ENERGY REQUIREMENTS FOR BREEDING IN THE MACCOA DUCK

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1. INTRODUCTION

The almost exclusively aquatic, small ducks in the genus *Oxyura* are remarkable for having, proportionate to body size, the largest eggs of all Anatidae, yet clutches are large and incubation periods are short (Lack 1968). Incubation is performed solely by the female, and the clutch is not insulated with a layer of down (Kear 1970a). Males and females undergo a complete moult of feathers twice a year (Siegfried 1970, 1973a). These phenomena may be linked with extra-energy demands.

The present paper focuses on the energy requirements for reproduction in free-living Maccoa Ducks *Oxyura maccoa*. The energy demands of breeding females are considered in relation to gonad and egg production, incubation and brood care. Breeding males require extra energy mainly for defence and advertisement of territory, and for courtship of females. Energy budgets are constructed for males and females, facilitating explanation of the adaptive significance of aspects of the Maccoa Duck's breeding biology.

2. STUDY AREA

The fieldwork was carried out during 1972-76 at two irrigation dams (16 and 14 ha) on the farms "Klawervlei" and "Meerlust", near Faure (33° 56′S, 18° 40′E), and at a series of ponds at a sewage farm, near Paarl (33° 42′S, 19°

01'E), in the south-western Cape, South Africa. The dams contained water permanently, but water levels fluctuated seasonally. Winter (June - August) is the cool, rainy season. Summers (December - February) are hot and dry, and water levels normally drop about 20% in the dams. Between 15 and 20 Maccoa Ducks usually occurred at "Klawervlei", and we suspect that the population was permanently resident there. The population at "Meerlust" fluctuated more; with an influx of about 30 birds resulting in a maximum population of about 50 birds in winter each year. Maccoa Ducks nested regularly in emergent rushes *(Typha)* and occasionally in other cover on the banks of islands.

3. MATERIALS AND METHODS

The behaviour of free-living Maccoa Ducks, at various stages in their breeding and non-breeding cycles, was recorded during dawn-dusk periods (Siegfried & van der Merwe 1975, Siegfried, Burger & van der Merwe 1976, Siegfried, Burger & Caldwell in press), using "focal animal" and "instantaneous scan" methods described by Altmann (1974). Specimens of adult birds, eggs and ducklings were collected for examination in the laboratory. Data on egg, nest-air and ambient temperatures were obtained (Siegfried *et al.* in press). The energy cost of incubation was determined, using methods devised by Kendeigh (1963) and subsequently refined by Drent (1970).

Fresh and incubated eggs were separated into shell, shell membrane and contents. Embryos were dissected and the liver, yolk remnants and allantoic fluid were separated from the remainder of the body. All parts were weighed while fresh and dried at 60°C in an extractor oven until constant mass was obtained. The parts were finely ground for subsequent analyses. Calorific values were determined, using a Gallenkamp ballistic bomb calorimeter. Fats were extracted, using ether and alcohol (Leshner, Litwin & Squibb 1972). This involved adding 0.5 ml ethyl alcohol and 10 ml methyl ether to 0.5 g of each ground and dried sample. The mixture was shaken for 30 min, centrifuged for 5 min at 2000 rpm and the supernatant fluid, containing the fat, was decanted. The process was repeated and the fat-free sample was dried at 60°C.

Only actively feeding adults were collected, and all such birds were observed for extended periods before they were shot. Duration of feeding spells, and duration and number of foraging dives per feeding spell, were recorded for each bird before collection, and, based on individuals which rested for not less than 2 hr prior to beginning a feeding spell, it was possible to estimate rates at which feeding birds ingested food. Gullets and gizzards of the shot birds were treated as described in Siegfried (1973b). A 3.5 l Ekman grab was used to obtain samples of the muddy ooze (containing the Maccoa Duck's food) at those sites at which the birds were observed feeding. These samples were taken immediately after each bird had been shot. Additional

samples, taken regularly at feeding sites, yielded data on seasonal change in biomass of food potentially available to the birds. All animals in the mud samples were identified, wherever possible, to family level, sorted and counted. They were weighed while fresh, and dried at 60°C until constant mass was obtained. Energy content, obtained by bomb calorimetry, varied between 4.6 and 5.7 kcal/g for the different organisms. Consequently, a mean value of 5.0 kcal/g was taken as representative for all food organisms at all times of the year (see Driver, Sugden & Kovach 1974).

The feathers of the culled adult birds were plucked, and then dried and ground for calorific analysis. Each bird was separated into: the integument, consisting of skin; subdermal fat; gonads; and, the carcase. Each portion was weighed, minced and blended until thoroughly homogenized. Numerous random aliquots were taken (see Brisbin 1968). The aliquots were oven-dried to constant mass. Additional aliquots were analysed for lipid content, using a cold-hexane-extraction method (Dreosti & Wiechers 1962).

4. FOOD AND FEEDING

The Maccoa Duck feeds almost exclusively by diving, straining food objects from the soft mud overlying the bottoms of ponds. Chironomid midge (Tendipedidae) larvae and pupae feature prominently in the bird's diet (Table 1). Feeding Maccoa Ducks ingested food at a rate of 7 - 96 mg (dry weight) per dive (Table 2). On average, this represents an energy intake of 0.22 kcal/dive or 0.50 kcal/min; 54% being contributed by midge larvae and pupae which contained about 20% of the gross energy potentially available in the mud (Table 3). In calculating energy budgets we assumed that 90% of the ingested energy is assimilated, since most of the food organisms are soft-bodied animals.

Based on seven separate, aggregated samples, biomass of chironomid larvae and pupae averaged 20 mg/l (S.D. ± 30, range 3-79 mg/l) at sites at which breeding Maccoa Ducks were observed feeding immediately prior to our sampling the mud. This value falls within the range of the bi-monthly means which suggest that no great changes occurred seasonally in the biomass of the chironomid larvae and pupae at Klawervlei (Table 4). However, seasonal change in the depth of the waterbody did occur and this, and other factors, might have influenced the distribution and area of mud, and so could have affected the quantity of midges available as food for Maccoa Ducks. We know that changes in substrate type affect the density of midge larvae and pupae, but at present we lack data on the patchy distribution of different substrata in the waterbody.

5. SOCIAL ORGANIZATION

Breeding male Maccoa Ducks are strongly territorial, advertising and defending their presence in discrete areas with fixed boundaries embracing

Table 1. Food items in the oesophagi of adult Maccoa Ducks (8 ♂♂, 5 ♀♀) collected in January, February, March, July, October and December.

Food item	% occurrence	% frequency (no. objects)	% aggregate dry weight
Tendipedidae (larvae, pupae)	100	34	45
Ostracoda	46	59	32
Gastropoda	15	2	19
Other organisms	15	5	4

Table 2. Duration and number of dives, and food intake of Maccoa Ducks during feeding spells.

Bird No.	Sex	Mass [a] (g)	Duration foraging spell (min)	Duration under water (min)	No. dives	Total food intake (dry weight) (mg)	Food intake (dry weight) per dive (mg)
1	♂	732	14	12.1	33	2080	63
2	♂	792	18	12.0	27	300	11
3	♀	794	7	3.5	14	1341	96
4	♀	732	8	3.2	43	315	7

[a] Excludes gonads and materials in gullet and gizzard.

Table 3. Energy intake by Maccoa Ducks and energy potentially available to the birds during feeding spells.

Bird no.	Gross energy intake (kcal/min)	Energy intake derived from midges (kcal/min)	Gross energy potentially available in mud (kcal/l)	Energy potentially available from midges in mud (kcal/l)
1	0.743	0.298	0.105	0.042
2	0.084	0.084	no data	no data
3	0.958	0.366	0.790	0.125
4	0.197	0.153	0.045	0.020

Table 4. Dry-weight biomass (mg/l) of midge (Tendipedidae) larvae and pupae in mud at Klawervlei.

	Midge biomass			Midges as % of total faunal biomass of mud	No. samples	No. sampling days
	$\bar{x}$	S.D.	range			
Jan.—Feb.	20	±10	3— 35	49	15	4
March—April	40	±20	21— 76	34	10	2
May—June	50	±40	6—164	50	20	4
July—Aug.	50	±20	22— 61	43	5	1
Sept.—Oct.	10		2— 10	33	5	1
Nov.—Dec.	30	±20	1— 65	54	28	5

open water and stands of emergent vegetation. Females move through the territories for purposes of feeding and for selecting nesting cover and/or fittest mates. Polygyny occurs and there is no social courtship or pair-bond in the normally accepted sense. A successful male can have one or more females nesting in his territory. The territorial male does not attend the female when

she is off the nest and takes no part in the rearing of the young. The incubating female does not restrict her feeding to the male's territory. Females with broods wander freely, and are very aggressive toward conspecifics and other birds (Siegfried 1976).

Non-breeding Maccoa Ducks associate in loose congregations on the water, males and females mixing freely in loafing flocks. The males assume a dull female-like plumage, in contrast to the bright dress they wear during the breeding season (Siegfried 1968).

6. BREEDING SEASON

In the south-western Cape, the Maccoa Duck breeds from July to April with a peak in egg-laying occurring in October-November; and egg-laying continues at a relatively high level during the austral summer (Fig. 1). To be noted is that the Maccoa Duck's breeding peak occurs about two months later than the main breeding period of dabbling ducks (Siegfried 1969a). Both the North American Ruddy Duck *Oxyura jamaicensis* and the Australian Blue-bill *O. australis* display similar time-lags relative to dabbling ducks. Siegfried (1977) has indicated that in parts of Canada the Ruddy Duck's delay in onset of breeding is related to the availability of suitable nesting cover. However, we think it unlikely that a similar condition prevails in the south-western Cape where new vegetative growth of *Typha capensis,* the Maccoa Duck's usual nesting cover, begins in July and the plants flower in December each year (Fig. 1).

7. GONAD PRODUCTION

There are no data on the actual development of the ovary and oviduct in the Maccoa Duck. In the related, and slightly smaller, North American Ruddy Duck the fully developed gonad has a fresh mass of 55 g (Siegfried 1977). A combined ovary and oviduct mass of 85.4 g was obtained for a Maccoa Duck collected during the egg-laying phase of her reproductive cycle. Assuming a calorific content of 2 kcal/g and an efficiency of production of 70% (King 1973), the estimated energy required for ovary and oviduct growth in the Maccoa Duck is 244 kcal.

A maximum mass of 17 g (wet weight) was obtained for a male Maccoa Duck's testes, representing about 2% of the bird's 805 g body weight. King (1973) has shown for several species of birds that the calorific cost of testicular synthesis is, even at a maximum, less than 1% of the birds' basal metabolic rate. This cost is negligible, and is ignored here.

8. EGG PRODUCTION

Mean mass of a fresh Maccoa Duck egg is 88 g (Siegfried 1969b). An adjusted mean value of 195 kcal per 88 g egg was obtained, based on the

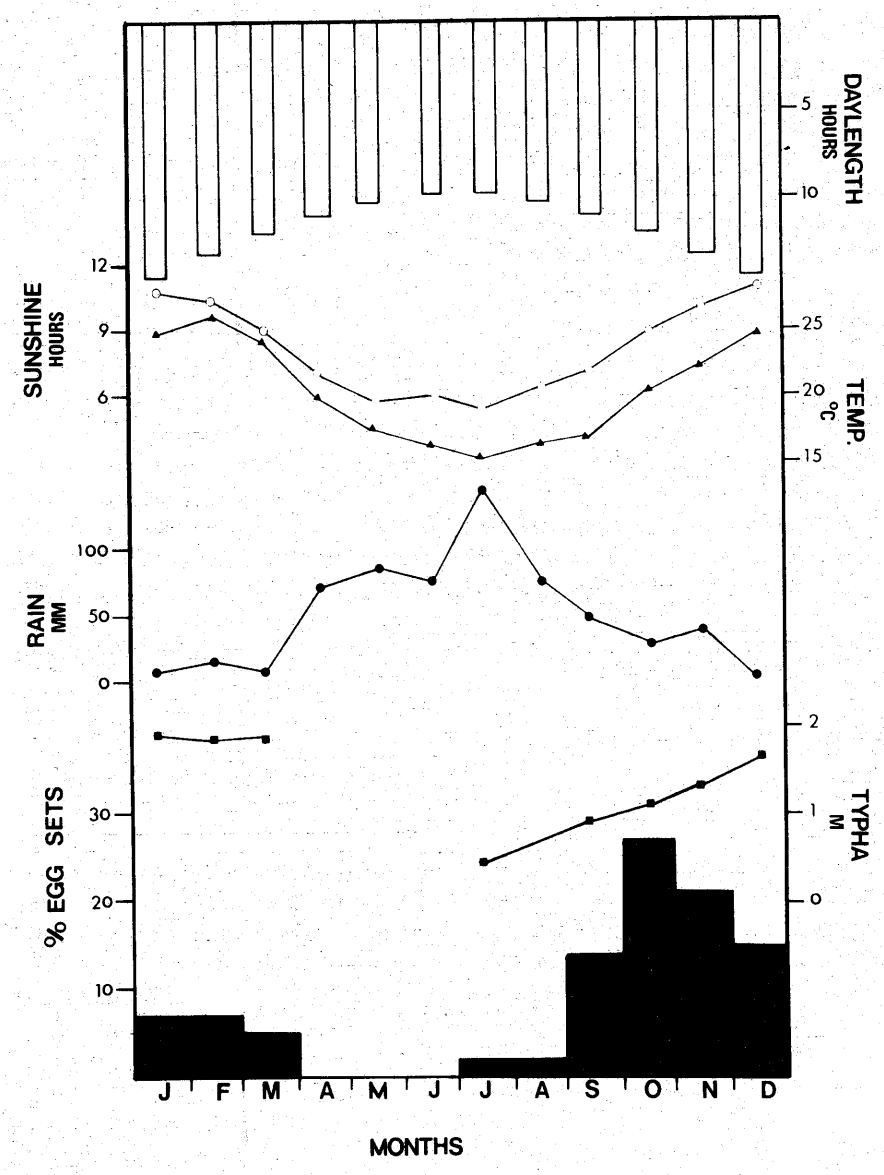

Fig. 1. Breeding season of the Maccoa Duck, in relation to average air temperature, rainfall, sunshine, daylength and growth of longest leaf shoot of *Typha capensis* in the south-western Cape. Shaded columns represent clutches (n = 148) entered according to the months in which they were known to have been completed, and plotted as percentages for the period 1959-1976. Norms for the meteorological parameters are based on data supplied by S.A. Weather Bureau.

energy contents of two fresh eggs. One egg would have cost 278 kcal to produce, assuming a 70% efficiency of production (King 1973).

The frequency distribution of Maccoa Duck clutches is skewed to the right (Fig. 2), and several deviations from a normal distribution appear when the data are plotted on arithmetic probability paper. The most marked deviation occurred at a clutch size of nine, which may be the maximum clutch possible for one female. The mean clutch size was six, when clutches of 10 and more eggs were ignored. These extra-large clutches are believed to be due to intraspecific nest parasitism (Clark 1964).

The Maccoa Duck requires twice as much energy to produce an egg as does the Mallard *Anas platyrhynchos,* even though the Mallard is a considerably larger bird (Table 5). A comparative measure of the effort

Table 5. Energy cost of egg production in the Anatidae. Data for species other than the Maccoa Duck taken from King (1973: 94—95).

Species	Body mass (g)	Basal metabolic rate (kcal)	Egg mass (g)	Clutch size	Energy for egg (kcal)	Energy for clutch (kcal)	Energy for egg / BMR	Energy for clutch / BMR
Canada Goose *Branta canadensis*	5,000	239.5	163	6	372.6	2,235	1.56	9.3
Mallard *Anas platyrhynchos*	1,100	78.8	54	11	138.8	1,527	1.76	19.4
Cinnamon Teal *Anas cyanoptera*	335	34.4	32	10	82.3	823	2.39	23.9
Lesser scaup *Aythya affinis*	650	53.6	44	9	113.1	1,018	2.11	19.0
Maccoa Duck *Oxyura maccoa*	907	68.6 [a]	88	6	278.3	1,670	4.06	24.3

[a] based on Aschoff & Pohl (1970).

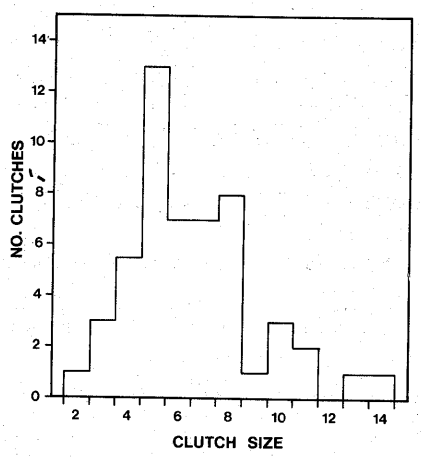

Fig. 2. Frequency of Maccoa Duck clutches (complete egg-sets) in the south-western Cape.

involved in egg production can be obtained by relating the daily cost of egg production to the basal metabolic rate of the bird. In the five species compared here, the female lays on average one egg per day during the laying period (King 1973; pers. obs.). If clutch size is assumed to be equal to the period of rapid follicular growth in days, then the maximum daily energy requirement for egg production is equivalent to the energy content of a single egg (King 1973). The daily energetic cost would be reduced marginally if follicular growth took place over a longer period. Even so, the Maccoa Duck has by far the greatest daily energetic requirement of the five species considered here (Table 5). However, in the four duck species the total energy requirement per clutch, as a multiple of the basal metabolic rate, is very similar. Presumably this reflects the evolutionary compromise between the opposing selection pressures for egg size, clutch size and energy allocation for egg production.

9. INCUBATION

The incubation behaviour of the Maccoa Duck is described by Siegfried *et al.* (in press) who also report data on nest-air, egg and ambient temperatures. The energy cost of incubation was calculated, using Kendeigh's (1963) formula

kcal/bird = $n.\ w.\ h.\ b.\ (te - tna)\ i\ (1 - c.a.)$

n = no. eggs in clutch (6)
w = mean mass of egg (88 g)
h = specific heat of egg (0.8 cal g^{-1}, based on King & Farner 1961)
b = cooling rate of eggs (0.66°C/°C/hr in a clutch of six, based on Siegfried *et al.* in press)
$(te - tna)$ = temperature gradient between egg and nest-air (6.3, based on Siegfried *et al.* in press)
i = time interval in hr
c = % eggs' surface covered by female (22%, based on Siegfried *et al.* in press)
a = nest attentiveness of female (72%, see Table 6).

It was computed that in a 24-hr period a female expended 35.17 kcal on incubating a clutch of six eggs (Table 6). The female Maccoa Duck covers the eggs with the feathered ventral surface of the thorax and abdomen. This

Table 6. Mean daily egg temperature and energy cost of incubation for a clutch of six Maccoa Duck eggs.

	No. of hours	Nest attentiveness of female (hr)	Mean egg temperature (°C)	Energy cost of incubation of clutch (kcal)
Daytime	15	0.71	33.5	21.38
Night-time	9	0.80	34.8	13.79
Daily	24	0.72	34.1	35.17

area was measured as 126.6 cm² (Siegfried *et al.* in press). This represents 15% of the female's total surface area, as computed from Meeh's formula

$$S = 10W^{0.67}$$

where W is mass (g) and S is surface area (cm²) of bird (Drent & Stonehouse 1971). The mass of an incubating female Maccoa Duck was taken as 761 g (see Appendix 1), and the bird's surface area was 835 cm².

King (1973) believes that the energy necessary for incubation is met by the normal loss of heat from the incubating bird, without additional energy expenditure. According to Kendeigh (1973), however, additional energy is necessary for incubation. For the Maccoa Duck, if one assumes that body heat is lost equally over the whole of the bird's surface area, 15% of the basal metabolic heat should be lost from the brood area. This assumption is incorrect, since some areas of the body, such as the feet, can lose heat more readily than others (Caldwell & Cornwell 1975; pers. obs.). Heat is also lost by evaporative cooling in the mouth and throat. The assumption, however, allows an estimate of the maximum amount of heat which would normally be lost via the brood area. This amounts to 9.0 kcal/24 hr, for a 761 g female Maccoa Duck with a BMR of 60.3 kcal/24 hr. based on Aschoff & Pohl's (1970) formula for nonpasserines. Clearly, 9.0 kcal/24 hr is not nearly enough energy for effective incubation of a normal clutch.

The minimum total energy expended by the female during incubation of six eggs is estimated at 86.47 kcal/24 hr (60.3 - 9.0 + 35.17 kcal/24 hr). During incubation the bird's metabolism could thus be expected to increase 1.43 times its basal rate. For the Maccoa Duck, it appears that Kendeigh (1973) is correct in stating that increased energy is required for incubation. Similar conclusions were arrived at by El-Wailly (1966), who studied the food intake of the Zebra Finch *Taeniopygia guttata* during incubation.

Unlike most ducks, oxyurines do not line their nests with down (Kear 1970a). In the Maccoa Duck this results in increased heat loss from the eggs, with a corresponding increase in the energy cost of incubation (Siegfried *et al.* in press). Clutch configuration and nest materials partly offset this loss. Based on the relative rates of heat loss from an egg suspended in air (1.26°C/°C/hr) and in association with other eggs of similar temperature in a nest (0.66°C/°C/hr) the saving in the Maccoa Duck amounts to 48%, compared to 54% in the Mallard (calculated from data in Caldwell & Cornwell 1975). Furthermore, in the Maccoa Duck the total cost of one hour of continuous incubation per gram egg per degree C gradient is 0.612 cal. In the Mallard the total cost amounts to 0.448 cal/g/°C difference (Caldwell & Cornwell 1975). The ratio of these costs is 1 : 1.37, which provides some indication of the magnitude of the extra energy demands of incubation in the Maccoa Duck. Presumably, this extra cost is offset by the saving in body heat to the female during her feeding spells off the nest. Maccoa Ducks have a relatively large surface-to-volume ratio, and their mode of feeding,

Table 7. Mass of shell, water and fat, and energy content in Maccoa Duck eggs. Egg 1 contained a six-day-old embryo. Egg 2 was fresh and unincubated.

	(g)	Fat (g)	Calorific value (kcal/g)	Energy content of egg (kcal)
Egg 1				
Shell	10.40	—	—	
Water	56.06	0	0	
Mixed contents	22.57	11.24	8.10	182.82
Egg 2				
Shell	9.90	—	—	
Water	50.37	0	0	
Mixed contents	24.69	11.21	8.19	202.21

Table 8. Mass of water, fat and components of embryos and their energy content in Maccoa Duck eggs. Egg 3 contained a 23-day-old embryo. Egg 4 and its duckling were analysed 15 hours after hatching.

	(g)	Fat [a] (g)	Calorific value (kcal/g)	Energy content of egg (kcal)
Egg 3				
Water	47.60	0	0	
Yolk remnant	9.96	5.21	8.03	79.97
Liver of embryo	0.37	0.19	7.39	2.73
Body of embryo (minus liver)	10.36	3.91	7.14	73.97
Allantoic fluid	0.69	0.02	4.09	2.82
Membranes	0.65	0.01	5.49	3.57
Totals	69.63	9.34		163.00
Egg 4				
Water	44.76	0	0	
Yolk remnant	4.75	2.71	8.06	38.30
Liver of embryo	0.76	0.34	7.86	5.27
Body of embryo (minus liver)	14.87	5.82	7.17	106.61
Allantoic fluid	0.36	0.01	3.72	1.34
Membranes	0.39	0.01	5.56	2.17
Totals	65.80	8.89		153.70

[a] fat values for liver (50 mg/100 mg) and allantoic fluid (3 mg/100 mg) taken from Romanoff (1967).

involving complete submergence in water, must place considerable thermoregulatory demands on them. The loss of insulation consequent on providing down for the nest lining might place excessive demands on the feeding bird.

The developing avian embryo produces heat, in addition to that supplied by the incubating parent, and this may amount to 70% of the total heat necessary for incubation during the last day or two before hatching (Drent 1970). The production of heat by Maccoa Duck embryos was calculated, using data in Tables 7 and 8. The incubation period is 25 - 26 days (Siegfried *et al.* in press). After 23 days of incubation 39 kcal, or 19.3% of the maximum

Table 9. Energy expenditure of avian embryos during incubation.

Species	Energy content of fresh egg (kcal)	Energy expended by embryo (kcal)	Percent available energy expended	Source
House Wren *Troglodytes aedon*	1.6	0.9	55	Kendeigh (1963)
Herring Gull *Larus argentatus*	144.4	57.9	40	Drent (1970)
Domestic fowl *Gallus domesticus*	90.9	25.3	28	Romyn & Lokhorst (1960)
Domestic duck *Anas platyrhynchos*	138.7	39.7	29	Kashkin (1961)
Maccoa Duck *Oxyura maccoa*	202.2	48.5	24	This study

total energy content (202 kcal) of a fresh egg, had been expended by the developing embryo. Similarly, a 26-day-old embryo, 15 hr after hatching, had used 48 kcal, or 24.0% of the maximum total energy content of a fresh egg (Table 8). This accords well with the expected energy loss of 48.44 kcal for a Maccoa duckling hatching at 67% mass of the fresh egg mass (Drent pers. comm.). In fact the mean mass of newly hatched Maccoa ducklings is 56 g (S.D. ± 3 g, $n = 31$), which is about 64% of the mass of an average 88 g egg.

Matthews & Evans (1974) related decreasing nest attentiveness of White-headed Ducks *Oxyura leucocephala* with increasing self-sufficiency of well-developed embryos towards the end of the incubation period. It is apparent that Maccoa Duck embryos contribute relatively little heat towards offsetting the total energy cost to the incubating parent (Table 9).

One of the consequences of this is that the female Maccoa Duck has to produce more heat for incubation than a similarly-sized bird with altricial young. Among the species considered in Table 9, the hatchling House Wren *Troglodytes aedon* is nidicolous, altricial and psilopaedic (hatched without down), and depends entirely on the parents for food and thermoregulation (Kendeigh 1963). The chick of the Herring Gull *Larus argentatus* is nidicolous, initially altricial and ptilopaedic (hatched with some down); it depends on the parents for food and initial thermoregulation (Drent 1970). The domestic fowl and duck are nidifugous, precocial and ptilopaedic, and are not entirely dependent on the parents for food and thermoregulation. The Maccoa duckling is precocial, nidifugous, ptilopaedic and largely independent of the parents, although members of broods do keep together and remain with the female for several weeks (Clark 1964).

Lack (1968) suggested that comparatively large eggs are an adaptation for producing precocial chicks, allowing greater food reserves on hatching. The Maccoa Duck lays very large eggs in relation to body weight, and the ducklings begin feeding in an energy-demanding manner (diving) almost immediately after hatching. Eggs producing precocial chicks have a higher

fat content than those producing altricial chicks (Romanoff & Romanoff 1949). Lipids comprised about 48% of the dried contents of Maccoa Duck eggs (Table 7). However the high calorific value of the contents suggests that there may have been incomplete extraction of the total lipids in the eggs. Using the formula given by Ricklefs (1974) the eggs should have contained about 67% lipids if the calorific value of 8.19 kcal/dry g is correct. Nevertheless, it is obvious that Maccoa Duck eggs contain substantial amounts of lipids.

The greatest energy reserve of a duckling is the remnant of the yolk, enclosed in the hatchling's viscera (Table 8). Energy reserves from the yolk sac are transferred to the subepidermal fat layer and the liver (Kear 1965, 1970b). The Maccoa duckling's liver increases in size after hatching, although the duckling may not yet be feeding (Table 8). Kear (1970b) found that tolerance to cold and starvation and the ability to feed energetically were greater in the Tufted Duck *Aythya fuligula,* a diving duck, than in the Mallard, a dabbling duck.

10. ACTIVITY OF FEMALES

Data on the diurnal activity of adult female Maccoa Ducks, at various stages of the annual cycle, are set out in Table 10. About 70 days are required to complete a female's reproductive cycle, from time of egg formation to independence of the brood. Incubating females were observed to feed assiduously whenever they were off their nests. Females fed frequently in short spells alternating with longer bouts of incubation throughout the day. Mean daily nest attentiveness was 72% (Siegfried *et al.* in press). The time used for incubation was made up largely of time normally spent resting by non-breeding females, with reduced amounts of time spent on other activities as well (Table 10). Females accompanying young broods

Table 10. Per cent diurnal time (dawn-dusk) spent on activities by breeding and non-breeding female Maccoa Ducks.

Activity	Incubating female	Brood accompanying female	Non-breeding female (summer)	Non-breeding female (winter)
Rest	—	27.1	41.5	57.2
Preen and bathe	7.0	9.9	14.8	15.4
Swim	2.1	12.5	3.7	4.3
Dive (feed)	31.9	50.5	40.0	23.1
Incubate	59.0	—	—	—
Months in which observations were made	February	February	Dec.—Feb.	April—Aug.
No. hours observation	48	14	145	161
Method of observation [a]	Focal	Focal	Scan	Scan
No. individual female ducks observed	1	1	10	26

[a] Based on Altmann (1974).

Table 11. Chasing activity of a female Maccoa Duck with three ducklings aged 19 days. The female and her brood were observed continuously for 14 hours.

Birds chased	No. of chases
Male Maccoa Ducks	7
Female Maccoa Ducks	16
Coots *Fulica cristata*	28
Shoveller *Anas smithii*	1
Pochards *Netta erythropthalma*	2
Dabchicks *Podiceps ruficollis*	14
Black-necked Grebes *Podiceps nigricollis*	2
Cormorant *Phalacrocorax africanus*	1
	71

spent considerable time on feeding, and seldom rested during daytime. The female parent does not tolerate other birds near her brood, and may spend much time and energy on chasing activity (Table 11).

11. ENERGY EXPENDED BY FEMALES

Table 13 presents data on energy expended diurnally by female Maccoa Ducks, based on metabolic rates for the activities of birds at various stages in the annual cycle (Table 12). Since the metabolic rates of the females did not differ much for a particular activity, seasonal differences in overall energy expenditure were largely due to differences in the allocation of time to various activities. It appears that the varying amount of time spent on feeding resulted in the most significant changes in the energy expended. Feeding is by diving exclusively and is, energetically, the most expensive activity.

Table 12. Metabolic rates (kcal/hr) for various activities performed by breeding and non-breeding female Maccoa Ducks.

Activity	Incubating female	Brood-accompanying female	Non-breeding female (summer)	Non-breeding female (winter)
Basal Metabolic Rate [a]	2.5	2.3	2.3	2.1
Rest (1.24 × BMR) [a]	3.1	2.9	2.9	2.6
Preen and bathe (2 × BMR) [b]	5.0	4.6	4.6	4.2
Swim (4.1 × BMR) [b]	10.3	9.4	9.4	8.6
Dive (8 × BMR) [b]	20.0	18.4	18.4	16.8
Incubate (1.43 × BMR)	3.6	—	—	—
Mass (g) of female [c]	761[d]	673[d]	677[d]	600[d]

[a] based on Aschoff & Pohl (1970).
[b] based on Siegfried *et al.* (1976).
[c] excludes mass of gonads and contents of gullet and gizzard.
[d] see Appendix 1.

Table 13. Mean hourly (dawn to dusk) energy expenditure (kcal/hr) of breeding and non-breeding female Maccoa Ducks.

Activity	Incubating female	Brood-accompanying female	Non-breeding female (summer)	Non-breeding female (winter)
Rest	—	0.79	1.20	1.49
Preen and bathe	0.35	0.46	0.68	0.65
Swim	0.22	1.18	0.35	0.37
Dive (feed)	6.38	9.29	7.36	3.88
Incubate	2.12	—	—	—
Totals	9.07	11.72	9.59	6.39

Table 14. Percent diurnal time and mean hourly (dawn to dusk) energy expenditure of breeding (territorial) and non-breeding male Maccoa Ducks (adapted from Siegfried *et al.* 1976).

Activity	Breeding male (summer)		Non-breeding male (winter)	
	(%)	(kcal/hr)	(%)	(kcal/hr)
Rest	29.0	0.96	58.4	1.93
Preen and bathe	10.0	0.53	15.4	0.82
Swim	27.0	2.95	4.5	0.49
Dive (feed)	21.0	4.47	21.2	4.51
Display	13.0	0.87	0.5	0.03
Totals	100.0	9.78	100.0	7.78

12. ACTIVITY AND ENERGY EXPENDED BY MALES

A territorial male Maccoa Duck spends one-third of the daytime on active behaviour associated with reproduction. Territorial males averaged 297 displays per 15-hr day, or about one display every 3 min. Active defence of territory occupied 15% of a male's time, adding an estimated 20% to the energy that a non-breeding male would spend on self-maintenance. Active courtship of females occupied another 15% of the male's time, adding a further 18% to the energy spent by a non-breeding male on self-maintenance. The increase in time spent on reproductive behaviour over that of a non-breeding male is achieved mainly through decrease of time allocated to resting by the non-breeder. Territorial males increased energy expenditure by a factor of 1.3, but devoted the same proportion of time as non-breeders to actual feeding (Table 14, adapted from Siegfried *et al.* 1976).

13. MOULT

Adult Maccoa Ducks replace all their feathers twice annually (Siegfried 1970). Average mass (dry weight) of a full complement of feathers was 29 g (25.0 - 32.7, n= 3) and 27 g (24.4 - 29.8, n= 2) for males and females respectively. Males moult before and after breeding. Females moult before

breeding, but the timing of the second moult has not been determined precisely. We have a few observations of brood-caring females with growing remiges, and these observations are not restricted to late-in-the-season breeders. However, we cannot say at present whether it is normal for breeding females to moult whilst still caring for young ducklings.

Energy content of Maccoa Duck feather tissue varied between 4.87 and 5.14 kcal/g. We have taken 5.0 kcal/g as an approximate value representative of all Maccoa Duck feather tissue, bearing in mind that feathers consist almost exclusively of the protein keratin (5.5 kcal/g). If we consider a female Maccoa Duck to take 30 days (which may be a little long for the remiges and a little short for the body plumage) to complete the moult, then 27 g of feathers represents the production of 4.5 kcal/day of which about 25% goes into the remiges and rectrices during that time. At this stage, we cannot say by how much a moulting Maccoa Duck increases its daily energy requirements, since in birds generally the increase in metabolic rate during moult is complex and involves both the cost of growing feathers and the thermoregulatory response to decreased insulation of the moulting bird.

14. ENERGY BUDGETS

Energy output by the female Maccoa Duck during the laying period amounts to an average of 13.7 kcal/hr, which is far greater than at any other time. Table 15 summarises the diurnal hourly energy costs for female Maccoa Ducks at various stages of their breeding cycle. Unfortunately, we do not have any information at present on the nocturnal activities of females, other than for incubating birds. Thus it is not possible to make comparisons of daily energy expenditure and energy intake.

The average diurnal hourly debit balance for incubating birds is 0.85 kcal. However, the average daily debit balance for incubating females amounts to 39.6 kcal, or 990 kcal for the 25-day incubation period (Table 16). This debit averages 1.65 kcal/hr. Obviously this is more than the diurnal hourly debit of 0.84 kcal. Females show decreased nest attentiveness during the day, and

Table 15. Mean hourly (dawn to dusk) energy budgets of female Maccoa Ducks in summer (December—February) and winter (April—June).

	Energy output [a] (kcal/hr)	Energy intake [b] (kcal/hr)	Balance (kcal/hr)
Incubating (summer)	9.07	8.23	—0.84
Brood-caring (summer)	11.72	13.64	+ 1.92
Non-breeding (summer)	9.59	10.80	+ 1.21
Non-breeding (winter)	6.39	6.23	—0.16

[a] based on data in Table 13.

[b] based on data in Table 10 and an assimilated energy intake rate of 0.43 kcal/min for an incubating female (see Table 16) and 0.45 kcal/min for other birds (see Table 3 and assuming an assimilation efficiency of 90%).

spend correspondingly more time feeding. Nest attentiveness is high at night (Siegfried *et al.* in press), so that the rate of energy intake declines and the debit balance increases. During the day the cost of rewarming the eggs after each of the bouts off the nest is partly offset by the generally higher ambient temperatures. The duration of the inattentive period is positively correlated with the increase in ambient temperature (Siegfried *et al.* in press).

In this context, we draw attention to the possibility of solar-assisted incubation when the female is off the nest during the day. As there is no down in the nest the eggs are exposed, and though there is usually some overhead cover the eggs are partially insolated, at least during the midday period. Furthermore the matt surface of the eggs, in contrast to the glossy texture of most duck eggs, might serve to reduce reflected radiation, thereby enhancing the insolation effects. Whether these materially influence egg temperatures has yet to be demonstrated.

Brood-caring females appear to have a credit balance during daytime, as do non-breeding females in summer (Table 15). However, a female caring for newly-hatched ducklings broods them at night, during which time she does not normally feed. Moreover, if moult during the brood-caring phase is normal, then the presumed increased metabolic costs associated with moult would provide an additional tax on the brood-caring female's energy resources. In sum, everything points to the breeding female having to spend more energy than she can gain, commencing at the onset of egg-laying through until into the brood-caring phase of the annual cycle.

A non-breeding bird in winter spends about 50% less time feeding than a breeding bird, and apparently operates a balanced energy budget. We do not attach any significance to the slight apparent energy debit exhibited by females in winter. Rather this probably represents an artefact of the necessarily crude approximations involved in constructing these energy budgets.

Table 16. Mean daily energy budget of a female Maccoa Duck during the incubation period.

Activity	Time (hr)	Energy output [a] (kcal)	Energy intake [b] (kcal)
Preen and bathe	1.2	6.00	0
Swim	0.2	2.06	0
Dive (feed)	5.3	106.00	136.74
Incubate	17.3	62.28	0
Total	24.0	176.34	136.74

[a] based on metabolic rates in Table 12 and 24-hr observation periods of two incubating birds.
[b] based on 0.43 kcal/min derived from data on frequency and duration of dives of females during spells off their nests, biomass of food organisms in the mud in which the females were observed to feed, the oesophageal contents of individual birds collected while they were feeding in the mud, and an estimated 90% assimilation efficiency of the bird for the food organisms ingested.

The daily energy expenditure for non-breeding birds can be estimated from the formula

$$DEE = 317.7W^{0.7052}$$

where DEE is daily energy expenditure in kcal, and W is the body weight of the bird in kg (King 1974). From this it is calculated that a non-breeding female Maccoa Duck would expend 241 kcal/24-hr in summer and 221 kcal/24-hr in winter. These estimates are 1.05 and 1.44 times greater than our diurnal hourly values expanded to a 24-hr period. However, it needs to be stressed that the value of constructing energy budgets is not in quantifying exactly the various energy gains and losses, but in the identifying of relative expenditures in each activity in relation to the likely gains.

Territorial, breeding males devote the same proportion (16%) of daytime as non-breeders to actual feeding, but increase their overall daily energy expenditure by a factor of about 1.3 (Siegfried *et al.* 1976). The breeding male apparently incurs an energy debt.

An energy reserve, in the form of body fat, is essential for egg-production and incubation in the Maccoa Duck. Egg production might require the diversion of as much as 126 g (9.5 kcal/g) of depot lipids for a six-egg clutch. The female's daily energy deficit of 39.6 kcal during incubation would require mobilization of about 104 g of fat for the 25-day incubation period. A female collected at the start of her incubation phase contained fat depots amounting to 142 g, whereas 58 g of fat was found in a female shot in the second week of her brood-caring phase. The 84 g difference is close to the calculated loss (88 g) in body weight during incubation (Appendix 1), and is not too far removed from the estimated depletion (104 g) of body fat. Thus, a pre-laying female could require to accumulate about 200 g in fat depots to assure sufficient energy for egg-production and successful incubation. The Ruddy Duck is capable of storing this amount of fat, and so is the larger Maccoa Duck (Siegfried 1977, and unpublished). These ducks are similar to the Eider Duck *Somateria mollissima* in which the female accumulates about 300 g of fat as an energy source during incubation (Gorman & Milne 1971). However, the female Eider Duck weighs about three times as much as the Maccoa Duck and does not produce a heavier clutch. Male Maccoa Ducks also accumulate substantial fat depots prior to breeding, and these energy reserves are utilized during the period that the male is territorial (pers. obs.). Presumably, those males which can maintain fat reserves longest are able to maintain territories longest, and so increase their opportunities for repeatedly inseminating numerous females.

In our generalizations about the energy budgets of Maccoa Ducks, we have made numerous assumptions and we have incorporated crude estimates based on small samples. We are aware of many deficiencies in the approach, but we are confident in stating that both sexes require to accumulate relatively large energy reserves, in the form of fat, before onset of breeding.

Fat depots amounting to 20% and more of the birds' body weight are apparently required for successful breeding.

15. CONCLUSIONS

As expressed above (Section 4), we have reservations concerning our data on the seasonal availability of food to Maccoa Ducks in the south-western Cape. For the moment, however, we postulate that the availability of benthic food organisms, in respect to both quantity and quality, was similar in all seasons, and that at least socially-dominant Maccoa Ducks were able to feed at approximately the same level of efficiency at all times of the year. This premise is crucial to some of the concepts developed here. In any event, we will argue that, the regular winter influx of Maccoa Ducks into our study area (Section 2, Siegfried, Ball, Frost & McKinney 1975) suggests that food is not limiting onset of breeding then or in early spring, when other waterfowl normally breed. Furthermore, we have demonstrated that Maccoa Ducks spend a maximum amount of time loafing and a minimum amount of time feeding outside of the summer breeding season.

We suggest that by delaying breeding until relatively late in the year, the Maccoa Duck is taking advantage of the extended period of daylight and warm ambient temperatures which occur then, and which assist in reducing the energy tax demanded of both sexes and of the incubating female especially. The adaptiveness of the female's behaviour during the incubation period has been pointed up elsewhere (Siegfried *et al.* in press). It suffices here to say that the female feeds frequently in short spells alternating with longer bouts of incubation throughout the day, and even at night. Since the eggs in the nest cool faster than they heat up, recovery time, after the parent has returned to incubate, is longer than exposure time. The time lost for embryonic development is least, in relation to exposure time, at relatively high ambient temperatures (Siegfried *et al.* in press). The precocial, almost exclusively aquatic Maccoa duckling, which has to dive for its food, presumably has the best chance of surviving to fledging when water as well as air temperatures are relatively high; all other conditions being equal during the year.

A combination of food and ambient temperature conditions appears to be important among factors controlling the geographical and seasonal distribution of breeding in members of the genus *Oxyura*. The small oxyurines tend to be resident in warm-temperate climate-zones (Siegfried 1976), and apparently the birds are intolerant of cold water (Siegfried 1973c). All the species, which have proportionately large eggs, appear to delay onset of breeding until ambient temperatures are relatively high. The North American Ruddy Duck experiences an energy-drain "problem" during incubation (Siegfried *et al.* in press) similar to that of the Maccoa Duck and, in this context, ambient temperature, acting through incubation, may be crucial in controlling the breeding range of all the small oxyurines.

We suspect that a female Maccoa Duck's reserves, in the form of body fat, may not uncommonly be so reduced during, or at the end of, egg production as to leave little or no spare energy available for incubation. Should the female fail to make good the deficit through not being able to ingest sufficient food at this time, incubation could not begin or continue. We found several deserted fresh egg-sets and partially incubated clutches in our study area, and the same phenomenon is known to occur elsewhere (pers. obs.). This suggests that desertion of eggs is not unusual before and during incubation.

For the oxyurines, it seems likely that a diving mode of feeding resulted in selection for precocial chicks, requiring large, energy-rich eggs (Lack 1968). After egg production, the energy reserves of a female may not be always sufficient for successful incubation. A female would be spared the loss of her "investment", in the eggs, and would save the extra cost of energy needed for incubation, if the eggs could be incubated by some other bird. The precocity and self-sufficiency of Maccoa ducklings make them "pre-adapted" for parasitism, in a situation in which the hatchling is not fed by the parents. Nest parasitism has been recorded several times for the Maccoa Duck, both intraspecifically (Clark 1964) and interspecifically (Dean 1970, Lees-May 1974). The Maccoa Duck and several other oxyurines are facultative parasites (Weller 1968), occasionally laying their eggs in other birds' nests but usually incubating their own eggs. This may represent a phase in the evolution of obligate parasitism. The South American Black-headed Duck *Heteronetta atricapilla,* a member of the Oxyurini, is an obligate parasite (Weller 1968).

16. SUMMARY

The Maccoa Duck *Oxyura maccoa* is a small diving bird which obtains its food by straining invertebrates, mainly Tendipedidae larvae and pupae, from the soft, muddy ooze overlying the bottoms of ponds. The species tends to breed late in the year, when ambient temperatures are relatively high, in the south-western Cape, South Africa. The female produces large eggs, resulting in precocial ducklings. The ducklings obtain their food by diving, soon after hatching. Gonad development in the female was estimated to cost 244 kcal. The egg, weighing 88 g, costs 278 kcal to produce, much more, in relation to the producer's metabolic rate, than any other anatid egg studied to date. Incubation of six eggs required 35.17 kcal per day, increasing the female's metabolic rate. Each embryo contributes a maximum of 48 kcal to the cost of incubation, mostly during the last few days of incubation. The ducklings have large energy reserves at hatching. The time spent by the female on incubation and brood care is made up largely of time spent resting by non-breeding females. The time spent by breeding males on territorial defence and courtship is achieved mainly through decrease of time allocated to resting by non-breeding males. Breeding birds apparently spend more energy than they gain by feeding, and the problem of maintaining a positive energy balance while breeding is overcome largely through the parents' capacity to store large energy reserves in the form of subcutaneous and visceral deposits of fat. Ambient temperature, rather than availability of food, acting through incubation, may be crucial in controlling onset of breeding and the breeding range of all the small members of the genus *Oxyura.* For the female Maccoa Duck, maximum daily energy output occurs during egg production, and the female may not always be able to mobilize sufficient energy for successful incubation. Facultative intraspecific and interspecific nest parasitism occurs in Maccoa Ducks, saving certain females the energy cost of incubation and brood care. This may represent a phase in the evolution of obligate parasitism.

17. ACKNOWLEDGEMENTS

We thank Sue Frost, for assistance in the field and in the laboratory, and M. H. Currie for supplying the weights of newly hatched ducklings. Dr. R. H. Drent gave helpful advice. The study was supported financially by the Council for Scientific and Industrial Research and the University of Cape Town.

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19. APPENDIX 1

MASS OF FEMALE MACCOA DUCKS

Fresh specimens, weighed after removal of gonads and materials in the oesophagus and gizzard, included three non-breeding females, $\bar{x} = 600$ g $\pm$ 16 S.D. in winter (June-August); a female with four-week-old ducklings, 673 g; and an egg-laying female, 907 g. A mean summer (December-February) mass for females was calculated using all five specimens, $x_x = 677$ g $\pm$ 135 S.D., since the population in summer consisted of pre-breeding and post-breeding birds. The mass of an incubating female (= 761 g) was derived from the mass of the laying female (= 907 g), on the basis of incubating female Ruddy Ducks *Oxyura jamaicensis* weighing 84% of the mass of laying females (Siegfried 1977).