

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

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Summary

1. The life history of the cliff swallow bug *Oeciacus vicarius* is closely associated with that of the cliff swallow *Hirundo pyrrhonota* during the bird's three month breeding period in the Nearctic region.
2. The bugs are long lived, feed rapidly and lay eggs in several clutches that hatch in three-five days. Nymphs mature in approximately ten weeks and will mate and reproduce as long as food is available.
3. The proportion of newly emerged male bugs is equal to that of females. Mating occurs before winter when the ovaries of the female are still undeveloped. Spring bug populations contain proportionately more females, which may disperse, feed and lay eggs without re-mating.
4. Bugs (predominately adults) aggregate in the necks of the nests in colonies that were inhabited by birds the previous year. The arrival of the migratory swallows is characterized by "communal flighting" and exploration of the nests in several colonies. Bugs may disperse between colonies by clinging to the base of feathers at this time.

Key words : Cimicidae — Cliff swallow — Hirundinidae — Resource variability — Mating system — Nearctic region.

Résumé

BIOLOGIE ET ÉCOLOGIE D'*OECIACUS VICARIUS* (HEMIPTERA : CIMICIDAE), LA PUNAISE DE L'HIRONDELLE AMÉRICAINE À FRONT BLANC. 1. La biologie de cette punaise est étroitement associée à celle de son hôte *Hirundo pyrrhonota*, pendant la période de reproduction de trois mois de l'oiseau dans la région néarctique.

2. Les punaises ont une durée de vie importante, se nourrissent rapidement et pondent en plusieurs fois leurs œufs qui éclosent en trois à cinq jours. Les nymphes arrivent à maturité en dix semaines environ et les adultes qui en sortent s'accoupleront et se reproduiront aussi longtemps que la source de nourriture sera disponible.

3. Les mâles et les femelles sont en nombre égal à l'émergence. L'accouplement apparaît avant l'hiver au moment où les ovaires de la femelle ne sont pas encore développés. Les populations du printemps contiennent proportionnellement plus de femelles qui peuvent se disperser, se nourrir et pondre sans avoir à s'accoupler de nouveau.

4. Dans les colonies qui étaient habitées par les oiseaux l'année précédente, les punaises (surtout les adultes) se rassemblent dans le

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couloir d'entrée des nids. L'arrivée des hirondelles migratrices est caractérisée par des vols en bandes et par l'exploration des nids dans plusieurs colonies. Les punaises peuvent se disperser entre les colonies en s'accrochant à ce moment à la base des plumes des oiseaux.

Mots-clés : Cimicidae — Hirondelle à front blanc — Hirundinidae — Variabilité des ressources — Système d'accouplement — Région néarctique.

Introduction

The nest-dwelling ectoparasites of the cliff swallow *Hirundo pyrrhonota* Vieillot (Hirundinidae) are resource specialists that offer a productive system for investigating the co-evolution of life history patterns. The colonial nesting habits of the cliff swallow, which builds a protective domed nest of mud, encourage parasite maintenance and transmission of ectoparasites. Several species of blood-feeding arthropods use the nest substrate for shelter, oviposition and to establish contact with the host. Where colonies are re-occupied each year, the three month breeding period of the cliff swallow limits its specialized ectoparasites to a short feeding period before host migration and a food resource deprivation that lasts nine months. However, in Oklahoma, swallows abandon some nesting sites for up to several years (Hopla and Loye, 1983), and thus the ectoparasites sheltered in the durable nests and the crevices behind them are forced to endure starvation for prolonged periods.

The present paper examines the cliff swallow bug, *Oeciacus vicarius* (Horvath). This is a hemimetabolous, wingless cimicid that feeds on the swallow in all stages of development. Its degree of dependency on the host is intermediate between that of a free-roaming, facultative predator and the constant host association of obligatory parasites (Dogiel, 1964). Some aspects of the biology of cliff swallow bugs have been reported by Myers (1928), Foster and Olkowski (1968), Chapman (1973), Hayes *et al.* (1977), Smith and Eads (1978), Rush (1981), Gorenzel *et al.* (1982) and Loye and Hopla (1983). Reproductive adaptations to ectoparasitism in the swallow bug are related to the use of a patchy food resource that changes in space (between colonies) and time (within and between years) (*sensu* MacArthur, 1968). This study examined the life history response of the swallow bug to its host in the field and laboratory.

Material and methods

Cliff swallow colonies were studied in west-central Oklahoma in Caddo and Grady countries.

The primary study colony was RY, "Ryburn cliff colony" (ca. 750 nests) a colony occupied in 1978, vacant in 1979 and used again in 1980. The dense center portion of 550 nests was protected by an overhang where nests remained intact over the years, while the edge nests were exposed in vertical cliff fissures. Other cliff nesting sites were PAB, newly constructed in 1981 (ca. 1 300 nests) and SE, which had been used before 1979 and was sampled in 1982 (870 nests). Two bridges were sampled: GC (Grady co.), a colony of more than 1 000 nests, built under a 25 m highway bridge over Buggy creek and used each year by swallows (1979-83). Wilson's bridge (WB) colony was newly built in 1982 in a 2 m high culvert (550 nests) and was reused by swallows in 1983 (100 nests).

To monitor population dynamics and sex ratio, ectoparasites were collected by sampling nests most months from March 1980 to September 1983, using a randomized quadrat system. A ladder was used to remove nests up to 8 m into the lower 1/3-1/2 of the colony. The ectoparasites were harvested from the nests by breaking them into enamel pans (Loye and Hopla, 1983). In addition, samples of the "neck" portion of the nest were collected for observation of the dispersal stages and sex of bugs in spring aggregations and compared with the body of the nests. Neck samples were initially collected in groups of 20, and 19 more samples treated each neck and associated nest separately. Sex ratio (proportion of adults that were male) of newly emerged bugs was determined by holding field collected, engorged fifth instar nymphs (collected July, 1982) and allowing them to molt to sexual maturity.

Feeding trials employed cliff swallow nestlings and suckling mice. These were placed in small paper bags with the top edge rolled back to simulate a nest with crevices on all sides. Bugs were fed for two hours (21 h-23 h) in darkness. For comparison with field data, development time and age structure were investigated in captive bug populations. The colonies were established to reflect the contemporary age structure of a pre-breeding season population in nature and were established from whole-nest collections taken in April, 1982. The colonies were held

in three jars, at 28°C, L : D 14/10 photoperiod and 70-75 % humidity and provided with a continuous supply of suckling mice. The number of individuals in each instar was recorded each week. Finally, to assess reproductive status and sperm presence, field collected female bugs were dissected in 0.9 % saline and examined with phase-contrast microscope (200 ×).

Results

PHENOLOGY

Swallow 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 (fig. 1). Bugs were most numerous in colonies that were used by swallows the previous year. When the birds arrived, bugs fed and were dispersed by clinging to the base of feathers. Eggs were laid on the nest within 24 hours of feeding. The swallow nestlings hatched in mid-June and the numerous bugs engorged and moved actively over the cliff face and base, at night and during the day in shady areas. In direct sunlight the bugs became immobile and rested inside and outside of the nests.

When the young swallows fledged and migrated in July, the engorged bugs formed dense aggregations and molted in nests and crevices behind the nests (fig. 1). An example of this clustering effect was observed in a sample of 11 nests from the center of RY colony (August) : three nests contained no bugs, a four nest sample averaged 207 bugs/nest and groups of 1 300, 2 586, 3 474 and 6 048 bugs occurred in each of four other nests. No observable factor was seen to influence the formation of aggregations. After the swallow emigration, bugs sheltered in crevices as well as in nests. In late July, five similar crevices, 1 m below the nests on the cliff face, were inspected. Four of these 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 (fig. 2).

LIFE CYCLE

The mating of engorged bugs was observed on nests in June and August. In two laboratory observations of mating (18 October 1982) the male clung

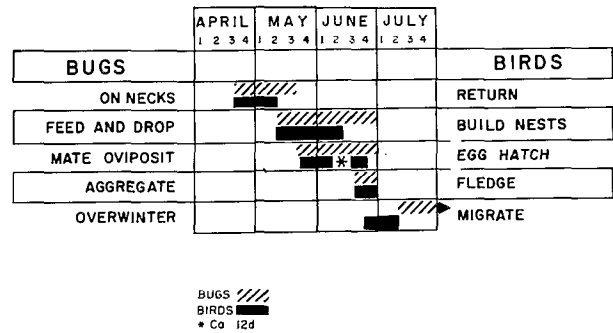


FIG. 1. — Life history phenology of swallow bugs and cliff swallows in Caddo Co., Oklahoma, 1979-84.

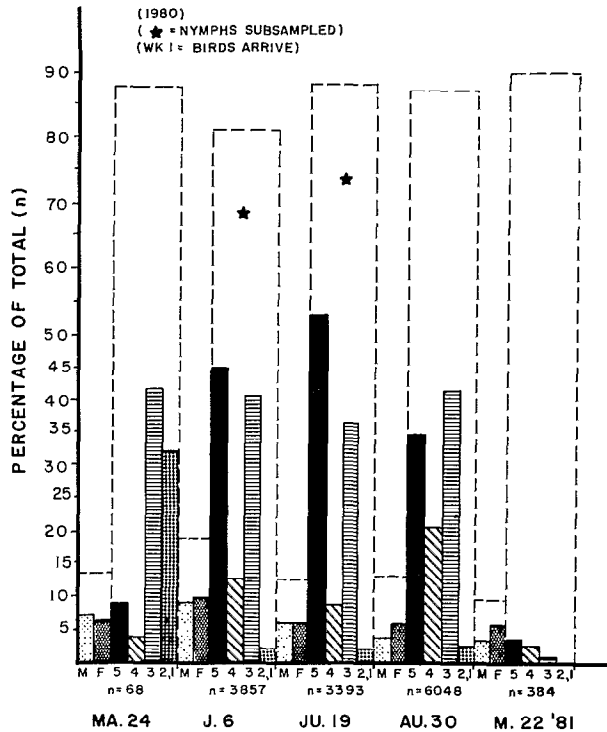


FIG. 2. — Age structure of field collections of cliff swallows bugs.

to the female's thorax with his legs, curled his abdomen and probed under the right side of the arched abdomen of the female for 30 ad 60 seconds, respectively. The male moved away and the female remained arched for several seconds. Cimicids mate by "traumatic insemination" (Usinger, 1966), in which the male inserts the aedeagus between the fifth and sixth abdominal sternites of the female bug,

bypassing her genitalia. The internal morphology of *Oeciacus* is comparable to *Cimex lectularius* in which a spermatheca is lacking and sperm is freely released into the haemocoel of the female and migrate to a seminal conceptacle (Usinger, 1966).

Mating also occurred in newly emerged adults. Viable sperm was found clustered around the undeveloped ovaries of newly emerged females in five of 19 bugs dissected at the end of July, 1983. All overwintering females dissected had been 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 commenced in January although mature eggs were not observed until after the first blood-meal in May.

Before swallows returned (April, 1983) female bugs were collected from nests, and held without males and allowed to feed on suckling mice. Six of 30 female bugs laid eggs (36 eggs total, 90 % hatched). Insemination probably occurred in these females in July or August of the previous year and they were able to lay eggs without mating again. Virgin females which emerged in the laboratory did not lay eggs after feeding.

In the field, eggs were usually found on the inner nest surface and cliff face but the outer surface was also used when the bugs were numerous. The eggs were laid in groups of two-ten over a three day period. An average of 16 (range 7-27) eggs were laid by engorged female bugs collected from an active swallow colony (7 July, 1982, $n = 9$, 92 % hatched). Seven females dissected from the same sample contained a mean of 19 eggs (range 8-25) and some of these eggs had eye spots, indicating that hatching was imminent. When females were fed continuously on suckling mice in the laboratory they laid fewer eggs: 25 females laid 128 eggs, an average of six per bug (90-100 % hatching success). Female bugs dissected one week after being fed in the laboratory ($n = 44$) contained eight eggs each (one per ovariole).

Eggs developed red eye spots within three days of being laid. The first nymphs hatched after three-five days and fed after 24 hours. Molting occurred only after complete engorgement. Adult bugs ($n = 10$) emerged approximately 60 days after the eggs hatched. Feeding was initiated by touching the hosts' skin repeatedly with the proboscis. Feeding bugs elevated the abdomen, became immobile and were not easily dislodged. Bugs engorged on swallow nestlings readily, in 10-30 seconds. Feeding time to engorgement on suckling mice took approxi-

mately 8 minutes (mean 7 mn 52 s, range 1 mn 15 s-29 mn; $n = 27$ fourth instar to adult bugs). After feeding, bugs dropped and moved away from the host to defecate.

When swallows were absent, engorged bugs were found with other animals that used the cliff swallow nests (Loye, 1985). Two species of bats were found in the swallow colonies. One female *Myotis velifer* and more than 600 bugs were collected in an artificial plaster nest (July, 1980). Several *M. velifer* females (September, 1979) and an *Eptesicus fuscus* male (October, 1979) were also collected (Hopla and Loye, 1983). A nest of the eastern phoebe, *Sayornis phoebe*, a common associate of cliff swallows (Hopla and Loye, 1983; Loye, 1985) contained 3 393 engorged and newly molted bugs (RY, July, 1980). House sparrows, *Passer domesticus*, used swallow nests at GC from March to October (Hopla and Loye, 1983). A nest used by sparrows in early May, before the swallows returned, contained 1 735 bugs. 75 % of these were nymphs, which suggests that the bugs were actively reproducing. A simultaneous sample of four adjacent nests unoccupied by birds contained engorged bugs. These feeding records indicate that alternate hosts provide blood meals for bugs.

The bugs entered the nine month period of swallow absence as newly emerged adults and nymphs with large abdominal fat deposits (dissection of 82 females, nine males, seven nymphs). Adipose diminished in bugs collected as the winter progressed ($n = 108$ females, 9 males, 5 nymphs).

Survival trends in adults and nymphs in winter nest samples indicated that mortality was high. In the winter of 1980-1981, the average number of bugs at RY decreased by 99 % from August (6 058 bugs/nest) to March (68 bugs/nest) but the age structure changed very little (fig. 2). Similarly, the average number of bugs/nest in eight nests collected at the new bridge colony (WB) decreased by approximately 95 % from July (2 347 bugs/nest) to April (116 bugs/nest). Bugs survived in a colony that was not used by swallows for three consecutive years but by the fourth year no bugs were collected in the nests. In the laboratory bugs have not survived longer than one year without feeding.

POPULATION BIOLOGY

The age structures of field sampled (RY) and laboratory bug populations were similar: a higher proportion of nymphs (80-90 %) occurred during the

population growth period in June and July (fig. 2 and 3). At RY, first and second instar nymphs were numerous only during the first month. Adult bugs did not exceed 15 % of the total populations at any time in RY. In comparison, the field collections at SE used to establish the laboratory colony were 43 % adult bugs.

ufficient to allow complete development during the three month swallow breeding season.

A female biased sex ratio in the bugs prevailed in all field collections except those in late July when nestlings fledged. Field collections of bugs in late July had a sex ratio of 0.43 (n = 241 newly emerged fifth instar nymphs) and 0.52 (n = 393) in adults. The sex ratio in laboratory colonies was also female biased (0.3 at initiation) for the first eight weeks. At the ninth week, when adult bugs began to emerge the proportion of male bugs increased to 0.5.

Dispersal was examined in terms of departure of bugs from the necks of nests and arrival at new colonies. If bugs congregated for purposes of dispersal then the proportion collected in the neck of a nest (approximately 1/20 of the internal surface area of the entire nest) would be expected to be greater than 5 % of the total bugs. 28 % (238) of 822 bugs were collected on necks of 19 nests (April 25, 1984) a much greater proportion than predicted. Adult bugs were significantly more abundant on necks than were nymphs (47 % of 238 adults versus 28 % of 584 nymphs, $\chi^2 = 27.28, p < 0.01$).

The dispersal of inseminated females to new colonies was examined by testing aggregations between the neck and body of the nest. A strong female bias was found in all May samples (necks 77 % females, n = 376, 70 necks ; nests 72 % females, n = 348, 20 nests). However, there was no significant difference between the number of females collected in May (weeks 1 and 3) on the necks and the body of the nest (sex ratio : 0.23 vs 0.28). A sample of 19 necks and the associated nests (25 April, 1983 ; sex ratio 0.4 ; n = 280 bugs) did not significantly differ between females in necks and nests (χ^2 test).

Newly-built nesting colonies provided an opportunity to observe site colonization by bugs. The new colonies observed were WB, a bridge (1981) and PAB, a cliff (1982). The bridge colony was built in April and was several miles from the nearest colony, too distant to permit the introduction of bugs by crawling. The introduced population contained more female bugs than males (sex ratio : 0.33, n = 277 adults, 11 nests, late May and early June). The predominance of early instar bugs in May (75 %, n = 12, four nests) and in early June (80 %, n = 338, seven nests) indicated a rapidly growing population. After WB was used a second year (April, 1983) the bugs had a sex ratio of 0.32 (n = 74 adults, 16 nests) with 42 % adults (n = 175 bugs) in April.

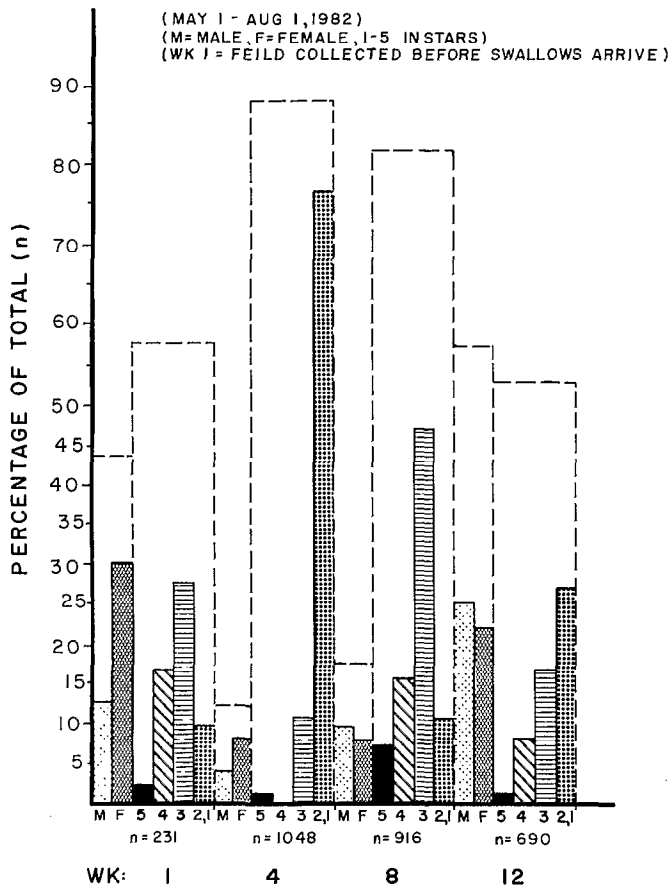


FIG. 3. — Age structure of laboratory populations of cliff swallow bugs.

Population changes were observed for 12 weeks in laboratory populations (fig. 3). The laboratory populations were initiated with 231 bugs (April, 1983), 57 % of which were nymphs. In four weeks the proportion of nymphs increased to 88 % (n = 1 048, 76 % in the first instar). At eight weeks 82 % of 916 bugs were nymphs, but only 12 % were first instars. The total number of bugs decreased to 690 by the time of adult emergence at 12 weeks. The maturation time for bugs (10-12 weeks) was suf-

In contrast, bugs from the cliff colony (PAB) had a sex ratio of 0.51 ($n = 115$, 11 nests) and 37 % of the bugs were adults in early June. This age structure was similar to that of the bugs sampled at an older colony (RY) (late May, 1980) where the sex ratio was 0.42 ($n = 19$ adults, 12 nests) with 25 % adults ($n = 79$ bugs). PAB cliff was 300 m from an old colony and crawling was a likely mode of dispersal for bugs. In the course of observation bugs have been collected up to 50 m from this colony.

Discussion

Host activities strongly influence the behaviour and development of cliff swallow bugs. In May, returning cliff swallows hover and explore old nests, a "communal flighting" described in sand martins by Jolley and Storer (1945). Bugs aggregating in the necks of the nests can move onto the swallows for dispersal to other colonies. Mobilization of ectoparasites to the nest entrance may be due to positive phototaxis as occurs in the newly emerged adults of the bird flea, *Ceratophyllus styx* (Humphries, 1969). Many nidicoles exhibit rapid location and utilization of hosts for dispersal and feeding (Humphries, 1969; Webb, 1979; Marshall, 1981). In late July and August the dense clusters of bugs in nests leads to a high variance in the number of average bugs per nest. Behavioural changes in the bugs such as aggregation at necks, movement away from hosts after feeding and clustering are respectively, responses to the host's arrival, availability, departure and absence.

Reproductive effort in the bugs reflects the pattern of food availability. A changeable resource presence may result in high juvenile mortality and a reproductive response in bugs (Hirschfield and Tinkle, 1975; Warner, 1980) such as repeated egg laying (Charnov and Schaffer, 1973). The low reproductive effort invested in several small batches of eggs may allow a flexible schedule of oviposition, continuing as long as the bugs can feed. For instance, swallow bugs reproduced and developed in swallow nests that were used by house sparrows at GC colony for several months after the swallows migrated. Iteroparity may require repeated mating (Warner, 1980) which is common in cimicid bugs (Usinger, 1966; Ryckman, 1958). Traumatic insemination may facilitate multiple mating in male bugs as well. The age structure of the bug population is also comparable to other animals living in an unpre-

dictable environment with high juvenile mortality (Stearns, 1976). A rapid rate population increase occurs during the period of nestling development. Adult bugs were always present, but newly emerged adults predominated after approximately ten weeks in the laboratory and field. Because bugs overwinter in all stages and lay eggs in several batches, the age distribution is spread out over time and adults mature 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) and was followed by prolonged sperm storage.

Bugs introduced to the new bridge colony (WB) began reproduction later and exhibited a female biased sex ratio in the comparatively few adults in its rapidly expanding population. Older colonies on cliffs, where bugs overwinter in greater numbers than on bridges (Loye, in preparation), contain relatively more males and adults at the time of the birds return in the spring.

The presence of proportionately more females at the new bridge colony may indicate that they disperse more often than males or nymphs. Dispersal assures the bugs of blood meals and egg laying opportunities if they successfully migrate to a new nesting colony site.

In summary, the cliff swallow bug's life history is characterized by: iteroparity, few young, a lengthy maturation time, adult emergence throughout the breeding season and a long lifespan (Loye and Hopla, 1983). This life history pattern, termed "bet-hedging" (Schaffer, 1974; Stearns, 1976; Tallamy and Denno, 1981) is predicted by variable juvenile mortality. The pre-diapause mating found in these bugs is also anticipated as a strategy of organisms facing cyclic periods of stress (Williams, 1975). The impact of resource predictability on these life history adaptations may be assessed by comparing life histories between populations inhabiting cliff and bridge habitats or geographic areas where colony usage varies in its reliability.

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