INCUBATION BEHAVIOR OF RUDDY AND MACCOA DUCKS

W. R. SIEGFRIED
A. E. BURGER
AND
P. J. CALDWELL

The small ducks in the genus *Oxyura* are remarkable for having, proportionate to body size, the largest eggs of all Anatidae, yet clutch-sizes 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 1970).

This paper describes the incubation behavior of the North American Ruddy Duck (*Oxyura jamaicensis*) and the South African Maccoa Duck (*O. maccoa*) which were studied under natural field conditions.

STUDY AREAS, MATERIALS AND METHODS

Ruddy Ducks were studied during 1971 in southwestern Manitoba, Canada (Siegfried 1976). Maccoa Ducks have been studied over several years in the south-western Cape, South Africa (Siegfried 1976). In both species, nesting wild birds were studied from onset of laying to hatching of eggs. The behavior of nesting birds was watched, with the aid of binoculars and telescopes, from blinds. Data on egg, nest-air and ambient temperatures were obtained, using electronically driven, multi-channel telethermometers and paper-chart recorders. Nests and their contents were instrumented according to general procedures described by Caldwell and Cornwell (1975).

For the Ruddy Duck, 3 eggs were probed with thermistors on the day that the clutch (6 eggs) was completed. The nest was built over water (23 cm deep) in a stand of emergent *Scolochloa festucacea* and *Carex atherodes*. Egg and nest-air temperatures were monitored continuously for 24 days until hatching occurred on 21 July 1971. A second, and similarly sited, nest was observed during daylight for a total of 16 hr on 1–3 July 1971. The blind housing the observer was situated 9 m from the nest. This nest contained a clutch of 6 eggs plus one Redhead (*Aythya americana*) egg. Hatching occurred on 8 July. These two nests and their females are referred to as (A) and (B) respectively.

For the Maccoa Duck, two clutches ((A) and (B)) were observed from start of incubation, but intensive study was restricted to the last 10 days of the incubation period (25 days). Both nests were built in rushes (*Typha* sp.) over land about 1 m from open water. Blinds were sited 6 m from the nests. For nest (A), 2 eggs in a clutch of 5 were probed with thermistors and temperatures of eggs and nest-air were monitored continuously for 60 hr; a total of 34 hr of visual observations was obtained during the day and night on 25–29 January 1973. Hatching occurred on 2 February. Nest (B) contained a clutch of 10 eggs. Continuous records of nest-air (4 thermistors in nest) and ambient temperatures were obtained for 95 hr during February 1975 when a total of 28 hr of visual observations was made. Hatching occurred on 9 February.

Since egg temperatures at times undergo little or no change when birds leave their nests (pers. obs.), the use of egg temperatures alone can produce misleading results in deducing time spent on or off the nest. Observations of Maccoa and Ruddy ducks and data on changes in nest-air temperature were used as often as possible in checking the accuracy of time on or off the nest. Although the samples of observations are small, we have no reason to suspect the accuracy of our data. The female Maccoa Duck responsible for nest (A) had been marked earlier in the season by means of a plastic nasal-saddle, allowing observers to recognize the bird during absences from the nest. None of the other females was marked and consequently could not be observed continuously during periods away from the nest. Only the Maccoa Duck was watched while off its nest at night, with the aid of moonlight.

RESULTS

SIZE OF EGGS AND FEMALES

For the Maccoa Duck mean fresh egg mass was 88 ± 8.4 g (n = 8) and mean standard linear dimensions were 66.2 ± 1.8 × 50.7 ± 1.4 mm (n = 55). Using these data and conversion formulae given by Romanoff and Romanoff (1949 : 109), it was calculated that a Maccoa Duck egg has a surface area of 95.7 ± 4.7 cm^2. A clutch of 6 eggs would thus have a surface area of 574 cm^2. Two dead adult female Maccoa Ducks had a mean brood area of 127 cm^2. Ruddy Ducks are similar in size to Maccoa Ducks and there is little difference in the size of the eggs between the two species (Delacour 1959). In both species the females do not develop unfeathered brood patches, but incompletely cover the eggs with the feathered ventral surface of the thorax and abdomen; the feet being lifted clear of the eggs.

FEMALES ON NESTS

The attentive period is that time spent on the nest by the parent bird. In the Ruddy Duck mean daily nest attentiveness was similar throughout incubation (table 1). However, bouts of attentiveness increased in frequency and decreased in duration as incubation progressed (table 2). In both species mean

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TABLE 1. Mean daily percent nest attentiveness for Ruddy and Maccoa ducks.

Species	Week in incubation	Attentiveness			No. hrs data recorded by machine
		Daylight[a]	Darkness[b]	24-hr day	
Ruddy Duck (A)	1	82	78	81	106
	2	76	93	81	144
	3	76	97	83	92
Maccoa Duck (A)	3	71	80	72	60
Maccoa Duck (B)	3	67	81	73	95

[a] 0600 : 2200 for Ruddy Duck; 0530 : 1930 for Maccoa Duck.
[b] 2200 : 0600 for Ruddy Duck; 1930 : 0530 for Maccoa Duck.

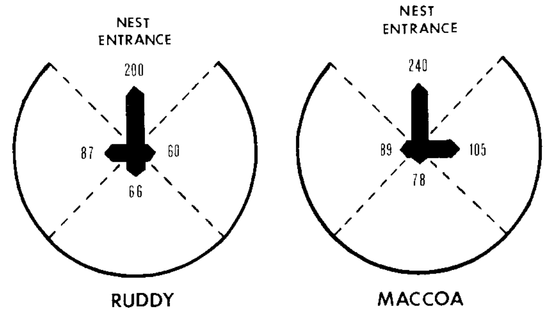

FIGURE 1. Fractional composition of time (daytime only) incubating birds spent sitting with foreparts of their bodies in one of four quadrants. Numbers indicate actual time (min) spent in each quadrant.

bouts of attentiveness were longer at night than during daytime (table 2). In the Maccoa Duck bouts were also significantly longer ($P < 0.05$) (Steel and Torrie 1960 : 74) in the morning than in the afternoon period (table 3).

Periods of undisturbed incubation between positional changes made by the female during attentive bouts are called "incubation spells." In both species, incubation spells occurred regularly and frequently, and in the Maccoa Duck were longest at night (table 4). During daytime, females were observed to sit facing the entrances of their nests for approximately half of the time devoted to incubation spells (fig. 1).

No correlation ($P > 0.05$) between ambient temperature and length of incubation spell was found in the Maccoa Duck (fig. 2). Long incubation spells occurred when nest-air temperatures approached the temperature of the eggs in the nest (fig. 3). Female Maccoa Ducks were observed to become very restless when nest-air temperature rose above incubation temperature of the eggs. Mean daily egg temperatures were 34.1°C for the Maccoa Duck during the 3rd week of incubation, and for the Ruddy Duck 32.1, 34.6, and 34.7°C for the 1st, 2nd and 3rd weeks respectively of incubation. At no time did internal egg temperatures fall outside a range of 25–39°C for the Maccoa Duck and 21–39°C for the Ruddy Duck.

In both species, females frequently and regularly interrupted incubation to make positional changes by rotating on their nests (table 4). During series of consecutive changes in position, the birds showed no

TABLE 2. Mean duration (min) ± one SD and range of nest attentive bouts for Ruddy and Maccoa ducks. Data recording periods as in table 1.

Species	Week in incubation	Duration of bouts			No. bouts in 24-hr day
		Daylight[a]	Darkness[b]	24-hr day	
Ruddy Duck (A)	1	173 ± 99 20 – 390 n = 20	186 ± 118 30 – 400 n = 9	117 ± 103 20 – 400 n = 29	4.3
	2	140 ± 134 30 – 700 n = 31	299 ± 164 100 – 520 n = 9	176 ± 154 30 – 700 n = 40	6.6
	3	82 ± 52 20 – 270 n = 32	537 ± 81 430 – 600 n = 4	136 ± 158 20 – 600 n = 36	9.3
Maccoa Duck (A)	3	112 ± 58 42 – 245 n = 11	132 ± 51 65 – 205 n = 7	120 ± 55 42 – 245 n = 18	8.6
Maccoa Duck (B)	3	60 ± 37 8 – 172 n = 27	121 ± 55 36 – 204 n = 12	79 ± 52 8 – 204 n = 39	13.3

[a] 0600 : 2200 for Ruddy Duck; 0530 : 1930 for Maccoa Duck.
[b] 2200 : 0600 for Ruddy Duck; 1930 : 0530 for Maccoa Duck.

TABLE 3. Mean duration (min) ± one SD and range of nest attentive bouts according to morning and afternoon periods for Maccoa Ducks.

Species	Week in incubation	Attentiveness	
		Morning[a]	Afternoon[b]
Maccoa Duck (A)	3	132 ± 71 42 – 245 n = 6	88 ± 28 60 – 125 n = 5
Maccoa Duck (B)	3	88 ± 33 58 – 172 n = 11	41 ± 25 8 – 85 n = 16

[a] 0530 : 1200.
[b] 1200 : 1930.

tendency to keep on turning in the direction taken by the initial turn (*vide* Siegfried and Frost 1975). While changing position, females frequently "paddled" and "billed" (terms after McKinney 1952) their eggs.

FEMALES OFF NESTS

In both species females frequently left their nests during the hours of darkness as well as in daytime. The females were observed to feed assiduously whenever they were off their nests during daylight. The Maccoa Duck was observed feeding during darkness as well. This was not proven for the Ruddy Duck, although non-incubating birds were observed (by means of a "night-scope") feeding during darkness.

Spells spent off the nest were similar in duration for both species (table 5). In the Maccoa Duck the mean periods off the nest did not differ significantly ($P > 0.05$) between the two females studied:

Female (A) $\bar{x}$ and SD = 34 ± 17 min (n = 15)

Female (B) $\bar{x}$ and SD = 35 ± 16 min (n = 33)

Nor was there a significant ($P > 0.05$) difference between nocturnal and diurnal periods off the nest; thus it appears that daylight in itself did not necessarily affect the duration of periods spent off the nest. Absences, however, were significantly longer ($P < 0.05$) in the afternoons than in the mornings (table 6). Increasing ambient temperatures, generally highest in the afternoons, correlated with an increase in the duration of the Maccoa Ducks' absences from the nest (fig. 4). The Ruddy Duck also left its nest longer when ambient temperatures were relatively high (table 7).

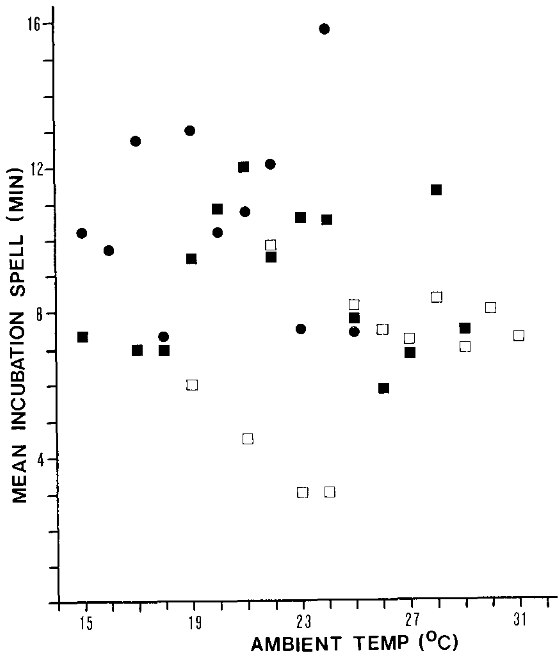

FIGURE 2. Mean duration (min) of incubation spells in relation to ambient temperature for the Maccoa Duck. Solid and open blocks indicate diurnal (0530 : 1930) spells for females at nests (A) and (B) respectively; solid circles indicate nocturnal (1930 : 0530) spells for female at nest (B).

TABLE 4. Mean duration (min) ± one SD and range of incubation spells for Ruddy and Maccoa ducks.

Species	Week in incubation	Incubation spell		
		Daylight[a]	Darkness[b]	24-hr day
Ruddy Duck (B)	2	7.8 ± 4.5 2 – 18 n = 53	No data	No data
Maccoa Duck (A)	3	8.9 ± 6.4 1 – 28 n = 114	No data	No data
Maccoa Duck (B)	3	8.1 ± 4.0 1 – 30 n = 156	10.9 ± 3.2 1 – 39 n = 131	9.4 ± 5.2 1 – 39 n = 287

[a] 0600 : 2200 for Ruddy Duck; 0530 : 1930 for Maccoa Duck.
[b] 2200 : 0600 for Ruddy Duck; 1930 : 0530 for Maccoa Duck.

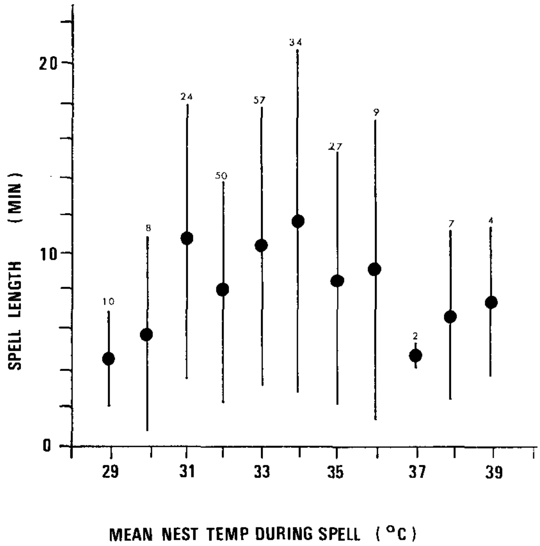

FIGURE 3. Mean duration (min) ± one SD of incubation spells in relation to nest-air temperature for the Maccoa Duck. Numbers indicate sample size.

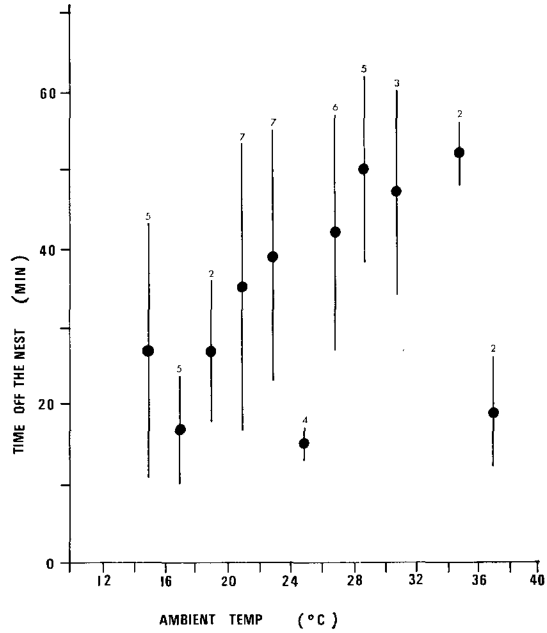

FIGURE 4. Mean duration (min) ± one SD of inattentive periods in relation to ambient temperature for the Maccoa Duck. Numbers indicate sample size, the data grouped in 2°C class intervals.

The cooling rate of a Maccoa Duck egg in the laboratory was determined using procedures and precautions advocated by Kendeigh (1973). The cooling rate is expressed by the regression $y = 0.21\ x - 0.09$, where x is temperature difference between the egg and the air and y is the drop in internal egg temperature per 10 min. This yields a cooling rate of 1.26 °C/°C/hr, agreeing with the expected value interpolated from known cooling rates of other avian eggs in the laboratory (Drent 1975). Frost and Siegfried (in press) found that for the Moorhen (*Gallinula chloropus*) cooling rates of an egg in clutches of 5 and 6 were 57% and 52% respectively of the laboratory determined value for one egg cooling alone. Applying this modification to Maccoa Duck eggs, the cooling rate of an egg in a clutch of 5 is 0.72 °C/°C/hr. This is higher than 0.38 °C/°C/hr derived through the regression $y = 0.064\ x + 0.28$ from data on natural cooling rates of Maccoa Duck eggs in a clutch of 5 in nest (A) in the field. However, the expected cooling rate for eggs in a clutch of 5 does not differ from the observed value to an extent that cannot be explained by factors such as radiated heat

TABLE 5. Mean duration (min) ± one SD and range of periods off the nest for Ruddy and Maccoa ducks. Observation periods as in table 1.

Species	Week in incubation	Periods off nest		
		Daylight[a]	Darkness[b]	24-hr day
Ruddy Duck (A)	1	33 ± 21 10 – 100 n = 20	70 ± 76 10 – 240 n = 8	44 ± 46 10 – 240 n = 28
	2	41 ± 32 10 – 170 n = 33	37 ± 27 10 – 80 n = 6	40 ± 31 10 – 170 n = 39
	3	27 ± 14 10 – 80 n = 33	25 20 – 30 n = 2	27 ± 14 10 – 80 n = 35
Maccoa Duck (A and B pooled)	3	36 ± 16 11 — 71 n = 34	31 ± 17 13 — 70 n = 14	34 ± 17 11 — 71 n = 48

[a] 0600 : 2200 for Ruddy Duck; 0530 : 1930 for Maccoa Duck.
[b] 2200 : 0600 for Ruddy Duck; 1930 : 0530 for Maccoa Duck.

TABLE 6. Mean duration (min) ± one SD and range of periods spent off the nest according to morning and afternoon periods for Maccoa Ducks.

Species	Week in incubation	Periods off nest: Morning[a]	Periods off nest: Afternoon[b]
Maccoa Duck (A and B pooled)	3	29 ± 16 11 – 60 n = 17	42 ± 17 12 – 71 n = 17

[a] 0530 : 1200.
[b] 1200 : 1930.

TABLE 7. Percentage of mean daily time spent off the nest in relation to ambient temperature for the Ruddy Duck. Observation periods as in Table 1.

	Week in incubation	$T_a \leqslant 15°C$	$T_a \geqslant 20°C$
Ruddy Duck (A)	1	18.0	19.5
	2	8.2	17.8
	3	3.7	28.4

and heat produced by the well-developed embryos (in 3rd week in incubation) which must have influenced the result.

Unless exposed to direct sunlight or in very warm conditions, eggs normally cool in the absence of the parent. Since eggs cool faster than they heat up (Drent 1970), recovery time, after the parent has returned to incubate, is longer than the exposure time. Time lost for embryonic development is the sum of exposure time and recovery time. The time lost for embryonic development was least, in relation to exposure time, at high ambient temperatures no matter what the exposure time (fig. 5).

DISCUSSION

In comparing Ruddy and Maccoa ducks and in generalizing about their behavioral adaptations for incubation, it must be stressed that only 2 females of each species were studied and that the results are derived from small samples.

It appears that small body size and large eggs have been key factors in shaping the incubation behavior of Ruddy and Maccoa ducks. Incubating oxyurines manage to cover at any one time only a portion of a clutch, with uncovered eggs at the periphery cooling relatively fast. A female frequently changes position on the clutch and moves the eggs, probably in order to compensate for the discrepancy between surface area of the clutch and the bird's body, related to the need to apply equal heat to all eggs in the clutch.

Incubation has been studied thoroughly in very few anatids. However, in many species females are known to leave their nests normally only twice a day to feed (Kendeigh 1952). In the Ruddy and Maccoa ducks, the females feed frequently in short spells alternating with longer bouts of incubation throughout the day. The related White-headed Duck (*Oxyura leucocephala*) also frequently leaves its eggs unattended (Matthews and Evans 1974). This suggests a relatively greater need to feed and/or that ambient temperatures are relatively favorable for leaving the eggs unattended. Female Ruddy and Maccoa ducks experience severe losses in body condition and weight during incubation and their energy reserves are depleted by the end of the incubation period (Siegfried, in press; Siegfried, Burger and Frost, unpubl. data).

In the Mallard (*Anas platyrhynchos*) eggs in an uncovered clutch cool almost twice as fast as eggs under a covering of down (Caldwell and Cornwell 1975). Oxyurines do not line their nests or cover their eggs with down. Since rewarming of the eggs takes more time than the preceding cooling period during which the clutch is exposed, every absence from the nest costs the parent extra energy and time and extends the incubation period (Drent 1975). Although frequent and ir-

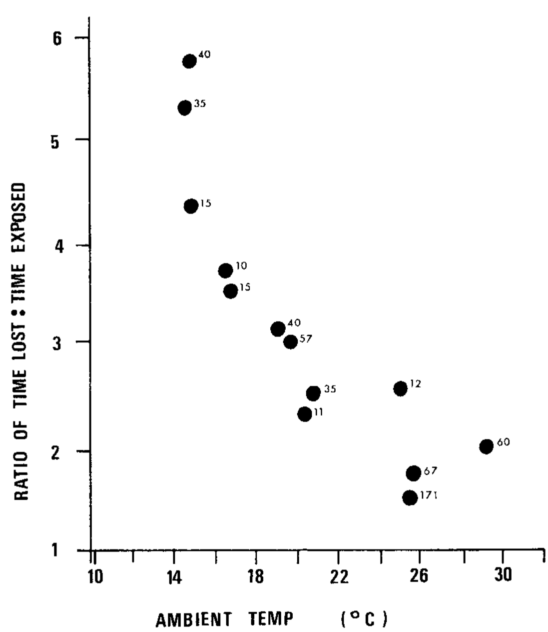

FIGURE 5. The ratio of time lost for embryonic development (exposure time + recovery time) to the duration (min) of parental inattentiveness (exposure time) in relation to ambient temperature for the Maccoa Duck. Numbers indicate duration (min) of individual inattentive periods.

regular short recesses are overall more costly than fewer and longer ones, short intensive foraging spells of 30–60 min duration allow Ruddy and Maccoa ducks to eat quantities of food equal or close to the capacity of the esophagus and proventriculus (based on dissections of ducks which had been collected while feeding). Thus, for the incubating parent relatively long recesses (i.e., 3 hr) would involve unnecessary exposure of the eggs.

Oxyurines feed in ponds where food appears to be abundant and freely available (Siegfried 1973, in press). A combination of favorable food and ambient temperature conditions appears to be important among factors controlling the geographical and seasonal distribution of successful breeding in Ruddy and Maccoa ducks (Siegfried 1976). Oxyurines tend to breed during the warmest time of the year and in areas within warm-temperate climate-zones (Delacour 1959). Ambient temperature, acting through incubation, may be crucial in determing the northern geographical limit of the breeding range of migratory populations of the Ruddy Duck.

SUMMARY

The paper describes the incubation behavior of the North American Ruddy Duck (*Oxyura jamaicensis*) and the South African Maccoa Duck (*Oxyura maccoa*) under natural field conditions. Females feed frequently in short spells alternating with longer bouts of incubation throughout the day. While incubating, a female frequently changes position on the nest and moves the eggs, probably in order to compensate for the discrepancy between surface area of the clutch and the bird's body, related to the need to apply equal heat to all eggs in the clutch. It appears that small body size and large eggs have been key factors in shaping the incubation behavior of Ruddy and Maccoa ducks.

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FitzPatrick Institute, Zoology Department, University of Cape Town, Rondebosch 7700, South Africa. Address of third author: Division of Biology, Kansas State University, Manhattan, Kansas 66506. Accepted for publication 9 March 1976.