AN ABSTRACT OF THE THESIS OF John Mark Perkins for the Master of Science in Biology presented 31 May 1977.

Title: Bat Homing

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

[redacted]

Richard Forbes, Chairman

[redacted]

John H. Wirtz

[redacted]

Larry I. Crawshaw

[redacted]

Robert W. Rempfer

A model proposed by Wilson & Findley (1972) to test for randomness in bat homing was applied to results of homing studies on big brown bats (*Eptesicus fuscus*) and, when possible, to published studies on homing by other bats.

BAT HOMING

by

JOHN MARK PERKINS

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

Portland State University
1977

TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

The members of the Committee approve the thesis of John Mark Perkins presented 31 May 1977.

[redacted]

Richard Forbes, Chairman

[redacted]

John H. Wirtz

[redacted]

Larry I. Crawshaw

[redacted]

Robert W. Rempfer

APPROVED:

[redacted]

W. Herman Taylor, Head, Department of Biology

[redacted]

Stanley E. Rauch, Dean, Graduate Studies and Research

ACKNOWLEDGEMENTS

Many individuals helped to make this study a success. Special thanks are due Dr. Richard Forbes whose encouragement and help was greatly appreciated during the course of the work. I would also like to thank the other members of my committee Drs. Larry Crawshaw, Robert Rempfer, and John Wirtz.

People below deserve special mention for advice and participation: Drs. Stephen P. Cross and Russell Davis, my wife, Nancy D. Perkins, Pat Hickey, Pat Runyan, Lloyd D. Taylor and Clara Sabbe.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Many investigators assumed migrating bats utilized special navigational aides. In the first recorded homing experiment on bats, Gyles (1883) displaced the animals about 0.5 miles from their roost and noted that when released they flew directly back to it.

Early experimenters (Eisentraut, 1936; Casteret, 1938; Mohr, 1934 and Poole, 1932) used leg, ear, and wing tags to discover that homing among migratory bats was usually poor at distances less than 10 km., good at middle distances, and again poor at long distances.

Griffin (1940) showed that bats caught, banded and released near their colony were as likely to be recaptured as those which were released at a distance from it. He hypothesized that the bats associated the capture/release location with the trauma of being banded; hence they deserted the area. Griffin obtained two records of bats which were released at a distance from the colony and later were recaptured between the release site and the capture site. These records led him to postulate that cave bats had a well developed homing instinct. In later papers, Gifford and Griffin (1960) and Twente (1955) noted movements of distant releases to alternate roosts near the capture site. By checking these alternate day roosts and using radioactive tags, Punt and Nieuwenhoven (1957) increased the detection of returns.

By 1957, distance return records were available for several species of bats and their speed of return was studied. Cockrum (1956) and Mueller and Emlen (1957) noted that percentages of returns were not high enough to demonstrate accurate or direct homeward orientation by bats, as opposed to wandering and/or exploratory flights until "familiar area"[1] was reached. Mueller's (1963) studies of *Myotis lucifugus* led him to postulate that returns at faster than 4 mph (about 1/4 of normal flight speed) were in excess of what one might expect on the basis of a random search by a bat. Several of Mueller's experiments attempted to identify mechanisms used by bats in homing by comparing the returns of test bats to those of control bats. Mueller found no difference in performance between young adults and old adults, varying wind speeds and directions, cloud cover at night, vision, olfaction, topographic familiarity, light density or direction, and group coherence (numbers released all at once, all returning together to the capture site). Mueller applied Wilkerson's (1952) test for random search by birds to his data on bats. Mueller assumed that the bat's search for familiar territory ended after a designated

---

[1] Defined as the area traversed by a bat in normal undisturbed movements.

time, ignoring reports (Hitchcock and Reynolds, 1942; Bels, 1952; Dulic, 1957) of returns from distant releases later than one year after release. His findings were inconclusive.

Davis (1966) recognized two types of homing experiments: Type A, in which release is at a point within the bat's familiar area; and Type B, in which release is at a point outside of the familiar area. Three types of homing ability were described: 1) ability to home within familiar area; 2) ability to maintain a directional flight even when in unfamiliar area; and 3) ability to approximate the correct direction of the familiar area when in unfamiliar territory. Differences Davis observed in homing abilities of immatures compared to adults were thought to result from lack of flight capability, undeveloped homing ability, and/or differing locality loyality. Davis found that seasonal factors affected the homing of the pallid bat, *Antrozous pallidus*, significantly. An inverse relationship was found between number of returns and distance of release from colony. These findings confirmed those of Kowalski and Wojtusiak,(1952), Mueller (1963), and Hassell (1963). Release also apparently affected percentages of returns (Davis, 1966; Mueller, 1963; Hassell and Harvey, 1965) from various directions from the colony.

Davis (1966) concluded that Type 1 homing occurred in all bats, since they were able to leave roosts, forage, *etc.*, and return to the roost before sunrise. Davis speculated that Type 2 homing probably involved some learning and experience by bats. He considered returns from distances of 250 and 450 mi. by *Eptesicus fuscus* as possible evidence for Type 3 homing (Table II).

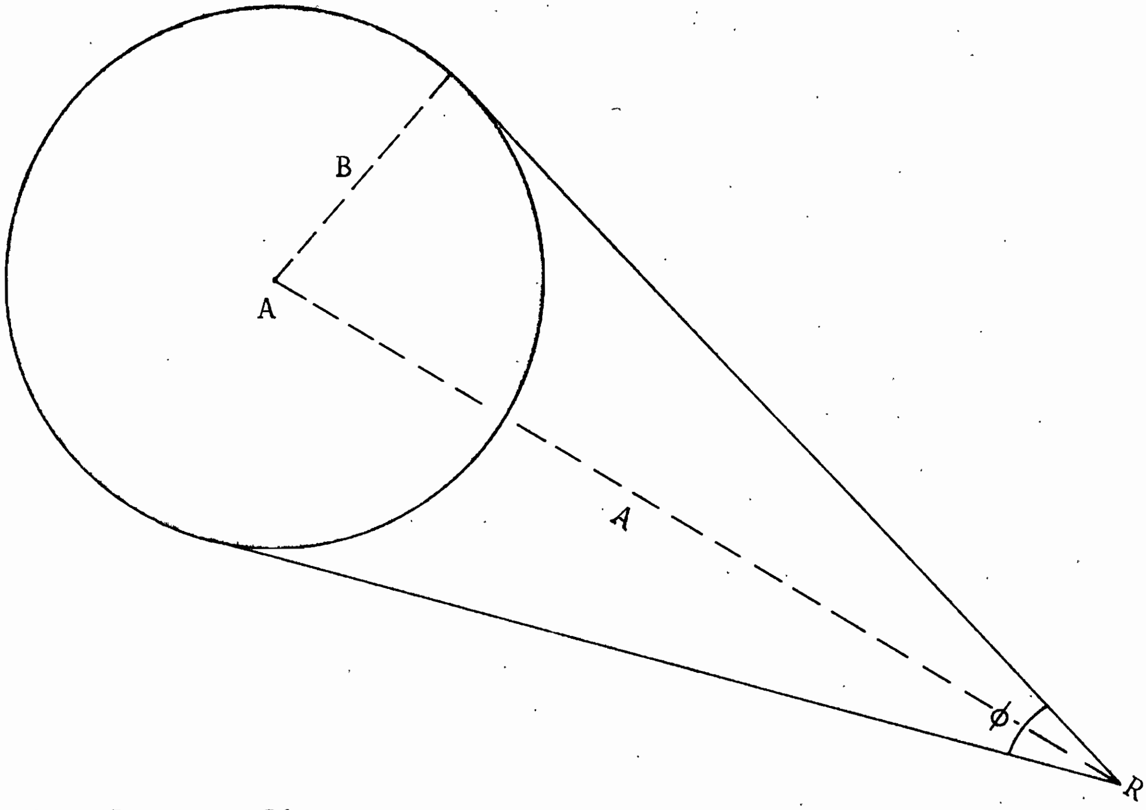
Navigation by bat employing celestial, rotational, or magnetic cues was rejected by Davis and others as an explanation of types 2 and 3 homing. So was use of information on routes traveled gathered in transit by bats before release. Davis regarded echolocation as important in Type 1 homing, but not in Types 2 and 3.

Statistical analysis of homing performances of blinded bats *versus* normal controls (Mueller, 1963; Williams *et al.*, 1966, 1967; Davis and Barbour, 1966, 1969; Stones and Branik, 1969) revealed no significant difference in percent returns of blinded and non-blinded bats. However, blinded bats returned more slowly and oriented themselves at the release site at a slower rate than did non-blinded ones. Release site orientation usually involves circular flight followed by a direct departure, or random movements over the release area. The latter was displayed most often by the blinded bats. Stones and Branik (1969) reported that deafened bats flew when released, but none homed, compared to about 30% homing for controls and blinded bats. R. Davis (pers. comm.) reported that most of the bats he deafened refused to fly.

Wilson and Findley (1972) suggested that homing might result from a random process, and chose a non-migratory bat, *Myotis nigricans,* to study. A model (hereinafter called the W-F model) was proposed, based upon the assumption that bats will fly randomly from a release point in a straight line until familiar territory is reached.

Figure 1 shows how expected returns may be calculated. Within the bat's familiar territory (circle) expected returns are 100%. As distance from the familiar territory increases, the probability of return decreases; at point R, that probability = $\frac{\theta}{360}$:. Figure 2 shows the expected and observed returns obtained by Wilson and Findley, based on a familiar area of 13 km. Table I shows a summary of Wilson and Findley data.

This study involves three phases. First, a summer colony of *E. fuscus* was investigated to determine whether the W-F model is applicable to this migratory species. *E. fuscus* was chosen because females seem to have a high locality loyality to the summer nursery (Humphrey & Cope, 1976). If the model is applicable, familiar area can be determined, and possibly hibernacula discovered, as *E. fuscus* is usually a sedentary bat and migratory movements are not of great distances. Secondly, the model was applied, where possible, to previously recorded work. A summary of other homing experiments is found in Table II. Finally, anomalies and non-random homing are discussed.



A = Capture Site

R = Release Site

= 2 (sin $^B/4$)

Probability of return = $\frac{\theta}{360}$

Figure 1. Wilson-Findley Model for Randomness in Bat Homing

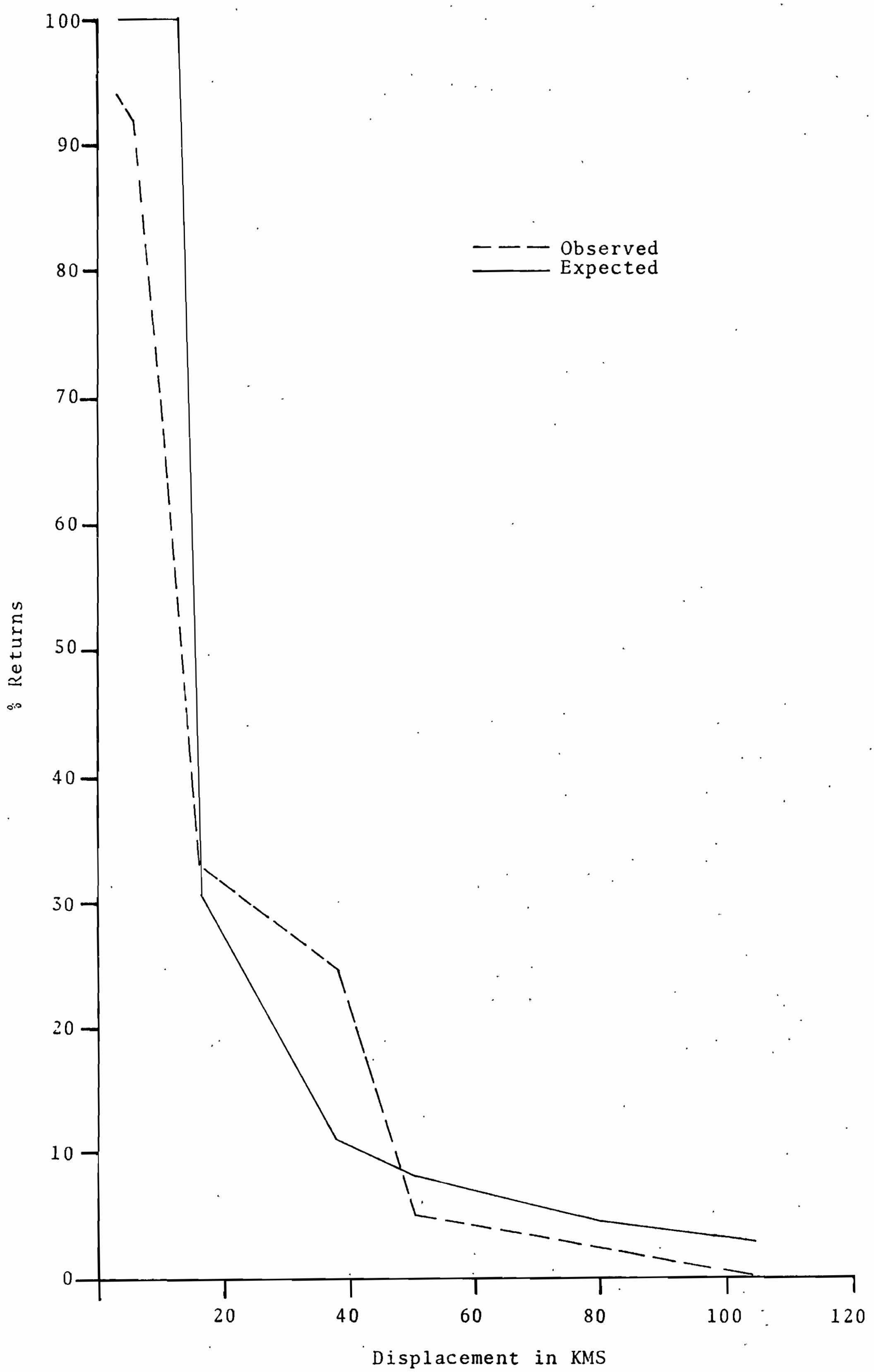


Figure 2. Expected and Observed Returns of *Myotis nigricans*.

TABLE I

ACTUAL AND EXPECTED HOMING PERFORMANCE OF *Myotis nigri*

Distance (km)	Number Released	Number Returns	Number E
3.5	17	16	17
5	12	11	12
10	17	12	17
16	12	4	3.
38	16	4	1.
50	39	2	3.
104	21	0	.

[1] Wilson & Findley (1972)

TABLE II

SUMMARY OF PUBLISHED HOMING PERFORMANCES OF BATS

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Rhinolophus hipposideros				
5.0	36	16	44	Issel (19
5.6-13.0	32	0	0	"
0.001	2	2	100	Kowalski
0.003	2	2	100	
0.007	2	2	100	
0.3	3	1	33	
0.4	1	0	0	
0.6	4	1	25	
2.2	10	4	40	
2.5	6	2	33	
3.1	3	2	67	
3.4	4	2	50	
3.7	2	0	0	
4.3	2	1	50	
5.0	2	1	50	
7.4	4	1	25	
8.1	3	0	0	
9.9	4	0	0	
10.5	3	1	33	
14.9	7	1	14	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Macrotus waterhousii				
42	31	2	6	Davis (1
Phyllostomus hastatus				
6.25	48	39	48	Williams
10	10	8	10	
12	11	5	11	
16	20	15	20	
17	10	5	5	
20	42	22	14	
21	10	3	3	
30	25	7	5	
40	25	3	4	
Myotis austroriparius				
18	80	18	23	Rice (19
31	25	2	8	"
45	100	8	8	"
108	100	0	0	"
178	79	0	0	"
Myotis capaccinii				
1.2	9	0	0	Lanza (1

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis dasycneme				
3.7	5	3	60	Punt & Ni
Myotis daubentoni				
4.4	42	2	5	Punt & Ni
Myotis grisescens				
38	225	48	22	Gunier &
75	212	59	27	
100	50	8	16	Harvey, e
100	50	2	4	
100	50	4	3	
100	50	3	6	
56	?	3	?	Tuttle (1
66	?	6	?	
68	?	7	?	
80	?	38	?	
130	?	3	?	
Myotis keenii				
8	1	1	100	Davis (19

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis lucifugus				
100	52	2	4	Cagle & C also Co
20	40	16-18	80-90	Cope, Koo (1961
4	46	?	?	Cope, Mum
10	179	?	?	
66	59	?	?	
77	229	?	?	
82	66	?	?	
93	133	?	?	
107	181	?	?	
120	118	?	?	
12	113	5	4	Davis & H
12	12	0	0	
17	102	5	5	
17	26	0	0	
51	64	0	0	
5	8	4	50	Gifford &
10	158	55	35	
15	331	43	13	
17.5	10	0	0	
20	10	5	50	
30	122	23	19	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis lucifugus (Continued)				
50	135	6	4	Gifford &
36	5	1	20	Griffin (
3	10	3	30	Griffin (
10	140	17	12	
12	73	6	8	
20	10	2	20	
24	5	1	20	
33	2	1	50	
36	24	6	25	
66	49	2	4	
156	82	7	8	
61	19	2	11	Hitchcock
3.2	93	37	40	Hitchcock
68	223	83	37	
70	55	1	2	
76	114	52	46	
180	78	2	3	
1.3	?	1	?	Mohr (193
2.8	?	1	?	
12.5	?	3	?	
17.5	?	4	?	
30	?	3	?	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis lucifugus (Continued)				
12	200+	(all but 1)	100	Mohr (194
25	162	0	0	Mohr (19
55	70	29	41	Mohr (195
250	?	2	?	Reported
.3	60	54	90	Mueller (
5	527	295	56	
10	151	66	44	
15	786	377	48	
20	128	49	38	
25	702	217	31	
30	91	34	37	
40	70	15	21	
50	66	9	13	
60	72	7	10	
5	109	60	55	Mueller &
10	58	30	52	
15	57	16	28	
20	60	10	17	
30	50	18	36	
40	50	11	22	
50	50	9	18	
60	50	8	16	
10	20	4	20	Poole (19

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis lucifugus (Continued)				
18	10	0	0	Poole (19
270	34	2	6	Schramm (
228	77	20	25	Smith & H
32	11	4	36	Stones &
Myotis myotis				
114.9	27	0	0	Bels (195
10	1	1	100	Casteret
124	17	1	6	
26	40	9	23	Eisentrau
95	22	1	5	
27.9	?	?	?	Eisentrau
13	74	12	16	Issel (19
?	?	1	?	Krzanowsk
1.2	6	1	17	Lanza (19
5.6	3	1	33	
11.2	4	1	25	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis mystacinus				
13	11	2	18	Issel as
3.7	10	1	10	Punt & Ni
Myotis nattereri				
3.7	?	1	?	Punt & Ni
Myotis nigricans				
6.2	17	12	70	Wilson (1
2.2	17	16	94	Wilson &
3.1	12	11	92	
10	12	4	33	
23.8	16	4	25	
31.2	39	2	5	
65	21	0	0	
Myotis oxygnathus				
82	15	1	7	Dulic (19
1.2	14	6	43	Lanza (19
5.6	6	3	50	
11.2	6	1	17	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis sodalis				
5	40	23	58	Davis & B
15	40	21	53	
25	50	31	62	
40	100	51	51	
20	35	10	29	Griffin (
150	44	2	5	
12	25	17	68	Hassell (
24	25	16	64	
36	25	14	56	
48	25	9	36	
60	51	16	34	
72	49	8	16	
84	50	9	18	
96	75	9	12	
108	77	6	8	
120	98	5	5	
132	100	6	6	
144	100	4	4	
200	1472	555	38	Hassel &
20	100	18	18	Mueller (

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Myotis thysanodes				
20	10	2	20	Davis (1
20	14	1	7	
21	15	1	7	
28	110	35	29	
Myotis velifer				
28	68	6	9	Cockrum
5 30	119	4	3	Hayward
38	72	3	4	
40	1	1	100	
7	52	1	2	Twente (
26	28	3	11	
Lasionycteris noctivagans				
107	3	1	33	Davis &
Pipistrellus pipistrellus				
.5	3	3	100	Gyles (1
1.2	10	6	60	Ryberg (
6.8	303	7	2	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Nyctalus noctula				
1.9	30	7	23	Bels (195
3.1	28	7	25	
24.8	29	16	55	
28.6	30	4	13	
71.4	30	6	20	
77.6	29	10	35	
86.9	30	2	7	
103.1	30	0	0	
104.3	28	3	11	
114.9	60	2	3	
6.2	?	?	?	Ryberg (1
13	?	?	?	
23.6	?	0	0	
27.9	?	?	?	
147.2	10	1	10	
Eptesicus fuscus				
20	20	14-18	70-90	Cope, Koo (196
40	47	15-19	32-40	
100	11	8-11	73-100	
250	36	31	85	
250	18	1	6	
35	25	20	80	Davis (19
55	12	11	92	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Eptesicus fuscus (Continued)				
102	5	4	80	Davis (19
105	61	15	25	
120	9	4	44	
328	22	1	5	
500	78	0	0	
15	32	9	28	Gifford &
54	13	0	0	
19	6	5	83	Griffin (
95	9	2	22	Hall & Da
20	5	2	40	Howell &
5	5	3	60	Phillips
15	11	3	27	
20	12	5	42	
40	23	7	30	
45	7	1	14	
10	98	10	10	Reynolds
340	18	2	11	Smith & G
450	155	7	5	
60	8	2	25	Tibbetts

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Eptesicus serotinus				
6.8	38	8	21	Havekost
22.4	?	2	?	
Nycticeius humeralis				
96	145	26	18	Cope & Hu
38	38	3	8	
56	26	?	?	
96	27	7	26	
Barbastella barbastellus				
3.7	?	1	?	Punt & Ni
Plecotus auritus				
37.3	9	2	22	Ryberg (1
Plecotus townsendii				
28	54	4	7	Cockrum (
23	37	0	0	Davis (19
24	1	1	100	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Miniopterus schreibersii				
10	138	42	30	Casteret
124	1	0	0	
12	1	0	0	Lanza (19
Antrozous pallidus				
1.4	2	2	100	Davis (19
5	5	5	100	
8	15	2	13	
8	9	0	0	
10	15	5	33	
10	8	8	100	
14	19	8	42	
14	17	8	48	
14	20	2	10	
14	10	2	20	
15	6	0	0	
19	5	4	80	
21	48	33	69	
23	9	2	22	
25	9	8	90	
30	19	8	37	
30	17	10	59	
30	18	6	33	
30	20	14	70	
30	16	8	50	
30	24	6	25	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Antrozous pallidus (Continued)				
32	112	2	2	Davis (1!
32	18	12	67	
37	11	2	18	
37	8	3	38	
42	6	2	33	
49	6	2	33	
49	2	1	50	
50	20	8	40	
50	34	2	6	
51	7	3	42	
55	27	12	44	
55	12	1	8	
56	20	9	45	
58	3	0	0	
59	6	1	17	
59	10	3	30	
62	3	0	0	
63	2	0	0	
68	12	3	25	
68	7	2	29	
70	5	1	20	
80	21	0	0	
92	20	0	0	
102	14	0	0	
108	26	1	4	
328	6	0	0	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Tadarida brasiliensis				
5	216	48	22	Davis (19
5	64	27	42	
10	60	25	42	
19	59	17	29	
21	8	1	13	
30	29	6	21	
30	21	5	24	
30	28	3	11	
30	26	1	4	
37	40	1	3	
38	91	27	30	
42	59	18	31	
49	3	0	0	
51	2	0	0	
55	14	1	7	
55	2	0	0	
55	38	0	0	
55	341	23	7	
56	7	5	71	
59	61	17	28	
65	89	23	26	
76	3	1	33	
108	25	5	20	
108	94	22	23	
195	69	22	32	
328	16	2	13	

TABLE II (Continued)

Distance (Miles)	Number Released	Number Returned	Percent Returns	
Tadarida brasiliensis (Continued)				
85	19	9	47	LaVal (1
60	6	1	17	Tibbetts

@Includes some blinded bats.

Some general information on the *E. fuscus* colony is presented (Appendix A and B).

MATERIALS AND METHODS

Study Site

The *Eptesicus fuscus* colony studied was situated at Camp Namanu, 7.0 mi North of Sandy, Multnomah County, Oregon, at an elevation of 350 m. Dominant vegetation is second growth Douglas fir, averaging about 12 m in height. Two rivers converge within 1000 m of the camp. Two day-night roost sites were used by *E. fuscus*. Since there appeared to be an exchange of individuals between them, both were considered as a single nursery. Roosts were a 5-8 X 100 X 120 cm south-facing crack between an external chimney and the exterior wall of one building, and an adjacent dwelling's attic from which the only apparent exit was under a south-facing covered porch approximately 10 m from from the chimney roost (Figure 3a).

Capture Techniques

A 2 X 8 m nylon mist net and a double-frame bat trap (Tuttle, 1974) arranged randomly along two of the three open sides of the porch were used to capture bats. The mist net was mounted on two 3/4" x 96" aluminum poles set in the ground. The only major modification to the bat trap was the use of 1/2 lb. test monofilament nylon fishing leader in place of the recommended wire. Netting times

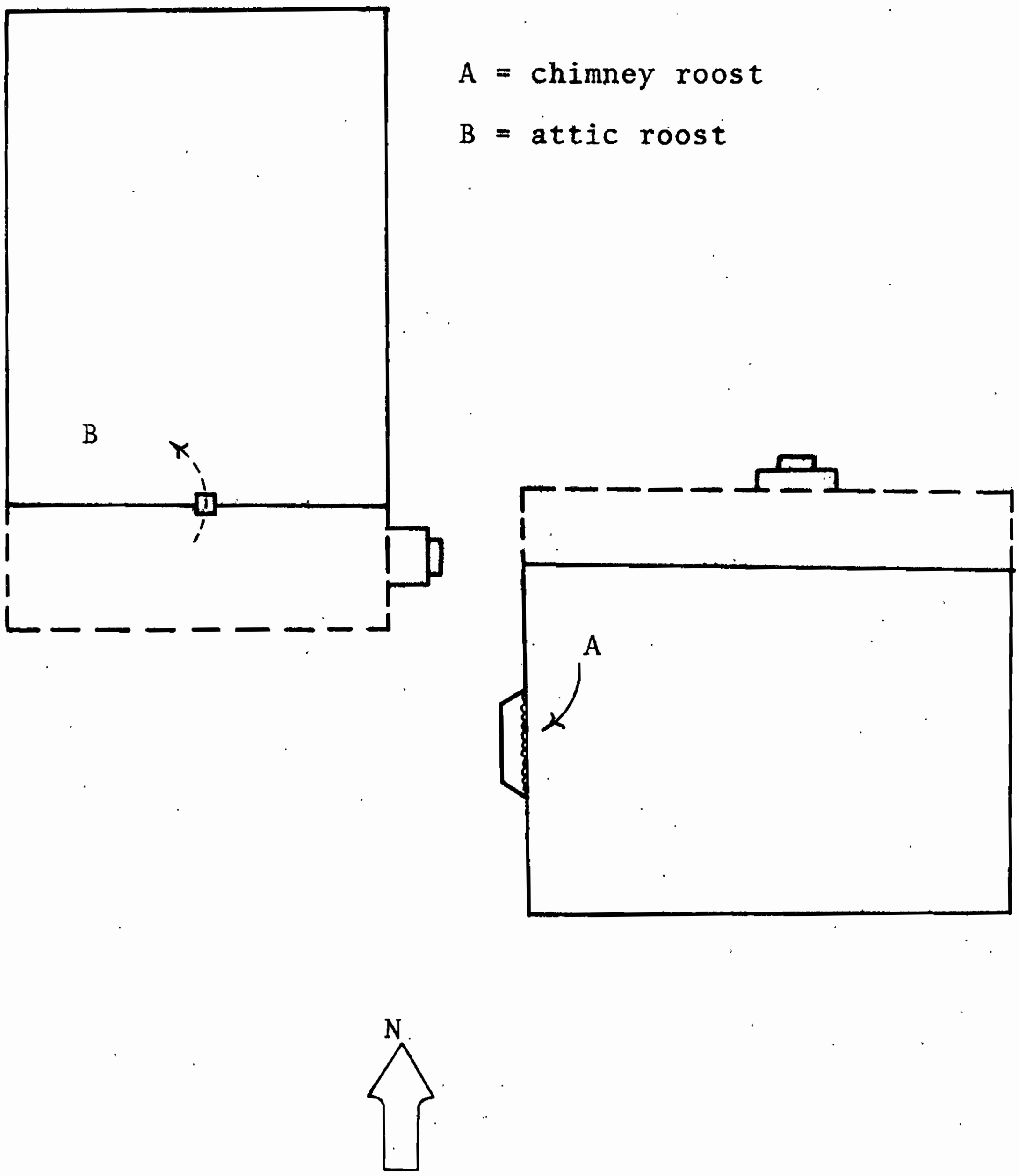


Figure 3a. Roosts used by *E. fuscus* in this study.

extended from 30 min before civil sunset until the bats were no longer observed to be flying and found at the night roosts, nursing young or grooming. Captured bats were placed in canvas bags until being marked and released.

Because excessive netting and handling places undue stress upon bats (Stebbings, 1966), collection was terminated when females appeared close to parturition, and was resumed approximately 16 days after most births occurred. Trap days were also limited to a maximum of two per week until the last week of the study when an extra trap night was used, attempting to collect all individuals in the colony.

Marking And Observations

Three methods of marking were employed. Night observations were made possible by attaching gelatinous capsules with glue dorsally to the cervical area and injecting the capsule with Cyalume$_R$ Chemical Light (Buchler, 1976). Temporary marking was done by punchmarking the right chiropatagium (Bonaccorso and Smythe, 1972) and dying the holes with a white liquid dye, normally used for ear branding cattle. Plastic wing bands (Bonaccorso, *et al.*, 1976) were applied to right forearms for a more permanent record of selected individuals.

Two observers, using 7 x 40 binoculars, observed flying bats at the nursery and upon release in the homing experiments. When possible, released bats were also observed as long as possible by using a hand-held Bushnell 40X spotting scope.

Transportation And Release

Only adults were used in homing experiments. Ten bats per release site were transported via auto to points that approximated as closely as possible the four compass directions. Releases of single individuals and of all individuals simultaneously were used. Care was taken to be certain each bat was flying and gone from view before leaving the release site. Returns were noted by recapture at or near the nursery colony. Time of return within the period of study was not considered, only whether a return was made.

U. S. National Forest Service Maps were used to determine aerial distances from release points. Except for two occasions (the northernmost release points), releases were made the same night of capture.

Additional Activities

Forearm measurements of adults were taken with HeliosR Vernier dial calipers. Each individual was inspected for parasites and wing damage. Dates were noted for parturition and first capture of young. A Schnabel population index was used to estimate changes in populations of the colony itself, and in numbers of females, males, and of juveniles as a group and by sex (Giles, 1971). <u>Cyalume$_R$</u> was used for determining individuals in the nursery after the young were weaned.

<u>Application Of W-F Model To Data From Published Studies</u>

The W-F model was applied to published studies that presented sufficient data for its use. X^2 values are calculated, ($P \geq 0.010$), and reported in the tables.

RESULTS - EXPERIMENTAL STUDIES

The study colony exhibited two "familiar areas" of approximately equal sizes, and homing consistent with these areas. Figure 3b shows the areas and approximate distances of possible migration. Table IIIa contains the homing results. The diameter of both areas is approximately 20 mi, well within the expected range previously recorded for known movements of this species.

Rhinolophus hippsideros

Strelkov (1969) and Roer (1972) reported that this species is relatively sedentary. Issel (1950) recorded migratory movements with a mean of 1.2 mi. This mean was used in Kowalski and Wotjusiak's (1952) homing tests. Results of my X^2 tests are shown in Table IIIb, and Figure 4, and suggest that returns are probably random. Issel's (1950) results could not be used in this test because specific returns from specific distances were not available.

Macrotus waterhousii

Only one homing test is reported, not enough for the X^2 evaluation (0 degrees of freedom). Barbour and Davis (1969) report *M. waterhousii* as sedentary, moving only about 5-10 mi. If 5 mi is used as a radius, then the expected return for the one test would be 1 of 31, very

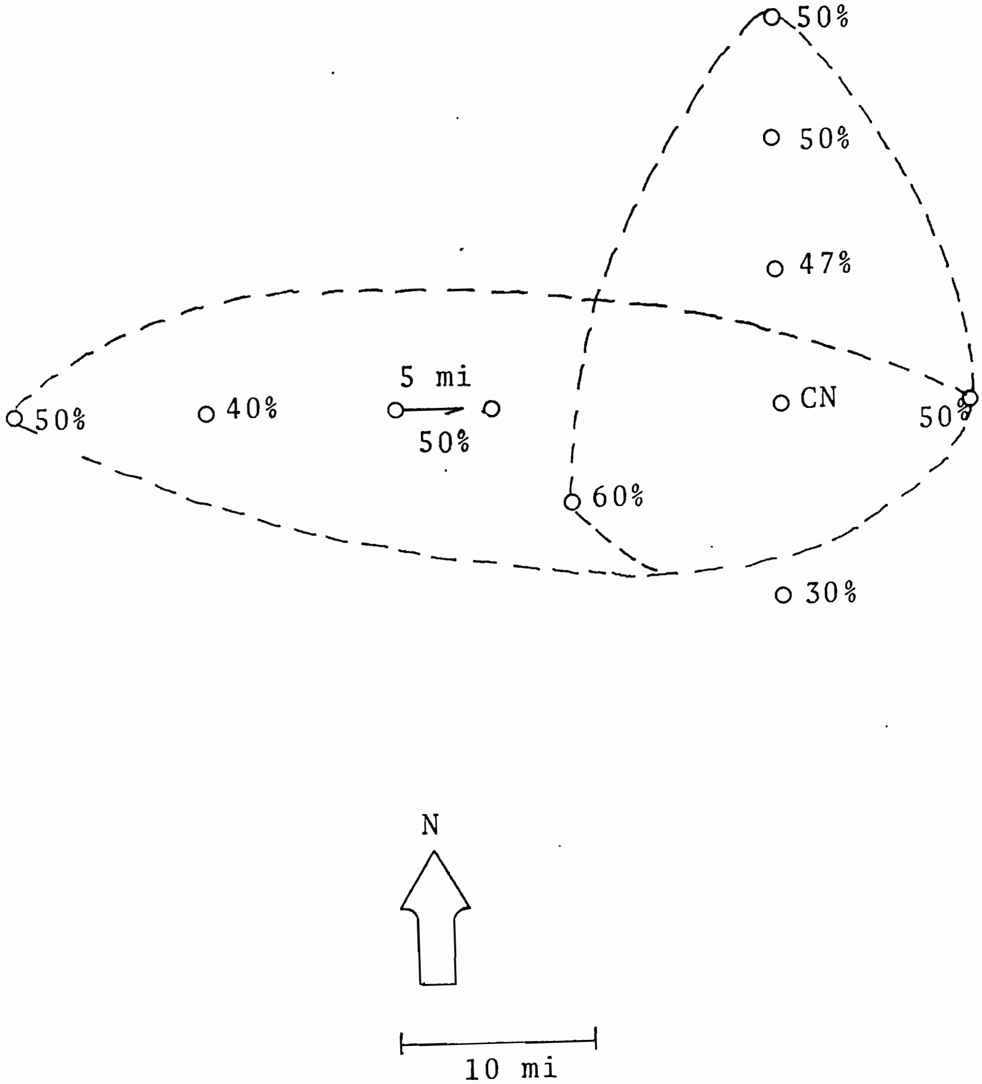


Figure 3b. Indicated familiar area by homing returns of Camp Namanu bats.

TABLE IIIa

RETURNS OF CAMP NAMANU BATS WITH NUMBERS OF RELEASES AND RETURNS FROM EA
IN RELATION TO DISTANCE AND DIRECTION. X^2 VALUES FOR ACTUAL ANI
EXPECTED RETURNS ARE CALCULATED

Total Released	Released from Attic	Released from Chimney	Direction & Distance	Total Returns	Returns from Attic	Returns from Chimney
10	6	4	10 mi S.	5	3	2
10	5	5	10 mi E.	3	1	2
10	7	3	10 mi W.	6	5	1
10	6	4	7 mi N.	4	1	3
10	7	3	15 mi W.	5	4	1
10	6	4	15 mi N.	5	4	4
13	6	7	20 mi W.	6	4	2
16	12	4	25 mi W.	6	4	2
10	3	7	20 mi N.	5	1	4
						TOTAL

TABLE IIIb

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Rhinolophus hippside*

Distance (Miles)	Number Released	Number Returns	Number Expected
.001	2	2	2
.003	2	2	2
.007	2	2	2
.3	3	1	3
.4	1	0	1
.6	4	1	4
2.2	10	4	2
2.5	6	2	1
3.1	3	2	1
3.4	4	2	1
3.7	2	0	0
4.3	2	1	0
5.6	2	1	0
7.4	4	1	0
8.1	3	0	0
9.9	4	0	0
10.5	3	1	0
14.9	7	1	0

[1] Kowalski & Wotjusiak, 1952

TOT

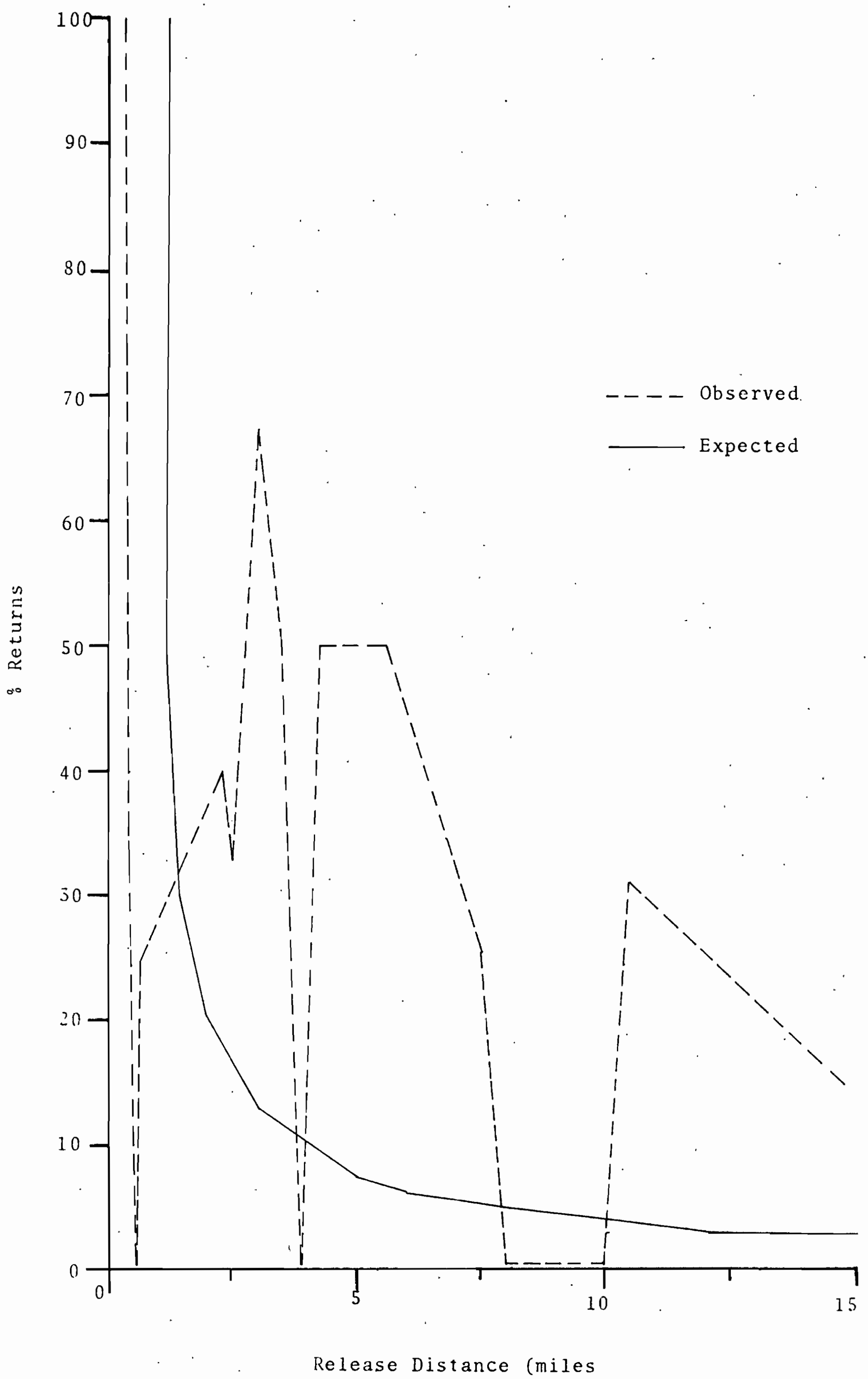


Figure 4. Expected and Observed Returns of *R. hippsideros*

close to that of 2 returns of 31 released (Davis, 1966).

Phyllostomus hastatus

Experimental data indicate that the edge of familiar territory is approximately 17 mi (Williams, *et al.*, 1966, 1967). Table IV and Figure 5 show the homing results and demonstrate that returns from beyond 17 mi were probably random. Because exact release numbers (5-22 individuals) were not reported, the percent recovery was used to calculate the closest number between 5 and 22 and the resulting number assumed as the number released; *e.g.*, 36% recoveries x 11 = 3.96 or 4, the closest to an integer of 36% of any number from 5 to 22.

Myotis austroriparius

Rice (1957) recorded both migratory movements and homing experiments. The mean of migratory movements was about 10 mi homing randomness was calculated from this mean. Table V and Figure 6 show results indicating randomness.

Myotis capaccinii, M. dasycneme, M. daubentoni, M. keeni, And *M. nattereri*

One homing experiment per species did not yield sufficient data for this analysis. Migratory movements of these bats are not well understood. *M. nattereri* moves frequently from one nest site to another during the summer, further

TABLE IV

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Phyllostonus*

Distance (Miles)	Number Released*	Number Returns	Number Ex
6.25	48	39	48
10	10	8	10
12	11	5	11
16	20	15	20
17	10	5	5
20	42	22	14
21	10	3	3
30	25	7	5
40	25	3	4

*The above figures are as close as can be determined from the literat
figures as to actual numbers were given.

[1] Williams, *et al.*, 1966, 1967.

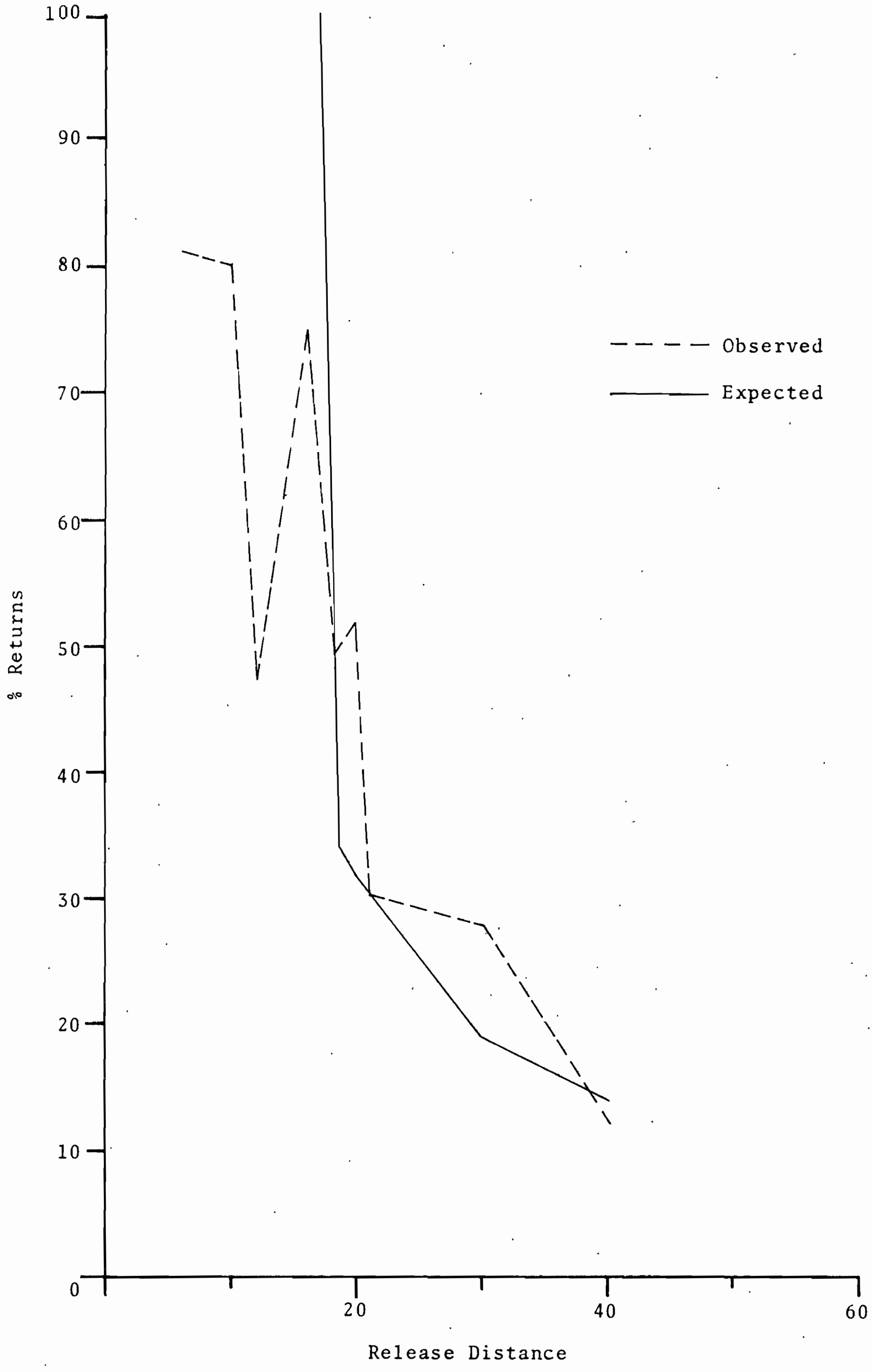


Figure 5. Expected and Observed Returns of *P. hastatus*.

TABLE V

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis austr*

Distance (Miles)	Number Released	Observed Returns	Expecte
18	80	18	18
31	25	2	3
45	100	8	6
108	100	0	3
178	79	0	2

[1] Rice, 1957

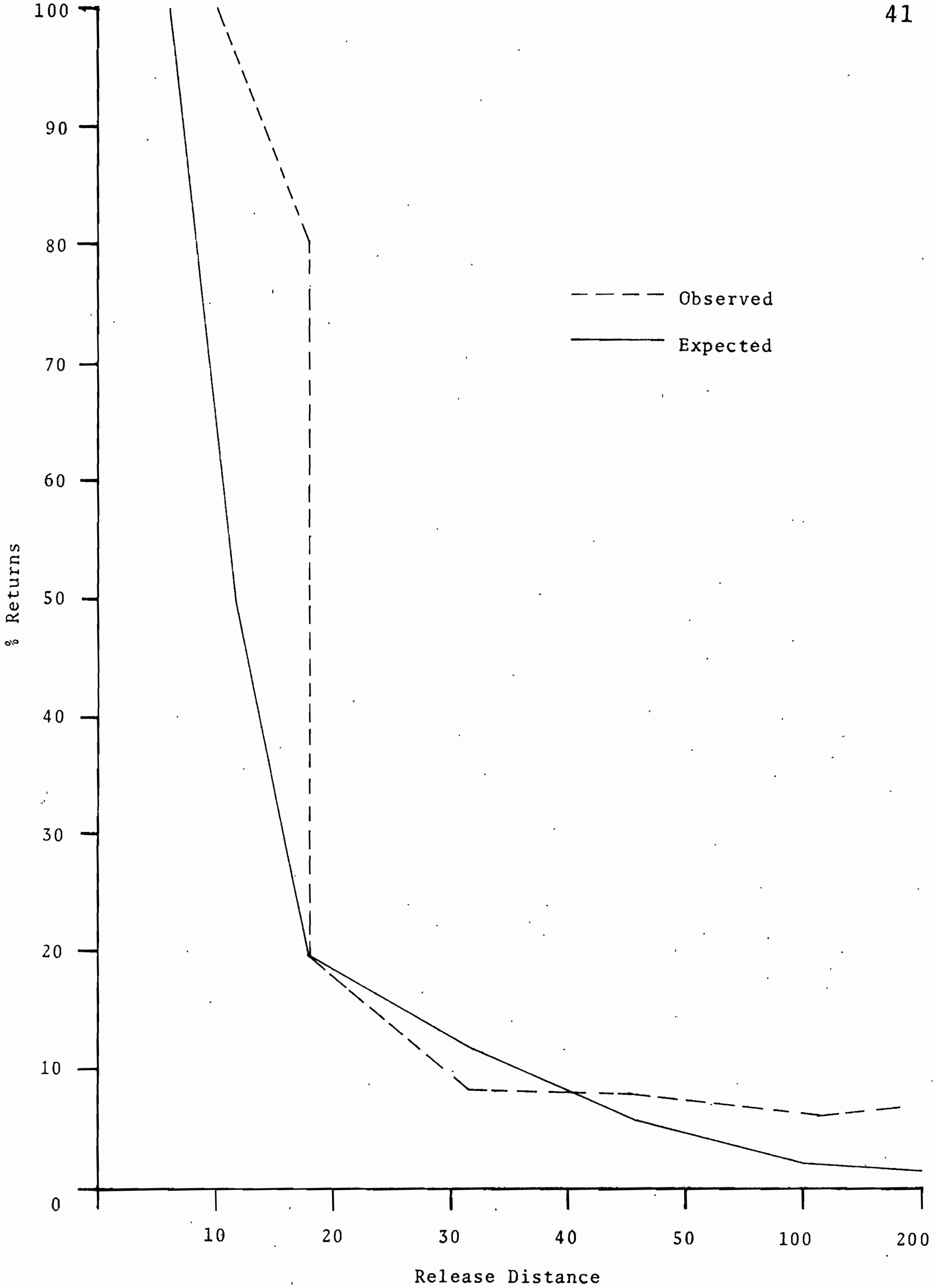


Figure 6. Expected and Observed Returns of *Myotis Austroriparius*

complicating the issue of an adequate test for this species (Lauffens, 1973).

Myotis grisescens

Tuttle (1961) did not report numbers released, so his data cannot be used here. Harvey, *et al.*, (1976) reported migratory movements of about 32 mi this figure was used as the radius of familiar area. Results (Table VI) indicate randomness. Gunier and Elder (1971) show possible movements of about 25 mi in an East-West direction and possible southward movements of about 45 mi. The 38 mi release point was North of the colony; a radius of 25 mi was used for those results. The Southwest release of 75 mi indicated use of the 45 mi distance as a radius. (Migratory movements indicate an ellipse as opposed to a circle.) Table VII also indicates randomness in *M. grisescens*.

Myotis lucifugus

Data from Mueller (1963) shows returns are not random. Data indicate an ellipse of 5 mi North-South of the colony, 5 mi West, and 15 mi East as a familiar area. Returns from 30 and 40 mi are the ones which give values not indicative of randomness. Davis and Hitchcock (1965) give known migratory range for two of the homing studies as approximately 25 mi. Only adults are considered in Table VIII. Juveniles were only volant for about one week; their strength and experience were assumed to be minimal. The known data again

TABLE VI

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis gris*

Distance (Miles)	Number Releases	Number Returns	Number Ex
100	50	8	5
100	50	2	5
100	50	4	5
100	50	3	5

[1] Harvey, *et al.*, 1976.

TABLE VII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis gri*

Distance (Miles)	Number Releases	Number Returns	Number E
38	225	48	5
75	212	59	4

[1] Gunier and Elder, 1971.

TABLE VIII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis luc*

Distance (Miles)	Number Releases	Number Returns	Number E
12	54	6	9
17	42	5	5

[1]Hitchcock and Davis, 1965.

supports the randomness hypothesis.

Hitchcock and Reynolds (1942) lack data on bat migratory movements and good recovery techniques (due to materials and chosen roost sites), making homing results uncertain. It was noted that the known colonies are on the Thames River drainage, and at distant releases near the river one might expect adults to attempt to follow it, suggesting a 50% probability of return. Using this premise, Table IX indicates homing was random at distant releases in Ontario. Hitchcock and Reynold's (1942) New England experiment lacks sufficient data on migratory movements and homing to indicate a familiar area.

Mueller and Emlen (1957) report homing on bats from the same location as Mueller (1963). Using the same ellipse as for Mueller's (1963) work, the returns are random if those from a distance of 5 mi (expected 100%) are neglected due to disturbance of bats and release too close to the colony (Table X, Figure 7).

The reports of Hitchcock (1943), Cagle and Cockrum (1943), Smith and Hale (1953), Griffin (1936, 1940b), Schramm (1967), Cope, Mumford, and Wilson (1958), Mohr (1934, 1942, 1953), Cope, Koontz, and Churchwell (1961), and Stones and Branik (1969) all lack sufficient data for this analysis.

TABLE IX

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis luc*

Distance (Miles)	Number Releases	Number Returns	Number E
76	88	47	4
68	66	30	3
68	82	37	4

[1] Hitchcock & Reynolds, 1942.

TABLE X

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis luc*

Distance (Miles)	Number Releases	Number Returns	Number E
10	58	30	2
15	57	16	1
20	60	10	1
30	50	18	1
40	50	11	
50	50	9	
60	50	8	

[1] Mueller and Emlen, 1957.

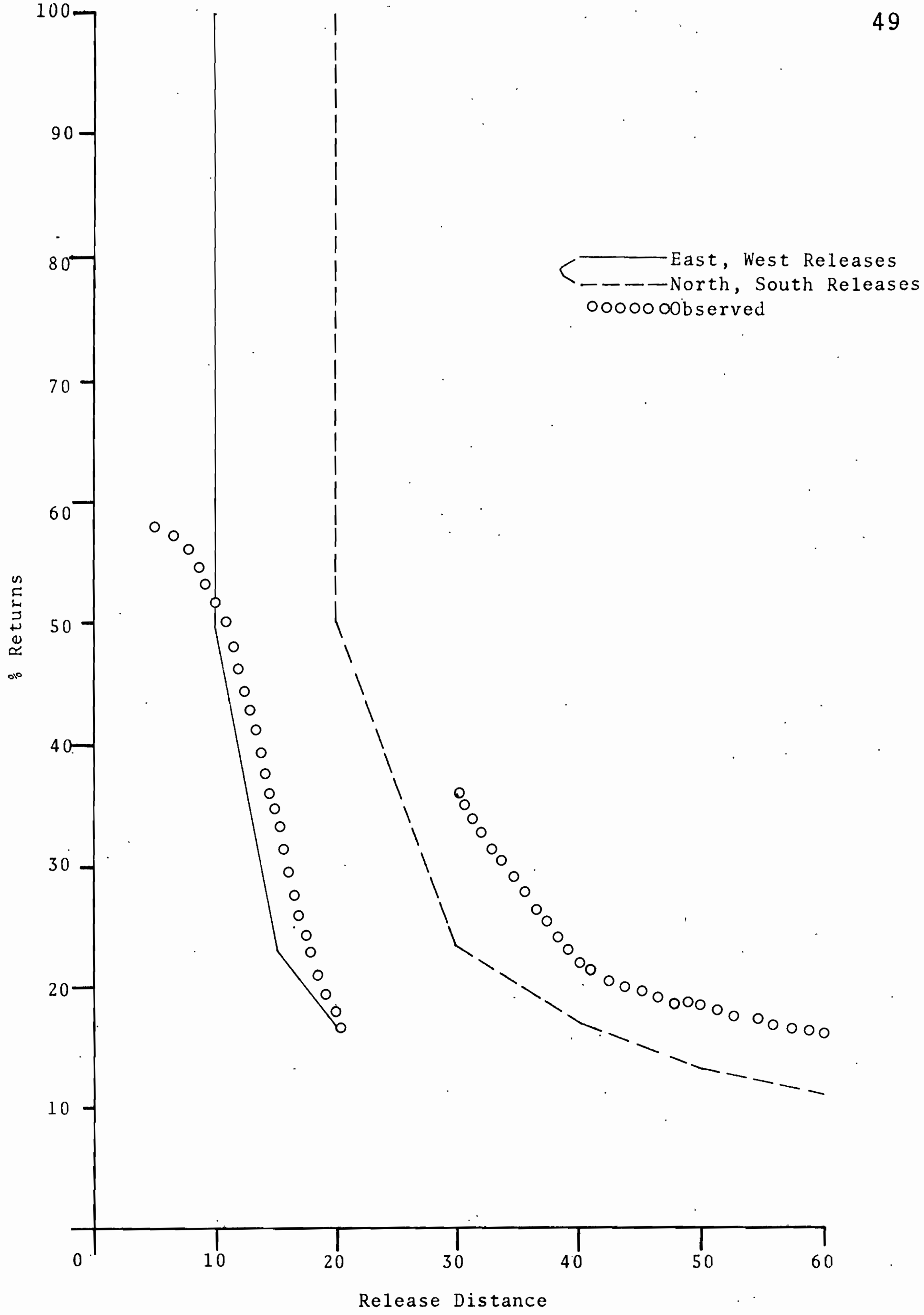


Figure 7. Expected and Observed Returns of *Myotis lucifugus*

Myotis myotis

All reports on homing in this species were applicable except for those of Krzanowski (1960). Results are based on a 5 km (3.1 mi) radius of familiar territory and movement (Strelkov, 1969, Heerdt and Sluiter, 1960, 1961). Table XI and Figure 8 suggest that homing in *M. myotis* is probably random.

Myotis mystacinus

Only 2 homing experiments are available (Punt and Nieuwenhoven, 1957, and Roer, 1960); the familiar area is again considered to be 5 km [3.1 mi (Strelkov, 1969)]. Results (Table XII) suggest randomness in homing for this species.

Myotis oxygnathus

Strelkov (1969) reports this species has a migratory behavior similar to *M. myotis*. The 2 homing experiments (Lanza, 1958, and Dulic, 1957) indicate this is probably true, Table XIII and Figure 9 show that homing results indicate randomness and a familiar territory of about 5 km.

Myotis sodalis

Hassell (1963) reports migratory movements of about 30-36 mi among bats which he used in the homing experiment (other *M. sodalis* migrate up to 200 mi North from this hibernacula). Using 36 mi as a radius of familiar territory

TABLE XI

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis m*

Distance (Miles)	Number Releases	Number Returns	Number E
1.2	6	1	6
5.6	3	1	1
10 11.2	5	2	1
13	74	12	9
26	40	9	6
95	22	1	1
115	27	0	0
124	17	1	0

[1] Eisentraut, 1936; Casteret, 1938; Issel, 1950; Bels, 1952; Lanza, 1

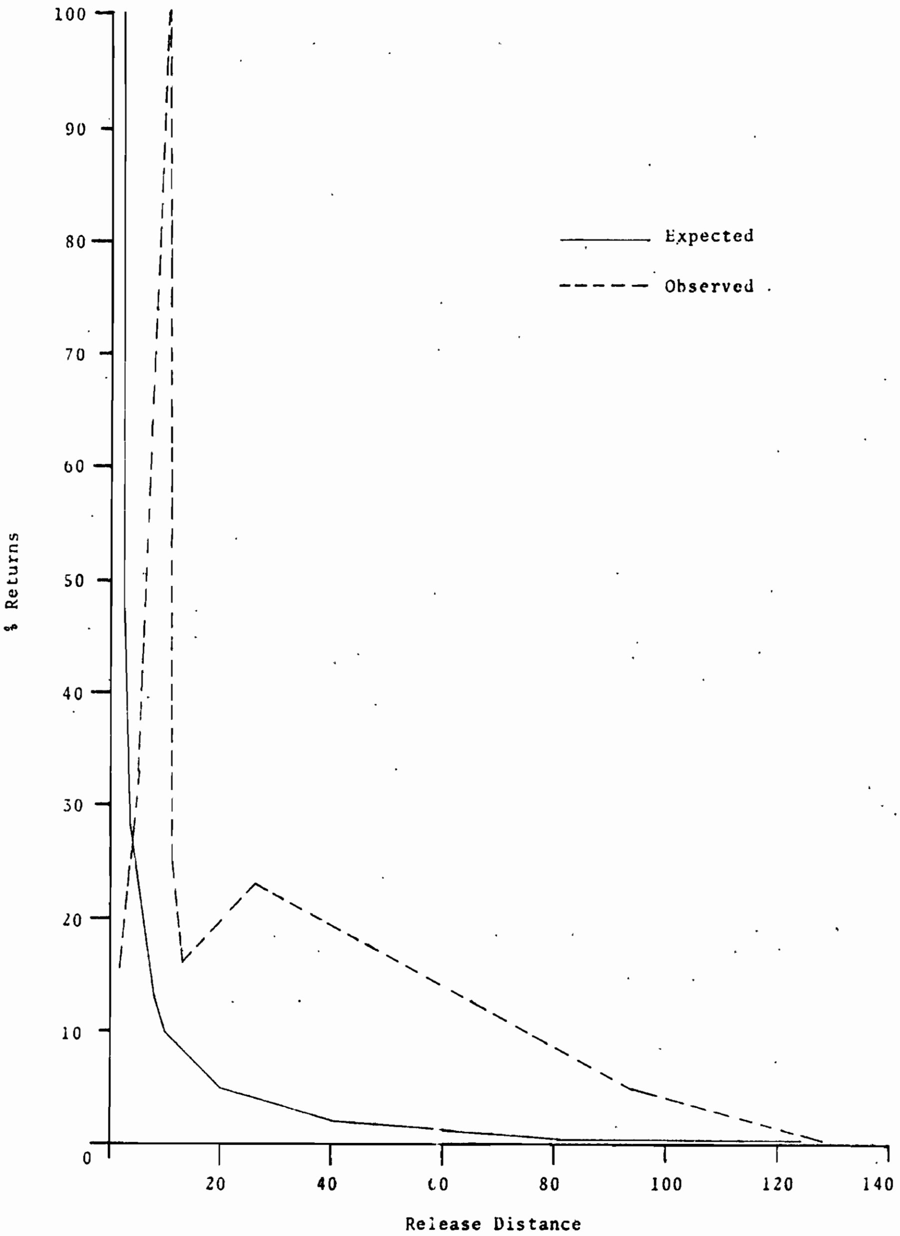


Figure 8. Expected and Observed Returns of *Myotis myotis*

TABLE XII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis mys*

Distance (Miles)	Number Released	Number Returns	Number E
3.7	10	1	1
13	11	2	1

[1]Punt & Nieuwenhoven, 1957; Issel as by Roer, 1960.

TABLE XIII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis oxy*

Distance (Miles)	Number Released	Number Returns	Number E
1.2	14	6	14
5.6	6	3	3
11.2	6	1	1
82	15	1	1

[1] Lanza, 1958 and Dulic, 1957.

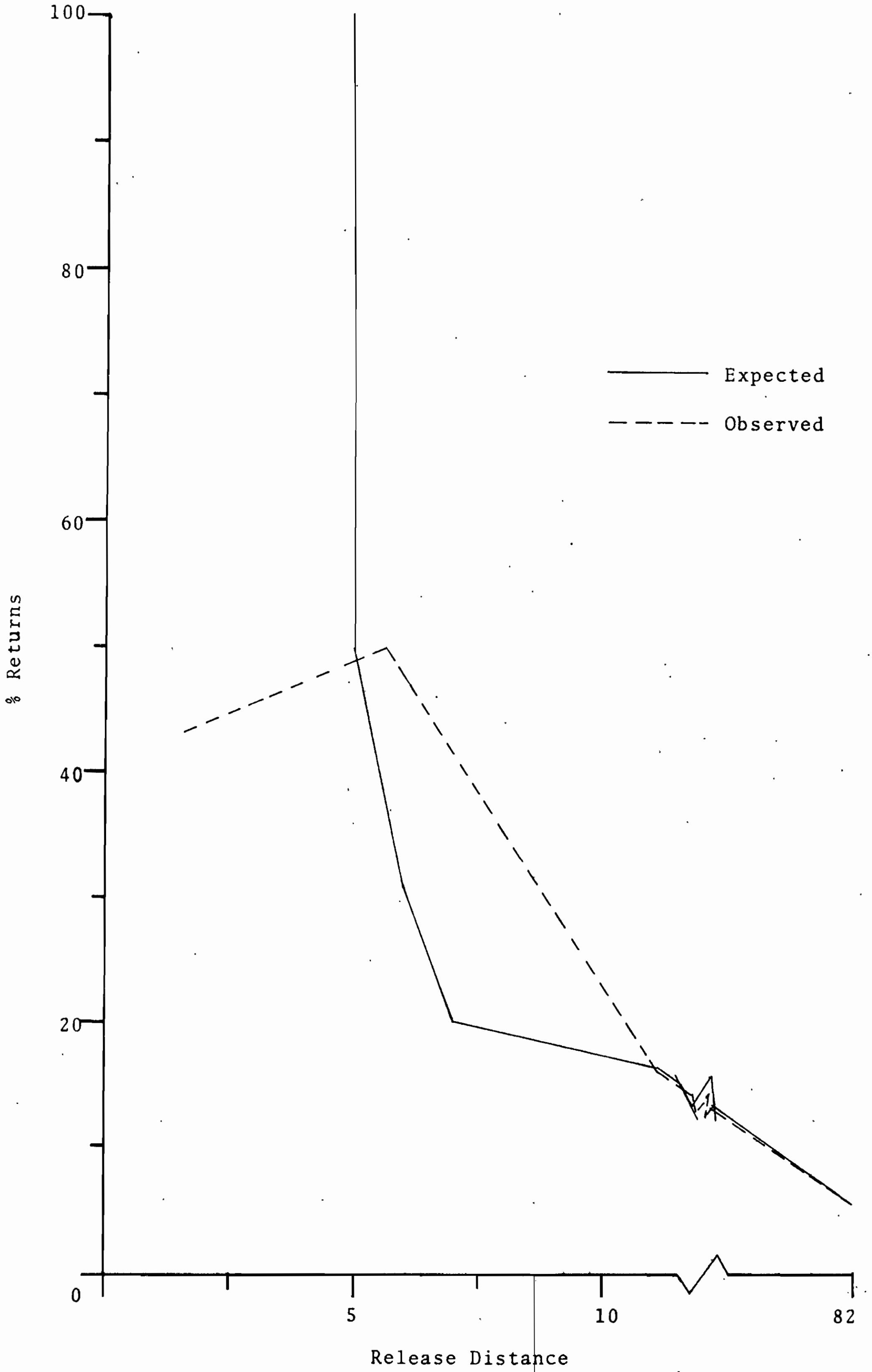


Figure 9. Expected and Observed Returns for *M. oxygnathus*

(all were released from the west) and assuming, *M. sodalis* use the Ohio drainage as possible aid to navigation (Hall, 1962), probability determination includes the possibility of flying to the river and then following the river course. This also indicates a 50% probability that the bat will fly in the correct direction when the river is reached. This technique was used for all 3 homing experiments from Bat Cave, Carter Co., Kentucky, found in Table XIV (Barbour and Davis, 1965, and Hassell and Harvey, 1965). Figure 10 contains only work by Hassell (1963), as his was the most extensive. The results indicate randomness.

Myotis thysanodes

Davis (1966) provided the only homing data on this species. Migratory studies and known movements are almost non-existent. If the model is used for Davis' results, the diameter of the familiar area of the study group is from 4 to 22 mi, with approximately 11 mi as a mean.

Myotis velifer

Only 4 experiments of Twente (1955), Cockrum (1956), and Hayward (1961) are usable for this test. Twente and Tinkle and Patterson (1965) report migrations up to 90 mi in winter, but agree with Barbour and Davis (1969) that most are permanent residents.

Assuming the ones from Hayward (1961), Twente (1955), and Cockrum (1956) are sedentary, a radius of 4-5 mi of

TABLE XIV

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis sodalis*[1]

Distance (Miles)	Number Releases	Number Returns	Number Expected
5	25	17	25
12	25	16	25
15	20	24	20
24	25	16	25
25	25	17	25
36	25	14	13
40	50	35	50
48	25	9	9
60	51	16	15
72	49	8	12
84	50	9	10
96	75	9	11
108	77	6	11
120	98	5	11
132	100	6	10
144	100	4	9
200	500	335	335
200	500	165	165
200	500	80	63
			TOTAL

[1]Hassell, 1963; Hassell and Harvey, 1965; Barbour & Davis, 1965.

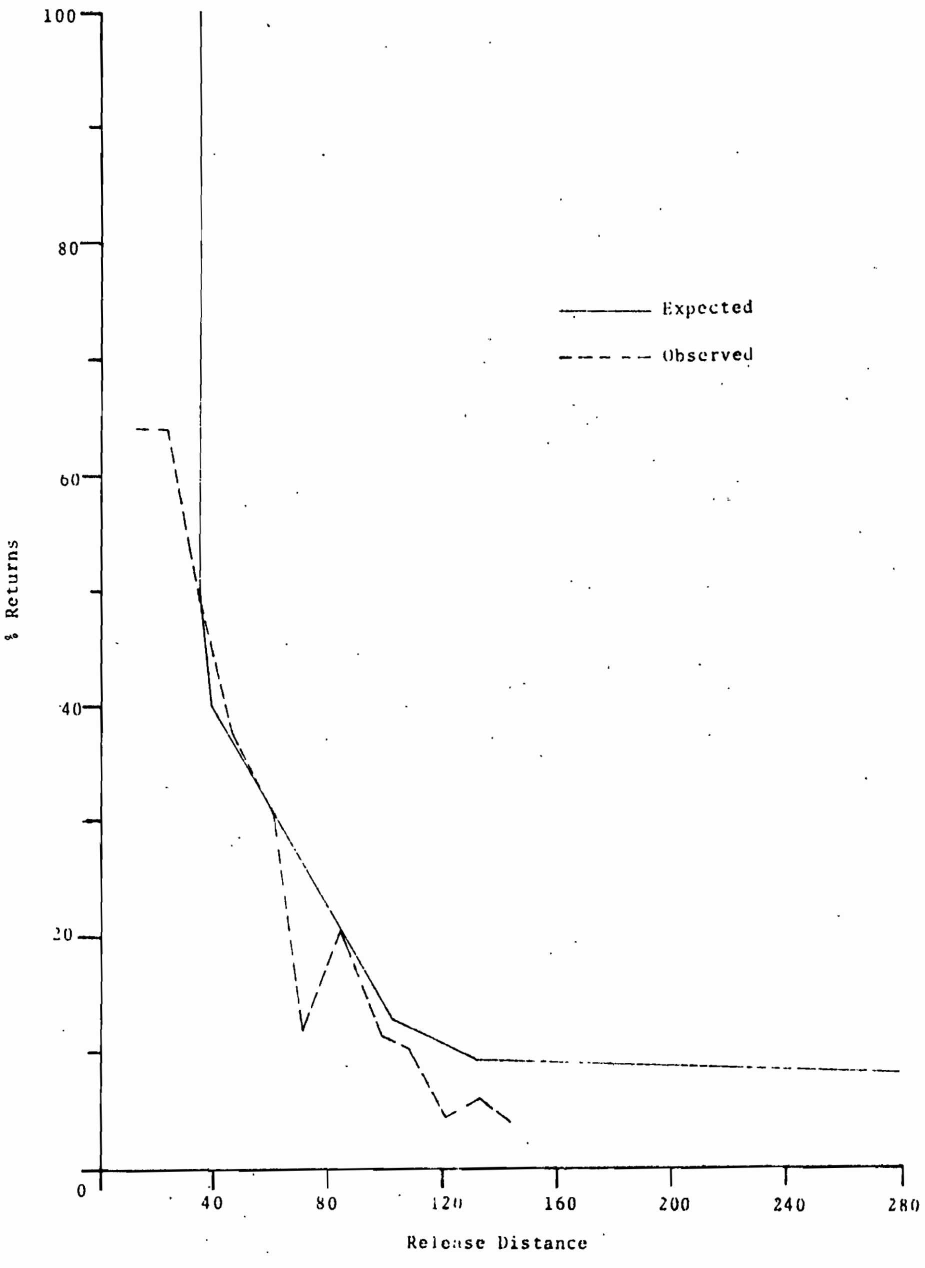


Figure 10. Expected and Observed Returns for *Myotis sodalis*

of familiar area is possible. Results in Table XV indicate no randomness in homing if 5 mi is used as a familiar area radius.

<u>*Nyctalus noctula*</u>

Ryberg's (1947) information is incomplete, but he does report that *N. noctula* is relatively sedentary and a year round resident in Sweden. Sluiter and Heerdt (1953, 1954, 1956, 1957, 1958, 1959, 1965) were cautious in reporting and interpreting the long flights (migratory?) of *N. noctula* from the Netherlands, as opposed to flights over only a very short distance (less than 5 mi). Strelkov (1960) compares the long flights from the Netherlands to those of migration in the U.S.S.R. as being approximately in the same direction and of the same distance. Behavioral notes indicate that nurseries may include a diversified group, some long migrators and other short migrators. If we assume this to be correct, returns from distances of greater than five miles should contain equal numbers of the population and those with a longer migratory range should home at approximately the 100% level until the edge of their familiar area is reached. Using this as a modification of the model, and applying it as though selection of bats for the homing tests were random, and 1/2 are from the long migrators (about 60 mi) and 1/2 from the short migrators (about 5 mi), the returns and X^2 values do not indicate randomness in

TABLE XV

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Myotis ve*

Distance (Miles)	Number Releases	Number Returns	Number E
7	52	1	10
26	28	3	1
28	68	6	3
38-40	73	3	2

[1] Twente, 1955; Cockrum, 1956; Hayward, 1961.

homing for *N. noctula*.

If assumptions are made that all of the colony is composed of either long or the short migrators, the X^2 values still indicate that the Wilson and Findley model does not fit for randomness.

Plecotus townsendii

Pearson, *et al.*, (1952) recorded migratory movements of up to 20 mi, but indicated that most were of considerably shorter distance. Strelkov (1969) indicates less than 20 km migrations for the genus *Plecotus*. A familiar area for Western *P. townsendii* appears to be about 20 mi. Table XVI displays results of Cockrum (1956) and Davis (1966) to be random for this species, if a diameter of 10 mi is assumed.

Eptesicus fuscus

Beer (1955), Griffin (1940a, b), Mumford (1958) and Phillips (1966) note migratory movements of 3.5 to 142 mi with the mean approximately 13 mi. A 26 mi diameter might be suitable for this species, since the nursery and hibernacula colonies may be composed of many subcolonies, migrating in different directions (Beer, 1955; Phillips, 1966). A radius of 13 mi was used for the experiments of Phillips (1966), Howell and Little (1924), Griffin (1940), Tibbetts (1956), Hall and Davis (1958), and Gifford and Griffin, (1960). Tables XVII, XVIII, and XIX and Figures 11, 12, and

TABLE XVI

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Plecotus to*

Distance (Miles)	Number Releases	Number Returns	Number E
23-24	38	1	5
28	54	4	6

[1]Davis, 1966 and Cockrum, 1956.

TABLE XVII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Eptesicus*

Distance (Miles)	Number Releases	Number Returns	Expecte
5	5	3	5
15	11	3	4
20	12	5	3
40	23	7	3
45	7	1	1

[1]Phillips, 1966.

TABLE XVIII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Eptesicus*

Distance (Miles)	Number Releases	Number Returns	Expecte
15	38	13	12
19	6	5	2
20	5	2	1
54	13	0	1
60	8	2	1
95	9	2	1

[1]Gifford & Griffin, 1960; Hall & Davis, 1958; Howell & Little, 1924; Tibbetts, 1960.

TABLE XIX

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Eptesicus f*

Distance (Miles)	Number Releases	Number Returns	Number Ex
20	18	18	2
40	47	19	4
100	11	11	1
250	54	32	2

[1] Cope, Koontz, & Churchwell, 1961.

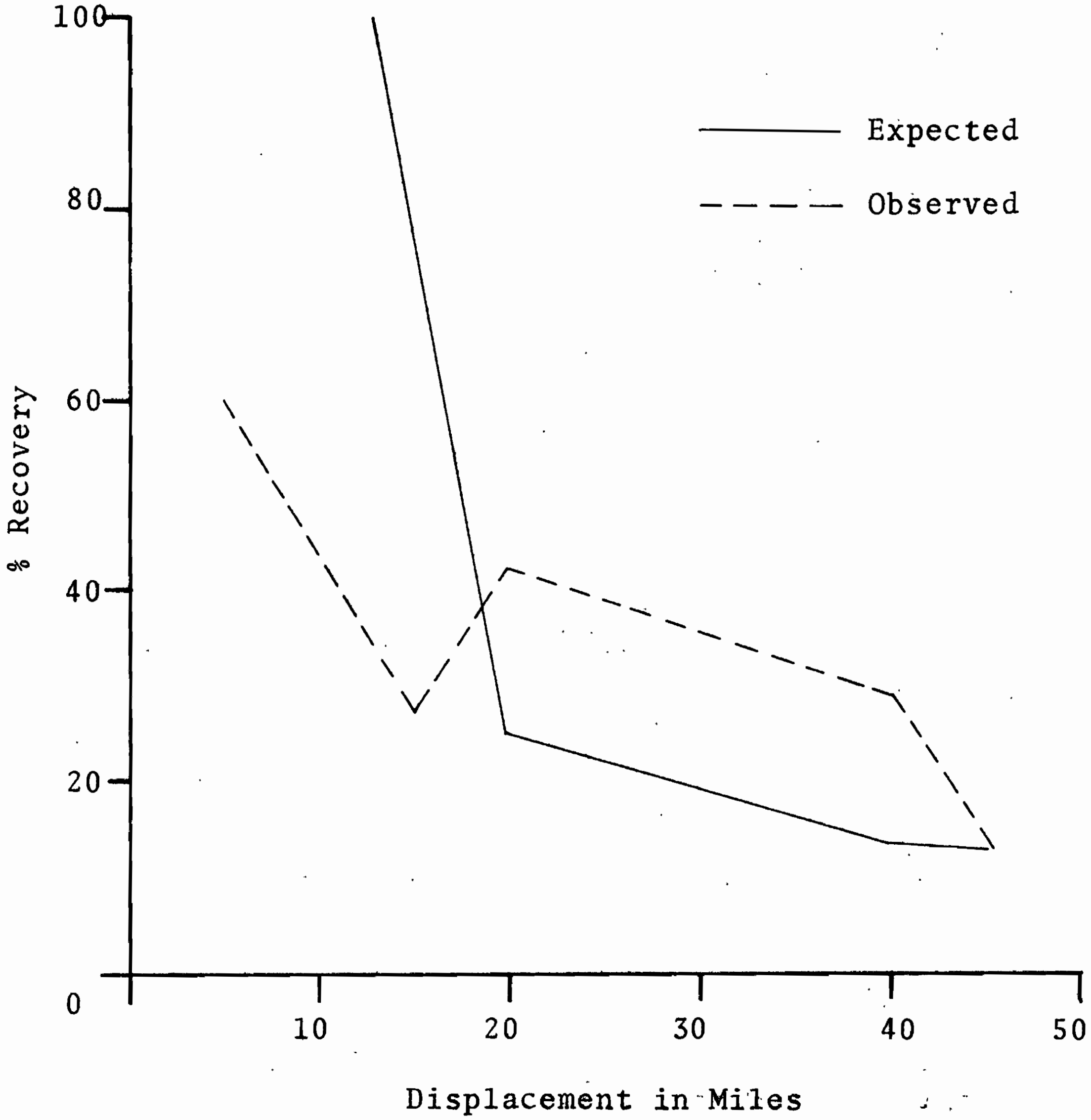


Figure 11. Expected and Observed Returns for *E. fuscus*.

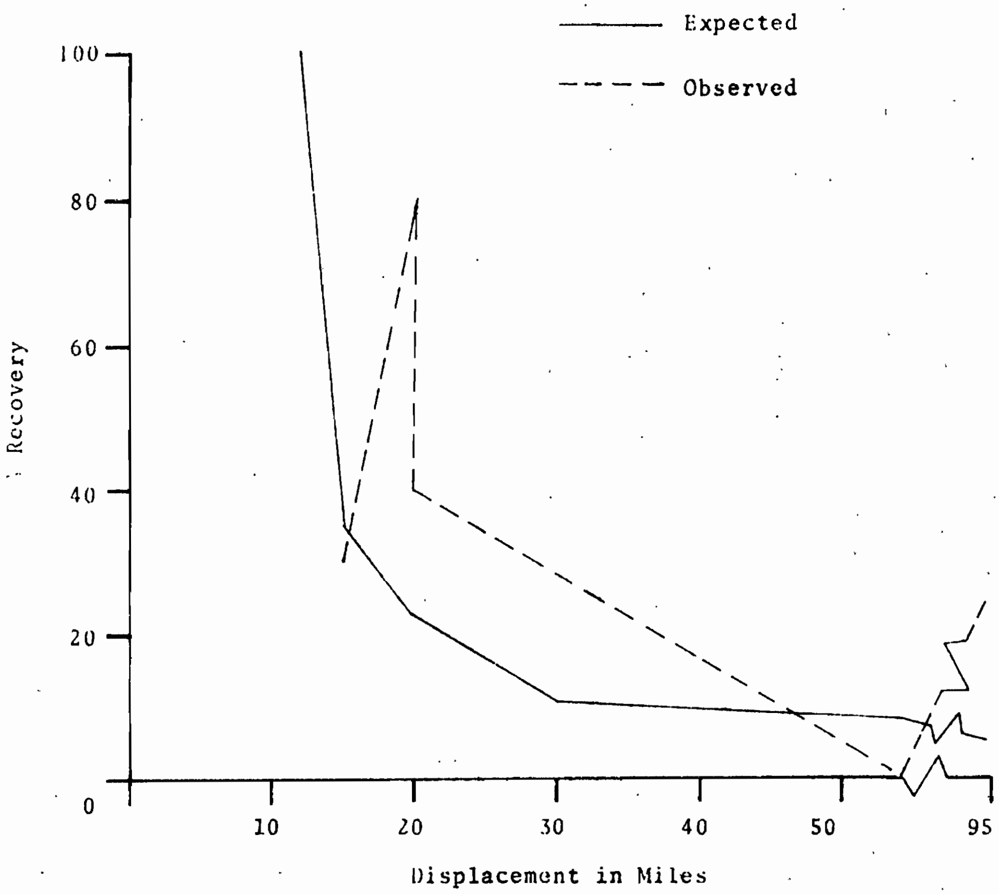


Figure 12. Expected and Observed Returns for *E. fuscus*.

and 13 indicate randomness for *E. fuscus* in these experiments.

Reynolds' (1941) experiments were not used because his search for returns was hampered by roost location and time. Cope, Koontz, and Churchwell (1961) indicate an area (from homing results) larger than the migratory maximum noted by Mumford (1958). It is interesting to note that both colonies are from the same general area in Indiana. If the 250 miles are used as the edge of the familiar area, Table XIX indicates randomness.

Davis' (1966) work suggests an area of approximately 100 mi, well within the longest known migratory movements. Using this number as the familiar area radius, Table XX and Figure 13 show the results, suggesting randomness.

Eptesicus serotinus and *Plecotus auritus*

Insufficient data again prevent application of the W-F model. Ryberg (1941) and Strelkov (1969) report *P. auritus* migratory movements of 20 km. At that distance Ryberg's result of 2 returns from 9 releases at 60 km is close to the expected 1 return.

Antrozous pallidus

Davis (1966) reports homing with sufficient data for application from four sites. All four indicate an area with a radius of approximately 30-36 mi. The known movements of this species are less than 30 mi (Davis, 1966), but no firm

TABLE XX

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Eptesicus*

Distance (Miles)	Number Released	Number Returns	Number E
35	25	20	
55	12	11	
102	5	4	
105	61	15	
120	9	4	
328	22	1	
500	78	0	

[1]Davis, 1966.

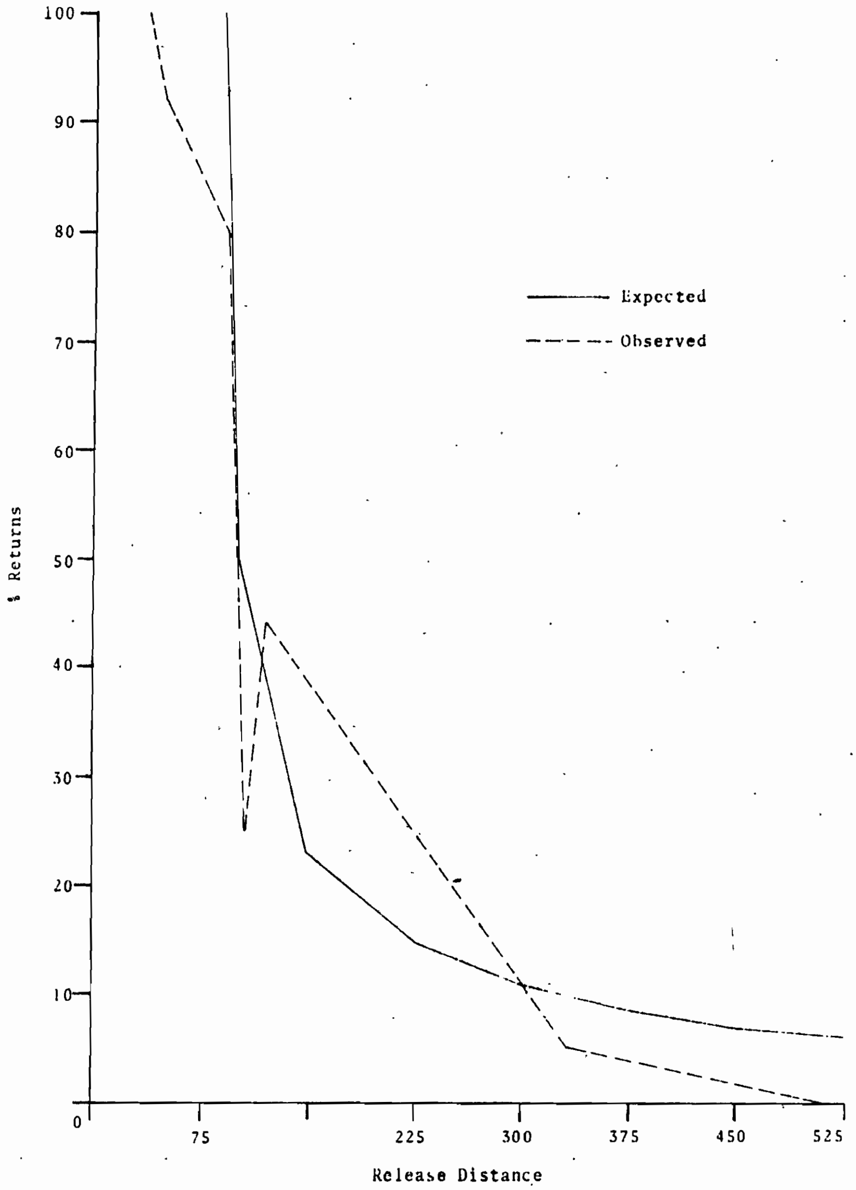


Figure 13. Expected and Observed Returns for *E. fuscus*.

data are available on movements between nurseries and hibernacula. Tables XXI and XXII, and Figures 14 and 15 show results which suggest randomness.

TABLE XXI

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Antrozous*

Distance (Miles)	Number Releases	Number Returns	Number
5	5	5	
10	5	5	
19	4	4	
42	6	2	
59	6	1	
108	19	1	

[i] Davis, 1966

TABLE XXII

ACTUAL AND EXPECTED HOMING PERFORMANCES OF *Antrozous pallidus*[1]

Distance (Miles)	Number Releases	Number Returns	Number Expected
10	4	4	4
21	48	33	48
25	9	8	9
30	36	14	18
30	19	7	9
30	17	10	9
30	18	6	9
32	18	12	9
37	11	2	3
49	8	3	2
50	20	8	4
56	20	9	4
59	10	3	2
63	2	0	0
68	12	3	2
68	7	2	1
70	5	1	1
102	14	0	1
328	6	0	0
			TOTAL =

[1] Davis, 1966

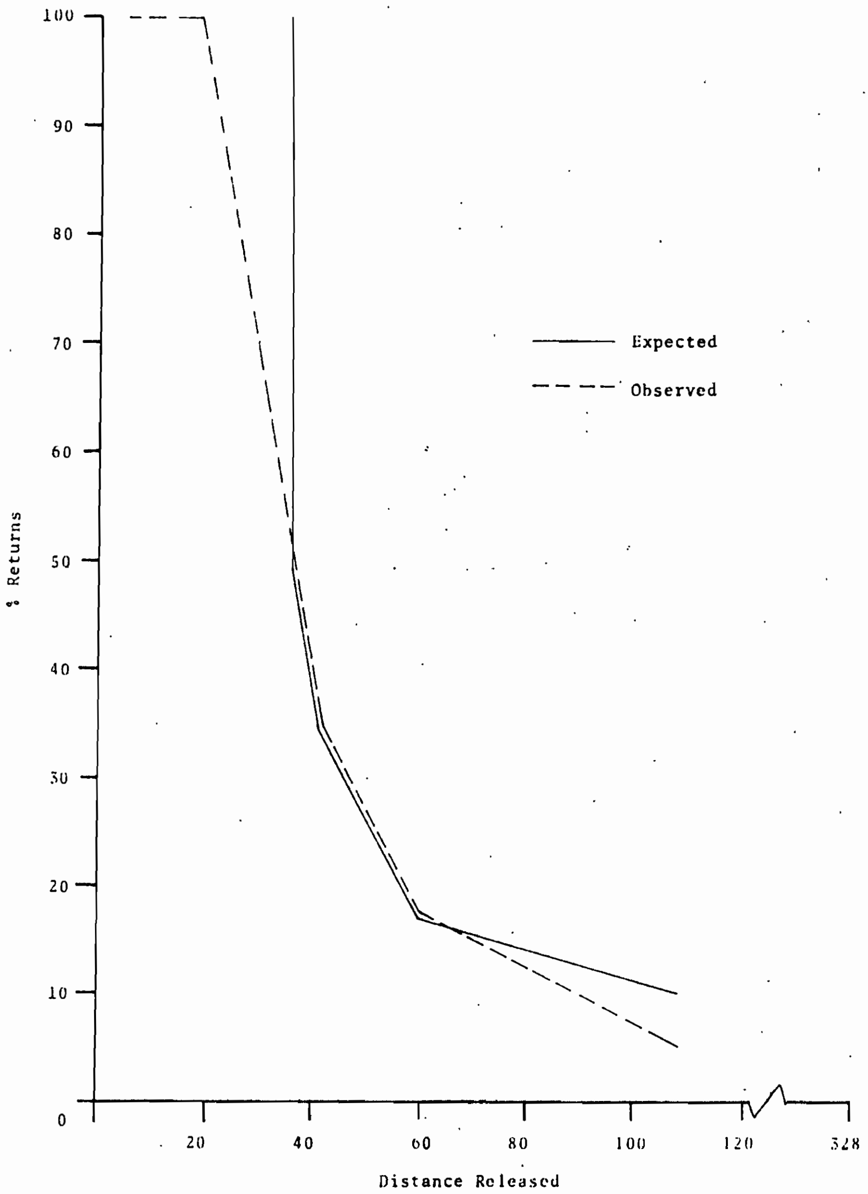


Figure 14. Expected and Observed Returns for *Antrozous pallidus*.

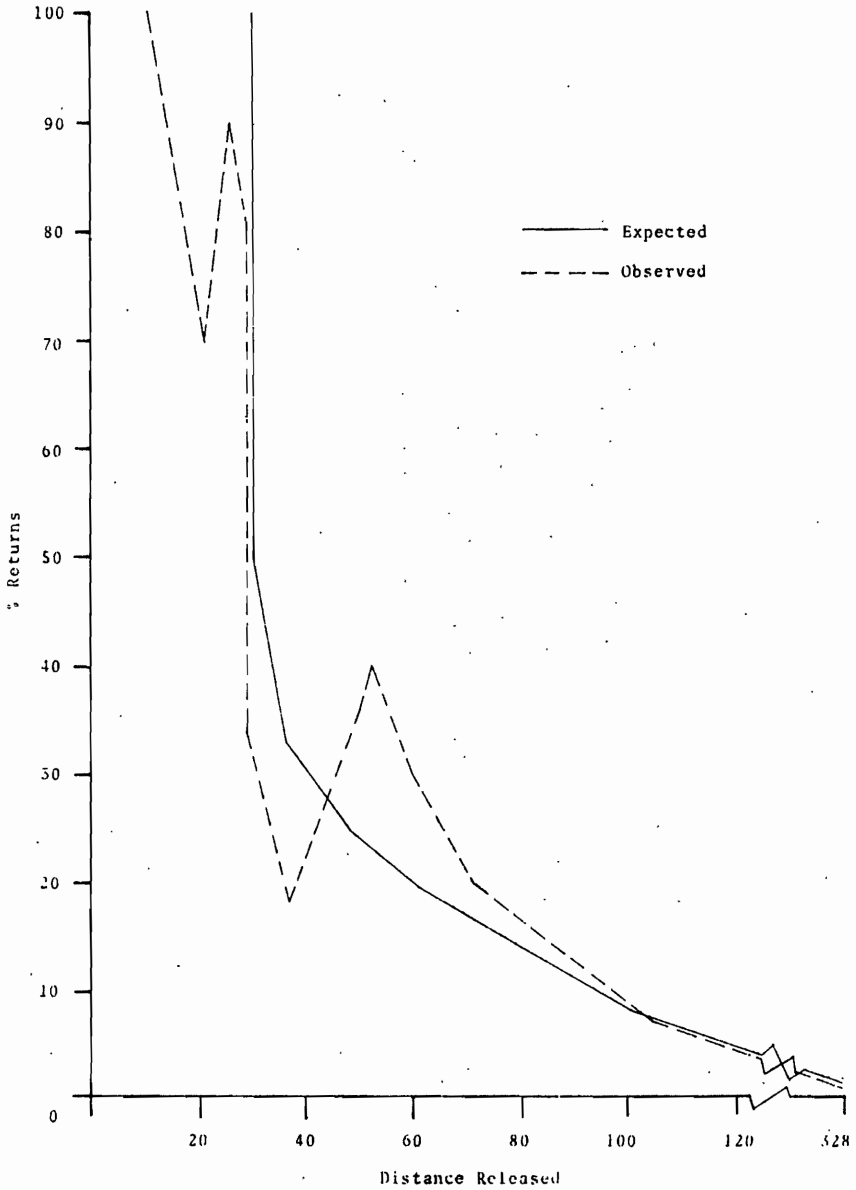


Figure 15. Expected and Observed Returns for *Antrozous pallidus*.

DISCUSSION

Application of the W-F model to literature reports of bat homing in tropical and temperate microchiropterans reveals that 25 of 29 applicable studies indicate homing randomness outside familiar territory (Type A). As Davis (1966) predicted, no record of Types 2 or 3 homing was encountered. The suggestion of non-randomness in four experiments may reveal lack of understanding of movements in migration or inadequate investigation of nearby roosts where returned bats may have gone because of disturbance (Griffin, 1940a).

Homing data from the *E. fuscus* in this study also suggest reasons why data from the 4 non-random experiments may not provide correct results. Circular or ellipitical assumed areas may not be true pictures of the familiar area of colonial bats. My study colony consisted of 2 separate day roosts, between which individuals were known to move. During the 2 weeks immediately after parturition, when trapping and mist-netting were suspended, no roost changes were noted. Table XXIII shows number of returns from directions by roost, the attic returns mostly from the East and the chimney roost mostly from the North. This indicates that there may be 2 or more distinct parts to the colony, as has been reported for many North American bats (Barbour and Davis, 1969; Humphrey & Cope, 1976; Griffin, 1940 a, b).

Several checks of the roosts on warm days during the winter of 1976-77 revealed no sign of any of the bats at the colony site or in the indicated migratory areas. That none were found is not unusual as only 74 were permanently banded (juveniles and adults), and normal recovery success is only about 3%.

Movement through familiar territory is probably accomplished by a combination of echolocation, vision, and memory. Blinded bats return from shorter distances at about the same percentages as controls (Barbour and Davis, 1969; Mueller, 1963) indicating echolocation may be important at short homing distances. Barbour and Davis (1969) and Williams, *et al.*, (1967) report that some species of bats have visual ability to distinguish topographic features. Griffin (1958) and Heerdt and Sluiter (1968) reported the ability of bats to memorize cues and later to use the memorized information.

CONCLUSIONS

Comparisons of homing success between juveniles and adults (Hitchcock and Reynolds, 1942; Davis, 1966) indicate that flight, migratory-area and wandering movements expand the familiar area for adults. The facts that bats fly certain patterns consistently (Barbour and Davis, 1969), that wandering usually occurs in < 5% of the population (Griffin, 1940a, b), and that roost attachment is strong (Humphrey & Cope, 1976), indicate that most (at least) conform to the normal movements of the colony.

Care should be taken in accepting the W-F model as applicable for all microchiropteran species. Some species do not depend on echolocation for navigation; most, however, do. Likewise, most microchiropterans may home randomly from unfamiliar territory while others may utilize special navigational ability as yet unknown.

Combining these findings with the applications of the model leads to the hypothesis that microchiropteran flight ability and navigation across terrain from hibernacula is probably based on memory, vision and echolocation. Homing from outside the familiar area is probably random. Return percentages are based on release distance and area radius.

SELECTED BIBLIOGRAPHY

Bailey, V. 1936. The Mammals and Life Zones of Oregon. North American Fauna No. 55, 416 p.

Barbour, R. W. and W. H. Davis. 1969. Bats of America. The University Press of Kentucky. 286 p.

Beer, J. R. 1955. Survival and movements of banded big brown bats. J. Mammal. 36:242-248.

Bels, L. 1952. Fifteen years of bat banding in the Netherlands. C. V. Dukkerij v/h cl. Goffin-Masstricht. 99 p.

Bonaccorso, F. J. and N. Smythe. 1972. Punchmarking bats: An alternative to banding. J. Mammal. 53: 389-390.

Bonaccorso, F. J., N. Smythe and S. R. Humphrey. 1976. Improved techniques for marking bats. J. Mammal. 57:181-182.

Buchler, E. R. 1976. A chemiluminescent tag for tracking bats and small nocturnal mammals. J. Mammal. 57: 173-176.

Cagle, F. R. and L. Cockrum. 1943. Notes on a summer colony of *Myotis lucifugus lucifugus*. J. Mammal. 24:472-492.

Casteret, N. 1938. Observations sur une colonie de Chauvessouris migratrices. Mammalia 2:29-34.

Christian, J. J. 1956. The natural history of a summer aggregation of the big brown, bat, *Eptesicus fuscus*. Amer. Mid. Natur. 55:66-95.

Cockrum, E. L. 1949. Longevity in the little brown bat, *Myotis l. lucifugus*. J. Mammal. 30:433-434.

Cockrum, E. L. 1956. Homing movements, and longevity of bats. J. Mammal. 37:48-57.

Cope, J. B., R. E. Mumford and N. Wilson. 1958. Some observations on a summer colony of *Myotis lucifugus*. Proc. Ind. Acad. Sci. 67:316-321.

Cope, J. B., K. Koontz and E. Churchwell. 1961. Notes on homing of two species of bats, *Myotis lucifugus* and *Eptesicus fuscus*. Proc. Ind. Acad. Sci. 70: 270-274.

Cope, J. B. and S. R. Humphrey. 1967. Homing experiments with the evening bat, *Nycticeius humeralis*. J. Mammal. 48:136.

Cross, S., *et al*. 1976. A survey of bat populations and their habitat preferences in southern Oregon. NSF study through Southern Oregon State College. 89 p.

Davis, R. 1966. Homing performance and homing ability in bats. Ecological Monographs 36:201-237.

Davis, W. H. and H. B. Hitchcock. 1965. Biology and migration of the bat *Myotis lucifugus* in New England. J. Mammal. 46:296-313.

Davis, W. H. and J. W. Hardin. 1967. Homing in *Lasionycteris noctivagans*. J. Mammal. 48:323.

Davis, W. H., R. W. Barbour and M. D. Hassell. 1968. Colonial behavior of *Eptesicus fuscus*. J. Mammal. 49:44-50.

Davis, W. H. and R. W. Barbour. 1970. Homing in blinded bats (*Myotis sodalis*). J. Mammal. 51:182-184.

Dulic, B. 1957. Report and some results obtained by the first bat-banding in P. R. Croatia. Larus, 9-10: 208-215.

Eisentraut, M. 1936. Ergebnisse der Fledermausberingung nach dreijahrige Versuchzeit. Zeitsch. Morph. Okol. Teire 31:1-26.

Eisentraut, M. 1950. Dressurversuche zur Feststellung eines optischen Orientierrungsvermogen der Fledermause. Jhft. Ver. Vaterl. Naturk. Wurttemberg 106:34-45.

Eisentraut, M. 1957. Aus dem leben der Fledermause und Flughunde. Fischer Verlag, Jena. 175 p.

Engels, W. L. 1936. Distribution of races of the brown bat (*Eptesicus*) in western North America. Amer. Mid. Natur. 17:653-660.

Gates, W. H. 1937. Notes on the Big Brown Bat. J. Mammal. 18:97-98.

Gates, W. H. 1941. A few notes on the evening bat, *Nycticeius humeralis* (Rafinesque). J. Mammal. 22:53-56.

Gifford, C. E. and D. R. Griffin. 1960. Notes on homing and migratory behavior of bats. Ecology 41:378-381.

Giles, R. H., Jr. (editor) 1971. Wildlife Management techniques, 3rd edition. Edward Bros., Ann Arbor, Mich. 633 p.

Griffin, D. R. 1936. Bat banding. J. Mammal. 17:235-239.

Griffin, D. R. 1940a. Notes on the life histories of New England cave bats. J. Mammal. 21:181-187.

Griffin, D. R. 1940b. Migrations of New England bats. Harv. Mus. Comp. Zool. Bull. 86-217-246.

Griffin, D. R. 1945. Travels of banded cave bats. J. Mammal. 26:15-23.

Griffin, D. R. 1958. Listening in the dark. Yale Univ. Press, New Haven, Conn. 413 p.

Gunier, W. J. and W. H. Elder. 1971. Experimental homing of gray bats to a maternity colony in a Missouri barn. Amer. Mid. Natur. 86:502-506.

Gutherie, M. J. 1933. Notes on the seasonal movements and habits of some cave bats. J. Mammal. 14:1-19.

Gyles, G. 1883. Homing instinct in bats. Zoologist 7:173.

Hall, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading Pub. Mus. Art Gallery, Sci. Pub. #12, 68 p.

Hall, J. S. and W. H. Davis. 1958. A record of homing in the big brown bat. J. Mammal. 39:292.

Handley, C. O., Jr. 1956. Bat *versus* ant. J. Mammal. 37:279.

Harvey, M. J., D. H. Snyder, A. E. Perry, J. W. Hardin and M. L. Kennedy. 1976. Homing of gray bats, *Myotis grisescens*, to a hibernaculum. Amer. Mid. Natur. 96:497-498.

Hassell, M. D. 1963. A study of homing in the Indiana bat, *Myotis sodalis*. Tran. Kentucky Acad. Sci. 24:1-14.

Hassell, M. D. and M. J. Harvey. 1965. Differential homing in *Myotis sodalis*. Amer. Mid. Natur. 74: 501-503.

Havekost, H. 1960. Die Beringung der Breitflugelfledermaus (*Eptesicus serotinus*) in Oldenberger Land. Bonner Zool. Beitrage, Sonderheft 11:222-233.

Hayward, B. J. 1961. The natural history of the cave bat, *Myotis velifer*. Ph.D. Dissertation (unpublished), Univ. Ariz., Tucson. 119 p.

Heerdt, P. F. and J. W. Sluiter. 1953. The results of bat banding in the Netherlands in 1952. Naturalist Maandbl. Maastricht, 42:101-104.

Heerdt, P. F. and J. W. Sluiter. 1954. The results of bat banding in the Netherlands in 1954. Naturalist Maandbl. Maastricht 43:85-88.

Heerdt, P. F. and J. W. Sluiter. 1955. The results of bat banding in the Netherlands in 1955. Naturalist Maandbl. Maastricht 45:62-64.

Heerdt, P. F. and J. W. Sluiter. 1956. The results of bat banding in the Netherlands in 1956. Naturalist Maandbl. Maastricht 46:13-16.

Heerdt, P. F. and J. W. Sluiter. 1957. The results of bat banding in the Netherlands in 1957. Naturalist Maandbl. Maastricht 47:39-41.

Heerdt, P. F. and J. W. Sluiter. 1958. The results of bat banding in the Netherlands in 1958. Naturalist Maandbl. Maastricht 48:96-98.

Heerdt, P. F. and J. W. Sluiter. 1959. The results of bat banding in the Netherlands in 1959. Naturalist Maandbl. Maastricht 49:42-44.

Heerdt, P. F. and J. W. Sluiter. 1960. Resutlaten van het vleermius-onderzoek in Nederland in 1960. Levende Natuur. Arnhem 64:156-162.

Heerdt, P. F. and J. W. Sluiter. 1961. Resutlaten van het vleermius-onderzoek in Nederland in 1961. Levende Natuur. Arnhem 65:87-92.

Heerdt, P. F. and J. W. Sluiter. 1965. Notes on the distribution and behavior of the Noctule Bat (*Nyctalus noctula*) in the Netherlands. Mammalia, Paris 29: 463-477.

Hitchcock, H. B. 1943. Banding as an aid in studying activities of the little brown bat, *Myotis lucifugus*. Mich. Acad. Sci. Arts and Lett. 29:277-279.

Hitchcock, H. B. and K. Reynolds. 1942. Homing experiments with the little brown bat, *Myotis lucifugus*. J. Mammal. 23:258-267.

Howell, A. B. and L. Little. 1924. Additional notes on California bats. J. Mammal. 5:261-263.

Humphrey, S. R. and J. B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. J. Mammal. Spec. Pub. #4.

Issel, W. 1950. Oekologische Untersuchungen an der Kleinen Hufeisenase (*Rhinolophus hipposideros*, Bechstein) im mittleren Rheinland und unterem altmühltal. Zool. Jahrb., Abt. f. Systematic 79:71-86.

Jones, J. K., Jr., R. P. Lampe, C. A. Spenrath, and T. H. Kunz. 1973. Notes on the distribution and natural history of bats in southeastern Montana. Occ. Pap. Mus. Tex. Tech. Univ. 15:1-12.

Kowalski, K. and R. J. Wojtusiak. 1952. Homing experiments on bats, part 1. Bull. Acad. Polonaise Sci., Cracovie, Ser. B(ii):33-56.

Krutzsch, P. H. 1946. Some observations on the big brown bat in San Diego, California. J. Mammal. 27:240-242.

Krzanowski, A. 1960. Investigations of flights of Polish bats, mainly *Myotis myotis* (Borkhausen 1797). Acta Theriologica 4:175-184.

Kunz, T. H. 1971. Reproduction of some Vespertilionid bats in central Iowa. Amer. Mid. Natur. 86:477-486.

Kunz, T. H. 1974. Reproduction, growth, and mortality of the Vespertilionid bat, *Eptesicus fuscus*, in Kansas. J. Mammal. 55:1-13.

Lanza, B. 1958. Inanellamento di chirotteri nella zona di ostia antica (Roma) e risultati di esperrienze sul ritorno al luogo di cattura. Annal. del Museo, Divico di Storia Naturale "G. Doria" Genova 2:1-8.

Lauffens, G. 1973. Beitrage zur Biologie der Fransen Fledermause (*Myotis nattereri*). Zeitschrift fuer Saeugetierkunde 38:1-14.

LaVal, R. K. 1973. Observations on the biology of *Tadarida brasiliensis cynocephala* in southeastern Louisiana. Amer. Mid. Natur. 89:112-120.

Mills, R. S., G. W. Barrett and M. P. Farrell. 1975. Population dynamics of the big brown bat (*Eptesicus fuscus*) in southwestern Ohio. J. Mammal. 56: 591-604.

Mohr, C. E. 1934. Marking bats for later recognition. Proc. Penn. Acad. Sci. 8:26-30.

Mohr, C. E. 1942a. Results of 10 years of bat marking in Pennsylvania. Proc. Penn. Acad. Sci. 16:32-36.

Mohr, C. E. 1942b. Bat tagging in Pennsylvania turnpike tunnels. J. Mammal. 23:375-379.

Mohr. C. E. 1953. A survey of bat banding in North America 1932-1951. American Caver 14:3-13.

Mueller, H. C. 1963. Homing and distance-orientation in bats. Ph.D. dissertation (unpublished). Univ. Wisc., Madison. 102 p.

Mueller, H. C. and J. T. Emlen. 1957. Homing in bats. Science 126:307-308.

Mumford, R. E. 1958. Population turnover in wintering bats in Indiana. J. Mammal. 39:253-261.

Patterson, P. and W. H. Davis. 1958. Variation in size among adult *Eptesicus fuscus*. Kent. Acad. Sci., Tran. 29:1-4.

Pearson, O. P., M. R. Koford, and A. K. Pearson. 1952. Reproduction of the lump-nosed bat, (*Corynorhinus rafinesque*) in California. J. Mammal. 33:273-320.

Phillips, G. L. 1966. Ecology of the big brown bat (Chiroptera:Vespertilionidae) in northeastern Kansas. Amer. Mid. Natur. 75:168-198.

Poole, E. L. 1932. A survey of the mammals of Berks County, Pennsylvania. Read. Pub. Mus. Art Gallery, Bull. 13:15-19.

Punt, A. and P. J. Nieuwenhoven. 1957. The use of radio-active bands in tracing hibernating bats. Experienta 13:51-54.

Reynolds, K. 1941. Notes on homing and hibernation in *Eptesicus fuscus*. Canadian Field-Natur. 55:132.

Rice, D. W. 1957. Life history and ecology of *Myotis austroriparius* in Florida. J. Mammal. 38:15-32.

Roer, H. 1960. Vorlaufige Ergebnisse der Fledermaus Beringnung und literatureubersicht. Bonner Zool. Beitr., Sonderheft 11:234-263.

Roer, H. 1972. Zur bestandsentwicklung der Kleinen Hufeisnase (Chiroptera, Mamm.) in westlichen Mitteleuropa. Bonn. Zool. Beitr. Heft 4:325-337.

Ryberg, O. 1947. Studies on bats and bat parasites. Bokforlaget Svensk. Natur. Stockholm, 330 p.

Schramm, P. 1957. A new homing record for the little brown bat. J. Mammal. 38:514-515.

Smith, E. 1957. Experimental study of factors affecting sex ratios in the little brown bat. J. Mammal. 38:32-39.

Smith, E. and K. Hale. 1953. A homing record in the bat, *Myotis lucifugus*. J. Mammal. 34:122.

Smith, E. and W. Goodpaster. 1958. Homing in non-migratory bats. Science 127:644.

Stebbings, R. E. 1966. Bats under stress. Studies in Speleology 1:168-173.

Stones, R. C. and L. P. Branik. 1969. Use of hearing in homing by two species of *Myotis* bats. J. Mammal. 50:157-160.

Strelkov, P. P. 1969. Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. Acta Zool. Cracoviensia; Tom XIV. Nr. 16:393-440.

Tibbetts, T. 1956. Homing instinct of two bats, *Eptesicus fuscus* and *Tadarida mexicana* (Mammalia: Chiroptera) Southwestern Natur. 1:194.

Tinkle, D. W. and I. G. Patterson. 1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. J. Mammal. 46:612-633.

Tuttle, M. D. 1961. In Bat banding News. 2:35.

Tuttle, M. D. 1974. An improved trap for bats. J. Mammal. 55:475-477.

Twente, J. W. 1955. Aspects of a population study of cavern-dwelling bats. J. Mammal 36:379-390.

Walley, H. D. 1970. Movements of *Myotis lucifugus lucifugus* from a colony in LaSalle County, Illinois. Trans. Ill. St. Acad. Sci. 63:409-414.

Wilkerson, D. H. 1952. The random element in bird 'navigation'. J. Exp. Biol. 29:532-560.

Williams, T. C., J. M. Williams and D. R. Griffin. 1966. The homing ability of the neotropical bat, *Phyllostomus hastatus*, with evidence for visual orientation. Anim. Behav. 14:468-473.

Williams, T. C., J. M. Williams and D. R. Griffin. 1967. Radio tracking of homing bats. Science 155:1435-1436.

Wilson, D. E. 1971. Ecology of *Myotis nigricans* (Mammalia:Chiroptera) on Barro Colorado Island, Panama Canal Zone. J. Zool. 163:1-13.

Wilson, D. E. and J. S. Findley. 1972. Randomness in bat homing. Amer. Natur. 106:418-424.

Wilson, N. 1958. Another instance of bat *versus* ant. J. Mammal. 39:438.

Wimsatt, W. A. 1944. Notes on the breeding behavior, pregnancy, and parturition in some Vespertilionid bats of the eastern United States. J. Mammal. 26: 23-33.

APPENDIX A

Forearm Size Variation

Engels (1936) observed that in *E. fuscus* females were 4-5% larger than males. Phillips (1966) reported skull length, zygomatic breadth, wingspan, and total length to be significantly smaller for males than for females. Patterson and Davis (1968) found the total length and forearm length of females to be significantly larger than for males; however, tail length was not significantly different between sexes. Total length and forearm length values were found to be least variable; in live bats the forearm is the easiest and most accurate to measure.

Forearms, including carpals, of all adults captured were measured to the nearest 0.1 mm. Mean (M), standard deviation (SD) and variance (V) for each sex are displayed in Table XXIII and Figure 16, above the findings of Patterson and Davis. Females were found to be significantly larger than the males ($\underline{z}$ = 7.284).

TABLE XXIII

COMPARISON OF SOME MEASUREMENTS OF *E. fuscus* FROM CAM
WITH THOSE OF PATTERSON AND DAVIS (1968)

	E. fuscus from Camp Namanu					
	FEMALES					
	No.	M	SD	V	No.	M
Forearm	74	47.9	1.947	4.05	21	46.8
	E. fuscus from Patterson and Davis (1968)					
Forearm	92	47.8	1.433	3.10	32	46.5
Body	92	76.4	3.024	3.96	32	67.0
Total Length	92	122.3	4.480	3.65	32	115.5
Tail	92	45.8	2.837	6.19	32	44.9

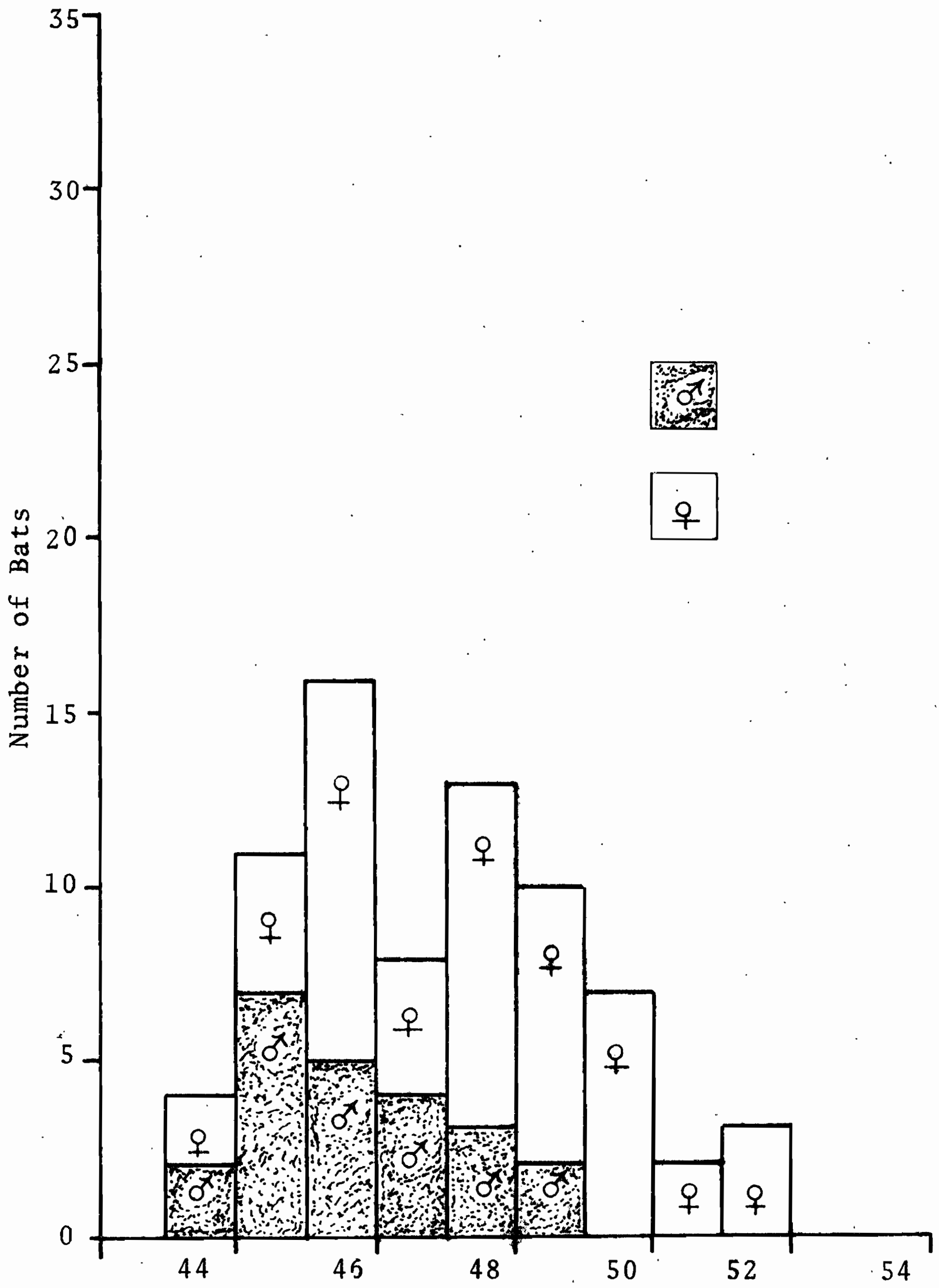


Figure 16. Forearm Length in mm

APPENDIX B

NATURAL HISTORY NOTES

Behavior

The flight of *E. fuscus* was usually straight, and certain patterns were often repeated by the same bat on different nights. Feeding was noted at three distinct sites: the clearing immediately outside the roost; over the river; over an open commons area of the camp (Fig. 17). Two drinking areas were utilized - a boating pond, and the section of the river that coincided with the aforementioned feeding site. Although data were insufficient for analysis, it appeared that the bats preferred a specific feeding site (as noted by Barbour and Davis, 1969), and a specific drinking site.

Usually one or two bats emerged at a time, beginning at about 3 min past civil sunset. Bats often continued to emerge for over two hours (Fig. 18). Immediately after emergence a short circling flight occurred, followed by a direct flight to the drinking site. About a fourth of the bats flew to the feeding site first, and then drank after feeding. This may help to explain the findings of Cross, *et al*. (1976) of two peaks of activity of *E. fuscus* over a water hole.

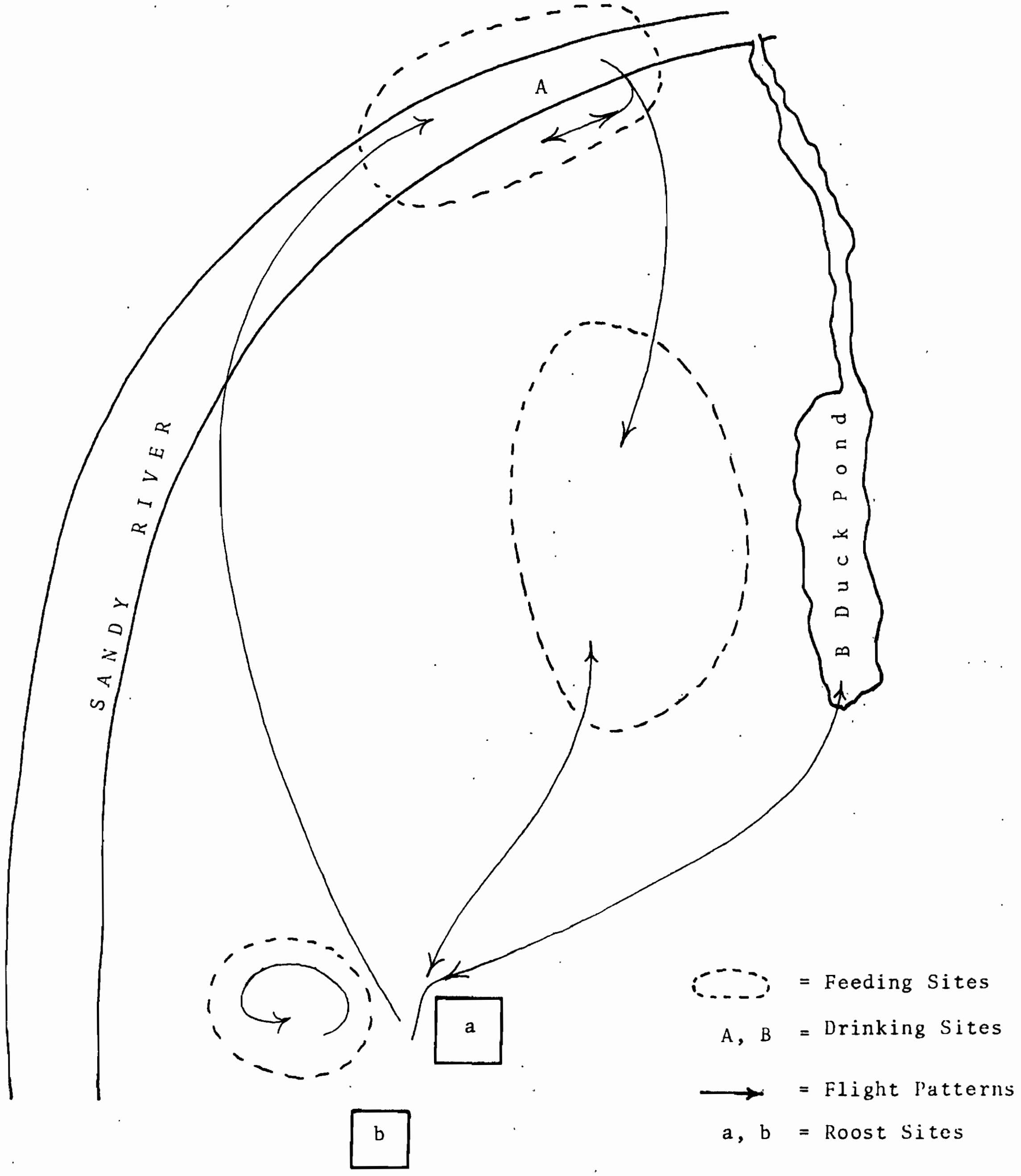


Figure 17. Preferred feeding and drinking sites of Camp Namanu bats.

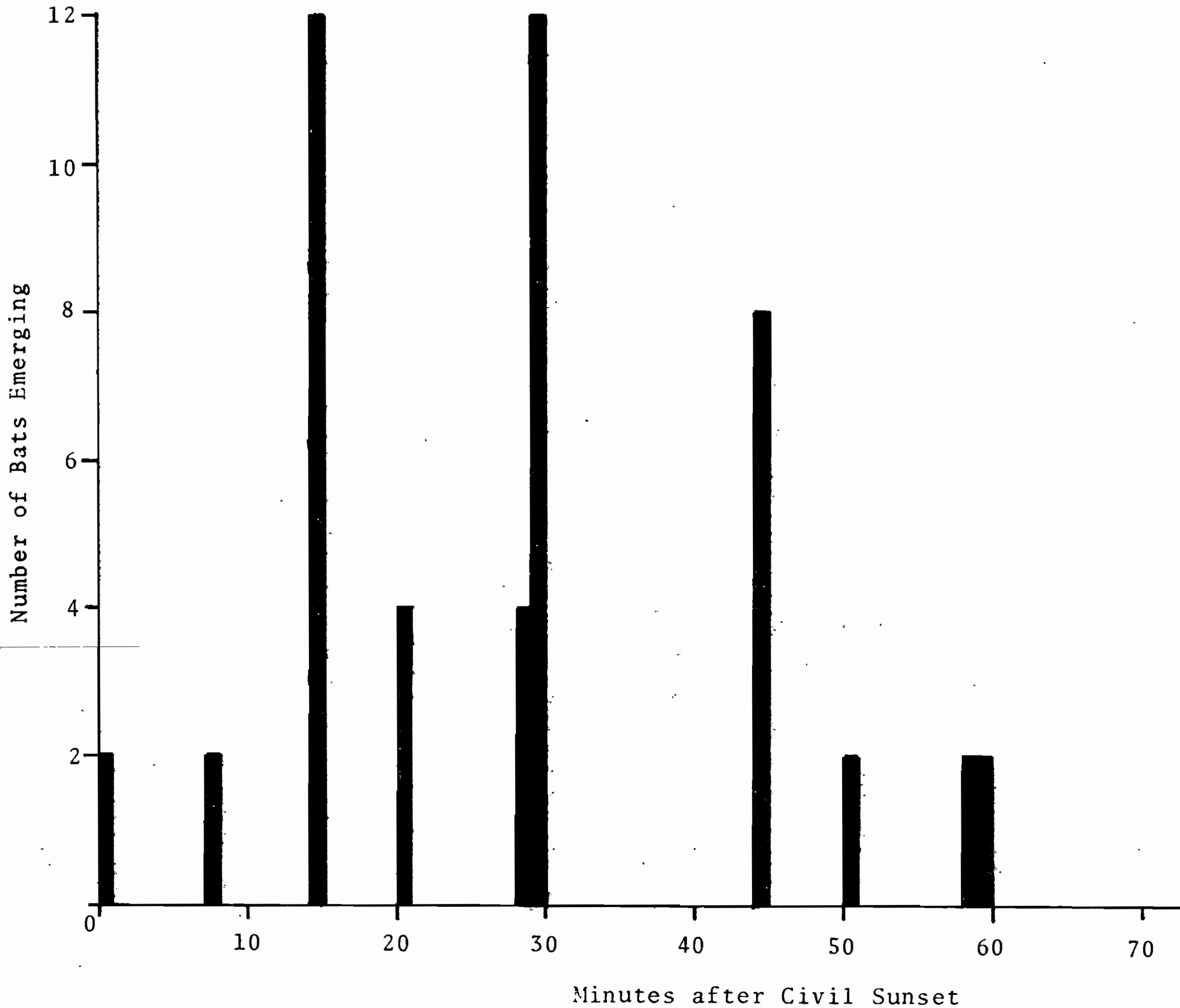


Figure 18. Emergence times of *E. fuscus* at Camp Namanu.

A study of the colony's guano was not conducted; however one insect eaten was the flying carpenter ant. Handley (1956) and Wilson (1958) reported finding big brown bats each with the head of an ant firmly attached by its mandibles to the side of the bat's face. We captured 3 such bats during the ants' flying period, two females with the ant head attached to the lower lip, and a male with one attached to his ear. Preference was exhibited by individual bats for one of the two day roosts. However, excessive disturbance (a combination of workers and campers) at certain times probably caused movement from one roost to the other. Exchange was noted between both roosts. No rejection or aggression to outsiders from either roost was seen.

Male Populations

Before females gave birth, the number of males present in samples was approximately 36% of the total. Postnatally, their numbers dropped to 17%. As the young became volant, numbers of males increased until they once again reached about 30%.

Ectoparasites

Barbour and Davis (1969) report mild to destructive levels of mites and *Cimex pilosellus* in *E. fuscus* nursery colonies. Various species of fleas have also been reported. Careful search of each bat captured produced only 5 mites, one flea, and 2 *C. pilosellus*. No ectoparasites were found on any juveniles. Among adults, less than 11% of the population studied was externally parasitized. All parasites but the flea were first observed in the ears or the fur of the occipital region.

Reproduction And Growth

Barbour and Davis (1969) indicate that parturition time varied with latitude (Table XXIV). In this study the first births noted were on 2 July; most young were born within the next two days. Gates (1937, 1941) noted a similarly short interval for *E. fuscus* births. Parturition here occurs about the same time as in Montana (Jones, *et al.*, 1973), despite the fact that the mean temperatures are lower in that state than in western Oregon.

The first volant young were captured on August 3, 1976, about four weeks after the first births. Kunz (1974) also reported volancy at about 4 weeks, and that the size of the young at 10 weeks was 85-90% of that of the adults. Young of my colony were not measured until about the sixth week; then only the lack of ossification in the phalanges allowed the separation of the juveniles from the adults. At 6 weeks the forearm measurements were that of an adult (Table XXV). Perhaps more rapid maturation is associated with higher latitudes.

Population numbers could only be estimated by capture-recapture methods, due to the inaccessability of one portion

TABLE XXIV

PARTURITION VARIANCE OF *E. fuscus* BY LATITUD

LOCATION	LATITUDE	DATES	
Louisana	32° North	Lat May	Gates
San Diego, Ca.	33° North	Late May	Krutz
Los Angeles, Ca.	34° North	Mid-June	Howel
Central Kentucky	38° North	Early June	Davis
Maryland	39° North	Late May	Chris
Central Kansas	39° North	Early June	Kunz
Central Iowa	43° North	Late June	Kunz
Southwest Ohio	43° North	Mid-June	Mills
New England	45° North	Early-Mid July	Griff
Western Oregon	45° North	Early July (?)	Baile
Portland, Oregon	45° North	Early July	This
Montana	46° North	Early July	Jones

TABLE XXV

JUVENILE FOREARM MEASUREMENTS OF *E. fuscus* FROM CAMP NAMAN

	RANGE	MEAN	PERC
MALES	42.1mm - 49.1mm	45.8mm	
FEMALES	45.5mm - 49.0mm	47.7mm	

of the roost in the later weeks of the study. Schnabel's formula, $N = \frac{M\,n}{x}$, where N is the total estimated, M is the number previously marked in the population, n is the number captured and x is the number of captures marked, was used. The adult female population was estimated to be 60.

Christian (1956) indicated a 7% postnatal mortality for *E. fuscus*; this contrasts with Kunz (1974) prenatal loss of 34%, indicating that the accumulative loss by weaning is about 40% (Beer, 1955). Wimsatt's (1944) study of mature and ruptured follicles in *E. fuscus* indicates a prenatal loss of up to 34%. If the 26 young netted are considered to be approximately 60% of all possible births, then the number of young would be 43 if no deaths occurred. The approximate number of young per female would be 0.74, somewhat below the 0.85-0.95 numbers previously reported (adjusted for eastern *E. fuscus*, where 2 young are normal, by dividing ratios by two). No females with severe wing damage were ever found to be lactating or nursing a juvenile. If these females are subtracted from the reproducing adult female population, then the ratio rises to 0.84, very close to reported ratios. One factor which could be responsible for a large postnatal loss was a 10-day period in early July during which temperatures rarely rose above 65° F. Also, the handling of the bats may have induced some bats to abandon the colony and their young.