View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by University of Montana

University of Montana
ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, & Professional Papers
Graduate School

1992

The effect of nest density on the respiratory environment of bank swallow burrows

David Nusbaumer
The University of Montana

Follow this and additional works at: https://scholarworks.umt.edu/etd
Let us know how access to this document benefits you.

Recommended Citation

Nusbaumer, David, "The effect of nest density on the respiratory environment of bank swallow burrows" (1992). *Graduate Student Theses, Dissertations, & Professional Papers*. 7042.
https://scholarworks.umt.edu/etd/7042

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.

Maureen and Mike
MANSFIELD LIBRARY

Copying allowed as provided under provisions of the Fair Use Section of the U.S. COPYRIGHT LAW, 1976.
Any copying for commercial purposes or financial gain may be undertaken only with the author's written consent.

University of
Montana

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

THE EFFECT OF NEST DENSITY ON THE RESPIRATORY ENVIRONMENT OF BANK SWALLOW BURROWS.

by

David Nusbaumer
B.S. George Mason University, 1987

Presented in partial fulfillment of the requirements for the degree of

Master of Arts

University of Montana
1992

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

Feb. 27, 1992
Date

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UMI Number: EP37843

All rights reserved

INFORMATION TO ALL USERS
The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript
and there are missing pages, these will be noted. Also, if material had to be removed,
a note will indicate the deletion.

UMI
Dissertation Publishing

UMI EP37843

Published by ProQuest LLC (2013). Copyright in the Dissertation held by the Author.

Microform Edition © ProQuest LLC.
All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code

ProQuest

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Nusbaumer, David, D., M.A., February 1992 Zoology

The Effect of Nest Density on the Respiratory Environment of Bank Swallow Burrows. (39 pp.)

Director: Delbert L. Kilgore, Jr. DLK

Diffusion is an important mechanism for the exchange of gases between animal burrows and the external environment. Colonial, burrowing birds construct nests close to neighboring burrows. The proximity of burrows could influence the diffusion of gases between nests and the free atmosphere, resulting in elevated concentrations of CO_2 in burrows located in regions of high nest density. Gas samples were collected from nest chambers of 32 active bank swallow burrows (8 surrounded by 0, 1, 2, or 3 neighboring burrows) and analyzed for CO_2 concentration. Other variables that may influence the respiratory environment were also evaluated (i.e., nest depth, biomass of occupants). An analysis of covariance was used to determine the effect of nest density on burrow CO_2 with depth, biomass, and distance from ground surface as covariates. There was a small non-significant increase in CO_2 with nest density (P=0.138). The effects of burrow depth, biomass, and distance from ground surface, were also insignificant, P = 0.062, P = 0.251, and P = 0.148, respectively. Studies conducted on unoccupied bank swallow nest indicate that the respiratory environment in unoccupied bank swallow nest cavities is affected by the gaseous environment in adjacent nests due to the diffusive movement of gases between burrows. These data suggest that inter-nest diffusion of gases in active burrows may be masked by the effects of other mechanisms of exchange that influence the respiratory environment.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ACKNOWLEDGMENTS

I would like to thank the members of my advisory committee, Dr. Andrew Sheldon, and Dr. David Patterson for their assistance in the development of a workable experimental design and for their editorial and technical assistance in the preparation of this manuscript. I would especially like to thank my major professor, Dr. Delbert L. Kilgore, Jr. for his assistance and support throughout my tenure as a graduate student at the University of Montana.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE OF CONTENTS

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF FIGURES

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF TABLES

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

INTRODUCTION

Bank Swallows nest colonially. They excavate their burrows in vertical cliffs of sandy soil along rivers, and at man-made disturbed sites. However, burrow placement within a colony is not uniform. Burrows are concentrated in the center of the colony with lower nest density along the periphery (Stoner 1936, Petersen 1955). Burrow location within the colony affects reproductive success (Emlen 1971). Occupants of centrally located nests have higher fitness than those nesting in burrows on the periphery of the colony. The successfulness of birds in centrally located nests is due to increased facilitation of breeding, reduced predation pressure, and a lower incidence of nest abandonment (Emlen 1971, Hamilton 1971, Hoogland and Sherman 1976,). However, the close proximity of burrows in the central area of the colony potentially interfers with diffusion gradients. Because diffusion is an important mechanism of gas exchange between occupants of burrows and the free atmosphere (Wilson and Kilgore 1978, Withers 1978), CO_2 and O_2 levels in central burrows should be higher and lower, respectively, than those at the periphery (Furilla 1980).

The physiological mechanisms for coping with an elevated burrow CO_2, for example, increased ventilation

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Colby et al 1987), and enhanced blood buffering (Darden 1972, Chapman and Bennett 1975), all increase the energy demands of an organism. Therefore, burrows with a high CO_2 concentration will be energetically more costly to inhabit than burrows with lower CO_2 levels.

The principal question being asked in this study is whether or not burrows in the center of a bank swallow colony have respiratory environments with higher CO_2 concentrations than nests in the peripheral areas. To answer this question it was first necessary to determine how CO_2 levels in burrows change during the breeding season. A follow up study of inter-nest diffusion was also conducted.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

METHODS

STUDY SITE

The study site was a commercial sand pit (Polson Ready-mix Concrete) on the west side of the Flathead Valley, approximately 2 miles south of Polson, Montana (47°40'N, 114°06'W). The soil at the study site is composed of well sorted sand and gravel deposited by a glacial meltwater stream during the Pinedale ice age (Alt and Hyndman 1986). Study colonies were located in south and east facing banks in 1989, and 1990, respectively.

COLLECTION AND ANALYSIS OF GAS SAMPLES

Burrow air samples were withdrawn into 10cc greased, ground glass syringes from lengths of polyethylene tubing (PE 90) placed into the nest chamber and extended out of the burrow opening. Each syringe was fitted with a three way stopcock and a blunted 23 gauge needle. Prior to collection of samples, 4 cm^3 (approximately 4 times the tubing dead space) of gas was withdrawn and purged to the atmosphere before a 6 cm^3 sample was collected for analysis. All gas samples were analyzed within three hours of collection. CO_2 concentrations

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

were measured with a Scholander micro-gas analyzer (Scholander 1947).

SEASONAL VARIATION IN BURROW CARBON DIOXIDE LEVELS

Thirty-two randomly selected active bank swallow burrows were studied. Nests were asigned to one of two groups of sixteen. Gas samples were collected from each of the burrows within a group twice weekly throughout the nestling period (June 31 to July 20 1989). CO_2 levels in these gas samples were measured as described above. The age of nestlings within burrows in this part of the study was estimated from size of chicks and feather development (Wickler and Marsh 1981).

EFFECT OF NEST DENSITY ON RESPIRATORY ENVIRONMENT.

During the 1989 breeding season 25 nests in a colony of approximately 150 burrows were randomly selected and assigned to one of four density categories depending on the number of active neighboring nests within a 25 cm radius. Ten nests had no active neighboring nests (category 1), seven had 1 or 2 neighboring nests (category 2), eight had 3 or 4 neighboring nests (category 3), and seven had five or more active neighboring nests (category 4) . Gas samples were withdrawn from the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

experimental burrows late in the nestling period when CO_2 concentrations were at a maximum. The number of chicks present in these burrows at the time gas samples were withdrawn was also recorded. The depth of each experimental burrow was measured after the young had fledged. Samples of soil surrounding 20 of the experimental burrows were also collected at the end of the breeding season and analyzed for porosity (Jacobs and Reed 1964).

In 1990, 25 additional nests were randomly selected from a colony of approximately 60 nests. Seven of these experimental burrows had no active neighboring nests (category 1), ten had 1 or 2 neighboring nests (category 2),and nine had 3 or 4 neighboring nests (category 3). Gas samples were collected from these burrows on July 14 or 16. Depth of each burrow was determined. After burrow depth was measured chicks were removed from the burrows and their total mass was measured to the nearest 0.1g. Chicks were then returned to the nest and the burrow reconstructed.

INTER-NEST DIFFUSION

Carbon dioxide levels were experimentally elevated in the burrows surrounding 7 bank swallow nests. After the completion of the 1990 breeding season two

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

burrows with one neighboring burrow within a 25 cm radius, two with two neighbors, two with three neighbors, and one with four neighboring burrows were selected and a sampling tube inserted into the nest cavity. A length of P.E. tubing was also positioned in each neighboring burrow along with a length of 1/8 OD diameter copper tubing. The entrances of the neighboring burrows were then sealed with foam insulation (Great Stuff). Two short pieces of large diameter plastic tubing were passed through the foam insulation to serve as exhaust vents for gas flow. After the foam plugs hardened, a gas mixture containing 5% CO_2, and 12% O_2 was introduced into the neighboring nests through the copper tubing. Gas flow into the neighboring nests was maintained from pressurized tanks at approximately. 0.62 $l \cdot min.^{-1}$ for the first five minutes, then reduced to approximately. 0.38 $l \cdot min^{-1}$ thereafter. Measurements of pressure within the neighboring burrows indicated that the vent tubes prevented any increase in pressure. Gas samples were withdrawn from both experimental and neighboring burrows 30min, 1h, 3h, 7.5h, and 20h following the introduction of the gas mixture into the neighboring nests and then analyzed as described above.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

RESULTS AND DISCUSSION

SEASONAL VARIATION IN BURROW CARBON DIOXIDE LEVELS

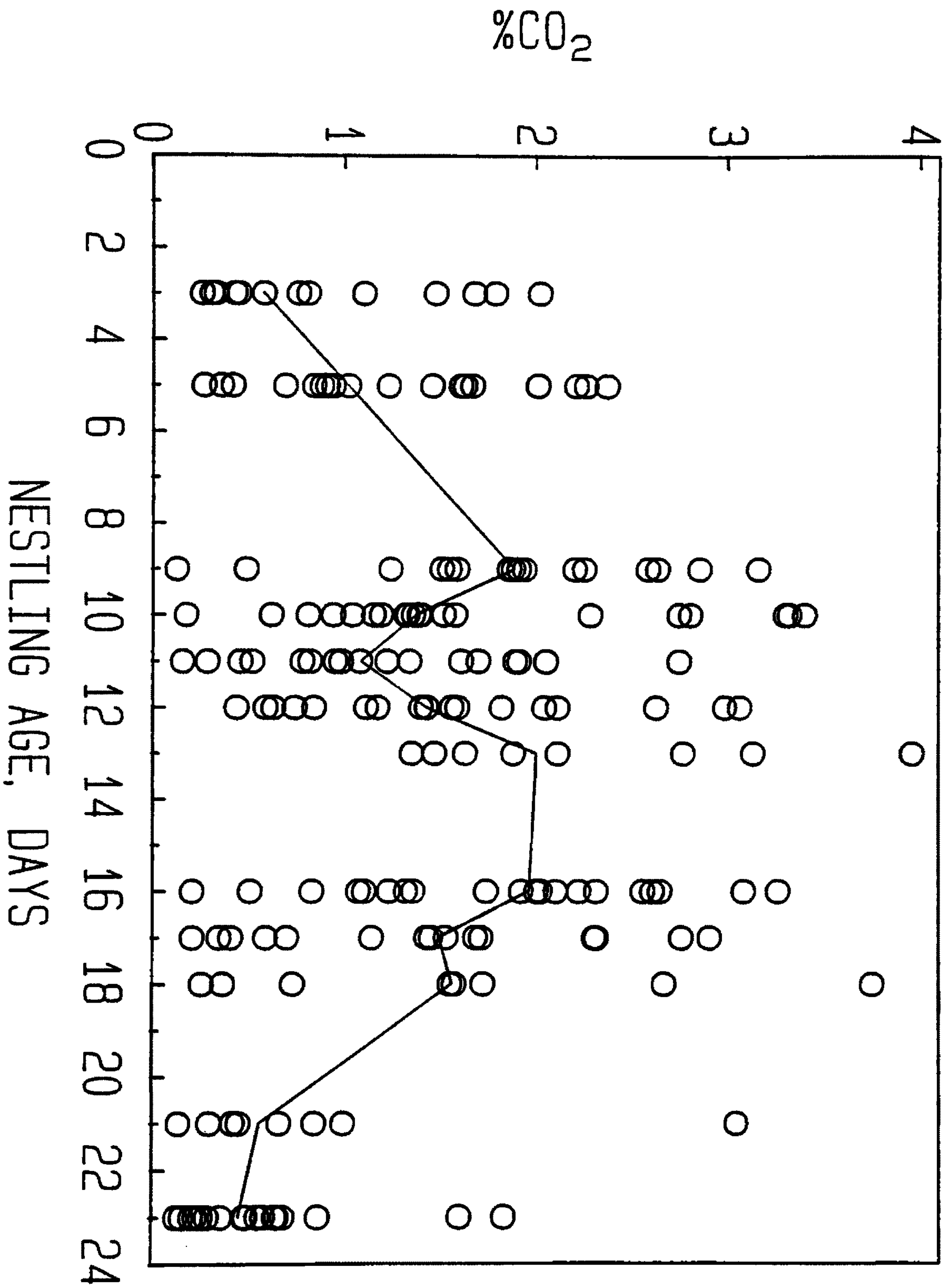
The CO_2 concentration in bank swallow burrows generally increases during the breeding season, but declines near the end of the season (Fig. 1). The build-up of CO_2 in burrows correlates with nestling development and growth (i.e., age). Gas samples collected from cavities early in the nestling period (ca. 3 days post hatching) had a mean CO_2 concentration of 0.86%. From day 9 to day 17 mean CO_2 concentration averaged 1.64%. However, mean CO_2 concentrations began to fall at 21 days post hatching. At the end of the breeding season; at 23 days post hatching, the mean CO_2 levels in these burrows was 0.59%. Carbon dioxide levels measured in this study tend to be somewhat lower than those observed by other investigators (Furilla 1980).

The observed relationship between burrow CO_2 levels and increasing age of the chicks from day 3 to day 17 is undoubtedly due to the increase in metabolizing mass within the nest cavities, and therefore an increase in the production of CO_2 (Wickler and Marsh 1981). The decline in nest cavity CO_2 concentrations that occurred between day 17 and day 23 might be due to the activities of the chicks as they near fledging. For example,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE 1. Seasonal variation in CO_2 levels within bank swallow burrows during the nestling period. Line = median values (n=32)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Petersen (1955) noted that 12 day old nestlings waited to receive food approximately 6 inches from the burrow entrance, and chicks near fledging often met their parents at the burrow opening. As chicks spend more time near the burrow entrance CO_2 in the nest cavity expectably would decline.

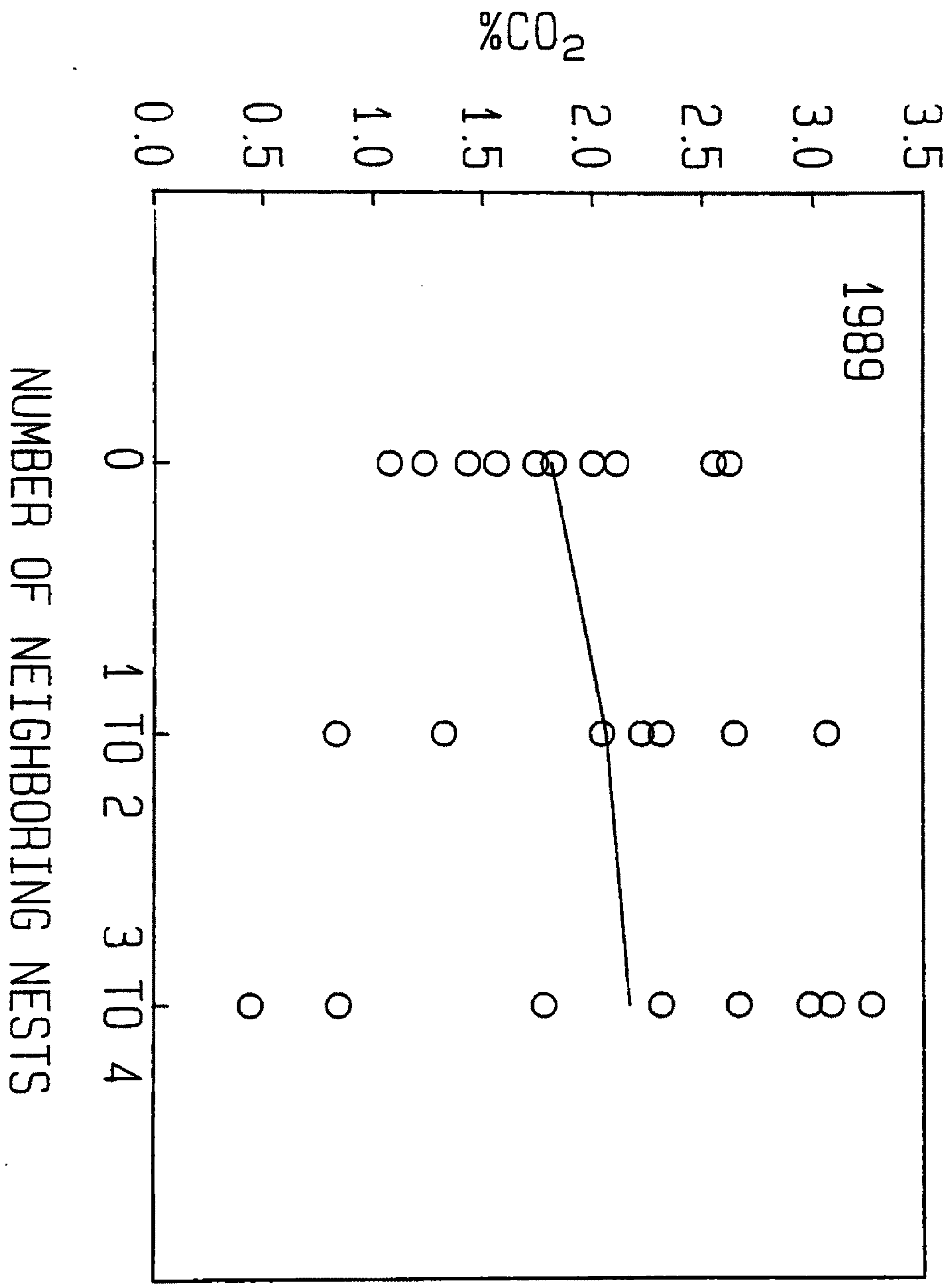
EFFECTS OF NEST DENSITY ON RESPIRATORY ENVIRONMENT

In 1989, mean CO_2 level was elevated somewhat in burrows with up to 3 or 4 active neighboring nests (Fig. 2). This slight increase in CO_2 was not statistically significant ($\underline{P} > 0.05$) when analyzed with an analysis of covariance using the number of chicks and burrow depth as covariates (Table 1). In an earlier study, Wickler and Marsh (1981) demonstrated a significant relationship between nestling mass and burrow CO_2. Because there is a high degree of breeding synchrony between adjacent nests (Emlen 1971, Hoogland and Sherman 1976), chicks in the same colony of approximately the same age should have similar masses. Therefore, chick number is a reasonable indicator of biomass within a nest. In my study number of nestlings had a significant effect on maximal burrow CO_2 level ($\underline{P} = 0.002$). Wickler and Marsh (1981) also showed that burrow depth significantly affects cavity CO_2 concentrations. However, in my study burrow

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE 2. Carbon dioxide levels in bank swallow burrows surrounded by different numbers of active burrows. Line passes through mean. Data were collected during the 1989 breeding season.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE 1. Analysis of covariance of CO_2 levels within bank swallow burrows surrounded by different numbers of active burrows. Number of chicks within the burrow (Biomass), burrow depth (Depth), and verticle distance (Vert) between the burrow entrance and top of the bank were included in the analysis as covariates. Data from 1989 breeding season.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ANALYSIS OF COVARIANCE

SOURCE OF VARIATION	SS	DF	MS	F	P
COVARIATES					
DEPTH	0.646	1	0.646	2.075	0.167
BIOMASS	4.283	1	4.283	13.767	0.002
VERT	0.108	1	0.108	0.348	0.563
MAIN EFFECT					
NEST DENSITY	0.856	3	0.285	0.917	0.453
RESIDUAL	5.600	18	0.311		

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

depth was not a significant determinant of maximal CO_2 concentration (P = 0.16)(Table 1). Carbon dioxide levels in nests with 5 or more adjacent burrows were lower than those in the other categories (1.47%CO_2). These low CO_2 concentrations are the result of reduced activity in the neighboring burrows. When large numbers of nests are constructed in a very small area of the sand bank, the tunnels are more likely to coalesce, which will lead to their abandonment (Hoogland and Sherman 1976). Consequently, data from burrows with 5 or more neighboring nests were not included in the analysis of nest density effects on CO_2 levels and are not shown in Fig. 2.

In 1990, mean maximal CO_2 level was slightly higher in burrows with up to 3 or 4 neighboring nests (category3). The difference was not statistically significant when analyzed with an analysis of covariance using biomass and burrow depth as covariates (P = .14)(Table 2, Fig 3). Biomass was the weight of the chicks in each nest at the time of sampling. Biomass does not explain a significant portion of the variation in burrow CO_2 level (P = 0.25) (Table 2) nor does burrow depth (P = 0.062) (Table 2).

In my 1989 and 1990 studies I found no significant effect of nest density on the gas composition of active bank swallow burrows. If diffusion is the primary mechanism of gas exchange in burrows, as suggested by

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE 2. Analysis of covariance of CO_2 levels within bank swallow burrows surrounded by different numbers of active burrows. Weight of chicks within the burrow (Biomass), and burrow depth (Depth) were included in the analysis as covariates. Data from the 1990 breeding season.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

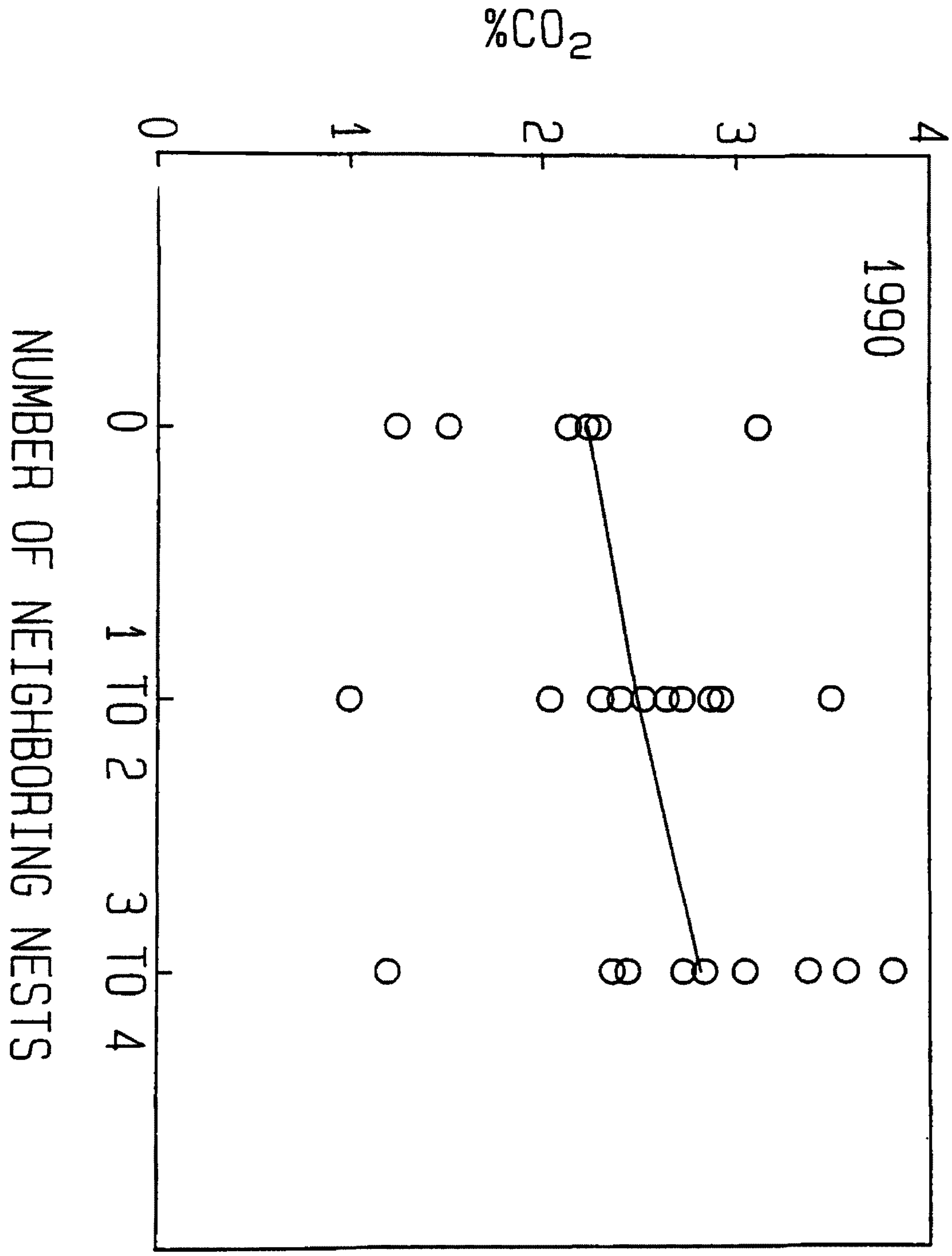
ANALYSIS OF COVARIANCE

SOURCE OF VARIATION	SS	DF	MS	F	P
COVARIATES					
DEPTH	1.552	1	1.552	3.892	0.062
BIOMASS	0.557	1	0.557	1.396	0.251
MAIN EFFECT					
NEST DENSITY	1.741	2	0.870	2.183	0.138
RESIDUAL	8.373	21	0.399		

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE 3. Carbon dioxide levels in bank swallow burrows surrounded by different numbers of active burrows. Line passes through mean. Data were collected during the 1990 breeding season.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Wilson and Kilgore (1978), Withers (1978), Furilla (1980) and Maclean (1981), then burrows within areas of the colony with high nest density should have had higher levels of CO_2 than those in lower nest density areas of the colony (Furilla 1980). My data would then suggest either that diffusion is not as important as suspected or that other mechanisms of gas exchange predominate in bank swallow burrows.

INTER-NEST DIFFUSION

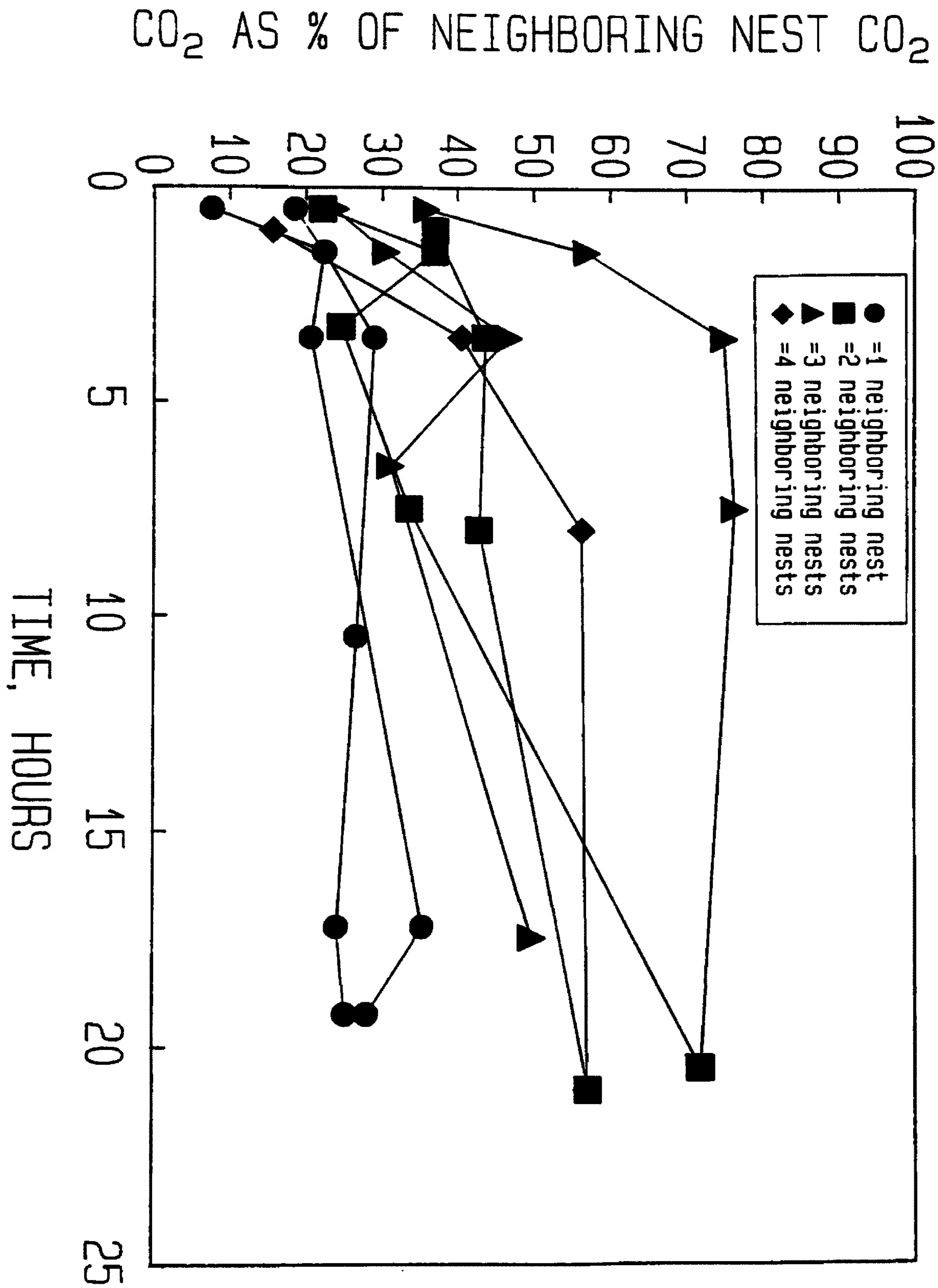
In unoccupied burrows, CO_2 levels are elevated when a high CO_2 gas mixture is introduced into neighboring nest cavities (Fig.4). Furthermore, this rise in CO_2 concentration occurs rapidly, reaching a new steady-state level usually within 1 to 3 hours. While I have insufficient data for statistical analysis, there is a trend for the final steady-state CO_2 levels in the experimental burrows to be elevated as the number of neighboring burrows filled with a high CO_2 mixture is increased from 1 to 3. Filling more than 3 neighboring nests with the CO_2 gas mixture does not seem to cause a furthur increase in steady-state CO_2 levels within the experimental burrows.

These results indicate that the respiratory environment in unoccupied bank swallow nest cavities will be affected

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE 4. CO_2 levels in unoccupied bank swallow nests surrounded by different numbers of unoccupied neighboring nests filled with a 5% CO_2 12% O_2 gas mixture.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

by the gaseous environment in adjacent nests due to the diffusive movement of gases between burrows. The fact that a similar effect is not detectable in active nests suggests that inter-nest diffusion may be masked by the effects of other mechanisms of exchange that influence the respiratory environment. For example, Ar and Piontkewitz (1989) determined that the movement of adult bee eaters, another colonial burrow nesting bird, may account for a substantial flux of gas (0.5 l/per visit) into and out of the nest. The adult birds act as pistons as they move through the burrow. White et al (1978) suggested that surface wind movements along the front of the bank or cliff may account for a substantial amount of gas movement. Also, bulk flow of gases due to thermal convection may have an effect on gas movement (Howe and Kilgore 1987, White et. al, 1978). Therefore, models of gas exchange based on diffusion only may not be adequate to explain the gas composition of bank swallow burrows.

CONCLUSION

Seasonal changes in the concentration of CO_2 in bank swallow burrows are mostly affected by changes in metabolizing mass of the nest occupants i.e., nestling age, and is little influenced by nest density.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The number of active neighboring nests had no significant effect on the respiratory environment of bank swallow burrows. However, substantial diffusive exchange can be demonstrated experimentally, between adjacent unoccupied nests. This suggests that in an active bank swallow colony the movement of gas between burrows and the free atmosphere involves multiple mechanisms (diffusion, bulk flow due to parental movement, venturi effect, and thermal gradients) and cannot be explained adequately by models based on diffusion alone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LITERATURE CITED

Alt, D. and D.W. Hyndman 1986. Roadside geology of Montana. Mountain press publishing Co., Missoula. MT

Ar, A., Piontkewitz Y. 1989. Whole nest gas exchange in bee-eaters. Proceedings of the international union of physiological sciences XVll. pp 389.

Chapman, R.C., and Bennett Albert F. 1975. Physiological correlates of burrowing in rodents. Comp. Biochem. Physiol. Vol. 51A, pp. 599-603.

Colby, C., D.L. Kilgore,Jr. and S. Howe 1987. Effects of hypoxia and hypercapnia on V_T, f, and V_I of nestling and adult bank swallows. Am. J. Physiol. 253: R854-R860

Darden, T.R. 1972. Respiratory adaptations of a fossorial mammal, the pocket gopher (Thomomys bottae). J. Comp. Physiol. 78, 121-137.

Emlen, S. T. 1971. Adaptive aspects of coloniality in the bank swallow. Abstr. Am. Zool. 11:47

Furilla, R.A. 1980. Ecological and physiological correlates of tunnel nesting in the bank swallow Riparia riparia, with reference to the cliff swallow Petrochelidon pyrrhonata. M.S. thesis. University of Alaska, Fairbanks.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295-311

Hoogland, J. L. and P. W. Sherman 1976. Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecological Monographs 46: 33-58

Howe, S. and D. L. Kilgore 1987. Convective and diffusive gas exchange in the nest cavities of the norther flicker (Colaptes auratus). Physiol. Zool. 60(6): 707-712

Jacobs, H. S. and R. M. Reed 1964. soils laboratory exercise source book. American Society of Agronomy. Madison, Wisconsin.

Maclean, G. S. 1981. Factors influencing the composition of respiratory gases in mammal burrows. Comp. Biochem. Physiol. 69A: 373-380.

Marsh, R. L. 1979. Development of endothermy in nestling bank swallows (Riparia riparia).Physiol. Zool. 52: 340-353

Petersen, A.J. 1955. The breeding cycle in the bank swallow. The Wilson Bulletin. Vol. 67, No. 4

Scholander, P. F. 1947. Analyzer for accurate estimation of respiratory gases in one-half cubic centimeter samples. J. Biological Chemistry. 167(1)

Stoner, D. 1936. Studies on the bank swallow Riparia riparia riparia (Linnaeus). Roosevelt Wild Life Annals. 4(2): 122-233

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

White, F. N., G. A. Bartholomew, and J. L. Kinney 1978. Physiological and ecological correlates of tunnel nesting in the European bee-eater *Merops apiaster*. Physiol. Zool. 51: 140-148

Wickler, S. J. and R. L. Marsh 1981. Effects of nestling age and burrow depth on CO_2 and O_2 concentrations in the burrow of the bank swallow (*Riparia riparia*). Physiol. Zool. 54(1): 132-136

Wilson, K. J. and D. L. Kilgore Jr. 1978. The Effects of location and design on the diffusion of respiratory gases in mammal burrows. J. Theor. Biol. 71: 73-101

Withers, P. C. 1978. Models of diffusion-mediated gas exchange in animal burrows. American Naturalist 112(988): 1101-1112

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX I

SOIL POROSITY

Porosity affects the rate of diffusion of gases through soil (Wilson and Kilgore 1978). The porosity (%pore space) of soil surrounding twenty-one randomly selected bank swallow burrows is given in Table I-1. Mean ($\pm$ 1SD) porosity was 39.4$\pm$1.6%, (Table I1). Soil porosity was determined by the method described by Jacobs and Reed (1964).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE I-1. Percent pore space of samples from the soil surrounding 21 bank swallow burrows.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE I-1:
POROSITY OF THE SOIL SURROUNDING BANK SWALLOW BURROWS.

SOIL SAMPLE	BULK MASS(g)	BULK VOLUME(ml)	BULK DENSITY(g/ml)	PARTICLE DENSITY(g/ml)	%PORE SPACE
1	157.0	106.45	1.47	2.5	41.2
2	162.5	106.45	1.53	2.5	38.8
3	168.0	106.45	1.58	2.5	36.8
4	162.0	106.45	1.52	2.5	39.2
5	159.5	106.45	1.50	2.5	40.0
6	160.0	106.45	1.50	2.5	40.0
7	163.0	106.45	1.53	2.5	38.9
8	164.0	106.45	1.54	2.5	38.4
9	158.5	106.45	1.49	2.5	40.4
10	166.0	106.45	1.56	2.5	37.6
11	168.5	106.45	1.58	2.5	36.8
12	166.5	106.45	1.56	2.5	37.6
13	157.0	106.45	1.47	2.5	42.2
14	164.0	106.45	1.54	2.5	38.4
15	161.5	106.45	1.52	2.5	39.2
16	152.5	106.45	1.43	2.5	42.8
17	155.5	106.45	1.46	2.5	41.6
18	163.0	106.45	1.53	2.5	38.8
19	160.0	106.45	1.50	2.5	40.0
20	162.0	106.45	1.52	2.5	39.2
21	159.5	106.45	1.50	2.5	40.0
					39.4±1.6%

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX II

RELATIONSHIP BETWEEN DISTANCE OF BURROW FROM TOP OFBANK AND MAXIMAL BURROW CO_2 FRACTIONAL CONCENTRATION.

The vertical distance between the top of the bank to the top of the burrow entrance was measured for each nest cavity studied in 1989.

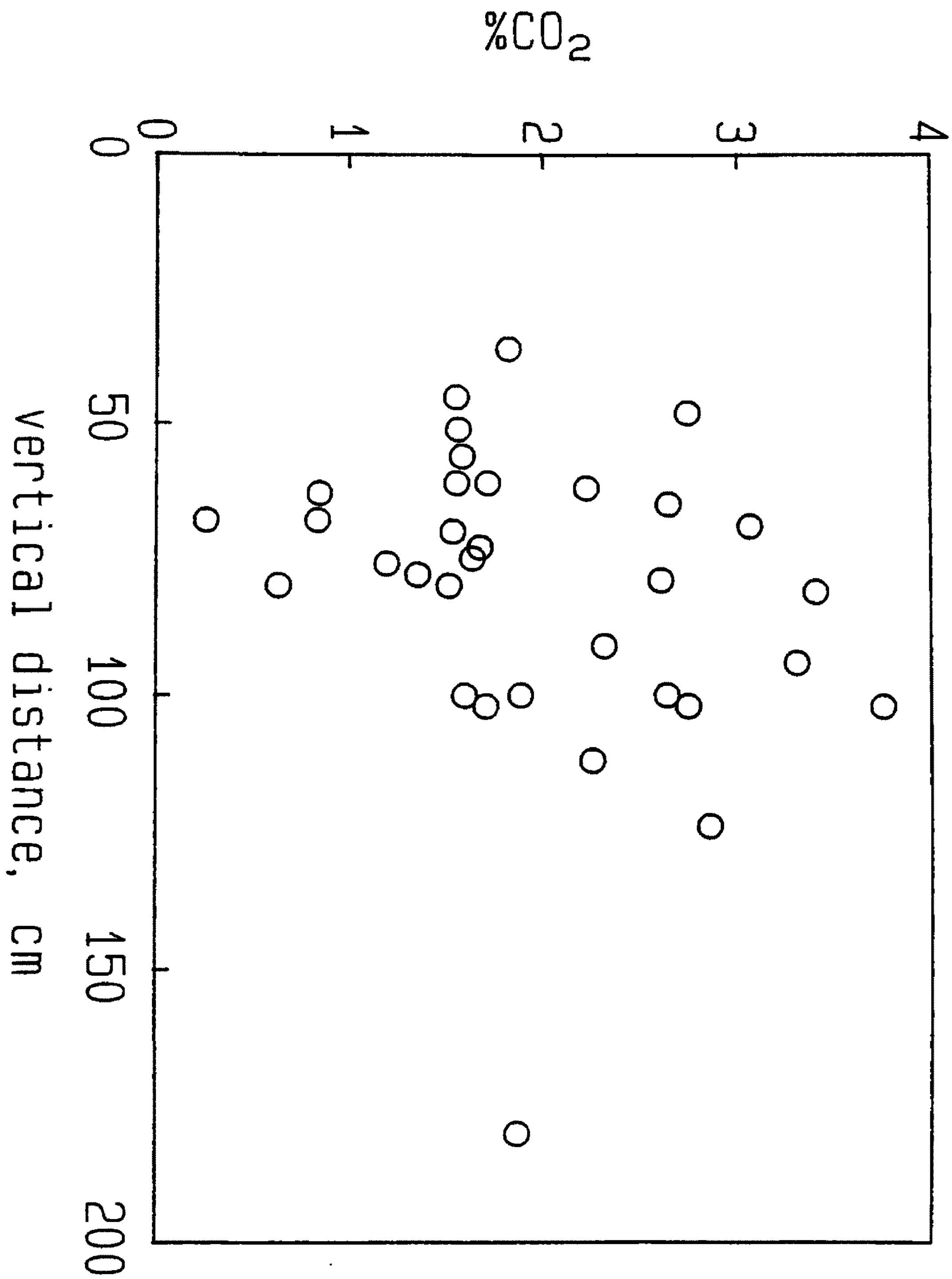
The vertical distance between a burrow and the soil surface may influence the diffusive exchange between the burrow and the free atmosphere. Topsoil contains a relatively large amount of organic material which holds a great deal of moisture. Because diffusion is much slower in water than in air, the water contained in the topsoil may impede the diffusive exchange of gases between the nest cavity and the free atmosphere. Respiration of soil microbes may also reduce the diffusion gradient for CO_2. Also, diffusion distances are reduced in burrows located close to the surface. Fig II-1 is a regression of peak CO_2 in burrows on vertical distance from the top of the cliff. Vertical distance does not explain a significant portion of the variation in maximal CO_2 level ($\underline{P}$= 0.15, n=33 , R^2=.07).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE II-1. CO_2 levels in bank swallow burrows located at different distances from the top of the bank.

Points are peak values.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX III

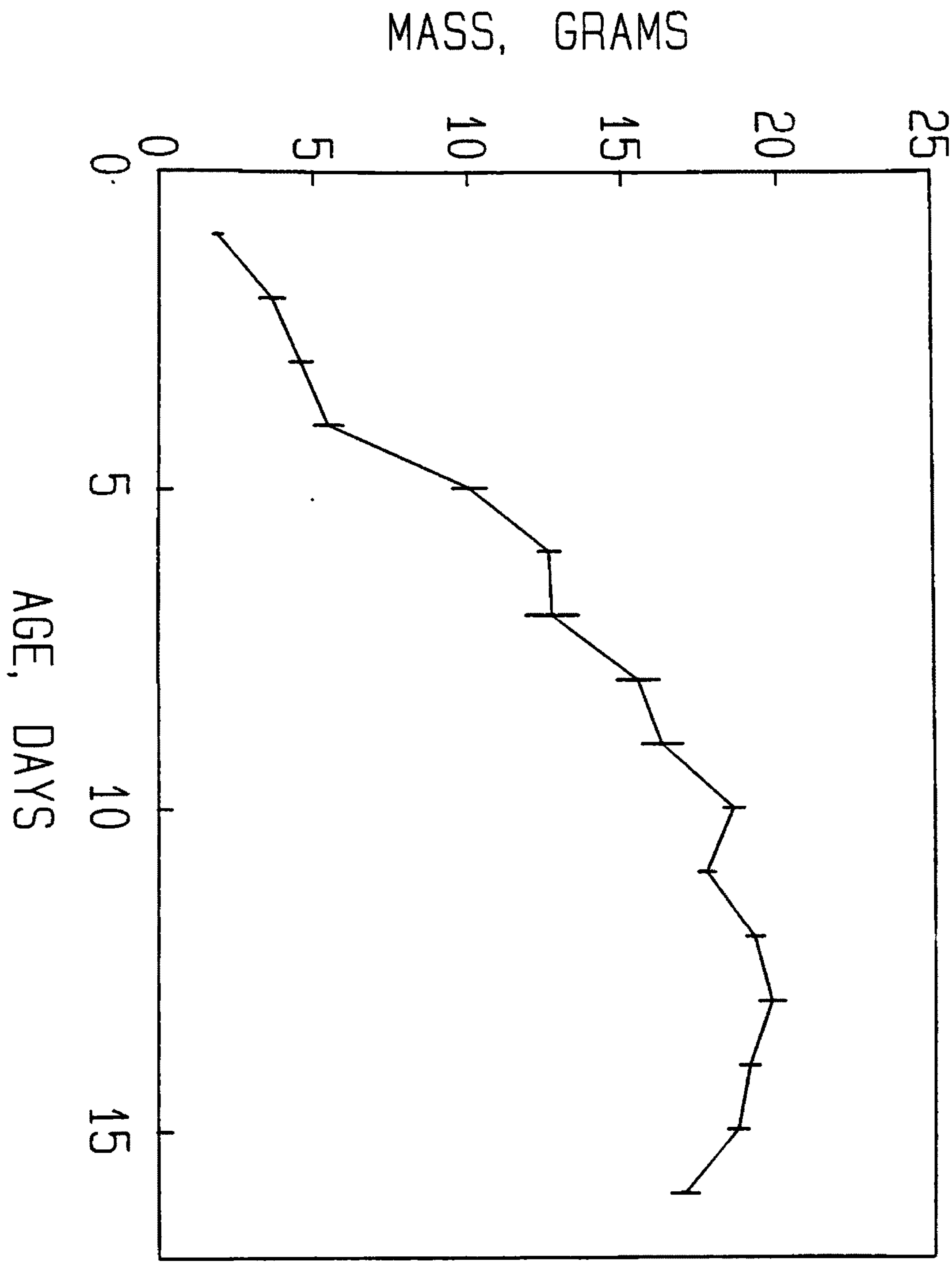
GROWTH CURVE FOR BANK SWALLOWS

Bank swallow nestlings increase in mass during development to a peak of 19 grams at 13 days of age. Between 13 days and fledging, mass of nestlings decreases until adult mass is attained (Fig. III-1). The age-mass curve obtained in this study is similar to that reported by Marsh (1979).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FIGURE III-1. Growth curve for bank swallows. Values are means ± SD. n=8.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE III-1. Data for bank swallow growth curve.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table III-1

Chick age, days	Chick mass, grams	Chick age, days	Chick mass, grams
1	1.89	7	11.39
1	2.65	7	15.89
1	2.15	7	15.87
1	2.72	7	13.80
1	1.55	8	15.11
1	1.56	8	14.23
1	1.15	8	15.04
1	2.35	8	16.04
1	1.98	8	12.02
1	1.62	8	18.01
1	1.31	8	15.41
2	4.01	8	17.81
2	2.85	9	17.00
2	4.14	9	18.69
3	4.72	9	17.40
3	6.19	9	13.77
3	5.19	9	14.72
3	4.60	9	14.61
3	3.43	9	12.7
3	4.32	9	14.68
3	2.71	9	18.94
3	3.17	9	18.60
3	5.86	9	17.42
3	6.21	10	18.70
3	4.17	10	19.80
4	4.71	10	17.88
4	5.88	10	17.13
4	3.77	10	17.75
4	4.92	10	18.44
4	7.12	10	17.17
4	5.08	10	19.08
4	6.89	10	17.70
5	10.23	10	19.60
5	10.18	10	20.25
5	8.14	11	17.47
5	8.78	11	18.76
5	11.42	11	17.48
5	11.40	11	17.46
6	12.67	11	18.77
6	10.82	11	17.24
6	13.09	11	16.85
6	13.01	11	17.01
6	12.97	12	18.86
6	13.02	12	18.75
7	12.38	12	20.91
7	10.67	12	19.17
7	9.12	12	18.58
7	12.38	12	19.25

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chich age, days	Chich mass, grams
12	17.59
12	18.20
12	19.12
12	19.89
12	20.28
13	18.39
13	17.64
13	19.61
13	20.46
13	19.98
13	20.91
13	19.56
13	20.98
14	19.55
14	18.77
14	19.35
14	18.12
14	19.27
14	19.45
14	19.81
14	20.50
14	17.69
14	19.22
14	16.85
15	17.37
15	19.85
15	18.94
15	19.61
15	18.74
15	18.55
15	18.38
15	17.32
16	16.07
16	17.27
16	17.40

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.