ENERGETICS OF INCUBATION IN FREE-LIVING ORANGE-BREASTED SUNBIRDS IN SOUTH AFRICA

JOSEPH B. WILLIAMS

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, Rondebosch, South Africa 7700

Abstract. Using the single-sample variant of the doubly labeled water method (DLW), I quantified the field metabolic rate (FMR) and water flux of female Orange-breasted Sunbirds (*Nectarinia violacea*) during the incubation period. Concurrent to DLW measurements, I examined their incubation behavior and microclimate. These are the first measurements of FMR and water flux for a nectarivorous bird during incubation and the first for an Old World sunbird species. For 10 incubating female Orange-breasted Sunbirds (mean mass = 9.5 g), CO_2 production averaged 13.3 ml/hr, which corresponds to a FMR of 66.2 kJ/day, one of the highest values reported for a bird of its size. Among female passerines, the ratio of FMR to basal metabolic rate (BMR) is typically near 3.0, but for female Orange-breasted Sunbirds, the ratio of FMR/BMR is near 6.5. This suggests that during incubation females are working near their maximum capacity. Females generally lost mass during experimental periods; birds with high mass loss have elevated FMRs. Females consumed 14.7 ml H_2O/day, slightly more than twice that expected based on body size.

Attentiveness of females averaged 39.4 min/hr, while incubation bouts and inattentive periods averaged 11.9 min and 6.7 min, respectively. Females stayed away from their nests for long periods in the late afternoon, especially during inclement weather. Egg temperature averaged 34.7°C for all experimental periods combined. When females were absent for extended periods, eggs cooled to ambient temperatures, often near 10°C. This is a temperature well below the physiological zero temperature. The FMR of females increased significantly with decreasing operative temperature. One observation suggested that when in negative energy balance, females lower their body temperature while on the nest at night. These are the first data suggesting that sunbirds use hypothermia as an energy conservation mechanism in the field.

Key words: Incubation; avian energetics; energetics; doubly labeled water; water flux; Orange-breasted Sunbird; Nectarinia violacea.

INTRODUCTION

Because they nest in environments where ambient temperatures often fall below optimum levels for proper embryological development, parent birds must supply heat to their eggs while also providing for their own needs for self-maintenance, two mutually exclusive behaviors. In many species, both parents share incubation duties (bilateral continuous incubation, BCI), allowing one partner to forage while the other sits on the nest. In other species, males provision the female while she alone incubates the eggs. In both situations, eggs are covered almost continuously and egg temperature tightly controlled (Skutch 1976). In some orders, especially the Passeriformes, a different incubation strategy has evolved: the incubating partner, usually the female, is unassisted by her mate (gynelateral intermitent incubation, GII; Williams 1991). This

dictates that she balance the regulation of egg temperature with fulfilling her own nutritional requirements. The partitioning of time and energy between these two behaviors can affect reproductive performance by influencing hatching sucess and the length of the incubation period (Lyon and Montgomerie 1987, Nilsson and Smith 1988).

Contemporary views of avian life-history evolution often focus on the nestling or post-fledgling period as the period of peak energy demand when energy considerations play a key role in the outcome of the reproductive bout (Nur 1988, Murphy and Haukioja 1986, Weathers and Sullivan 1989). The incubation period has been perceived as a time of relatively low energy demand for parents owing to reduced activity of the incubating parent and the insulating capacity of the nest which is thought to reduce thermoregulatory demands (King 1974, Walsberg and King 1978). In contrast, Yom-Tov and Hilborn's (1981) model for the energy budget of Great Tits

(*Parus major*) predicted that females may experience a negative energy balance during incubation, despite the fact that in this species the male sometimes feeds the female at the nest. More data are needed to resolve these issues.

Considering the few studies that have reported the field metabolic rate (FMR) of free-living birds during both the incubation and nestling phase of reproduction, there is little evidence that female energy expenditures are reduced compared to their expenditures during the nestling period for females that receive no aid during incubation (Williams 1991). In GII systems, several factors contribute towards elevated energy expenditure of the female. These are as follows: (1) The steady state act of incubation requires added heat production above normal thermoregulatory costs when incubating females are exposed to ambient temperatures below their lower critical temperature (Kendeigh 1952, Weathers 1985). (2) Rewarming of eggs after recesses requires increased energy expenditures (Vleck 1981, Biebach 1986). (3) In temperate areas, females typically incubate eggs early in the spring when ambient temperatures are low and food resources may be diminished (Mertens 1977). (4) Females may make nearly as many trips to and from the nest during incubation as they do when feeding young (Haftorn 1978, Williams 1987). Additionally, attentiveness of 60–80% of each daylight hour significantly curtails foraging time and females may have difficulty finding sufficient food to balance their needs under some circumstances (Skutch 1962, Walsberg 1983). Taken together, these considerations suggest that for GII systems, the incubation period can be challenging with respect to energy balance for the female.

I measured the FMR of incubating female Orange-breasted Sunbirds (*Nectarinia violacea*), a small nectarivorous bird endemic to the protea-heath (fynbos) vegetation of South Africa, while simultaneously quantifying their microclimate and incubation behavior. Orange-breasted Sunbirds are sexually dimorphic with males having a yellow-orange breast and a dark iridescent green head, while females are olive-gray on the back and yellowish-green on the belly (MacClean 1984). During the fall and winter months (February–August), males establish a territory in which the female builds a tightly woven, well-insulated, domed nest, usually less than 1 m above ground (Skead 1967). The female typically lays two eggs which she alone incubates, and the male does not provide food to his mate. Incubation lasts 14–15 days (Broekhuysen 1963; Williams, unpubl. data). These birds are unusual in that they breed during the austral winter when temperatures are relatively cool and frequent rainstorms occur (Jackson and Tyson 1971). Within their rather restricted range, mean daily air temperatures average around 12–15°C, with nighttime lows of near 6–8°C during June and July. On average, rain falls about 12 days during each of these two months (Thompson 1975).

Few studies have successfully applied the standard doubly labeled water technique to incubating birds because most species are prone to nest abandonment when disturbed at this time. With the advent of the single-sample variation of the DLW method (Ricklefs and Williams 1984, Williams and Dwinnel 1990), it is now possible to circumvent some of these difficulties making such measurements more tractable. Of the few studies that have measured FMR in nectarivorous birds, all have been completed during the non-breeding season (Weathers and Stiles 1989). I report here the first measurements of FMR for a nectarivorous bird during the incubation period, and the first measurements of FMR for a sunbird species.

STUDY AREAS AND METHODS

STUDY AREAS

This study was conducted from 1 April–4 August 1989 at two sites. The first was a north-facing slope in the Outeniqua mountains about 50 km east of Unionville, South Africa. The plants on which sunbirds were feeding in this area consisted of *Erica* sp. and several species of *Protea*, mainly *P. nerifolia* and *P. repens*. My second site lay in the Hottentots Holland mountains, 3 km north of Kleinmond, South Africa. Sunbirds were primarily feeding on *E. sessifolia*, *P. compacta* and *P. magnifica* during my study. Day et al. (1979) present a more detailed description of fynbos vegetation.

DOUBLY LABELED WATER PROCEDURES

My protocol for using the single-sample variant of the DLW method has been detailed elsewhere (Williams and Dwinnel 1990). In brief, this consisted of netting a female sunbird at the nest in the late afternoon, whereupon she was weighed, banded, and injected with DLW, and immediately released. The entire process required about 5 min. I injected birds with 50 μl of water con-

taining 95 atom % O–18 and 0.8 mCi tritium with a calibrated Hamilton syringe. Because of the nectar diet of sunbirds and consequent high water turnover, the volume of isotopes injected was somewhat higher than normally prescribed (Nagy 1983). The day after injection, I monitored the attentiveness (minutes in the nest per hour) of the female until she was recaptured that evening, either by continuously recording changes in egg temperature (see Davis et al. 1984), or by timing to the nearest second, the number of minutes spent in the nest as determined by visual observation. About 24 hr after injection, birds were renetted at the nest, weighed, and a 60 μl blood sample taken from the brachial vein. Three uninjected birds were also bled for determination of background levels of isotopes. Blood samples were flame-sealed in glass microhematocrit capillary tubes and stored under refrigeration pending analysis of isotope concentration.

Carbon dioxide production was calculated from equation 5 of Ricklefs and Williams (1984). To determine the average water fraction of Orange-breasted Sunbirds, I sacrificed four females and one male, removed their feathers, and dried the carcasses at 70°C to constant mass. Total body water averaged 64.3 ± 0.8% (100 × g H_2O/g wet mass intact bird). The natural logarithm of the initial ratio of isotopes, ln O_i/H_i, was estimated by netting another eight birds, six females and two males, injecting them with DLW, and after a 1 hr equilibration period (Williams and Nagy 1984), removing a 60 μl blood sample. For control birds, ln(O_i/H_i) averaged -10.1193 ± 0.0440 (range -10.0228 to -10.1741). Blood samples from control birds and from incubating females were microdistilled under vacuum to obtain pure water (Wood et al. 1975), then the distillate assayed in 10 μl aliquots for tritium activity (see Williams 1987). The O–18 contents of water samples were measured in triplicate at the laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles. The coefficient of variation for these measurements averaged 0.496%. Webster and Weathers (1989) validated the single-sample DLW method on Verdins (*Auriparus flaviceps*); results based on one-sample calculations differed from simultaneous gravimetric determinations of CO_2 production by less than 0.5% on average.

To calculate water influx and efflux, I used equations 6 and 5 of Nagy (1975). For a constant injection volume, the relationship between specific activity and the milliliters dilution in the body water is described by the equation $C_0 = XY$, where Y = the specific activity of tritium (cpm), X = the total ml of body water, and C_0 is a constant (Nagy 1984). For the sample of control Orange-breasted Sunbirds, $C_0 = 94,810 \pm 5,186$ ml H_2O × cpm. I estimated the initial concentrations of tritium in the body water pool using this equation.

CO_2 production was used to estimate energy consumption with the factor 21.5 J/ml CO_2. This assumes that the diet of sunbirds consisted of 90% nectar and 10% insects (Skead 1967). Nectar has a heat equivalent of 21.1 J/ml CO_2 (Carpenter 1948), and the heat equivalent of insects was assumed to be 24.6 J/ml CO_2 (Williams and Nagy 1985). Estimates of basal metabolism (BMR) were derived using the equation of Aschoff and Pohl (1970).

OPERATIVE TEMPERATURE

Operative temperature (T_e) is defined as the temperature of an isothermal blackbody enclosure with the identical convective conditions as the actual environment and which would result in the same net sensible heat flow to or from an animal with the same surface (Winslow et al. 1937) or body core temperature (Bakken 1976). Functionally, it is essentially the temperature of a metabolically inert body of the study animal under a given combination of microclimatic conditions. Operative temperatures were measured from plumage-covered copper casts manufactured according to the methods of Bakken et al. (1983). For each injected female, I placed three models of females near the nest. One was affixed to the top of vegetation, and thus received full sun; another was perched on a small limb within the vegetation; and a third model was placed within an Orange-breasted Sunbird nest, positioned at the same height and oriented with the entrance facing the same direction as the nest of the injected female. Additionally, I placed an anemometer (Thornthwaite Associates, model 901-LED) which had previously been calibrated in a wind tunnel against a pitot tube, at nest height within a stand of vegetation similar to the vegetation surrounding the nest of the injected bird. The output of thermocouples and anemometer was routed to a Campbell Scientific Corp. data logger (model 10X), which accumulated data for each minute and recorded data as an average for each 15 min interval.

TABLE 1.   Mean body mass, field metabolic rate, and water flux for female Orange-breasted Sunbirds during incubation.

| Animal | Body mass | | FMR | | Water influx (ml H_2O/day) | Period (day) | Date (1989) |
	Mean (g)	Change (%/day)	(ml CO_2/hr)	(kJ/day)[a]			
11	8.8	−7.7	17.02	88.4	17.0	0.89	25 May
52	9.2	−4.1	12.62	59.9	11.3	1.06	28 May
53	9.1	−2.0	14.47	67.9	13.6	1.11	31 May
55	9.9	−1.9	14.10	72.0	19.3	1.07	18 July
56	9.5	−1.0	11.74	57.5	13.4	1.07	21 July
57	10.1	−1.9	13.33	69.5	16.3	1.03	26 July
58	9.7	−5.0	12.97	64.9	11.8	1.03	28 July
59	9.5	−2.1	12.44	61.0	20.5	1.03	1 Aug
60	10.0	1.0	11.75	60.6	13.6	1.03	3 Aug
61	9.6	−1.0	12.16	60.2	9.9	1.08	4 Aug
Mean	9.5	−2.6	13.26	66.2	14.7	1.04	
(SD)	(0.4)	(2.4)	(1.6)	(9.1)	(3.5)	(0.06)	

[a] Units of CO_2 production converted to units of energy using the relation 21.1 J/ml CO_2.

EGG TEMPERATURE

For each injected female and several that were not injected, I implanted a 40-gauge thermocouple within an egg and cemented it in place with dental resin (see Davis et al. 1984). Subsequently, the data logger recorded egg temperature each minute of the day and every 15 min at night. I positioned the thermocouple junction about 1 mm below the upper surface of the egg such that temperature measurements would reflect the temperature experienced by the embryo. Egg temperatures were monitored from the time of injection until the female was recaptured.

STATISTICS

Statistical analyses were performed with SPSS computer software. Means are presented ±1 SD. Null hypotheses were rejected at a significance level of $P = 0.05$.

RESULTS

FIELD METABOLIC RATE

For 10 incubating female sunbirds with a mean body mass of 9.5 ± 0.4 g, CO_2 production averaged 13.26 ml CO_2/hr, which translates to 66.2 kJ/day (Table 1). Females generally lost mass during experimental periods with a mean loss of −2.6%/day; birds with high mass loss tended to have high FMRs (one-tailed test, $r = 0.64$, $P = 0.02$). Water influx averaged 14.7 ml/day for this group of birds.

Bill length increases as Orange-breasted Sunbirds mature and can be used as a crude index of age (Skead 1967). Birds with longer bills had a lower FMR ($r = -0.822$, $P = 0.002$), suggesting that older and more experienced birds had a lower FMR.

INCUBATION BEHAVIOR

For 10 female Orange-breasted Sunbirds, attentiveness varied from a low of 33.4 min at 16:00–17:00 hr, to a high of 52.6 min at 18:00–19:00 hr and averaged 39.4 ± 4.8 min/hr during daylight hours (Fig. 1A). The first inattentive period (period of absence) in the morning was usually about 20 min before sunrise which occurred about 07:25 hr, and females typically settled on the nest for the night about 10–20 min after sunset, which was at about 17:40 hr.

Attentive periods, or the duration of each incubation bout, varied from 8.7 to 14.5 min and averaged 11.9 ± 1.7 min (Fig. 1B). Around midday when temperatures were highest, females tended to stay at the nest longer. Recesses averaged 6.7 ± 1.2 min (Fig. 1C). Females remained away from the nest longer in the late afternoon, apparently foraging in anticipation of their night fast.

Nest visitation rate ranged from 2.5 to 4.1 visits/hr (Table 2). For all females combined, differences between hour intervals during the day were not significant (Analysis of variance [ANOVA], $F = 1.1$, $P > 0.4$). Interindividual comparisons of average nest visitation showed some females made significantly fewer trips to the nest staying on the nest longer at each attentive period (ANOVA, $F = 5.4$, $P < 0.001$), but females that made more frequent trips to the nest did not have a higher FMR than females that made fewer trips.
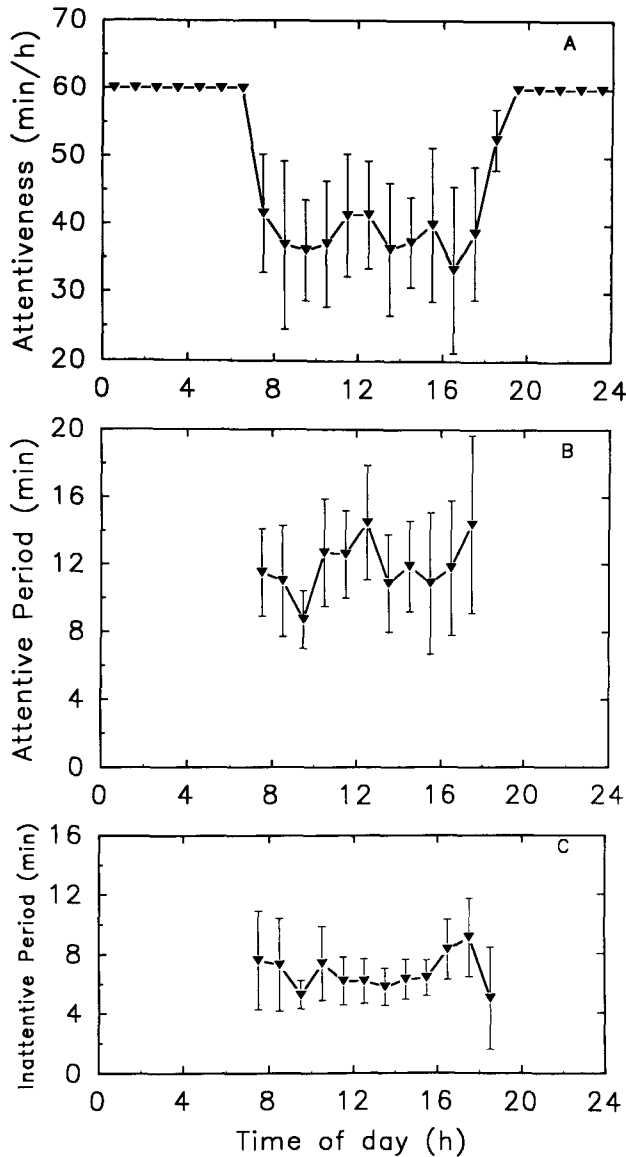
FIGURE 1. (A) Attentiveness, defined as min/hr in the nest, of female Orange-breasted Sunbirds as a function of the time of day. Vertical bars represent 95% confidence intervals. Sunrise occurred at about 07:25 hr, and sunset about 17:40 hr. (B) Attentive periods, the minutes spent on the nest each incubation bout, for female Orange-breasted Sunbirds as a function of the time of day. (C) Inattentive periods (minutes) of female Orange-breasted Sunbirds as a function of the time of day.

EGG TEMPERATURE

For each hourly interval, mean egg temperature ranged from a low of 24.6°C between 17:00 and 18:00 hr to a high of 37.4°C between 19:00 and 20:00 hr (Fig. 2). Some females spent long periods off their nests between 17:00 and 18:00 hr, especially on days of inclement weather when eggs cooled to near ambient temperature, often around 10–15°C. Overall egg temperature averaged 34.7 ± 2.9°C ($n = 11$ eggs).

OPERATIVE TEMPERATURE AND WIND

During winter, May–August, mean temperature of taxidermic mounts varied with the position

TABLE 2.   Nest visitation of female Orange-breasted Sunbirds in South Africa ($n = 11$).

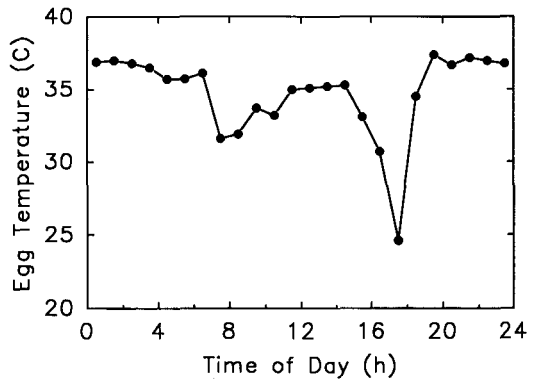| Time of day (hr)	Mean visits/hr	95% CI
07:00–08:00	2.6	1.0
08:00–09:00	3.3	1.2
09:00–10:00	4.1	0.9
10:00–11:00	3.2	1.2
11:00–12:00	3.1	1.0
12:00–13:00	2.7	0.7
13:00–14:00	3.5	1.1
14:00–15:00	3.1	1.1
15:00–16:00	3.0	1.2
16:00–17:00	3.2	1.8
17:00–18:00	2.5	0.6
Mean	3.1	

FIGURE 2.   Mean egg temperature maintained by female Orange-breasted Sunbirds as a function of the time of day. The low average egg temperature during the interval 17:00–18:00 hr was a result of several females staying off their nests for the entire interval.

of the mount (Fig. 3A). The model affixed to the top of vegetation and thus exposed to full sun, averaged the highest T_e, around 25°C at midday, while the model within a nest gave the lowest T_e readings. At night, temperature readings for all models fell below 10°C, and on some days in May, below freezing. Wind speeds at 1 m varied with time of day with the highest readings occurring in the afternoon (Fig. 3B).

Female sunbirds altered their incubation behavior in concert with T_e (Fig. 4A). As mean T_e increased (T_e averaged for each 15 min of experimental period), females increased their time away from the nest ($r = 0.57$, $P = 0.03$, $n = 8$). Additionally, the FMR of females increased as the average T_e declined (Fig. 4B). If this analysis is restricted by using only values for T_e during the daytime, the relationship between T_e and FMR remains statistically significant ($r = 0.79$, $P = 0.01$, $n = 8$).

HYPOTHERMIA

Inclement weather can impede the foraging routine of Orange-breasted Sunbirds, and under such circumstances, short-term energy problems may arise for incubating females. One such event apparently occurred on the night of August 4 after a rainstorm that day. In the Hottentots Holand mountains, the number of blooms available to sunbirds had markedly declined by early August. Of the 25 pairs of Orange-breasted Sunbirds on my study area, four had nests with eggs at this time. A female that maintained egg temperature above 34°C for the two previous nights apparently went into a controlled hypothermia on the

night of August 4, resulting in a drop in egg temperature to about 29°C (Fig. 5). On this night, she warmed her eggs to temperatures above 34°C until about 03:00 hr, whereupon egg temperature declined to about 29°C. After feeding during her first morning recess the following day, she restored egg temperature to above 35°C, an egg temperature that she maintained while in the nest for the rest of the day. If the thermocouple-equipped egg was shifted in some way by the female away from her brood patch during the night, a similar pattern to the one observed could result, a possibility that I cannot completely eliminate. However, I ran thermocouple wires through the bottom of nests and wires were taped to vegetation, thereby preventing the egg from moving in the nest. Of 10 Orange-breasted Sunbird nests that had eggs with thermocouples, in no case did such a shift in the thermocouple-equipped egg occur. On the first recess of the female on August 5, I checked for the position of the egg and found it unmoved from its location of the previous two days. Movement of the egg probably did not account for the observed pattern.

DISCUSSION

The avian incubation period is often considered a time of low energy demand relative to other phases of the reproductive cycle (Walsberg and King 1978). This idea finds support when BCI systems are examined; FMRs of females during incubation are often lower than when they are feeding young (Williams 1991). In contrast, for
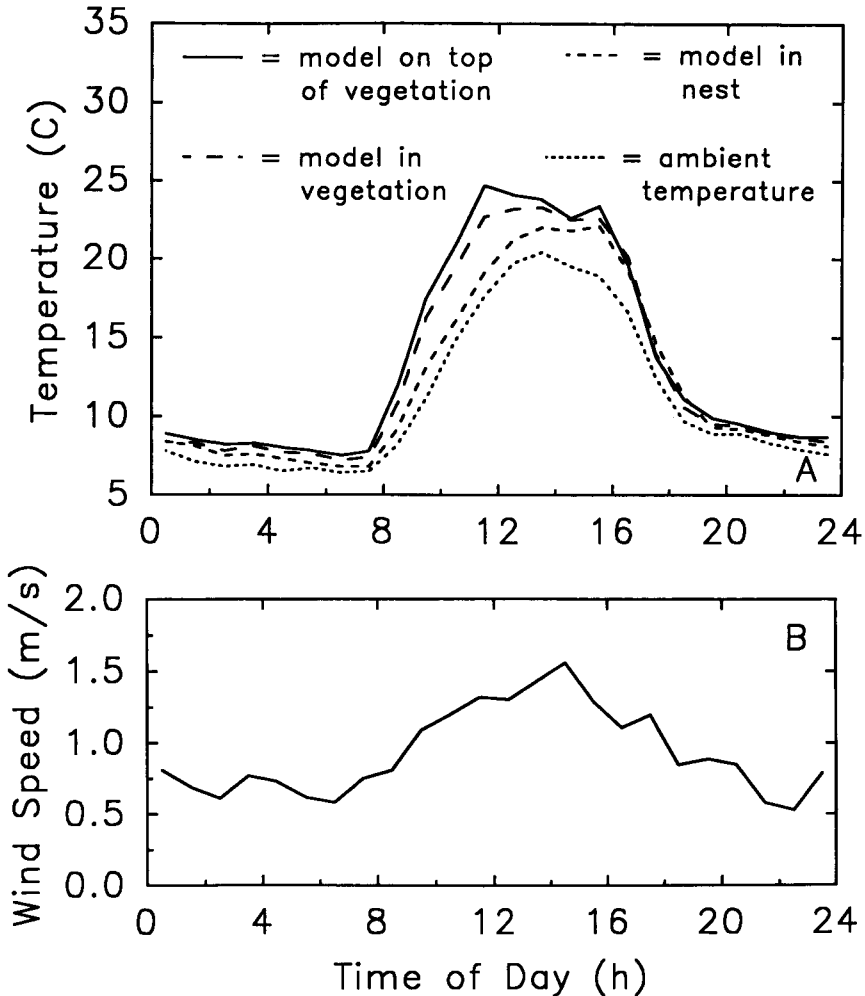
FIGURE 3. (A) Operative temperature (T_e), as measured by taxidermic mounts of female Orange-breasted Sunbirds, in three different locations, and air temperature at 1 m as a function of the time of day. (B) Mean wind speed as a function of the time of day for all days of the study.

GII systems, FMRs of incubating females do not differ from or even exceed values for females feeding young. Relatively high energy expenditure coupled with a reduction in the available foraging time (females spend 60–80% of each hour on the nest, Skutch 1976), may indicate that in some situations incubation could be more energetically stressful than previously believed. Many females that incubate unaided by their mates lose mass, a phenomenon interpreted by some as a genetically programmed anorexia that lowers power requirements necessary for flight during the forthcoming nestling period (see also Sherry et al. 1980, Norberg 1981). The alterna-

tive hypothesis, that incubating females are unable to procure enough food to meet their requirements, remains untested for the specific case of GII females that lose mass.

Incubating female Orange-breasted Sunbirds have one of the highest weight-specific FMRs recorded (Table 3), even when compared to hummingbirds which are thought to have high energy expenditures because they forage in flight (Walsberg 1983, Weathers and Stiles 1989). Though the Bronze-tailed Plumeleteer has a mass-adjusted FMR somewhat higher than female Orange-breasted Sunbirds (Weathers and Stiles 1989), this information was based on one bird,
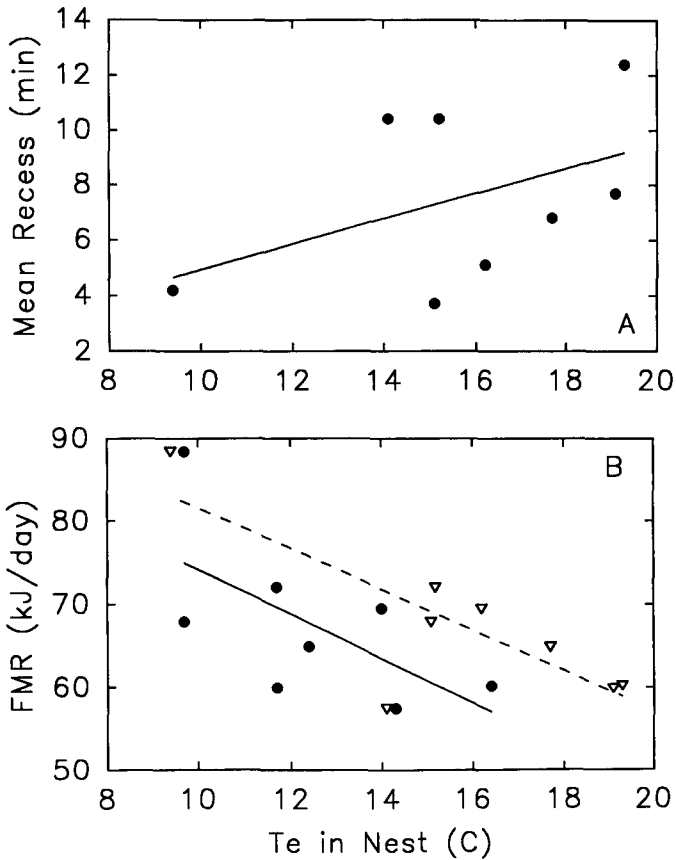
FIGURE 4. (A) Inattentive periods for female Orange-breasted Sunbirds as a function of average T_e within the nest. (B) FMR for female Orange-breasted Sunbirds as a function of average T_e within the nest. Dashed line and unshaded triangles represent average T_e during daylight hours only, filled circles and solid line represent T_e during entire 24 hr day ($n = 8$ in both cases).
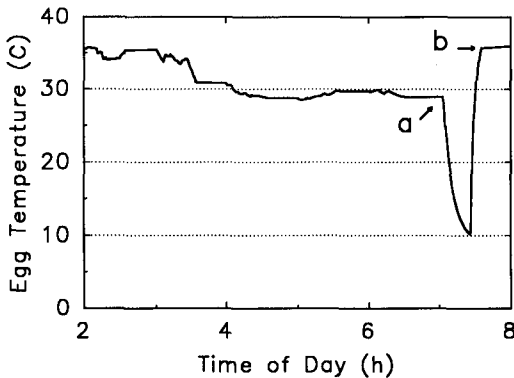

FIGURE 5. Egg temperature for an incubating female Orange-breasted Sunbird during the early morning of August 5. At point a, the female left the nest to forage, and at b she returned to incubate her eggs.

making further data necessary before firm conclusions can be drawn.

Allometric comparisons further emphasize the remarkable high FMR of female Orange-breasted Sunbirds during incubation. Based on 62 species of birds, the equation of Williams et al. (1992) predicts a FMR of 45.1 kJ/day for a 9.5 g bird. Sunbird females had a FMR of 66.2 kJ/day, which surpasses the prediction by 147%. An equation constructed from data for species that forage in flight (Walsberg 1983) yields an estimate of 55.6 kJ/day. This is about 20% lower than I have found for Orange-breasted Sunbirds, even though these birds do not hover while feeding.

The power requirement of free-living birds relative to a standard measure of metabolism, such as basal metabolism, may indicate the physio-

TABLE 3.   Field metabolism of small nectarivorous birds. For the three species of hummingbird and the Eastern Spinebill, FMR measured during non-breeding season.

Species	Mass (g)	FMR (kJ/day)	FMR $(kJ/g^{0.704} \times day)$ [a]	FMR/BMR	Source
Anna's Hummingbird					
(*Calypte anna*)	4.5	32.0	11.1	3.5	Powers and Nagy 1988
Crowned Woodnymph					
(*Thalurania colombica*)	4.9	38.0	12.4	6.2	Weathers and Stiles 1989
Bronze-tailed Plumeleteer					
(*Chalybara urochrysia*)	7.2	58.0	14.4	7.0	Weathers and Stiles 1989
Eastern Spinebill					
(*Acanthorhychus tenuirostris*)	9.7	53.0	10.7	2.5	Weathers and Stiles 1989
Orange-breasted Sunbird					
(*Nectarinia violacea*)	9.5	66.2	13.5	6.5 [b]	This study

[a] Mass-adjusted values based on allometric equation for non-passerine birds (Williams et al. 1992). The slope of the line of this equation is 0.704.
[b] BMR based on Aschoff and Pohl (1970) equation for passerines in rest phase.

logical work load of birds (Drent and Daan 1980). This ratio holds considerable theoretical interest because the maximum sustainable energy expenditure of birds may be constrained physiologically. Individuals that approach this energetic ceiling may incur a fitness cost. Indeed, among insects, high rates of energy expenditure reduce lifespan (Schmid-Hempel and Wolf 1988). Although Drent and Daan (1980) posited that the theoretical maximum sustainable rate of energy expenditure should lie near 4 × BMR, recent evidence shows that during breeding some birds can exceed this value (Bryant 1991). Using different criteria, Weathers and Sullivan (1989) suggested that FMRs of 5.2 × BMR may be nearer the maximum working capacity of birds. Among female passerines, this ratio of FMR/BMR is typically near 3.0, but for female Orange-breasted Sunbirds the ratio of FMR/BMR lies near 6.5. This may indicate that during incubation females are working near their maximum capacity. It is difficult to conceive that females work at even higher levels during other phases of reproduction.

Since ratios of physiological work load depend on accurate assessment of both FMR and BMR, my use of the Aschoff and Pohl (1970) equation to predict BMR might be questioned, especially because some hummingbirds, the New World ecological equivalents of Old World sunbirds, have unusually high BMRs (Kruger et al. 1982). However, Prinzinger et al. (1989) studied 13 sunbird species and found the resting metabolic rate closely followed allometric predictions. Additionally, in Lesser Double-collared Sunbirds (*Nectarinia chalybea*; mass = 8.4 g), a congeneric

species that inhabits many of the same areas as Orange-breasted Sunbirds, BMR was 12.9 kJ/day. This is within 13% of the Aschoff and Pohl prediction (14.9 kJ/day; Leon, unpubl.). These data suggest that the BMR of Orange-breasted Sunbirds can be reasonably approximated using the Aschoff and Pohl equation.

On a day-to-day basis, small birds have limited energy reserves (Jones and Ward 1976, Walsberg 1983). If incubating Orange-breasted Sunbirds expend energy near their maximum sustainable capacity as I have suggested, then one might expect that females could experience a negative energy balance during periods of inclement weather. I have presented evidence that females lower their body temperature while on the nest at night, perhaps as a response to energy shortage. In the laboratory, females that are well fed do not display hypothermia even at ambient temperatures lower than encountered in this study (Prinzinger et al. 1989). These are the first data that suggest that sunbirds use hypothermia as an energy conservation mechanism. Females likely use such a tactic as a last resort, because lowering egg temperature for prolonged periods could lengthen incubation and diminish reproductive sucess (Clark and Wilson 1981).

Consumption of a liquid diet such as nectar mandates a high rate of water influx. Allometric predictions of water influx based on data from 46 species of birds (Williams et al. 1992) yields an estimate of 7.3 ml/day for a 9.5 g bird. My result for Orange-breasted Sunbirds, 14.7 ml/day, is near twice the predicted value. Mass-adjusted water influx rates for Orange-breasted Sunbirds are higher than Anna's Hummingbirds or East-

TABLE 4. Water influx of nectarivorous birds.[a]

Species	Mass (g)	(ml/day)	Water influx (ml/day × $g^{0.874}$)[b]
Anna's Hummingbird	4.5	7.38	1.28
Crowned Woodnymph	4.9	11.81	2.89
Bronze-tailed Plumeleteer	7.2	14.38	2.56
Eastern Spinebill	9.7	8.78	1.23
Orange-breasted Sunbird	9.5	14.7	2.05

[a] Sources as in Table 3.
[b] The slope of the line relating water flux to mass in birds is 0.874 (Williams et al. 1992).

ern Spinebills, a nectarivorous bird of Australia, but not as high as values for two tropical hummingbirds, the Crowned Woodnymph and Bronze-tailed Plumeleteer (Table 4).

The incubation behavior of Orange-breasted Sunbirds appears fairly consistent within the Cape Province. On Table Mountain in Cape Town, females spent an average of 38.7 min/hr on their nest during the day and the duration of inattentive periods averaged about 8.0 min (Broekhuysen 1963). These findings agree with my results that attentiveness averaged 39.4 min/hr and the mean for inattentive periods was 6.7 min. Both studies indicated that females tended to stay away from the nest longer in the early morning or evening, the former likely a result of energy depletion during the nighttime fast and the latter in anticipation of it.

Many studies have shown a correlation between attentiveness and air temperature with females increasing the amount of time that they spend at the nest when ambient temperatures decline (Kendeigh 1952). More recently, some authors have suggested that females with GII adjust their attentiveness in direct response to fluctuations in egg temperature, which they monitor through sensory receptors located in their brood patch (White and Kinney 1974, Davis et al. 1984). Female Orange-breasted Sunbirds responded to decreasing operative temperatures within the nest by decreasing the length of their inattentive periods. As attentiveness increases, their FMR is elevated likely because the act of warming eggs at these low temperatures is energetically expensive (Weathers 1985).

For optimum embryonic development, females must control the temperature of their eggs within fairly narrow bounds (Lundy 1969, Drent 1975). Deviations from optimum egg temperature for prolonged periods can cause abnormal development or can lengthen the incubation period which could enhance the risk of predation, and thus lower fitness (Webb 1987). Most female passerines adjust their incubation rhythm such that egg temperature is maintained well above the physiological zero temperature of approximately 25–27°C, below which embryonic development ceases (Haftorn 1988). Females will abandon their eggs for long periods during foul weather, presumably because of energy stress. Orange-breasted Sunbirds generally conform to this pattern keeping their eggs above 35°C at night and maintaining an average temperature between 32 and 34°C during the day. On several occasions, especially during stormy weather, however, females stayed off their nest for over 60 min during the late afternoon. This resulted in an average egg temperature below the physiological zero temperature. It is unlikely that females would leave their eggs for such long periods when ambient temperatures were relatively low unless they needed to overcome an energy deficit or to store energy reserves for use during the forthcoming nighttime fast.

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