BREEDING ECOLOGY OF MANED DUCKS

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The research reported in this thesis is my own original work except where acknowledged otherwise.

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To Vi and Leckie

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Preface

This thesis is written as a series of six papers (Chapters 2-7), plus an Introduction, a Conclusion, and four Appendices. Therefore, the style changes throughout the thesis according to the editorial style of the specifically targetted journal for each chapter. Details of the methods and study areas are given in the introductory section of each chapter; and references are listed at the end of each chapter. The journals which the chapters have been published in, or submitted to, are listed in the Table of Contents, and at the beginning of each chapter.

ABSTRACT

This study investigates body condition, behaviour, and laying characteristics of maned ducks to determine their nutritional requirements for breeding, the roles of the sexes in acquiring this nutrition, and the mechanisms that regulate clutch size and laying in the species. The study was undertaken on the southern tablelands of New South Wales and the Australian Capital Territory, in southeastern Australia. Maned ducks are medium-sized (750-1050 g), grazing ducks which are common throughout much of Australia. They have sustained pair bonds and biparental care of young. Only females incubate.

Body fat levels were estimated from carcass analysis of shot ducks, and from morphological measurements of live-trapped ducks. Body weights and fat contents of non-breeding ducks were highest during spring and summer and lowest in autumn and winter. Fat levels and body weights of females increased between autumn/winter and the pre-laying period, and fat levels and body weights of males increased during spring. Female maned ducks always fed more than males, but males were more alert than females. Protein content of females did not vary with season, but

protein content of males was lower in winter. Females stored fat, but not protein, for egg production. During laying and incubation, female maned ducks expended a total of 50 g of their body fat, or ~ 70% of the fat they had stored prior to laying. They provided ~ 40% of the fat content of their clutch from this stored fat. Breeding males lost fat between incubation and brood care. Outside the breeding season, paired females were fatter than unpaired females; but fat content of paired and unpaired males did not differ during the non-breeding season. Body condition of maned ducks was related to food availability, their breeding activity, sex, and in females to pair status.

Intraspecific nest parasitism was recorded in 31% of clutches containing ≥ 5 eggs laid by maned ducks in artificial nest boxes. This is within the range for other cavity - nesting waterfowl. Parasitism was more frequent in 1987 than in 1988. Less rain fell during pre-laying and laying in 1987 (209 mm) than in the same periods in 1988 (309 mm). Rain enhances the growth of pasture grazed by maned ducks. The higher incidence of parasitism in the drier year suggests that individual ducks used nest parasitism to enhance their chance of reproductive success in the year when food was relatively scarce.

The mean size of maned duck clutches did not differ between years, but the proportion of females that bred did. Neither adding nor removing eggs affected clutch size of maned ducks; adding eggs to clutches did not increase nest desertion, nor did it reduce fat levels of females in late incubation or egg hatchability; and survival of ducklings in larger broods was similar to that in smaller ones. Fat levels of females at the end of laying were independent of the size and fat content of their clutches. Fat levels of laying females increased seasonally, but clutch sizes did not show any seasonal trend. Clutch sizes of individual females were inversely related to the mean fat content of their eggs.

During egg production and incubation, female maned ducks thus used a large amount of the energy they had stored prior to laying. Males helped females accumulate this energy (in the form of fat) by being vigilant while their mates fed. The lack of effect of clutch manipulation on measures of reproductive success, the lack of correlation between fat levels of females at the end of laying and either the size or fat content of their clutches, the negative correlation between egg fat and clutch size, and the

lack of association between brood size and duckling survival, suggest that clutch size in maned ducks is proximately, and ultimately, regulated by the size of the female's fat reserve.

Similar clutch sizes between years but different proportions of females breeding, apparent trade-offs between egg fat and clutch size, and seasonal increase in fat level of laying females, indicate that females lay when they reach the level of body fat required for their own particular clutch size. Females appear to trade the benefits and costs of breeding or not breeding, of differing clutch sizes with differing egg fat contents, and different times of laying to produce the number of eggs that corresponds to their individual ability to accumulate nutrients for egg production.

TABLE OF CONTENTS

Appendix 1. Patterns of egg-laying in prairie ducks. Auk 102: 896-897.

Appendix 2. Abdominal fat and percentage water as predictors of body fat in adult maned duck, *Chenonetta jubata*. Aust. Wildl. Res. 15: 231-234.

Appendix 3. Weight changes and reproduction in female blue-billed and musk ducks, compared with North American ruddy ducks. Wildfowl 39: 98-101.

Appendix 4. Food addition, clutch size, and the timing of laying in American coots. Condor 91: 493-494.

CHAPTER 1.

INTRODUCTION

INTRODUCTION

The nutritional requirements of the ducks, geese and swans that breed in the temperate northern hemisphere have been investigated in considerable detail, allowing the strategies of different species to be identified and classified (Owen and Reinecke 1979, Thomas 1988). By contrast, the nutritional requirement of southern breeding waterfowl are poorly known. Comprehensive understanding of the reproductive ecology of waterfowl requires a global perspective, and therefore the strategies of southern temperate and tropical ducks, geese and swans need to be understood, as well as of those of the temperate north. Because of their different environments and adaptations, research on the breeding strategies of southern and tropical waterfowl can advance understanding of the reproductive ecology of all waterfowl (Anatidae).

This thesis addresses two aspects of the ecology of a temperate Australian species of duck. Firstly, it investigates annual changes in body condition and behaviour of maned ducks *Chenonetta jubata* Latham, to determine the nutritional requirements of males and females during breeding, and how they acquire this nutrition. Secondly, it investigates the mechanisms that regulate individual clutch size and laying patterns in female maned ducks. These findings are then discussed in the contexts of the behaviour and habitat use of maned ducks, and of ducks generally.

The body condition of a bird is its level of stored nutrients, usually measured as body mass (= weight), or as fat and/or protein content. Only preliminary data are available on changes in body condition of breeding Australian waterfowl. Female black swans *Cygnus atratus* became heavier prior to breeding in a relatively predictable habitat, but did not gain weight before laying where environmental conditions were unpredictable (Braithwaite 1976, 1977). Female Pacific black ducks *Anas superciliosa*, grey teal *Anas gibberifrons*, chestnut teal *Anas castanea*, hardheads *Aythya australis*, blue-billed ducks *Oxyura australis* and musk ducks *Biziura lobata* gained variable amounts of weight between non-breeding and laying (varied from 9% in grey teal to 87% in blue-billed ducks) (Norman and Hurley 1984, Briggs 1988, 1990), but relations between these weight increases and the birds' subsequent reproductive success were not investigated. No studies have determined changes in body composition of Australian waterfowl relative to their breeding requirements, the sources of nutrients used by females for egg production, or the effects of laying, incubation, attending a breeding female, or brood caring, on body condition of either males or females.

Control of clutch size and laying patterns (timing and duration of laying, egg characteristics) in waterfowl are incompletely understood, although several hypotheses exist (Winkler and Walters 1983). Ultimate determinants of clutch size and associated laying patterns may be the ability of the female to store nutrients for egg formation, her food supply during laying, her incubation ability, parental ability to raise ducklings, predation, egg viability, and trade-offs between annual reproductive effort and residual reproductive value (Williams 1966, Lack 1967, Johnsgard 1973, Braithwaite 1977, Arnold *et al.* 1987). Proximate determinants are usually considered to be the food supply for the laying female, or her body condition at the beginning of egg production (Johnsgard 1973, Ankney and MacInnes 1978, Drent and Daan 1980, Hamann *et al.* 1986, Rockwell *et al.* 1987, Ankney and Afton 1988). Proximate and ultimate factors together can influence laying characteristics of ducks, especially through their nutritional effects on the ability of the female to form eggs (Winkler and Walters 1983, Eldridge and Krapu 1988). I specifically investigated hypotheses relating annual clutch size and laying patterns to nutrition and parental ability of individual maned ducks. The study was not long enough to measure their lifetime reproductive success, and hence I could not study trade-offs between reproductive effort and reproductive value.

Maned ducks are an ideal species for investigating relations between body condition, behaviour and breeding patterns in Australian waterfowl because; unlike many Australian ducks Maned Ducks are sexually dimorphic; they are monogamous with persistent pair bonds; they graze on land; they are abundant; they will nest in artificial nest boxes as well as in natural tree hollows; they are easy to catch and individually colour band; some ducks remain present all year in suitable habitats; and they have been the subject of a previous comprehensive study (Frith 1967, Kingsford 1986, 1989a, 1989b, Briggs unpubl. data). These characteristics mean that; individuals can be trapped for measurements of body condition at the same sites throughout the year; pair status of individual ducks can be monitored; clutches are easy to find and to manipulate; and males and females can be easily recognised from a distance.

The specific aims of the study reported in this thesis were as follows:

1. To develop equations for predicting body fat levels in live maned ducks from measurements of their body size and mass (Chapter 2).

2. To ascertain whether behaviour of maned ducks varies with sex or time of year (Chapter 3).

3. To determine effects of environment, sex, breeding activity and pair status on body condition of maned ducks, and to find out how females acquire nutrients for egg production (Chapter 4).

4. To determine whether intra-specific egg parasitism occurs in maned ducks, and to ascertain its costs and benefits to host and parasitic maned ducks (Chapter 5).

5. To determine whether clutch size of maned ducks can be altered by experimental removal or addition of eggs during laying (Chapter 6).

6. To understand how clutch size in maned ducks is regulated, particularly whether it is controlled proximately and/or ultimately by the nutritional status of the female (Chapter 7).

7. To interpret the conclusions of Chapters 2-7 in the context of our current understanding of the breeding ecology and behaviour of maned ducks, and of waterfowl generally (Chapter 8).

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CHAPTER 2.

MORPHOLOGICAL PREDICTION OF BODY CONDITION IN MANED DUCKS

Aust. Wildl. Res. 16: 605-609.

Aust. Wildl. Res., 1989, **16**, 605–9

Morphological Prediction of Body Condition in Maned Ducks

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Abstract

Best-fit regression equations for estimating body-fat levels from morphological measurements of maned ducks (*Chenonetta jubata*) were developed. The cube of [body weight/(sternum × tarsus × bill length)] plus the square of skinfold thickness was the best predictor of body fat in females ($r^2 = 0 \cdot 81$). The cube of (body weight × skinfold thickness) was the best predictor in males ($r^2 = 0 \cdot 75$). These regression equations accurately estimated fat level in all seasons except females in winter, when estimated values were significantly higher (paired t test, $P < 0 \cdot 02$) by 18% than actual levels. Body weight alone predicted protein content well in males ($r^2 = 0 \cdot 81$) and less well in females ($r^2 = 0 \cdot 61$). These equations enable long-term and relatively cheap monitoring of body condition in trapped maned ducks.

Introduction

Body condition influences both survival and fecundity in several species of waterfowl (Ankney and MacInnes 1978; Raveling 1979; Haramis *et al.* 1986). 'Condition' can imply either or both stored fat and protein but usually refers to fat. Most studies of effects of body condition on reproductive success and mortality have used dead rather than live birds. Fat and protein can be determined accurately and precisely, if laboriously, by solvent extraction and ashing or from water content of carcasses (Child and Marshall 1970; Dobush *et al.* 1985; Briggs and Thornton 1988).

Body condition can also be estimated in live birds from species-specific prediction equations containing morphological measurements. Such equations have been developed to estimate fat, and sometimes protein, in several species of waterfowl (Bailey 1979; Wishart 1979; Gauthier and Bédard 1985; Ringelman and Szymczak 1985; Hohman and Taylor 1986; Moser and Rusch 1988). Equations relating body fat, or protein, and body morphology are determined by carcass fat extraction and ashing followed by regression analysis. The resulting formulae can be used to estimate fat, and protein, levels in live birds.

The major aim of this study was to develop equations for predicting body fat from morphological measurements in live maned ducks. Relationships between body weight and protein were also determined. The study is part of a larger investigation into fat dynamics and reproductive ecology in maned ducks. Equations for predicting body fat from carcass water content and abdominal fat weight of maned ducks have been published previously (Briggs and Thornton 1988).

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Methods

In all, 130 maned ducks (78 males and 52 females) were shot on or near Lake Eucumbene (36°15'S., 148°15'E.) in southern New South Wales between March 1985 and November 1986. During the same period, a further three males and one female were collected near Canberra (35°15'S.,149°10'E.), 100 km north of Lake Eucumbene, and two males and one female were obtained from north-western New South Wales (29°45'S.,144°15'E.). Only post-juvenile ducks, distinguished by an absence of notched tail feathers (Hochbaum 1942), were used in this study. Maned ducks without notched tail feathers are usually at least 4 months old (Briggs, unpublished data).

The carcasses were weighed fresh (to nearest 10 g), checked for brood patches, frozen, thawed and measured. Sternum, tarsus and exposed culmen (bill) lengths (to nearest 0·1 mm) and skinfold thickness of right breast and middle abdomen (to nearest 0·1 mm) were measured. Skinfold thickness (i.e. subcutaneous fat) was measured with a Holtain adiposimeter as used for humans (Gauthier and Bédard 1985). The carcasses were then plucked and sheared and cut open to determine reproductive status. Females were regarded as breeding if their largest follicle was >4 mm in diameter or their oviducts were enlarged. Incubating ducks were those with brood patches. Males were regarded as breeding if their left testis was $\geqslant$18 mm long (Norman and Hurley 1984). Ducks from Lake Eucumbene were placed into seasonal and reproductive categories. Categories for males were breeding ($n = 17$), post-breeding ($n = 21$), late summer ($n = 11$), autumn ($n = 18$) and winter ($n = 8$). Categories for females were breeding ($n = 10$), incubating ($n = 4$), post-breeding ($n = 10$), late summer ($n = 11$), autumn ($n = 8$) and winter ($n = 6$). Six Lake Eucumbene ducks could not be readily placed into these categories and were excluded from the seasonal analyses.

Carcasses were dried to constant weight in a forced-air oven at 60°C. The dried carcasses were ground and four subsamples were taken: two for fat and two for ash determination. Fat was extracted for 24 h, using Soxhlet apparatus with carbon tetrachloride as the solvent (Green and Eberhard 1983). Ash was determined by combustion in a muffle furnace at 500°C for 6 h. Percentage fat and ash (both the mean of two samples) from subsample extraction were converted to total body fat and ash, using dry carcass mass (excluding feathers). Analyses were repeated if subsample percentages differed by more than 1%. Dry carcass mass minus ash minus fat was regarded as protein (Hohman 1986). Ash, and hence protein, were determined for 69 of the males and 40 of the females.

Relations between fat and predictor variables (body weight, combined breast and abdomen skinfold thickness, and product of sternum, tarsus and bill lengths) were determined by regression analysis. Males and females were analysed separately. Structural measurements (unaltered, squared, cubed, and to the fourth power) were introduced into the regression equations either alone or in various combinations (products or ratios). Variables were included in the final equations only if their partial regression coefficients were significantly different from zero ($P<0\cdot05$).

Effects of season and reproductive status on the accuracy of estimated fat levels were determined by paired t tests of estimated and true fat levels of ducks in each seasonal and reproductive category. Relationships between other variables, including body weight and protein, were investigated by simple regression and correlation analyses. Statistical tests follow Sokal and Rohlf (1981) and Zar (1984).

Results

The cube of (body weight × combined breast + abdomen skinfold thickness) explained 75% of the variation in body-fat mass in male maned ducks (Table 1). The cube of [body weight/(sternum × tarsus × bill length)] plus the square of (combined breast + abdomen skinfold thickness) provided the best prediction of female fat mass ($r^2 = 0\cdot81$) (Table 1). Skinfold thickness accounted for more variation in fat levels in both sexes ($r^2 = 0\cdot60$) than did body weight (males, $r^2 = 0\cdot32$; females, $r^2 = 0\cdot27$) (Table 1). Body weight/(sternum × tarsus × bill length) explained more variation in female fat levels ($r^2 = 0\cdot42$) than in males ($r^2 = 0\cdot27$) (Table 1).

The equations accurately estimated fat in maned ducks in all seasonal or reproductive categories (paired t tests, $P>0\cdot05$) except females in winter ($t = -3\cdot47$, $P<0\cdot02$). The average predicted fat of females collected during winter was 18% higher than their actual level (43·7 *v.* 36·9 g).

Body weight was a good predictor of protein levels in female maned ducks ($r^2 = 0\cdot61$) and was particularly so in male ducks ($r^2 = 0\cdot81$) (Table 1). Fat and protein were correlated more highly in males ($r = 0\cdot53$, $P<0\cdot001$) than in females ($r = 0\cdot24$, $P>0\cdot10$). Correlations of (sternum × tarsus × bill length) with protein and fat were stronger in females ($r = 0\cdot30$, $r = -0\cdot28$, $P<0\cdot10$) than in males ($r = 0\cdot14$, $r = -0\cdot10$, $P>0\cdot10$).

Table 1. Regressions of body fat (F) and protein (P) on combinations of body weight (BW), combined breast and abdomen skinfold thickness (SF), and sternum × tarsus × bill length (STB) of male and female maned ducks

Fat, protein and body weight are in grams; skinfold thickness and sternum, tarsus and bill lengths are in millimetres. Significance of all *F* ratios: $P<0\cdot001$

Sex	Equation	r^2	F
Male	$F=22\cdot7+11\cdot6(BW\times SF)^3/10^{11}$ [A]	0·75	$F1,81=236\cdot9$
	$F=-132\cdot9+0\cdot214BW$	0·32	$F1,81=37\cdot6$
	$F=-84\cdot7+19\cdot9SF$	0·60	$F1,81=120\cdot1$
	$F=-76\cdot5+20\cdot0(BW\times10^3/STB)$	0·27	$F1,81=29\cdot6$
	$F=8\cdot4+0\cdot157(BW\times10^3/STB)^3$	0·29	$F1,81=33\cdot9$
	$F=-7\cdot5+0\cdot091(BW/10^2)^3$	0·32	$F1,81=38\cdot4$
	$P=19\cdot8+0\cdot183BW$	0·81	$F1,67=280\cdot9$
Female	$F=-19\cdot1+105\cdot5(BW\times10^2/STB)^3+0\cdot676(SF)^2$ [A]	0·81	$F2,51=113\cdot6$
	$F=-136\cdot9+0\cdot224BW$	0·27	$F1,52=19\cdot3$
	$F=-41\cdot6+12\cdot8SF$	0·60	$F1,52=79\cdot5$
	$F=-124\cdot1+26\cdot7(BW\times10^3/STB)$	0·42	$F1,52=37\cdot1$
	$F=-6\cdot6+0\cdot196(BW\times10^3/STB)^3$	0·46	$F1,52=44\cdot2$
	$F=-8\cdot5+0\cdot099(BW/10^2)^3$	0·27	$F1,52=19\cdot6$
	$P=45\cdot6+0\cdot157BW$	0·61	$F1,38=60\cdot5$

[A] Equations of best fit.

Discussion

Measurements of body dimensions such as bone lengths are commonly used in avian condition indices to adjust body weight for structural size. Body weight is divided or reduced by a linear dimension (Chappell and Titman 1983) or by the product of three linear variables (Piersma 1984) to estimate fat. Dividing body weight by the product of three linear variables produces a linear value since body weight is volumetric and hence three-dimensional. As fat is also three-dimensional, body weight divided by the product of three linear variables should be cubed before it is used in a regression equation for fat prediction. The cube of [body weight/(sternum × tarsus × bill length)], when combined with skinfold thickness squared, provided the equation of best fit for fat estimation in female maned ducks (Table 1). However, the best-fit equation for estimating fat in males was multidimensional; division by linear structural variables did not increase the variance explained by regression.

Fat and protein are highly correlated in male maned ducks but not in females. Thus, males may gain and lose fat and protein together. Protein levels are related to structural size in females but not in males. Thus, females may gain and lose fat independently of protein levels. These intersexual differences in fat and protein dynamics are reflected in the fat-prediction equations. Division of body weight by structural size improves fat predictability in females because it corrects body weight for its protein component. Male body weight does not need correcting by protein content for fat prediction because amounts of fat and protein present are well correlated.

Scaling body weight to structural size improves prediction of fat levels in some species of waterfowl (Bailey 1979; Wishart 1979; Ringelman and Szymczak 1985; Moser and Rusch 1988) but not in others (Chappell and Titman 1983; Gauthier and Bédard 1985). Differences in relations between fat, protein and structural size may cause this interspecific variability. Sexual differences in relations between fat, protein and structural size in waterfowl have not been explored in the published literature.

Protein may vary with fat in male maned ducks but not in females because of their physiological and behavioural differences. Females store some fat for egg production and incubation, but not protein (Briggs, unpublished data). Male maned ducks are very attentive to their mates and aggressive towards other individuals, especially during the reproductive period (Kingsford 1986; Briggs, unpublished data). Female anatids generally choose their mates (Rohwer and Anderson 1988) and may be influenced by characteristics such as body size (Wishart 1983). Larger male maned ducks have more protein (muscle) for nest prospecting and for guarding their mates and young from predation and conspecific aggression than do smaller males. But being too heavy is disadvantageous for ducks of either sex because it reduces flying ability (Tome 1984 and references therein). Thus, females who do not need extra protein reserves may benefit by storing only fat, whereas males need protein for breeding activities and may benefit by acquiring both fat and protein.

The regression equations accurately predicted fat mass in male and female maned ducks in the seasonal and reproductive categories except for females in winter. The equation overestimated fat during this season. That this bias may result from a relatively high ratio of subcutaneous to abdominal fat reserves during winter is supported by the asymptotic relationship between abdominal fat and total body fat in females (Briggs and Thornton 1988). Fat females carry a higher proportion of abdominal fat than do thin ones. Hence, thin females presumably carry a relatively higher proportion of subcutaneous fat relative to total levels.

The equations developed here provide a simple, accurate, and generally reliable technique for determining fat reserves in live or dead maned ducks. Live birds can be trapped, colour-banded, measured for fat determination, released, and their subsequent behaviour monitored. Dead birds can be obtained by various methods, including hunter surveys. The estimation equations can be used to track population body condition or to study trapped and marked individuals. Maned-duck fat levels vary with food availability indexed by weather conditions, and females use some stored fat for reproduction (Briggs, unpublished data). Fat level may therefore be a good measure of individual maned-duck breeding performance, as it is in other waterfowl (Ankney and MacInnes 1978; Krapu 1981), and of population status or demographic vigour (Caughley 1977). Results of investigations into maned-duck fat levels in relation to environment and reproductive status and success will be published in later papers.

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CHAPTER 3.

SEXUAL AND ANNUAL DIFFERENCES IN ACTIVITY BUDGETS OF MANED DUCKS.

Emu 90: in press.

Sexual and Annual Differences in Activity Budgets of Maned Ducks

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Summary

Briggs, S.V. (19). Sexual and annual differences in activity budgets of Maned Ducks. *Emu* .

Maned Ducks fed for between 28% (males) and 32% (females) of the day in summer, and 56% (males) and 64% (females) in autumn. Females always fed more than males, but males were more alert. Flock size and vigilance, as well as feeding and resting times, were inversely related in both sexes. Increased daylength prior to laying allowed females to increase their feeding time. I hypothesise that females fed more than males and males were more alert than females, to allow females to maintain body condition during the year. Females in better condition prior to breeding would build up fat reserves for laying

and incubation more quickly, which would provide reproductive advantages to both pair members.

Introduction

Sexual and seasonal variability in activity patterns of waterfowl have been observed frequently (Siegfried 1974; Dwyer 1975; Asplund 1981; Fox & Madsen 1981; Kingsford 1986a; Paulus 1988). Females, especially when breeding, commonly feed more than males and males are more vigilant than females (Dwyer 1975; Asplund 1981; Kingsford 1986a; Paulus 1988). These differences have been attributed to the female's need to acquire food and store reserves for egg formation and for maintenance while incubating (Fox & Madsen 1981; Kingsford 1986a; Hohman *et al*. 1987). Sexual differences in feeding and alertness have been reported during the breeding season in Maned Ducks *Chenonetta jubata* by Kingsford (1986a). The study reported here investigated activity patterns in Maned Ducks both during the breeding season and outside it. It formed part of an investigation into factors regulating reproductive success in the species. The specific aims of this study were to answer the following questions. 1. Do activity budgets of the sexes differ? 2. Do activity budgets of each sex vary with time of year? 3. Does female feeding time increase before or during egg production?

The Maned Duck is an Australian duck that grazes like a goose. It has persistent pair bonds, biparental care of young; females store fat for egg production, and some individuals (approximately 50% in my general study area) are sedentary (Kingsford 1986a; Briggs unpubl.). The diet of Maned Ducks on the southern tablelands of New South Wales consists mostly of pasture grasses and legumes (Kingsford 1989).

Methods

The study was undertaken in parkland adjacent to Gungahlin Cemetery, near Canberra (lat. 35°15'S; long 149°10'E) in southeastern Australia. Temperatures in the study area varied from an average of 28°C maximum in January and February 1987 to 0°C minimum in June and July 1986. The habitat was exotic grasses and legumes, with scattered trees, and an artificial lake. The pasture was mown and watered. Wild Maned Ducks feed and breed in such environments readily. Most egg laying in the region of the study site occurred in August and September and most incubation was in September and October (Briggs unpubl.). Broods of Maned Ducks were present between October and January.

Activity patterns were determined from a total of 125 hours of diurnal behavioural recording. Maned Ducks appear to feed mainly during the day, although they may graze at night sometimes, especially under floodlights or moonlight (Kingsford 1986a; pers. obs.). Activity was recorded during five sessions each of one hour, on one or two consecutive days every two weeks between March 1986 and 1987. Each of the hourly sessions was randomly chosen from within five, three hourly periods between 0500 h and 2000 h. Data from these five sampling sessions of one hour's duration were averaged to give one set of daily activity figures, every two weeks.

Activity was recorded by instantaneous sampling (Altmann 1974). The behaviour of one male and one female duck, chosen arbitrarily from the flock regardless of pair status, was recorded every 20 seconds during the observation hour. Behavioural categories were feeding (grazing, upending, surface picking, dabbling), resting (awake or asleep), locomotion (walking, running, swimming), comfort (preening), social (courtship, display, aggression by or to individual), vigilant (alert), and other (drinking, bathing, ingesting grit, flying). Most (>99%) feeding behaviour was grazing. Feeding included the time between pecks while walking with head down but not the time spent walking between food patches. Only flying within the site was recorded, not flying between sites. Hence, flying time was considerably underestimated. Female Maned Ducks are away from their nests for less than four hours per day during incubation (pers. obs.; Davey and Fullagar pers. comm.). Hours of behaviour of incubating females were consequently overestimated, because time spent incubating was not recorded.

Only behaviour of post-juvenile birds (Eisenmann 1965; Kingsford 1986b) was studied. Pair status was recorded between August and November (the main breeding period). Paired ducks were either known to be so from their colour bands, or were males and females in close proximity without mutual aggression, and away from other ducks. The number of ducks present from August to November was insufficient to separate the results for paired and unpaired birds. Data from birds in flocks, paired birds, solitary birds, and birds of uncertain status, were therefore combined. From June to November, which includes the pre-breeding (June) as well as the breeding season (July-November), is referred to as winter/spring. December to May is referred to as summer/autumn. Rainfall data were obtained from the Canberra office of the Bureau of Meterology, and temperatures were obtained from the CSIRO Ginninderra Experiment Station. Statistical tests follow Sokal and Rohlf (1981) and Zar (1984). Precision figures are standard errors.

Results

The average daily number of ducks at the study site ranged from 280 in autumn to 16 in late winter. The mean number present during winter/spring was 45 ± 11 ($\underline{n}$=12) and during summer/autumn was 171 ± 22 (n=12). Between 64% and 79% of females, and 56% and 69% of males were obviously paired between August and November. Less than 6% of females and 15% of males were obviously unpaired during this period. Percent feeding times of males and females were not correlated with the numbers of ducks at the study site, but percent vigilance times were (Spearman rank correlations, females, $r = -0.57$, $n = 25$; males, $r = -0.61$, $n = 25$, both $P < 0.01$). Disturbance from humans, dogs and unknown causes was greater during summer/autumn than during winter/spring. Ducks were disturbed sufficiently to fly or run back to the pond an average of 4.8 ± 0.4 (n=12) times per five hours between December and May, compared with 2.7 ± 0.4 (n=12) times per five hours between June and November.

The percentage of time that males and females spent feeding increased between late summer (both sexes 34%, 4.3h) and autumn (females, 64%, 6.8h; males, 55%, 5.8h) (Figures 1, 2). Percent feeding time in males then fell slowly during winter, followed by a large fall in late spring and early summer 1986/87 (Figure 1). Female feeding activity followed a similar trend to males, but with a pronounced autumn peak (Figure 2). Proportions of the day spent feeding rose again in both sexes in summer 1987. Percent feeding times in males and females were inversely correlated with daylength (Table 1). The number of hours that Maned Ducks fed varied similarly to percentage times, with smaller increases in autumn, increases rather than decreases in late winter and early spring, and smaller decreases in late spring because of daylength changes. Males and females increased their feeding time during winter and early spring by almost 2 h as a result of increasing daylength. However, these increases in feeding time (females 1.8 h; males 1.7 h between June and October) were less than the daylength increase during the same interval (3.7 h). The sexes differed in that the hours that females spent feeding increased steadily between June and October, whereas feeding by males increased initially and then decreased as vigilance increased. Females always fed for a greater proportion of the day than males (Wilcoxon paired - sample test, $\underline{T} = 0$, $\underline{n}=25$, $\underline{P} < 0.001$).

Insert Figures 1, 2, Table 1 hereabouts

Percent feeding time was negatively related to resting in both sexes, and to comfort time in females (Figures 1,2, Table 2). Percent resting was positively correlated with daylength in both sexes (Table 1), and resting time was highest during late spring and early summer (Figures 1, 2). Males were more vigilant than females (Wilcoxon paired - sample test, $\underline{T}=5$, $\underline{n}=25$, $\underline{P} < 0.001$). Males, and to a lesser extent females, were more alert during winter/spring than during summer/autumn (Wilcoxon two - sample test, females, $\underline{U}=110.5$, $\underline{n}=12$; males, $\underline{U}=112.5$, $\underline{n}=12$, both $\underline{P} < 0.05$). Male vigilance increased during winter/spring by over 1 h, whereas female vigilance rose by less than 0.5 h. Females walked and swam less during winter/spring than during summer/autumn (Wilcoxon two-sample test, $\underline{U}=112.0$, $\underline{n}=12$, $\underline{P}< 0.05$) (Table 3). The difference between the two seasons was not significant in males. Females spent more time in social encounters than did males (Wilcoxon paired-sample test, $\underline{T}=65.5$, $\underline{n}=12$, $\underline{P}< 0.01$) (Table 3).

Insert Tables 2, 3 hereabouts

Discussion

Annual patterns

Percent grazing time decreased with warmer and wetter weather in spring (1986 winter/spring rainfall 409 mm), and increased during dry weather in late summer and autumn (1986/87 summer/autumn rainfall 231 mm), and with cold in winter. Total grazing time decreased in late spring. Conversely, resting time was highest during late spring and early summer, and lowest in autumn and winter. Waterfowl often reduce their feeding time with higher food quality, and increase it when food quality declines (Owen 1980; Paulus 1988). Maned Ducks digest very little cellulose and rely largely on starch and sugars for their carbohydrate intake (Johns 1986). Thus, the quality and quantity of their food would have been highest in spring, and lowest in autumn and winter. Pasture growth largely depends on rainfall and temperature (Donald 1970;

Fitzpatrick & Nix 1970; Spedding 1971), and pasture quality is affected by the stage of the growing season. Nutrients (protein and carbohydrates) are generally concentrated in newly emerged shoots of grasses and other herbs, and foraging conditions for waterfowl are usually best early rather than late in the growing season (Owen 1980; Thomas & Prevett 1982; Sedinger 1984; Prevett *et al.* 1985; Sedinger & Raveling 1986).

Females did not increase their percent feeding time prior to and during laying. The duration of their feeding time increased, but was less than the increase in daylength during the same period. Therefore, female Maned Ducks apparently acquired the protein and fat used in egg production from increased pasture quality and quanity in spring, as well as from the longer days in which to graze, rather than from feeding for a greater proportion of the day. Pre-laying and laying females may also have conserved energy by flying and walking less.

An inverse relation between flock size and vigilance has been found in other birds, including other waterfowl (Caraco 1979; Lendrem 1983a; Westcott and Cockburn 1988). Although the correlation between vigilance and group size can be confounded by other factors such as food availability (Elgar 1989), more individuals can watch for predators in larger flocks. Hence, individual vigilance is reduced and feeding time increases. Flocking during dry periods when food is scarce thus may benefit individual Maned Ducks by allowing them to increase their feeding time. Increased vigilance by both sexes during breeding may be caused partly by reduced flock size (often a pair). The seasonal difference in alertness was not caused by external disturbance. Disturbances sufficient to flush the ducks were more common during summer/autumn when vigilance was lower, than in winter/spring when vigilance was higher.

Sexual differences

Female Maned Ducks grazed more than males, and males were more alert. Females spent more time in obvious social behaviour, mostly inciting (Johnsgard 1965) than males. Both sexes allocated similar amounts of time to resting, locomotion and comfort behaviour. Various hypotheses have been advanced to account for the sexual differences in vigilance and feeding that have been found in breeding waterfowl (Asplund 1981; Lendrem 1983b; Hohman *et al*. 1987; Kingsford 1986a; Lessells 1987; Mayhew 1987; Rohwer & Anderson 1988). These differences also occur in non-breeding waterfowl, although less frequently (Paulus 1988).

Kingsford (1986a) attributed sexual differences in feeding and alertness of breeding Maned Ducks to males watching for predators, while females fed to acquire and maintain nutrient reserves for breeding. Kingsford's explanation can be modified to account for sexual differences in feeding and alert behaviour between non-breeding, as well as between breeding Maned Ducks. The species is monogamous and most pair members stay together semi-permanently or permanently (Kingsford 1986a; Briggs unpubl. data). I therefore hypothesise that females always fed more than males, and males were more alert than females, to allow females to maintain body condition during the year. Weather, and consequently food availability for Maned Ducks, can be unpredictable prior to and during breeding. Females store as fat some of the energy they need for egg production and incubation (Briggs unpubl.). Maintaining fat reserves outside the reproductive period would allow female ducks to acquire more nutrients for egg formation and incubation, more rapidly prior to laying. Rohwer and Anderson (1988) have proposed that seasonally monogamous ducks pair some time prior to laying for a similar reason. Female waterfowl who commence breeding in better condition are more likely to lay a larger clutch and successfully hatch their eggs than those in poorer condition (Ankney & MacInnes 1978; Krapu 1981; Aldrich & Raveling 1983; Ankney & Afton 1988; Briggs unpubl.). Thus, males who watch for predators to allow their mates greater feeding time throughout the year would gain a reproductive advantage.

The hypothesis could be tested in Maned Ducks firstly, by comparing feeding and vigilance times of known paired and unpaired ducks in the same flock, outside the breeding season. Greater allocation of time to vigilance and feeding by paired males and females respectively compared with unpaired ducks, would support the hypothesis. Such a test would require a large, sedentary population of colour banded ducks. The hypothesis could be tested secondly, by comparing fat levels of paired and unpaired females outside the breeding season. This test would require trapping, and measuring fat reserves of females of known pair status.

The particularly high levels of male vigilance during egg laying in late August, September and October may also have reduced the chance of insemination of paired females by extrapair males. Goodburn (1984) showed that male Mallards *Anas playtyrhynchos* guarded their female partners during the time they could be fertilised. Extrapair copulations are common in several species of waterfowl (McKinney *et al*. 1983) and have been observed in Maned Ducks (Kingsford 1986a; Briggs unpubl.).

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TABLE 1 Spearman rank correlations between daylength and proportions of time spent in each activity. _n_ = 25.

Activity	Females	Males
Feeding	-0.73**	-0.63**
Resting	+0.77**	+0.75**
Locomotion	+0.31	+0.35
Comfort	+0.12	+0.02
Social	-0.54*	-0.51*
Vigilance	-0.20	-0.14

** _P_<0.001

* _P_<0.01

TABLE 2 Spearman rank correlations between proportions of time Maned Duck spent feeding and proportions in other activities during the year. _n_ = 25.

Activity	Females	Males
Resting	-0.87**	-0.66**
Locomotion	-0.21	-0.23
Comfort	-0.50*	-0.33
Social	+0.11	+0.05
Vigilance	+0.25	-0.07

** _P_<0.001

* _P_<0.01

Captions to figures

Figure 1. Annual diurnal activities of male Maned Ducks expressed as percentage of day.

Figure 2. Annual diurnal activities of female Maned Ducks expressed as percentage of day.

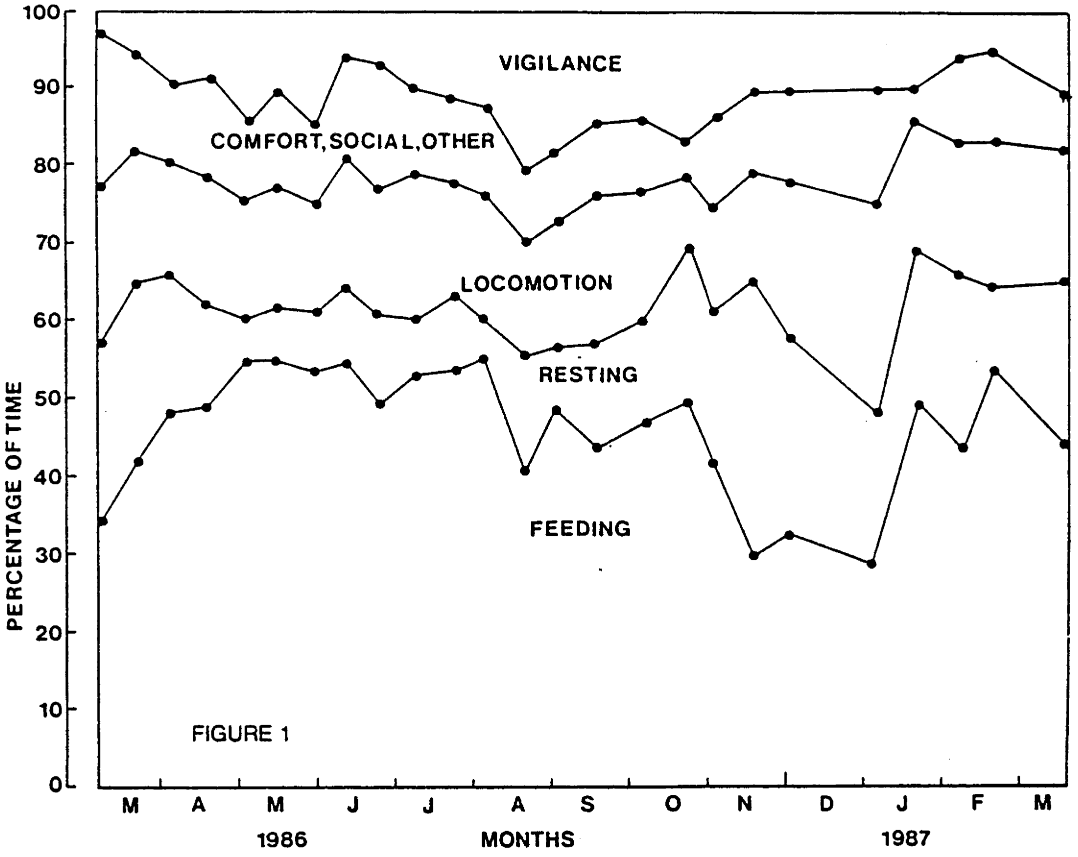

FIGURE 1

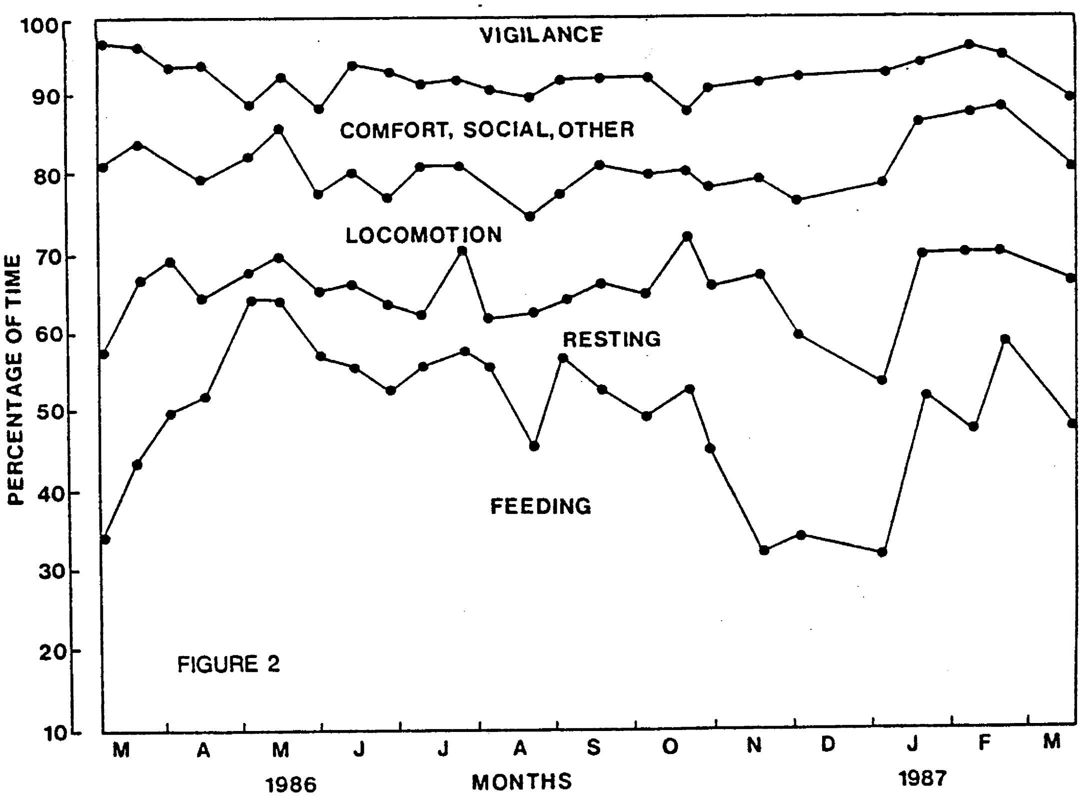

FIGURE 2

CHAPTER 4.

EFFECTS OF BREEDING AND ENVIRONMENT ON BODY CONDITION OF MANED DUCKS *CHENONETTA JUBATA*

Submitted to Emu.

Effects of Breeding and Environment on Body Condition of Maned Ducks *Chenonetta jubata*

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Summary

Briggs, S. V. (19). Effects of breeding and environment on body condition of Maned Ducks *Chenonetta jubata*. *Emu*

Body weights and fat levels of non-breeding Maned Ducks on the southern tablelands of New South Wales and in the Australian Capital Territory were highest during spring and summer and lowest during autumn and winter. Fat levels and body weights of female ducks increased between autumn/winter and pre-laying, and they increased during spring in males. Protein levels of females did not vary with season, but protein levels in males were significantly ($\underline{P} < 0.05$) lower in winter. Prior to laying, females stored fat but not protein for egg production. They used 44% of their pre-laying fat while laying, and contributed 42% of the fat required to produce their clutch from stored reserves. During incubation they used a further 47% of the body fat present at the beginning of incubation. During laying and incubation, Maned Duck females expended a total of 50 g of their body fat, or ~ 70% of their average fat content prior to laying. Body condition of Maned Ducks was related to food availability, breeding activity, sex, and pair status in females.

Introduction

The body condition of an animal is its level of stored nutrients (Reinecke et al. 1988). Body condition can be measured crudely as body mass (= weight), or more accurately as fat and/or protein content. Body mass alone is usually an inaccurate index of condition, particularly of the fat component, because an animal's mass or weight depends on its structural size as well as on its lipid and protein stores (Piersma 1984; Ringelman & Szymczak 1985; Moser & Rusch 1988). Direct measures of fat and protein are good indicators of condition (Sears 1988), but depend on carcass analysis. They are thus useless in studies of live animals. Fortunately, indirect measures of fat levels (and of protein levels if necessary) in waterbirds can be obtained by scaling body weights of live individuals by indices of their structural size (Bailey 1979; Chappell & Titman 1983; Piersma 1984; Briggs 1989).

Waterfowl (Anatidae) store nutrients for breeding, and for maintenance when food intake is low. Depending on the environment and species, female waterfowl store all, some, or very little of the energy and protein they require for egg production, and for maintenance during incubation (Owen & Reinecke 1979; Tome 1984; Halse & Dobbs 1985; Mainguy & Thomas 1985; Brown & Frederickson 1987; Ankney & Afton 1988; Harvey et al. 1989). Males may also store nutrients for use during reproduction (Raveling 1979a; Krapu 1981;

Hohman 1986). Outside the breeding season, shortage of food causes waterfowl to lose condition (Wishart 1979; Joyner et al. 1984), and nutrients may be stored to buffer against this loss (Reinecke et al. 1982).

Most previous studies of condition in waterfowl have been done in Europe or north America, where ducks and geese generally migrate to nest. Many of these studies provide a limited perspective on condition in waterfowl because they are necessarily restricted to their breeding or wintering periods (see Hohman et al, 1988). Winter is the usual time of food shortage in the cool temperate regions of the northern hemisphere, but dry weather can also reduce food supplies for waterfowl (Davies & Cooke 1983; Miller 1986). Dry weather is particularly likely to reduce food for waterbirds in the parts of Australia that have a warm climate and erratic rainfall. Unlike their northern temperate counterparts, Australian waterfowl do not usually migrate to nest, and most occupy a range of climatic regions (Frith 1967). Thus annual studies are possible using Australian species, giving a wider perspective on body condition of waterfowl than is often possible elsewhere.

Among Australian waterfowl, Maned Ducks are a particularly good species for condition studies because they are easy to capture, can be readily identified from individually coloured leg bands, some individuals remain in the same location all year, and the species occurs in a variety of habitats (Blakers et al. 1984; Kingsford 1986; Briggs unpubl.). Maned Ducks are largely terrestrial grazers, feeding on pasture grasses and legumes (Kingsford 1989a), and they nest in tree cavities (Frith 1967). As in most other ducks , only females incubate. Further information on their ecology can be found in Frith (1967), Kingsford (1986, 1989a, b), Dawson et al. (1989), Briggs (1990a) and Lawler (1990).

This study was designed to answer the following questions. 1) Do body, fat and protein masses of Maned Ducks vary with food availability? 2) How do reproductive activities (laying, incubating, attending a laying or incubating female, brood caring) affect body, fat and protein masses of Maned Ducks? 3) How do female Maned Ducks acquire nutrients for egg production? This paper deals with body condition in breeding and non-breeding Maned Ducks of both sexes. It investigates effects of environment, sex, breeding activity and pair status on mean measurements of body condition. A later paper will address the effects of body condition in individual Maned Duck females on their laying patterns and clutch sizes.

Methods

The study was done in two areas of the southern tablelands of New South Wales, including the enclosed Australian Capital Territory. Maned Ducks (n = 1059) were trapped within 60 km of Canberra (lat. 35° 15'S; long. 149° 10'E), and also shot (n = 163) on and near Lake Eucumbene (lat. 36° 15'S; long. 148° 15'E). The main trapping sites were two suburban parklands which were watered during dry periods and periodically mown, and three rural properties which were grazed by domestic livestock. Ducks were captured in traps baited with grain (McNally & Falconer 1953) and set near ponds or dams.
Trapped ducks were aged from their tail feathers (Kingsford 1988) as adults ($\geq$ 4 months post-hatching (Briggs unpubl.) or juveniles, and uniquely colour and numerically banded (Australian Bird Banding Scheme Authority No. 1034). Only data from adult ducks were used in this study.

Trapped females were weighed (to nearest 10g) and measured (sternum, tarsus and exposed culmen lengths to nearest 0.1 g), and the thickness of their subcutaneous fat (abdomen and right breast to nearest 0.1g) was determined with an adiposimeter (Gauthier & Bédard 1985; Briggs 1989). Twenty six females caught while laying or incubating in nest boxes were weighed and measured in the same way. The fat content (dry weight) of individual Maned Ducks was estimated from sex-specific regression equations, based on their body weight, subcutaneous fat thickness, and morphological measurements (Briggs 1989).

Ducks were trapped every month between July 1985 and February 1988, and in July 1988. Breeding females were trapped in nest boxes in 1986, 1987 and 1988.

All captured females were checked for signs of breeding. Females with both a swollen abdomen and a pelvic bone spread > 15 mm were regarded as laying, as were all females with pelvic spreads > 20 mm. Females with a brood patch were regarded as incubating. Females trapped ≤ 2 weeks prior to laying, backdated from subsequent recapture or resighting, were regarded as pre-laying. Laying females could be distinguished by eye using binoculars, from their swollen abdomens. Trapped males were also weighed, and the thickness of their breast and abdominal subcutaneous fat layer determined as for females. Trapped males that were paired with known breeding females were assigned to the reproductive category of their mate (pre-laying, laying, incubating). Paired females and males were ascertained from their sustained close proximity to each other, and their repelling of other ducks (Briggs 1990a), and they were subsequently recognised from their colour bands.

Body weights and fat levels of the trapped males and females were first separated by sex, and then according to whether the ducks were known to be breeding (laying, incubating, brood caring), or not known to be breeding (including pre-layers). The data from the non-breeding ducks (including pre-layers) were then combined by month of capture. Mean monthly weights and fat levels were then calculated. Data from the breeding ducks were combined according to the year they were trapped and whether they were laying, incubating or brood caring. Not all sites were trapped every month, but monthly fat levels of non-breeding male and female Maned Ducks did not differ significantly between sites (ANOVAS, all months, $\underline{P} > 0.05$). Also, some marked individuals moved between the study sites.

Mean monthly fat levels of non-breeding males and females were separately regressed against an index combining pasture growth with available feeding time (mean maximum monthly temperature x rainfall in the two previous months x mid-monthly daylength) (= food availability) to investigate effects of food availability on duck condition. Temperature and rainfall together largely determine pasture growth in the Canberra area (Fitzpatrick and Nix 1970), and Maned Ducks appear to feed mainly during the day (Kingsford 1986; Briggs pers. obs.). The number of degrees that mean monthly maximum temperatures exceeded 25° C were subtracted from 25° (e.g. 28° = 22°), prior to incorporating temperatures above 25° C in the index. I did this to account for limitations to the growth of temperate pasture plants at high temperatures (see Fitzpatrick and Nix 1970; Nix 1982). Rainfall and temperature infomation were obtained from the

Bureau of Meteorology, and the CSIRO Ginninderra Experiment Station. Fat data from recaptured ducks were included in the plotted means (Figures 1, 2), but they were excluded from the monthly mean fat levels used in the regression analyses. I did this to ensure that the monthly data points were independent of each other.

The mean fat level of females caught at the end of laying/beginning of incubation (distinguished by their swollen abdomen, wide pelvic spread and brood patch) was subtracted from the mean fat level of females caught at the beginning of laying (≤ 1 week prior to laying, determined by back dating from subsequent recapture or resighting), to determine the average fat loss during laying. Based on the number of light and dark rings in their yolks (Romanoff & Romanoff 1949), eggs of Maned Ducks take approximately seven days to develop in the female (Briggs unpubl.). The average fat loss during laying was then divided by 10.7, which was the average clutch size in the study area between 1986 and 1988 (Briggs unpubl.), to determine the fat loss per egg laid. Fat loss of females during incubation was calculated by regressing the fat content of individual females on the their stage of incubation in days. All the females trapped in nest boxes were caught at known stages of incubation; and the stages of incubation of some ducks caught in traps were determined by backdating from later sightings with ducklings. Fat levels of females caught at the end of laying/beginning of incubation were entered at day zero in the regression analysis of fat loss during incubation. Females recaptured in the same year during laying or incubation were excluded from the regression analyses of fat losses during incubation, as were females known to be renesting.

Maned Ducks were shot between March 1985 and November 1986. Fat and protein (= ash-free lean dry mass) content of these ducks were determined by solvent extraction and by ashing the dried carcasses (Briggs 1989). Fat, and protein (which includes carcass carbohydrate (≤ 2% of wet weight in Wood Ducks <u>Aix sponsa</u> (Drobney 1982) and ash-free gut contents), were expressed as dry weights. Data from these ducks were grouped into seasonal and breeding categories according to the season in which the ducks were shot, and the state of their reproductive organs (Briggs 1989). Data from trapped ducks and shot ducks were analysed separately because of climatic differences between Canberra (altitude 600 m) and Lake Eucumbene (altitude 1200 m), and because fat levels of the ducks from the two sites were determined differently. All means are presented as ± <u>s</u>.<u>e</u>.

Results

The number of females trapped each month varied from 2-38 (2-50 including recaptures); the number of males varied from 6-54 (7-62 including recaptures). No Maned Ducks in wing moult were shot or trapped. The months when laying, incubating, and brood caring Maned Ducks were captured are shown in Table 1. Fat levels and body weights of both sexes varied seasonally and with reproductive activity, but females varied more than males (Figures 1, 2, Table 2). Both sexes were fattest and heaviest during spring and summer. Females were thinnest and lightest in autumn, and males were thinnest and lightest in autumn and winter. Females became fatter and heavier during winter as well as during spring, and therefore they gained condition prior to breeding earlier than males did. Fat levels and weights of males remained low during winter, and increased in spring. The index of pasture growth and time available for feeding (= food availability) explained significant proportions of variance in the fat levels of males (r^2 = 0.34, $F_{1,32}$ = 16.2, $P < 0.001$) and of females (r^2 = 0.27, $F_{1,32}$ = 11.6, $P < 0.01$).

(Insert Tables 1, 2, Figures 1, 2 hereabouts)

Female weight increased by 10% (from a mean annual low value of 780 g to 853 g), and female fat content increased by 70% (from a mean annual low of 37 g to 63 g), between autumn and the pre-laying period (Figures 1, 2, Table 2). Female fat levels increased by 95% (37 g to 72 ± 7.2 g (n = 8)) from their mean annual low to the beginning of laying. Males gained 3% (from 792 g to 817 g) in weight, and 34% (38 g to 51 g) in fat between winter and pre-laying (Figures 1, 2, Table 2). Incubating females, males with incubating mates, and both sexes with broods, had less fat than non-breeding birds in the same season (Figure 1). Females lost fat and percentage fat content between pre-laying and incubation, but not between incubation and brood care (Table 2). Males lost fat and percentage fat between pre-laying and laying, and between incubation and brood care, but not between laying and incubation (Table 2). Female Maned Ducks lost an average of 32 g of fat during laying (from 72 ± 7.2 g (n=8) at the beginning of laying to 40 ± 3.6 g (n = 10) at the end of laying/beginning of incubation (ANOVA, $F_{1,16}$ = 18.2, $P < 0.01$)). This equals 44% of their average pre-laying fat level of 72 g, and 3.0 per egg laid (assuming the average clutch size of 10.7 eggs (Briggs unpubl.)). They lost a further 18 g of fat during incubation (the average length of incubation is 34 days (Briggs unpubl.)). This equals 47% of their average fat content at the beginning of incubation, and a fat loss of 0.53 g per day of incubation (Figure 3).

(Insert Figure 3 hereabouts)

Paired females were significantly fatter ($\bar{x}$ = 51 ± 4.8 g of fat, n = 13) during the non-breeding period (January - May), than were unpaired females ($\bar{x}$ = 33 ± 5.3, n = 6) (ANOVA, $F_{1,17}$ = 5.2, $P < 0.05$). During the same period fat levels of paired ($\bar{x}$ = 41 ± 2.8 g, n = 9)) and unpaired males ($\bar{x}$ = 42 ± 7.4 g, n = 8) did not differ.

Body and fat masses of the shot Maned Ducks were similar to those of the trapped ducks (Figures 1, 2, Tables 2, 3). Fat and body weights and percentage fat levels of the shot ducks were lowest in winter, and highest post-breeding and in late summer (Table 3). Protein levels of females did not vary significantly (_P_ > 0.05) with seasonal or reproductive categories (Table 3). In contrast, mean protein content of males was significantly (_P_ < 0.05) lower in winter than at other times of the year (Table 3). Protein remained a constant proportion of body mass in both sexes, whereas the proportion of fat varied, especially in females (Tables 2, 3).

(Insert Table 3 hereabouts)

Discussion

The climate in the study areas is relatively seasonal; most rain falls in winter/spring; and winters are cold and summers are hot. Consequently, pasture growth is high during spring, early summer and autumn (Fitzpatrick & Nix 1970). Growth is most vigorous in spring because high temperatures cause a water deficit in late summer which reduces growth of pasture during autumn (Kingsford 1989b). Pasture quality (= protein plus soluble carbohydrate content) is also higher in the early part of the growing season, rather than in the later part (Owen 1980; Prins &

Ydenberg 1985; Sedinger & Raveling 1986). Maned Ducks gained fat during spring and early summer from feeding on the abundant new pasture of high quality, as do other grazing waterfowl (Raveling 1979b). Both sexes lost weight and fat when food availability (pasture growth) was low due to dry weather in Canberra, or cold weather at Lake Eucumbene. Thus, fat levels in these Maned Ducks were related to their food availability (temperature x rainfall in previous two months x daylength), and possibly also to pasture quality.

Behavioural differences explain why, on average, females gained weight and fat during winter, whereas males stayed thin and light until spring. During autumn and winter females generally grazed more and were less vigilant than males (Briggs 1990a). This behavioural difference between the sexes resulted in paired females being significantly fatter during the non-breeding period than unpaired females. Most females were paired during this period (Briggs 1990a, unpubl.). Thus, females on average gained condition during winter, whereas males, on average, did not. Long-term, continuous pair bonds allow female Maned Ducks to maintain their body condition outside the reproductive period (see Briggs 1990a) when food availability can be uncertain, and thus to increase their fat content rapidly prior to laying. This would enhance the reproductive success of the pair because females use stored fat for egg production.

Males and females had different protein dynamics. Females did not lose protein, even during cold and dry weather (winter at Lake Eucumbene), whereas males did. Ducks can use body protein for energy during periods of extreme physiological stress (Reinecke et al. 1982). Male Maned Ducks apparently did this whereas females did not, possibly because females with depleted body protein cannot ovulate normally. The lack of annual variation in the percentages of protein in both sexes is the result of the relatively constant ratios between protein and water in both male and female Maned Ducks (Briggs unpubl.), as in several other waterfowl (Johnson et al. 1985; Ringelman & Szymczak 1985), combined with the large contribution of protein plus water (~ 90%) to the body mass of Maned Ducks (Briggs unpubl.). Thus, most of the mass of a Maned Duck consists of protein plus water which covary, resulting in a relatively invariable ratio of protein to body weight regardless of the absolute protein content of the duck.

Female Maned Ducks lost fat during laying and incubation but not while attending ducklings. They accumulated this fat for 3-6 months before laying. Females did not store protein for laying or incubation. Instead, they directly ingested protein for egg production, and thus apparently relied on protein-rich, new pasture (see Raveling 1979b; Owen 1980) being available during laying. Maned Duck eggs contain an average of 7.1 g of fat and 7.3 g of protein (Briggs unpubl.). Females therefore supplied 3.0/7.1 (= 42%) of the fat content of each egg from their own fat store, and incorporated 44 g of fat or its equivalent, and 78 g of protein, for egg production from dietary sources during laying (assuming an average clutch size of 10.7 eggs (Briggs unpubl.)).

The percentage increases in weight (10%) and fat content (70%) of female Maned Ducks from their annual, non-breeding minima to their pre-laying or laying maxima were much lower than in Blue-billed Ducks *Oxyura australis* (weight increase 73%) (Briggs 1988) Cackling Geese *Branta canadensis minima* (weight increase of 57%; fat increase 833%) (Raveling 1979a), or Giant Canada Geese *Branta canadensis maxima* (36%; 125%) (McLandress & Raveling 1981) However, they were similar to those in Musk Ducks *Biziura lobata* (weight increase 24%) (Briggs 1988), Ruddy Ducks *Oxyura jamaicensis* (21%; 60%) (Tome 1984), Hardheads *Aythya australis* (weight increase 18%) (Briggs 1990b), Wood Ducks (15%; 165%) (Drobney 1982), Ring-necked Ducks *Aythya collaris* (14%; 34%) (Hohman 1986), Pacific Black Ducks *Anas superciliosa* (weight increase ~ 9%) (Briggs 1990b) and Grey Teal *Anas gibberifrons* (weight increase 9%) (Briggs 1990b).

The proportion (~40%) of a Maned Duck's clutch derived from stored fat was also less than in many waterfowl, notably Arctic nesting geese (~ 100%) (Newton 1977) and Wood Ducks (88%) (Drobney 1980), but similar to Ruddy Ducks (35%) (Tome 1984), and higher than White-winged Scoters *Melanitta fusca deglandi* (~0%)(Brown & Frederickson 1987). However, the proportion of their pre-laying body fat (44%) that female Maned Ducks used to produce their eggs was higher than in many waterfowl, including Lesser Snow Geese *Anser caerulescens caerulescens* (25%) (Ankney & MacInnes 1978), Giant Canada Geese (26%) (Mainguy & Thomas 1985), White-winged Scoters (26%) (Brown & Frederickson 1987), Common Eiders *Somateria mollissima* (26%) (Korshgen 1977), and Ruddy Ducks (31%) (Tome 1984), but lower than in Ring-necked Ducks (>57%) (Hohman 1986), Cackling Geese (68%), (Raveling 1979a), and Wood Ducks (71%) (Drobney 1982). Thus, the percentage increase in fat level of female Maned Ducks up to laying was low for waterfowl (although about average for ducks), but the proportion of fat stored prior to laying that was used during laying was above average for waterfowl generally.

The daily loss in body fat of female Maned Ducks during incubation (0.53 g) was lower than in several other waterfowl, including Northern Shovelers *Anas clypeata* (4.5 g) (Ankney & Afton 1988), Cackling Geese (5.3 g) (Raveling 1979a), but similar to others, for example, Wood Ducks (0.6 g) (Drobney 1982), and higher than others such as Ring-necked Ducks (0.3 g) (Hohman 1986). The proportion of fat left at the end of laying which was subsequently lost during incubation (47%) was about average for waterfowl (varies from 85% in Lesser Snow Geese to 20% in Ring-necked Ducks (Ankney and MacInnes 1978; Hohman 1986).

These variations in body condition of male and female Maned Ducks with time of year and breeding status can be understood from their ecology. Maned Ducks live and breed in a variety of regions of Australia, from arid to well-watered, and from those with predictable rainfall patterns to those where rainfall, and consequently wetland availability, are erratic (Blakers <u>et al</u>. 1984). Selection is likely to favour individual waterfowl that store the necessary, but not more than the necessary, amount of nutrients for breeding prior to laying (Mainguy & Thomas 1985). Eggs are a moderately high energetic cost to Maned Ducks (7.1 g fat/egg x 10.7 eggs per female (Briggs unpubl.) = 76 g fat <u>cf</u>. their body fat content of ~ 40 g - ~ 80 g), but females can and do, feed in their breeding area while laying (Kingsford 1989a; Briggs pers. obs.). Individuals must be able to stop nesting and fly elsewhere if wetlands dry out during laying, but they do not have to migrate long distances after breeding. Therefore, females can ingest food directly for egg production, they must not be too heavy to fly adequately (see Briggs 1988) during laying, and they do not have to keep fat reserves for post-breeding migration (although males and females may have to leave their breeding site immediately after their young fledge). Consequently, the females gain benefit by storing some, but not all, of the nutrients required for egg formation, and by using a high proportion of these nutrients (in the form of fat) during laying and incubation. Females presumably store fat rather than protein, because protein is heavier than fat (protein is stored in combination with water (Johnson <u>et al</u>. 1985) whereas fat is not (Blem

1976)), and because protein is not required for maintenance during incubation.

Male Maned Ducks lost fat while their mates were laying, and during brood care, but not while their mates were incubating. Males lost an average of 22 g of fat from pre-laying to brood care or 40% of their pre-laying level. Most of this was used during the laying period and while attending broods. Male waterfowl often, but not always, lose fat while attending pre-laying and laying females (Raveling 1979a; Ankney & Afton 1988; Drobney 1982). In particular, males with pre-laying and laying females frequently reduce their feeding time, become more vigilant and thus lose body fat (Hohman 1986), as did these Maned Ducks (Briggs 1990a, pers. obs.). Also, males with pre-laying and laying females often fly more, and spend more time repelling other males (Owen & Reinecke 1979). Male Maned Ducks with young reduce their feeding time, and become more alert (Kingsford 1986). The reduced time that males spent feeding, together with their increased time spent vigilant during pre-laying and brood care, and while their mates were laying, allowed female Maned Ducks greater feeding time during egg production and while attending ducklings.

Fat levels of female Maned Ducks at the end of incubation were low (20 g). Male assistance with raising young appears to prevent further depletion in fat levels of females while they are caring for young. Without male assistance with ducklings, the fat level of females with broods could fall sufficiently to cause starvation. Furthermore, their likelihood of being predated would probably increase because they would need to feed more and consequently be less vigilant. This intra-pair co-operation in Maned Ducks, which operates both inside and outside the breeding season is likely to have evolved in association with their long term and continuously maintained pair bonds (Kingsford 1986; Briggs unpubl.; see Breitwisch 1989).

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Table 1. Months in which laying, incubating and brood caring Maned Ducks were trapped for condition measurements. n.d., no data.

	Laying	Incubating	Brood caring
Females			
1985	Aug., Oct., Nov.	Sept. - Nov.	Oct., Nov.
1986	June - Oct.	Aug. - Nov., Jan.*, Feb.*	Sept., Oct.
1987	July - Oct., Dec.	Aug. - Nov.	Sept., Oct., Dec.
1988	n.d.	July - Nov.	n.d.
Males			
1985	Aug.	Sept. - Nov.	Oct.
1986	July - Sept.	Aug. - Oct.	Oct.
1987	July - Sept.	Sept. - Oct.	Sept., Oct., Dec.
1988	n.d.	n.d.	n.d.

* Jan., Feb. 1987

Table 2. Mean body mass (g) (± *s.e.*) and estimated fat levels (g) (± *s.e.*) of trapped Maned Ducks. Figures in parentheses are percentages of body weight. Combined 1985 - 1988 data.

	Pre-laying	Laying	Incubating	Brood caring
Females				
Mass	853±14 n = 19	870±9 n = 49	837±7 n = 77	805±16 n = 10
Fat	62.6±4.2 (7.3) n = 19	48.0±2.5 (5.5) n = 49	28.2±1.3 (3.4) n = 77	26.9±2.8 (3.3) n = 10
Males				
Mass	817±11 n = 16	822±12 n = 14	795±11 n = 25	791±13 n = 6
Fat	51.5±4.9 (6.3) n = 16	39.2±2.5 (4.8) n = 14	38.2±1.5 (4.8) n = 25	29.4±1.7 (3.7) n = 6

Table 3. Mean carcass composition (g)(± s.e.) of Maned Ducks in seasonal and reproductive (see Briggs 1989) categories. Mass is wet body weight; protein and fat are expressed as dry weights. Figures in parentheses are percentages of body weight. Different letters indicate significantly different weights ($P < 0.05$) by ANOVA and Student-Newman-Keuls test (Zar 1984). Protein data from females collected in late summer and autumn were combined prior to analysis. n.a., not applicable. Combined 1985 and 1986 data.

	Late summer (Feb.- March)	Autumn (Apr.- May)	Winter (June - July)	Breeding (July - Nov.)	Incubating (Sept.)	Post breeding (Oct. - Jan.)
Females						
Mass	861±10a n = 18	843±24a n = 8	809±33b n = 8	882±20a n = 14	863±15a n = 6	898±16a n = 14
Fat	60.6±6.2b (7.0) n = 18	46.1±4.5b (5.5) n = 8	37.3±2.5b (4.6) n = 8	57.4±4.5b (6.5) n = 14	38.4±13.6b (4.4) n = 6	92.5±11.2a (10.3) n = 14
Protein	175±60 (20.3) n =4	185±1.4a (21.9) n = 2	171±8.0a (21.1) n =8	186±3.8a 21.1) n = 14	188±1.5a (21.8) n = 6	184±2.6a (20.4) n = 14
Males						
Mass	915±15a n = 21	908±18a n = 19	783±21c n = 10	858±14b n = 21	n.a.	890±14a n =24
Fat	59.9±4.7b (6.5) n =21	47.0±3.0c (5.2) n = 19	36.6±4.2c (4.7) n = 10	47.1±5.8c (5.5) n = 21	n.a.	75.6±8.6a (8.5) n = 24
Protein	194±7.6a (21.2) n = 5	188±5.7a (20.7) n = 12	163±4.7b (20.8) n = 10	179±2.4a (20.9) n = 21	n.a.	187±2.6a (21.0) n = 24

Captions to figures

Figure 1. Mean monthly fat levels of trapped, non-breeding Maned Ducks (▲); and mean annual fat levels of laying females or males with laying females (●), incubating females or males with incubating females (●), brood caring males or females (●) (in sequential order of laying, incubating, brood caring), monthly rainfall for Canberra (|), and mean monthly maximum temperature for Canberra (•). Vertical bars on the data means are standard errors. An open circle indicates that only one sample was available.

Figure 2. Mean monthly body mass of trapped, non-breeding Maned Ducks (▲); and mean annual fat levels of laying females or males with laying females (●), incubating females or males with incubating females (●), brood caring males or females (●) (in sequential order of laying, incubating, brood caring), monthly rainfall for Canberra (|), and mean monthly maximum temperature for Canberra (•). Vertical bars on the data means are standard errors. An open circle indicates that only one sample was available.

Figure 3. Loss in body fat from female Maned Ducks during incubation. Fat level of duck at known stage of incubation (○). The regression equation is: Fat in grams = 38.2 - [0.53 x (Days of incubation)], $\underline{r}^2 = 0.29$, $\underline{F}_{1,50} = 20.5$, $\underline{P} < 0.001$

FIGURE 1

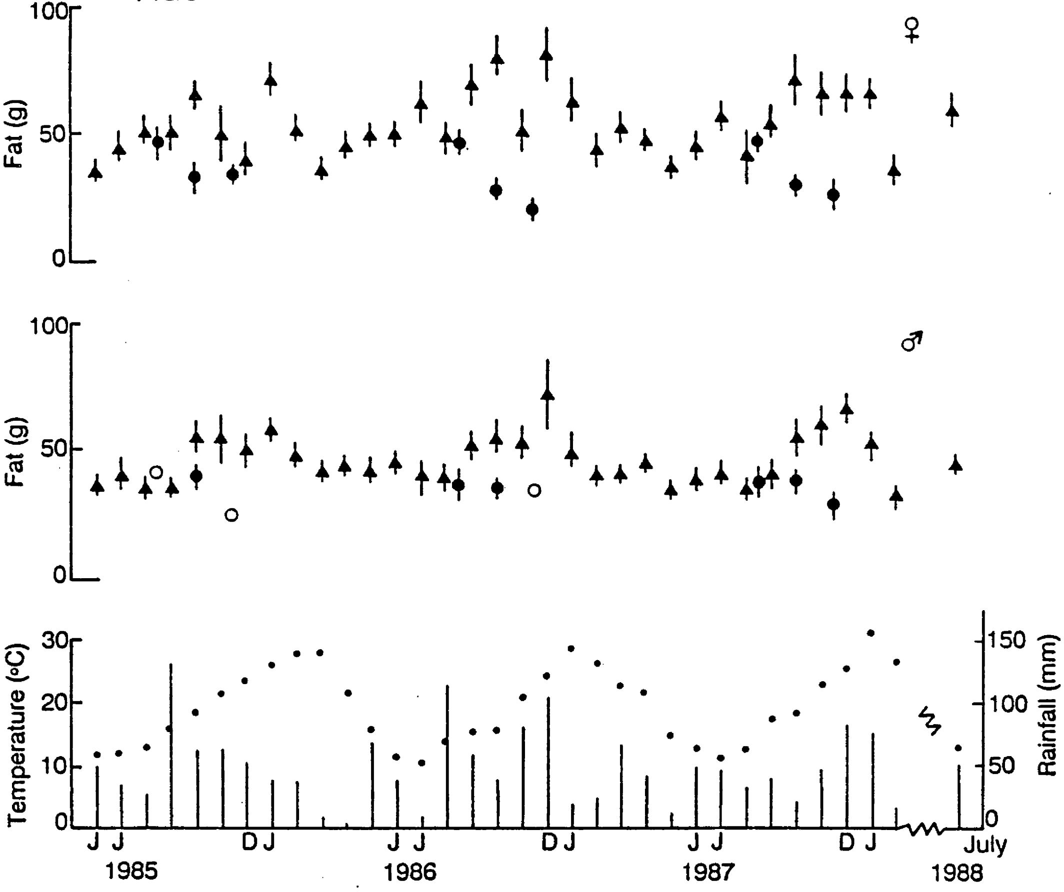
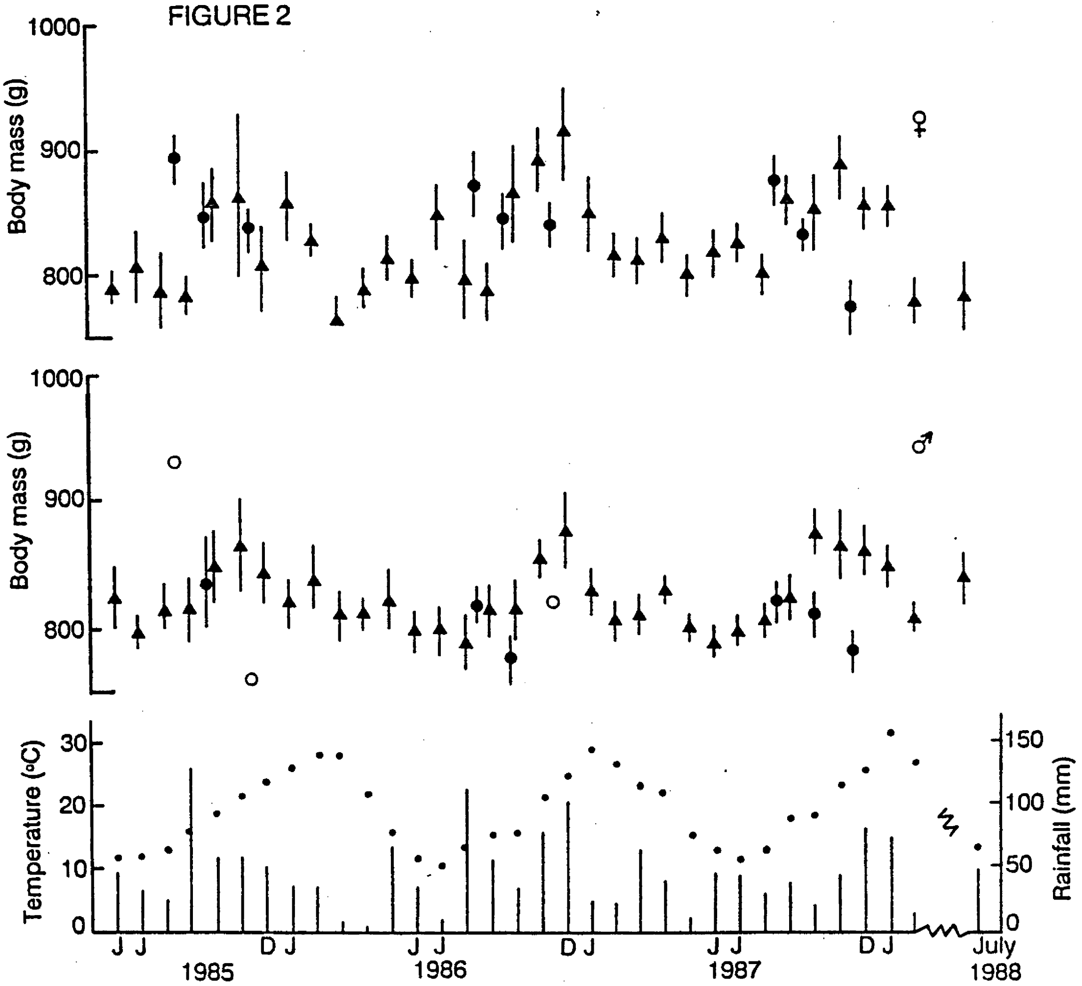


FIGURE 2



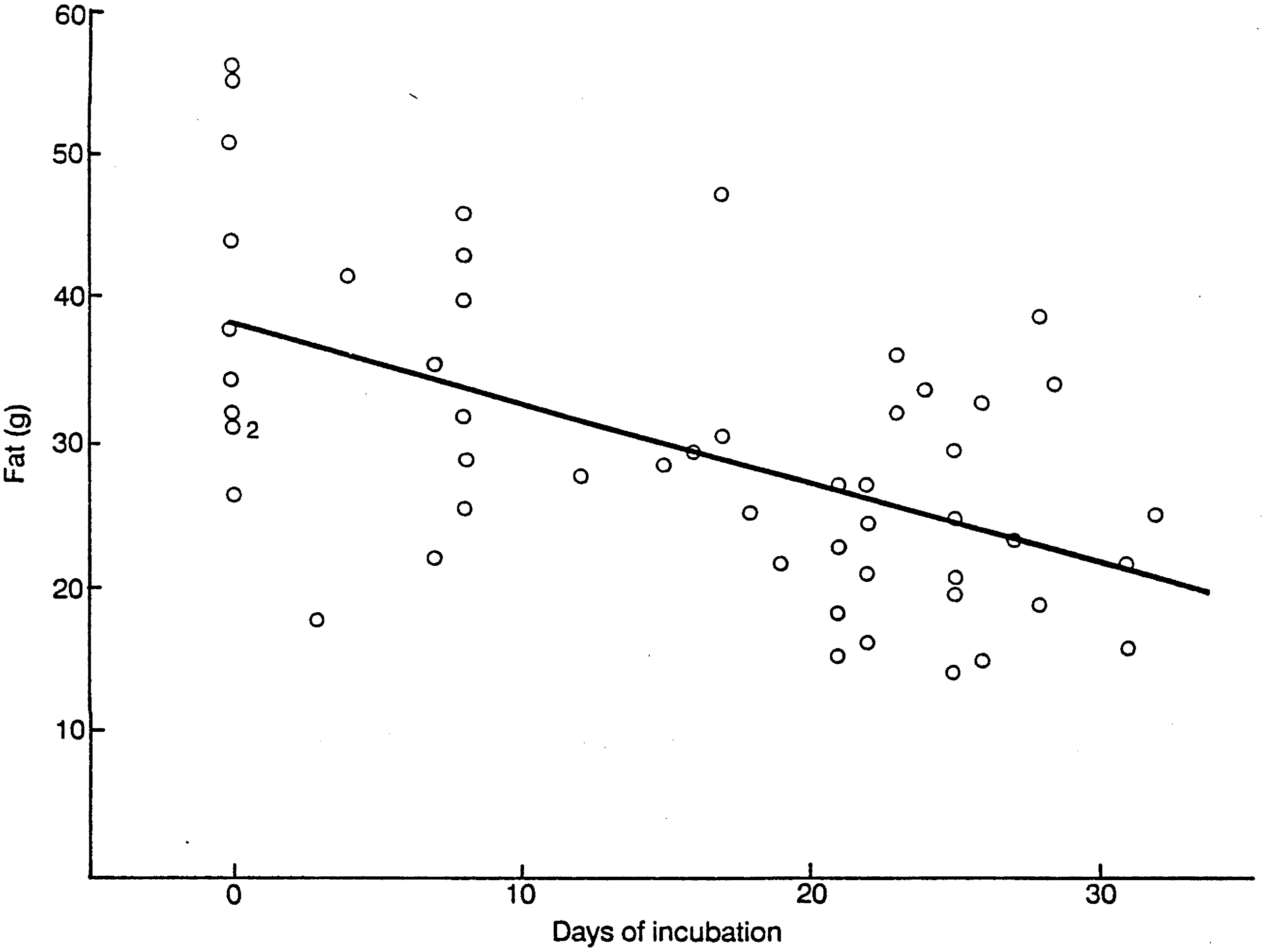


FIGURE 3

CHAPTER 5.

PARASITIC LAYING IN MANED DUCKS *CHENONETTA JUBATA*: MANIPULATION OR MUTUALISM?

Submitted to J. Anim. Ecol.

PARASITIC LAYING IN MANED DUCKS *CHENONETTA JUBATA*: MANIPULATION OR MUTUALISM?

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Running head: Parasitic laying in maned ducks

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Lyneham, A.C.T. 2602, Australia.

SUMMARY

(1) Intraspecific nest parasitism was recorded in 31% of clutches containing $\geq$ 5 eggs laid by maned ducks in nest boxes near Canberra. This is within the range for other cavity - nesting waterfowl.

(2) Frequency of parasitism was higher in 1987 (62% of incubated clutches) than in 1988 (27% of incubated clutches). Less rain fell during the laying period in 1987 (209 mm) than during the same period in 1988 (309 mm). Rain enhances the growth of pasture grazed by maned ducks. The higher incidence of parasitism in the drier year suggests that individual maned ducks used nest parasitism as a salvage strategy, to enhance their chance of reproductive success when food was relatively scarce.

(3) Natural and artificial parasitism did not reduce clutch size of hosts, fat levels of incubating females, nor egg hatchability. Nor did they appear to increase nest desertion. Larger broods survived as well as smaller ones. The relationship between host and parasitic maned ducks thus seemed to be mutualism, rather than manipulation of the host by the parasite.

INTRODUCTION

Intraspecific nest parasitism has been recorded in sixty-four species of waterfowl (Anatidae) (Rohwer & Freeman 1989). Recent research on this type of parasitism has focused on its ecological and behavioural causes (Semel, Sherman & Byers 1988; Lank *et al.* 1989a; Rohwer & Freeman 1989), and on its costs and benefits to host and parasite (Eadie, Kehoe & Nudds 1988). I investigated parasitic laying in maned ducks *Chenonetta jubata* (Latham). This Australian duck nests in tree cavities, grazes like a goose, and has biparental care of young and long-term pair bonds (Frith 1967; Kingsford 1986a). The particular aims of this study were; (a) to compare the frequency of parasitic laying in maned ducks *Chenonetta jubata* (Latham) with its frequency in other waterfowl (Anatidae) species; and (b) to ascertain the benefits and costs to host and parasite of intraspecific nest parasitism in maned ducks. Parasitic laying has not been reported in maned ducks previously, although Kingsford (1989b) postulated its existence from brood data.

METHODS

The study area was four parkland sites near Canberra (35°15'S; 149°10'E) in southeastern Australia. The habitat was modified woodland, consisting of improved pasture with scattered trees, mostly *Eucalyptus* spp. Natural cavities in which maned ducks nested commonly, were abundant in these eucalypt trees. Constructed nest boxes were also available in the study area for the maned ducks to nest in.

Sixty nest boxes and four natural cavities in trees at the sites were checked for nesting activity every four days during the 1987 and 1988 breeding seasons (June to December). Two cavities were checked weekly in 1986. The boxes were in groups of between five and twenty-four, and the tree cavities were alone or near a nest box. Boxes within groups were separated by 5 m to 500 m, and the groups of boxes were separated by 3 km to 8 km. All the boxes and two of the tree cavities were visible from at least one other box or cavity. Two of the tree cavities were not visible from another tree cavity or nest box.

Active nests were visited daily in 1987 and 1988, usually in the afternoon, to count and number eggs, and to manipulate experimental clutches. All eggs were numbered. Experimental clutches were randomly assigned to control, addition or removal treatments. Control clutches were not manipulated other than by numbering eggs. All new eggs, after the fourth one, were removed from removal clutches (manipulated without egg addition), and one egg was added to addition clutches (artificially parasitized) each day that an egg was laid, once four eggs were present. All experimental clutches were laid in nest boxes.

When more than one egg was laid in a nest per day; the extra eggs were regarded as parasitic (supernumerary eggs). This method of detecting parasitism is commonly used, although it can underestimate the true rate of parasitism by excluding parasitic eggs laid on a day that the host fails to lay (MacWhirter 1989). In 1988 but not in 1987, supernumerary eggs were removed from control nests, and all except the one left as an addition egg were removed from addition nests. Supernumary eggs were left in nests in 1987. The number of skipped days recorded after I found each nest (= number of days when no eggs were deposited) was multiplied by the ratio of host clutch size to the number of host eggs deposited after I found each nest, to determine the number of skipped days per clutch. I excluded obviously predated clutches from the analyses of nest desertion and egg hatchability. One clutch of 24 eggs found in 1987 was excluded from the clutch size analyses, but included in the analyses of rates of egg deposition. Total clutch size refers to the number of eggs in a nest; host clutch size refers to the number of eggs presumed to have been laid by the host female (total ± removal or addition eggs - parasitic eggs).

Twenty-three incubating females were caught on their nests in late incubation in 1987 and 1988. They were colour-banded, weighed and measured, and their fat content estimated from a regression equation which predicts body fat from powers of body mass and external measurements (Briggs 1989). The number of eggs laid after incubation began was ascertained in all but three nests in 1987 and 1988. The status (developed embryo or not) of unhatched eggs remaining in nests after hatching was determined in 1988. Broods of ducklings were surveyed approximately once per week at the four study sites in 1986, 1987 and 1988. Broods were identified by the colour-banded adults which accompanied them (putative parents). All the ducklings in a brood were considered dead if their mother was seen feeding or resting for several minutes or seen on two separate occasions, without the ducklings. Ducklings in broods were aged using plumage characteristics (Kingsford 1986b).

I assumed that clutches were incubated when down was deposited and eggs were warmed. My results apply to these incubated clutches, to eggs laid prior to incubation, and to data from 1987 and 1988, unless otherwise stated. Deserted, unincubated clutches of $\leq$ 4 eggs were excluded from all analyses. Data were also available from five non-experimental clutches found in natural cavities in the study area between 1986 and 1988. Percentage data were arcsin transformed prior to analysis of variance to improve normality. Rainfall figures were obtained from the

Canberra office of the Bureau of Meterology. Means are reported as ± S. E.

RESULTS

Unoccupied nest boxes were available throughout the study. Fifty clutches containing ≥ 5 eggs were found in the study area during 1987 and 1988. Thirty-five of these were incubated. At least one parasitic egg was laid in 62% of incubated nests ($n = 13$) in 1987, in 27% of incubated nests ($n = 22$) in 1988, and in 31% of the incubated plus unincubated clutches found in both years. An average of 4.4 ± 0.8 ($n = 14$) superumerary eggs was deposited per nest parasitized during laying in 1987 and 1988, or 1.7 per nest studied ($n = 35$). The incidence of parasitic eggs per nest did not differ significantly between 1987 (5.3 ± 1.3, $n = 8$) and 1988 (3.2 ± 0.7, $n = 6$) (ANOVA, $F_{1,12} = 1.6$, $P > 0.10$). Twenty-three percent of eggs laid in nests in 1987 were parasitic, compared with 13% in 1988. After incubation began, an average of 2.2 ± 0.2 ($n = 23$) eggs were laid per nest affected, or 1.6 eggs per nest investigated ($n = 32$). No eggs laid during incubation in 1988 hatched. Preterm embryos were found in 47% of these eggs; the rest were undeveloped, and presumably infertile.

No eggs were laid in some nests on some days. The average number of days when no eggs were laid in an incubated nest (= zero-days corrected for stage of finding each clutch) in 1987 and 1988 was 4.4 ± 0.6 ($n = 35$). Host clutch size measured at the start of incubation did not decrease significantly with increased number of skipped days per egg laid by the host female ($r = -0.275$, d.f. = 33, $0.10 > P > 0.05$; 0-3 zero-days, clutch size = 10.6 ± 0.4, $n = 18$; 4-13 zero days, clutch size = 10.8 ± 0.4, $n = 16$). Nor did smaller clutches include significantly more skipped days than larger ones (clutch size $\leq$ 10, zero days = 5.9 ± 1.1, n = 14; clutch size $\geq$ 11, zero days = 3.5 ± 0.6, n = 20, ANOVA, $F_{1,32}$ = 4.0, 0.10 > P > 0.05).

Desertion during laying (30%) was not significantly more frequent in naturally parasitized nests (36%, n = 22) than in unparasitized ones (25%, n = 28) (χ_1^2 = 0.7, P > 0.25). Sample sizes were too small to test the effect of natural parasitism on desertion during incubation, or effects of artificial parasitism on desertion during laying or incubation. However, natural parasitism did not appear to cause increased desertion during incubation (naturally parasitized nests, n = 22, 33% deserted; nests not parasitized, n = 15, 27% deserted). And artificially adding extra eggs to clutches did not obviously increase nest desertion in incubated plus unincubated clutches during laying (control clutches, n = 20, 30% deserted; removal clutches, n = 15, 33% deserted; addition clutches, n = 15, 27% deserted), nor in incubated clutches during incubation (control clutches, n = 11, 18% deserted; removal clutches, n = 8, 50% deserted; addition clutches, n = 8, 38% deserted). Interestingly, the experimental treatment itself (either removal or addition of eggs) did appear to increase desertion during incubation.

Fat levels of host females in late incubation were unaffected by natural or artificial enlargement of their clutches (Table 1). Hatchability (the percentage of eggs hatching in successful nests (Rohwer 1985)) was unaffected by natural or artificial parasitism, clutch size or year (Table 2). Neither natural nor artificial parasitism influenced host clutch size (Table 3). Mean, total clutch size in natural cavities in the study area was similar to host clutch size in nest boxes (Table 3). Survival of ducklings did not decrease with increased size of total clutch or brood (Table 4). Instead, percent mortality in larger broods was generally lower than in smaller ones (Table 4). However, no young survived in 1988 from hatching to 5-8 weeks in four artificially parasitized (addition) clutches for which data were available, compared with a mean survival of 29% ± 14.6 survival in three unparasitized (control) clutches.

DISCUSSION

Comparison with other waterfowl

The percentages of nests parasitized by maned ducks were in the range observed in other cavity-nesting waterfowl (Rohwer & Freeman 1989). Semel and Sherman (1986) and Semel, Sherman and Byers (1989) suggested that parasitism by wood ducks *Aix sponsa* L. increased when they bred in easily visible nest boxes, which were close to each other. This may be true in this population of maned ducks also. Mean, total clutch size of unmanipulated clutches in inconspicuous, natural cavities in trees in my study area was similar to host (unparasitized) clutch size of Maned Ducks breeding in nest boxes (Table 3). As with other ducks (Andersson 1984; Rohwer & Freeman 1989), nest parasitism was not due to shortage of nest sizes *per se*, although my data do not exclude the possibility that competition for particular sites increased its incidence (see Eadie, Kehoe and Nudds 1989). Rohwer & Freeman (1989) predicted that intraspecific nest parasitisim should be common in birds with self-feeding young, especially in species that nest in cavities and those nesting at high densities. Relatively high rates of parasitism in the study population of maned ducks fit their predictions.

Benefits and costs to the parasite

Incubation is long (34 days) in maned ducks (S. Briggs, unpublished data). Incubating females leave their nests for only 2 - 4 h in every 24 h (P. Fullagar & C. Davey, unpublished data), and thus have limited time to feed. During incubation, they lose 50% of the fat present at the end of laying (S. Briggs, unpublished data). Because non-incubating females feed for at least 4.5 h per day (Briggs 1990) incubating females are likely to have an energy deficit. Laying in another female's nest would benefit the parasite by removing this cost of incubation. Males feed little and are particularly vigilant for predators during the early weeks of brood care (Kingsford 1986a), suggesting that both parents are vulnerable to predators while raising ducklings. Parasitic birds may therefore reduce their risk of predation by avoiding incubation and duckling care.

Parasitism by maned ducks was higher in 1987 than in 1988. The 1988 pre-laying and laying period (June - October) was considerably wetter (309 mm of rain) than the same period in 1987 (209 mm). Pasture growth in the Canberra area varies with rainfall (Fitzpatrick & Nix 1970). Maned ducks are mainly grazers (Kingsford 1989a), and their production of broods is depressed by low pasture growth (Kingsford 1989b). The higher incidence of parasitism in 1987 compared with 1988, suggests that maned ducks used nest parasitism to avoid the costs of incubation and brood rearing in the poorer breeding year. Lank *et al.* (1989a) inferred that female snow geese *Chen caerulescens caerulescens* (L.) in low physiological condition used parasitism for the same reason. Inability to store sufficient reserves for producing eggs, as well as for maintenance during incubation and while raising ducklings would provide an advantage to parasitic birds. Regular occurrences of such an inability would select for parasitism as a salvage strategy (Eadie, Kehoe & Nudds 1988) in maned ducks, as in snow geese (Lank *et al.* 1989a).

Parasitism can also operate as a mixed strategy, which differs from parasitism as a salvage strategy. Mixed strategy parasitic females lay eggs in the nests of others as well as laying in their own nests and raising their own young (Lank *et al.* 1989a). Parasitic females using such a strategy reduce their chance of total reproductive failure by not "putting all their eggs in one basket" (Payne 1977; Rubenstein 1982). A mixed strategy was unlikely in these maned ducks because their clutch size did not decrease with increased zero-egg days.

Only half the eggs deposited by parasitic females were laid during the host's laying period. The other half, which were presumably parasitic, were laid during incubation, and generally did not hatch. They thus represented a net cost to the parasite in lost reproductive effort. Low hatching success of eggs laid during the host's incubation period is the principal disadvantage of parasitic laying (Lank *et al.* 1989b).

Benefits and costs to the host

There were no obvious fitness disadvantages (reduced clutch size, increased nest desertion, reduced hatchability, reduced female fat level, increased duckling mortality) to pairs raising enlarged clutches. Survival of large broods was similar to survival of smaller ones. This lack of cost and a possible benefit of raising ducklings from parasitic eggs support the findings of Eadie and Lumsden (1985). These authors noted that nest parasitism in common goldeneyes *Bucephala clangula* (Gmelin) was not deleterious to host females and may have enhanced survival of their own ducklings. Host maned ducks could benefit from enlarged clutches and mixed broods by reduced mortality of their young through diluted risk of predation, or from increased group vigilance (Nudds 1980; Andersson 1984). Enlarged group size is a common mechanism for reducing predation in animals (Pulliam and Caraco 1984). Nest parasitism in maned ducks generally seems to benefit the parasite (and her mate) without reducing the reproductive success of the host (and her mate). The relationship therefore seems more one of mutualism (*sensu*

Maynard-Smith 1982), than manipulation of the host by the parasite (*sensu* Krebs and Davies 1981).

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I thank A. Cockburn, J. Eadie and R. Titman for ideas, R. Kingsford and particularly A. Cockburn for reading drafts, W. Lawler for installing nest boxes, S. Thornton and W. Lawler for assisting with brood surveys, and the Australian Bird Banding Scheme for bird bands. Funds were provided by the National Parks and Wildlife Service (N.S.W.). Facilities and study sites were provided by the Division of Wildlife and Ecology, CSIRO, Australian National University, Fernhill Park, Yowani Country Club and Gungahlin Cemetery.

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able 1. Mean fat (g) levels ± S.E. (*n*) of host female maned ducks aught in late incubation in 1987 and 1988, according to clutch anipulation treatment, whether naturally parasitized or not, and heir total clutch size (host clutch - eggs removed experimentally + ggs added experimentally or naturally) at their time of capture ± .E. Fat levels did not vary significantly with treatment, natural arasitism or total clutch size (ANOVAS, all $P > 0.25$).

		Female fat levels	
Nest category	Mean total clutch size	Fat	Stage of incubation (days)
Experimental			
Control	12.7±0.6	22±1.9 (11)	24±0.9
Removal	6.4±1.0	28±3.9 ((5)	24±1.4
Addition	19.3±2.2	26±1.2 (7)	21±0.4
Natural*			
Not parasitized	12.2±1.2	24±2.0 (13)	23±1.0
Parasitized	14.7±2.2	26±2.1 (10)	23±0.6
Clutch size**			
4-11 eggs	7.4±1.0	26±3.0 (7)	24±1.0
12-31 eggs	15.9±1.2	24±1.7 (16)	22±0.8

* Combined control and manipulated clutches.

** Determined from average host clutch size in unmanipulated clutches (11 eggs) (S. Briggs, unpublished data).

Table 2. Mean percent hatchability ± S.E. ($\underline{n}$) of maned duck nests in 1987 and 1988, according to clutch manipulation treatment, whether naturally parasitized or not, and total clutch size in late incubation. Hatchability did not vary significantly with treatment, natural parasitism or clutch size (ANOVAS, all $\underline{P} > 0.25$).

Nest category	Hatchability
Experimental	
Control	84.5 ± 2.6 (14)
Removal	74.4 ± 9.6 (4)
Addition	77.4 ± 9.4 (5)
Natural *	
Parasitized	79.9 ± 3.9 (7)
Not parasitized	81.7 ± 4.0 (16)
Clutch size**	
4 - 11	82.7 ± 4.3 (11)
12 - 20	79.8 ± 4.3 (12)

* Combined control and manipulated clutches

** Determined from average host clutch size in unmanipulated clutches (11 eggs) (S. Briggs, unpublished data).

Table 3. Host clutch size ± S.E. (n) of maned ducks laying in unparasitized (control), naturally parasitized (control) and artificially parasitized (addition) nests in nest boxes (1987, 1988), and total clutch size ± S.E. (n) of maned ducks laying in unmanipulated nests in tree cavities (1986, 1987, 1988).

Nest category	Clutch size
Nest boxes	
Not parasitized	10.8±0.4 (10)
Naturally parasitized	10.5±0.6 (4)
Artificially parasitized	10.4±0.5 (11)
Cavities	
Non-experimental	10.6±0.8 (5)

Table 4. Percentage ± S.E. (n) of ducklings surviving in maned duck broods according to original size* of clutch or brood. Clutches deserted during incubation are excluded. Data are from combined 1986, 1987, 1988, and control, manipulated and non-experimental clutches. Sample sizes vary because not every brood was seen at each age. Survival of ducklings did not vary significantly with either measure of clutch size or with brood size (ANOVAS, all $P > 0.05$).

	Percent survival to age (weeks)		
Clutch/brood size*	0 - 2	3 - 4	5 - 8
Clutch size prior to hatching			
4-12	56.6 ± 14.0 (8)	41.2 ± 13.1 (8)	31.0 ± 11.6 (7)
13-20	64.4 ± 11.0 (8)	24.8 ± 13.2 (10)	22.5 ± 12.6(10)
Hatched clutch size			
4-10	54.4 ± 16.7 (8)	31.0 ± 13.2 (10)	12.5 ± 8.2 (8)
11-16	93.4 ± 6.3 (7)	47.0 ± 21.2 (6)	48.1 ± 17.9 (7)
Brood size at 0-2 weeks			
1-8	-	60.6 ± 9.6 (20)	45.1 ± 10.8(17)
9-17	-	67.4 ± 10.1 (18)	62.6 ± 11.7(14)

* Size categories determined from average clutch size of host in late incubation in all clutches (12 eggs) - average number of unhatched eggs (2 eggs) (= 10 eggs), and average size of broods from unmanipulated clutches (8 ducklings) (S. Briggs, unpublished data).

CHAPTER 6.

EXPERIMENTAL MANIPULATION OF CLUTCH SIZE IN MANED DUCKS.

Submitted to Wildfowl.

Experimental manipulation of clutch size in Maned Ducks.

S.V. BRIGGS

Clutch size of Maned Ducks was not affected by removal or addition of eggs. This supports the hypothesis that the level of the female's nutrient store proximately controls clutch size in this species. Clutch manipulation experiments can be used to test the hypothesis that the level of nutrients stored by the female limits her egg production, in indeterminately laying birds. Clutch manipulation should not be used alone to distinguish determinately from indeterminately laying species.

The aim of this study was to determine whether clutch size of free-living Maned Ducks *Chenonetta jubata* can be altered by experimental removal or addition of eggs during laying, and thus to test the hypothesis that the size of the female's nutrient store proximately limits clutch size in this species. This hypothesis was first stated by Lack (1966: 6-7), and developed by Klomp (1970), Ankney and MacInnes (1978) and Drent and Daan (1980). It states that clutch size is controlled by the female's nutrient reserves, i.e., food has a direct proximate effect on clutch size through its influence on female physical condition (Klomp 1970). In this context, the term nutrient implies either or both fat or protein. The nutrient reserve hypothesis is refuted in an indeterminate layer, if addition or removal of eggs causes the clutch size of individuals to decrease or increase (Klomp 1970). This is because egg manipulation should not affect clutch size, if it has been set by nutrients stored before clutch manipulation (Anderson 1989).

Determinate and indeterminate laying in birds were described by Cole (1917), who stated that the number of eggs laid by determinate layers is set when laying begins, whereas the number of eggs laid by indeterminate layers depends on stimuli after laying commences.

He also suggested a practical test for distinguishing indeterminate layers; they keep laying if eggs are removed as laid. This test of indeterminate laying has commonly but erroneously been used as its definition. It is not an absolute test because indeterminate species, with the inherent capacity to vary their clutch size during laying, cannot do so if their levels of stored nutrients limit their egg production (Klomp 1970, Winkler & Walters 1983). Birds that keep laying as their eggs are removed, generally rely on daily food input, rather than accumulated reserves for egg production (Perrins & Birkhead 1983).

Egg removal and addition experiments thus test whether clutch size in indeterminate breeders is limited by the female's stored nutrient level (Klomp 1970, Briggs 1985), rather than whether the species is indeterminate or not. Determinate or indeterminate laying should be determined by ovary inspection to ascertain the number and relative size of developing follicles, rather than by egg removal or addition experiments. Several authors have given details of ovarian development in indeterminate and determinate layers (Davis 1955, Klomp 1970, Gilbert 1971, Porter & Wiemeyer 1972, Ankney & MacInnes 1978, Drobney 1980, Houston et al. 1983, Follett 1984). There are more developing follicles in indeterminate layers than the final clutch size, and they form a series in decreasing size. This contrasts with the follicles in determinate layers which are more similar in size, and equal to the final clutch size.

Maned Ducks were chosen for the study because they nest in tree holes and in artificial nest boxes. Hence their clutches are easy to manipulate. Maned Ducks are grazers and ecologically resemble geese (Kingsford 1986). They are common in semi-arid to humid temperate Australia (Blakers et al. 1984).

Methods

The experiments were conducted during the 1987 and 1988 breeding seasons near Canberra (lat. 35° 15'S; long. 149° 10'E) in southeastern Australia. The study area was modified woodland, and included university grounds, golf fairways, artificial ponds and pasture grazed by domestic stock. Maned Ducks use such environments readily. All clutches used in the experiment were found in nest boxes. Only clutches that were subsequently incubated were included in the analyses. A nest was regarded as deserted during laying if an interval of greater than six days passed with no egg laid. Incubation was considered to commence with maintenance of egg warming. Some incubated clutches were deserted before hatching.

Potential nests were checked for new eggs every four days. New clutches were randomly allocated between treatments as they were found. Active nests were visited daily for manipulation, usually in the afternoon. All eggs were removed, numbered, measured, and depending on treatment, replaced. Two measures of clutch size were used, number of eggs at the beginning of incubation, and number in the third week of incubation or at nest desertion. Clutch size at the beginning of incubation was used in most analyses, because later in incubation additional eggs may be laid parasitically (Briggs, unpubl.data). Eggs deposited at a greater rate than one per nest per day were considered parasitic. Such extra eggs were excluded from the analyses. One nest of 24 eggs in 1987 was also excluded. At least three females contributed to this nest, and it was probably abandoned by one female and taken over by another. Clutches larger than twice the mean size are usually the result of laying by more than one female (Yom-Tov 1980).

Treatment schedules were as follows. Control nests were not manipulated; all eggs above four were removed from removal nests; and one egg was added to addition nests each day that an egg was laid, once four eggs were present. Clutches were manipulated after four eggs had been laid for the reasons given by Rohwer (1984, 1986). In 1988, parasitic eggs were also removed from control nests, and one was left as the added egg in addition nests. These slight differences in control and addition treatments between 1987 and 1988 were because of the previously unknown high levels of parasitic laying found in 1987. Since the treatment differences were minor and had no measurable effects on clutch size, the 1987 and 1988 clutch data were combined where appropriate. Four Maned Ducks were collected for ovarian examination in 1986 and 1988. Three of these were collected about 20 km from the study site and one (in 1986) about 500 km to the north.

Results

Maned Ducks show sequential development of a large number of follicles (Table 1), and therefore can be classed as indeterminate layers.

Neither adding nor removing eggs affected clutch size at the beginning of incubation in 1987 (one way ANOVA, $\underline{F} = 0.99$, df = 2,10, $\underline{P} > 0.25$), 1988 (one way ANOVA, $\underline{F} = 1.41$, df = 2,19, $\underline{P} > 0.25$) or the two years combined (combined data, one way ANOVA, $\underline{F} = 0.37$, df = 2,32, $\underline{P} > 0.25$) (Table 2). The mean clutch size at the beginning of incubation was 10.7 (SE = 0.24, $\underline{n} = 35$). Clutch size in late incubation was larger by an average of 1.6 (SE = 0.26, $\underline{n} = 31$) eggs than at the start of incubation, but also showed no treatment effect (combined data, one way ANOVA, $\underline{F} = 0.78$, df = 2,29, $\underline{P} > 0.25$). Eggs laid during incubation rarely hatched, and were presumably the result of nest parasitism (Briggs, unpubl. data).

Discussion

These results are consistent with a direct relation between stored nutrient reserves and clutch size in an indeterminately laying bird. The results therefore fail to refute the nutrient limitation hypothesis for proximate control of clutch size in Maned Ducks. The separate findings that female Maned Ducks store fat prior to laying, and lose it during egg production (Briggs, unpubl. data), are also consistent with proximate control of clutch size in this by species by the nutrient level of the pre-laying female.

The timing of egg manipulation can affect the consequent response of the laying female (Andersson & Eriksson 1982, Winkler & Walters 1983, Duncan 1986). At some point during laying, a female's clutch size is set and further follicular development is inhibited (Klomp 1970). Common Goldeneyes *Bucephala clangula* did not reduce their clutch size when eggs were added to their nests late ($\geqslant 5$ eggs laid) in laying; but did when eggs were added early (< 5 eggs laid). Goldeneyes develop three (rarely four) follicles at the same time, even though they produce clutches of more than 10 eggs (H.G. Lumsden, unpubl. data, quoted in Thomas 1988). Thus, their final clutch size is set before the fifth egg is laid, and late, experimental addition of eggs will not affect the clutch size of host females, whereas early manipulation will. Unlike those of Goldeneyes, developing follicles of Blue-winged Teal *Anas discors* (Rohwer 1984) and Maned Ducks (Table 1, Briggs unpubl. data) show a continuous progression in size from large to small. Thus, manipulating clutches of Maned Ducks (and of Blue-winged Teal) after four or five eggs have been laid should be sufficiently early to induce a host response if such a response was possible.

Egg manipulation studies by Rohwer (1984) with wild and captive Mallards *Anas platyrhynchos* and wild Blue-winged Teal produced similar results to mine in wild Mallards and Teal. However, removing eggs increased the clutch size of some captive Mallards which were fed *ad libitum*. This difference between wild and captive ducks may be caused by different food availability, and hence different sources of material for eggs in wild and captive birds. Krapu (1981) found that wild Mallards used endogenous (stored) fat to produce eggs, and showed that their clutch sizes were positively correlated with their levels of stored lipids. Conversely, Batt and Prince (1978) found that clutch sizes in captive Mallards given *ad libitum* food were independent of female body weight.

Other species of waterfowl also show a positive association between stored nutrient control of clutch size and lack of response to egg manipulation, and *vice versa*. Clutch size in Wood Ducks *Aix sponsa* appears to be limited by the fat reserve of the female (Drobney 1980, Drobney & Frederickson 1985). Wood Ducks did not significantly reduce their clutch size when eggs were experimentally added to their nest (Heusmann *et al.*1980). Arctic-nesting geese do not lay extra eggs to replace those experimentally removed, and their clutch sizes are strongly related to their level of body reserves just prior to laying (Ankney & MacInnes 1978, Raveling 1979, Winkler & Walters 1983, Thomas 1988). Conversely, Common Goldeneyes reduced their clutch size when eggs were added artificially to their nests (prior to their clutch size being fixed) (Andersson & Eriksson 1982). Although they carry fat reserves, Goldeneyes depend on invertebrates consumed on their breeding grounds for the formation of their entire clutch (H.G. Lumsden, unpubl. data, quoted in Thomas 1988). Their lower clutch size in response to egg addition is consistent with relying on exogenous (ingested) food for egg formation, rather than on stored reserves.

In conclusion, determining the source of nutrients for egg production is essential for understanding clutch size regulation in birds. Clutch manipulation experiments can be used in indeterminately laying species to test the hypothesis that clutch size is limited by the level of the female's nutrient reserve. Such experiments should preferably be conducted in association with food manipulation studies (Hochachka & Boag 1987, Briggs 1989), ovarian examination, and analysis of female body condition (Ankney and Afton 1988).

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TABLE 1. Number of follicles of different size classes in breeding Maned Ducks

Follicle sizes (mm)	Date specimen collected			
	14 Oct 86	10 July 88	17 July 88	31 July 88
Post-ovulatory	0	0	0	2
Atretic	0	0	0	2
Egg	1	0	0	1
15	1	0	0	0
9	0	0	0	1
6-6.9	0	0	1	0
5-5.9	2	0	9	4
4-4.9	2	0	4	6
3-3.9	2	11	10	9
2-2.9	Numerous	9	Numerous	Numerous
< 2	Numerous	Numerous	Numerous	Numerous

TABLE 2. Mean (± 1 SE) clutch sizes of Maned Ducks

Incubation	Year	Treatment		
		Control	Removal	Addition
Start of incubation				
	1987	10.7±0.4	12.0±0.9	11.7±1.2
	n	6	4	3
	1988	10.8±0.4	10.0±0.4	9.9±0.4
	n	9	5	8
	1987+1988	10.7±0.3	10.9±0.6	10.4±0.5
	n	15	9	11
Late incubation				
	1987+1988	12.7±0.5	11.9±1.0	11.6±0.8
	n	15	7	10

CHAPTER 7.

NUTRITIONAL REGULATION OF CLUTCH SIZE AND LAYING IN MANED DUCKS.

To be submitted to Auk.

NUTRITIONAL REGULATION OF CLUTCH SIZE AND LAYING IN MANED DUCKS

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Running head: Clutch size and laying in Maned Ducks.

Abstract. - I investigated whether clutch size and laying patterns in Maned Ducks (*Chenonetta jubata*) were affected by the nutritional status of the laying females. Previous studies have shown that neither adding nor removing eggs affected clutch size of host Maned Ducks; that adding eggs to clutches did not increase nest desertion, nor did it reduce egg hatchability or fat level of females in late incubation; and that survival of ducklings in larger broods was similar to their survival in smaller ones. This study showed that fat levels of the female Maned Ducks at the end of laying were independent of the size and total fat content of their clutch; that clutch size and fat content of eggs varied inversely; and that the mean size of clutches did not differ between years but the proportion of females that bred did. The study also demonstrated that fat levels of females increased seasonally. The results are consistent with proximate and ultimate effects of nutritional factors, particularly the size of the female's fat reserve, on laying and clutch size of Maned Ducks. The study indicated that breeding females may trade the relative benefits and costs of early and late laying, high and low egg fat content, and small and large clutches to produce the clutch size that is optimum for them.

PROXIMATE control of clutch size in waterfowl (Anatidae) has been related to the nutrition of the laying female, either to her food supply during laying, or to the size of her pre-laying nutrient reserve (Bengston 1971, Ankney and MacInnes 1978, Raveling 1979, Drent and Daan 1980, Drobney 1980, Krapu 1981, Winkler and Walters 1983, Ankney and Afton 1988, Eldridge and Krapu 1988) (Fig. 1). Nutritional control of clutch size in waterfowl is usually assumed to operate by females either increasing their level of stored nutrients prior to laying, or by feeding as much as possible during egg formation; and then by laying the maximum number of eggs allowed by the size of their nutrient reserve and/or their rate of food intake (Drent and Daan 1980, Winkler and Walters 1983). This mechanism of clutch control where clutch size increases with the nutritional level of the female can be termed the continuous model (Fig. 1).

However, nutrition may proximately control avian clutch size by a different mechanism from that of the continuous model. Females may have a pre-determined clutch size, and commence laying as soon as they have stored sufficient nutrients and/or ingested sufficient food to produce this pre-determined number of eggs. This mechanism of clutch control, I term the threshold model (Fig. 1). Under the threshold model, if a female's nutritional level was too low to produce her full clutch, she would not breed rather than lay fewer eggs. Both clutch size and the decision to lay are proximately determined by nutritional factors in both models (see Fig. 1), but their methods of operation are different. Which of the two mechanisms (continuous and threshold) control clutch size in a species can be determined by the species' responses to good and poor nutritional conditions for breeding (Table 1).

Since Maned Ducks, in common with most other ducks store fat for egg production, but obtain protein for their eggs by feeding during laying (Ankney and Afton 1988, Briggs Chap. 4), their individual clutch sizes are likely to be influenced by the size of their fat reserves and/or by their intake of fat and protein during laying. The hypothesis that the fat reserve of the female proximately regulates clutch size of ducks cannot be tested directly (Ankney and Afton 1988), so I adopted an alternative approach of testing predictions of the hypothesis.

The general hypothesis of proximate regulation of clutch size by the amount of the female's fat reserve, firstly predicts that artificially adding or removing eggs will not affect the number of eggs that a female lays (Klomp 1970, Briggs 1985, Chap. 6). Secondly, it predicts that the fat level of female ducks at the end of laying will be independent of the size and total fat content of their clutch, i.e., clutch size is related to the pre-laying fat level of the females rather than to their post-laying level (Korschgen 1977, Ankney and MacInnes 1978, see Drent and Daan 1980: Fig. 1)). Thirdly, it predicts that the fat content of a female's eggs and her clutch size will be inversely related (see Rohwer 1988). The alternative hypothesis, that clutch size is regulated proximately by the female's food intake during laying rather than by her level of stored fat, predicts that females will continue to lay when eggs are removed from their nests (Briggs Chap. 6); that the clutch size of individual females will be unrelated to their pre-laying fat level, but will be inversely correlated with their post-laying fat level (Ankney and MacInnes 1978); and that clutch size and fat content of component eggs will be unrelated.

(Insert Figure 1, Table 1 hereabouts)

Nutrition for the laying female, either in the form of endogenous reserves or exogenous food availability, can regulate clutch size in waterfowl by ultimate, evolutionary processes (Lack 1967), as well as by proximate means (Winkler and Walters 1983) (Fig. 1). The hypothesis that clutch size is ultimately controlled by the amount of nutrients available to females for egg formation, either by their feeding during laying or from their body reserves, predicts that artificially adding eggs to clutches will not reduce fat levels of females in late incubation, the hatchability of their eggs, or their brood survival, nor will it increase their rate of nest desertion (Pellis and Pellis 1982, Rohwer 1985, Lessells 1986). That is, the hypothesis predicts that clutch size is constrained by the demands of egg formation, rather than those that occur post-laying. The alternative hypothesis, that clutch size is regulated ultimately by processes that occur post-laying predicts that hatching success and duckling survival will be reduced in enlarged clutches. The hypothesis that stored fat ultimately regulates clutch size also predicts an inverse relation between clutch size and egg fat (Lack 1967, Rohwer 1988).

I tested these hypotheses in Maned Ducks *Chenonetta jubata*. Female Maned Ducks of this species store fat prior to breeding for later use during egg production (44% of pre-laying reserves are used during laying; 42% of fat in their clutch comes from stored reserves (Briggs, Chap. 4)), and while incubating (47% of post-laying reserves are used during incubation (Briggs Chap. 4). They do not store protein for egg production (Briggs Chap. 4). I investigated whether clutch size in Maned Ducks is regulated proximately and/or ultimately by the nutritional status of the laying female (Fig. 1), either by the size of her fat reserve prior to laying, or by the amount of food available to her during egg formation. I also investigated the mechanism (continuous or threshold) by which proximate, nutritional control of laying and clutch size might operate in Maned Ducks (Table 1, Fig. 1), and measured other relevant laying parameters (duration, timing, egg characteristics).

METHODS

Study species and area. - Maned Ducks are grazers, and feed on pasture grasses and legumes (Kingsford 1989a). They occur in a wide variety of habitats in Australia (Frith 1967, Blakers et al. 1984). Their food availability is determined largely by rainfall (Frith 1967, Fitzpatrick and Nix 1970, Kingsford 1989b). The females nest in tree cavities, and readily use artificial nest boxes (Frith 1967, Briggs Chap. 5, 6). Both males and females can breed at one year of age (Briggs unpubl. data). Further information on their ecology can be found in Frith (1967), Kingsford (1986a, 1989a, b) Briggs (1990, Chap. 4) and Lawler (1990). The study was undertaken near Canberra (35° 15', 149° 10' E) on the southern tablelands of southeastern Australia. Details of the study area are given in Briggs (1990, Chaps. 4, 5, 6).

Breeding female and clutch data. - Twenty four nest boxes and 2 tree cavities in the study area were searched for nests every week in 1986. In 1987 and 1988, 60 nest boxes and 4 natural cavities were searched for nests every 4 days. Active clutches were visited weekly in 1986, and daily in 1987 and 1988. New eggs were weighed (to nearest 1 g) (1987 and 1988 only), measured (length and breadth to nearest 1 mm), and numbered during these visits. In 1987 and 1988, eggs were added to and removed from some clutches (after 4 eggs had been laid), and effects of this egg manipulation on clutch sizes of host females were ascertained (Briggs Chap. 6). The effects of enlarged clutches on egg hatchability (= percentage of eggs that hatch in successful nests (Rohwer 1985)), nest desertion, duckling survival, and on fat levels (Briggs 1989) of females in late incubation (17-28 days) were also determined in 1987 and 1988 (Briggs Chap. 5). Known extra eggs in clutches that had been parasitized (= more than 7 eggs per week in 1986, and more than 1 egg per day in 1987 and 1988) were excluded from analyses of clutch size. I assumed that the number of non-parasitic eggs laid in a nest equalled the clutch size of the host female (see Briggs Chap. 5). However, which eggs belonged to the parasitic female could not be determined, so all eggs in a clutch were included in the analyses of egg characteristics. Parasitic eggs did not comprise more than 31% of the total (host plus parasite) number of eggs in any clutch.

All clutches used in this analysis had ≤ 4 eggs when found. Laying interval was expressed in days, and calculated as the number of days from finding an active nest to the beginning of incubation, divided by the number of host eggs laid during the same period. The date that laying commenced was the Julian date of finding the clutch minus the number of host eggs present, corrected for laying interval. Incubation was considered to commence with down deposition and constant egg warming. Fat levels of incubating females trapped in late incubation in 1986, 1987 and 1988 (Briggs

1989, Chaps. 4, 5) were extrapolated back to the end of laying (= beginning of incubation), and to the beginning of laying (0-7 days before the first egg was laid), using data on average fat loss during incubation (0.53 g per day), and during laying (3.0 g per egg) from Briggs (Chap. 4). Data from 7 individually marked females, whose clutches were found in 2 or 3 years, were available to estimate repeatabilities of clutch and egg characteristics (Lessells and Boag 1987).

Ducks were captured during 1986 and 1987 in the study area in traps set near waterbodies and baited with grain (Briggs Chap. 4). The total number of captured, adult (≥ 4 months old (Kingsford 1986b, 1988; Briggs unpubl. data)) females that were laying (determined by their wide pelvic spread and/or swollen abdomen (Briggs Chap. 4)), incubating (with brood patches (Briggs Chap. 4)) and with young, were calculated as a proportion of all adult females trapped in the study area during the 1986 and 1987 breeding seasons (July - October). All ducks caught on nests and in traps were measured, individually colour and numerically banded, and released. Broods were surveyed weekly during and following breeding in 1986, 1987 and 1988 (July - December). Ducklings were aged from their plumage (Kingsford 1986b).

Egg analyses. - In 1987, 40 eggs were removed from 6 nests (range of 3-18 eggs removed per nest, including parasitic eggs), and in 1988, 32 eggs were removed from 10 nests (range of 1-7 eggs removed per nest) to determine their fat and protein content. All eggs analysed were collected within 24 h of being laid, and were frozen, thawed, and hardboiled at 100°C. The combined yolks and albumen of all eggs except 12 collected in 1988 were separated from their shells leaving the membranes attached to the shells. The combined yolks and albumen were then oven-dried to constant weight at 60°C, and weighed. Fat was extracted from the yolks plus albumen of individual eggs in a Soxhlet apparatus for 24 h, using carbon tetrachloride as the solvent (see Briggs 1989). The oven-dry residue of each egg remaining after fat extraction (the shell-free lean dry mass) was regarded as protein. Shell membranes (see Alisauskas and Ankney 1985) from 12 of the eggs collected in 1988 were combined with the yolk and albumen for fat extraction and residue weighing, rather than discarded with the shell. Data from eggs treated this way were not used in the comparison of egg composition between years.

Data from all eggs analysed were used in the regression analyses (with a dummy variable indicating the method of preparation) for predicting fat and protein content of eggs from their size. Fat (F)(g) and protein (P)(g) content of eggs were regressed against egg length (L)(mm), breadth (B)(mm), fresh mass (g), LB^2, year of laying (Y)(1987=1, 1988=2, and method of preparation (S)(shell membranes excluded = 1, membranes included = 2) to determine which equations explained most variance in dry fat and protein content of individual eggs. Independent variables for estimating egg fat and protein were retained in the prediction equations only if their partial regression coefficients were significantly different from zero ($P<0.05$). Fat and protein content of eggs that were measured and left in clutches to be incubated, were calculated from these equations. Protein content was calculated for eggs measured in 1986-88; fat content was only calculated for eggs measured in 1987 and 1988. The number of light and dark rings in the yolks of 4 eggs collected in 1988 were counted after they were hardboiled, but before they were oven-dried. The number of rings in the yolk of an egg equals its development time in days (Romanoff and Romanoff 1949:202). Statistical tests follow Sokal and Rohlf (1981) and Zar (1984). All values reported are means ± SE unless otherwise stated.

RESULTS

Previous studies. - Experimentally adding or removing eggs did not affect the number of eggs laid by host female Maned Ducks (Briggs Chap. 6). Extra eggs added to clutches did not increase desertion of nests by females or egg hatchability, nor did they reduce fat levels of females in late incubation (Briggs Chap. 5). Percentage mortality in larger broods was not higher than in smaller ones (Briggs Chap. 5).

This study. - The fat content of individual eggs was best predicted by: $F = -9.58 + 0.30\ Y + 0.18\ L + 0.14\ B$ ($r^2 = 0.43$, $F_{3,68} = 18.5$, $P < 0.001$). Protein content of individual eggs was best predicted by: $P = -17.54 + 0.62\ S + 0.13\ L + 0.40\ B$ ($r^2 = 0.74$, $F_{3,68} = 65.9$, $P < 0.001$). The average number of rings in a sample of 4 eggs was 6.5 ± 0.3; thus eggs of Maned Ducks take approximately 7 days to develop.

There were no significant ($P > 0.05$) differences between years in clutch size, distribution of clutch sizes ($G_3 = 3.86$), size of broods between 1 and 14 days old, distribution of brood sizes ($G_8 = 14.95$), average laying date, laying interval, length and breadth of eggs in incubated clutches, or measured protein content of eggs removed from clutches (Table 2).

(Insert Table 2 hereabouts)

Conversely, the date that laying commenced (1987, 18 July; 1988, 20 June), the number of broods (1-14 days old) (1986, 43; 1987, 24; 1988, 47), and the proportion of adult females trapped between July and October that were laying, incubating or with ducklings (1986, 25/49; 1987, 33/103; $G_1 = 4.94$, $P < 0.05$) showed marked annual differences between 1987 and the other two years, as did rainfall during the pre-laying and laying periods (June-October; 1986, 303 mm; 1987, 208 mm; 1988, 309 mm). The mean level of fat measured in eggs removed from clutches did not differ significantly between 1987 ($n = 6$ clutches) and 1988 ($n = 5$ clutches) ($\bar{x}$

= 7.1 ± 0.25, $F_{1,9}$ = 2.94, $P > 0.05$), but the eggs collected in 1988 contained more fat for their length and breadth (average of an extra 0.3 g/egg from the regression equation), than those collected in 1987.

Clutch size increased with the the fat level of female Maned Ducks at the beginning of laying (Fig. 2). Fat levels of females at the end of laying were not related to their clutch size (r^2 = 0.01, $F_{1,28}$ = 0.38, $P > 0.10$), to the total fat content of their clutch (r^2 = 0.02, $F_{1,22}$ = 0.65, $P > 0.10$), or to the total protein content of their clutch (r^2 = 0.00, $F_{1,27}$ = 0.00, $P > 0.10$). The mean fat content of component eggs decreased as clutch size increased and *vice versa* (Fig. 3), but clutch size was not related to mean egg protein (r^2 = 0.02, $F_{1,38}$ = 0.83, $P > 0.10$). The inverse relation between egg fat and clutch size was greater early in laying than later (before 8 August, $r^2 = 0.37$, $F_{1,11}$ = 7.04, $P < 0.05$; after 8 August, r^2 = 0.04, $F_{1,20}$ = 0.86, $P > 0.10$ (Fig. 3). Reduced egg fat in larger clutches did not wholly compensate for increased clutch size; larger clutches contained more total fat than smaller ones (Fig. 3, Table 3).

(Insert Figures 2, 3, Table 3 hereabouts)

Neither clutch size, brood size (1-14 days) nor egg composition declined seasonally (combined 1986, 1987, 1988 data; clutch, r^2 = -0.00, $F_{1,40}$ = 0.13, $P > 0.10$; brood, r^2 = 0.00, $F_{1,99}$ = 0.02 , $P >$ 0.10; egg fat, r^2 = 0.06, $F_{1,33}$ = 2.06, $P > 0.10$; egg protein, r^2 = 0.04; $F_{1,38}$ = 1.45,

$P>0.10$). The fat level of females at the end of laying increased with laying date (Fig. 4). The fat level of pre-laying females also showed a weak increase with time (r^2 = 0.39, $F_{1,22}$ = 3.95, 0.10 > P > 0.05).

(Insert Figure 4 hereabouts)

Repeatabilities of clutch size (0.37, $F_{6,9}$ = 2.32, $P>0.10$), laying date (0.39, $F_{6,9}$ = 2.44, 0.10> $P>0.05$, egg dimensions (length, 0.34, $F_{6,9}$ = 2.15, $P>0.10$; breadth, 0.46, $F_{6,9}$ = 2.93, 0.10> $P>0.05$), and laying interval (0.34, $F_{6,9}$ = 2.15, $P>0.10$) were moderate; but the sample sizes were small and the F ratios were not significant.

DISCUSSION

The absence of any effect of adding or removing eggs on clutch size, the absence of a relation between fat level of post-laying females and either the size of their clutch or its total fat content, and a negative correlation between clutch size and egg fat, all are consistent with proximate determination of clutch size in Maned Ducks by the size of the female's fat reserve (Korschgen 1977, Ankney and MacInnes 1978, Rohwer 1988, Briggs Chap. 6). Although the data are confounded, the positive relation between the fat reserve of pre-laying females and the size of their clutch also indicates that clutch size in Maned Ducks, as in other waterfowl (Drent and Daan 1980, Winkler and Walters 1983, Ankney and Afton 1988), is proximately regulated by the fat level of the female at the beginning of egg formation (Hamann and Cook 1989).

The lack of annual variation in clutch size, together with the lower number of broods and fewer females breeding in the drier year strongly suggest that Maned Ducks laid a pre-determined number of eggs, using the threshold mechanism of clutch regulation (see Table 1). That is, they commenced ovulation when they attained the level of fat storage required for forming their clutch, and then laid the number of eggs corresponding to that fat level. Nutritional control of laying and clutch size in Maned Ducks by such a threshold mechanism is supported by other data. Crome (1986), working in south-western New South Wales, and Kingsford (1989b), working near my study area, found that the number of clutches and broods produced by Maned Ducks varied fivefold between years with different environmental conditions. Kingsford's (1989b) study also showed that average brood size (1-7 day old ducklings) of Maned Ducks was not significantly lower in a drought year.

Whether the continuous or threshold mechanism (see Fig. 1) of clutch control by proximate nutritional factors regulates clutch size in waterfowl other than Maned Ducks can be determined using the predictions in Table 1. Ankney and MacInnes (1978) specifically rejected the concept of a threshold mechanism for controlling clutch size in Lesser Snow Geese (*Chen caerulescens caerulescens*). Their conclusion is supported by the annual variation in clutch size in Lesser Snow Geese found by other authors (Davies and Cooke 1983). The threshold model is also unlikely to apply in

Canada Geese (*Branta canadensis*). Clutch size in some races of this species is proximately determined by female nutrient levels, but clutch size and distribution of clutch size varied between years (MacInnes et al. 1974, Raveling and Lumsden 1977, MacInnes and Dunn 1988). However, the threshold model may apply to Lesser Scaups (*Aythya affinis*). Clutch size in this species did not vary between years, but the rate of non-breeding did (Afton 1984). Female Lesser Scaups only bred when conditions were suitable for them as individuals, and when their probability of breeding success was high (Afton 1984). The reasons why some species use the threshold, rather than the continuous mechanism of proximate clutch control are unknown. Both Maned Ducks and Lesser Scaups breed in seasonally variable environments (Frith 1967, Afton 1984, Kingsford 1989b, Lawler 1990). Perhaps the threshold mechanism allows female ducks that nest in erratic environments to evaluate whether environmental conditions are right for breeding, better than the continuous mechanism does. In this context, it is worth noting Duncan (1987a) found that the clutch size in Pintails (*Anas acuta*) did not vary between years, in spite of drought in one year of his study. Pintails also nest on ephemeral waterbodies whose availability varies between years (Duncan 1987a).

The absence of any effect of adding eggs to clutches on fat levels of females in late incubation, or on their levels of nest desertion or egg hatchability, and the absence of reduction in survival rates of ducklings with increased brood size, are all consistent with ultimate control of clutch size in Maned Ducks by nutritional factors, either by the level of the female's stored reserves or by the availability of food to her during laying. The negative relation between clutch size and egg fat is consistent with ultimate regulation of clutch size by the size of the female's fat store (Lack 1967, Rohwer 1988). These conclusions are also supported by other evidence. Kingsford (1986a:126) noted that the amount of time that Maned Duck parents were vigilant did not increase with their brood size. He therefore concluded that clutch size in Maned Ducks was determined by the female's ability to form eggs, rather than by behavioural constraints on parents. In this respect, Maned Ducks are similar to other waterfowl (Dow and Fredga 1984, Rohwer 1985, Lessells 1986, but see Pellis and Pellis 1982).

Ultimate regulation of clutch size in waterfowl by the food available to the laying female for egg production has been proposed by Lack (1967), Batt and Prince (1979) Winkler and Walters (1983) and Rohwer (1985). Other authors considered that nutrients available to the female determine clutch size proximately (Johnsgard 1973, Ankney and MacInnes 1978, Duncan 1987a, Ankney and Afton 1988). This study did not refute either of the hypotheses that the nutritional level of female Maned Ducks regulates their clutch size proximately, and ultimately, through the amount of fat stored by the pre-laying female.

Proximate (by the threshold mechanism), and ultimate regulation of clutch size in Maned Ducks, by the size of the female's fat reserve poses the following questions. Why do some females lay smaller clutches than others? Why do they commence laying with say, only sufficient fat reserves for an 8 egg clutch when extra time spent storing more fat would permit a 12 egg clutch? The answer may be that individual Maned Ducks trade the costs and benefits of large and small clutches, low and high egg fat, and late and early laying to produce their optimum clutch size and egg fat content, according to their own ability (= quality).

Smaller clutches require less body fat than larger ones. Therefore, they could presumably be laid sooner in the season, because fat levels of females increased seasonally. Early laying is generally advantageous to ducks because their chance of reproductive success declines seasonally (Toft et al. 1984). Early laying is likely to specifically enhance the breeding success of Maned Ducks in many habitats because pasture growth and quality, and wetland availability decrease towards the end of the breeding season, and the number of predators of ducklings increases (Kingsford 1986a: 71, Lawler 1990).

Therefore, females who forage efficiently and build up their fat reserves rapidly, would do best to lay early, and either produce as large a clutch as possible or a smaller clutch with as much egg fat as possible. Conversely, females who forage inefficiently and are slow at acquiring body fat would have to trade the advantages and disadvantages of laying a small clutch sooner or a larger clutch later in the season, as well as consider their ability to produce eggs with sufficient fat for survival of embryos and young ducklings (Rohwer 1986, Duncan 1987b). Thus both early and late laid clutches would vary in size with no consistent trend with time, and the negative correlation between clutch size and egg fat would be stronger during the earlier part of the breeding season, as occurred in these Maned Ducks.

Maned Duck females may therefore lay the number of eggs that optimize their own individual reproductive success as do Great Tits (*Parus major*) (Pettifor et al. 1988). Individual Great Tits differ in their ability to raise chicks; each female accordingly lays the size of clutch from which she and her mate can maximize recruitment of their young (Pettifor et al. 1988). Artificially adding eggs to clutches did not reduce survival of ducklings after hatching in Maned Ducks (Briggs Chap. 5), because brood rearing is not a constraint on their reproductive success, as it is in altricial species such as Great Tits. However, Maned Ducks may be practising a similar strategy as Great Tits except that egg production rather than caring for young constrains their reproductive success. The quality of individual Maned Duck females may vary (e.g. with access to food, age, experience, rapidity of fat build-up prior to laying, male attentiveness), causing breeding birds to make the decision to lay, and to adjust their clutch size and laying patterns (timing, egg composition) according to their individual ability.

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TABLE 1. Alternative predictions of continuous and threshold mechanisms for proximate control of clutch size in waterfowl by nutritional factors.

Continuous	Threshold
1. Little change in proportion of adult females that breed between good and poor breeding years.	1. High proportion of adult females breeding in good years, low proportion in poor years
2. Large clutches in good years, small clutches in poor years, and hence high annual variability in mean clutch size.	2. Little variation in clutch sizes of individuals, or in mean clutch size between years.
3. Skewed distributions of clutch size according to breeding conditions (to the left in good years, to the right in poor years).	3. Little change in distribution of clutch sizes between years.

TABLE 2. Mean values (± 1 SE) of breeding variables of Maned Ducks that did not vary significantly (ANOVAS, all $P>0.05$) between years.

Variable	Mean	df	F
Clutch size[a]	10.7 ± 0.3	2,43	2.43
Brood size[a]	8.1 ± 0.7	2,207	3.01
Laying date[a]	24 Aug ± 3 days	2,47	0.22
Laying interval[b]	1.6 ± 0.01 days	1,31	0.01
Egg length[b]	58.8 ± 0.44 mm	1,35	2.60
Egg breadth[b]	41.3 ± 1.25 mm	1,35	0.04
Egg protein[b]	7.3 ± 0.15 g	1,9	0.46

[a] Tested for differences between 1986, 1987 and 1988.

[b] Tested for differences between 1987 and 1988.

TABLE 3. Effect of clutch size and estimated egg fat (g) on estimated total clutch fat (g) and incremental increase in clutch fat (g) with clutch size. Data from Figure 3.

Clutch size	Estimated egg fat	Estimated clutch fat	Incremental increase in clutch fat
8	7.4	58.9	-
9	7.3	65.6	6.7
10	7.2	72.2	6.6
11	7.1	78.6	6.4
12	7.1	84.9	6.3
13	7.0	91.1	6.2
14	6.9	97.1	6.0

Fig. 1. Diagramatic representation of hierarchy of hypotheses and mechanisms of nutritional control of clutch size in waterfowl.

Fig. 2. Relation between fat level (g) of pre-laying female Maned Ducks and their clutch size. The fat level of pre-laying females was calculated as: fat level at the end of laying + (clutch size x average fat loss from females per egg laid)(Briggs Chap. 4). Statistical analysis of the relation is not appropriate because the data are confounded (clutch size is a component of both axes).

Fig. 3. Relation between clutch size and mean fat content (g) of component eggs. The regression equation is: Cutch size = 7.9 - (0.07 x Egg fat). $r^2 = 0.12$, $F_{1,33} = 4.7$, $P < 0.05$. (▲), laying commenced before 8 August; (△), laying commenced after 8 August.

Fig. 4. Relation between laying date (Julian date) and fat level (g) of individual females at the end of laying. The regression equation is: Female fat level = 2.4 + (0.16 x Lay date). $r^2 = 0.23$, $F_{1,22} = 6.5$, $P < 0.05$.

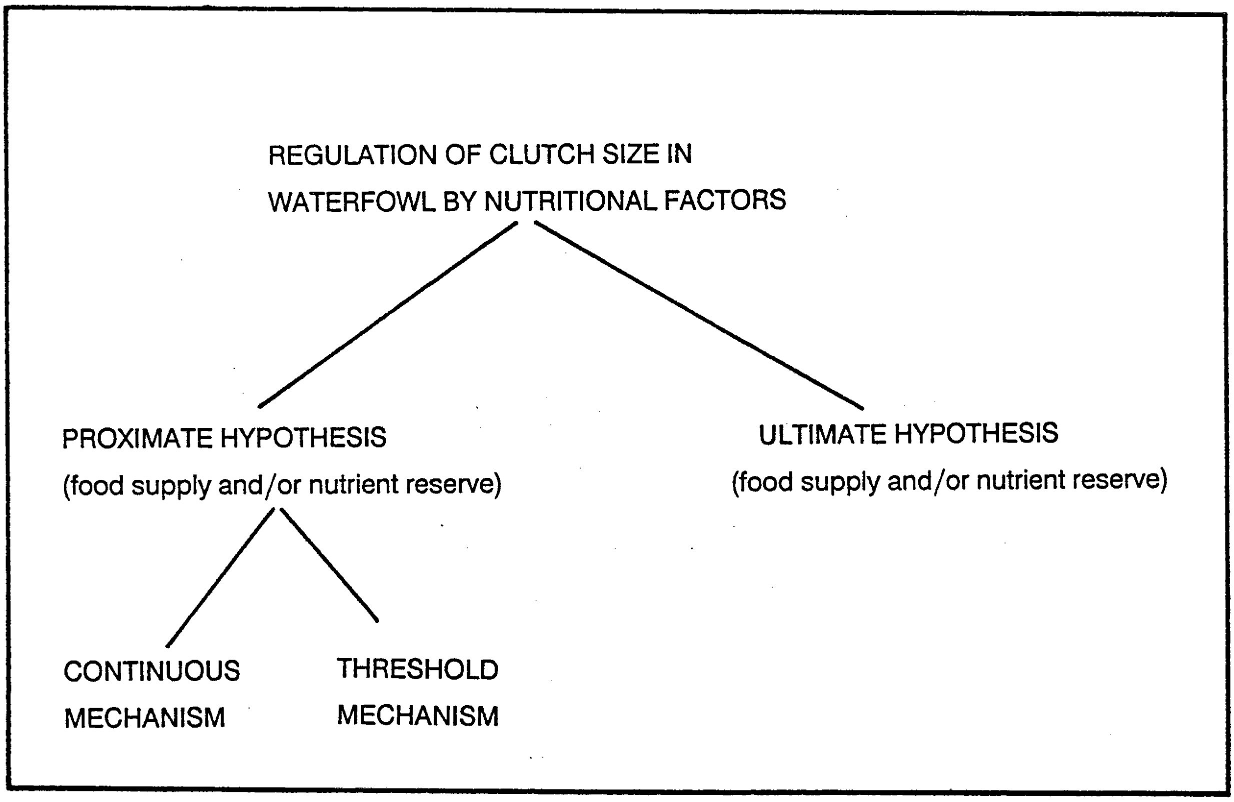

FIGURE 1

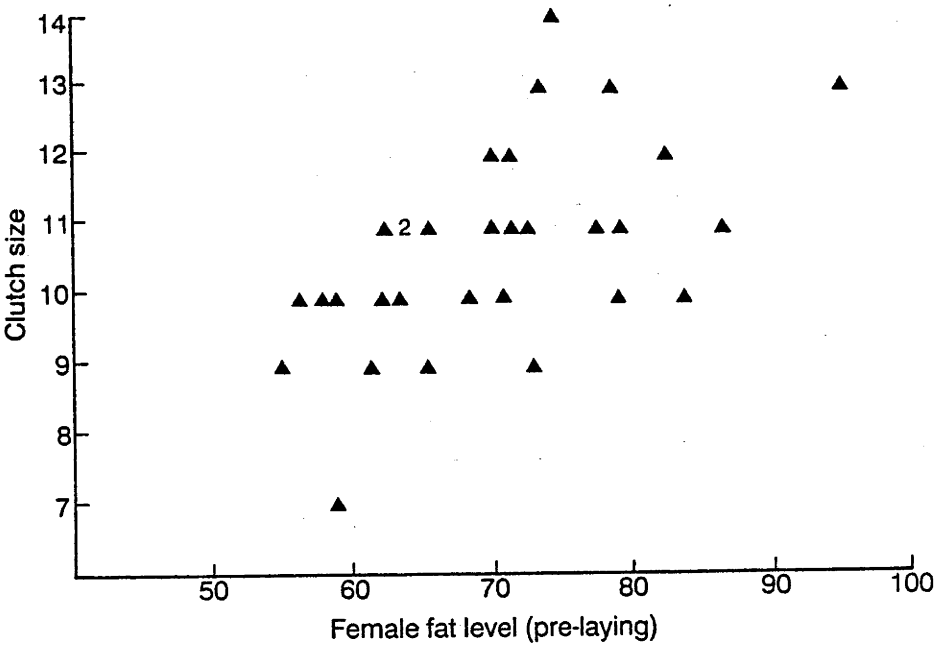

FIGURE 2

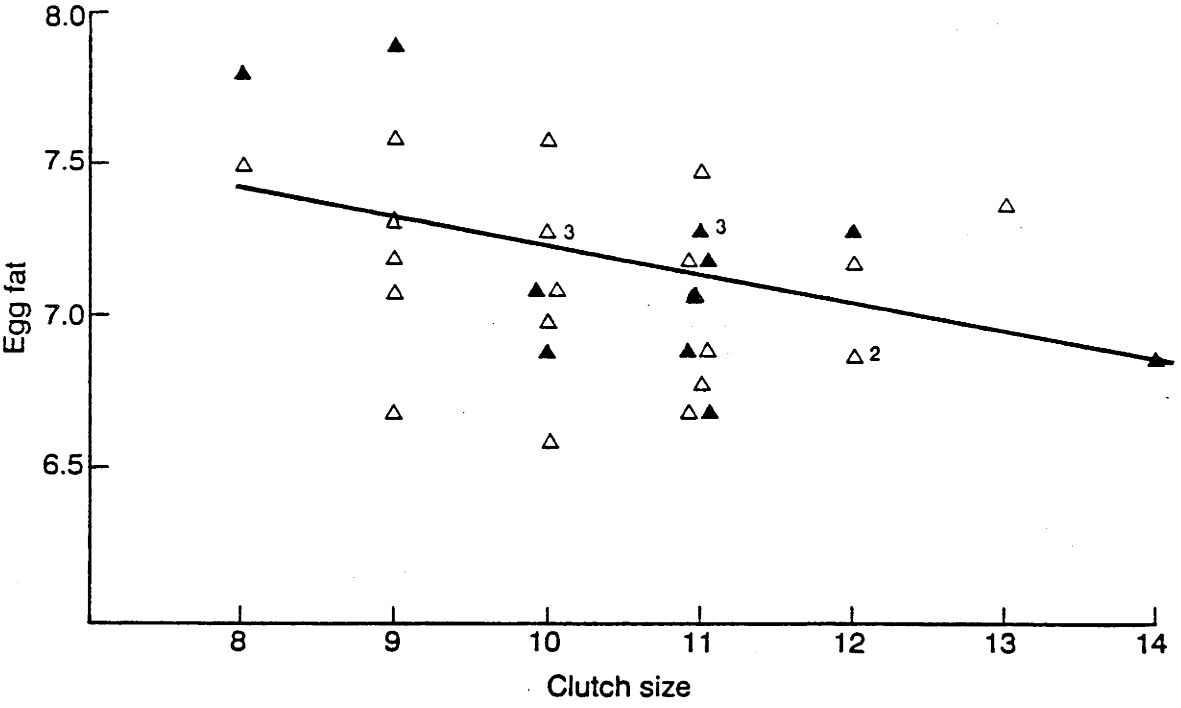

FIGURE 3

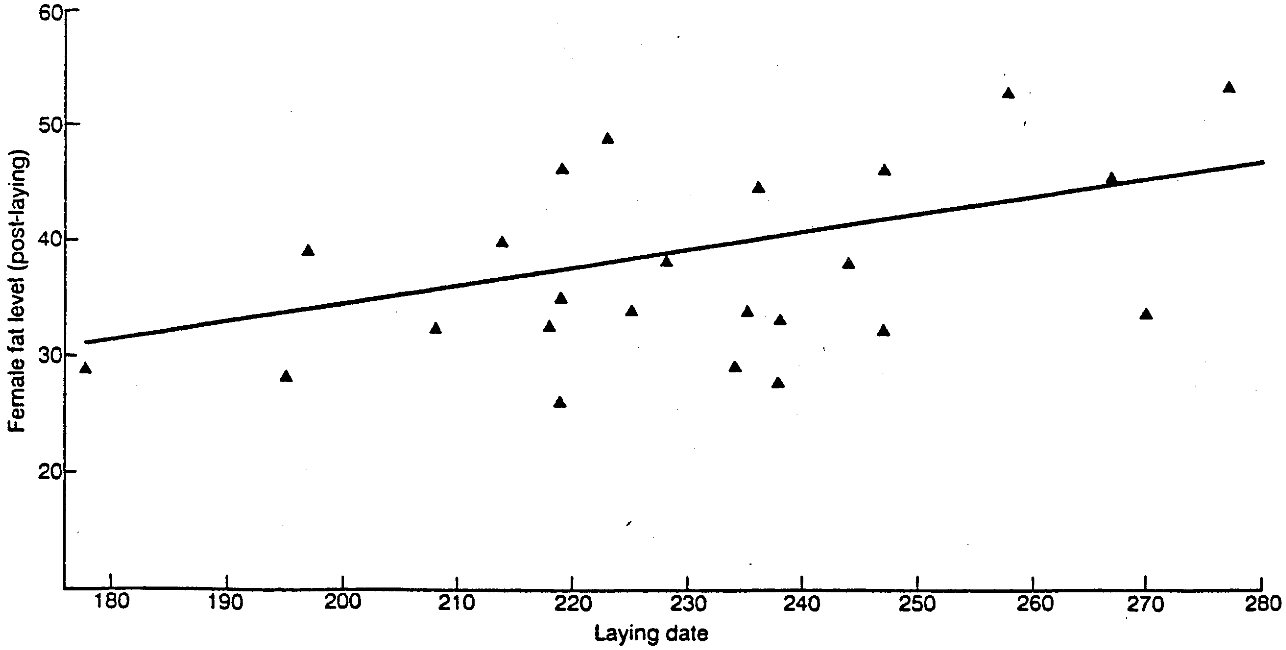

FIGURE 4

CHAPTER 8.

CONCLUSIONS.

CONCLUSIONS

Reproduction is energetically expensive for female maned ducks. During laying and incubation females lose 70% of their average pre-laying fat content; there is strong evidence that clutch sizes are regulated by the amount of fat that females store prior to laying; and some females lay parasitically in other females' nests, which removes the parasites' costs of incubation and brood care. However, neither the percent increase in fat content of female maned ducks prior to laying, nor the proportion of their clutch derived from stored fat, is particularly high compared with other waterfowl. Female maned ducks do not store any protein for egg production.

The study has demonstrated that paired males help their female mates to retain body fat. Females feed more than males while males are more alert than females throughout the year; females gain fat earlier prior to nesting than do males; and paired females are fatter during the non-breeding period than unpaired females whereas fat levels do not differ between paired and unpaired males. Only males lose fat between incubation and brood care, and therefore they contribute energetically to raising their ducklings.

Maned ducks breed throughout south-eastern and south-western Australia (Blakers et al. 1984), frequently on or near ephemeral wetlands. Such ephemeral wetlands can dry and flood unpredictably, and nesting does not occur regularly under such conditions. Throughout much of their range, maned ducks breed whenever conditions are suitable regardless of time of year (Frith 1967, Lawler 1990).

The nature of their habitat means, firstly, that maned ducks must be able to respond rapidly when the right environmental conditions occur for breeding (see Frith 1967, Kingsford 1986, 1989, Lawler 1990). Second, females must not lose their mobility by becoming too heavy prior to laying, in case their breeding habitat disappears. Third, females must not drop their body fat reserves too low, in case their breeding wetlands dry out at the end of brood rearing. Thus, females maintain body fat during the non-breeding period for later use in reproduction; they increase their body fat further prior to laying and expend most of their fat reserves during laying and incubation; but they do not lose further body fat during brood care, following incubation.

Maintenance of stored fat during non-breeding, further acquisition of fat prior to laying, use of most of their fat reserves during egg production and incubation, and no further loss of body fat after incubation, would not be possible for female ducks breeding in unpredictable environments without continuous, sustained pair bonds and male assistance with brood care, as occur in maned ducks. Sustained pair bonds and male assistance with raising ducklings are uncommon in ducks, although they are relatively more common in southern hemisphere and lower latitude species than in higher latitude, northern hemisphere ones (McKinney 1985, Fullagar *et al.* 1988, Norman and McKinney 1987, Brewer 1989, Buitron and Nuechterlein 1989, McKinney and Brewer 1989, but see Savard 1985, Gauthier 1987). The different pairing and brood caring behaviours of southern hemisphere and near tropical ducks, compared with northern, cool temperate species, may be related to their different breeding environments and consequently their different patterns of nutrient acquisition and use for breeding. Unpredictable and aseasonal breeding habitats may favour mate retention and male brood care (see Fullagar *et al.* 1988, Rohwer and Anderson 1988).

Relations between breeding behaviour of Australian waterfowl, their environments, and how they gain and use the nutrients they require for reproduction present an absorbing field for further study.

Some unanswered questions about the breeding ecology of maned ducks are as follows. How do females choose their mates? Do they use cues that predict future male breeding ability? What are the characteristics of parasitic females, and their mates? Are parasitic females in poorer condition than females that lay normally? Do the rates and degrees of fat acquisition prior to laying differ between individual females? Does fat acquisition vary with the age or experience of females, or their mates? Do the proportions of stored and ingested nutrients in their eggs differ between females? Do females use stored body fat while ingesting high protein food for egg formation? How repeatable are laying characteristics of individual females (clutch size, time of laying, egg characteristics) between years? What happens to the body condition of females that lose their mates from predation early in brood care? Some of these questions can be answered by experimental manipulation, some require detailed observations of wild and/or captive birds, and some cannot be answered readily with current technology. All would test and extend the observations and hypotheses reported and proposed in this thesis.

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APPENDIX 1.

PATTERNS OF EGG-LAYING IN PRAIRIE DUCKS.

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Patterns of Egg-laying in Prairie Ducks

S. V. Briggs[1,2]

Cole (1917) defined an indeterminate layer as one that both extends laying when eggs are removed and curtails laying when eggs are added to the nest. Rohwer (1984) experimentally showed that some captive, wild-stock Mallards (*Anas platyrhynchos*) extended laying when eggs were removed, but the same treatment did not induce extended laying in wild Mallards or wild Blue-winged Teal (*Anas discors*), in smaller samples of Gadwalls (*Anas strepera*), Northern Shovelers (*Anas clypeata*), or Canvasbacks (*Aythya valisineria*), or in a Green-winged Teal (*Anas crecca*). Nor did wild Blue-winged Teal curtail breeding when eggs were added to their nests. Rohwer (1984) removed and added eggs during the first part of the laying period in his experiments. The fourth and all subsequent eggs were removed from wild birds, the third and subsequent eggs were removed from captive birds, and 6 or 8 eggs were added to nests that already contained 2 or 3 eggs.

From these experiments, Rohwer (1984), (1) concluded that wild ducks do not lay indeterminately, as has been reported previously (Delacour 1964, Andersson and Eriksson 1982), and (2) suggested that nutrition is not the proximate determinant of clutch size in prairie ducks because eggs had to be removed for extended laying to occur. These conclusions may not be valid.

In a review of clutch-size determination in birds, Klomp (1970: 102) gave a critical test for distinguishing between direct and indirect proximate effects of food on clutch size of indeterminate layers. Indeterminate layers will not protract laying when eggs are removed from the nest if food has a direct proximate effect, but will if the effect of food is indirectly proximate. By extension, laying will not be curtailed when eggs are added if the effect of food is direct, but will be if it is indirect. Food has a direct proximate effect on clutch size if it influences the physical condition of the female, so that the number of eggs produced is determined by the amount of material available for yolk and albumin production. Food has an indirect proximate effect on clutch size if it influences the physiological mechanism controlling ovarian activity. The critical point is that laying will not be extended or curtailed in indeterminate layers if food has a direct proximate effect on clutch size.

Whether food has either or both proximate and ultimate effects on clutch size is unclear. Rohwer (1984) suggested that food is not a proximate determinant. Bengston's (1971) data on diving ducks imply the reverse. Ankney and MacInnes (1978) suggested that clutch size in female Lesser Snow Geese (*Chen caerulescens caerulescens*) is determined by the size of her nutrient reserves, and hence that much variation in clutch size between females is caused by proximate rather than ultimate factors. Batt and Prince (1979) considered laying date to be the main factor controlling clutch size in Mallards and noted that the proximate effect of food may not be the only reason for variation in laying date. Their results indicated that food ultimately affects individual laying date, and hence clutch size. But they did not specifically reject a proximate influence of food on clutch size.

Rohwer's (1984) data on clutch manipulation in wild ducks are consistent with a direct proximate effect of food on clutch size of an indeterminate layer. His data from some captive ducks are consistent with an indirect proximate effect of food on clutch size of an indeterminate layer. None of his data refute the possibility that ducks are indeterminate layers or that their clutch size is influenced proximately by food. I suggest that the question of whether wild ducks are determinate or indeterminate layers remains unresolved. Further experimental studies appear warranted.

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APPENDIX 2.

ABDOMINAL FAT AND PERCENTAGE WATER AS PREDICTORS OF BODY FAT IN ADULT MANED DUCK, *CHENONETTA JUBATA*.

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Abdominal Fat and Percentage Water as Predictors of Body Fat in Adult Maned Duck, *Chenonetta jubata*

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Abstract

We derived 10 best fit regression equations for estimating body fat mass in maned duck carcasses. Body fat can be estimated from abdominal fat mass (females, $R^2 = 0\cdot86$; males, $R^2 = 0\cdot81$), percentage water (combined sexes, $R^2 = 0\cdot83$), and the Child–Marshall index (combined sexes, $R^2 = 0\cdot91$). We recommend that body fat be estimated by the Child–Marshall equation where carcasses can be dried, and by abdominal fat equations otherwise.

Introduction

Relations between waterfowl reproduction and survival and their body fat deposits have attracted considerable attention (e.g. Ankney and MacInnes 1978; Drobney 1980; Krapu 1981; Baldassare *et al.* 1986; Hepp *et al.* 1986; Hohman 1986), both at the individual and population level. Measuring body fat by solvent extraction is time-consuming and costly. Hence the interest in fat levels has stimulated development of fat indices which are reliable and cheap (see Bailey 1979; Johnson *et al.* 1985).

We are investigating body fat levels in maned duck, *Chenonetta jubata*, in relation to reproductive state and environment. As part of this study we derived three indices of absolute body fat in adult birds. One index is based on weight of abdominal fat and two are based on water content of the carcass. All three indices have been used previously for predicting waterfowl fat levels (Woodall 1978; Wishart 1979; Campbell and Leatherland 1980; Chappell and Titman 1983; Thomas *et al.* 1983; Whyte and Bolen 1984; Gauthier and Bedard 1985; Hohman and Taylor 1986).

Study Area and Methods

Maned duck were obtained from Lake Eucumbene (36°15'S.,148°15'E.) in southern New South Wales. Specimens for predicting body fat from abdominal fat were collected every 6–8 weeks between February 1985 and October 1985. Specimens for predicting body fat from carcass water content were collected every 6–8 weeks between August 1985 and July 1986.

Carcasses were weighed fresh, frozen, thawed, shaved and cut open, and the abdominal fat deposits [=omental fat (Woodall 1978)] removed. Carcasses and fat deposits were then dried separately to constant weight in a forced-air oven at 60°C, weighed and recombined. Feathers were dried, weighed separately and included with the dry carcass weights for determinating water content. The dried carcasses, including abdominal fat deposits, were then ground and two subsamples taken for fat analysis. Fat was extracted for 24 h using Soxhlet apparatus with carbon tetrachloride as the solvent (Green and Eberhard 1983). Percentage fat determined from subsample extraction was converted to total body fat using dry carcass mass (excluding feathers). Analyses were repeated if the two subsample percentages differed by more than 1%.

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The Child–Marshall index of body fat is based on carcass water content (Child and Marshall 1970). It has the following form:

Child–Marshall index = wet carcass mass − water mass/C,
where C = water mass/fat-free mass,
and thus
Child–Marshall index = wet carcass mass − fat-free mass.

This index relies on the assumption that water forms a constant proportion of fat-free carcass mass, i.e. that C is a constant which, once derived for a species, can be used repeatedly; then only measurements of wet carcass mass and water mass are necessary to calculate the index.

Relationships between predictor variables (abdominal fat, percentage water and Child–Marshall index) and the predicted variable (total body fat) were determined by regression analysis (Sokal and Rohlf 1981). Measurement errors in the predictor variables were assumed to be small relative to their ranges. We used linear models for relationships between percentage water, the Child–Marshall index and body fat, and linear and quadratic models for abdominal fat and body fat.

Table 1. Relationships between abdominal fat (AF), percentage body water (BW), the Child–Marshall index (CM) and total body fat (*Y*) in maned duck measured by solvent extraction

Abdominal fat and total body fat are in grams; '*b*' = slope of the regression where equations are in the form of $y=a+bx$; *using sex specific C values; **using combined sex C value (0·690)

Sex	*n*	Predictive equation	R^2	*F*	d.f.	SE of *b*
		Abdominal fat				
F	24	$Y=34{\cdot}99+7{\cdot}10\mathrm{AF}$	0·78	78·9	1, 22	0·57
F	24	$Y=28{\cdot}06+15{\cdot}22\mathrm{AF}-0{\cdot}83\mathrm{AF}^2$	0·86	66·8	2, 21	–
M	29	$Y=40{\cdot}85+5{\cdot}79\mathrm{AF}$	0·81	115·9	1, 27	0·55
		Percentage water				
F	38	$Y=775{\cdot}5-11{\cdot}16\mathrm{BW}$	0·85	203·0	1, 36	0·79
M	40	$Y=665{\cdot}9-9{\cdot}38\mathrm{BW}$	0·81	157·8	1, 38	0·75
F,M	78	$Y=700{\cdot}1-9{\cdot}94\mathrm{BW}$	0·83	363·8	1, 76	0·52
		Child–Marshall index				
F	38	$Y=11{\cdot}70+0{\cdot}80\mathrm{CM}$	0·90	325·8	1, 36	0·04
M	40	$Y=11{\cdot}80+0{\cdot}78\mathrm{CM}$	0·91	381·2	1, 38	0·04
*F,M	78	$Y=11{\cdot}65+0{\cdot}79\mathrm{CM}$	0·91	731·8	1, 76	0·03
**F,M	78	$Y=12{\cdot}19+0{\cdot}78\mathrm{CM}$	0·90	702·4	1, 76	0·03

Results and Discussion

Abdominal fat, percentage water and the Child–Marshall index are all good predictors of body fat in adult maned duck (all $P<0{\cdot}001$). All best fit equations were linear, except for the regression of total body fat in females on abdominal fat mass which was quadratic (Table 1, Fig. 1). Piersma (1984) found that a quadratic equation provided the best fit between weight of abdominal fat and weight of total fat in great crested grebe, *Podiceps cristatus*.

The slopes of the lines did not differ significantly ($P>0{\cdot}10$) between the sexes in any of the simple regression equations. Nor did the values (mean ± SE) of C differ significantly between male (0·693 ± 0·002) and female (0·687 ± 0·002) maned ducks. But the Child–Marshall equation determined with sex-specific C values was a better predictor of body fat for the combined sexes than that determined with the mean C value; 0·690 (see Table 1). Thus, when estimating body fat of maned duck from percentage water, use the equation for the combined sexes; when estimating from the Child–Marshall index, use the combined sexes equation with sex-specific C values; and use separate equations for each sex when estimating body fat level from abdominal fat mass.

Water content of fat-free carcass mass (C) in adult maned ducks is close to constant (coefficient of variation: ♀♀, 1·5%; ♂♂, 1·8%). This agrees with the findings of Johnson *et al.* (1985) for the white-fronted goose, *Anser albifrons*, and with Child and Marshall (1970) for a range of non-waterfowl species. But it conflicts with the results of Campbell and Leatherland (1980) who found considerable variation in the ratio in lesser snow goose, *Anser c. caerulescens*.

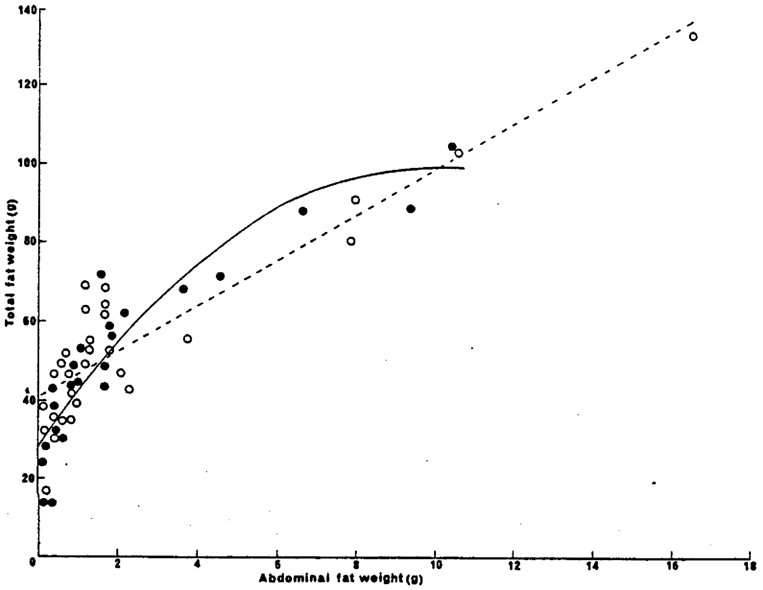

Fig. 1. Relationships between abdominal fat and total body fat in adult maned duck: (●——●), females; (O----O), males.

All three methods of estimating fat are relatively simple and cheap. The Child–Marshall index is the most precise of the three predictive indices that we tested. We recommend its use in studies of body fat where carcasses can be destroyed or where water content can be determined with labelled water (Hulbert and Grant 1983). Alternatively, mass of abdominal fat can be used to estimate fat levels in shot ducks without affecting their culinary value (Woodall 1978).

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APPENDIX 3.

WEIGHT CHANGES AND REPRODUCTION IN FEMALE BLUE-BILLED AND MUSK DUCKS, COMPARED WITH NORTH AMERICAN RUDDY DUCKS.

Wildfowl 39: 98-101.

Weight changes and reproduction in female Blue-billed and Musk Ducks, compared with North American Ruddy Ducks

S.V. BRIGGS

Introduction

Tome (1984) has recently published details of weight changes in North American Ruddy Ducks *Oxyura jamaicensis* in relation to their breeding status. Prior to this, Siegfried *et al.* (1976) published some limited data for Maccoa Ducks *O. maccoa*. In the present paper data on female weight changes in two Australian oxyurids, Blue-billed Ducks *O. australis* and Musk Ducks *Biziura lobata*, are summarised. The question is asked – does female body weight increase prior to laying, and if so, by how much? Body weight changes in Blue-billed and Musk Ducks are then compared with those in related North American Ruddy Ducks and Maccoa Ducks.

Study area and methods

The Blue-billed and Musk Ducks were collected at Barrenbox Swamp (34°10'S; 145°50'E), an irrigation water storage lake in inland south-eastern Australia. A full habitat description of Barrenbox Swamp is given in Braithwaite and Frith (1969a). A sample of ducks was collected by shooting each month they were present between September 1962 and April 1967 (Braithwaite and Frith 1969b). Musk Ducks were present at Barrenbox Swamp all year while Blue-billed Ducks were absent or less abundant between March and May (autumn). Each duck specimen was assigned to 1 of 6 reproductive categories modified from Tome (1984):-

Pre-breeding: Corresponds to Tome's "Arrival" stage. Largest follicle <8 mm. Collected between June and November (breeding period).

Pre-laying: Identical with Tome's category.

Laying: Identical with Tome's category.

Incubation: Collected with brood patch, on nest incubating, or with regressing follicles.

Brood rearing: Collected with downy young.

Non-breeding: Largest follicle <8 mm. Collected between December and May (non-breeding period).

Wing area of female Blue-billed Ducks was obtained from three captive yearling birds (other wing clipped, second generation in captivity), measured according to Raikow (1973). The average wing length of these captive ducks was the same as in wild birds (Frith 1977).

No identifiably incubating or brood rearing Blue-billed Ducks were collected. The collection period spanned 4 1/2 breeding seasons.

Results

Female Blue-billed and Musk Ducks both gained weight prior to laying (Table 1). Blue-billed Ducks increased in body weight by an average of 212 g between pre-breeding and pre-laying and by a further 157 g between pre-laying and laying (total increase of 46% from pre-breeding to laying). Their body weight had increased by 28% between non-breeding and pre-breeding, giving a total increase of 87% between non-breeding and laying ((73% when corrected for egg mass in laying birds – Table 3). There were no data on weights

Table 1. Body weights in female Blue-billed and Musk Ducks in relation to breeding status (means ± s.e.).

Breeding stage	Blue-billed Duck	Musk Duck
Pre-breeding	798±16.8	1338±16.8
n	47	144
Pre-laying	1010±45.0	1665±43.8
n	11	21
Laying	1167±27.6	1641±33.4
n	10	13
Incubation	–	1397±87.6
n		4
Brood rearing	–	1223±22.1
n		21
Non-breeding	624±16.4	1346±22.6
n	26	98

Wildfowl 39 (1988): 98–101

of incubating and brood-rearing Blue-billed Ducks.

Musk Ducks increased in weight by an average of 327 g (24%) between pre-breeding and pre-laying (Table 1). Mean pre-laying weight was not significantly different from mean laying weight. Females of this species lost weight during incubation (244 g) and brood rearing (a further 174 g). This total weight loss was greater than that gained prior to laying.

Females of both species had relatively low body masses during the non-breeding period (Table 1). They differed in that average Musk Duck weight did not increase during the pre-breeding period, whereas Blue-billed Duck pre-breeding weight was higher (174 g) than for non-breeding.

Discussion

The percentage weight change in Blue-billed Ducks prior to laying is amongst the highest recorded in waterfowl to date. It compares with the large weight increases in breeding geese and eider ducks. For example, Cackling Geese . *Branta canadensis minima* increase their weight by 46% from spring migration to pre-laying, and 57% from midwinter to pre-laying (Raveling 1979). Common Eiders *Somateria mollissima* increase by 25% between winter and pre-laying, and American Eiders *S.m. dresseri* by 32% between pre-breeding and laying (Milne 1976; Korschen 1977).

The large percentage and absolute weight gain in breeding Blue-billed Ducks and the large absolute gain in Musk Ducks contrast with the much smaller weight gain in North American Ruddy Ducks. When laying these last increase by only 123 g or 21% of their body weight (Tome 1984). Maccoa Ducks, closely related to Blue-billed Ducks, may also substantially increase in body weight prior to laying. Seigried *et al.* (1976) report a weight difference of 307 g (51%) between three non-breeding (= pre-breeding) females and one laying individual.

Why is there this difference between Ruddy Ducks and Blue-billed, Musk and Maccoa Ducks? Two factors related to body mass in ducks may be important. Firstly, flying imposes a constraint on weight gain in birds. As Tome (1984) has highlighted, North American Ruddy Ducks have a low wing area to body weight ratio (buoyancy index) compared with waterfowl in other tribes. He suggested that this factor prevents them from increasing their breeding body weight. Large weight gains in Blue-billed and Musk Ducks might thus be possible if they have higher wing areas relative to body weight than North American Ruddy Ducks.

Relations between body weight and wing size in Blue-billed, Musk, Maccoa and North American Ruddy Ducks are shown in Table 2. Breeding Musk and Maccoa Ducks have slightly greater wing length to body weight ratios than Blue-billed and North American Ruddy Ducks. But breeding Blue-billed Ducks have similar wing lengths relative to body weight as breeding North American Ruddy Ducks, and lower wing area to body weight ratios (buoyance index) (Table 2). Consequently, breeding female Blue-billed Ducks have no advantage in wing size and this factor cannot explain their marked increase in reproductive body weight compared with North American Ruddy Ducks.

A second factor which could be related to

Table 2. Maximum (breeding) and minimum (pre-breeding or non-breeding) body weight (g), wing length (mm), wing length divided by cube root of body weight, wing area (cm^2) and Bouyancy Index[a] (Hartman 1961) in female oxyurids. Data from Siegfried *et al.* (1976), Johnsgard (1978) and Tome (1984).

	Body weights		Wing	Wing ÷ $\sqrt[3]{}$ weight		Wing	Buoyancy Index[a]	
Species	max	min	length	max	min	area	max	min
Blue-billed Duck	1167	624	153	26.2	30.6	360	1.80	2.22
Musk Duck	1665	1338	185	29.0	30.6	–	–	–
N.A. Ruddy Duck	739	582	139	26.7	28.3	326	2.00[b]	2.16[b]
Maccoa Duck	907	600	169	30.5	34.1	–	–	–

[a] square root of wing area divided by cube root of body weight

[b] calculated from wing area in Raikow (1973) and body weights in Tome (1984)

breeding body weight is clutch mass. All oxyurids have large eggs and consequently large clutch masses relative to their body mass, compared with other waterfowl (Lack 1967). A large pre-laying increase in body mass might enhance clutch mass, since stored reserves can influence clutch size in anatids (Ankney and MacInnes 1978; Drent and Daan 1980). However, North American Ruddy Ducks have a larger clutch mass than Blue-billed, Musk or Maccoa Ducks (Table 3), so that clutch mass and body weight increase are not positively related in these four species.

It is suggested that the answer to the question lies in the different movement patterns of the species. North American Ruddy Ducks are migrants (Johnsgard 1978), and fly several hundred kilometres between their wintering and breeding grounds. Good flying ability is hence essential for breeding and survival in this species, as suggested by Tome (1984). Blue-billed, Musk and Maccoa Ducks have no such constraints. Blue-billed Ducks make local seasonal movements, but do not regularly migrate long distances prior to breeding, and Musk Ducks are mainly sedentary (Blakers *et al.* 1984). Maccoa Ducks are also sedentary or move locally (Siegfried *et al.* 1976; Johnsgard 1978). Differences in breeding habitat may additionally contribute to the species' differences in weight gain. North American Ruddy Ducks often breed in relatively small, discrete wetlands between which they must fly to find nest sites (Tome 1984). Conversely, Blue-billed and Musk Ducks usually breed in interconnected or larger waterbodies (Frith 1977) in which they can move largely by swimming.

I therefore suggest that low breeding weight gain in North American Ruddy Ducks compared with Musk, Maccoa, and especially Blue-billed Ducks can be attributed to this difference in their movement patterns. The sedentary or locally mobile species consequently can store more reserves for breeding. These data thus support Tome's (1984) conclusions concerning the constraining effect of wing area on weight increase prior to breeding in female North American Ruddy Ducks.

Further investigations of this subject await accurate information on movement patterns and weight changes in other oxyurid species, and details of carcass composition changes relative to breeding in Blue-billed and Musk Ducks.

Table 3. Average egg mass (g), clutch size and clutch mass as a percentage of laying body mass in female oxyurids. Data from Siegfried *et al.* (1976), Frith (1977), Johnsgard (1978) and Tome (1984).

Species	Egg mass	Clutch size	Clutch mass %
Blue-billed Duck	90	5.5	42%
Musk Duck	128	2.8	22%
N.A. Ruddy Duck	73	7.6	75%
Maccoa Duck	88	5	49%

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Summary

Female Blue-billed and Musk Ducks both increase in body weight prior to breeding. Blue-billed Ducks increase by 369 g (46%) and Musk Ducks by 327 g (24%) between pre-breeding and breeding. These weight gains, especially in Blue-billed Ducks, are high compared with those in related North American Ruddy Ducks. It is suggested that this difference is because North American Ruddy Ducks have to migrate long distances to breed whereas Blue-billed and Musk Ducks do not.

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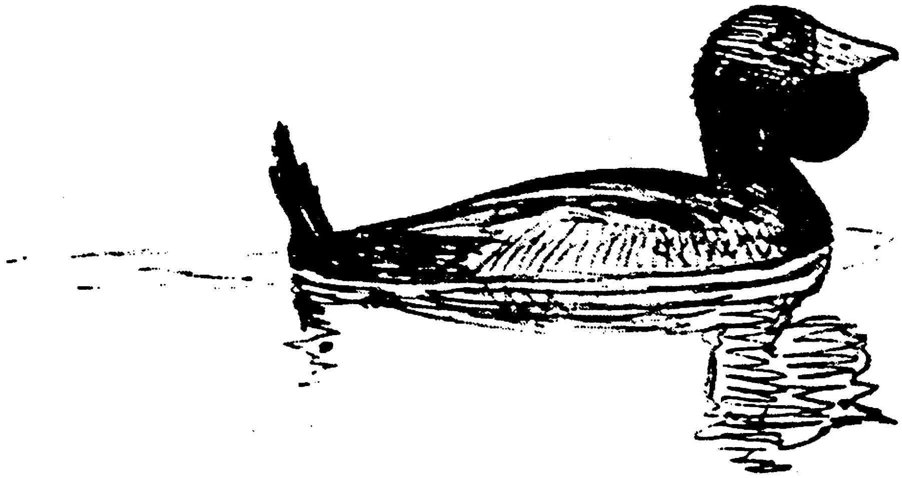

APPENDIX 4.

FOOD ADDITION, CLUTCH SIZE, AND THE TIMING OF LAYING IN AMERICAN COOTS.

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The Condor 91:493–494

COMMENTARY

FOOD ADDITION, CLUTCH SIZE, AND THE TIMING OF LAYING IN AMERICAN COOTS

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Hill (1988) has recently published a study showing that supplemental feeding increased egg mass but did not affect laying date or clutch size in American Coots (*Fulica americana*). She added food (protein content 26%) to coot breeding territories in 1982, from the last week of March until the end of June. The coots in her study area started laying around the end of April in 1982, with median hatch date 13 June. Thus Hill added food from approximately 1 month before laying commenced to hatching.

Alisauskas and Ankney (1985) found that 85% of the lipids required for egg production in coots came from stored reserves. Although Hill (1988) stated otherwise, Alisauskas and Ankney (1985) determined that these energy reserves were acquired prior to arrival at the breeding site. They found that, unlike fat, most protein (72% of requirements) for egg formation is acquired exogenously on the breeding grounds. Thus, adding food to coot breeding territories provides extra protein for eggs but not extra fat.

Supplementary food has been shown to enlarge or advance all, some, or none of clutch size, egg size, and laying date in several species of birds (Davies and Lundberg 1985, Hochachka and Boag 1987, Hochachka 1988, and references therein). Consistent, between-species effects of added food on egg production should not be expected. In particular, the impact of added food on laying date, clutch size, and egg mass will depend on four factors: when food is added relative to when it is obtained from the environment, relative contributions of endogenous and exogenous resources to egg formation, whether food is naturally limiting, and whether laying date and clutch characteristics are plastic, i.e., indeterminate.

Assuming that laying date, clutch size, and egg mass are plastic, then the following relations should occur. Additional food during the time of reserve acquisition should advance laying date in species that use endogenous reserves and need to reach a condition threshold for breeding (Drent and Daan 1980), because the reserves are acquired sooner. Adding food during this time will increase clutch size and egg mass in such species only if naturally available food is limiting. (Species, like coots, that accumulate fat reserves for breeding before or during migration [Alisauskas and Ankney 1985], may be constrained in when they commence breeding by migration itself. Weather may determine migration, and hence laying date, irrespective of nutritional conditions.) Supplementary food during the breeding period will enlarge clutch size, egg mass, and/or advance laying, only in species that rely on exogenous resources, and only if naturally available food is limiting. Consequently, food added to the breeding territory will affect neither clutch size, nor egg mass, nor laying date if these are determined by endogenous reserves stored prior to arrival on the territory, or naturally present in quantities in excess of their needs.

These generalizations can be checked by determining effects of food supplementation on laying date, clutch size, and egg mass, in relation to timing of nutrient acquisition for egg production in individual species. Such food experiments should include separate treatments of food added prior to, and during, egg laying. Nonmigratory species should be used where possible. Simultaneous monitoring of nutrient reserves, food resources, and egg production is required. This is currently difficult if not impossible (Ankney and Afton 1988), and some of the methodology is controversial (Murphy 1986, Alisauskas et al. 1987, Murphy 1987).

Effects of food supplementation could also be tested on species whose relative use of endogenous and exogenous resources for egg laying is known. For example, Eurasian Kestrels (*Falco tinnunculus*) provide support for these postulated relationships between sources of nutrient for egg production and effects of food addition. Food supplied prior to laying increased clutch size and advanced laying date in this species in poor food years, but did not affect laying date (no data for clutch size) in good food years (Dijkstra et al. 1982). Kestrels form eggs from endogenous reserves (Drent and Daan 1980). Sources of nutrients for clutch formation in species for which results of food provisioning experiments are known (Davies and Lundberg 1985, Hochachka and Boag 1987, and references therein) could also be ascertained. Determining sources of nutrients for egg formation should be done with care because species may vary in their use of endogenous and exogenous resources for laying depending on their environment (Batt and Prince 1978, Krapu 1981, Hohman 1986).

These interpretations and the results of Hill's (1988) experiment strongly suggest the following. Firstly, clutch size and laying date in American Coots are largely determined by endogenous lipid and protein reserves acquired prior to laying. Secondly, natural protein resources in the breeding territories are in excess of their needs, and do not determine clutch size or laying date. Thirdly, egg mass is controlled by, and probably limited by, protein levels in the breeding territories. This third conclusion is supported by Hill's findings that larger eggs were produced by coots in the food-enhanced territories, and that larger eggs generally had relatively more albumen (mostly protein solids) than yolk (solids mostly lipid, with some protein [Alisauskas 1986]). The data of Hill (1988) demonstrate that protein availability in the breeding territory has little or no effect on clutch size of coots. They thus support the conclusions of Ankney and Afton (1988) that the role of protein in regulating clutch size of temperate nesting waterfowl has been overstated. Perhaps this is the case also for other wetland birds, such as coots.

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