

INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.
2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.
3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.
4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.
5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

**University
Microfilms
International**

300 N. Zeeb Road
Ann Arbor, MI 48106

8506404

Loye, Jenella E.

THE CLIFF SWALLOW BUG OECIACUS VICARIUS (CIMICIDAE:
HEMIPTERA), NATURAL HISTORY AND POPULATION ECOLOGY

The University of Oklahoma

PH.D. 1984

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark .

1. Glossy photographs or pages _____
2. Colored illustrations, paper or print _____
3. Photographs with dark background _____
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages _____
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) 37 seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Dissertation contains pages with print at a slant, filmed as received _____
16. Other _____

University
Microfilms
International

—

THE UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

The cliff swallow bug Oeciacus vicarius (Cimicidae:
Hemiptera), natural history and population ecology.

A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
Doctorate of Philosophy

by
JENELLA E. LOYE
Norman, Oklahoma

1984

THE CLIFF SWALLOW BUG OECIACUS VICARIUS (CIMICIDAE:
HEMIPTERA), NATURAL HISTORY AND POPULATION ECOLOGY.

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF ZOOLOGY

by George E. Knyla

Paul H. Lamb

L. Beatt

Frank J. Sontestner

Mark A. Roberts

Joseph White

ACKNOWLEDGEMENTS

First I must thank my major advisor, Dr. C. E. Hopla for his dedication to sharing this project and our many joint research projects as well. I thank the members of my committee Dr. Howard Larsh, Dr. Mark Roberts, Dr. Vernon Scott, Dr. Frank Sonleitner and Dr. Gary White for their interest and suggestions. And thanks to Charles Brown, Scott Carroll, Brian Chapman, Alan Covich, John Emlen, Bruce Francy, Ken Gage, Victor Hutchinson, Tom Scott, Bill Shepard, Gordon Smith and Rex Thomas for discussions and ideas on this topic. Scott Carroll and Dave Loye provided years of intellectual, editorial and emotional support. And my thanks to all the Loyes and Buck and Minnow for their encouragement and patience. This dissertation was produced due to the generosity of Ric Charnov and the University of Utah, for which I am grateful. Graphs were executed by Laura Karcher.

This research was conducted while a research assistant to C. E. Hopla and a teaching assistant in the Department of Zoology at the University of Oklahoma. Additional funding was provided by the Graduate College of The University of Oklahoma, Sigma XI and Winifred Loye.

Paper I was prepared for submission to the Bulletin of the Society of Vector Ecology. Papers II and III were prepared for submission to The Journal of Ecological Entomology.

TABLE OF CONTENTS

LIST OF TABLES.....v

LIST OF ILLUSTRATIONS.....vi

PAPER I Host-effects on feeding and survival of the
polyphagous cliff swallow bug (Oeciacus
vicarius: Cimicidae: Hemiptera).

Abstract.....1

Introduction.....2

Materials and Methods.....3

Results.....4

Discussion.....8

Literature Cited.....12

Tables.....14

Table headings.....19

Figures.....20

Figure headings.....21

PAPER II The natural history and ecology of the cliff
swallow bug Oeciacus vicarius (Cimicidae:
Hemiptera).

Abstract.....21

Introduction.....22

Materials and Methods.....23

Results.....29

Discussion.....32

Literature Cited.....38

Tables.....42

Table headings.....45

Figures.....	46
Figure headings.....	48
PAPER III Population ecology of the cliff swallow bug	
<u>Oeciacus vicarius</u> (Cimicidae:Hemiptera).	
Abstract.....	50
Introduction.....	51
Materials and Methods.....	52
Results.....	54
Discussion.....	63
Literature Cited.....	67
Tables.....	70
Table headings.....	73
Figures.....	74
Figure headings.....	79

LIST OF TABLES

PAPER I

TABLE	Page
I Vertebrates found associated with cliff swallow nesting habitats.....	16
II Feeding of cliff swallow bugs: the number and percentage of bugs that fed when give access to different hosts.....	17
IIIa Average blood meal weight (mg) of <u>O. vicarius</u> fed on two hosts.....	18
IIIb Average blood meal weight of <u>O. vicarius</u> fed on mice.....	18
IV Percentage survival of cliff swallow bugs for 6 weeks after feeding on various hosts.....	19
V Percentage of survival of adult <u>O. vicarius</u> over 3 months after feeding on two hosts (1982).....	20

PAPER II

TABLE	
I Cliff swallow bug and swallow activities in Caddo Canyons, Oklahoma (Ryburn Cliff 1980).	42
II Laboratory development of bugs.....	43
III Field collections of bugs.....	44

PAPER III

TABLE	
I Cliff swallow colonies in Caddo and Grady Co.s Oklahoma: history of use, 1979-83.	70
II Effect of location in colony on nestling weight and total bugs in transect samples.....	71

III Effect of location on total bugs and nestling
mortality in 30 nest transect samples (taken
after fledging late July, 1982).....72

LIST OF ILLUSTRATIONS

PAPER I

FIGURE	Page
I <u>O. vicarius</u> survival: collected in February and June, 1981. Fed on nestling cliff swallows and suckling mice (2 hrs); held at 78% relative humidity	15

PAPER II

FIGURE	
I Bug development in laboratory colonies, April 11-June 6, 1983.....	46
II Sex ratio of field collected bugs: mean and range by month.....	47

PAPER III

FIGURE	
I Maximum, average and minimum temperatures, precipitation and bird presence (I—I) (wk 1-4: April, wk 5-8: May, wk 9-12: June, wk 13-16 July, wk 17-20 August).....	74
II Cliff swallow bugs/nest/month, 1979-84 samples. A comparison of colonies used by swallows 1 nesting season (birds present), bridges used each year (bridges) and colonies unused one year (birds absent).....	75
III Cliff swallow bugs/nest in two new colonies: PAB (1981-82), on a cliff and WB (1982-83), in a culvert.....	76
IV Cliff swallow bugs/nest at Ryburn cliff (1980-81).....	77
V Cliff swallow bugs/individual nest at PAB colony (1981 and 1982)	78

PAPER I

Host-effects and survival of the polyphagous cliff
swallow bug (Oeciacus vicarius:Cimicidae:Hemiptera).

HOST-EFFECTS ON FEEDING AND SURVIVAL OF THE POLYPHAGOUS
CLIFF SWALLOW BUG (OECIACUS VICARIUS:CIMICIDAE:HEMIPTERA).

J.E.LOYE

ABSTRACT

The cliff swallow bug Oeciacus vicarius, is a hematophagous ectoparasite associated with the cliff swallow (Hirundo pyrrhonota). The unpredictable availability of the swallow as a food resource leads to food deprivation in the cliff swallow bug for periods of 9 or more months. I examined the effect of different hosts on the percent of adult and nymphal bugs feeding, blood meal weights, survivorship and fecundity. Adult bugs fed readily on swallow nestlings, suckling mice and chicks. Nymphs fed more frequently on swallow nestlings. Blood meal weight did not vary significantly between hosts. Adult bugs showed no significant difference in survival between hosts, but nymphs fed on swallow nestlings survived longer than those fed on suckling mice. Survival of female bugs was greater (20% of 60) than male bugs (7% of 41) over 12 months. The average number of eggs/female bug collected from swallows nests was 16 (range 7-27, n=9) and dissections of field collected females averaged 19 eggs/female (8-25, n=7). Females fed on suckling mice in the lab laid 6 eggs/female (128 eggs, n=25) or contained 8 eggs upon dissection. Polyphagy may allow O. vicarius to supplement an ephemeral food resource, the blood of the cliff swallow, with alternative hosts that are transient residents of the bridges and cliffs where the swallows nest.

INTRODUCTION

Oeciacus vicarius Horvath 1912 is a nidicolous ectoparasite of the colonially nesting cliff swallow (Hirundo pyrrhonota) throughout the bird's breeding range in the continental United States. I have reported elsewhere on the phenological and life history relationships of the insect to its host (Loye and Hopla 1983), and several other authors have contributed observations of bug's behavior (Smith and Eads 1978), influence on nestling cliff swallow mortality (Chapman 1982) and status as a vector and overwintering mechanism for Fort Morgan virus, a relative of Western Equine Encephalitis (Hayes et al 1977).

Here I report that O. vicarius takes blood meals from a variety of vertebrates other than the cliff swallow. Alternative hosts are especially common during the swallows nine month migratory absence, when the bugs remain in and around the durable mud nests. The swallows do not return to each colony every year, but I have found that bug populations may persist in deserted colonies as many as four years (Loye and Hopla 1983). Non-swallow hosts may be ecologically significant in the long-term maintenance of O. vicarius populations, and therefore of its micro-organismal associates as well.

In complementary laboratory work, I investigated the ability of the cliff swallow bug to feed and survive on other vertebrates. Captives were reared on suckling mice, chicks, house sparrows (Passer domesticus which often nests in cliff swallow colonies), and cliff swallow nestlings. In addition, because suckling mice are often employed as the sole host of O. vicarius in laboratory studies (e.g.

Rush 1981), I compared the weights of blood meals taken by adult and nymphal bugs on suckling mice versus cliff swallow nestlings.

MATERIALS AND METHODS

Cliff swallow bugs were collected for laboratory work in May and June (1981 and 1982) from swallow nests on cliffs in the Caddo Canyons area of central Oklahoma. The bugs collected in May had overwintered for several months without feeding. For feeding trials host animals were held in 1000 ml beakers, each containing a wire mesh platform capped with filter paper which allowed a space below the host where the bugs rested before and after feeding. The straight walls of the glass beaker effectively contained the bugs. Bugs were allowed to feed for 2 hours (18-2000 hrs). Feeding trials were conducted during three periods: 1) 1 June - 7 July 1981 and 2) 6-21 November, 1981 and 3) 22 June - 16 July, 1982. In July, 1981 the bugs were fed at weekly intervals. During later feeding periods the bugs were fed only once and held in starved condition after collection. The following hosts were each offered separately: cliff swallow nestlings (6-10 days old), suckling mice (3-4 days), chicks (3-4 days) and sparrow nestlings (6-10 days). Blood was visible in the digestive tract of the bugs after feeding and I used this condition to determine the proportion of bugs feeding on each host.

After feeding the groups of bugs were placed in 4 dram shell vials with a one inch square filter paper folded for clinging and egg laying. The vials were covered with cotton organdy or nylon mesh which was secured with a rubber band. Bugs were also held in pairs in glass 76 X 8 mm tubes plugged with cotton (1b and 1c). The bugs were

held at 78% RH, 22 C and LD 14/10. The fed bugs in period 1 were monitored for longevity at 6 weeks (trial 1a), 9 weeks (1b, July-Sept.) and 12 months (1c, July-May). Survival of male and female bugs was monitored in 1981 (1b, 1c) as well. Group 1b was newly emerged adult bugs (121 females, 62 males) which were given access to two hosts for 24-72 hours (July 17-19, 1982) and 1c was 101 adults (60 female, 41 male) collected in May and early June, 1981 and fed for 2 hours. Both 1b and 1c were held in pairs in glass (76 X 8mm) tubes plugged with cotton.

Blood meal weight of bugs fed on swallow nestlings and suckling mice was determined in trials 1a, 2 and 3. Groups of adult and nymphal bugs were fed in June and July of 1981 and 1982. Separate pools of 50 bugs (male, female and instars 4 and 5) were fed on suckling mice in November, 1981. The bugs were weighed in groups on a Sartorius balance (0.0001-200.0g) before and after feeding. The average blood meal weight was calculated by dividing the difference in weight by the number of bugs that fed.

RESULTS

ALTERNATE HOSTS:

Transient residents that have been found in or directly adjacent to cliff swallow nests when swallows are absent include 3 classes of vertebrates. Reports of 11 species of birds, seven mammals and 2 reptiles are summarized in Table 1. Nesting passerine birds and migratory or overwintering bats were found often and are probably the most important alternate hosts for the nidicolous ectoparasites.

In the fall of 1979 and 1980 engorged cliff swallow bugs were collected in cliff swallow nests used by groups of Myotis velifer bats (Hopla and Loye 1984). In preliminary laboratory trials of alternate hosts cliff swallow bugs took blood meals from the bats, pigeon nestling and a young gecko. In the field, the bugs fed readily on humans.

FEEDING PATTERNS:

The feeding trials showed no significant variation in the number of adult bugs that fed on the individual hosts when offered access for 2 hours (Table 2). In contrast, nymphs fed significantly more frequently on swallow nestlings than on suckling mice or chicks. In pooled groups of adult and nymphal bugs given access to swallow or sparrow nestlings, more bugs fed on swallow nestlings than sparrow nestlings (Table 2). During feeding trials the nymphs showed less direction in movement towards non-swallow hosts than adult bugs. The preferred feeding sites for the bugs were the heavily vascularized areas of the feet, tail, axial and inguinal areas in all hosts.

BLOOD MEAL WEIGHT:

Mean blood meal weight was not significantly different between hosts (Table 3a). The average weight of the blood meal taken each week in trial 1a (June-July 1981) from swallow nestlings was 0.85 mg for adults and 1.1 mg for fifth instar bugs. Trial 1b (1982), in which the bugs were not fed from the time of spring collection until feeding, blood meal weights were lower for adult bugs (0.52 mg) and higher for nymphs (2.0 mg). In November, 1982 blood meal weight

values were comparable to those of July 1982, both groups were starved from the time of collection until feeding on suckling mice. There was no significant difference in blood meal weight of male vs female bugs fed on suckling mice (trial 1c) (0.49 mg vs 0.57 mg respectively; Table 3b). The average blood meal weight of the fifth instar nymph was almost twice that of adults (0.81 mg; Table 3b). The blood meal weight represented more than 50% of the average pre-feeding weight in all nymphal instars, (Table 3b), while adult bugs imbibed an average of 23.6% of their weight.

SURVIVAL

Summer survival over 6 weeks (trial 1a) varied between developmental stages. Nymphs fed on swallows lived significantly longer than nymphs fed on any other hosts (Table 4). However, adult bugs that fed on swallows lived no longer than those fed on mice. There was significantly higher mortality in adult bugs fed on sparrow nestlings and chicks (Table 4).

Over twelve months (trial 1c), more female cliff swallow bugs survived than males (Fig.1). The greatest mortality occurred within two weeks of feeding: 50% of female bugs and 80% of the males had died. By seven months 20% of the females (n=60) and 7% of the males (n=41) remained alive. The host species providing a blood meal had no apparent effect on longevity of the bugs; however the two male bugs that lived until May 1982 were fed on cliff swallows.

Survival of newly eclosed adult female and male bugs (fed on nestling swallows and suckling mice, 17 July 1982) was evaluated.

(trial 1b, Table 5). Female mortality was lower (63%, n=121) than male (88%, n=62) after 4 weeks. By 8 weeks, 92% of the female and 89% of the male bugs were dead. The host species had no effect on survival.

OVIPOSITION

Fecundity in field collected females (1st week July, 1981; n=9) averaged 16 eggs/female (range 7-27). Females dissected from the same sample (n=7) contained an average of 19 eggs/female (range 8-25). This was considerably higher than oviposition rates of lab fed bugs. Females that fed on swallow nestlings or suckling mice (48-72 hours with host n=38 and 62 respectively) did not differ significantly in number of eggs laid from those fed on swallows (mean=6.0, range 4-10; n=8) versus mice (mean=8, range 4-17, n=5). However, eggs were laid by 21 % of the group that fed on swallows compared to 8 % of those fed on mice.

DISCUSSION

The cliff swallow bug is polyphagous and thus less specialized in its host requirement than the flea and the ticks that are also cliff swallow ectoparasites (Loye and Hopla 1983). A trend towards specific feeding on cliff swallows as hosts was seen in laboratory trials. The nymphal swallow bugs fed and survived more successfully and females laid more eggs when the cliff swallow was the blood meal source. However alternate hosts have been found to be suitable for development and reproduction in the bugs (Rush, 1981). The wide range of vertebrate species found in association with the cliff swallow bug may alleviate the periods of starvation that the bug might endure in the absence of its preferred host.

The observed differences in feeding patterns between adults and nymphs may result from stadial variation in the degree of starvation. The female bugs collected in the field in July had large adipose reserves and immature ovaries that are indicative of recent eclosion. These reserves of adipose tissue present in summer, were absent in winter and spring. Thus, females that overwintered probably emerged the previous summer and survived 9 months of starvation. In contrast, the nymphs had very little adipose tissue during any season of the year. The stress of starvation was reflected in a high overwintering mortality of the juveniles (Loye and Hopla 1984). Starved nymphs in poor condition may also have reduced feeding ability which could account for a smaller proportion of nymphs feeding in lab trials. Perhaps the ability to withstand starvation and feed readily when a host becomes available is greater in adult bugs.

The blood meal size differences between 1981 and 1982 reflect difference in feeding history. Chapman (1982) notes that recent feeding may act as a deterrent to further feeding. The bugs were fed 6 times at weekly intervals in 1981, while those in 1982 were fed once, after collection in nests that were not yet inhabited by birds. Blood meal size was consistent between starved bugs fed in November 1981 and those starved and fed once in 1982. Remnants of undigested blood in the gut in the repeatedly fed bugs may account for a smaller average blood meal weight in 1982. Cimicid bugs feed repeatedly until replete, they are easily disturbed and may drop and move to another site to resume feeding (Usinger 1966). The time for engorgement may be longer after starvation stress.

High mortality occurred rapidly in the newly emerged bugs. These bugs had been gathered after feeding on swallows in the field and molted to adulthood in the lab. Feeding and holding conditions did not vary from trial 1c, mortality rates were similar. The adults that were newly emerged after overwintering as nymphs may comprize a short-lived reproductive stage whose offspring become the diapausing, overwintering population that emerges in late July.

Short term survival observations were undertaken due to the anticipation of high mortality rates in juvenile bugs and overwintering adults. Survival in the lab was enhanced by grouping the bugs, perhaps due to microclimate effects of aggregating.

The bugs that were held for 12 months must have overwintered as adults, as blood feeding is required for the development of juveniles and these adults were collected before the swallow returned. Thus the

period of retention in the laboratory was a second season of survival for them. The high early mortality rates are explained by the age of the bugs. A long life span of 18-20 months is consistent with predictions of a life history featuring a reliance on unpredictable food resources (Stearns 1976). The greater survival of inseminated females would also be advantageous for the perpetuation of cliff swallow bugs after the starvation stress of host absence (Williams 1975). These differences are an avenue for ongoing investigations on variation in response to resource periodicity.

A larger fat reserve may be responsible for the greater survivorship of females. Yanovski and Ogston (1982) found that female Cimex hemipterus took a larger blood meal than males. This is not the case in O. vicarius, but the female may, none-the-less, overwinter with greater stored resources. Hinton (1964) considered sperm to be a source of protein for the starved female cimicid. If this is the case, sex differences in mortality may suggest that insemination occurs before overwintering (Loye, manuscript).

The rate of oviposition in field collections differs from that recorded by Rush (1981) who found egg deposition/week/female to average 8.6 (range 0-17) for first generation colonized bugs reared on suckling mice at 24 C. The number is similar to the egg numbers found in my lab colonies. The number of eggs laid by female bugs in the lab contrasts with those found in the field. Blood fed bugs collected in the field were more heavily replete with blood and exhibited higher fecundity than those fed in the laboratory. Temperature and humidity may have been suboptimal for a complete feeding response or egg

development as Davis (1964) found in C. lectularis which laid eggs most readily at 27 C.

The differences in host-effect on the cliff swallow bug indicate that the bugs' generalized feeding habits are an avenue for the exploitation of a broad resource base in the absence of the cliff swallow. Although the number of bugs feeding and fecundity were greater when cliff swallows were the hosts, mice, sparrows and chicks were all found to be adequate blood meal sources for cliff swallow bugs. The nests in cliff swallow colonies may persist for many years, but the birds do not return to all colony sites annually. Thus the bug's ability to use transient vertebrates may enhance survival during periods of prolonged host absence. My findings, and those of Rush (1981) show that the cliff swallow bug can be readily colonized in the laboratory. It offers a valuable model for further investigation of the physiology, behavior and vector competence of an ectoparasite that is also readily accessible for ecological study in the field.

LITERATURE CITED

- Chapman, R. F. 1982. The insects: structure and function. 3rd. edition. Harvard University Press, Cambridge, MA.
- Cook, B. 1972. Hosts of Argas cooleyi and Ornithodoros concanensis (Acarina:Argasidae) in a cliff face habitat. J. Med. Entomol., 9:315-317.
- Davis, N. T. 1964. Studies of the reproductive physiology of Cimicidae (Hemiptera). I. Fecundation and egg maturation. J. Insect. Physiol., 10:947-63.
- Hayes, R. O., Francy, D. B., Lazuick, J. S., Smith, G. C. and Gibbs, E. R. 1977. Role of the cliff swallow bug (Oeciacus vicarius) in the natural cycle of a western equine encephalitis related alpha-virus. J. Med. Entomol., 14:257-262.
- Hinton, H. E. 1964. Sperm transfer in insects and the evolution of haemocoelic insemination. In: K. G. Highnam, Insect Reproduction, Symposium no. 2, Roy. Entomol. Soc. London, 95-107.
- Hopla, C. E. and J. E. Loye 1983. The ectoparasites and micro-organisms associated with cliff swallows in West-central Oklahoma. I. Ticks and Fleas. Bull. Soc. of Vector Ecology, 8(2): 111-121.
- Loye, J. E. and C. E. Hopla 1983. The ectoparasites and micro-organisms associated with cliff swallows in West-central Oklahoma. II. Life history patterns. Bull. Soc. of Vector Ecology, 8(2):79-84.
- Myers, L. E. 1928. The american swallow bug, Oeciacus vicarius

- Horvath (Hemiptera, Cimicidae). *Parasit.*, 20(2):159-172.
- Rush, W. A. 1981. Colonization of the swallow bug in the laboratory. *Ann. Entomol. Soc. of Am.*, 74(5):556-59.
- Smith, G. E. and R. B. Eads 1978. Field observations on the cliff swallow Petrochelidon pyrrhonota (Viellot) and the swallow bug, Oeciacus vicarius Horvath. *J. Wash. Acad. Sci.*, 68(1):23-26.
- Sooter, C. A., E. E. Bennington and L. B. Daniels 1954. Multiple use of cliff swallow nests by bird species. *Condor*, 56(5):309.
- Sutton, G. M. 1967. Oklahoma birds: their ecology and distribution, with comments on the avifauna of the Southern Great Plains. O. U. Press, Norman, Oklahoma. 674 pp.
- Usinger, R.L. 1966. Monograph of Cimicidae. (Hemiptera-Heteroptera). Thomas Say Foundation vol.7, 585 pp.
- Williams, G. C. 1975. Sex and evolution. Princeton Univ. Press, Princeton, N.J.
- Yanovski, A. D. and C. W. Ogston 1982. Sex differences in size of blood meal in the bed bug Cimex hemipterus (Hemiptera:Cimicidae). *J. Med. Entomol.*, 19(1):45-47.

Table 1: Vertebrates found associated with cliff swallow (Hirundo pyrrhonota) nesting habitat.

Vertebrate	State	Reference
BIRDS		
Bank swallow <u>Riparia riparia</u>	CA	Usinger 1966
Barn swallow <u>Hirundo rustica</u>	CO	Smith & Eads 1978, OK Loye pers. obs.
Blk rosy finch <u>Leucosticte atrata</u>	CO	Sooter et al 1954
Canyon wren <u>Cartherpes mexicanus</u>	OK	Loye pers. obs.
Eastern Bluebird <u>Sialis sialis</u>	OK	Loye pers. obs.
Eastern Phoebe <u>Sayornis phoebe</u>	OK	Hopla & Loye 1984
House sparrow <u>Passer domesticus</u>	TX	Cook 1972, OK Hopla & Loye 1984
Rock dove <u>Columbia livia</u>	CO	Smith & Eads 1978, OK Loye pers. obs.
Say's phoebe <u>S. say</u>	CO	Smith & Eads 1978, OK D.S. Wood pers. obs.
Starling <u>Sturnus vulgaris</u>	CO	Smith & Eads 1978, OK Hopla & Loye 1984
White-winged dove <u>Zenaida asiatica</u>	AZ	Loye pers. obs.
MAMMALS		
Bat <u>Eptesicus fuscus</u>	TX	Cook 1972, OK Hopla & Loye 1984
Bat <u>Myotis velifer</u>	TX	Cook 1972, OK Hopla & Loye 1984
Bat <u>Pipistrellus subflavus</u>	TX	Cook 1972
Bat <u>Tadarida brasiliensis</u>	TX	Cook 1972
Deermouse <u>Peromyscus leucopus</u>	OK	Sutton 1967, Hopla & Loye 1984
Woodrat <u>Neotoma cinerea</u>	CA	Usinger 1966
Woodrat <u>Neotoma floridana</u>	OK	Hopla & Loye 1984
REPTILE		
Rat snake <u>Elaphe obsoletus</u>	OK	Hopla & Loye 1984
Tree lizard <u>Urosaurus ornatus</u>	AZ	Loye pers. obs.

Table 2: FEEDING OF CLIFF SWALLOW BUGS (OECIACUS VICARIUS):

THE NUMBER AND PERCENTAGE OF BUGS THAT FED WHEN GIVEN ACCESS TO DIFFERENT HOSTS.

Host:	Swallow	Mouse	Chick	Sparrow
Bugs: fed/total placed with host (%fed)				
1981				
Adult	127/175 (73)	54/86 (63)	47/71 (66)	354/560 (63)**
Nymph	663/940 (71)	370/792 (47)***	284/457 (62)**	pooled
1982				
Adult	211/271 (78)	183/259 (71)	—	—
Nymph	105/278 (38)	35/185 (19)**	—	—

** p<0.01 Difference between bugs fed on swallows and other hosts.

*** p<0.001

TABLE 3a: AVERAGE BLOOD MEAL WEIGHT (mg) OF O. VICARIUS FED ON TWO HOSTS. (mg , mean \pm SD, (number of bugs sampled)).

Host:	Swallow	Mouse
1981 (July)		
Adult	0.85 \pm 0.0003 (28)	1.2 \pm 0.0007 (40)
Nymph	1.1 \pm 0.0009 (196)	0.57 \pm 0.0005 (50)
1982 (July)		
Female	0.52 \pm 0.0003 (30)	0.33 \pm 0.0005 (27)
Nymph	2.0 \pm 0.0019 (50)	3.2 \pm 0.0029 (50)

TABLE 3b: AVERAGE BLOOD MEAL WEIGHT OF O. VICARIUS FED ON MICE. (mean \pm SD).

Host: Mouse only

November	No.	a. Average Wt.	b. Average Wt.	% b/a
1981	examined	of bug (mg)	blood meal (mg)	
Female	50	2.5 \pm 0.0003	0.57 \pm 0.0005	23.6
Male	50	2.2 \pm 0.0001	0.49 \pm 0.0004	23.6
Nymph 5	50	1.4 \pm 0.00006	0.81 \pm 0.0006	56.3
Nymph 4	50	0.84 \pm 0.0002	0.44 \pm 0.0003	57.4
Nymph 3-2	50	0.62 \pm 0.00004	0.44 \pm 0.0001	70.7

TABLE 4: PERCENTAGE SURVIVAL OF CLIFF SWALLOW BUGS FOR 6 WEEKS
AFTER FEEDING ON VARIOUS HOSTS (N).

Bugs surviving/total given access (% survival)

Hosts:	Swallow	Mouse	Chick	Sparrow
Adult	89 (191)	83 (145)	71 (75)**	60 (105)**
Nymph	97 (1114)	93 (850)**	81 (714)**	68 (783)**

** $p < 0.01$ Mortality difference between bugs fed on swallows and those
on other hosts.

*** $p < 0.001$

TABLE 5: PERCENTAGE OF SURVIVAL OF ADULT O. VICARIUS OVER 3 MONTHS AFTER FEEDING ON TWO HOSTS (1982).

Host:		Swallow	Mouse	Total
month	sex			
17 July	female	100 (n=59)	100 (n=62)	100 (n=121)
fed	male	100 (n=29)	100 (n=33)	100 (n=62)
Aug.	female	27	37	37
	male	28	18	19
Sept.	female	5	21	8
	male	6	15	11

TABLE HEADINGS

Table 1. Vertbrates found associated with Cliff Swallow (Hirundo
Pyrrhonota) nesting habitat.

Table 2. Feeding of Cliff Swallow bugs (Oeciacus vicarius):
The number and percentage of bugs that fed when given access to
different hosts.

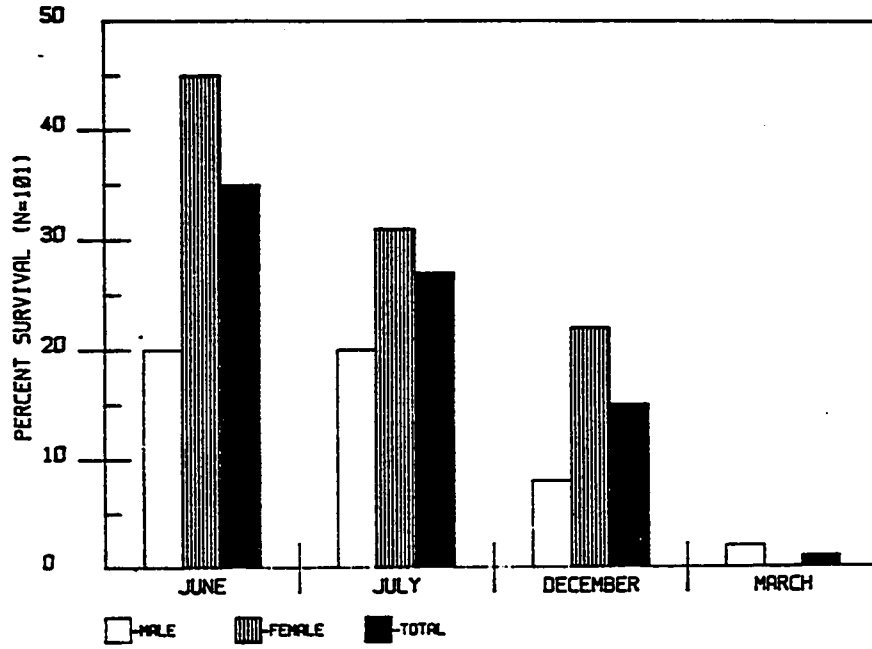
Table 3a. Average blood meal weight (mg) of O. vicarius Fed on
twon hosts.

Table 3b. Average blood meal weight of O. vicarius fed on mice.

Table 4. Percentage survival of Cliff Swallow bugs for 6 weeks after
feeding on various hosts.

Table 5. Percentage of survival of adult O. vicarius over 3
months after feeding on two hosts (1982).

Figure 1: *O. vicarius* survival: Collected in February and June, 1981. Fed on nestling cliff swallows and suckling mice (2 Hrs); held at 78% relative humidity.



PAPER II

The natural history and ecology of the cliff swallow bug
Oeciacus vicarius (Cimicidae:Hemiptera).

The Natural History and Ecology of the Cliff Swallow
Bug (Oeciacus vicarius:Cimicidae:Hemiptera).

Abstract

1. The cliff swallow bug Oeciacus vicarius (Horvath), is a nest-dwelling, polyphagous ectoparasite of the cliff swallow Hirundo pyrrhonota.

2. The life history of the bug is closely tied to that of the swallow during its three month breeding period in the Neartic.

3. Bugs, (predominately adults) anticipate the arrival of the migratory swallows by aggregating in the necks of the nests in colonies that were inhabited by birds the previous year.

4. Swallow use of cliff colonies is unpredictable and bugs disperse between colonies by clinging to the base of the swallows' feathers while feeding.

5. Adaptations to an ephemeral host-food resource include iteroparity, few young, a lengthy maturation time, univoltine life cycle and a long life.

6. Newly emerged bugs mate before overwintering at a time when the sex ratio is male biased. Spring collections are biased towards females which may lay eggs as soon as they feed, without re-mating.

Introduction

The nest-dwelling ectoparasites of the cliff swallow are resource specialists that offer a productive system for investigation of co-evolution of life history patterns. The colonial nesting habits of the cliff swallow, which builds a protective domed nest of mud, lend themselves to parasite maintenance and transmission. The swallow nest is the focus of the life-cycles of four species of nidicolous insects: a bug, flea and two ticks (Loye and Hopla 1983). The nest provides a substrate for oviposition, shelter and most important, host proximity. The three month breeding period of the cliff swallow limits its specialized ectoparasites to a short feeding interval before host migration and a food resource deprivation that lasts a minimum of 9 months. In cliff nesting sites in Oklahoma swallows may not reuse the nests for several years (Hopla and Loye 1983).

The cliff swallow bug, Oeciacus vicarius (Horvath), was chosen as a subject for a study of vector ecology that might exhibit a degree of dependancy on a host that is between a free-roaming, facultative predator and a host dependant, obligatory parasite (Dogiel 1964). Reports on life-history patterns and host associations for the cliff swallow bug have been limited (Myers 1928, Foster and Olkowski 1968, Chapman 1973, Hayes et. al. 1977, Rush 1981, Gorenzel and Salmon, 1982). Here I report on some adaptations to parasitism in the swallow bug and its ecology and life

history as they relate to use of patchy food resources in space (colonies) and time (years), (see MacArthur 1968).

Methods

Field observations were made in cliff swallow colonies located in west-central Oklahoma in Caddo and Grady counties. The primary study site was 'Ryburn cliff colony' (RY) (ca. 750 nests), a comparatively large, old colony occupied in 1978, vacant in 1979 and used again in 1980. It had a dense center portion (ca. 550 nests) built under a protected overhang that is typical of Oklahoma cliff colonies. On the western edge of RY nests occurred along vertical cliff fissures. Other cliff colonies were PAB, newly constructed in 1981 (ca. 1300 nests) and SE, (sampled in 1982; 870 nests) which was used before 1979 and was considered 'old'. Two bridges were sampled: Buggy creek (GC: Grady co.) an old colony (>1000 nests that was built on a 25 m. highway bridge over Buggy creek and used each year by swallows (1979-83). Wilsons' bridge (WB) colony was newly built in a 2 m. high culvert (1982; 550 nests) and occupied in 1983 (100 nests).

Nest collections were chosen using a randomized quadrat system of 4 nest samples. These were taken by placing a ladder up to 8 m. into the lower 1/2-1/3 of the colony. Harvesting of the ectoparasites was described in Loye and Hopla (1983). Neck samples from nests were taken for observation of dispersal stages and sex ratio in spring aggregations of the bugs. The samples were compared between

necks and the body of the nest. Initial neck samples were collected in groups of 20, a further study treated each neck and associated nest separately (n=19 nests). Deviation from normality was used to describe clustered dispersion of bugs between individual nests. The sex ratio of newly emerged bugs in the field was determined by collection of engorged fifth instar nymphs (July, 1982). Sex ratio is defined as the proportion of adults that were male.

Laboratory feeding trials used cliff swallow nestlings and suckling mice, which were placed in a paper bag with the top edge rolled back to simulate a nest with crevices on all sides. Bugs were fed for 2 hours (2100-2300) in the dark. Laboratory colonies of bugs were established from whole-nest collections taken in April, 1982 to reflect the age structure of a population in nature. Colonies were held in jars, provided with a continuous supply of suckling mice and assayed each week. Bugs were held at 28 C, L:D 14/10 photoperiod and 70-75% humidity (humidity above 80% caused mold and death).

The reproductive status of females was discerned by dissection in 0.9% saline and examination with phase-contrast microscopy (200X) for live sperm presence.

Results

Phenology

The bugs began to aggregate on the necks of the nests in April, before the swallows' return. They were found in and

on the necks until mid-May, when nest building and repair commenced (Figure 1). Bugs were most numerous in colonies inhabited the previous year. When the birds arrived, the bugs fed and were dispersed by clinging to the base of feathers. The bugs laid eggs soon after a blood-meal.

Bugs fed actively on nestlings that hatched in mid-June. Feeding behaviour was characterized by active movement of engorged bugs on the cliff face and base, principally at night and during the day in shady areas (RY 1980). When the sun struck the nests the bugs became flattened and immobile, resting on the inside and outside of the nests.

When young swallows fledged and migrated in July, dense aggregations of passive, engorged bugs were found in some nests and crevices behind the nests (Figure 1). The aggregating bugs were molting, often to adulthood. Clustering was observed in a sample of 11 nests from the center of RY colony (August): three nests contained no bugs, four nests held an average of 207 bugs/nest and groups of 1300, 2586, 3474 and 6048 bugs were in each of 4 other nests. The use of the nest that year by birds was not observably linked to clustering. Previously empty crevices contained bugs after the swallow migration. In late July, I examined five comparable crevices 1 meter below the colony: 4 were empty and one crevice held 386 bugs. The bugs in molting clusters were moribund and did not disperse readily when disturbed. Overwintering bugs were predominately third

to fifth instar nymphs, and adults (Table 1).

Life cycle

Reproduction

Engorged adults were observed mating on nests in June and August. In two laboratory observations (18 October, 1982) the male clung to the females' thorax with his legs, curled his abdomen under the right side of the arched abdomen of the female, and probed with the aedeagus (30 and 60 seconds, respectively). The male moved away and the female remained arched for several seconds. Mating occurred via 'traumatic insemination' (Usinger 1966) where the male inserts the aedeagus between the 5th and 6th abdominal sternites of the female bug. The internal morphology of Oeciacus is comparable to Cimex lectularis in which a spermatheca is lacking (Usinger 1966) and sperm is freely released into the haemocoel of the female and migrates to a seminal conceptacle (Usinger 1966).

Mating occurred in newly emerged adults. Viable sperm was found clustered around the ovaries in newly emerged females in 5 of 19 bugs dissected at the end of July (1983). Overwintering females were inseminated (n=10, January; n=8, April 1984) with the sperm apparently contained within the seminal conceptacle as it could not be visualized until the ovaries were squashed. Ovarian development had commenced in January although mature eggs were not observed until after the first blood-meal in May.

In April (1983) 30 females were collected from nests and held away from males and 6 of these laid eggs (36 eggs total, 90% hatch) when fed on suckling mice. Insemination probably occurred in these females in July or August of the previous year and they were able to lay eggs without mating again. Laboratory reared virgin females did not lay eggs after feeding.

The average number of eggs laid by engorged female bugs collected from an active swallow colony (7 July, 1982) was 16 (range 7-27, n=9 females, 92% hatched). Eggs were usually found on the cliff face and inner nest surface but the outer surface was used when population density was high. The eggs were laid in groups of 2-10 over three day periods. Seven females dissected from the same sample contained a mean of 19 eggs (range 8-25) and a few eggs had eye spots. Females fed continuously on suckling mice in the laboratory laid fewer eggs: 6/female with 90-100% hatching success (128 eggs, n=25 females). Females dissected 1 week after being fed in the laboratory (n=44) contained 8 eggs each (one per ovariole).

The eggs developed red eye spots within three days of being laid. The first nymphs hatched at 3-5 days and fed after 24 hours. Molting occurred only after complete engorgement. Adult bugs (n=10) emerged approximately 60 days after the eggs hatched. Developmental trends are illustrated in Figure 1.

Feeding was initiated by touching the hosts' skin

repeatedly with the proboscis. Feeding bugs elevated the abdomen, became immobile and were not easily dislodged. Engorgement on swallow nestlings was rapid and took less than 10-30 seconds. Feeding time on suckling mice took approximately eight minutes (mean 7 min 52 sec, range 1 min 15 sec-29 min;n=27 fourth instar to adult bugs). The bugs dropped and moved away from the host to defecate. Eighty-nine percent of 107 bugs that fed on nestling swallows and suckling mice retreated to the darkened crevices of the paper bag (52% of these were engorged).

When the swallows migrated the bugs fed on other animals that used the cliff swallow nests (Loye manuscript submitted). Two species of bats were found in the swallow colonies: Myotis velifer, female, (July 1980) with more than 600 bugs were collected in an artificial plaster nest in the fall, M. velifer (females, Sept. 1979) and Eptesicus fuscus (one male, Oct. 1979) were also collected (Hopla and Loye 1983). Engorged bugs were found in all the nests that contained bats. The eastern Phoebe: Saynoris phoebe often nests in association with cliff swallows (Hopla and Loye 1983, Loye manuscript) one nest (RY, July 1980) contained 3393 engorged and newly molted bugs. House sparrows Passer domesticus also used nests in large numbers at Buggy Creek bridge from March to October (Hopla and Loye 1983) and were used as hosts by bugs. A cliff swallow nest used by sparrows in early May before the swallows return contained

1735 bugs and 75% of these were nymphs, which suggests that bugs were actively reproducing. Unused nests in a nearby four nest sample taken at the same time contained engorged bugs. These feeding records indicate that alternate hosts provide bloodmeals for bugs and that feeding does occur between April and October.

The bugs stopped feeding and entered the 9 month period of host absence as newly emerged adults and nymphs filled with abdominal fat deposits (dissection 82 females, 9 males, 7 nymphs). Adipose diminished in bugs collected as the winter progressed (n=108 females, 9 males, 5 nymphs).

Collections indicated a high overwintering mortality and similar survival trends in adults and nymphs. The average number of bugs at RY (1980; Table 2) decreased by 99% from August to March (6058 bugs/nest to 68 bugs/nest) but the age structure changed very little. The average bug/nest (n=8 nests) collected at WB decreased by approximately 95% from July (2347 bugs/nest) to April (116 bugs/nest). Some bugs were still found in nests even after 3 consecutive years without swallow use at Beach cliff colony, but by the fourth year no bugs were collected. In the laboratory bugs have not survived over 1 year without feeding.

Population Biology

The age structure of the field sampled populations (RY) was similar to that of the laboratory populations (Tables 1 & 2): a higher proportion of nymphs occurred

during the growth period in June and July. However, adults did not exceed 15% of the total at any time in field populations at RY while the initial collection at SE was higher.

A 12 week survey of developmental stadia in laboratory colonies illustrated the amount of increase and timing of changes in bug population structure (Table 1). The initial colonies contained 43% adult bugs (April 1983; n=231). After 4 weeks the proportion of nymphs increased rapidly from 57% to 88% (n=1048), first instar nymphs comprised 76% of these. By the eighth week nymphs were 82% of 916 bugs with only 12% first instars. A decrease in the total numbers of bugs coincided with adult emergence. One generation was completed in 10-12 weeks which was comparable to the time for adult arrival and nestling development in swallows (Loye manuscript).

The sex ratio was female biased in all field collections except those at the time of nestling fledging in late July (Figure 3). A female bias was also found in laboratory colonies during the first eight weeks of the ten week sample. Males predominated during the ninth week when the greatest proportion of adult bugs were newly emerged (Loye manuscript) During the twelfth week the population had a sex ratio of 0.5 which differed from the female bias of 0.3 at initiation. The field data was similar in late July with a sex ratio for newly emerged adults of :0.43 (n=241 fifth instar nymphs) and 0.52 (n=393) for adults in collections.

I examined the question of dispersal in terms of departure from the necks of nests and arrival at new colonies. If bugs congregated for purposes of dispersal than the proportion collected in the neck of a nest which was 1/20 of the surface area of the entire nest would be expected to be greater than 5% of the total bugs. Twenty eight percent (238 of 822) bugs were collected on necks of 19 nests (April 25, 1984) a much greater number than predicted. Adult bugs were significantly more abundant on necks than were nymphs (47% of 238 adults versus 28% of 584 nymphs, $\chi^2 = p < 0.01$).

I hypothesized that dispersing bugs would tend to be inseminated females. But, samples collected during the first and third weeks of May had no significant difference between the number of females on the necks of nests and the body of the nest (sex ratio: 0.23 vs 0.28). A strong female bias was found in these samples (necks 77% females, n=376, 70 necks; nests 72% females, n=348, 20 nests). A sample of 19 necks and the associated nests (25 April, 1983) with 280 adult bugs (sex ratio 0.4) also did not significantly differ between females in necks and nests (chi-square test).

Newly-built nesting colonies provided an opportunity to compare these patterns of sex bias and age structure with those in site colonization. The new colonies observed were Wilsons' bridge (WB) and a cliff, PAB (1982). The bridge was far removed from any possibility of crawling bug

introduction. Nests were under WB in April when nesting began so ectoparasites were presumed to be introduced. Female bugs predominated (sex ratio: 0.33, n=277 adults, 11 nests, late May & early June). In May newly hatched, early instar bugs dominated the population (75%, n=12, 4 nests) as in June (80%, n=338, 7 nests).

Bugs at PAB, in contrast, had a sex ratio of 0.51 (n=115, 11 nests) with 37% of the bugs adults in June. An older colony RY (late May, 1980) had a similar sex ratio of 0.42 (n=19 adults, 12 nests) and 25% adults (n=79 bugs). The sex ratio and age structure of bugs in PAB was comparable to an older colony. In its second year of use (1983), nests at Wilsons' bridge had a sex ratio of 0.32 (n=74 adults, 16 nests) and 42% adults (n=175 bugs) in April. Crawling may be a likely mode of dispersal on this cliff which was 300 m. from an old colony. I have collected actively moving bugs 50 m. from this colony. The older colonies had more male bugs and 25-40% adult bugs which were present before the birds arrived and active reproduction began. Bugs in the new bridge colony began reproduction later, due to later introduction of adults by swallows (late May), exhibited a more strongly female biased sex ratio and had proportionately fewer adults in the rapidly expanding population (June samples).

Discussion

Behaviour and development in cliff swallow bugs is

closely timed with host activities. Bugs on the necks of the nests were exposed to environmental forces and predation when host proximity was most probable. 'Communal flighting' in sand martins where a group hovers and explores old nests (Jolley and Storer 1945) is observed in cliff swallows returning to Caddo canyons (Hopla and Loye 1983). Aggregation of bugs in the necks of the nests allows movement onto the early visiting swallows for dispersal to colonies that were used by the birds. Humphries (1969) found positive phototaxis and concentration in the newly emerged adults of the bird flea Ceratophyllus styx on the necks of nests in the spring. This behaviour occurs in swallow fleas (Hopla and Loye 1983) and the same stimulus may mobilize the bugs. The rapid location and utilization of host presence by dispersing and feeding of bugs in is also seen in the response of fleas, ticks and other nidicoles (Humphries 1969, Webb 1979, Marshall 1981). The bed-bug, Cimex lectularis migrates to crevices after feeding (Usinger 1966), similarly, crawling away from the host and nest removes the delicate, engorged bugs from possible injury from host activities in the nest. In contrast, bugs that are disturbed by nest breakage move upward from the base of the cliff (Loye personal observation). Aggregation and thigmotaxis are common in parasitic hemipterans (Usinger 1966, Marshall 1981). The dense aggregations of bugs in some of the nests in a colony in late July and August explains

variance in average bugs per nest. Behavioral changes in the bugs such as aggregation at necks, movement away from hosts after feeding and clustering are a response to the hosts arrival, availability, departure and absence.

A reproductive effort tied to food availability is predicted by life-history theory as a short-term response to changable and unpredictable resource presence (Hirschfield and Tinkle 1975, Warner 1980). The oviposition pattern of repeated egg laying in cliff swallow bugs could result from secondary adaptations to high juvenile mortality (Charnov and Schaffer 1973) and unpredictable environmental parameters (MacArthur 1968, Warner 1980). The low reproductive effort invested in several small batches of eggs allows a flexible schedule of egg laying that is spread out as long as feeding can occur. The continuing development and reproduction of cliff swallow bugs in the sparrow nests at Buggy creek illustrates the flexibility of this tactic. Repeated mating is common in both sexes of cimicid bugs (Usinger 1966, Ryckman 1958). High juvenile mortality of bugs in a changeable environment predicts female polygamy (polyandry; Warner 1980), while traumatic insemination may facilitate successful male polygamy (polygyny).

A bug may feed several times on one or many hosts until engorged, thus, repeated, rapid feeding is a vehicle for disease transmission (James and Harwood 1979). Alternative hosts in the swallow colony may also enhance the chances of

micro-organism passage between vertebrate species. Little is known about the role of alternate hosts and micro-organisms transmission in the life cycle of cliff swallow bugs beyond feeding records (Smith and Eads 1978, Hopla and Loye 1983, Scott et. al. 1984, Loye manuscript submitted).

The age structure of the bug population is comparable to other animals living in an unpredictable environment with high juvenile mortality (Stearns 1976). A rapid rate of increase in the bugs occurs during the period of nestling development (Loye manuscript). Although adult bugs are always present, newly emerged adults predominate at the end of ca. 10 weeks both in the laboratory and the field. Since the bugs overwinter in all stages and lay eggs in several batches the age distribution is spread out over time and allows maturation of adults for as long as food is available. Females facing unpredictable mating opportunities due to overwintering mortality would have enhanced opportunity to produce offspring if mating occurred at the time when males were most numerous (Williams 1975).

Adult bugs predominate as dispersers in the necks of nests. However more females are present at the new colonies which may indicate that they are the major dispersers. Though dispersal may be an advantageous migration before the nest habitat deteriorates with disuse (Dingle 1972) it is more likely to assure blood meals and

egg laying opportunities at the nesting colony site.

In summary, the cliff swallow bug is characterized by adaptations to limited and unpredictable resources by: iteroparity, few young, a lengthy maturation time, one generation (and a partial second) and a long life (Loye and Hopla 1983). This life history pattern is predicted by 'bet-hedging' (Schaffer 1974, Sterns 1976, Tallamy and Denno 1981) with variable juvenile mortality. The pre-diapause mating found in these bugs is also anticipated (Williams 1975) as a strategy seen in animals facing cyclic periods of stress. The question of adaptation to resource predictability for the bug when cliff swallows return to cliff nesting sites at intervals as great as 5 years may be answered by comparative life history studies between habitat sites (cliffs and bridges) or geographic areas where colony usage is more or less cyclic.

PLEASE NOTE:

This page not included with original material. Filmed as received.

University Microfilms International

References

- Chapman, B. R. (1973). The effects of nest ectoparasites on cliff swallow populations. Ph. D. thesis, Texas technical University. Lubbock, Texas.
- Charnov, E. L. & Schaffer, W. M. (1973). Life history consequences of natural selection: Cole's result revisited. *American Naturalist*, 107, 791-793.
- Dingle, H. (1972). Migration strategies of insects. *Science*, 175, 1327-1335.
- Dogiel, V. A. (1964). *General Parasitology*. Oliver and Boyd, Edinburgh.
- Foster, W. A. & Olkowski, W. (1968). The natural invasion of artificial cliff swallow nests by Oeciacus vicarius (Hemiptera:Cimicidae) and Ceratophyllus petrochelodoni (Siphonaptera: Ceratophyllidae). *Journal of Medical Entomology*, 5, 488-491.
- Gorenzel, W. P. & Salmon, T. P. (1982). The cliff swallow: biology and control. Proceedings of the 10th Vertebrate Pest Conference. (Ed., R. E. Marsh), University of California, Davis, CA.
- Hayes, R. O., Francy, D. B., Lazuick, J. S., Smith, G. C. & Gibbs, E. R. (1977). Role of the cliff swallow bug Oeciacus vicarius in the natural cycle of a western equine encephalitis-related alpha-virus. *Journal of Medical Entomology*, 14, 257-262.

- Hirshfield, M. F. & Tinkle, D. W. (1975). Natural selection and the evolution of reproductive effort. Proceedings of the National Academy of Science, U.S.A, 72, 2227-2231.
- Hopla, C. E. & Loye, J. E. (1983). The ectoparasites and micro-organisms associated with cliff swallows in West-central Oklahoma. I. Ticks and fleas. Society of Vector Ecology Bulletin. 8(2), 111-121.
- Humphries, D. A. (1969). Behavioral aspects of the ecology of the sand martin flea Ceratophyllus styx jordani Smit (Siphonaptera). Parasitology, 59, 311-334.
- James, M. T. & Harwood, R. F. (1979). Herm's Medical Entomology. 7th Edition, Macmillan Co. London.
- Jolley, A. E. & Storer, R. (1945). Report on the sand martin inquiry 1944. pp 10-21. Leichester Literary and Philosophical Society., Ornithological section for Leicestershire and Rutland.
- Loye, J. E. submitted 1984, Society of Vector Ecology Bulletin. Host effects on feeding and survival of the polyphagous cliff swallow bug (Oeciacus vicarius: Cimicidae: Hemiptera).
- Loye, J. E. & Hopla, C. E. (1983). The ectoparasites and micro-organisms associated with cliff swallows in West-central Oklahoma II. Life history patterns. Society of Vector Ecology Bulletin, 8(2), 79-84.
- MacArthur, R. H. (1968). Selection for life tables in

- periodic environments. *American Naturalist*, 102, 381-383.
- Marshall, A. (1981). *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- Myers, L. E. (1928). The American swallow bug, Oeciacus vicarius Horvath (Hemiptera, Cimicidae). *Parasitology*, 20(2), 159-172.
- Ryckman, R. E. (1958). Description and biology of Hesperocimex sonorensis, new species, an ectoparasite of the purple martin (Hemiptera: Cimicidae). *Annals of the Entomological Society of America*. 51, 33-47.
- Rush, W. A. (1981). Colonization of the swallow bug in the laboratory. *Annals of the Entomological Society of America*. 74(6), 556-559.
- Scott, T. W. , Bowen, G. S. and Monath, T. B. 1984. Effects of Fort Morgan virus on avian host reproduction. *J. Trop. Med. and Hyg.* 33(5):981-991.
- Schaffer, W. M. (1974). Optimal reproductive effort in fluctuating environments. *American Naturalist*, 108, 783-790.
- Smith, G. E. & Eads, R. B. (1978). Field observations on the cliff swallow Petrochelidon pyrrhonota (Viellot) and the swallow bug, Oeciacus vicarius Horvath. *Journal of the Washington Academy of Science*, 69(1), 23-26.

- Stearns, S. C. (1976). Life history tactics: a review of the ideas. *The Quarterly Review of Biology*, 51, 3-47.
- Tallamy, D. W. & Denno, R. F. (1981). Alternative life history patterns in risky environments: an example from lacebugs. in: *Insects and life history patterns: geographic and habitat variation*. (eds: Denno, R. F. & Usinger, R. L. (1966). *Monograph of Cimicidae. (Hemiptera-Heteroptera)*. Thomas Say Foundation, Vol. 7.
- Warner, R. R. (1980). The coevolution of behavioral and life history characteristics. in: *Sociobiology: beyond nature/nuture?* (eds: Barlow, G. W. & Silverberg, J.) pp 151-188. American Association of Scientists symposium 35. Westview press, Boulder, Colorado.
- Webb, J. P. (1979). Host-locating behavior of nymphal Ornithodoros concanensis (Acarina: Argasidae). *Journal of Medical Entomology*, 16(5), 437-447.
- Williams, G. C. (1975). *Sex and Evolution*. Princeton University Press, Princeton, N.J.

Table 1: Cliff swallow bug and swallow activities in Caddo Canyons, Oklahoma (Ryburn cliff 1980).

	APRIL				MAY				JUNE				JULY				
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	
BUGS																	BIRDS
ON NECKS			////		■												RETURN
FEED AND DROP					////												BUILD NESTS
MATE OVIPOSIT					■		////		* ■								EGG HATCH
AGGREGATE											////						FLEDGE
OVERWINTER											■				////	▶	MIGRATE

BUGS ///
 BIRDS ■
 * Co. 12d

Table 2: Laboratory Development of Bugs.

Age structure of colony (May 1- August 1, 1982).

week	1	4	8	12
stage	n (%)	n (%)	n (%)	n (%)
male	31 (13)	45 (4)	93 (10)	175 (25)
female	69 (30)	80 (8)	71 (8)	155 (22)
adults	100 (43)	125 (12)	164 (18)	330 (57)
fifth	4 (2)	6 (1)	65 (7)	4 (1)
fourth	38 (17)	1 -	150 (16)	56 (8)
third	65 (28)	114 (11)	427 (47)	115 (17)
2nd & 1st	24 (10)	802 (76)	110 (12)	185 (27)
nymphs	131 (57)	923 (88)	752 (82)	360 (53)
total	231	1048	916	690
eggs	76	691	48	102

Table 3: Field collections of bugs.

Age structure of bugs in field collections-Ryburn 1980

month	May 24	June 6	July 19	August 30	March 22
week	1	6	8	14	
stage n (%)					
male	5 (7)	365 (9)	203 (6)	285 (5)	14 (4)
female	4 (6)	399 (10)	190 (6)	497 (8)	23 (6)
adult	9 (13)	764 (19)	393 (12)	782 (13)	37 (10)
fifth	6 (9)	796 (45)*	105 (53)*	63 (35)*	44 (4)*
fourth	3 (4)	203 (12)	18 (9)	38 (21)	30 (3)
third	28 (42)	719 (41)	73 (37)	76 (42)	34 (3)
2nd & 1st**	22 (32)	34 (2)	4 (2)	5 (3)	1 (1)
other	0 -	1335 -	2800 -	5084 -	238 -
nymphs	59 (87)	3087 (81)	3000 (88)	5266 (87)	347 (90)
total	68	3851	3393	6048	384
nests/sample	4	4	1	1	4

* nymphs subsampled for %

** first instar probably higher

Tables:

1. Cliff swallow bug and cliff swallow activities in Caddo Canyons, Oklahoma (Ryburn Cliff 1980).
2. Laboratory development of bugs.
3. Field collections of bugs.

Figure 1: Bug development in laboratory colonies: male, female and nymphs, April 11-June 6, 1983.

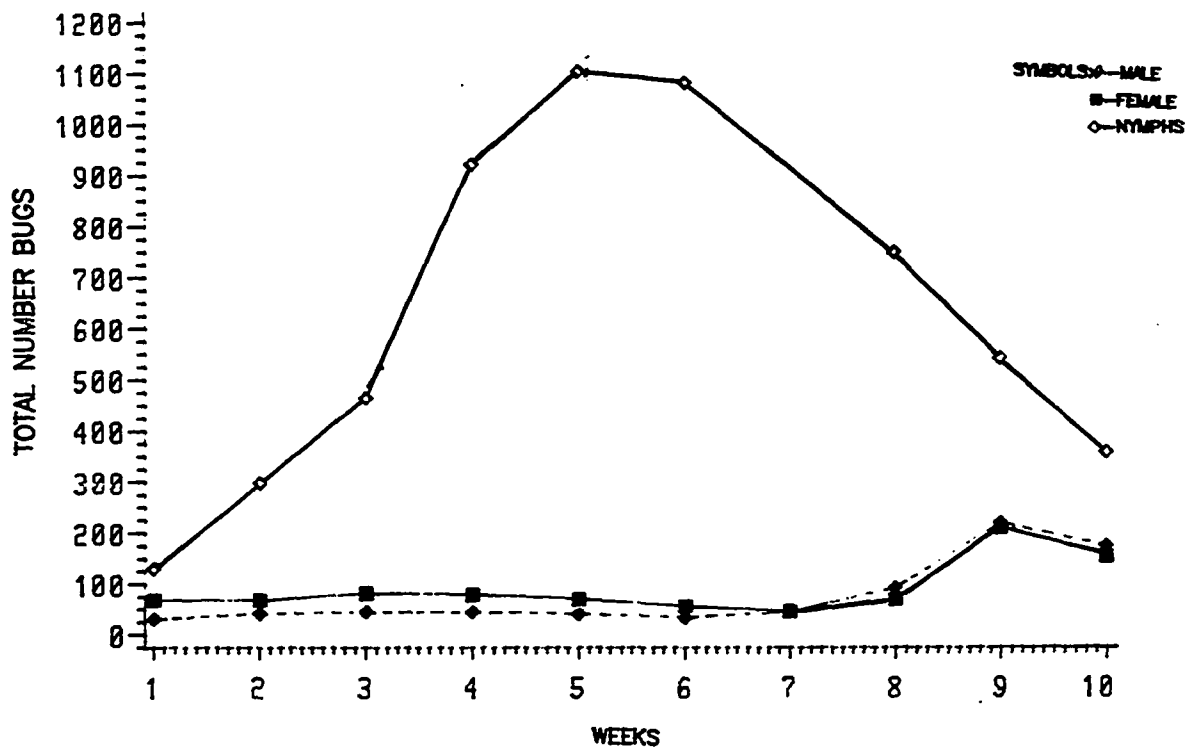
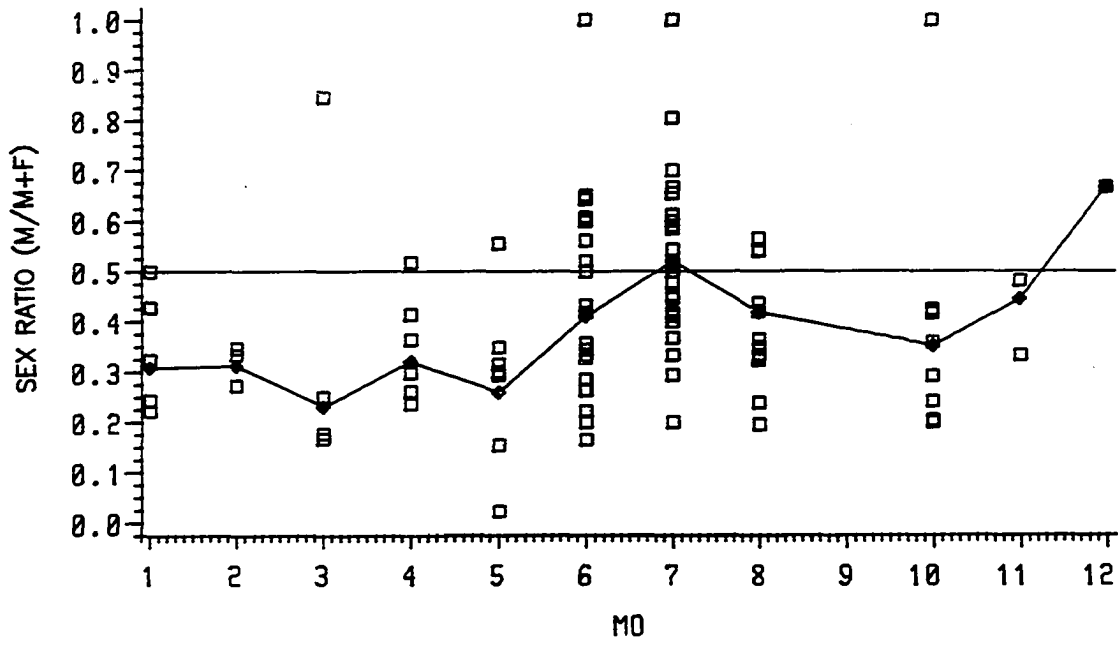


Figure 2: Sex ratio of field collected bugs: mean and range by month, 1980-83.



Figures:

1. Bug development in laboratory colonies, April 11-June 6, 1983.
2. Sex ratio of field collected bugs: mean and range by month, 1980-83.

PAPER III

Population ecology of the cliff swallow bug,
Oeciacus vicarius (Cimicidae:Hemiptera).

III Population ecology of the cliff swallow bug, Oeciacus vicarius. (Hemiptera: Cimicidae).

Abstract

1. Cliff swallow bugs are blood-feeding ectoparasites of the colonial cliff swallow.
2. The life history and population dynamics of the bug are closely adapted to the activities of its host.
3. The bugs respond behaviorally to the arrival of the birds by moving to the necks of the nests. Bugs disperse on the bodies of the birds to other colonies.
4. Cliff swallows are present in Oklahoma for 3 months (April-July) and the population increase of bugs is most closely correlated with time.
5. The use of nesting colonies by swallows varies: on cliffs, swallows depart synchronously and cliffs are abandoned for one or more years before being reused. Bug populations increase to very high levels and are maintained overwinter in protected crevices and nests on the cliffs.
6. In contrast, the bridges in this study were reused by swallows each year. Departure was spread out over 3 weeks. The density of bugs in bridge nests was significantly lower than on cliffs that were used that year, but not significantly different than cliff colonies abandoned for 1 year.
7. Bugs were fewer in newly built colonies and on the edges of older colonies, but nestling weight was significantly

lower as well.

8. Alternate hosts give an opportunity for bugs to feed and develop after swallows migrate.

9. A high variance in numbers of bugs/ nest illustrates aggregation.

INTRODUCTION

The role of many blood-sucking arthropods in disease transmission makes a knowledge of their life history and ecology of general medical interest. When such ectoparasites are specialists upon one or a few hosts, there is potential for quantifying patterns in the spatial and temporal distribution and abundance of the vector/host association exploited by micro organisms. The dense colonies of mud nests built by the cliff swallow (Hirundo pyrrhonata) offer a study area for the interaction of hosts and ectoparasites that is contained within a limited area of nesting habitat and accessible to researchers. The cyclic return of the swallows to the colony sites gives the long-lasting nesting sites a reliable, although unpredictable useage history. The ectoparasites of the cliff swallow are nidicolous to varying degrees and use the nest substrate as their primary habitat rather than the body of the host as in some more dependent species (Loye and Hopla 1983). The biology of the cliff swallow associates: ticks, fleas and cliff swallow bugs, is reflected foremost in an ability and adaptation to use an ephemeral food resource - the cliff

swallow (Loye and Hopla 1983).

Cliff swallow bugs (bugs) live in mud nests built by colonial cliff swallows on cliffs, bridges and barns. When the cliff swallow migrates south in July the bug remains behind to over-winter in the nests and associated crevices of the habitat. The nest and crevices on the cliff provide ameliorated habitat protecting the insects from the extremes of weather such as temperature fluctuations and dryness and brings the vertebrate host into association with blood feeding arthropods. A bug is faced with a period of starvation of 9 months or more before the periodic return of its food resource. The transitory presence of a migratory bird-host might lead to a responsive interaction with the bird in terms of the phenology of life histories and perhaps coevolution.

Microorganisms often utilize arthropod/vertebrate associations as maintenance and transmission components in their life-history. An alpha virus (Ft. Morgan virus) is maintained in overwintering cliff swallow bugs and circulates in both swallows and sparrows (Passer domesticus) during the birds' nesting period (Hayes et. al. 1977, Scott et. al 1984). The cliff swallow bug (Oeciacus vicarius) was found to be the vector of a new species of virus in Oklahoma (Hopla and Loye 1983) during studies of the ectoparasite ecology in the Oklahoma cliff swallow colonies. This paper examines the population biology of this vector, the cliff swallow bug, in relation to patterns in the availability of

the cliff swallow.

MATERIALS AND METHODS

Study site: The canyon system used in this study was 15 km east of Binger, and approximately 8 km north of Anadarko, in Caddo County Oklahoma. The Buggy Creek bridge colony was located in Grady County 29 km east of Binger Oklahoma. The U. S. Government Weather service, provided data for Anadarko, Caddo County, Oklahoma.

The cliff swallow colonies were visited each month and observations were made on the activities of the birds: absence, presence, dates of arrival, egg hatch, fledging and departure during 1979 to 1983.

Population density of the bugs was determined from samples of 4 associated nests in quadrats. Collections were taken each month except during the swallow breeding season. Quadrats were randomized by the sampler (using a random number table) with accessibility limited to 30 feet from the base of the cliff. Nests were removed with an entrenching tool and placed in a heavy paper bag which was then sealed in a large plastic bag. Nest material was broken, sieved and sorted in enamel pans. The ectoparasites were counted, sexed and developmental stadia determined; The mean number of bugs in a four nest sample were referred to as average bugs/nest.

Variation in density of bugs in colonies was determined using quadrat samples of nests. The average number of bugs/4 nest sample was tested for significant differences in

variance and mean between cliff colonies (birds present and without host usage), and bridge colonies where birds were present each yearly breeding season. Nine colonies were used in these tests (Table 1:1-9). Statistical tests used were ANOVA, Student-Neuman-Keuls and paired t-tests. Statistical analysis relied on SAS (Helwig and Council 1979). Chi-square and negative binomial tests were performed using Apple programs written by Dr. F. J. Sonleitner, University of Oklahoma, Norman, Oklahoma.

Further measure of bug density and distribution between sections employed transect samples. These were taken ca. 10.0 m X 0.5 m from the center of the colony to the sparsely nested edge, 1 m above the lower edge of the colony. Ten nests were collected in each area. Nestlings were weighed using a triple beam balance at ca. 12 days after hatching. Weights were taken during banding from 60 nests located in belt transects in 6 colonies. These weights were correlated with the numbers of bugs found in 10 nests collected from each section of the transects.

Results

I. Habitat and Ecology

Cliff swallow populations are an ample food resource for the bugs in their colonies during the season of use. The groups of nests are built on cliffs, bridges and barns. In Oklahoma the plains outside the canyon system are devoid of natural nesting sites and bridges are used.

The average size of the 9 colonies studied was 650 nests (range 100-1500). 'Small' colonies were those with fewer than 500 nests in use and 'large' colonies were those with more than 500 nests. Cliff swallow colonies were categorized as: 1. newly built on previously unused cliff substrate, 2. old, with nests present from the previous year, 3. on bridges or in culverts and 4. domestic, in barns (colonies are listed in Table 1).

Seasonal patterns in bird activity are illustrated in association with temperature and rainfall in Figure 1. Spring temperatures and precipitation increased at the time of the birds' return. Insect activity was great each spring when the moisture increased: Dipterans (Chironomidae, Tachinidae, Syrphidae, Sarcophagidae, Tipulidae); Homopterans (Cicadellidae, Membracidae); small Lepidopterans and flying ants were collected from the mouths of swallows during mist netting and banding. The swallows migrated when the summer was hot and dry and observable insect activity had decreased. Synchronous migration occurred at all cliff colonies, however the protected bridge over Buggy Creek harbored swallows for several weeks longer than the cliffs, and fledging and departure of the swallows was asynchronous.

II Population distribution

I compared the dynamics of O. vicarius populations in the nests between colonies that differed in bird usage and type of nesting habitat. Analysis of the effects of seven

parameters on the distribution and abundance of bugs was undertaken: 1. bird presence or absence, 2. cliff versus bridge habitat, 3. colony age, 4. colony size, 5. location within colonies, 6. individual differences in colony use by birds and 7. correlations of bird and bug interaction. Colonies were examined individually for differences within and between the parameters (ANOVA). If no significant difference was found between colonies I then pooled ~~samples~~ which increased the sample size of nests available for analysis.

I predicted that the presence of the swallows would cause the bug populations to be much higher during the birds breeding season. The effect of the seasonal presence of birds on the average bugs/nest was tested for each colony for May to August, the time of greatest bug abundance and September to April for each year from 1979 to 1983 by colony. Bug populations were tested seasonally within colonies (PC omitted). Only two older, large south facing cliff colonies had a significantly higher number of average bugs/nest during the period of swallow occupancy (RY'80, $n=32$ nests, $T=18.1$, $p<0.03$ and DG'82, $n=51$ nests, $T=12.8$, $p<0.06$). The absence of a significant difference over the seasons within colonies might suggest a low mortality over-winter that is not borne out by more intensive sampling (see fig. 4). The number of over-wintering bugs was not significantly different between colonies.

Cliff colonies in Oklahoma were not used for 2 consecutive years, this differs from the repeated use of Buggy Creek bridge in Caddo Co. as well as other bridge colonies I observed in Murray and Johnson counties Oklahoma. I speculated that cliffs might harbor higher numbers of ectoparasites which would suffer low over-wintering mortality due to the protection offered by cliff crevices in comparison to the colder, more exposed bridges where harborages were limited.

During the years when the birds were present in cliff colonies there were significantly higher average bugs/nest than either the years when birds were absent or from bridge colonies ($F=4.71$, $p<0.009$; fig. 2). There was no significant difference in bug numbers between bridges and the cliffs when birds were seasonally absent, indicating that the bug numbers are consistently lower in samples from the bridge habitats in spite of yearly use by the swallows ($n=195$ nests on the cliffs with birds, $n=71$ nests, cliffs without birds, $n=160$ nests bridge).

The introduction of bugs to new colonies was examined at one bridge and two cliff sites where no remnants of previous nests existed (WB'82, PAB'81, P82), as expected, these new colonies had fewer ectoparasites on the average during the breeding period than older colonies that already contained bugs and were used by swallows (SE'82, RY'83, WB'83, $p<0.05$, SNK, $n=134$, Fig. 3a&b, 4). In the three new colonies the number of ectoparasites increased over the

breeding season, and declined over the winter (Fig.3a & b).

Bug populations were compared between the newly built, inhabited colonies and the unused older colony sites during the ectoparasite overwintering period (August-April); there was no significant difference in average bugs/nest. Buggy Creek bridge, although used each year by swallows was comparable in average bugs/nest to the new colonies.

A comparison of two new colonies, PAB cliff (390 nests) and Wilson bridge, a 1.5 m high culvert (550 nests) illustrates the similarities in the average number of bugs per nest during the initial year of new colony establishment (Fig. 3a & b). The bridge colony maintained bugs in nests during the winter while the numbers of bugs in nests on the cliffs decreased due to movement to crevices. However, in May the average bugs/nest was once again the same. When the birds returned to the bridge the second year (1983) the numbers of bugs increased four-fold while those at the abandoned PAB decreased the second year of sampling.

Population increase in an older colony (RY 1980; Fig. 4) was much greater. Bugs in the new colony, PAB (1981) increased from 0 to 60 average bugs/nest and then dropped to 30 bugs/nest by August. In comparison, population increase in the older colony (RY) was 10 fold (from ca. 70 to 1050 average bugs/nest) over the swallow breeding period. Large numbers of bugs survive in previously built nests and associated crevices. The year after the colonies were used

a difference in numbers of average bugs/nest still existed between new and old colonies. Few bugs (0-10) were found in collections from PAB, while Ryburn maintained higher overwintering populations of bugs. An infestation of 2-3 pairs of house sparrows occurred at PAB in March, 1982. One sparrow nest contained 1735 bugs, many of which were blood fed. Such alternate hosts offer a route of survival for the bugs during the swallows absence.

A cost of coloniality to birds might be the increase in numbers of ectoparasites with colony size. Greater numbers of average bugs/nest were associated with increase in colony size from quadrat samples collected from 6 colonies: WB'82 and '83, PAB'82, P82, RY'83 and SE'82 during May-July when birds were present ($r^2 = 0.22$, $p < 0.001$, $n = 112$ nests). Two large colonies (WB'82, RY'83) had significantly higher average numbers of bugs/nest ($p < 0.05$, SNK) than the smaller more sparsely nested colonies.

I also looked at variation in bug numbers according to location within areas in the colonies: center (c), intermediate (i) and edge (e). The center of colonies typically had complete nests in close association. This was the area used first by the returning birds. Bugs in the center were anticipated to be greater in number due to previous usage, population buildup and movement of the bugs to the food source. Field collections of average bugs/nest were significantly different ($F = 11.39$, $p < 0.0001$, $n = 281$ nests, ANOVA) between locations for 4 large, older colonies

(WB'83, RY'83, SE, DG; April-August collections) with center nests containing the most bugs. All were densely nested large colonies. Bug populations at Wilson bridge differed between the center and edge ($G=139.0$, $p<0.01$, $n=48$ nests) the second year it was used by swallows (1983). The large Ryburn cliff colony had significantly higher numbers of bugs in the center area in 1980 ($G=917.6$, $p<0.01$, $n=62$) when it was a breeding colony and in 1981 ($G=71.0$, $p<0.01$, $n=29$) when birds were absent as well. Two other old, large colonies (SE'82 and DG'82) had significantly higher numbers of bugs/nest in the center ($G=51.4$ and 384.2 respectively, $p<0.01$, $n=35$ and $n=26$). Bug populations at three new colonies: two on cliffs (P82, PAB) and Wilson bridge showed no statistical difference in bugs between locations.

Bug population distribution within the colonies differed not only in location but varied in the usage of individual nests. Single nest samples taken at PAB in June of 1981 when birds had used the nests and then were absent the next year showed a wide variance in the total numbers of bugs indicative of a clustered dispersion (Fig. 5).

Seventeen individual nests were collected in April, 1984 (RY) and a significant clustering tendency was seen in the bugs (mean number=49, S.D.=41, C.V. 85%) before the arrival of the birds. In the late summer when birds were absent bugs were also found aggregated in great numbers in some nests (Loye manuscript).

III Host/Parasite interaction.

III Host/Parasite interaction.

Quadrat samples indicated that the bug population increased in response to the birds' arrival and use of the colonies. Further quantification of the host/parasite interaction and effect utilized belt transects of 60 nest/colony for weights and 30 nests/colony which were removed for comparison of bug density and nesting mortality.

The effect of colony size on the numbers of bugs and the nestling weights was determined using regression. A significant increase in the total number of bugs with colony size ($r^2 = 0.74$, $p < 0.001$) was similar to the quadrat samples. Nestling weight was also positively associated with increased colony size ($r^2 = 0.26$, $p < 0.001$).

The density of bugs was correlated with the presence of nestling swallows. Bugs increased rapidly and significantly in number from May when the adult birds arrived and laid eggs to July when fledging and migration occurred ($r = 0.26$, $p < 0.01$). The correlation between the numbers of bugs collected in the colony after the birds fledged and nestling weight (6 colonies) was significant ($r = 0.14$, $p < 0.001$).

The average nestling weight among the 4 colonies was grouped into 2 categories ($p < 0.05$, SNK; Table 2). The heavier nestlings were in the large SE, PC and WB colonies and lighter nestlings in P82 a new, small cliff colony. P82 was built several weeks after the other colonies and the young were abandoned when the adult birds departed.

An analysis between locations in 4 colonies showed difference in nestling weight in the center, intermediate and edge ($F=84.84$, $p<0.001$). The mean nestling weight was higher in the central nests (Table 2) than in the intermediate or edge sections. When specific colonies were examined in 1982 no differences in weight associated with location was seen in Wilson's bridge (WB) and Pugh cave (PC). Nestlings were heavier in the central area of SE, an old, sparsely nested cliff and P82 the new cliff colony. In 1983 nestlings (8-10 days old) were weighed at Wilsons' bridge and Ryburn cliff (RY) (during banding) these were also heavier in the center portion of the colony. The average weight at WB was 6.2 g. ($n=68$ birds) in the center and 4.6 g ($n=59$ birds) at the edge ($F=8.43$, $p<0.004$), Ryburn cliff was similar (6.9 g, $n=64$ birds, center; 4.7 g, $n=83$ birds intermediate; 3.7 g, $n=50$ birds edge; $F=10.07$ $p<0.0001$). It is notable that the central areas of SE and RY were protected overhangs, like PC cave.

A location effect was also seen in the total number of bugs collected in all 6 colonies after fledging (Table 3; $F=11.39$, $p<0.001$). However the area that contained the most bugs was not consistently the center in each colony, unlike the quadrat samples.

Clutch size was significantly associated with colony size ($F=5.62$, $p<0.0001$) and with location ($F=2.21$, $p<0.005$). Larger colonies and central locations had more chicks.

The mortality of nestlings was assessed by counting the dead left in the nests after fledging. The factors involved in death were unknown, however, mortality was consistently low in all 6 colonies (Table 3).

Discussion

The Caddo canyons may have sheltered cliff swallow colonies for hundreds of years (Hopla and Loye 1983). The microclimate of the canyons has higher humidity and water availability (Rice, 1960) and supports dense insect populations (personal observation). Emlen and Demong (1975) associated synchronized fledging in bank swallows with cyclic insect abundance. However, habitat and ectoparasites rather than food constraints between cliffs and Buggy creek bridge in my study may effect synchrony in the swallow departure. The insect availability does not observably differ between the bridge and cliffs used the year before but ectoparasite abundance did. Ectoparasite mortality may increase due to the limitations of overwintering sites such as crevices on bridges and the vibration from traffic which may increase nest loss (Scott, et. al. 1984).

The repeated use of cliff faces for colonial nesting has led to adaptations in the bugs using the nests to rapid response to food resource availability both in behaviour and life history strategy (Loye and Hopla 1983, Loye manuscript). Swallows are always present in the canyon system in May-July, but their absence from colonies causes a relative food shortage for the bugs (Andrewartha and Birch

1960). Some of the effects of this cyclic usage pattern are seen in the population ecology of the bugs.

The increase in bugs in response to the swallows' seasonal presence was lower at the two bridge colonies when compared with cliff colonies in use. In this context the continuous use of Buggy creek bridge compared with the periodic cliff colony disuse of 1 or more years makes the question of parasite effect on the birds choice of colony of great interest (Loye manuscript). Cliff substrates were used more often for nesting than the numerous bridges and barns available in the area. If ectoparasite buildup has an effect on nesting patterns independent of substrate (cliff, bridge or barn) then bridges or barns with very high numbers of ectoparasites would show a cyclic usage pattern. John T. Emlen, Brian Chapman (personal communication) and I have observed this. Secondly the removal of the numerous ectoparasites should encourage colony reuse by swallows. J. T. Emlen has demonstrated this by spraying nests in a heavily bug infested colony on a barn with insecticide, and observing reuse of those specific nests by swallows (personal communication). Bugs were introduced to colonies when birds were building new nests at PAB and WB (Loye manuscript, see also Foster and Olkowski 1968) but the numbers were low. However, newly built colonies like P82 were built later and perhaps greater nestling mortality occurred due to inclement weather. At two other newly built

colonies: Herrons' barn and Costello cliff (1980) no more than four bugs were collected in the nests after the breeding season. Both colonies were submitted to temperatures >100 degrees F. for weeks with the high nestling mortality (>90%) and lack of ectoparasites was attributed to heat.

The shelter offered by the nests attracts a variety of animals and may serve to maintain ectoparasites through periods of host absence (Loye submitted). The most protected areas of the cliffs are centrally located where nests are the most dense and these last longer than nests in other parts of the colony. An inconsistent clumped pattern of bug distribution within colonies is due to aggregating behaviour that is typical of nest dwelling cimicids (Usinger 1966).

The life cycle of the cliff swallow host makes them a briefly seasonal food resource for the bugs. As weeks pass and the bugs increase in numbers, the detrimental effect on the birds must undoubtedly become great. Chapman (1973) demonstrated important differences in blood picture and weight of nestlings in the same colony with and without ectoparasite stress. However, an increase in both ectoparasitism and nestling weight with colony size was observed in bank swallows by Hoogland and Sherman (1966). Trends of larger nestlings and bigger broods in larger colonies, and little difference in weight and mortality between colonies may be explained by parental provisioning

which compensates for stress caused by increased numbers of bugs (Emlen 1984).

Life history patterns of the bugs are characterized by a use of a patchy food resource in the colonies (Loye and Hopla 1983). The population ecology of cliff swallow bugs would be predicted to have an increasing, non-equilibrium growth type (Caswell 1982, Price 1980, Loye manuscript) with both rapid increase and decrease in numbers. Price (1980) defines a non-equilibrium population as one that does not fluctuate with a typical probability range around an average population size. Unstable populations are typified by a high variance which is found in O. vicarius. Highly aggregated or over-dispersed patterns are explored in the models of host/parasite interaction of Anderson and May (1978), who suggest that parasite accumulation differs in individual hosts. The facultative parasitism of cliff swallow bugs place the nest in the typical supportive role that the host plays for more dependent organisms (Marshall 1981). The wide variance in samples and clustering behaviour of cliff swallow bugs make an emphasis on the study of individual nests, or within patch population dynamics a necessity to further understanding of these organisms.

LITERATURE CITED

- Anderson, R. M. and May R. M. 1978. Regulation and stability of host-parasite population interactions I. regulatory processes. *J. An. Ecol.* 47:219-247.
- Andrewartha, H. G. and Birch, L. C. 1960. some recent contributions to the study of the distribution and abundance of insects. *Ann. Rev. Entomol.* 5:219-242.
- Caswell, H. 1982. Life history theory and the equilibrium status of populations. *Am. Nat.* 120(3):317-339.
- Chapman, B. B. 1973. The effects of nest ectoparasites on cliff swallow populations. Ph. D. thesis. Texas Tech. Univ., Lubbock, Tx.
- Emlen, J. T. 1952. Social behavior in cliff swallows. *Condor* 54(4):177-199.
- Emlen, J. T. personal communication.
- Emlen, S. T. 1984. The evolution of cooperative breeding. in: Krebs, J. R. and Davies, N. B. *Behavioral Ecology*. 2nd Ed. Sinauer Assoc. Inc., Sunderland, Ma. 493pp.
- Emlen, S. T. and Dejong, N. J. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. *Science* 188:1029-1031.
- Foster, W. A. and Olkowski, W. 1968. The natural invasion of artificial cliff swallow nests by Oeciacus vicarius (Hemiptera:Cimicidae) and Ceratophyllus petrochelodoni (Siphonaptera:Ceratophyllidae). *J. Med. Ent.* 5:488-491.

- Hayes, R. O., Francey, D. B., Lazuick, J. S., Smith, G. C. and Gibbs, E. R. 1977. Role of the cliff swallow bug (Oeciacus vicarius) in the natural cycle of a western equine encephalitis-related alpha-virus. J. Med. Entomol. 14:257-262.
- Helwig, J. T. and Council, K. A. 1979. Statistical Analysis system user's guide. Statistical Analysis System Institute, Raleigh, North Carolina.
- Hoogland, J. L. and Sherman, P. W. 1966. Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecol. Monog. 46:33-58.
- Hopla C. E. and Loye, J. E. 1983. The ectoparasites and micro-organisms associated with cliff swallows in West-central Oklahoma. I. Ticks and fleas. Bull. of Vector Ecol. Soc. 8(2):111-121.
- Loye, J. E. submitted Bull. Vector Ecology Soc. 1984. Host effects on feeding and survival of the polyphagous cliff swallow bug (Oeciacus vicarius:Cimicidae:Hemiptera).
- Loye, J. E. and Hopla, C. E. 1983. The ectoparasites and micro-organisms associated with cliff swallows in West-Central Oklahoma II. Life history patterns. Bull.Soc. Vector Ecology. 8(2):79-84.
- Marshall, A. 1981. The ecology of ectoparasitic insects. Academic Press, London 459pp.
- Price, P. W. 1980. The evolutionary biology of parasites. Princeton Univ. Press, Princeton, N. J. 237pp.
- Rice, E. L., 1960. The micro-climate of a relict stand of sugar maple in Devils canyon in Canadian County,

- Oklahoma. *Ecology* 41(3):445-453.
- Scott, T. W., Bowen, G. S. and Monath, T. P. 1984. Effects of Fort Morgan virus on avian host reproduction. *J. Trop. Med. and Hyg.* 33(5):981-991.
- Usinger, R. L. 1966. Monograph of Cimicidae (Hemiptera-Heteroptera). Thomas Say Foundation vol. 7, 585pp.

Table 1: Cliff swallow colonies in Caddo and Grady Co.s Oklahoma:
history of use, 1979-83.

colony	found	years used	# nests	description	areas
1. P82	'82*	82	125	cliff-sparse	1
2. SW	'79	80,81/83	250/300	" -dense	1
3. PAB	'81*	81/83	390/1300	" -"	2
4. RY	'79	78/80/83	350/740/850	" -"	3
5. DG	'82	82,83	570	" -"	2
6. PC	'81	81,83	800	" -"	3
7. SE	'80	82	870	" -"	3
8. WB	'82*	82,83	550/100	" -culvert	2
9. GC	'79	79-83	800/1500/350"	-bridge	5

/=break in use by swallows

*=newly built

sparse=nests touch on <3 sides dense=nests touch all sides

area= # nests separated from others by a strip of cliff
or bridge

Table 2: Effect of location in colony on nestling weight and total bugs in transect samples.

colony	section	nestling wt grams	(N)	variation ANOVA/SNK
SE	c	25.2± 2.0	(62)	
	i	20.8± 6.3	(67)	
	e	18.7± 5.5	(66)	F=26.9****
PC	c	22.0± 3.9	(60)	ns
	i	20.0± 5.3	(61)	
	e	20.8± 5.9	(54)	
WB	c	20.6± 4.5	(39)	ns
	i	19.3± 5.6	(52)	
	e	20.7± 2.7	(41)	
P82 !	c	13.5± 5.8	(24)	F=6.3**
	i	10.6± 3.4	(7)	
	e	8.7± 2.6	(20)	

!=weights differ from other groups F=57.01 ****(SNK)

**p<0.01

****p<0.0001

center-c, intermediate-i, edge-e.

Table 3: Effect of location on total bugs and nestling mortality in 30 nest transect samples (taken after fledging July 1982).

colony	section	total bugs	variation	nests with dead
SE	c	430	G=511.0**	0
	i	1048		0
	e	299		0
PC	c	1	G=339.6**	1 (4)
	i	0		1 (1)
	e	159		1 (2)
WB	c	710	G=20.3**	0
	i	552		0
	e	606		0
P82	c	304	G=30.0**	2 (1 & 3)
	i	184		2 (2)
	e	245		2 (2 & 3)
DG (n=5)	c	3810	G=2516.0**	0
	i	3729		0
	e	345		0
GC (n=6) (n=6)	c	1130	G=430.8 **	0
	e	170		0
-----no birds 1982-----				
SW	c	138	G=166.2 **	1 (1)
	i	449		0
	e	579		0
PAB	c	68	G=36.0 **	1 (1)
	i	108		0
	e	20		0

**=p<0.01

***=p<0.001

Table 1: Cliff swallow colonies in Caddo and Grady Co.s
Oklahoma: history of use, 1979-83.

Table 2: Effect of location in colony on nesting weight and total
bugs in transect samples.

Table 3: Effect of location on total bugs and nestling mortality
in 30 nest transect samples (taken after fledging July 1982).

Figure 1: Maximim, Average and minimum temperatures
 precipitation and bird presence. (I-----I)
 (wk 1-4: April, wk 5-8: May, wk 9-12: June,
 wk 13-16 July, wk 17-20 August).

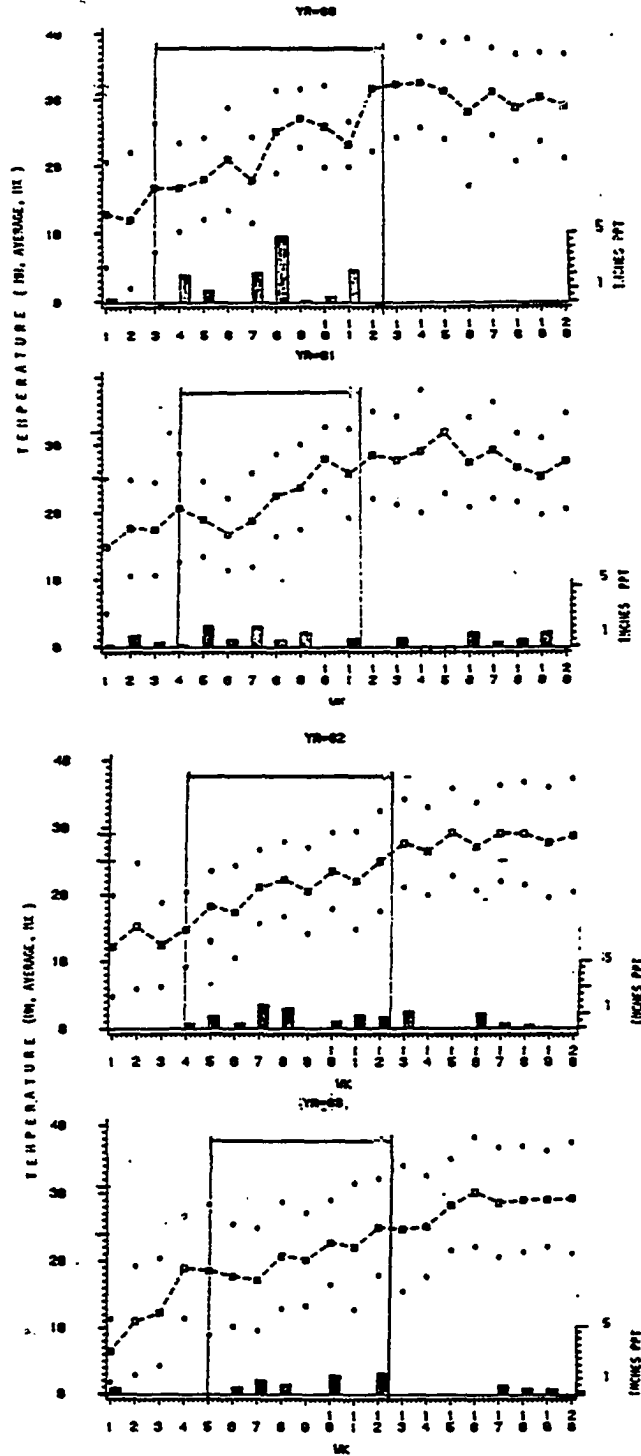


Figure 2: Cliff swallow bugs/nest/month, 1979-84.

A comparison of colonies used by swallows
1 nesting season (birds present), bridges
used each year (bridges) and colonies unused one
year (birds absent).

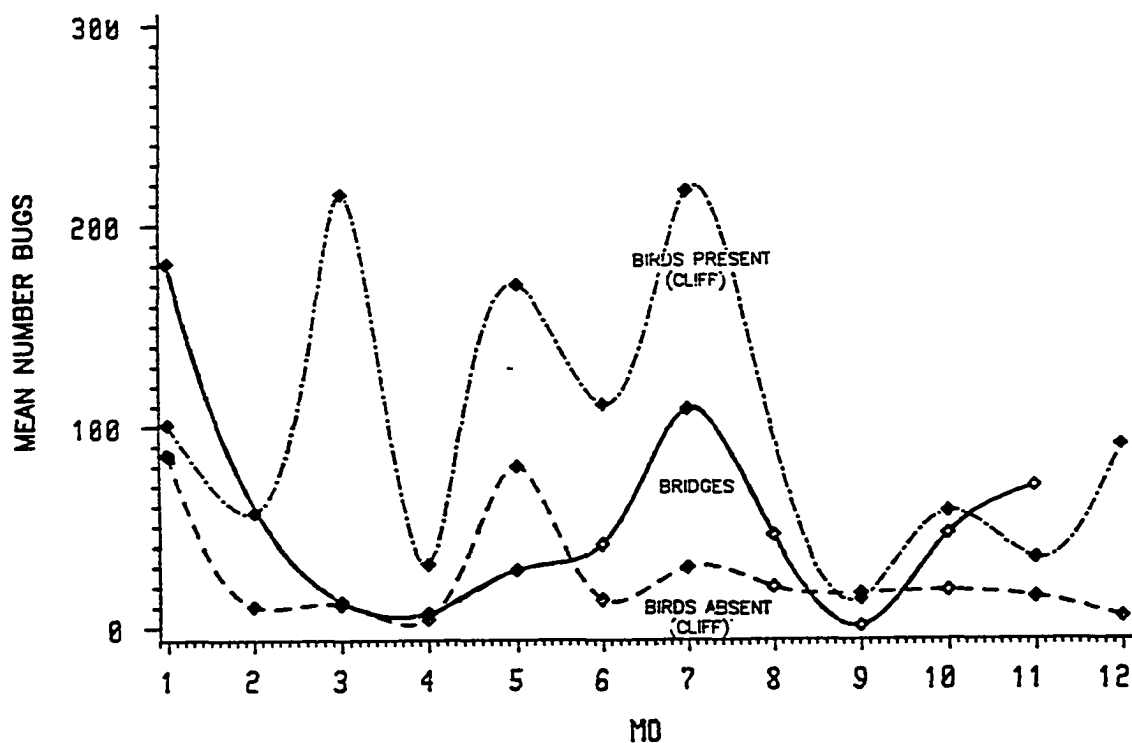
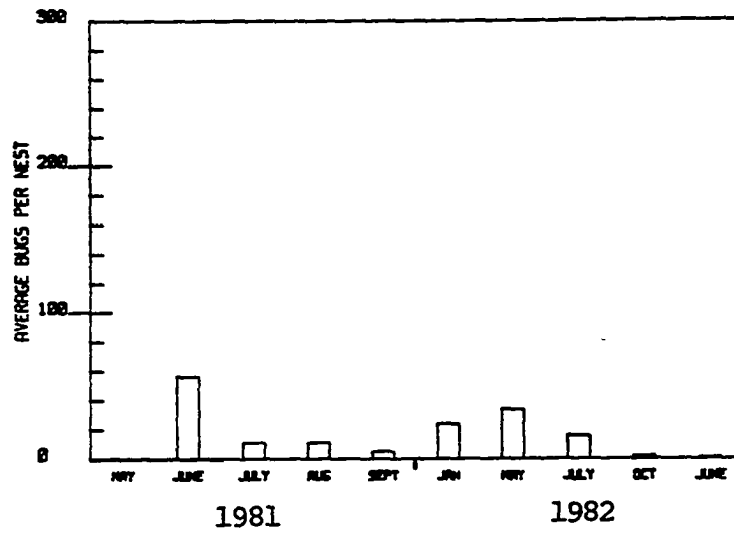


Figure 3: Cliff swallow bugs/nest in two new colonies :

PAB (1981-82), on a cliff and WB (1982-83), in a culvert.

PAB



WB

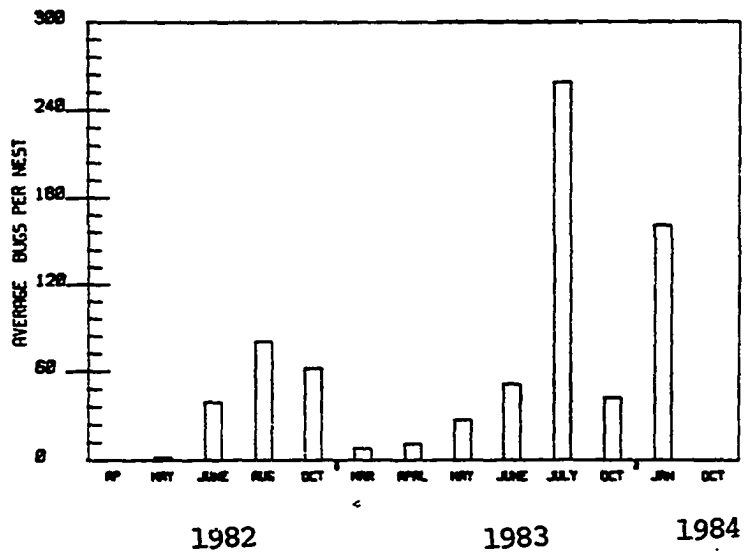


Figure 4: Cliff swallow bugs/nest at Ryburn cliff (1980-81).

RY

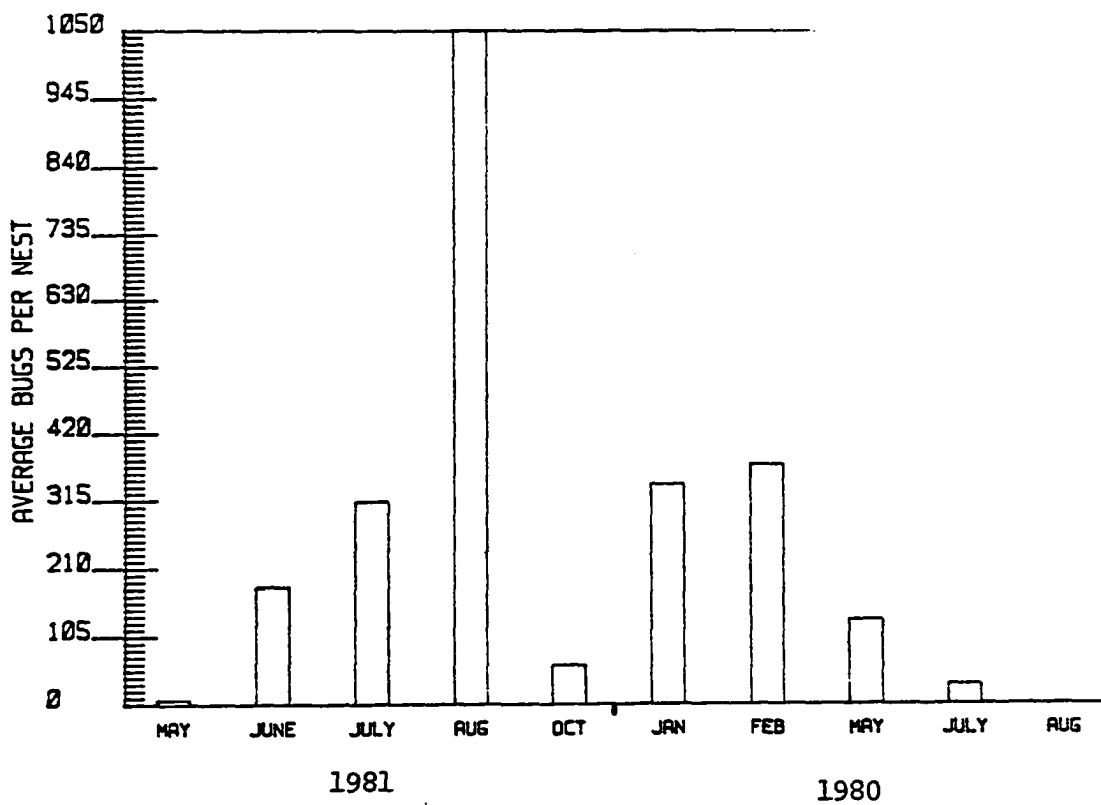


Figure 5: Cliff swallow bugs/individual nest at PAB colony
(1981 and 1982).

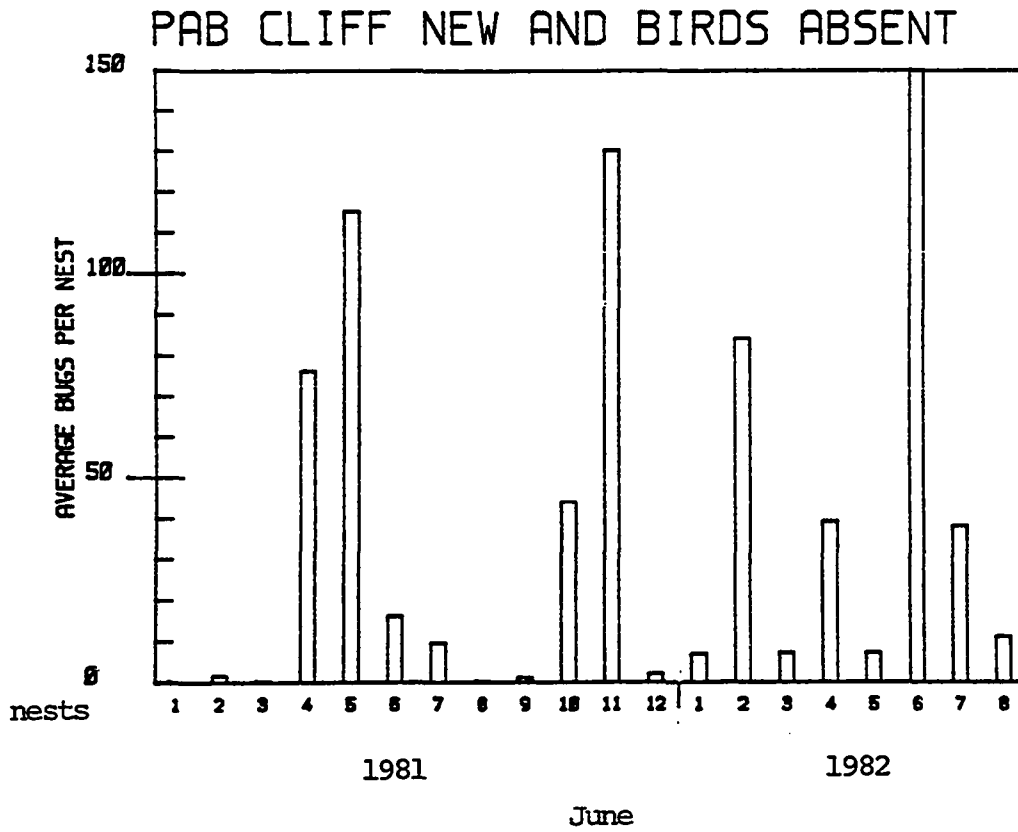


Figure 1: Maximim, Average and minimum temperatures
precipitation and bird presence (I-----I)
(wk 1-4: April, wk 5-8: May, wk 9-12: June,
wk 13-16 July, wk 17-20 August).

Figure 2: Cliff swallow bugs/nest/month, 1979-84 samples.

A comparison of colonies used by swallows 1 nesting
season (birds present), bridges used each year (bridges)
and colonies unused one year (birds absent).

Figure 3: Cliff swallow bugs/nest in two new colonies:

PAB (1981-82), on a cliff and WB (1982-83), in a culvert.

Figure 4: Cliff swallow bugs/nest at Ryburn cliff (1980-81).

Figure 5: Cliff swallow bugs/individual nest at PAB colony (1981 and
1982).