

# ACTIVITY BUDGETS OF MALE MACCOA DUCKS

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## ABSTRACT

The behaviour of breeding and non-breeding male maccoa ducks (*Oxyura maccoa*) was studied in South Africa. Individual ducks were observed continuously from sunrise to sunset in the wild, and all ritualized and non-ritualized behaviour was recorded. Diurnal time budgets of territorial and non-territorial males were translated into energy budgets, showing relative time and energy expenditures for resting, foraging, preening and bathing, territorial defence and courtship activities. A territorial male spent one-third of the daytime on active behaviour associated with reproduction. Territorial males averaged 297 displays per fifteen-hour day, or about one display every three minutes. Active defence of territory occupied 15 per cent of a male's time budget, adding an estimated 20 per cent to the energy a non-breeding male spent on self-maintenance. Active courtship of females occupied 15 per cent of a male's time budget, adding 18 per cent to the energy a non-breeding male spent 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 in the budget of the non-breeder. Territorial males increased energy expenditure by a factor of 1.3, but devoted the same portion of time as non-breeders to actual feeding (21 per cent). Energy- and time-saving strategies were associated with territorial defence and courtship, contributing towards optimization of time and energy budgeting.

## INTRODUCTION

In the life cycle of any animal, time, energy and behaviour together form a system – termed the exploitation system by Verbeek (1973). Reproduction requires extra time and energy above the needs of self-maintenance. Among individuals competing for resources, success is linked with the individuals' abilities and opportunities for performing appropriate behaviour at the right time. Very little is known quantitatively about the time and energy requirements attending behavioural aspects of reproduction, and the interplay of time, activity and energy has not been adequately investigated for any free-living bird (King 1973; Verbeek 1973). This requires the study first of time budgets and then the allocation of energetic costs to the various behavioural activities.

In the waterfowl (Family Anatidae) daily and seasonal time budgets have been determined for certain species (e.g. *Anas crecca*: Tamisier 1974), but we are unaware of any published accounts dealing with allotments of time for detailed behavioural patterns in individual ducks observed continuously from dawn to dusk in the wild. This paper deals with the daily time budgets of male maccoa ducks (*Oxyura maccoa*), and includes detailed quantitative accounts of behaviour and provisional information on energy budgets. The report contributes towards our ultimate objective, which is an ecological analysis of the adaptive significance of the maccoa duck's repertoire of behaviour.

## STUDY AREA AND METHODS

Wild maccoa ducks were studied in the south-western Cape, South Africa, in 1968, 1972 and 1973. Data were collected while observing individual birds continuously from dawn to noon on one day and again from noon until dusk on the following day. On several days observations were made continuously from dawn to dusk. Field-work extended over several days of uniformly fine weather in December, January, February, April, May and June. In December–February dawn-to-dusk observations were made during 05h30–20h30 (local time). In April–June dawn-to-dusk observations extended over 07h00–18h00.

We employed 'focal animal' and 'instantaneous scan' methods (Altmann 1974) to obtain activity records. Tape-recorders and binoculars were used. Observations were made from raised promontories overlooking bodies of water. Maccoa ducks seldom fly during daylight. They are almost exclusively aquatic, and are normally found dispersed over a body of water. The territorial behaviour of the species (Clark 1964; Siegfried & van der Merwe 1975) also greatly facilitated recognition and extensive continuous observation of individual birds. Two individuals were marked with plastic nasal-saddles (Bartonek & Dane 1964).

We recorded every conspicuous act of behaviour performed by focal birds. Thus complete numerical records were obtained for all major displays. Terminology for displays follows Siegfried & van der Merwe (1975). Preening includes all activity associated with the nibbling and oiling of feathers. Bathing is included with preening. Maccoa ducks forage almost exclusively by diving. Feeding includes all the time associated with diving and the pauses between each consecutive dive in a foraging bout. Resting includes sleeping. Swimming time is based entirely on movement from one place to another. A bout of any particular behaviour was regarded as interrupted when the bird resumed its previous behaviour within one minute of the start of the interruption. When the interruption lasted longer than one minute, then it and subsequent behaviours were designated as separate bouts.

## RESULTS

*Territorial, breeding males*

Maccoa ducks are promiscuous. Dominant males defend discrete territories during the breeding season. Territories encompass areas of open water and emergent vegetation. Females are attracted to these areas for feeding, mating and nesting (Clark 1964; Siegfried & van der Merwe 1975). Breeding occurs mainly in summer and extends from July to March in the south-western Cape (Siegfried 1969).

All data pertaining to territorial males were obtained through use of the 'focal animal' method (Altmann 1974). We observed individual males holding three separate territories.

On average, territorial males rested for 29 per cent of the daylight period (Table 1). The birds typically rested on water in the open. In 80 separate bouts of resting, we only twice recorded a territorial male on land. This bird spent two bouts, totalling 17 minutes, resting on the edge of a beach fringing an island in his territory. Males tended to use repeatedly the same resting places, frequently 'anchoring' themselves in floating vegetation before going to sleep. An individual was

recorded returning on 24 out of 26 occasions to rest at the same place after having foraged elsewhere in his territory. The territory of this male was divided into 10 equal quadrates and the time spent resting in each quadrate was recorded. Table 2 shows that the male spent most time resting in one particular quadrate.

Resting occurred at all times of the day, but males appeared to rest most often and for longer periods in the late morning and again in the late afternoon (Figure 1). Resting bouts were frequently interrupted briefly by the male performing usually one Independent Vibrating Trumpet Call display (IVTC), and then resuming his rest. Thirty-six per cent of all resting bouts ( $n = 80$ ) were interrupted for performance of IVTC. Resting bouts were short, averaging 19

TABLE 1

Mean daily (dawn to dusk) duration of activities of territorial male maccoa ducks during December, January and February.

<i>Activity</i>	<i>Per cent time</i>	<i>Number whole days observation</i>	<i>Number half days observation</i>	<i>Number hours observation</i>	<i>Minimum number individual birds</i>
Rest	29	2	8	89	3
Dive	29	2	8	89	3
Preen and bathe	10	2	8	89	3
Swim	19	2	8	89	3
Display	13	2	8	89	3

TABLE 2

Time spent by a male maccoa duck in resting in particular areas of his territory.

<i>Grid quadrate in territory</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>Minutes male 10 observed resting</i>	
Per cent time male resting	1	23	53	3	6	2	12	0	0	0	866

minutes (Table 3). Uninterrupted bouts tended to be shorter than those containing IVTC (Table 3).

Time expended on foraging, exclusively by diving, occupied as much of the day as resting (Table 1). However, 83 per cent of all diving bouts were interrupted for performance of displays, and diving bouts were shorter than resting bouts (Table 4). Based on the number of dives per bout multiplied by the number of bouts, males averaged 282 dives per fifteen-hour observation day, spending 16 per cent of the day underwater.

Preening and bathing occupied 10 per cent of the males' daily time expenditure (Table 1). Bouts typically were short, and occurred frequently throughout the day (Table 5; Figure 1). Thirty-two per cent of all bouts were interrupted for performance of displays.

Males spent 19 per cent of the day swimming (Table 1). This allocation is broken down to time spent on swimming associated with foraging, defence of territory and courtship. Table 6 shows that two-thirds of all swimming activity was associated with territorial defence, mainly involving bouts of Stretched Swim Display (Siegfried & van der Merwe 1975).

Time allotted to displays (excluding Stretched Swim) amounted to 13 per cent of the day (Table 1). Performance of displays was not correlated with a particular time of the day. For instance, two of the male's main displays, Independent Vibrating Trumpet Call (IVTC) and Vibrating Trumpet Call (VTC), occurred spread out more or less evenly throughout the day

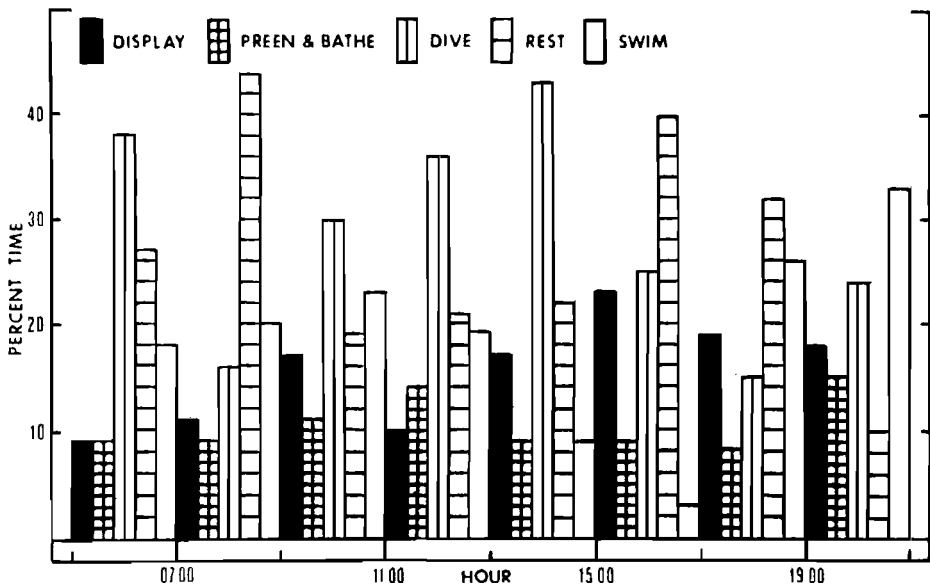


FIGURE 1

Daily pattern of time expenditure on activities by territorial, male maccoa ducks. Per cent of time spent on activities is analysed per two-hour period, based on observation periods given in Table 1.

TABLE 3

Daily frequency and duration of resting bouts of territorial male maccoa ducks. Observation schedule as in Table 1. Figures in parentheses are ranges.

<i>Mean number bouts</i>		<i>Mean bout duration (minutes)</i>		
<i>All bouts</i>	<i>Number uninterrupted by IVTC</i>	<i>All bouts</i>	<i>Uninterrupted by IVTC</i>	<i>Interrupted by IVTC</i>
13,3	8,5	19 ± 20 (S.D.)	17 ± 17 (S.D.)	24 ± 25 (S.D.)
(9-19)	(4-11)	(1-105)	(1-70)	(2-105)
<i>n</i> = 80	<i>n</i> = 51	<i>n</i> = 80	<i>n</i> = 51	<i>n</i> = 29

TABLE 4

Daily frequency and duration of diving bouts of territorial male maccoa ducks. Observation schedule as in Table 1. Figures in parentheses are ranges.

<i>Mean number bouts</i>		<i>Mean bout duration (minutes)</i>	<i>Mean number dives per bout</i>
<i>All bouts</i>	<i>Number uninterrupted by displays</i>	<i>All bouts</i>	<i>All bouts</i>
20,2	3,3	12 ± 10 (S.D.)	14 ± 13 (S.D.)
(18-23)	(1-5)	(1-47)	(1-51)
<i>n</i> = 121	<i>n</i> = 20	<i>n</i> = 121	<i>n</i> = 1 756

TABLE 5

Daily frequency and duration of preening/bathing bouts of territorial male maccoa ducks. Observation schedule as in Table 1. Figures in parentheses are ranges.

<i>Mean number bouts</i>		<i>Mean bout duration (minutes)</i>
<i>All bouts</i>	<i>Number uninterrupted by displays</i>	<i>All bouts</i>
21,8	14,8	4 ± 3 (S.D.)
(18-23)	(11-19)	(1-16)
n = 131	n = 89	n = 131

TABLE 6

Daily frequency and duration of swimming bouts of territorial male maccoa ducks. Observation schedule as in Table 1. Figures in parentheses are ranges.

<i>Swimming association</i>	<i>Per cent daily time</i>	<i>Mean number bouts</i>	<i>Mean bout duration (minutes)</i>
Territory defence	12	18,3 (13-22) n = 110	6 ± 6(S.D.) (1-40) n = 110
Courtship	6	10,6 (3-14) n = 64	4 ± 3 (S.D.) (1-20) n = 64
Forage	1	2,8 (2-6) n = 17	4 ± 3 (S.D.) (2-10) n = 17

(Figure 2). On average, an individual male performed one IVTC display every five minutes and one VTC display every 17 minutes during the day.

Individual displays occurred singly or in series with or without other displays (Siegfried & van der Merwe 1975). Water-flicking was recorded most frequently (Table 7). Excluding Water-flicking and Stretched Swim, males averaged 297 displays per fifteen-hour day, or roughly one display every three minutes. Displays frequently interrupted bouts of non-ritualized behaviour (Tables 3–5). Bouts of diving were interrupted most frequently, and displays were performed most intensively during these interruptions (Table 8). About 50 per cent of all the displays (excluding Water-flicking) given to females occurred during bouts of diving. Feeding females, exploiting patchily distributed food, tend to dive repeatedly in the same food-rich area, thus affording a male an opportunity for repeated performance of displays during pauses between dives (Siegfried & van der Merwe 1975).

Single displays and series of displays occurred also as bouts of behaviour quite independent of, and discrete from, other behaviour. This category constituted 59 per cent of all recorded displays, and about two-thirds of the displays in the category were directed at females (Table 9).

Although we were able to observe and record the context in which all activities occurred, it was not always possible to allocate precisely the number of displays or the time involved in terms of either purely male:male or male:female behaviour. Certain displays, e.g., Water-

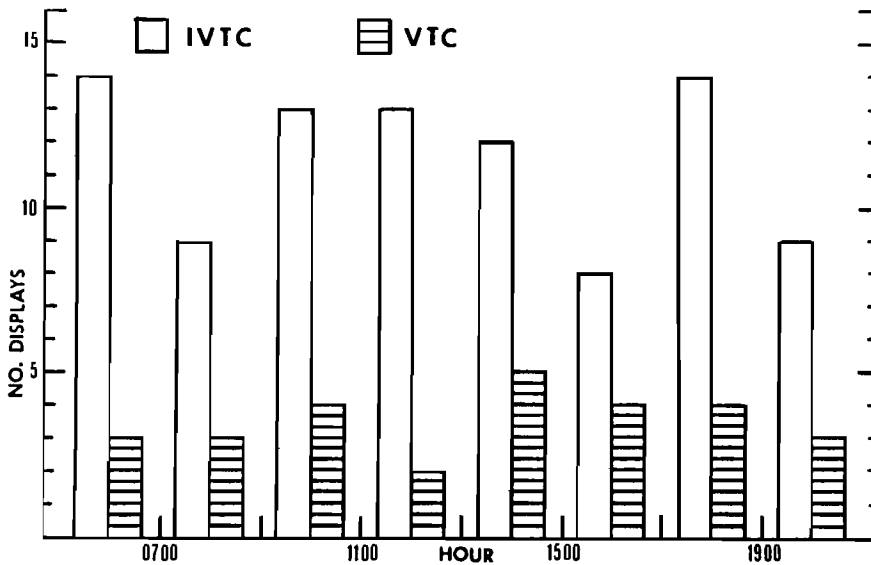


FIGURE 2

Daily pattern of frequency of Independent Vibrating Trumpet Call (IVTC) and Vibrating Trumpet Call (VTC) displays of territorial male maccoa ducks. Number of displays per hour is analysed per two-hour period, based on observation periods given in Table 7.

TABLE 7

Daily frequency of behaviours of territorial male maccoa ducks.

<i>Behaviours</i>		<i>Number whole days observation</i>	<i>Number half days observation</i>	<i>Number hours observation</i>	<i>Minimum number individual birds</i>
<i>Category</i>	<i>Mean daily number and range</i>				
IVTC	162 (104–254)	2	9	97	3
Pursue rival	9 (3–16)	2	8	90	3
Flee rival	1 (0–3)	2	8	90	3
Fight	1 (0–2)	2	9	97	3
Running flight	5 (1–13)	2	7	82	3
Souse	3 (0–4)	2	9	97	3
Lead swim	2 (1–5)	2	9	97	3
Ski	2 (1–5)	2	9	97	3
VTC	57 (10–130)	2	9	97	3
Dab-preening	3 (0–13)	1	7	67	3
Cheek-rolling	40 (4–60)	0	10	75	3
Swimming shake	12 (2–22)	0	10	75	3
Water-flicking	764 (430–1 270)	4	0	60	2

TABLE 8

Daily frequency of displays, excluding water-flicking, interrupting bouts of non-ritualized behaviour of territorial male maccoa ducks. Observation schedule as in Table 1.

<i>Behaviour</i>	<i>Mean number displays</i>	<i>Mean number minutes between interruptions</i>
Rest	8,8	29,1
Dive	99,0	2,5
Preen and bathe	10,8	8,4
Swim (to forage)	1,3	9,8



flicking, occur in series given by territory-holders in response to both females and rival males (Siegfried & van der Merwe 1975). A problem attends the time spent by territory-holders in advertising their status, either to females or to rivals. In addition to time spent on actively advertising and defending status, time spent on presumed passive advertising might be important, since territory-holders apparently elect to rest regularly at places that seemingly render them conspicuous to conspecifics.

While cognizant of these reservations we have, however, apportioned time spent on active behaviour associated with reproduction in relation to territory-holders' interactions with females and rival males (Table 10). On average, a territory-holder spent a total of 277 minutes, or 31 per cent of a fifteen-hour day interacting with males and females. Fifty-five per cent of this time embraced displays associated with bouts of swimming, of which some two-thirds involved

TABLE 9

Daily frequency of displays, excluding water-flicking, performed independently of non-ritualized behaviour of territorial male maccoa ducks. Observation schedule as in Table 1.

<i>Mean number displays</i>	
<i>Directed at rival males and associated with advertisement of territory-holder</i>	<i>Directed at females</i>
58	119

TABLE 10

Mean daily duration of behaviour performed by territorial male maccoa ducks and directed at females or rival males. Observation schedule as in Table 1.

<i>Behaviour directed at females (minutes)</i>	<i>Behaviour directed at rival males (minutes)</i>	<i>Not known (minutes)</i>
137	124	16

interactions with rival males. Overall, approximately half of all behaviour associated with reproduction was directed at females and half at males.

*Non-territorial, non-breeding males*

Out of the breeding season, male maccoa ducks assume a dull female-like plumage, and they congregate in flocks containing both sexes (Siegfried 1968; Clark 1974).

Table 11 and Figure 3 summarize data obtained by 'instantaneous scans' of non-territorial, non-breeding males. These observations were made at the same bodies of water that supported

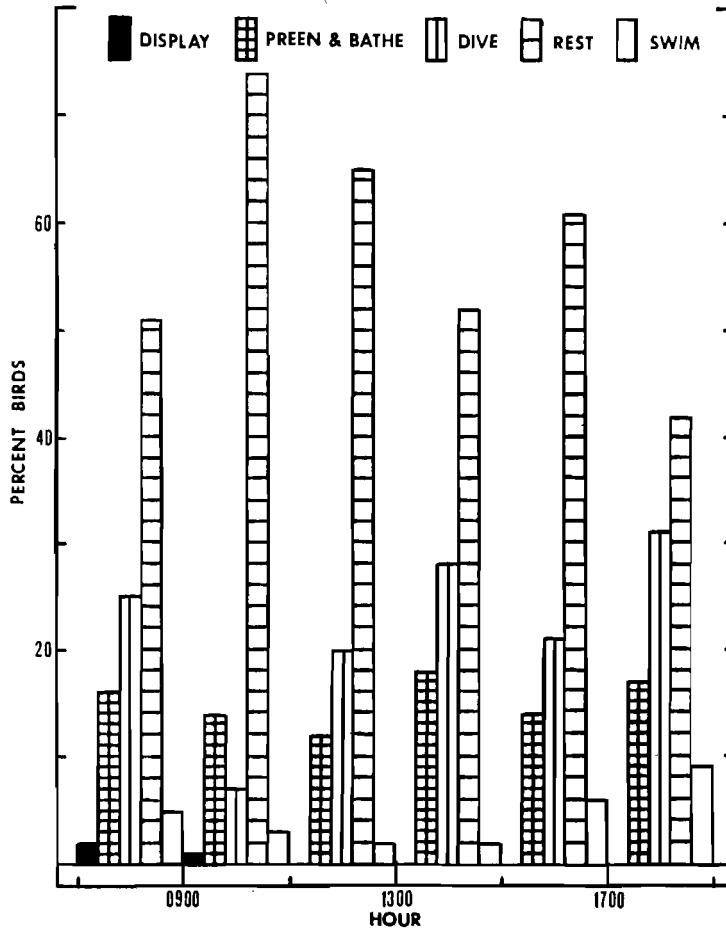


FIGURE 3

Daily pattern of frequency of activities of non-breeding, male maccoa ducks. Per cent of birds exhibiting activities is analysed per two-hour period, based on observation periods given in Table 11.

TABLE 11

Daily (dawn to dusk) duration of activities of non-breeding, non-territorial male maccoa ducks during April, May and June.

Month	<i>Per cent daily time spent on activities</i>					<i>Number half days observation</i>	<i>Number minutes observation</i>	<i>Number 'scans'</i>	<i>Number birds 'scanned'</i>
	<i>Rest</i>	<i>Dive</i>	<i>Preen and bathe</i>	<i>Swim</i>	<i>Display</i>				
April	60	20	17	3	0	2	760	36	390
April	54	27	16	3	0	2	660	32	612
May	60	19	16	4	1	2	690	37	962
June	60	19	12	9	1	2	580	36	276

TABLE 12

Mean daily (dawn to dusk) duration of activities of breeding (territorial) and non-breeding male maccoa ducks during December–February and April–June respectively.

Activity	<i>Breeding males</i>			<i>Non-breeding males</i>		
	<i>Minutes</i>	<i>%</i>	<i>Min/hr</i>	<i>Minutes</i>	<i>%</i>	<i>Min/hr</i>
Rest	259	29	17,4	395	60	35,4
Dive	259	29	17,4	142	21	12,7
Preen and bathe	89	10	6,0	94	14	8,4
Swim	170	19	11,4	34	5	3,0
Display	116	13	7,8	5	1	0,1
	893	100	60,0	670	101	59,6

breeding birds earlier in the year. Resting occupied most of the day, and the distribution of time spent on resting and diving (feeding) throughout the day varied very little from month to month. Resting and diving bouts were not interrupted by displays. Very few displays were observed. Males averaged 218 foraging dives per eleven-hour observation day, spending 16 per cent of the day underwater.

#### *Breeding and non-breeding males compared*

The major difference between the diurnal time budgets of territorial and non-breeding males was in time allocated to resting (Table 12). Territory-holders spent less time resting and were much more active. Actual feeding time (number foraging dives per unit time) amounted to 21 per cent in the budgets of both territorial and non-breeding males (see below). Casual observations made during two full-moon nights suggested that non-breeding birds did nothing else but sleep at night. However, the data are hardly sufficient to demonstrate that this is normal. Territorial males were active at night. Again, our data are inadequate, but we can demonstrate that certain displays, involving vocalizations, were performed by territorial males throughout the night (Table 13). Bouts of swimming occurred frequently as well, but at present we cannot quantify nocturnal behaviour.

#### *Energy budget*

Conversion of the maccoa duck's time budget into a crude energy budget is superficially a fairly straightforward process, since the birds operate at essentially three metabolic levels: resting, swimming and diving.

The caloric equivalent of resting (Basal Metabolic Rate) for a male maccoa duck of 820 g (755–890 g,  $n = 5$ ; mass excludes contents of oesophagus and gizzard) was determined through the formula given by Kendeigh (1970):

$$\text{BMR} = 0,534 W^{0,723} \text{ kcal/day*}$$

The cost of swimming in ducks is  $4,1 \times \text{BMR}$  (Prange & Schmidt-Nielsen 1970). Bathing and preening activity presumably has an energy cost between that of resting and swimming and was arbitrarily given a value  $2 \times \text{BMR}$ . Similarly, there are no actual data on caloric cost of diving in ducks and a value  $7 \times \text{BMR}$  was used, similar to the caloric cost of flying in birds (Tucker 1972). Thus, for the 820 g maccoa duck caloric costs were calculated as: 2,84 kcal/hr (resting); 11,64 kcal/hr (swimming); 5,68 kcal/hr (preening and bathing); and 22,72 kcal/hr (diving).

Energy cost of displays was taken as 7,16 kcal/hr, or  $2,52 \times \text{BMR}$ . Based on Table 7, 77 per cent of displays involved presumed low cost ( $2 \times \text{BMR}$ ) activities similar to preening (Cheek-rolling, Water-flicking and Dab-preening); 22 per cent (Lead-swim, VTC, IVTC and Swimming Shake) were more vigorous and rated  $4 \times \text{BMR}$ ; and, 1 per cent very vigorous activities (Running Flight, Souse, Ski and Fight) were rated  $8 \times \text{BMR}$ .

A further problem attends translation of the territorial maccoa duck's diurnal time budget

\*1 kcal = 4 186,8 joule.

TABLE 13

Number of IVTC and VTC vocalizations uttered by a territorial male maccoa duck at night (moon in last quarter).

<i>Hours</i>	2000-2300	2300-0200	0200-0500
Number vocalizations recorded	5	10	13
Number observation hours	6	6	6

TABLE 14

Mean hourly (dawn to dusk) time and energy budgets of breeding (territorial) and non-breeding male maccoa ducks during December-February and April-June respectively. 1 kcal = 4 186,8 Joule.

<i>Activity</i>	<i>Breeding males</i>		<i>Non-breeding males</i>	
	<i>Min/hr</i>	<i>kcal/hr</i>	<i>Min/hr</i>	<i>kcal/hr</i>
Rest	17,4	0,82	35,4	1,68
Dive	12,7	4,81	12,7	4,81
Preen and bathe	6,0	0,60	8,4	0,80
Swim	16,2	3,14	3,0	0,58
Display	7,8	0,93	0,1	0,01
	60,1	10,30	59,6	7,88

into an energy budget. The pause times on the surface between foraging dives normally are about constant for non-breeding males [ $\bar{x} = 9$  seconds (range = 5–13 seconds),  $n = 100$  dives]. Territorial males frequently spend more time pausing between dives, and in the process swim to positions favourable for intermittently displaying to females. The mean pause time for territorial males was 25 seconds (range = 5–37 seconds),  $n = 120$  dives. The difference of 16 seconds between the pause times of territorial and non-territorial birds was used to increase time spent swimming and to decrease time spent diving (cf. Tables 12 & 14).

Table 14 indicates that territorial males spent about 1,3 times more energy than non-breeding birds during daylight hours, assuming that the two sets of birds were of equal mass and were operating within the zone of thermal neutrality.

#### DISCUSSION

The breeding success of a male maccoa duck depends on the quality of the territory that the male controls (Clark 1964; Siegfried in press). Quality primarily depends on suitable nesting cover available to females and a spatially fixed food source available to females and the territorial male. Females enter a male's territory to feed there and/or to select a nesting site. Males competing for these resources, and through possession thereof the chance to inseminate females, will be successful only if they can economically defend a territory. The time and energy that a male can spend on courting females will depend on the time and energy remaining after self-maintenance and territorial defence costs have been met. Selection will have operated to optimize a territorial male's time and energy budgeting, through most efficient division of behavioural activity.

A territorial male spent one-third of the daytime on active behaviour associated with reproduction. This behaviour occurred throughout the day, as bouts of intensive activity alternating with resting periods. The increase in time spent on reproductive behaviour over that of a non-breeding male is achieved mainly through decrease of the time allocated to resting in the diurnal budget of the non-breeder. Territorial males are thus increasing energy expenditure by a factor of 1,3, but devote the same proportion of time (21 per cent) as non-breeders to actual feeding. This implies greater availability of food and/or enhanced feeding efficiency and/or the male's capacity to accumulate reserves of energy.

Active defence of territory (mainly chases and boundary swims) occupied 15 per cent of a breeding male's diurnal time budget, adding an estimated 20 per cent (1,61 kcal/hr) to the energy a non-breeding male spent on self-maintenance. It appears that less active, energetically relatively inexpensive, defence behaviour is frequently manifested through use of the IVTC display, and additional presumed passive advertisement of status by resting in a conspicuous place. Such energy-saving behaviour has dual function, serving to promote territorial defence through deterrence of subordinate intruders and in announcing the male and his territory to females.

Active courtship of females occupied at least 15 per cent of a breeding male's diurnal time budget, adding an estimated 18 per cent (1,41 kcal/hr) to the energy a non-breeding male spent on self-maintenance. Fifty-six per cent of all courtship behaviour occurred while the male was

closely associated with feeding females and when he himself was able to feed intermittently. Indeed, 70 per cent of all feeding by a male occurred when the male was associated with feeding females. This form of dual exploitation contributes towards optimization of time and energy budgeting.

From these considerations, the efficiency of a breeding male's behaviour involves both time and energy budgeting, and it is difficult to decide which of the two is most important. It appears, however, that selection has favoured optimization of time, since this would maximize opportunity for mating with most females. The problem of maintaining a positive energy budget while breeding appears to have been overcome largely through the male's capacity to store large energy reserves in the form of subcutaneous and visceral deposits of fat (Siegfried unpublished).

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