Oxygen Consumption and Organ Growth in Sooty Tern (*Sterna fuscata*) Embryos

Q. ZHANG AND G. C. WHITTOW
Department of Physiology, John A. Burns School of Medicine,
University of Hawaii, Honolulu, Hawaii 96822, USA

A previous report (Zhang and Whittow 1992) described the patterns of embryonic oxygen consumption and organ growth in the Wedge-tailed Shearwater (*Puffinus pacificus*). In the present study, similar data were obtained for the Sooty Tern. There are some similarities between the eggs of the two species. The sequence of events during pipping, which had an important effect on organ growth in shearwater embryos, is similar in terns and shearwaters (Pettit and Whittow 1983, Whittow 1985). The maturity of the hatchling is also similar; both are designated to be semiprecocial (Pettit et al. 1984). However, there are also differences between the two species as well. The incubation period of the Wedge-tailed Shearwater's egg, but not that of the Sooty Tern's, is prolonged (Whittow 1980). Incubation temperature is 3°C higher in the Sooty Tern (Rahn et al. 1976). Incubation also is different; the Sooty Tern lays its egg directly on the ground whereas the shearwater's egg is protected by the burrow in which it is laid.

Thus, there were reasons to expect similarities in embryonic organ growth between the two species, but also grounds for anticipating differences. So little is known about the patterns of embryonic organ growth in avian species that a careful comparison of organ growth in the Sooty Tern and Wedge-tailed Shearwater promised to shed further light on the factors affecting organ growth in avian embryos. For example, similar growth patterns in the two species might point to the importance of the pipping pattern and hatchling maturity in determining organ growth.

Methods.—Sooty Tern eggs were collected on Manana Island (20°20'N, 157°40'W), a small offshore island of Oahu in the main Hawaiian Islands. The exact age of the eggs was not known. The eggs were transported to the laboratory in plastic boxes packed with cotton. Approximately 90 min elapsed during transport. Eggs were incubated at 38°C and 60% relative humidity in a commercial, forced-draft, incubator (GQF, model 1202), and turned by hand (through 180°) at least twice daily. Data were collected from unpipped eggs, externally pipped eggs with star-fractured shells (Whittow 1985), eggs with pip holes, and hatchlings.

Oxygen consumption of the eggs and hatchlings was measured in a modified Scholander respirometer (Ackerman et al. 1980). The chamber containing the egg was immersed in a water bath at 38°C and the chamber was ventilated with air for 60 min before measurements began. All values of oxygen consumption were corrected to standard temperature (from the temperature of the introduced oxygen) and pressure and dry gas (STPD).

After oxygen consumption was determined, the egg was opened and the embryo carefully separated from the yolk sac. The wet mass of the embryo was determined on a Mettler balance (model H6) to the nearest 0.1 mg. The following linear dimensions of the embryo were taken with dial calipers: (1) whole-embryo length, top of head to tip of tail, with embryo in relaxed posture; (2) culmen length, tip of beak to beginning of nasal skin on upper mandible; (3) wing length, tip of wing to shoulder joint, with wing extended; (4) leg length, tip of middle toe to head of femur; (5) toe length, tip of nail to proximal fold in webbing between middle and lateral toe; (6) neck length, from lower mandible to 13th cervical vertebra. The embryo was then carefully dissected and the following organs and tissues were weighed wet on the Mettler balance: (1) leg muscles, muscles from both legs; (2) pectoral muscles, muscles from both sides; (3) heart; (4) liver; (5) stomach; (6) intestine; (7) lungs, including both lungs.
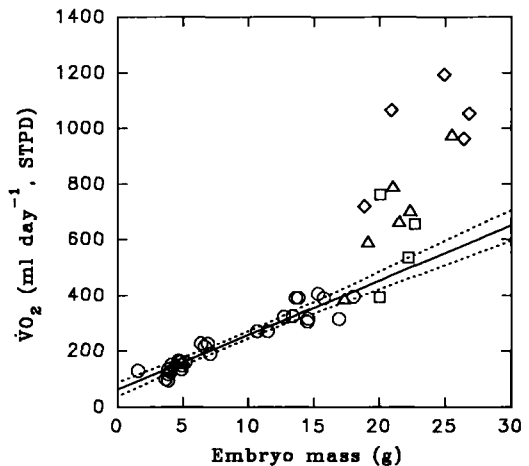

Fig. 1. Oxygen consumption ($\dot{V}_{O_2}$) of Sooty Tern embryos in relation to whole-embryo wet mass. Symbols used are: circle, unpipped eggs; square, externally-pipped eggs (star-fractured shells); triangle, eggs with pip holes; diamond, hatchlings. Solid line is linear regression of $\dot{V}_{O_2}$ (Y) on embryo mass (X) for unpipped eggs, and dots define 95% confidence limits. $\dot{V}_{O_2} = 61.682 + 19.632\ X$.
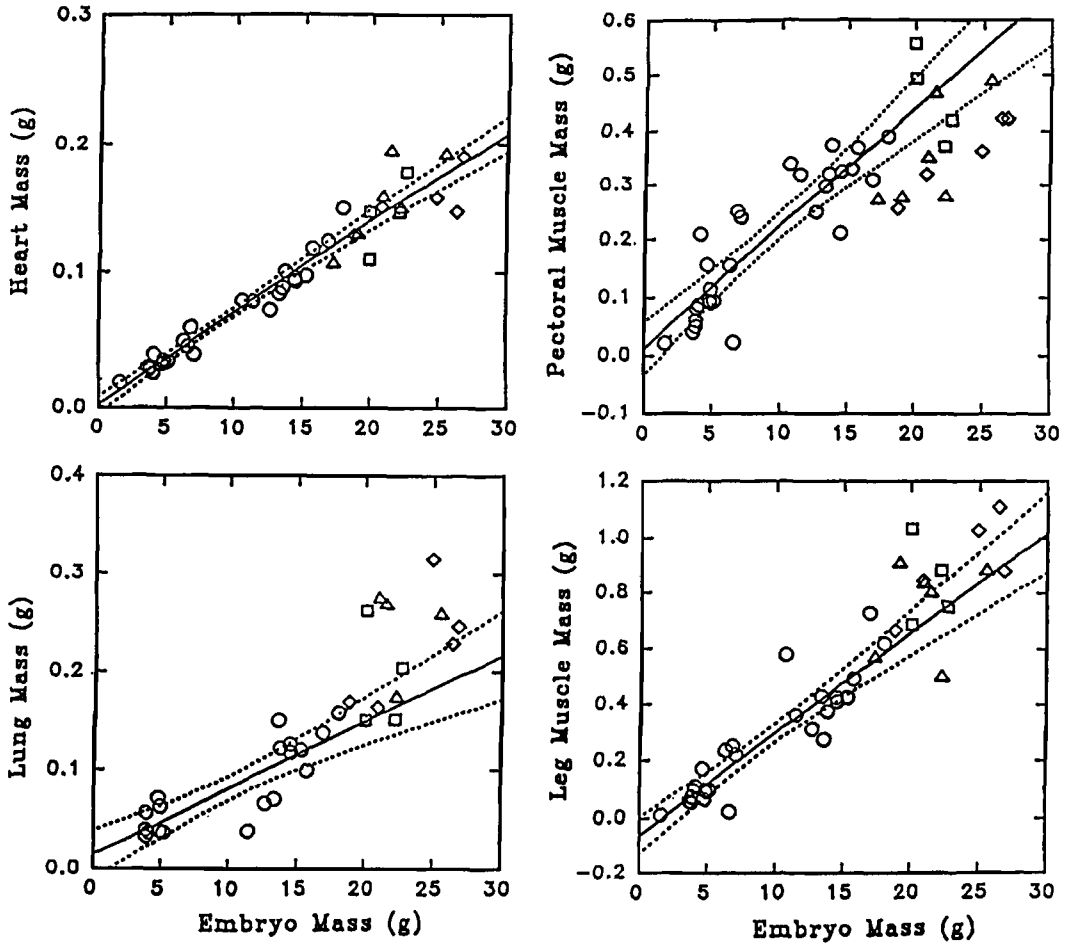
Fig. 2. Heart, lung, pectoral and leg muscle wet mass in relation to whole-embryo wet mass in the Sooty Tern. Equations for regression lines in Table 1; notations as in Figure 1.

As the age of the embryos was not known exactly, whereas the embryo mass could be measured precisely, all measured data were related to embryo mass. Organ mass was plotted against whole-body mass together with a linear regression line for the data from the unpipped eggs and the 95% confidence limits (Zhang and Whittow 1992).

Results.—The data for oxygen consumption ($\dot{V}_{O_2}$; Fig. 1) reveal that, in unpipped eggs, the oxygen consumption of the embryo increased linearly with body mass. After pipping occurred, there was a large increase in oxygen consumption, the highest $\dot{V}_{O_2}$ being recorded from hatchlings.

The data for organ mass are shown in Figures 2 and 3. Heart mass increased with the increase in the mass of the whole embryo, in unpipped eggs, pipped eggs, and hatchlings (Fig. 2). There was considerable variation in the lung data. The relationship between lung mass and whole-embryo mass was linear in unpipped eggs. After pipping there were greater increments in lung mass (Fig. 2).

The data for leg muscles from unpipped eggs formed a linear regression on embryo mass, with a tendency for growth to accelerate in pipped eggs and hatchlings (Fig. 2). In contrast, pectoral muscle growth tended to diminish in rate late in incubation, and in the hatchling the pectoral muscle mass was less than one-half that of the leg muscles (Fig. 2). The highest value for pectoral muscle mass was in an externally pipped egg.

The relationship between the mass of the stomach and embryo mass was linear (Fig. 3). In contrast, the intestine mass grew at an accelerated rate in pipped eggs, which also was the trend for liver mass.

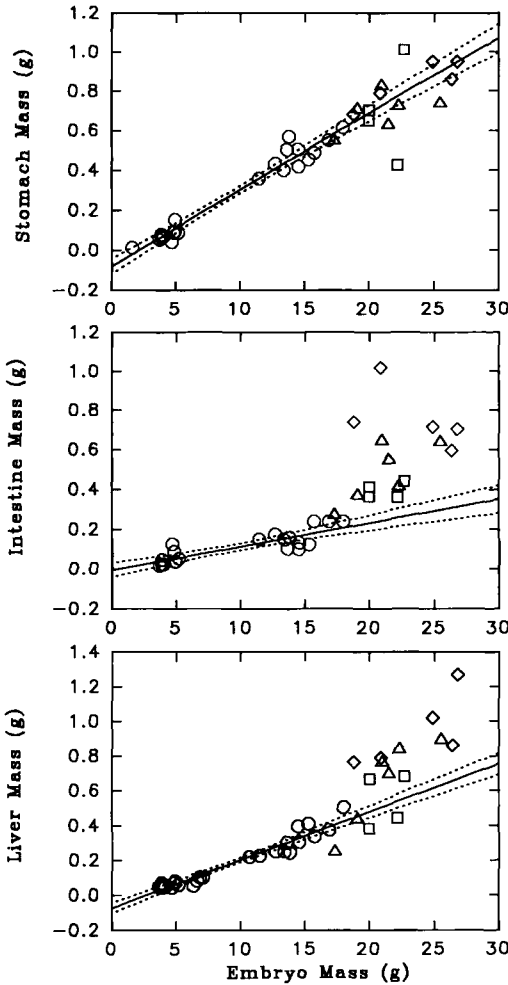The linear dimensions of the embryo increased rapidly at first and then the rate diminished as the em-

Fig. 3.   Stomach, intestine and liver wet mass in relation to whole-embryo mass in Sooty Tern (notations as in Fig. 1).

TABLE 1.   Coefficients for linear regression equations ($Y = a + bX$) of organ mass on embryo mass (g) for Sooty Tern embryos from unpipped eggs.

Organ	Intercept (a)	Slope (b)	r^a
Heart	0.00234	0.00685	0.98
Lungs	0.0151	0.00672	0.84
Pectoral muscles	0.0114	0.0214	0.88
Leg muscles	−0.0616	0.0360	0.91
Liver	−0.0726	0.0276	0.97
Stomach	−0.0796	0.0384	0.98
Intestine	−0.00439	0.0119	0.86

[a] Product-moment correlation coefficient.

precocial in their mode of development (Zhang and Whittow 1992).

Sooty Tern embryos differed from those of the Wedge-tailed Shearwater in that there was no plateau in the oxygen consumption of unpipped eggs just prior to pipping. Gas conductance of the shell of the Sooty Tern's egg is relatively greater than that of the Wedge-tailed Shearwater (Whittow 1984). Possibly, therefore, oxygen consumption of the shearwater's embryo just before pipping is constrained by the rate at which oxygen can diffuse into the egg through the microscopic pores in the shell. This may not be a factor in the Sooty Tern.

Oxygen consumption increased as much as 300% in pipped eggs and acceleration of growth of some organs occurred during pipping. This was most apparent in the intestine and liver (Fig. 3). The increase in oxygen consumption and organ growth may be related to the increase in embryonic lung mass in pipped eggs. The consumption of the albumen by embryos in pipped eggs (Freeman and Vince 1974) may also fuel accelerated growth after pipping. Pipping appeared to have little effect on growth of heart and stomach (Figs. 2 and 3), while the growth of pectoral muscle tended to diminish in pipped eggs (Fig. 2). Some differences were evident in the patterns of growth in pipped eggs in the tern and shearwater. Thus, in the Sooty Tern, growth of heart and stomach were not affected by pipping of the egg.

bryo mass increased (Fig. 4). In no instance was the rate of growth in the length of the embryo or its parts greater in pipped eggs than in unpipped eggs.

Discussion.—The oxygen consumption of embryos in unpipped eggs increased linearly with increasing embryo mass in the Sooty Tern (Fig. 1), as it had in the shearwater (Zhang and Whittow 1992). For the most part, organ mass also increased linearly with embryo mass during this period (Figs. 2 and 3). This is brought out in Figure 5. The steepest slope (Table 1) of organ mass on whole-embryo mass was for the stomach, followed by the leg muscles and liver, in unpipped eggs of both the Sooty Tern and Wedge-tailed Shearwater. Similarly, the lowest slopes were for the heart and lungs. The heart and lungs grew slowly also in domestic fowl embryos, which are more

TABLE 2.   Organ mass as percentage of hatchling wet mass in Sooty Tern and Wedge-tailed Shearwater.

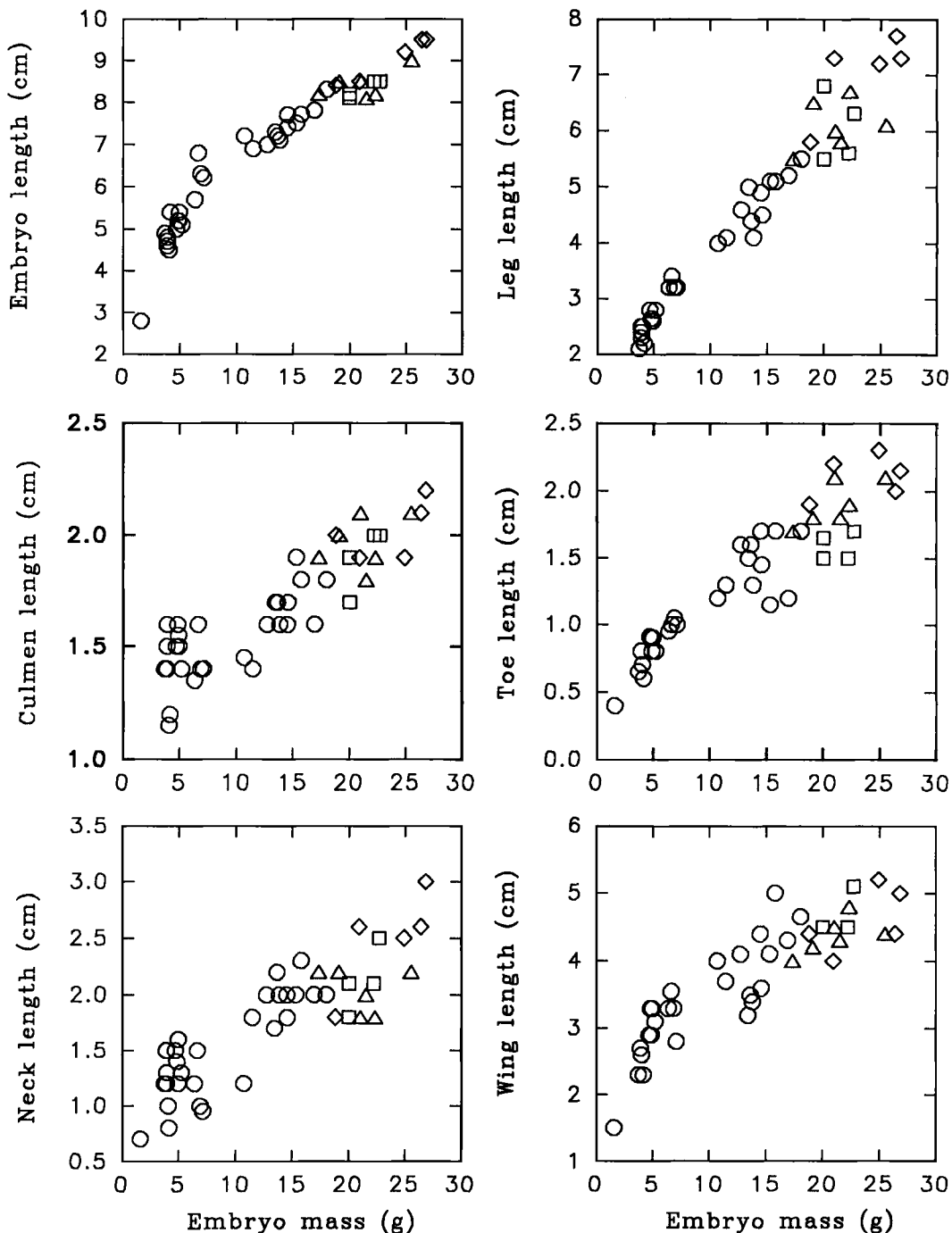| Organ	Sooty Tern	Wedge-tailed Shearwater[a]
Lungs	0.95	1.12
Heart	0.65	0.75
Liver	3.99	3.20
Intestine	3.21	2.58
Stomach	3.59	3.81
Pectoral muscle	1.51	1.34
Leg muscle	3.85	3.39

[a] Data from Zhang and Whittow (1992).

Fig. 4. Linear dimensions of Sooty Tern embryos in relation to embryo wet mass (symbols as in Fig. 1).

Table 2 lists the body composition, in terms of organ mass, of the Sooty Tern hatchling and, for comparative purposes, that of the Wedge-tailed Shearwater. The greatest difference between the two species was in the mass of the liver and intestine, which were 24 to 25% greater in the Sooty Tern. Relative organ size depends on hatchling maturity, a larger intestine being associated with a less mature hatchling (Whit-
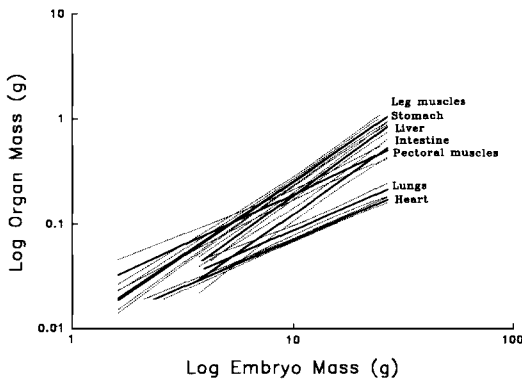
Fig. 5. Slope of linear regression of organ wet mass on whole-embryo wet mass in Sooty Tern embryos from unpipped eggs. Intercepts and slopes for regression lines in Table 1. Dotted lines define 95% confidence limits.

tow and Tazawa 1991). Growth in linear dimensions of embryos of Sooty Terns was similar to that in Wedge-tailed Shearwaters in that in no instance did the growth accelerate after pipping had occurred.

The striking feature of the results of the present investigation is how similar embryonic growth is in the Sooty Tern and Wedge-tailed Shearwater. The two species belong to different orders and differ substantially in body size. The shearwater's egg has a relatively longer incubation period (Whittow 1984). However, the two species have a similar sequence of events during pipping of the egg, and it is possible that the pattern of organ growth may be related to events during pipping. The strength of this argument is that pipping is known to have a considerable effect on the growth rates of some organs, but further studies of species with different modes of pipping are needed to substantiate this.

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Egg Formation, Brood Survival, and Cost of Reproduction as Clutch-size-determining Factors in Common Goldeneyes

MARKKU MILONOFF[1] AND PERTTI PAANANEN[2]
[1]*Evo Game Research Station, SF-16970 Evo, Finland; and*
[2]*Suihkola, SF-77600 Suonenjoki, Finland*

Three major explanations to account for clutch-size limitation in precocial birds such as Common Goldeneyes (*Bucephala clangula*) are: (1) food limitation for the laying female; (2) lower duckling survival in large broods; and (3) lower adult survival or reduced future fecundity among females laying large clutches and/or rearing large broods (i.e. the cost of reproduction; reviewed by Winkler and Walters 1983). Be-