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## Effects on nestling age and burrow depth on CO<sub>2</sub> and O<sub>2</sub> concentrations in the burrows of bank swallows (*Riparia riparia*)

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EFFECTS OF NESTLING AGE AND BURROW DEPTH ON CO<sub>2</sub>  
AND O<sub>2</sub> CONCENTRATIONS IN THE BURROWS OF  
BANK SWALLOWS (*RIPARIA RIPARIA*)<sup>1</sup>

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Gas samples were taken from the nest chambers of bank swallows (*Riparia riparia*) and analyzed for CO<sub>2</sub> and O<sub>2</sub> content. The mean CO<sub>2</sub> content was 2.62% with a maximum value of 5.58%, and the mean O<sub>2</sub> content was 17.83% with a minimum value of 14.61%. There was a positive and significant correlation of increasing CO<sub>2</sub> content with both increasing nestling age and increasing total metabolizing mass (adults plus young). With increasing metabolizing mass there is a linear increase in CO<sub>2</sub> content, which suggests no active regulation of gas concentrations. Burrow depth also affected CO<sub>2</sub>, particularly in burrows with older nestlings. The effect of depth is most likely due to the relative importance of convective exchange rather than to diffusion. The increase in CO<sub>2</sub> was proportional to the decrease in O<sub>2</sub> with a ratio of CO<sub>2</sub>:O<sub>2</sub> equal to 0.86.

INTRODUCTION

Burrowing animals may be exposed to consistently high levels of CO<sub>2</sub> and low levels of O<sub>2</sub> in the burrow air (see Withers 1978). Gas concentrations measured in natural and seminatural rodent burrows demonstrate that there is often prolonged exposure to hypoxic-hypercapnic atmospheres (Studier and Proctor 1971; Baudinette 1974; Maclean 1977). Less conspicuous, but presumably faced with identical problems, are birds which use burrows. Although not exposed for long periods of

their life cycle, burrow-nesting birds may have to cope with elevated CO<sub>2</sub> and depressed O<sub>2</sub>. Recently White, Bartholomew, and Kinney (1978) have demonstrated elevated levels of CO<sub>2</sub> in nesting burrows of the European bee eater (*Merops apiaster*). They identified several parameters which may act to counter excessive buildup of CO<sub>2</sub>, such as soil porosity, passive air movement, and convective currents set up by the birds. They did not, however, quantify which variables of the physical or biotic environment most influence the buildup of CO<sub>2</sub>.

We have examined the effects of burrow depth and nestling age on the concentrations of CO<sub>2</sub> and O<sub>2</sub> in burrows of bank swallows. Nesting bank swallows, *Riparia riparia*, excavate single-tunnel burrows to a depth of a meter or more which terminate in a nest chamber (Stoner 1936). This nest is occupied by two to seven nestlings and one or both parents for the entire night (Petersen 1955). Of particular interest were the maximum levels of CO<sub>2</sub> reached during the later developmental stages as the young obtain adult mass.

MATERIAL AND METHODS

Bank swallows, *Riparia riparia*, were found nesting in sandpits near Ann Arbor,

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Michigan, Washtenaw County. Construction of burrows and laying of eggs were followed closely during May and June of 1979. Burrows were constructed in banks of high sand content. A thin steel rod marked at 10-cm intervals and equipped with a small dental mirror and 6-V flashlight bulb attached to the distal portion of the rod permitted observation of the nests (Marsh 1979). When date of hatching was unknown, age was estimated by body mass and/or primary-feather length (Petersen 1955; Marsh 1979).

A thin copper tube ( $\frac{1}{8}$ -inch OD, 2.5 cm<sup>3</sup> total volume) attached the length of the rod permitted gas sampling. Gas samples were drawn from the nest chamber with gas-tight glass syringes fitted with three-way stopcocks. A 20-cm<sup>3</sup> volume was drawn from the nest and expelled to external air. Then a 30-cm<sup>3</sup> sample (approximately 1% of the estimated mean burrow volume) was drawn, sealed, and returned to the laboratory for analysis. Samples were equilibrated to 37 C, saturated with water, and analyzed for P<sub>CO<sub>2</sub></sub> and P<sub>O<sub>2</sub></sub> (mm Hg) using a Microtech 13 Blood Gas Analyzer. All gas samples were taken on clear, calm (winds less than 10 mph) mornings between 0500 and 0745 EDST.

#### RESULTS

The mean length of the bank swallow burrows was 90 cm (table 1), which is similar to other measurements of the burrows of this species (Stoner 1936). The mean CO<sub>2</sub> level inside occupied burrows was 2.62%, with a maximum of 5.58% and a mean O<sub>2</sub> level of 17.83% and a minimum value of 14.61% (table 1).

Preliminary data analysis demonstrated a significant ( $P = .0043$ ) positive correlation ( $r = .551$ ) between nestling age and CO<sub>2</sub> levels, despite only a small change in nestling mass after 8 to 10 days (Marsh 1979). Since CO<sub>2</sub> production is mostly a function of the metabolizing mass and not of age per se, age data were converted to a metabolizing mass. Because many of the nests were left intact throughout the developmental period, we have estimated the metabolizing mass, using the following assumptions: (1) The mass-specific metabolic rate of developing bank swallows changes by little more than 5% with age (Marsh 1979); (2) there was a mean of five young per nest (Hoogland and Sherman 1976; Marsh 1979; this study); and (3) one adult remains in the nest during the night (Petersen 1955). For any one age group, the mean mass of a nestling was obtained from the age-mass curve of Marsh (1979), multiplied by five and added to the mean mass of an adult (14.5 g [Marsh 1979]). The levels of CO<sub>2</sub> were significantly and positively correlated with the predicted metabolizing mass (fig. 1) as expressed by the linear regression equation for all burrows:

$$\%CO_2 = 0.74 + 0.030 M$$

$$(n = 43; r = .63; P < .0001;$$

$$S_b = 0.4; S_{y \cdot x} = 0.006),$$

where  $M$  = the predicted metabolizing mass in grams.

However, burrow depth also has an effect on CO<sub>2</sub> levels, particularly in the burrows with older nestlings (fig. 1, closed vs. open symbols). In order to reduce some of the influence of burrow depth, the population

TABLE 1  
BURROW GAS CONCENTRATIONS, BURROW DEPTH, AND  
AGE OF NESTLING BANK SWALLOWS

Variable	Sample Size	Mean	Range	SD
% CO <sub>2</sub> .....	36	2.62	.16-5.58	1.52
P <sub>CO<sub>2</sub></sub> (mm Hg).....	36	17.94	1.10-38.60	10.82
% O <sub>2</sub> .....	28	17.83	14.61-21.00	1.76
P <sub>O<sub>2</sub></sub> (mm Hg).....	28	123.8	101.1-145.61	12.2
Burrow depth (m).....	34	.90	.60-1.20	.17
Age of nestlings (days).....	31	8.5	0-19	6.6

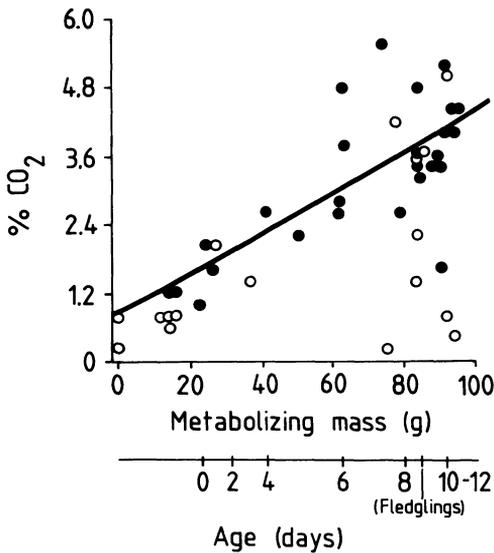


FIG. 1.—Burrow concentrations of  $\text{CO}_2$  plotted as a function of the predicted metabolizing mass of developing swallows (assuming one adult and five nestlings per burrow; see text). Closed symbols (●) represent longer burrows (0.9–1.2 m), and open symbols (○) represent shorter burrows (0.6–0.85 m). The line is the linear regression for the longer burrows only. Age in days, up to fledgling, is presented under the mass scale. There is a slight decrease in nestling body mass between day 12 and fledgling.

was divided into longer burrows ( $>0.9$  m) and shorter burrows ( $<0.9$  m). If only longer burrows are considered, then the correlation between  $\% \text{CO}_2$  and predicted metabolizing mass is improved (from  $r = .63$  to  $r = .71$ ). The regression equation for longer burrows only is:

$$\% \text{CO}_2 = 0.95 + 0.034 M$$

$$(n = 26; r = .71; P < .0001;$$

$$S_b = 0.49; S_{y \cdot x} = 0.006).$$

The intercept is not significantly different from zero ( $P = .0625$ ).

The effect of burrow depth is apparent, particularly when only older, larger ( $>60$  g) nestlings are considered (fig. 2). For the older nestlings, the regression equation for  $\% \text{CO}_2$  and burrow depth is:

$$\% \text{CO}_2 = -0.74 + 4.46 D$$

$$(n = 28; r = .50; P = .0073;$$

$$S_b = 1.42; S_{y \cdot x} = 1.53),$$

where  $D$  = burrow depth in meters.

When the combined effects of both metabolizing mass and burrow depth for all burrows are included in a multiple linear regression, more of the variance in  $\text{CO}_2$  levels is explained than when either depth or age alone is used:

$$\% \text{CO}_2 = -1.92 + 0.028 M + 3.1 D$$

$$[n = 43; r = .71; P < .0001;$$

$$S_b = 0.97; S_{y \cdot x}(M) = 0.005; S_{y \cdot x}(D) = 1.0].$$

The soil porosity was measured as 0.336 and water content was  $0.135 \text{ ml/cm}^3$ .

Our data show a good correlation between the decrease in  $\% \text{O}_2$  ( $\Delta \text{O}_2 = 21 - \% \text{O}_2$ ) and the increase in  $\text{CO}_2$  (fig. 3). This relation can be described by the linear regression equation:

$$\Delta \text{O}_2 = -0.13 + 1.15 (\% \text{CO}_2)$$

$$(n = 38; r = .98; P < .0001;$$

$$S_b = 0.12; S_{y \cdot x} = 0.04).$$

The slope is significantly greater than 1.0 ( $P = .0002$ ).

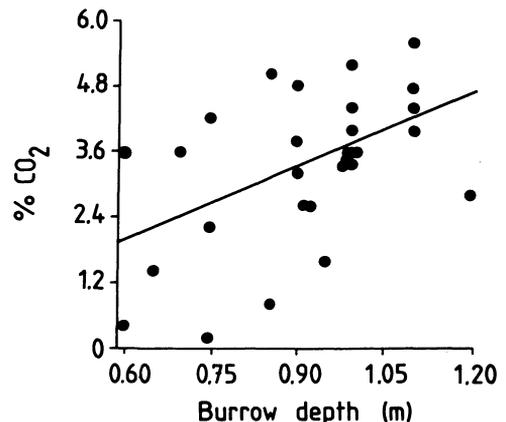


FIG. 2.—Concentration of  $\text{CO}_2$  in burrows of older, larger nestlings ( $>60$  g) as a function of burrow depth (in m).

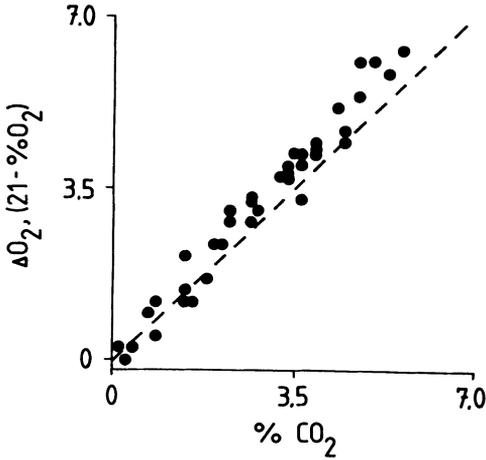


FIG. 3.—The decrement in burrow O<sub>2</sub> content ( $\Delta O_2 = 21 - \%O_2$  in burrows) compared with the increase in CO<sub>2</sub>. The dashed line equals a slope of 1.0.

#### DISCUSSION

Our data indicate that burrow depth is an important feature of nest construction which influences burrow gas concentrations (figs. 1 and 2). These results differ from predictions based on models of diffusion mediated gas exchange (Withers 1978; Wilson and Kilgore 1978). These models predict that burrow depth should have little effect on gas concentrations except in very short burrows. Calculations using the model of Withers (1978) indicate that the steady-state concentration of CO<sub>2</sub> in a 0.6-m burrow should be approximately 0.99 of that in a 1.2-m burrow. These calculations were based on the following measurements: soil porosity, 0.336; water content, 0.135 ml/cm<sup>3</sup>; nest chamber surface area, 750 cm<sup>2</sup>; and tunnel cross-sectional area, 18 cm<sup>2</sup>. In the colonial nesting system found in bank swallows, calculations predicated on these diffusion-based models are of limited utility. The tunnel systems of these birds are in tight clusters (see Stoner 1936; Petersen 1955) with nest chambers often within inches of one another. Because of the high degree of breeding synchrony between burrows (Hoogland and Sherman 1976), adjacent burrows are most often at a similar stage of the nesting cycle. However, both

models assume diffusion into a large mass of soil without the presence of nearby occupied burrows. Clearly, diffusional loss of CO<sub>2</sub> and gain of O<sub>2</sub> would be hampered under the conditions found in the bank swallow colonies. In all likelihood the influence of burrow depth is due to the importance of convective gas exchange in the burrows (White et al. 1978). Unfortunately, convective gas exchange is a complex process which, except for some two-entrance burrows (Vogel, Ellington, and Kilgore 1973), has not yet been adequately modeled (see White et al. 1978). Of particular interest in this regard is whether the buildup of CO<sub>2</sub> is a factor which limits the construction of deeper burrows.

We have shown that the burrow CO<sub>2</sub> concentration in the morning is proportional to the total mass of birds spending the night in the burrow (fig. 1). That the relationship between %CO<sub>2</sub> and mass is linear with an intercept of zero can be taken as evidence against active regulation of burrow gas concentrations. One would expect such regulation to be most important as nestlings reach peak body mass and therefore predict a leveling off of %CO<sub>2</sub> with increasing mass. Once dawn feeding begins, movements of parents (and fledglings) will presumably aid in correcting CO<sub>2</sub> and O<sub>2</sub> levels (White et al. 1978), but such movements cannot be described as primarily regulatory. The two values at 0 metabolizing mass (fig. 1) were obtained from burrows without nests. Both samples were taken during the early construction of the colony and may be above atmospheric CO<sub>2</sub> concentrations because of the early-morning activity of excavating adults or the presence of one or both adults in the partially completed burrow during the night.

The increase in CO<sub>2</sub> levels is proportional to the decrease in O<sub>2</sub> levels (fig. 3) and the ratio of CO<sub>2</sub>:O<sub>2</sub> is significantly less than 1.0 ( $P = .0002$ ). This could be accounted for by either a higher diffusion or absorption of CO<sub>2</sub> into the burrow walls or a respiratory quotient (RQ) of less than 1. The slope of the line obtained is that expected if the RQ

was 0.86. An RQ considerably less than 1.0 is reasonable to expect since our measurements were made shortly after the inactive phase of the bird's diurnal cycle.

The levels of CO<sub>2</sub> found in the deeper burrows with older nestlings could potentially cause serious respiratory problems for the birds. Levels of CO<sub>2</sub> similar to those found in this study can increase ventilation of birds severalfold (Fowle and Weinstein 1966; Ray and Fedde 1969). Also, a positive interaction between the elevated CO<sub>2</sub> and the reduced O<sub>2</sub> levels leads to marked increases in ventilation in ducks (Bouverot, Hill, and Jammes 1974). An increased ventilation in the face of the high external CO<sub>2</sub>

load of burrows would serve to equilibrate blood levels with high CO<sub>2</sub>. High blood CO<sub>2</sub> presents the potential problem of chronic acidosis. Chronic acidosis in fossorial mammals is countered by a number of regulatory mechanisms, including reduced ventilatory sensitivity to CO<sub>2</sub> (Darden 1972; Soholt, Yousef, and Dill 1973) and greater blood buffering capacity (Darden 1972; Chapman and Bennet 1975). Nothing is known of what mechanisms, if any, exist in burrow-nesting birds. The limited visual observations of bee eater nestlings in their nests suggest a greatly increased respiratory rate in the face of high CO<sub>2</sub> levels (White et al. 1978).

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