. Hunter Ltd.
- Immelmann, K. (1971) Ecological aspects of periodic reproduction. In "Avian Biology Vol I" pp 342-389. Eds Farner, D.S. and King, G.R., Academic Press, New York.
- Inglis, I.R. (1977) The breeding behaviour of the pink footed goose: behavioural correlates of nesting success. *Anim. Behav.* 25:747-764.
- Inglis, I.R. and Isaacson, A.J. (1978) The responses of dark-bellied Brent geese to models of geese in various postures. *Anim. Behav.* 26:953-958.
- Johnsgard, P.A. (1960a) Comparative behaviour of the Anatidae and its evolutionary implications. *Wildfowl Trust* 11th Ann. Rep, pp. 31-45.
- Johnsgard, P.A. (1960b) Pair formation mechanisms in *Anas* (Anatidae) and related genera. *Ibis* 102:616-618.
- Johnsgard, P.A. (1961a) The taxonomy of the Anatidae-A behavioural analysis. *Ibis* 103a:71-85.
- Johnsgard, P.A. (1961b) The tracheal anatomy of the Anatidae and its taxonomic significance. *Wildfowl Trust* 12th Ann. Rep. pp 58-69.
- Johnsgard, P.A. (1962) Evolutionary trends in the behaviour and morphology of the Anatidae. *Wildfowl Trust* 13th Ann. Rep. pp 130-148.
- Johnsgard, P.A. (1963) Behavioral isolating mechanisms in the family Anatidae. *Proc. Int. Orn. Congr.* 13:531-543.
- Johnsgard, P.A. (1965) Handbook of Waterfowl Behaviour. Cornell University Press, Ithaca.
- Johnsgard, P.A. (1973) Proximate and ultimate determinants of clutch size in Anatidae. *Wildfowl* 24:144-149.
- Johnsgard, P.A. and Buss, I. O. (1956) Waterfowl sex ratios during spring in Washington State and their interpretation. *J. Wildl. Manage.* 20:384-388.
- Johnson, D.H. (1979) Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Jones, P.J. and Ward, P. (1976) The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed Quelea *Quelea quelea*. *Ibis* 118:547-574.
- Jones, R.E. and Leopold, A.S. (1967) Nesting and interference in a dense population of wood ducks. *J. Wildl. Manage.* 31:221-228.
- Kaminski, R.M. and Prince, H.H. (1984) Dabbling duck-habitat associations during spring in Delta Marsh, Manitoba. *J. Wildl. Manage.* 48:37-50.
- Karr, J.R. (1980) History of the habitat concept in birds and the measurement of avian habitats. *Acta. Congr. Int. Orn.* 2:991-997.

- Kear, J. (1970) The adaptive radiation of parental care in waterfowl. In "Social Behaviour in birds and mammals", pp 357-392. Ed. J.H. Crook. Academic Press, New York.
- Kear, J. and Murton, R.K. (1976) The origins of Australian waterfowl as indicated by their photoresponses. Proc. 16th Int. Ornith. Congr. pp83-97.
- Kendall, M.G. (1957) A course in Multivariate Analysis. Griffin, London.
- Kendeigh, S.C. (1970) Energy requirements for existence in relation to size of bird. Condor 72:60-65.
- Kikkawa, J. (1968) Ecological associations of bird species and habitats in Eastern Australia; similarity analysis. J. Anim. Ecol. 37:143-165.
- Kim, J.-O. and Kohout, F.J. (1975) Multiple regression: subprogram regression, pp320-367 In "Statistical package for the social sciences". Nie, N.H., Hull, C.H. Jenkins, J.G., Steinbrenner, K. and Bent, eds. SPSS. 2nd ed. McGraw-Hill book Co. New York, N.Y.
- King, A.S. (1981) Phallus. In "Form and Function in birds Vol. 2" (King A.S. and Mclelland, J. eds) Academic Press London pp 107-147.
- King, J.R. (1973) Energetics of reproduction in birds. In "Breeding biology of birds", Ed. Farner, D.S. pp 78-107, Washington, D.C., Nat. Acad. Sci.
- Kinghorn, J.R. (1932) Wild ducks are not a serious pest of rice crops. Agric. Gaz. N.S.W 43:603-608
- Klecka, W.R. (1975) Discriminant analysis: subprogram discriminant. pp434-467. In "Statistical package for the social sciences". Nie, N.H., Hull, C.H. Jenkins, J.G., Steinbrenner, K. and Bent, eds. SPSS. 2nd ed. McGraw-Hill book Co. New York, N.Y.
- Klett, A.T. and Johnson, D.H. (1982) Variability in nest survival rates and implications to nesting studies. Auk 99:77-87.
- Klomp, H. (1970) The determination of clutch size in birds. Ardea 58:1-124.
- Korschgen, C.E. and Fredrickson (1976) Comparative displays of yearling and adult male wood ducks. Auk 93:793-807.
- Krapu, G.L. (1974) Food of breeding pintails in North Dakota. J. Wildl. Manage. 38:408-417.
- Krapu, G.L. (1981) The role of nutrient reserves in Mallard reproduction. Auk 98:29-38.
- Krapu, G.L. and Doty, H.A. (1979) Age related aspects of mallard reproduction. Wildfowl 30:35-39.
- Krapu, G.L. and Swanson, G.A. (1975) Some nutritional aspects of reproduction in prairie nesting pintails. J. Wildl. Manage. 39:155-162.
- Krebs, J.R. and Davies, N. B. (1981) Behavioural Ecology: An evolutionary approach. Blackwell Scientific Publications, Oxford.
- Krebs, J.R., MacRoberts, M.H. and Cullen, J.M. (1972) Flocking and feeding in the great tit *Parus major*-an experimental study-. Ibis 114:507-530.
- Kruuk, H. (1964) Predator and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour, Suppl. XI.
- Lack, D. (1948) Natural selection and family size in the starling. Evol. 2:95-110.
- Lack, D. (1954) The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.
- Lack, D. (1968) Ecological Adaptations for breeding in Birds. Methuen, London.
- Lamp, C. and Collett, F. (1976) A field guide to Weeds in Australia. Inkata Press, Melbourne.
- Landers, J.L. Fendley, T.T. and Johnson, A.S. (1977) Feeding ecology of Wood Ducks in South Carolina. J. Wildl. Manage. 41:118-127.
- Langlands, J.P. and Holmes, C.R. (1978) The nutrition of ruminants grazing native and improved pastures. I Seasonal variation in the diet selected by grazing sheep and cattle. Aust. J. Agric. Res. 29:863-874.
- Langlands, J.P. and Sanson, J. (1976) Factors affecting the nutritive value of the diet and the composition of rumen fluid of grazing sheep and cattle. Aust. J. Agric. Res. 27:691-707.
- Lavery, H.J. (1966a) Studies of waterfowl (Anatidae) in North Queensland. 1. Introduction, species, distribution and habitat. Qld. Agric. Anim. Sci. 23:573-590.
- Lavery, H.J. (1966b) Water storage provides homes for waterfowl. Qld. Agric. J. 92:594-597.
- Lavery, H.J. (1970a) Studies of waterfowl (Anatidae) in North Queensland. 5. Breeding. Qld. J. of Agric. and Anim. Sci. 27:425-436.

- Lavery, H.J. (1970b) The comparative ecology of waterfowl in north Queensland. *Wildfowl* 21:69-77.
- Lavery, H.J. (1971) Studies of waterfowl in North Queensland 6. Feeding methods and foods. *Qld. J. of Agr. and Anim. Sci.* 28:255-273.
- Lavery, H.J. (1974) Water conservation and waterfowl in north-eastern Australia. In "Man Made Lakes and Human Health" eds. Stanley, N.F. and Alpers, M.P., Academic Press, London.
- Lazenby, A. and Swain, F.G. (1973) Pasture species. In "Intensive pasture production", Ed., Lazenby, A. Angus and Robertson, Sydney.
- Lazurus, J. (1972) Natural selection and the function of flocking in birds: A reply to Murton. *Ibis* 114:556-558.
- Lazurus, J. (1978) Vigilance, flock size and domain of danger size in the whitefronted goose. *Wildfowl* 29:135-145.
- Lazurus, J. and Inglis, I. R. (1978) The breeding behaviour of the Pink-footed Goose: Parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62-87.
- Lebeda, C.S. and Ratti, J.T. (1983) Reproductive biology of Vancouver Canada geese on Admiralty island, Alaska. *J. Wildl. Manage.* 47:297-306.
- Lebrat, T. (1958) The Jump-flight of the Mallard, *Anas platyrhynchos* L., the Teal, *Anas crecca* L. and the Shoveler, *Spatula clypeata* L. *Ardea* 46:68-72.
- Leigh, J.H. and Mulham, W.E. (1965) Riverina Pastoral Plants. The Jacaranda Press, Brisbane.
- Leopold, F. (1951) A study of nesting wood ducks in Iowa. *Condor* 53:209-220.
- Lofts, B. and Murton, R.K. (1973) Reproduction in Birds. In "Avian Biology Vol. III". pp 1-107. Eds Farner, D.S. and King, J.R., Academic Press, New York.
- Lofts, B. and Murton, R.K. (1968) Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool.* 155:327-394.
- Lokemoen, J.T. (1973) Waterfowl production on stock-watering ponds in the northern plains. *J. Range Manage.* 26:179-184.
- Lorenz, K. (1941) Vergleichende Bewegungsstudien an Anatinen. *J. Ornithol.* 89, Erg, Bd.3:194-294.
- Lorenz, K. (1953) Comparative studies on the behaviour of Anatinae. *Avic. Mag.* 57:157-182; 58:8-77, 86-94, 172-184; 59:24-34, 80-91.
- McComb, W.C. and Noble, R.E. (1981) Nest-box and natural-cavity use in three mid-south forest habitats. *J. Wildl. Manage.* 45:93-101.
- McIlroy, J.C. (1978) The effects of forestry practices on wildlife in Australia: a review. *Aust. For.* 41:78-94.
- McKinney, F. (1965a) The comfort movements of Anatidae. *Behaviour* 25:120-220.
- McKinney, F. (1965b) Spacing and chasing in breeding ducks. *Wildfowl Trust 16th Ann. Rep.* p. 92-106.
- McKinney, F. (1970) The displays of four species of blue-winged ducks. *Living Bird* 9:29-64.
- McKinney, F. (1973) Ecoethological aspects of reproduction. In "Breeding biology of birds", pp 6-21. National Academy of Sciences, Washington, D.C.
- McKinney, F. (1975) The evolution of duck displays. In "Function and Evolution in Behaviour". Baerends, G., Beer, C. and Manning A. Eds. Clarendon Press, Oxford.
- McKinney, F. (1978) Comparative approaches to social behavior in closely related species of birds. *Advances Study Behav.* 8:1-38.
- McKinney, F., Cheng, K. M. and Bruggers, D.J. (1984) Sperm Competition in Apparently Monogamous Birds. In "Sperm Competition and the Evolution of Animal Mating Systems", pp 523-540. Ed. Smith, R.C., Academic Press, Orlando.
- McKinney, F., Derrickson, S.R. and Minneau, P. (1983) Forced copulation in waterfowl. *Behaviour* 86:250-294.
- McKinney, F., Siegfried, W.R., Ball, I.J. and Frost, P.O.H. (1978) Behavioral Specializations for River Life in the African Black Duck (*Anas sparsa* Eyton). *Z. Tierpsychol.* 48:349-400.
- McNally, J. and Falconer, O. (1953) Trapping and banding operations, Lara Lake, 1952. *Emu* 53:51-70.
- Mabbutt, J.A. (1970) Landforms. In "The Australian Environment" Ed. Leeper, G.W. fourth edition, CSIRO, Australia, Melbourne University Press.
- Mack, G.D. and Flake, L.D. (1980) Habitat relationships of waterfowl broods on South Dakota Stock ponds. *J. Wildl. Manage.* 44:695-700.
- Marriot, R.W. (1970) The food and water requirements of Cape Barren Geese (*Cereopsis novaehollandiae*). Ph.D Thesis, Monash University.

- Marriot, R.W. and Forbes, D.K. (1970) The digestion of Lucerne chaff by Cape Barren Geese, Cereopsis novaehollandiae Latham. Aust. J. Zool. 18:257-263.
- Martinson, R.K. and Hawkins, S. (1968) Lack of association among duck broodmates during migration and wintering. Auk 85:684-686.
- Martz, G.F. (1967) Effects of nesting cover removal on breeding ducks. J. Wildl. Manage. 31:236-247.
- Masters, J.R. and Milhinch, A.L. (1974) Birds of the shire of Northam about 100 km east of Perth, WA. Emu 74:228-244.
- Mayfield, H. (1961) Nesting success calculated from exposure. Wilson Bull. 73:255-261.
- Mayfield, H. (1975) Suggestion for calculating nest success. Wilson Bull. 87:456-466.
- Maynard Smith, J. (1977) Parental investment-a prospective analysis. Anim. Behav. 25:1-9.
- Mayr, E. (1976) Chairman's introduction. Proc. 16th Int. Ornith. Congr. pp173-175.
- Mead, R. (1971) A note on the use and misuse of regression models in ecology. J. Ecol. 59:215-219.
- Meier, A.H. and MacGregor, R. (1972) Temporal organisation in avian reproduction. Am. Zool. 12:257-271.
- Metcalf, N.B. (1984) The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? Anim. Behav. 32:986-993.
- Miller, H.W. and Johnson, D.H. (1978) Interpreting the results of nesting studies. J. Wildl. Manage. 42:471-476.
- Miller, K.J. (1976) Activity patterns, vocalisations, and site selection in nesting blue-winged teal. Wildfowl 27:33-43.
- Milton, K. (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by a generalist herbivore. Amer. Nat. 114:362-378.
- Minneau, P. and Cooke, F. (1979) Rape in the lesser snow goose. Behaviour 70:280-291.
- Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P. and Hall-Craggs, J. (1976) Visualising interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56:1-43.
- Morton, M.L. (1967) Diurnal feeding patterns in white-crowned Sparrows, Zonotrichia leucophrys gambelii. Condor 69:491-523.
- Moynihan, M. (1955) Some aspects of reproductive behavior in the Black-headed Gull (Larus ridibundus-L.) and related species. Behaviour Suppl. No. 4.
- Murton, R.K. and Westwood, N. J. (1977) Avian breeding cycles. Clarendon Press Oxford.
- Murton, R.K. (1971) Why do some birds feed in flocks? Ibis 113:534-536.
- Murton, R.K., Isaacson, A.J. and Westwood, N. (1966) The relationship between Wood-pigeons and their clover food supply and the mechanism of population control. J. Appl. Ecol. 3:55-96.
- Newton, I. (1977) Timing and success of breeding in tundra-nesting gessie. In "Evolutionary Ecology", pp113-126 eds Stonehouse, B. and Perrins, C., University Park Press, Baltimore, MD.
- Nichols, J.D. and Haramia, G.M. (1980) Sex-specific differences in winter distribution patterns of canvasbacks. Condor 82:406-416.
- Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. and Bent, D.H. (1975) SPSS: Statistical Package for the Social Sciences, 2nd edn. McGraw-Hill, New York.
- Nielsen, E.T. (1984) Relation of behavioural activity rhythms to the changes of day and night. Behaviour 89:147-173.
- Nix, H. (1982) Environmental determinants of biogeography and evolution in Terra Australis. In "Evolution of the Flora and Fauna of Arid Australia", pp 47-66. (Ed) Barker, W.R. and Greenslade, P.J.M. Peacock Public Relations.
- Noordwijk, A.J. van, Balen, J.H. van and Scharbo, W. (1980) Heritability of ecologically important traits in the Great Tit. Ardea 68:193-203.
- Norman, F. (1971) Movement and mortality of Wood Ducks banded in Victoria. Emu 71:57-60.
- Norman, F.I., Briggs, S. V. and Braithwaite, L.W. (1984) Some results from the 1979, 1980 and 1981 opening-day surveys of waterfowl hunters in New South Wales and Victoria. CSIRO Div. Wildl. Res. Tech. Memo. No. 20.
- Norman, F.I. and Mumford, L. (1982) Food of the chestnut teal, Anas castanea, in the Gippsland Lakes region of Victoria. Aust. Wildl. Res. 9:151-155.

- Norman, F.I., Thomson, L.W. and Hamilton, J.G. (1979) Use of habitat and diurnal activity of Pacific Black Duck, Chestnut Teal and Grey Teal at Serendip. *Emu* 79:54-62.
- North, A.J. (1913) Nests and eggs of birds found breeding in Australia and Tasmania. Vol IV Part I. Sydney, F.W. White, General Printer.
- Nudds, N.D. (1980) Theoretical considerations of diet selection by deer. *J. Wildl. Manage.* 44:735-740.
- Orians, G.H. (1969) On the evolution of mating systems in birds and mammals. *Amer. Natur.* 103:589-603.
- Owen, M. (1971) The selection of feeding site by white-fronted geese in winter. *J. Appl. Ecol.* 8:893-205.
- Owen, M. (1972) Some factors affecting food intake and selection in white-fronted geese. *J. Anim. Ecol.* 41:79-92.
- Owen, M. and Thomas, G.J. (1979) The feeding ecology and conservation of wigeon winters at Ouse Washes England. *J. Appl. Ecol.* 16:795-809.
- Palmer, R.S. (1972) Patterns of Molting. In "Avian Biology Vol. II". pp 65-101. Eds Farner, D.S. and King, J.R., Academic Press, New York.
- Parker, G.A., Baker, R.R. and Smith, V.G.F. (1972) The origin and evolution of gamete dimorphism and the male-female phenomenon. *J. Theor. Biol.* 36:529-553.
- Parr, D., Scott, M.D. and Kennedy, P.D. (1979) Autumn movements and habitat use by wood ducks in Southern Illinois. *J. Wildl. Manage.* 43:102-108.
- Partridge, L. (1978) Habitat selection. In "Behavioural Ecology: An evolutionary approach". Eds Krebs, J.R. and Davies, N.B. pp 351-376. Sunderland.
- Patterson, I.J., Young, C.M. and Tompa, F.S. (1974) The Shelduck population of Ytham estuary, Aberdeenshire. *Wildfowl* 25:16-28.
- Paulus, S.L. (1982) Gut morphology of Gadwalls in Louisiana in winter. *J. Wildl. Manage.* 46:483-490.
- Payne, R.B. (1969) Breeding seasons and reproductive physiology of Tricoloured Blackbirds and Redwinged Blackbirds. *Calif. Publ.* 90:1-117.
- Perrins, C.M. and Birkhead, T.R. (1983) Avian ecology. Blackie, Glasgow and London.
- Perry, D.R. A method of access into the crowns of emergents and canopy trees. *Biotropica* 10:155-157.
- Powell, G.V.N. (1974) Experimental analysis of the social value of flocking by starlings (*Sturnia vulgaris*) in relation to predation and foraging. *Anim. Behav.* 22:501-505.
- Pulliam, H.R. (1973) On the advantages of flocking. *J. Theor. Biol.* 38:419-422.
- Pulliam, H.R. and Millikan, G.C. (1982) Social organization in the nonreproductive season. In "Avian Biology, Vol. VI", Eds Farner, D.S., King, J.R. and Parkes, K.C., Academic Press, New York.
- Quinlan, E.E. and Baldassarre, G.A. (1984) Activity budgets of nonbreeding Green-Winged Teal on Playa Lakes in Texas. *J. Wildl. Manage.* 48:838-845.
- R.A.O.U. (1978) Recommended English names for Australian birds. *Emu* 77, Suppl. 245-307.
- Raveling, D.G. (1969a) Preflight and flight behavior of Canada Geese. *Auk* 86:671-681.
- Raveling, D.G. (1969b) Social classes of Canada Geese in winter. *J. Wildl. Manage.* 33:304-318.
- Raveling, D.G. (1979a) Traditional use of migration and winter roost sites by Canada Geese. *J. Wildl. Manage.* 43:229-235.
- Raveling, D.G. (1979b) The annual cycle of body composition of Canada geese with special reference to control of reproduction. *Auk* 96:234-252.
- Reed, A. (1975) Reproductive output of black ducks in the St. Lawrence estuary. *J. Wildl. Manage.* 39:243-255.
- Reinecke, K.J. and Owen Jr, R.B. (1980) Food use and nutrition of Black ducks nesting in Maine. *J. Wildl. Manage.* 44(3):549-558.
- Riggert, T.L. (1977) The biology of the Mountain Duck on Rottnest Island, Western Australia. *Wildl. Monogr.* No. 52.
- Ringelman, J.K. and Longcore, J.R. (1982) Survival of juvenile ducks (*Anas rubripes*) during brood rearing. *J. Wildl. Manage.* 46:622-628.
- Ringelman, J., Longcore, J.R. and Owen, R.B. (1982) Breeding habitat selection and home range of radio marked black ducks *Anas rubripes* in Maine. *Can. J. Zool.* 60:241-248.
- Rockwell, R.F. (1983) Life history studies of the Lesser Snow Goose. 1. The influence of age and time on fecundity. *Oecologia* 56:318-322.

- Rockwood, L.L. (1974) Seasonal changes in the susceptibility of Crescentia alata leaves to the flea beetle Oedynychus sp. Ecology 55:142-148.
- Romesburg, H.C. (1984) Cluster Analysis for researchers. Lifetime Learning Publications Belmont, California.
- Rowley, I. (1975) Bird Life. Collins, Sydney.
- Rowley, I. (1983) Re-mating in birds. In "Mate Choice", pp331-360. Ed Bateson, P., Cambridge University Press, Cambridge.
- Rubenstein, D.I. (1978) On predation, competition, and the advantages of group living. In "Perspectives in Ethology. Vol. 3. Social Behaviour". Ed. Bateson, P.P.G. and Klopfer, P.H. Plenum Press New York and London.
- Rudebeck, G. (1951) The choice of prey and modes of hunting of predatory birds with special reference to their selective effect II. Oikos 3:200-231.
- Rutgers, A. and Morris, K.A. (1970) Encyclopedia of aviculture 1. Blanford Press, London.
- Ruwaldt, J.J.Jr, Flake, L.D. and Gates, J.M. (1979) Waterfowl pair use of natural and man-made wetlands in South Dakota. J. Wildl. Manage. 43:375-383.
- Ryder, J.P. (1970) Clutch size evolution in Ross' goose. Wilson Bull. 82:5-13.
- Serventy, V.N., Pringle, J.D., Lindsay, T.R., Boles, W.E., Davies, S.J.J.F. and Serventy, D.L. (1985) The waterbirds of Australia. Angus and Robertson.
- Scott, M.L., Neisheim, M.C. and Young, R.J. (1976) Nutrition of the chicken. 2nd Ed. Ithaca, New York, M.L. Scott and Associates.
- Semple, A.T. (1970) Grassland improvement. London, Leonard Hill Books.
- Shapter, R.E. (1935) The chemical composition of certain pasture species at flowering and maturity. J. of Council Sci.Ind.Res. (Aust) 8:187-194.
- Shearer, L.A. (1960) Use of dugouts by breeding ducks. J. Wildl. Manage. 24:213-215.
- Short, J., Caughley, G., Grice, D. and Brown, B. (1983) The distribution and abundance of kangaroos in relation to environment in Western Australia. Aus. Wildl. Res. 10:435-451.
- Sibley, C.G. (1957) The evolution and taxonomic significance of sexual dimorphism and hybridization in birds. Condor 59:166-191.
- Sibley, R.M. (1981) Strategies of digestion and defecation. In "Physiological Ecology. An evolutionary approach to resource use". Ed. Townsend, C.R. and Calow, P. Sinauer Associates Inc.
- Siegfried, W.R. (1970) Wildfowl distribution, conservation, and research in southern Africa. Wildfowl 21:89-98.
- Siegfried, W.R. (1974a) Brood care, pair bonds and plumage in southern African Anatini. Wildfowl 25:33-40.
- Siegfried, W.R. (1974b) Time budget of behaviour among Lesser Scaups on Delta Marsh. J. Wildl. Manage. 38:708-714.
- Siegfried, W.R. (1979) Social behavior of the African comb duck. Living Bird 17:85-104.
- Siegfried, W.R. and Underhill, L.G. (1975) Flocking as anti-predator strategy in doves. Anim. Behav. 23:504-508.
- Skead, D.M. (1977) Diurnal activity budgets of Anatini during winter. Ostrich Suppl. 12:65-74.
- Sneath, P.H.A. and Sokal, R.R. (1973) Numerical Taxonomy. W.H. Freeman and Company. San Francisco.
- Sokal, R.R. and Rohlf, F.J. (1981) Biometry: The principles and practice of statistics on biological research. 2nd edition, W.H. Freeman and Co., San Francisco.
- Sokal, R.R. and Sneath, P.H.A. (1963) Principles in numerical taxonomy. W.H. Freeman and Company. San Francisco.
- Specht, R.L. (1970) Vegetation. In "The Australian Environment", Ed. Leeper, G.W. fourth edition, CSIRO, Australia, Melbourne University Press.
- Steel, R.G.D. and Torrie, J.H. (1960) Principles and procedures of statistics. McGraw-Hill Book Company, New York.
- Sugden, L.G. (1973) Feeding ecology of pintail, gadwall, American widgeon and Lesser Scaup ducklings. Can. Wildl. Serv. Rep. Ser. 24 45pp.
- Summers, R.W. (1983) The life cycle of the Upland Goose Chloephaga picta in the Falkland Islands. Ibis 125:524-544.
- Summers, R.W. (1985) The size and composition of Sheld-Geese populations and their food consumption on different vegetation types in the Falkland Islands. J. Appl. Ecol. 22:1-17

- Swanson, G.A. and Bartonek, J. (1970) Bias in food analysis of teal. *J. Wildl. Manage.* 34:739-746.
- Swanson, G.A., Krapu, G.L., Bartonek, J., Serie, J.R. and Johnson, D.H. (1974) Advantages in mathematically weighting waterfowl food habits data. *J. Wildl. Manage.* 38:302-307.
- Swanson, G.A. and Nelson, H.K. (1970) Potential influence of fish rearing programs on waterfowl breeding habitat. Pages 65-71 in E. Schneberger, ed. *A Symposium on the management of midwestern winter-kill lakes.* Amer. Fish Soc., North Central Div. 75pp.
- Taber, R.D. (1971) Criteria of sex and age. In *"Wildlife Management Techniques"*, (third edition) ed Giles, R.H. The Wildlife Society, Washington, D.C.
- Talent, L.G., Krapu, G.C. and Jarvis, R.L. (1982) Habitat use by mallard (*Anas platyrhynchos*) broods in south central North Dakota. *J. Wildl. Manage.* 46:629-635.
- Tamiasier, A. (1974) Etho-ecological studies of teal wintering in the Camargue (Rhône Delta France). *Wildfowl* 25:123-133.
- Tamiasier, A. (1976) Diurnal activities of Green-winged Teal and Pintail wintering in Louisiana. *Wildfowl* 27:19-32.
- Taylor, G.R., Friend, G.R. and Dudzinski, M.L. (1984) Influence of sampling strategy on the relationships between fauna and vegetation structure, plant lifeform and floristics. *Aus. J. Ecol.* 9:281-287.
- Thornwaite, C.E. (1931) The climate of North America according to a new classification. *Geogr. Rev.* 21:633-655.
- Timms, B.V. (1980) Farm dams. In *"An ecological basis for water resource management"*. Williams, W.D., (Ed), A.N.U. Press, Canberra.
- Todd, F.S. (1979) *Waterfowl: Ducks, Geese and Swans of the world.* Sea World Press, San Diego.
- Toft, C.A., Trauger, D.L., Murdy, H.W. (1984) Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Aythya*, Anatidae) and a proposed evolutionary explanation. *J. Anim. Ecol.* 53:75-92.
- Trivers, R.L. (1972) Parental investment and sexual selection. In *"Sexual Selection and the Descent of Man"*, Ed. Campbell, B. pp 136-177. Heinemann, London.
- Trivers, R.L. (1974) Parent-offspring conflict. *Amer. Zool.* 14:249-265.
- Verbeck, M. (1964) A time energy budget study of the Brewer Blackbird. *Condor* 66:70-74.
- Verner, J. (1965) Time budget of the male Long-billed Marsh Wren during the breeding season. *Condor* 67:125-139.
- Walters, J.R. (1982) Parental behaviour in Lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. *Evolution* 36:1030-1040.
- Ward, P. (1965) Feeding ecology of the Black-faced Cuckoo, *Cuculus quelea*, in Nigeria. *Ibis* 107:173-214.
- Ward, P. (1972) An appeal to physiologists reporting photoperiod experiments. *Ibis* 114:275.
- Weidman, U. (1956) Verhaltensstudien an der Sockente (*Anas platyrhynchos* L.) I. Das Aktionsystem. *Z. für Tierpsychol.* 13:208-271.
- Weller, M.W. (1959) Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.* 29:333-365.
- Weller, M.W. (1964a) General habits. In *"The waterfowl of the world"*. Vol IV pp15-34. Delacour, J. (Ed), Country Life, London.
- Weller, M.W. (1964b) The Reproductive cycle. In *"The waterfowl of the world"*. Vol IV pp35-79. Delacour, J. (Ed), Country Life, London.
- Weller, M.W. and Fredrickson, L.H. (1973) Avian ecology of a managed glacial marsh. *Living Bird* 12:269-291.
- Whitmore, R.C. (1979) Temporal variation in the selected habitats of a guild of grassland sparrows. *Wilson Bull.* 91:592-598.
- Wickler, W. and Seibt, U. (1983) Monogamy: an ambiguous concept. In *"Mate Choice"*. Ed Bateson, P. Cambridge University Press, Cambridge.
- Wiens, J.A. (1976) Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7 81-120.
- Wiens, J.A. (1983) Avian community ecology: an iconoclastic view. In *"Perspectives in Ornithology"* Eds. Brush, A.H. and Clark, G.A. Jr, Cambridge University Press, Cambridge.
- Williams, M. (1983) Mate choice in the Mallard. In *"Mate choice"*, Ed. Bateson, P. pp 297-309. Cambridge University Press, Cambridge.

- Winer, B.J. (1971) Statistical Principles in Experimental Design. McGraw-Hill, New York.
- Ydenberg, R.C. and Prins, H.H.T. (1981) Spring grazing and the manipulation of food quality by Barnacle geese (Branta leucopsis). J. Appl. Ecol. 18:443-454
- Yom-Tov, Y. (1980) Intraspecific nest parasitism in birds. Biol. Rev. 55:93-108.
- Zar, J.H. (1974) Biostatistical Analysis. Prentice-Hall Inc. Englewood Cliffs N.J.
- Zicus, M.C. (1981a) Flock behaviour and vulnerability to hunting of Canada geese (Branta canadensis) nesting at Crux Meadows, Wisconsin, U.S.A. J. Wildl. Manage. 45:830-841.
- Zicus, M.C. (1981b) Canada goose brood behavior and survival estimates at Crux meadows, Wisconsin. Wilson Bull. 93:207-217.

Appendix 1

Comfort behaviours performed by Maned Ducks, using the nomenclature of McKinney (1965a). Behaviours are listed according to context i) Basic situations ii) Secondary situations. (x)-recorded (-)-not recorded and (?) -not sure of either the nature or existence of the behaviour

	Basic	Secondary
<u>Shaking Movements</u>		
Body Shake	x	?
Wing Shake	x	-
Swimming Shake	?	-
Head Shake	x	x (preflight)
Head Flick	-	-
Tail Wag	x	x (postcopulatory)
Wing Flap	x	x (preflight; postcopulatory)
Foot Shake	x	-
Wing-Shuffle and Tail fan	?	?
<u>Stretching Movements</u>		
Wing-and-leg-stretch	x	-
Both-wings-stretch	x	x (preflight)
Jaw-stretch	x	-
<u>Cleaning Movements</u>		
Scratching	x	-
Foot-pecking	x	-
Bill-cleaning	x	-
Bill dip	x	-
Shoulder-rubbing	?	?
<u>Oiling:Preening</u>	x	-
<u>Nibble Preening</u>		
Occasional nibble preening	x	x (pair maintenance)
Nibbling with bill-dipping	-	-
Social preening	-	x
Washing	x	
Bathing	x	

Appendix 2

TABLE 2-A. GRAZING ACTIVITY Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE) (***=p<0.001, **=p<0.01, *=p<0.05, ns=p>0.05).

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	32394.49	12	2699.54	21.52	***
DAM	3408.55	3	1136.18	9.06	***
TIME	990.30	4	247.57	1.97	ns
DISTANCE	27133.51	5	5426.70	43.26	***
2-Way Interactions	37861.04	47	805.55	6.42	***
DAM TIME	714.57	12	59.55	0.48	ns
DAM DISTANCE	34311.12	15	2287.41	18.24	***
TIME DISTANCE	1885.88	20	94.29	0.75	ns
3-Way Interaction	6972.48	60	116.21	0.93	ns
DAM TIME DISTANCE					
Explained	77228.00	119	648.98	5.174	***
Residual	124929.80	996	125.43		
Total	202157.80	1115	181.31		

TABLE 2-B. DABBLING ACTIVITY Two-factor analysis of variance with unequal replication. Factors in the analysis were observation dam (DAM) and time of day (TIME). (***=p<0.001, **=p<0.01, *=p<0.05, ns=p>0.05)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	452.96	7	64.71	3.61	***
DAM	137.96	3	45.99	2.57	ns
TIME	288.01	4	72.00	4.02	*
2-Way Interaction	208.02	12	17.34	0.97	ns
DAM TIME					
Explained	660.97	19	34.79	1.94	*
Residual	2886.24	166	17.93		
Total	3547.21	185	19.71		

TABLE 2-C. LOADING ACTIVITY Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE) (***p<0.001, **p<0.01, *p<0.05, nasp>0.05)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	22348.68	11	2031.70	9.78	***
DAM	1892.17	3	630.72	3.04	*
TIME	4070.11	4	1017.53	4.90	***
DISTANCE	15227.93	4	3806.98	18.32	***
2-Way Interactions	30430.65	40	760.77	3.66	***
DAM TIME	1328.37	12	110.70	0.53	ns
DAM DISTANCE	22378.35	12	1864.86	8.98	***
TIME DISTANCE	5567.92	16	348.00	1.68	*
3-Way Interaction	13199.41	48	274.99	1.32	ns
DAM TIME DISTANCE					
Explained	65978.75	99	666.45	3.21	***
Residual	172462.83	830	207.79		
Total	238441.57	929	256.67		

TABLE 2-D. COMFORT ACTIVITY Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE) (***p<0.001, **p<0.01, *p<0.05, nasp>0.05)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	16681.57	12	1390.13	56.31	***
DAM	71.29	3	23.74	0.96	ns
TIME	195.34	4	48.84	1.98	ns
DISTANCE	16393.60	5	3278.72	132.80	***
2-Way Interactions	3290.69	47	70.02	2.84	***
DAM TIME	256.30	12	21.36	0.87	ns
DAM DISTANCE	1156.80	15	77.12	3.12	***
TIME DISTANCE	1750.99	20	87.55	3.55	*
3-Way Interaction	1702.71	60	28.38	1.15	ns
DAM TIME DISTANCE					
Explained	21674.97	119	182.14	7.38	***
Residual	24590.62	996	24.69		
Total	46265.59	1115	41.49		

TABLE 2-E. SOCIAL ACTIVITY Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE).
(***=p<0.001, **=p<0.01, *=p<0.05, ns=p>0.05)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects					
DAM	113.95	3	37.98	6.21	***
TIME	75.55	4	18.89	3.09	*
DISTANCE	73.39	4	18.35	3.00	*
2-Way Interactions					
DAM TIME	88.50	12	7.37	1.21	ns
DAM DISTANCE	310.94	12	25.81	4.24	***
TIME DISTANCE	103.96	16	6.50	1.06	ns
3-Way Interaction	307.42	48	6.40	1.05	ns
DAM TIME DISTANCE					
Residual	5131.19	830	6.10		

TABLE 2-F WALKING ACTIVITY. Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE)
(***=p<0.001, **=p<0.01, *=p<0.05, ns=p>0.05)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	3027.78	11	275.25	21.49	***
DAM	125.20	3	41.73	3.26	*
TIME	131.69	4	32.92	2.57	*
DISTANCE	2642.53	4	660.63	51.58	***
2-Way Interactions	837.97	40	21.49	1.68	ns
DAM TIME	248.36	12	20.70	1.62	ns
DAM DISTANCE	287.18	12	26.11	2.04	*
TIME DISTANCE	317.37	16	19.84	1.55	ns
3-Way Interaction	653.19	48	15.19	1.19	ns
DAM TIME DISTANCE					
Explained	4518.93	99	48.59	3.79	***
Residual	9913.08	830	12.81		
Total	14432.01	929	16.46		

TABLE 2-G. VIGILANT ACTIVITY. Three-factor analyses of variance with unequal replication. Factors in the analysis were observation dam (DAM), time of day (TIME) and distance from the dam (DISTANCE) (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	1053.71	12	87.81	4.82	***
DAM	120.07	3	40.02	2.20	ns
TIME	77.07	4	19.27	1.06	ns
DISTANCE	860.70	5	172.14	9.44	***
2-Way Interactions	1613.45	47	34.33	1.88	**
DAM TIME	107.50	12	8.96	0.49	ns
DAM DISTANCE	1324.96	15	88.33	4.85	*
TIME DISTANCE	153.08	20	7.65	0.42	ns
3-Way Interaction	1689.78	60	28.16	1.55	**
DAM TIME DISTANCE					
Explained	4356.94	119	36.61	2.01	***
Residual	17938.40	996	18.23		
Total	22295.34	1115	20.21		

TABLE 2-H. ON WATER ACTIVITY. Two-factor analysis of variance with unequal replication. Factors in the analysis were observation dam (DAM) and time of day (TIME). (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	2250.32	7	321.47	3.21	**
DAM	134.61	3	44.87	0.45	ns
TIME	1904.53	4	476.13	4.76	***
2-Way Interaction	759.78	12	63.32	1.58	ns
DAM TIME					
Explained	3010.09	19	158.43	1.58	ns
Residual	16823.27	166	100.14		
Total	19833.37	185	106.06		

Appendix 3

TABLE 3-A. DUCK NUMBERS Two-factor analysis of variance of duck numbers (transformed by $\log(x+1)$) in 1981 with unequal replication. Factors in the analysis were the property (PROPERTY) and the month of the year (MONTH) (ns=non significant at $p>0.05$)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	29.18	5	5.84	10.74	0.001
PROPERTY	26.40	2	13.20	24.29	0.001
MONTHS	2.78	3	0.93	1.70	ns
PROPERTY x MONTHS	6.96	6	1.16	2.13	ns
Explained	36.13	11	3.29	6.04	0.001
Residual	35.87	66	0.54		
Total	72.00	77	0.94		

TABLE 3-B. DUCK NUMBERS. Two-factor analysis of variance of duck numbers (transformed by $\log(x+1)$) in 1982 with unequal replication. Factors in the analysis were the property (PROPERTY) and the month of the year (MONTH) (ns=non significant at $p>0.05$)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	143.90	5	28.78	29.12	0.001
PROPERTY	140.71	2	70.34	71.20	0.001
MONTHS	3.19	3	1.06	1.08	ns
PROPERTY x MONTHS	14.77	6	2.46	2.49	0.03
Explained	158.66	11	14.42	14.60	0.001
Residual	97.83	99	0.99		
Total	256.49	110	2.33		

TABLE 3-C. DUCK NUMBERS Two-factor analysis of variance of duck numbers (transformed by $\log(x+1)$) in 1983 with unequal replication. Factors in the analysis were the property (PROPERTY) and the month of the year (MONTH) (ns=non significant at $p>0.05$)

<u>SOURCE OF VARIATION</u>	<u>SUM OF SQUARES</u>	<u>DF</u>	<u>MEAN SQUARE</u>	<u>F</u>	<u>SIGNIF OF F</u>
Main Effects	28.73	5	5.75	10.96	0.001
PROPERTY	27.51	2	13.76	26.24	0.001
MONTHS	1.22	3	0.41	0.78	ns
PROPERTY x MONTHS	7.11	6	1.19	2.26	0.04
Explained	35.85	11	3.26	6.22	0.001
Residual	48.75	93	0.52		
Total	84.60	104	0.81		

Appendix 4

Number of observations (n) made on each banded individual used in cluster analysis for flock structure.

<u>BAND No.</u>	<u>n</u>	<u>BAND No.</u>	<u>n</u>	<u>BAND No.</u>	<u>n</u>	<u>BAND No.</u>	<u>n</u>
F-58319	2	M- W	5	F-33645	2	M-58343	6
M-58304	11	F-58365	2	F-58370	5	M-58326	2
F-58307	3	M-58354	2	F-58325	3	F-30095	2
F- R/W	19	F-33688	2	M-58380	2	F-58280	2
M-30088	21	M-33670	2	M-58394	2	M- R/O	8
F-11620	25	F-33664	2	F-03440	4	F-11628	5
M-11619	24	F-03476	2	M-58270	3	M-11655	14
F-11616	10	F-33616	5	F-54409	3	M-13174	4
F-11683	5	M-11667	5	M-58350	4	M-13129	5
M-11676	7	M-58341	2	F-58367	4	F-11681	2
M-58348	2	M-33657	2	F-58393	6	M-58273	14
F-54485	2	F-33635	2	M-58369	6	F-58272	16
M-54437	7	M-58368	4	M-33610	2	M-33640	10
M-11675	6	M-58366	4	M-33608	6	F-33641	8
M-G/B1a	5	F-54463	3	F-33604	4		
F-58281	9	F-33620	2	F-03518	9		
F-13139	2	M-58309	2	M-58348	13		
F-11677	14	M-33605	2	F-33663	6		
F-03589	15	F-33606	4	F-33621	8		
M-58396	12	M-30098	2	M-33628	9		
F-58395	12	F-G/O/G	4	F-13189	11		
M-11699	9	F-54480	2	F-58276	3		
F-11682	11	F-13169	2	M-58275	3		
F-30096	6	M-33619	6	F-33676	3		
M-11642	4	F-G/B1u	6	M-33677	2		
F-11631	3	M-13157	4	M-33634	3		
F-58399	4	F-13158	6	M-30084	5		
M-11692	4	M-58389	6	M-13170	3		
F-54477	2	F-13160	5	F-11632	5		
F-11698	5	M-58328	6	M-13161	3		
F-11684	5	F-54470	15	M-03572	25		
F-58399	10	F-58362	17	F-11615	27		
M-33652	10	F-58360	7	M-11613	16		
F-33651	10	M-33667	5	F-11641	15		
F-13155	9	M-58398	3	F-54436	11		
M-58356	2	F-54467	2	M-13198	14		
M-30090	7	M-58390	2	F-11686	8		
M-58363	3	F-54419	2	M-13156	5		
F-58358	10	M-54448	3	F-58282	2		
M- O/O	2	F-54450	4	F-13154	8		

Appendix 5

TABLE 5-A. Schematic representation for four factor analysis of variance design. Repeated measures on Sex of the parent (1) and Behaviour (2) grouped over Age of ducklings (3) and Number of ducklings (4) in the brood. BROODS were 10 minute sample sessions for a particular brood. Behaviours were EHU-Extreme Head Up, HU-Head up, and GR-Grazing. T_{1111} is the frequency of Extreme Head up for the male of brood 1 which is aged A_1 and has N_1 (number of) ducklings

AGE OF DUCKLINGS	NO. OF DUCKLINGS	BROODS	M			F			SEX
			EHU	HU	GR	EHU	HU	GR	BEHAVIOUR
A_1	N_1	1	T_{1111}						
		4							
	N_2	5							
		15							
		16							
		19							
A_2	N_1	20							
		23							
	N_2	24							
		37							
		38							
		41							
A_3	N_1	42							
		51							
	N_2	52							
		63							
		64							
		75							
A_4	N_1	76							
		84							
	N_2	85							
		89							
		90							
		98							

TABLE 5-B. Four factor analysis of variance with repeated measures on sex of the paired Maned Duck (SEX) and the behaviours; extreme head up, head up and grazing (BEHAV). Other factors were age of ducklings (AGE) and number of ducklings in the brood (NO). Age groupings were (2-10), (11-22), (23-37), (38-68) days old. The three groups for number of ducklings in the brood were (1-5), (6-8), (9-16). The criterion measured was the amount of time spent by ducks in each behaviour over a ten minute sample. (*-p<0.05; **-p<0.01; ***-p<0.001)

BETWEEN SUBJECTS	DF	MS	F	SIGNIF
AGE	3	489015.70	3.90	*
NO	2	96357.34	0.77	ns
AGE By NO	6	152162.13	1.21	ns
SUBJ WITHIN GROUPS	86	12538.10		
WITHIN SUBJECTS				
SEX	1	108604.21	0.99	ns
AGE By SEX	3	230927.36	2.11	ns
NO By SEX	3	111871.29	1.02	ns
AGE By NO By SEX	6	8846.73	0.81	ns
SEX By SUBJ WITHIN GRPS	86	109594.10		
	DF	Error DF	F	SIGNIF
BEHAV	2	85	2.16	ns
AGE by BEHAV	6	170	3.12	**
NO by BEHAV	4	170	1.87	ns
AGE by NO by BEHAV	12	170	0.90	ns
SEX by BEHAV	2	85	21.43	***
AGE by SEX by BEHAV	6	170	3.59	**
NO by SEX by BEHAV	4	170	0.82	ns
AGE by NO by SEX by BEHAV	12	170	0.70	ns

Table 5-C. Summary analysis of variance on repeated measures data for mean duration parents performed the behaviours, performing extreme head up, head up and grazing, factor (BEHAV), within a ten minute interval. Factors are age of the ducklings (AGE)-the three groups (2-16); (17-35); (36-63) days represent the levels of this factor. Sex of the parent (SEX) and the number of ducklings in the brood (NO)- the three groups (1-5), (6-8), (9-16) represent the three levels of this factor. Data transformed by $\log(x+1)$ to overcome heterogeneity of variances

BETWEEN SUBJECTS	DF	MS	F	SIGNIF
AGE	2	0.47	0.25	ns
NO	2	2.48	1.29	ns
AGE By NO	4	0.69	0.36	ns
SUBJ WITHIN GROUPS	67	1.92		
WITHIN SUBJECTS				
SEX	1	0.93	4.98	*
AGE By SEX	2	0.05	0.28	ns
NO By SEX	2	0.18	0.94	ns
AGE By NO By SEX	4	0.05	0.25	ns
SEX By SUBJ WITHIN GRPS	67	0.19		
	DF	Error DF	F	SIGNIF
BEHAV	2	66	28.69	***
AGE by BEHAV	4	132	1.57	ns
NO by BEHAV	4	132	0.53	ns
AGE by NO by BEHAV	8	132	0.84	ns
SEX by BEHAV	2	66	8.96	***
AGE by SEX by BEHAV	4	132	1.42	ns
NO by SEX by BEHAV	4	132	2.03	ns
AGE by NO by SEX by BEHAV	8	132	0.60	ns

Number of Manned Ducks examined for body moults in 1982.

ADULTS													
FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC TOTAL													
JUVENALS.	Males	67	30	5	0	61	22	35	13	4	0	10	247
	Females	55	34	6	0	67	22	34	14	0	0	12	244
	Males	5	3	0	0	0	0	0	0	0	0	0	8
	Females	6	2	0	0	0	0	0	0	0	0	0	8
TOTAL 507													

Appendix 6

(manuscript submitted to Corella 3/1/86)

THE MOULTS AND PLUMAGES OF THE MANED DUCK
ON THE SOUTHERN TABLELANDS OF N.S.W.

R.T. Kingsford

Dept. of Zoology, University of Sydney, Sydney, N.S.W. 2006

moult and plumages of a wild population of Maned Ducks *Chenonetta jubata* were studied. Descriptions of duckling plumage development are presented so that they may be used to identify duckling age in the field. Characteristics of a distinct juvenal plumage are also described. The distribution of body moult shows a peak in moult activity at the beginning of the year and this, combined with the existence of a male "eclipse" plumage late in the year, suggests that there may be two body moults per year.

INTRODUCTION

The moults and plumages of the Maned Duck *Chenonetta jubata* have been little studied. The duckling plumage, however, has been described by Frith (1982). The purpose of the current study is to present data on the moult and plumage sequence of this species. These data were collected as part of a larger study on the behaviour and ecology of this species. Moult and plumage descriptions are based on data from 507 ducks that were captured during 1982 in the Southern Tablelands of New South Wales.

The moults and plumage sequences of waterfowl are notoriously complicated (Humphrey & Parkes 1964). Determination of the plumage sequence is often difficult because of variability among individuals. The present study presents a quantitative assessment of seasonal moult intensity and describes the patterns of plumage variation as well as the sequence of plumages. Particular importance is given to the description of a distinctive juvenal plumage (as defined by Dwight 1902).

METHODS

The study took place on the Southern Tablelands of NSW, on agricultural land, 16 km north of Taralga, during 1982 and 1983. As part of a banding programme, Maned Duck were caught in wheat baited traps (McNally & Falconer 1953) on farm dams. A total of 507 ducks was trapped and assessed for body moult, beginning in February 1982 (Table 1).

Birds were sexed and aged (adult or juvenal). Plumage state was scored, for all trapped birds by a single observer to avoid bias, following methods given by Billard & Humphrey (1972). Each bird was scored for moult in six body regions: breast, belly, flank, dorsal midline, head/neck region, and tail. Each region was scored from 0 to 3, representing no moult (0), light moult (1), moderate moult (2) and heavy moult (3) and the scores from the six regions were added, to form a total for each duck. An aggregate score of 0-2 indicated negligible moult; 3-7 light; 8-12 moderate; 13-18 heavy. A two factor analysis of variance was used to compare the effects of months by the sex of the duck. The square root transformation was used to improve normality. October scores were omitted from the analysis as no females were captured.

Two primary feathers of one wing were notched for all ducks trapped between June 1982 and December 1983. At any subsequent capture, examination of these feathers revealed if wing moult had occurred. Throughout 1983, records were also kept of any males which showed female-like plumage characteristics. Observations were also made on ducklings from 30 broods. The nomenclature follows that of Humphrey and Parkes (1959).

TABLE 2

Juvenal plumage development in ducklings of the Maned Duck.

	< 2 Weeks	2-3 Weeks	3 Weeks	4 Weeks	5 Weeks	6 Weeks
Down	Initially yellowish, characteristically dark coloured markings on the head and back	Markings less distinct, overall colour fading to light brown	on back, rump and head; as well as interspersed between feathers in other regions	head, back and rump	nape, mantle back and rump	head and back
Scapulars	-	-	evident	fully emerged	feathered	feathered
Breast and Belly	-	first feathers just emerging	some feathers fully emerged	fully feathered	feathered	feathered
Flanks	-	one or two feathers evident	some feathers fully emerged	fully feathered	feathered	feathered
Tail	-	-	first feathers appearing	quills apparent but feather not fully emerged giving characteristic "uplift" tail region	fully emerged	feathered
Flight feathers	-	-	-	first apparent	white of secondary feathers visible, primary feathers half grown	primaries almost fully grown

RESULTS

Table 2 presents plumage changes, as ducklings acquire the juvenal plumage collected from field observations. The most noticeable changes occur in the breast and belly, tail and flight feather regions. Juvenals (as defined by Eisenmann 1965) are capable of flight at fifty-seven days old (mean: 57 days $\pm$ 3 (S.E) $n=16$). Flying juvenals have still not attained full adult body size. Mean body weights for adults (756 ± 13.9 g (95% C.L.) $n=79$) and flying juvenals (707 ± 19.9 g (95% C.L.) $n=23$) captured in February were significantly different ($t_{100}=3.62$ $p<0.001$).

Juvenal plumage is similar to that of the adult female with both age categories possessing superciliary and suborbital lines of white feathers as well as similar body markings. Similarities are accentuated when a comparison is made with brown-headed males which have distinct markings. Nevertheless differences between juvenals and females do exist. Principally juvenals are a lighter colour than adult females. Juvenal breast feathers lack the brown bars that cross the top half of the female breast feather. Instead, an inverted white "Y" divides the two brown edges, as well, the feather has a more pronounced downy margin (Figure 1a). Flank feathers of females and juvenals also exhibit similar differences (Figure 1b). However, the differences between adult males and juvenals are more pronounced. The adult male breast feather is similar, in markings to the female, except darker (Figure 1a) but the adult male flank feather is quite different (Figure 1b). As well, there are some general differences. Juvenal scapulars differ by having a white edge so that spots can be seen on the juvenal's shoulder when they overlap. The scapulars of adults lack these markings. Finally, tail feathers of juvenals, unlike adults, are characteristically notched. The markings in the breast region of the juvenal produce the most noticeable difference between juvenals and females. The juvenal breast looks streaked, from a distance, in contrast to the mosaic pattern of adult breasts.

The onset of the first prebasic body moult was documented for one brood 88 days after hatching. Ducklings hatched in the spring of 1981 (September-November) had replaced the juvenal plumage with the first prebasic plumage by March 1982.

Overall adult body moult was similar between sexes (Figure 2), except that moult scores averaged higher in males ($F_{1,471}=4.52$, $p<0.05$). There was a discernable difference in the seasonal distribution of moult scores ($F_{7,471}=37.97$, $p<0.001$). More ducks were moulting in February, March and April than at any other time of the year ($p<0.001$). Very few birds were moulting in June and July. Moult scores increased again towards the latter part of the year (Figure 2).

Only four birds were consistently caught over a nine month period and these all showed heavy moult in February and March, little to no moult in June and July and light to moderate moult in August and September. Limited observations throughout 1983 showed a similar seasonal pattern.

A definite male "eclipse" plumage was found. Five of eight males banded in February-March 1983 and recaptured in December, adopted an "eclipse" plumage. This plumage is characterised by a few white feathers in superciliary and suborbital lines, a few female-like flank feathers amongst the distinctive barred ones of the male (Figure 1b) and some white feathers, characteristic of females, amongst the black feathers of the male belly and underbelly region. The brown feathers also appear lighter in the "eclipse". In one case a male was indistinguishable from a female except by cloacal examination. Males were also seen in "eclipse" while caring for their young in November and December.

Wing moult must have occurred in the latter months of 1983, since six out of the seven ducks banded in October 1983 and recaptured later in December that year, had renewed their primaries. Further, of the other twenty-five ducks captured for the first time in December 1983, all but three had flight feathers which appeared to be new. In 1982 however, the timing of wing moult was not so clear. None of six ducks banded in June 1982 and recaptured in August 1983 (over a year later), had renewed their flight feathers. Others, which had a shorter period between recaptures, also showed the same pattern.



Juvenal

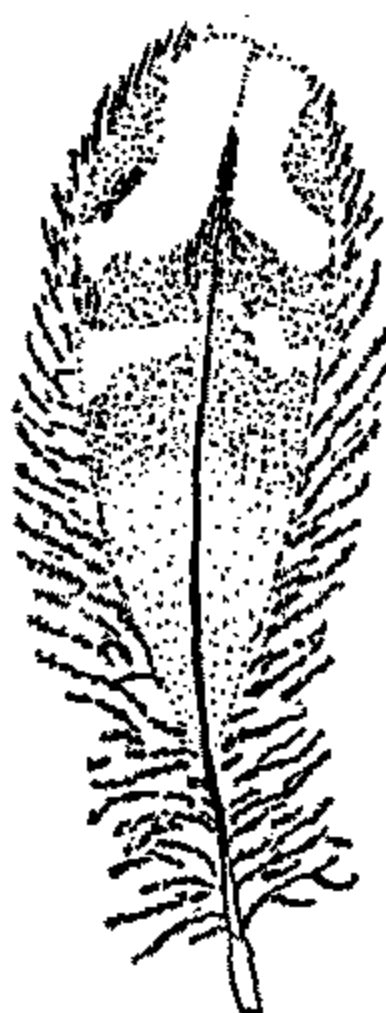


Female



Male

Figure 1a. Individual breast feathers of juvenal, adult female and adult male Maned Ducks.



Juvenal



Female



Male

Figure 1b. Individual flank feathers of juvenal, adult female and adult male Maned Ducks.

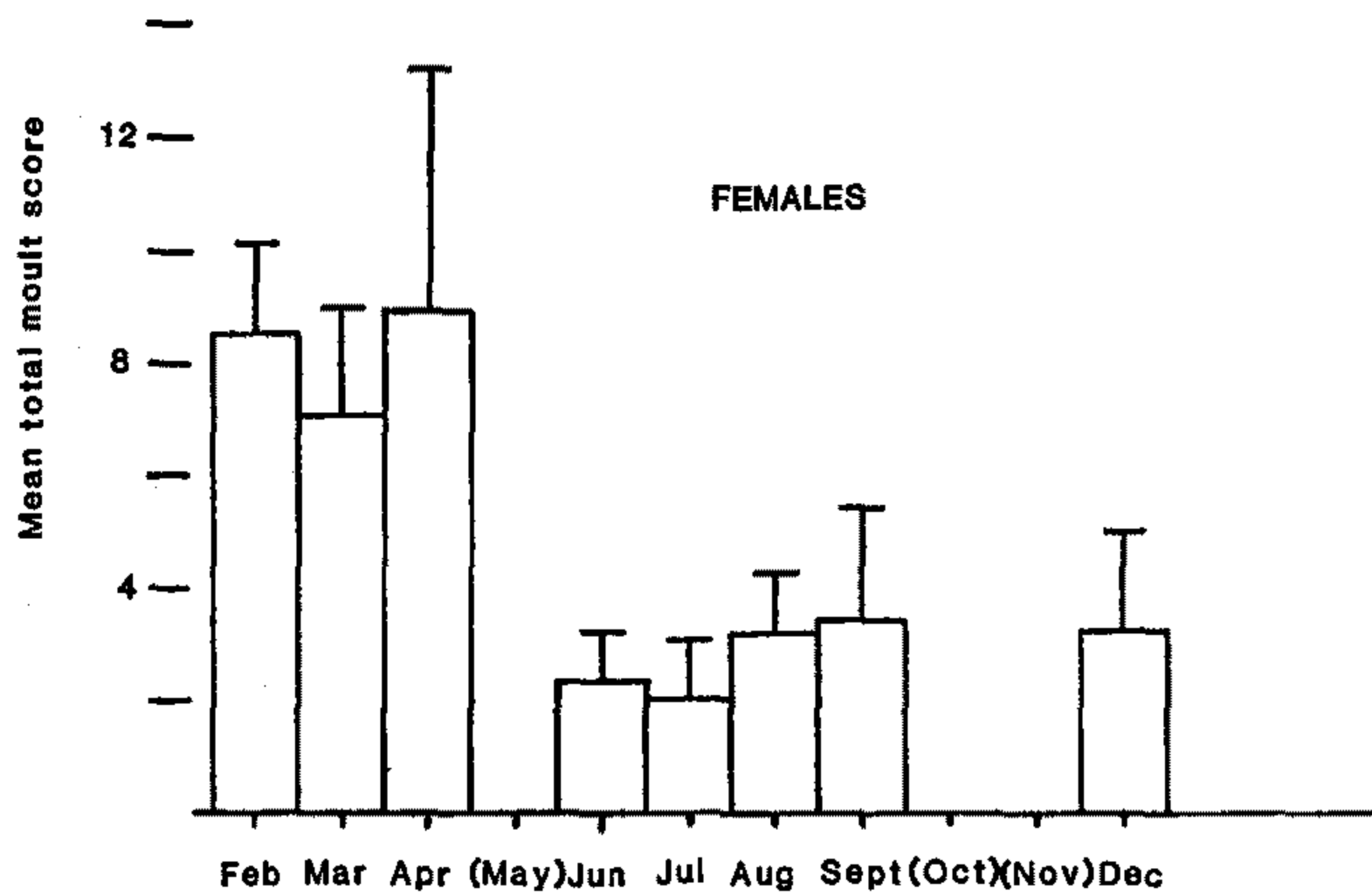
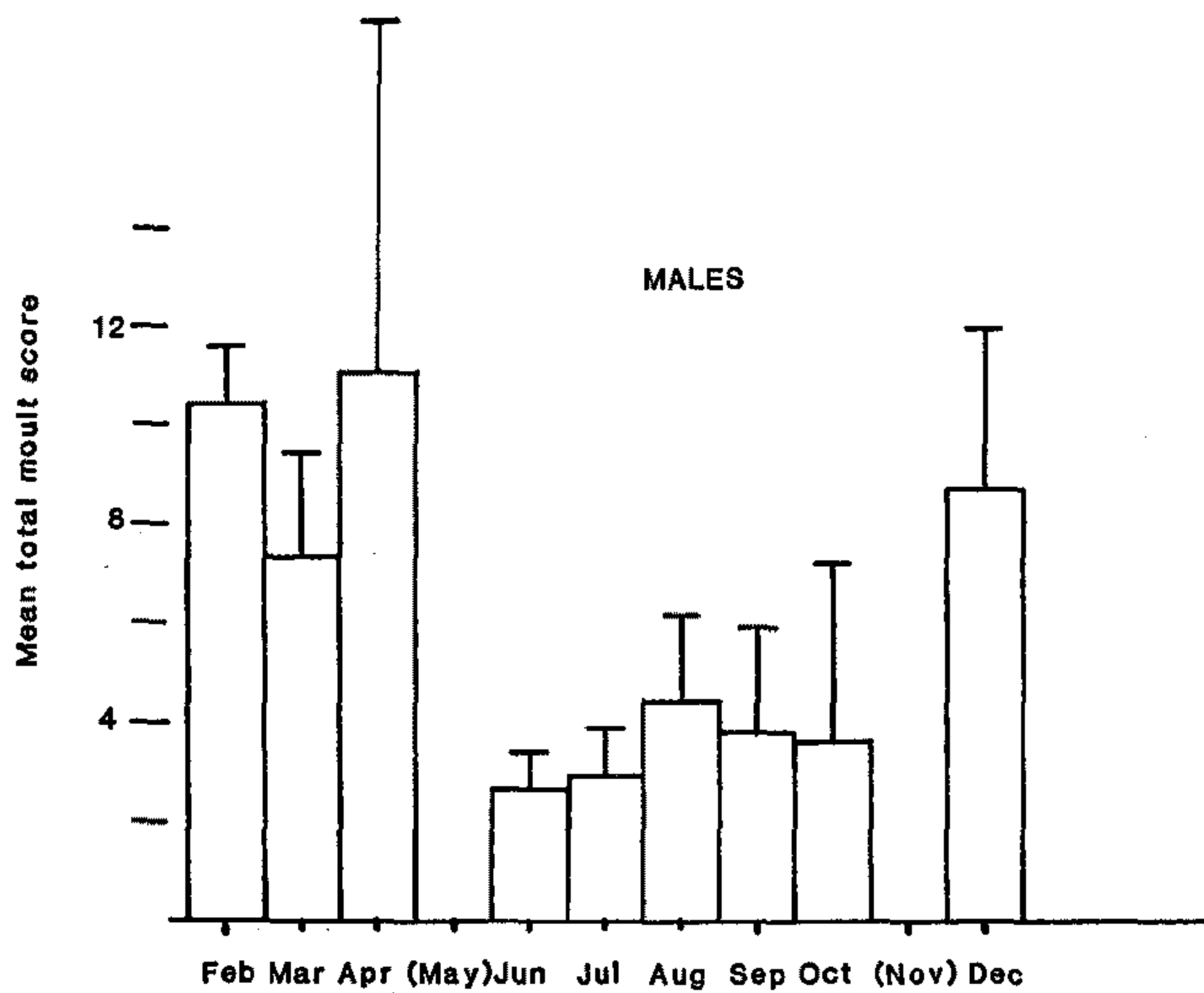


Figure 2. Monthly variation in the body moult of male and female Maned Ducks, with 95% confidence limits. No ducks examined for months in brackets.

DISCUSSION

JUVENAL PLUMAGE

Duckling development in the Maned Duck is similar to that found in the Gadwall *Anas strepera* (Oring 1968). There is early rapid growth of ventral feathering with a later development of the primary flight feathers. The description of duckling plumage development presented here should enable broods to be adequately aged in the field (Table 2). The fledging period observed is possibly inflated, as I recorded broods capable of flight only if I saw them fly. Juvenals are probably fledged before this.

The occurrence of a distinctive juvenal plumage follows the patterns found in other Anatinae (Oring 1968; Lavery 1972). There has however, been some confusion in the literature. Frith (1982) refers to juvenal Maned Duck as immatures, similar to the female but there are distinct differences, outlined here.

The first prebasic moult into basic, follows juvenal plumage. Frith (1982) found that the first appearance of male flank feathers, presumably marking the new basic, occurs three months after hatching. This study confirms the transitory nature of this plumage, as no ducks in juvenal plumage were captured later than March 1982 (Table 1). It is assumed that the juvenal wing is probably retained until the following moult into basic plumage, as in other waterfowl (Palmer 1972).

OTHER PLUMAGES

The inability to satisfactorily age ducks after the juvenal stage, obviously handicaps interpretation of subsequent moult patterns. Nevertheless, the occurrence of a distinguishable "eclipse" plumage in males provides evidence for the existence of at least two moults a year.

The "eclipse" plumage, not previously reported in Maned Duck (Johnsgard 1965), is considered to be the basic plumage in northern hemisphere waterfowl (Humphrey & Clarke 1964). Based on this assumption, interpretation of a possible annual sequence of plumages may be attempted. Males had adopted the "eclipse" plumage by December 1983. So, the increased moult activity in males in December 1982 could mark a prebasic moult into basic plumage with some ducks starting this moult earlier during August, September and October. Based on data from wing notching, ducks renewed their flight feathers some time between October and December 1983 which would coincide with moult into basic making this a complete moult as in other waterfowl. However, in 1982, some ducks did not renew their flight feathers for at least fourteen months. It is usual for waterfowl to renew their flight feathers at least once a year although some other Anatidae have been known to skip moults (Summers 1983). Climatic conditions may have affected this wing moult as the study area was experiencing a severe drought. It is interesting that no ducks were ever seen in wing moult during the study, lending further support to theories that Maned Duck wing moult on large bodies of water (Frith 1982), which were not present on the study site.

The basic plumage of Anatidae does not last long and is followed by the alternate plumage which occurs much earlier in ducks, during the autumn of the northern hemisphere (Humphrey & Clarke 1964). The high moult scores recorded during February and March may represent a prealternate moult.

This study shows that there is considerable variation in the moult state of individuals but also provides some evidence that this species conforms to the patterns found in most Anatinae; possessing a distinct juvenal plumage and two body moults a year. Future studies on the moult of known individuals are necessary in order to determine the full moult sequence.

ACKNOWLEDGEMENTS

I would like to thank Dr Peter Sale, Dr Peter Fullagar, Dr Richard Bradley, Sue Briggs, and David Giltrap for reviewing the manuscript. I would also like to thank Rosemary Kingsford for doing the feather drawings. This study was supported by funds from the University of Sydney Research Grant.

REFERENCES

- Billard, R.S. and Humphrey, P.S. (1972). Molts and plumage in the Greater Scaup. J. Wildl. Manage. 36: 765-775.
- Dwight, J., Jr. (1902). Plumage-cycles and the relation between plumages and moults. Auk 19: 248-255.
- Eisemann, E. (1965). The use of the terms "juvinal" and "juvenile". Auk 82: 105.
- Frith, H.J. (1982). Waterfowl in Australia, Sydney. Angus and Robertson.
- Johnsgard, P.A. (1965). Handbook of waterfowl behavior. Cornell University Press, Ithaca, N.Y.
- Humphrey, P.S. and Clark, G.A. (1964). The Anatomy of Waterfowl. Delacour, J. (ed) The Waterfowl of the world. Vol IV p167-232. Country Life, London.
- Humphrey, P.S. and Parkes, K.C. (1959). An approach to the study of molts and plumages. Auk 76: 1-31.
- McNally, J. and Falconer, D. (1953). Trapping and banding operations Lara Lake, 1952. Emu 53: 51-70.
- Lavery, H.J. (1972). Studies of waterfowl (Anatidae) in North Queensland. 8. Moults of the Grey Teal (*Anas gibberifrons gracilis* Buller). Qld J. Agr. Anim. Sci. 29:209-222.
- Oring, L.W. (1968). Growth, molts and plumage of the Gadwall. Auk 85: 355-380.
- Palmer, R.S. (1972). Patterns of moulting. Farner, D.S. and J.R. King (eds) Avian Biology Vol II p65-102 Academic Press, New York.
- Summers, R.W. (1983). Moults-skippping by Upland Geese *Chloephaga picta* in the Falkland Islands. Ibis 125: 262-263.