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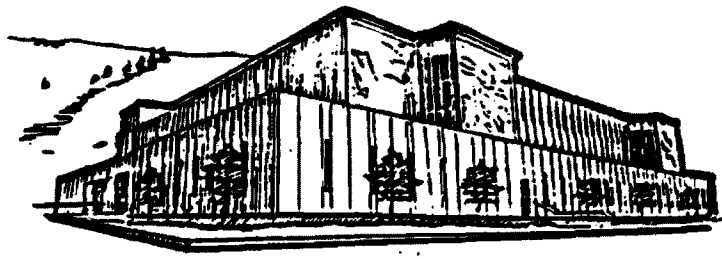
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University of  
**Montana**



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

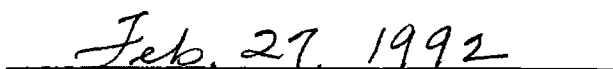
Master of Arts

University of Montana  
1992

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

Director: Delbert L. Kilgore, Jr. <sup>D.L.K.</sup>

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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> with depth, biomass, and distance from ground surface as covariates. There was a small non-significant increase in CO<sub>2</sub> 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.

## 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.

## TABLE OF CONTENTS

	Page
ABSTRACT.....	ii
ACKNOWLEDGMENTS.....	iii
LIST OF FIGURES.....	v
LIST OF TABLES.....	vi
INTRODUCTION.....	1
METHODS.....	3
Study site.....	3
Collection and analysis of gas samples.....	3
Seasonal variation in burrow carbon dioxide.....	4
Effect of nest density on respiratory environment..	4
Inter-nest diffusion.....	5
RESULTS AND DISCUSSION.....	7
Seasonal Variation in Burrow CO <sub>2</sub> .....	7
Effects of Nest Density on Respiratory Environment.	10
Inter-nest diffusion.....	20
CONCLUSIONS.....	23
LITERATURE CITED.....	25
APPENDIX I.....	28
APPENDIX II.....	31
APPENDIX III.....	34



## LIST OF FIGURES

FIGURE	PAGE
1 Seasonal variation in CO <sub>2</sub> levels within bank swallow burrows.-----	9
2 Mean maximal CO <sub>2</sub> levels in bank swallow burrows surrounded by different numbers of active burrows.-----	12
3 Mean maximal CO <sub>2</sub> levels in bank swallow burrows surrounded by different numbers of active burrows.-----	19
4 Carbon dioxide levels in unoccupied bank swallow nests surrounded by different numbers of unoccupied neighboring nests containing a 5% CO <sub>2</sub> 12% O <sub>2</sub> gas mixture.-----	22

### APPENDIX II

II-1 Carbon dioxide levels in bank swallow burrows located at different distances from the top of the cliff.-----	33
---	----

### APPENDIX III

III-1 Growth curve for bank swallows.-----	36
--	----

LIST OF TABLES

TABLE	PAGE
1 Analysis of covariance of CO <sub>2</sub> levels within bank swallow burrows surrounded by different numbers of active burrows (1989).-----	14

2 Analysis of covariance of CO <sub>2</sub> levels within bank swallow burrows surrounded by different numbers of active burrows (1990).-----	17
---	----

APPENDIX I

I-1 Soil porosity of a bank swallow nest site.-----	30
---	----

APPENDIX III

III-1 Growth curve data table.-----	38
-------------------------------------	----

## 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 interferes 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<sub>2</sub> and O<sub>2</sub> 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<sub>2</sub>, for example, increased ventilation

(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  $\text{CO}_2$  concentration will be energetically more costly to inhabit than burrows with lower  $\text{CO}_2$  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  $\text{CO}_2$  concentrations than nests in the peripheral areas. To answer this question it was first necessary to determine how  $\text{CO}_2$  levels in burrows change during the breeding season. A follow up study of inter-nest diffusion was also conducted.

## 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<sup>3</sup> (approximately 4 times the tubing dead space) of gas was withdrawn and purged to the atmosphere before a 6 cm<sup>3</sup> sample was collected for analysis. All gas samples were analyzed within three hours of collection. CO<sub>2</sub> concentrations

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 assigned 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<sub>2</sub> 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

experimental burrows late in the nestling period when CO<sub>2</sub> 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

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<sub>2</sub>, and 12% O<sub>2</sub> 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·min.<sup>-1</sup> for the first five minutes, then reduced to approximately. 0.38 l·min.<sup>-1</sup> 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.



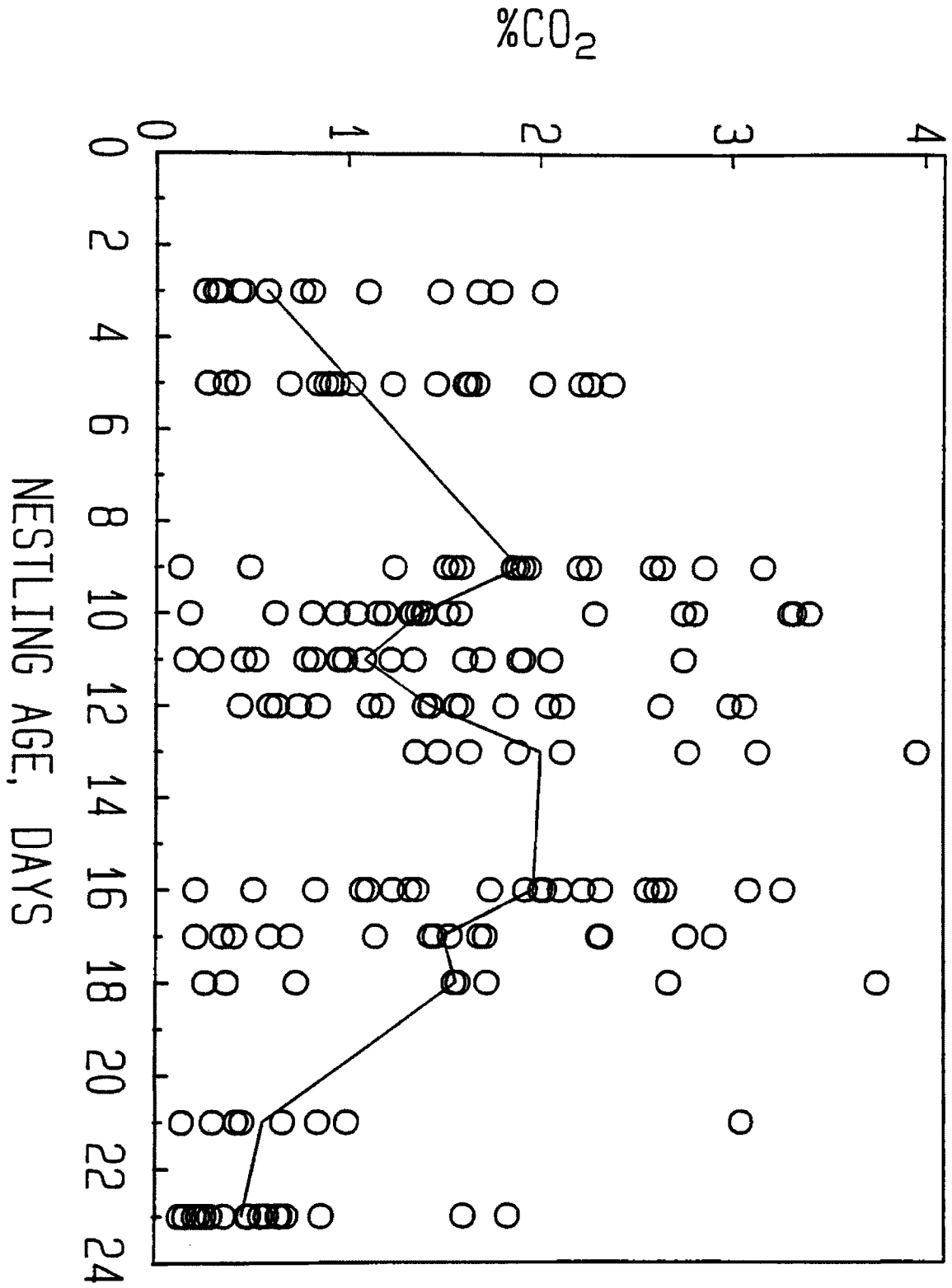
## RESULTS AND DISCUSSION

### SEASONAL VARIATION IN BURROW CARBON DIOXIDE LEVELS

The CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> concentration of 0.86%. From day 9 to day 17 mean CO<sub>2</sub> concentration averaged 1.64%. However, mean CO<sub>2</sub> concentrations began to fall at 21 days post hatching. At the end of the breeding season; at 23 days post hatching, the mean CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> (Wickler and Marsh 1981). The decline in nest cavity CO<sub>2</sub> concentrations that occurred between day 17 and day 23 might be due to the activities of the chicks as they near fledging. For example,

FIGURE 1. Seasonal variation in CO<sub>2</sub> levels within bank swallow burrows during the nestling period.  
Line = median values (n=32)



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  $\text{CO}_2$  in the nest cavity expectably would decline.

#### EFFECTS OF NEST DENSITY ON RESPIRATORY ENVIRONMENT

In 1989, mean  $\text{CO}_2$  level was elevated somewhat in burrows with up to 3 or 4 active neighboring nests (Fig. 2). This slight increase in  $\text{CO}_2$  was not statistically significant ( $P > 0.05$ ) 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  $\text{CO}_2$ . 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  $\text{CO}_2$  level ( $P = 0.002$ ). Wickler and Marsh (1981) also showed that burrow depth significantly affects cavity  $\text{CO}_2$  concentrations. However, in my study burrow

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.

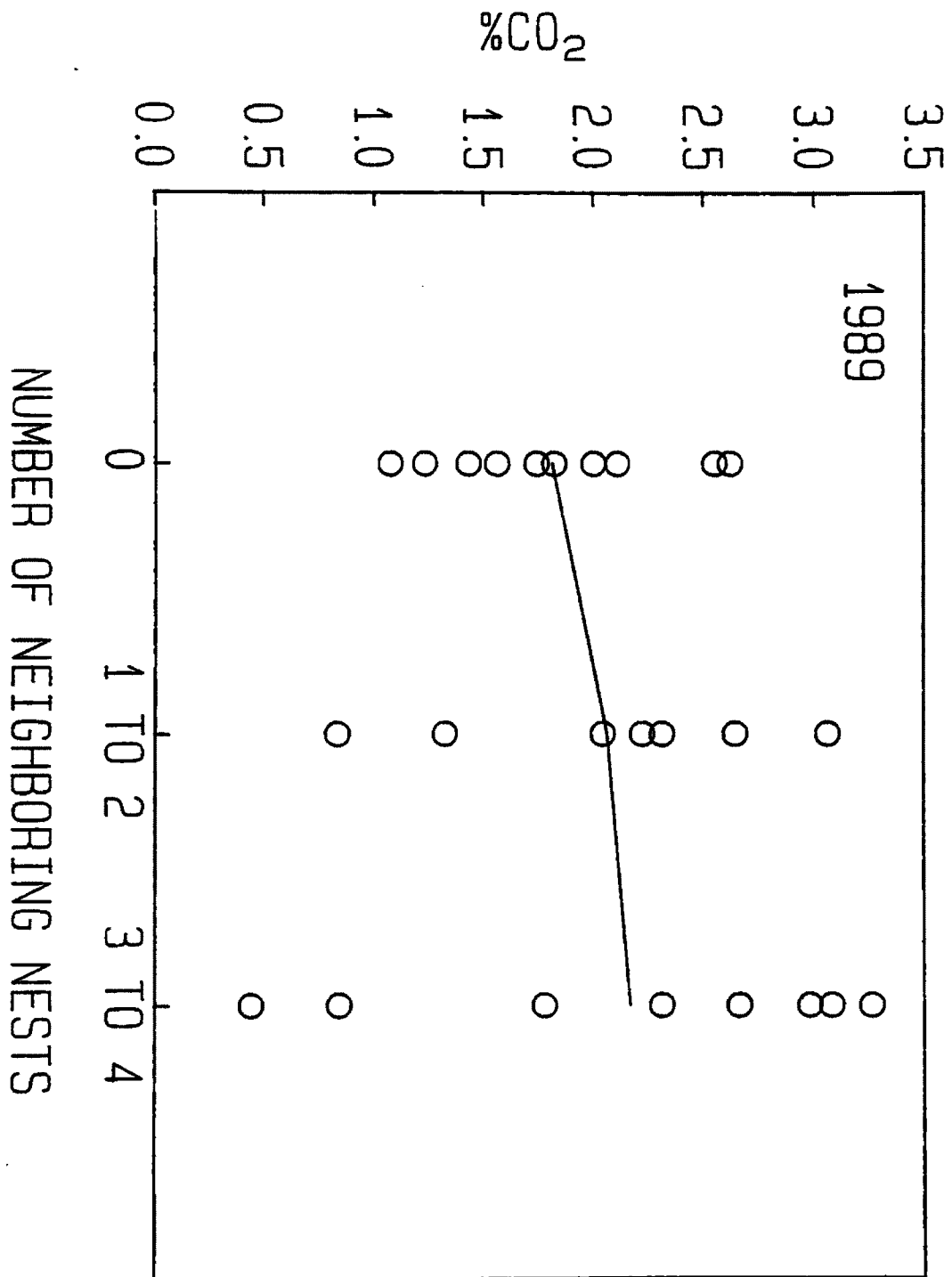


TABLE 1. Analysis of covariance of CO<sub>2</sub> levels within bank swallow burrows surrounded by different numbers of active burrows. Number of chicks within the burrow (Biomass), burrow depth (Depth), and verticle distance (Vert) between the burrow entrance and top of the bank were included in the analysis as covariates. Data from 1989 breeding season.

## 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		



depth was not a significant determinant of maximal CO<sub>2</sub> concentration ( $\underline{P} = 0.16$ )(Table 1). Carbon dioxide levels in nests with 5 or more adjacent burrows were lower than those in the other categories (1.47%CO<sub>2</sub>). These low CO<sub>2</sub> 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<sub>2</sub> levels and are not shown in Fig. 2.

In 1990, mean maximal CO<sub>2</sub> 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 ( $\underline{P} = .14$ )(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<sub>2</sub> level ( $\underline{P} = 0.25$ ) (Table 2) nor does burrow depth ( $\underline{P} = 0.062$ ) (Table 2).

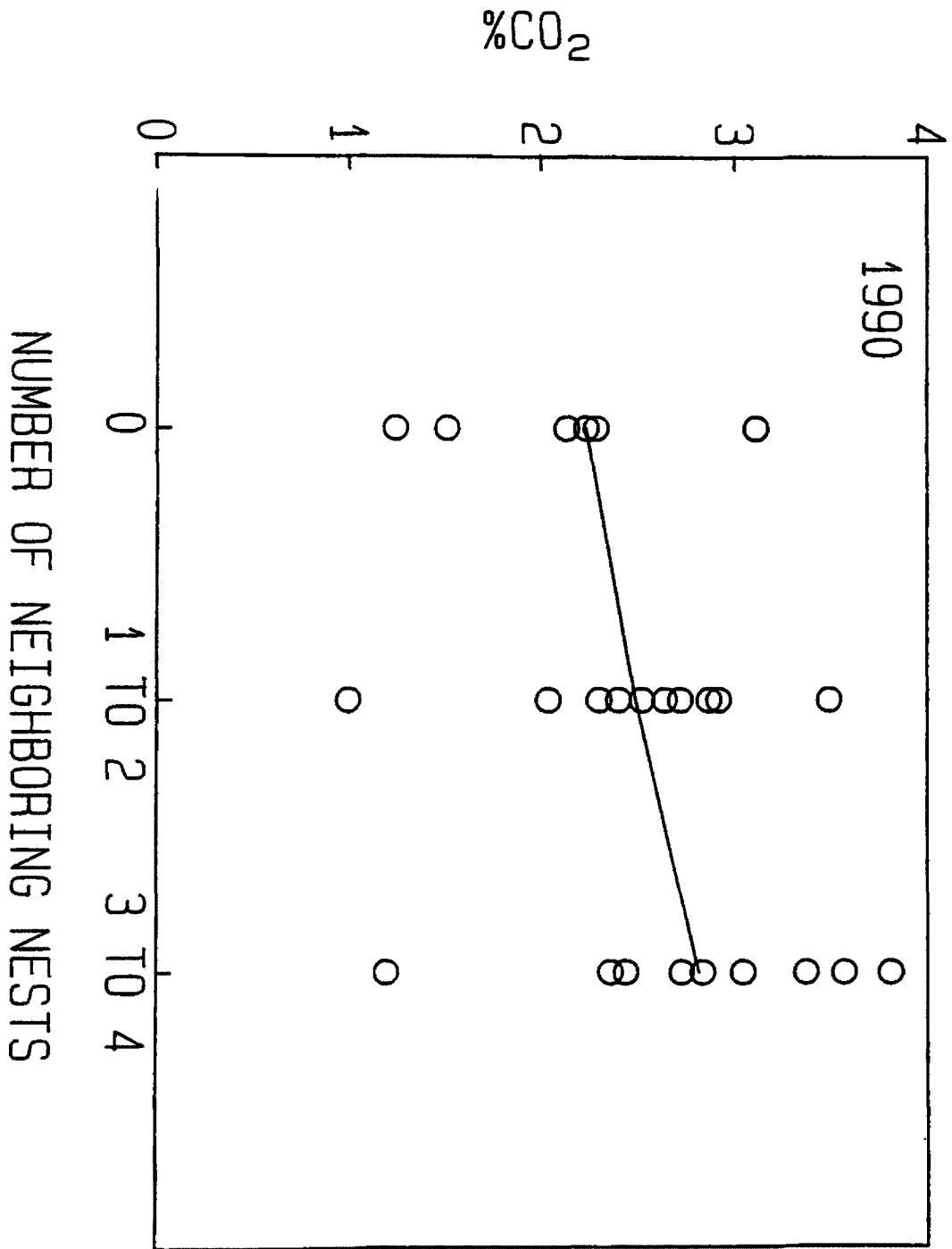
In my 1989 and 1990 studies I found no significant effect of nest density on the gas composition of active bank swallow burrows. If diffusion is the primary mechanism of gas exchange in burrows, as suggested by

TABLE 2. Analysis of covariance of CO<sub>2</sub> 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.

## 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		

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.



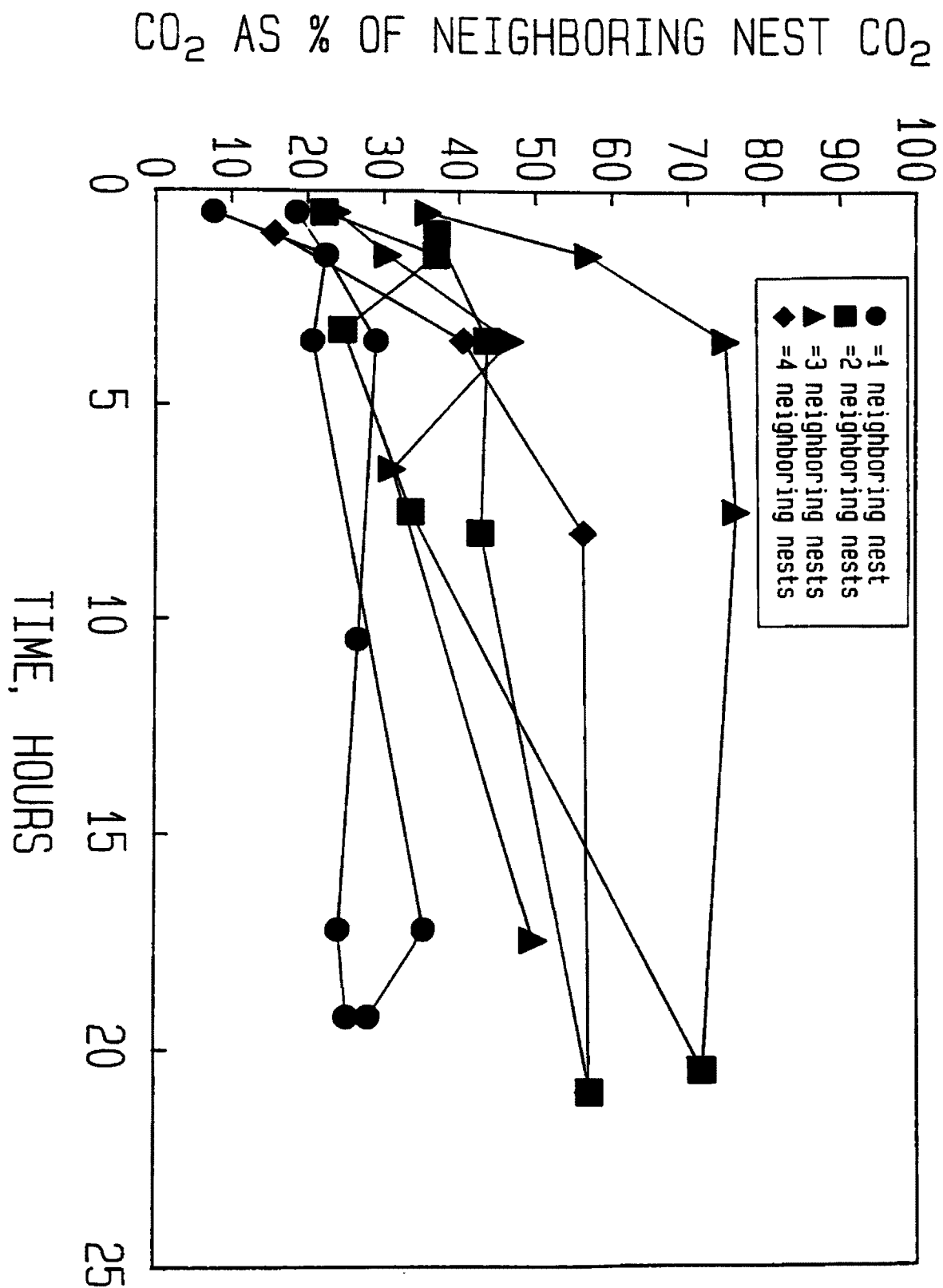
Wilson and Kilgore (1978), Withers (1978), Furilla (1980) and Maclean (1981), then burrows within areas of the colony with high nest density should have had higher levels of  $\text{CO}_2$  than those in lower nest density areas of the colony (Furilla 1980). My data would then suggest either that diffusion is not as important as suspected or that other mechanisms of gas exchange predominate in bank swallow burrows.

#### INTER-NEST DIFFUSION

In unoccupied burrows,  $\text{CO}_2$  levels are elevated when a high  $\text{CO}_2$  gas mixture is introduced into neighboring nest cavities (Fig.4). Furthermore, this rise in  $\text{CO}_2$  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  $\text{CO}_2$  levels in the experimental burrows to be elevated as the number of neighboring burrows filled with a high  $\text{CO}_2$  mixture is increased from 1 to 3. Filling more than 3 neighboring nests with the  $\text{CO}_2$  gas mixture does not seem to cause a further increase in steady-state  $\text{CO}_2$  levels within the experimental burrows.

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

FIGURE 4. CO<sub>2</sub> levels in unoccupied bank swallow nests surrounded by different numbers of unoccupied neighboring nests filled with a 5% CO<sub>2</sub> 12% O<sub>2</sub> gas mixture.





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<sub>2</sub> 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.

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.

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**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).

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

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

<b>SOIL SAMPLE</b>	<b>BULK MASS(g)</b>	<b>BULK VOLUME(ml)</b>	<b>BULK DENSITY(g/ml)</b>	<b>PARTICLE DENSITY(g/ml)</b>	<b>%PORE SPACE</b>
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
					<b>39.4±1.6%</b>



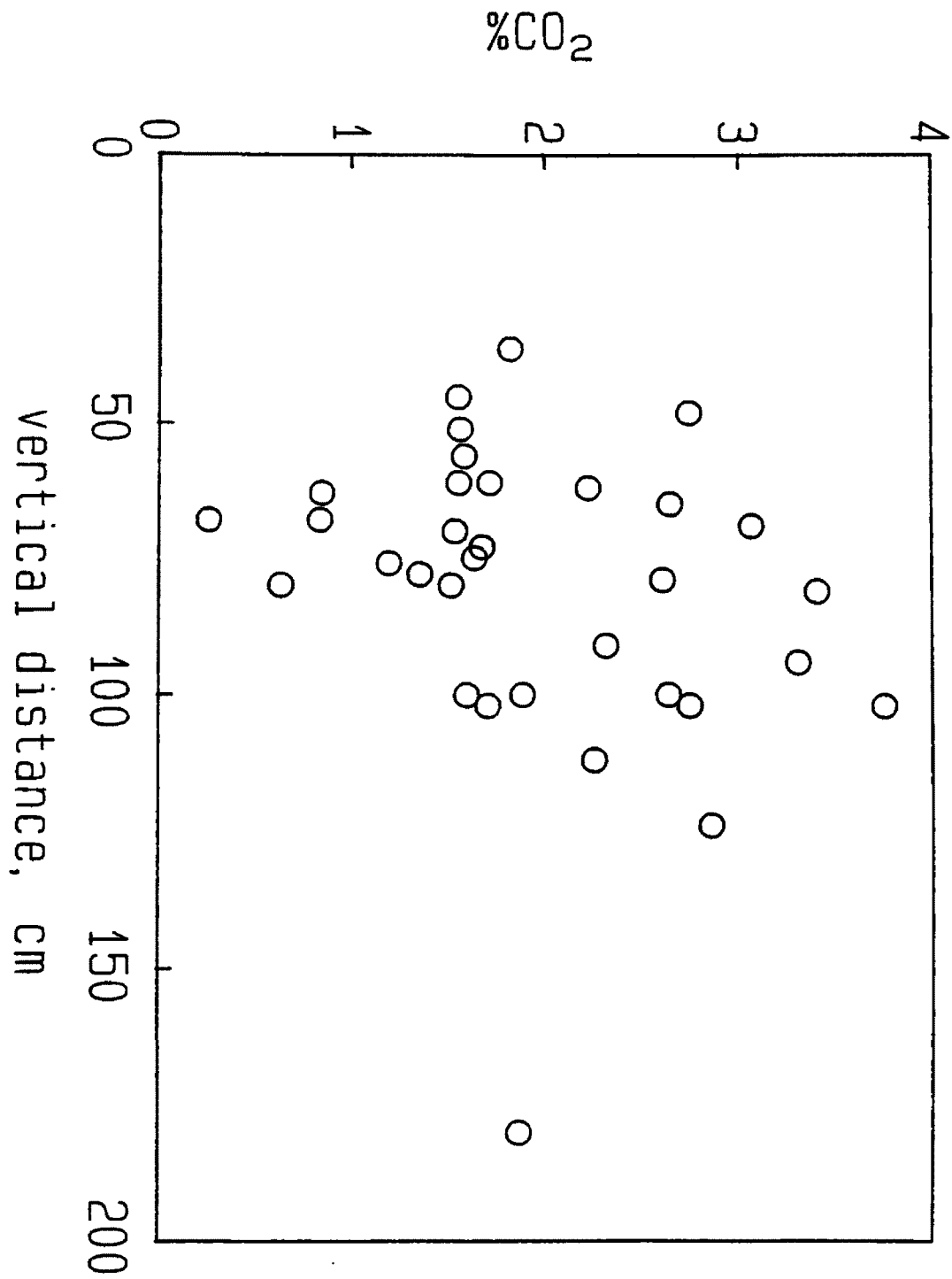
## APPENDIX II

RELATIONSHIP BETWEEN DISTANCE OF BURROW FROM TOP OF BANK  
AND MAXIMAL BURROW CO<sub>2</sub> 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<sub>2</sub>. Also, diffusion distances are reduced in burrows located close to the surface. Fig II-1 is a regression of peak CO<sub>2</sub> 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<sub>2</sub> level ( $P = 0.15$ ,  $n = 33$ ,  $R^2 = .07$ ).

FIGURE II-1. CO<sub>2</sub> levels in bank swallow burrows located at different distances from the top of the bank.  
Points are peak values.



## 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).

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

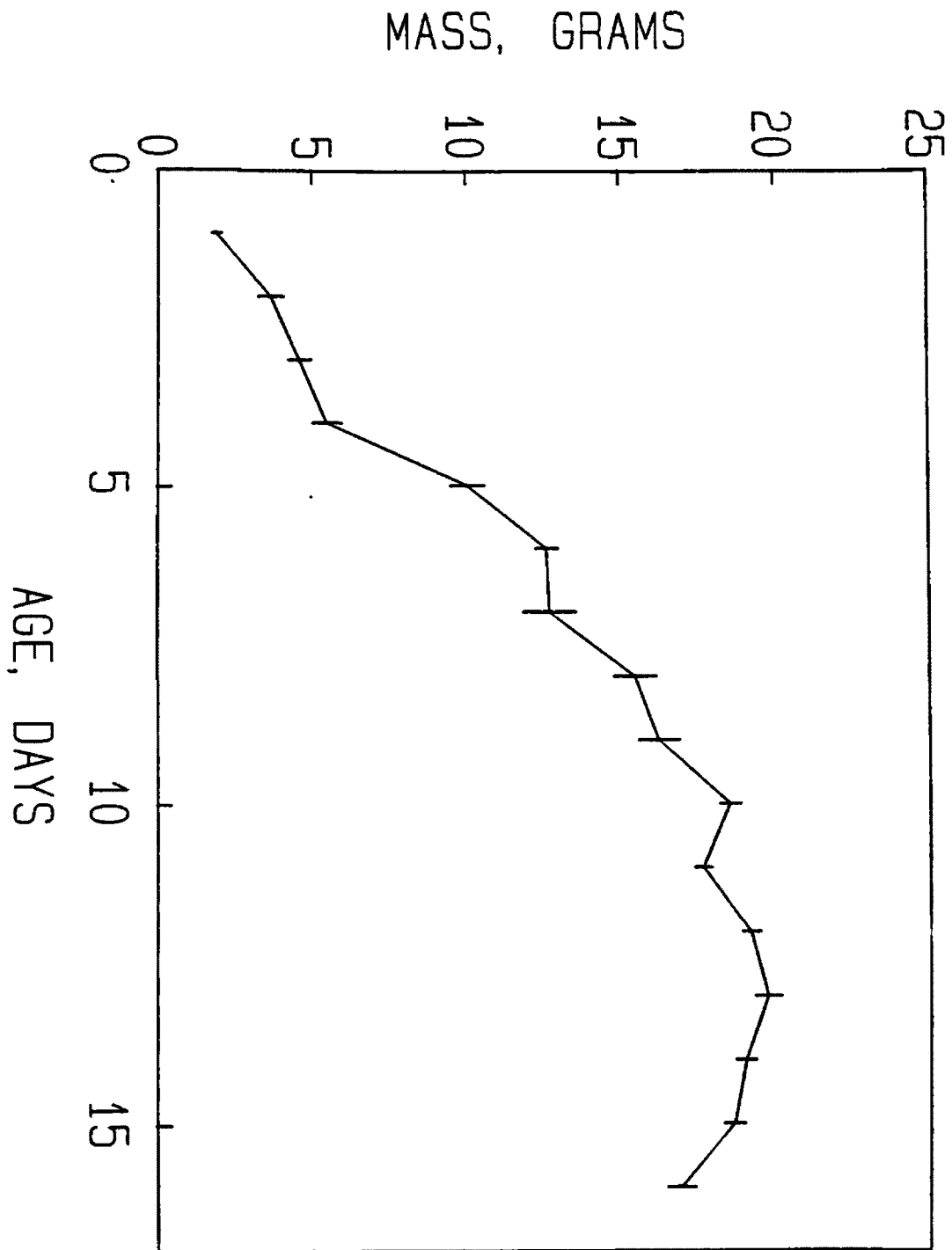


TABLE III-1. Data for bank swallow growth curve.

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



Chich age, days	Chich mass, grams
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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