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Biology of a Tydeid Mite, *Homeopronematus anconai* (n. comb.) (Acari: Tydeidae), Important in San Joaquin Valley Vineyards

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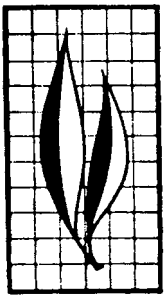
UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES



The taxonomy of *Homeopronematus anconai* (Baker 1943), new combination, is reviewed, and *Homeopronematus vidae* André 1980 is designated a new synonym.

The tydeid mite *H. anconai* has an egg, one larval, and three nymphal stages. Each postlarval stage begins with a prolonged period of quiescence following apolysis and preceding ecdysis. Quiescent phases are approximately as long as active immature phases. After adult female ecdysis, there is a short preoviposition period followed by a long reproductive period, during which up to 66 eggs per female are laid. When ample food is present, most of the eggs are laid early in the reproductive period. Mean generation time (T) is 20.6 days at 24 °C and 11.8 days at 30 °C.

Reproduction is arrhenotokous: unmated females produce male offspring only. The sex ratio is female-biased. An overall estimate of sex ratio is 2.2 females per male.

These mites have a clumped distribution in laboratory colonies. Quiescent stages, exuviae, and active larvae and adults are often aggregated near some physical feature such as a leaf vein or cotton strand, but aggregations also occur on otherwise apparently featureless leaf surfaces. Hungry *H. anconai* females spend more time on leaf surfaces with residues left by other *H. anconai* females, suggesting that tactile and/or chemical cues produced by the mites themselves may be partly responsible for the aggregation behavior. Female *H. anconai* have a photoperiodically induced, temperature-sensitive hibernal reproductive diapause. Diapausing females are mated but nongravid and are morphologically distinguishable in

Continued inside back cover.

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Biology of a Tydeid Mite, *Homeopronematus anconai* (n. comb.) (Acari: Tydeidae), Important in San Joaquin Valley Vineyards[1,2]

INTRODUCTION

ALTHOUGH TYDEID MITES COMMONLY OCCUR on the aerial portions of a wide variety of economically important plants, the biology of only a few tydeid species has been studied in the laboratory. Flaherty and Hoy (1971) successfully reared *Homeopronematus (Pronematus) anconai* (Baker) and *Pronematus ubiquitous* McGregor on pollen in the laboratory, and Schruft (1972) described the life history of *H. staerki* (Schruft) and *Tydeus goetzi* (Schruft). Brickhill (1958) studied the life history and feeding habits of *Paralorryia (Lorryia) ferula* (Baker) and *Triophtydeus (Tydeus) bakeri* (Brickhill). Thoreau-Pierre (1977) reared *Lorryia formosa* Cooreman in the laboratory, and several authors reared *Tydeus californicus* (Banks) (Fleschner and Arakawa 1953, Zaher and Shehata 1963, Soliman, Zaher and El-Safi 1974, Wahab, Yousef, and Hemeda 1974). Most of the laboratory work described in these papers centered around attempts to determine the food(s) used by these tydeid species and only incidentally yielded life history information.

The tydeid *H. anconai* plays a useful role as alternate prey for the predatory mite, *Metaseiulus (Typhlodromus) occidentalis* (Nesbitt) (Phytoseiidae), in San Joaquin Valley vineyards in California (Flaherty and Hoy 1971, Calvert and Huffaker 1974, Flaherty, Hoy and Lynn 1981). This article reports studies of the biology of *H. anconai* designed to yield information useful for incorporating this mite into a vineyard pest management program.

TAXONOMY

Confusion over the generic and specific name necessitated study of the taxonomy of this mite. The family Tydeidae was revised at the generic level (André 1979, 1980, 1981a, b) while our research was under way (1978-82). Colonies were initially identified as *Pronematus anconai* Baker, and that identification was confirmed by E. W. Baker (personal communication). Subsequently, André

[1] Accepted for publication August 15, 1983.

[2] Based on a thesis submitted by the senior author, in September 1982, to the Graduate Division, University of California, Berkeley, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology.

(1980) split the genus *Pronematus,* naming a new genus, *Homeopronematus,* comprised of two species—*H. vidae* André, a new species, and *H. staerki,* moved from *Pronematus.* His description of *H. vidae* was based in part on specimens provided by M. A. Hoy from a laboratory colony that was used in our research and originally identified as *Pronematus anconai.* André (1979, 1980, 1981a, b) did not discuss the species *anconai* in his revision. Taxonomic study led us to conclude that the description of *Homeopronematus* (André 1980) fits our colonies, whereas that of *Pronematus* (Baker 1965, 1968; Kuznetzov 1972) does not, and that *vidae* and *anconai* are conspecific, with *anconai* having priority. A description of *Homeopronematus anconai* (Baker) new combination follows, with a review of the taxonomy. *Homeopronematus vidae* is designated a new synonym of *H. anconai.*

Species redescription

Homeopronematus anconai (Baker), new combination

Pronematus anconai Baker 1943: 188-9; Baker 1968, 1094-5; Kuznetzov 1972, 11-12. *Homeopronematus vidae* André 1980, 113-16; new synonym.

Adult female. Tarsus I lacking claws and empodium; the four terminal setae and seta ft″ partially serrate (Fig. 1). All other leg and body setae completely serrate. Leg setation: I—8, 4, 3, 3, 1; II—6, 2, 3, 3, 1; III—6, 2, 2, 2, 1; IV—6, 2, 1, 2, 0. There are 11 pairs of dorsal setae on the hysterosoma, termed d1-5, l1, 4, 5, h1, h2, and ps by André (1980, 1981a) or D1-5, L1-5, and anals by Baker (1968), Kuznetzov (1972), and Kuznetzov and Livshitz (1973). Where differences in setal nomenclature occur in the following discussion, both designations are given. There are four pairs of aggenital setae (André 1980, 1981a); the pair anterior to the genital opening are short and appear forked (Fig. 2). Lobed striations cover the body (Fig. 1, 2, 3). Body length including gnathosoma is 232μ to 279μ; width 109μ to 118μ (Baker 1968, Kuznetzov 1972, André 1980).

Adult male. Smaller than the female, length 200μ, width 108μ (Kuznetzov 1972). Leg and dorsal setation as above. Femur IV is extended apically into a "hook"; the seta on genu IV is smooth rather than serrate and is recurved toward the hook at the base (Knop 1982). There are swollen areas just posterior and laterad to the D2 setae where the striation attenuates, although the lobes remain (Fig. 3 and Baker 1968). On males mounted in Hoyer's medium and observed with phase contrast, these areas appear as dark disks (Fig. 4). The male genital opening is more posterior and has one rather than four aggenitals (André 1979, 1980). The male has a Y-shaped aedeagus (Fig. 5).

Discussion

The genus *Homeopronematus* André 1980 is distinguished from *Pronematus* Canestrini sensu Baker 1968 by having 11 rather than 10 pairs of dorsal setae on the hysterosoma; seta L5 (h1) is missing in *Pronematus.* In addition, *Homeopronematus* has six setae rather than five on tarsi III and IV, and one seta rather than none on trochanters I and II.

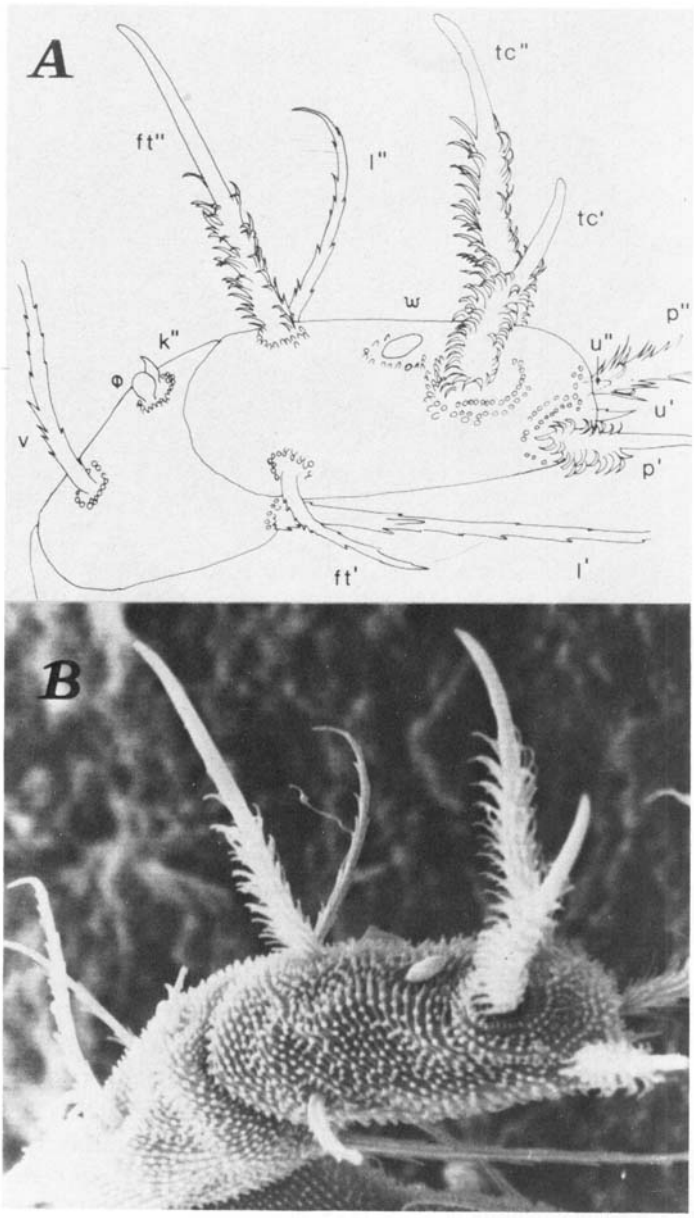

Fig. 1. A. Left tarsus I and tibia I of *H. anconai* male, 2200x. ft, fastigial; tc, tectal; p, proral; u, uniquinal (note u″ is located behind p″); k″, famulus; l, lateral; ω, tarsal solenidion; ϕ, tibial solenidion. Single prime = toward body of mite, double prime = away from the body; ω and ϕ are dorsal.

B. Scanning electron micrograph of left tarsus I and tibia I of male *H. anconai*, 2200x. Segments are somewhat collapsed due to fixation and dehydration. Mites fixed in 4 percent gluteraldehyde pH 6.6 in 1.0M phosphate buffer; post-fixed in OSO_4; dehydrated in ETOH, critical point drying with CO_2 as intermediate fluid; coated with gold-palladium in a sputter-coater. Coates and Welder Model 50 Field Emission SEM, Microscope Laboratory, University of California, Berkeley.

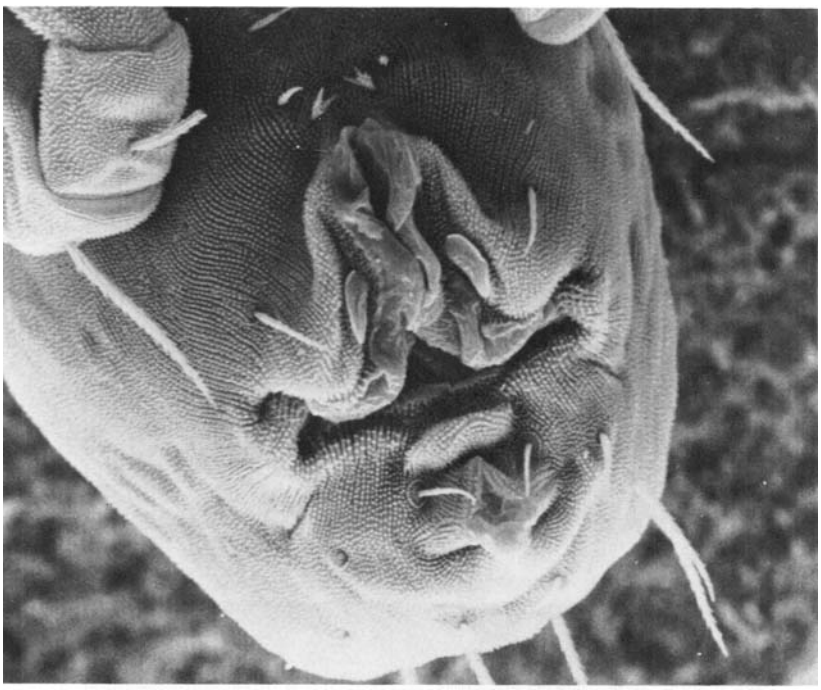

Fig. 2. Genital aperture of *H. anconai* female showing the short "forked" setae immediately anterior to the aperture (1500x). See Fig. 1B for SEM information.

Dr. E. W. Baker was kind enough to lend us a slide labeled "*Pronematus anconae* Baker, Type," containing two adult females. These females have the characters of *Homeopronematus* and not those of *Pronematus:* the leg setation is that of *Homeopronematus* and the dorsal setae L5 (h1) are visible on one of the two females (although obscured on the other). We conclude that *Homeopronematus* is the correct generic designation.

Distinguishing characters described for *anconai* include the partially smooth tarsal I setae and the "Y-like" female genital setae (Baker 1968, Kuznetzov 1972). The apical hook on the male femur IV is illustrated (Baker 1968), although not described in the text. Lobed striae are illustrated by Kuznetzov (1972). Baker (1968) did not see lobes on the striae of *P. anconai* females; however, the lobes are visible on his type specimens at 1000X magnification under oil with phase contrast.

André (1980) describes *H. vidae* with two figures, which illustrate the partially serrate tarsal I setae, the hook on male femur IV, and the lobed striae. Although he does not discuss the Y-like genital setae, females from the same laboratory colony that provided specimens for his description of *vidae* possess the Y-like genital setae (Fig. 2).

Since André's description of *vidae* fits the type specimens of *anconai* and the mites in the laboratory colonies, we conclude that they are conspecific, and that *anconai*, having priority, is the correct name for the species.

The two species in the genus *Homeopronematus, H. anconai* and *H. staerki,* are separated by André (1980) on the basis of shorter setal length and denser

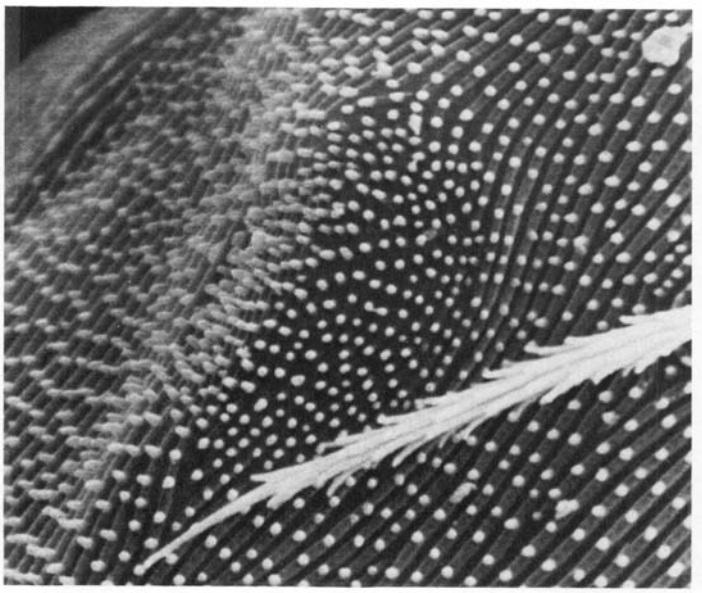

Fig. 3. Lobed striations of adult male *H. anconai* integument become attenuated in a circular area just behind the base of the D2 seta near the edge of the dorsum (7100x). See Fig. 1B for SEM information.

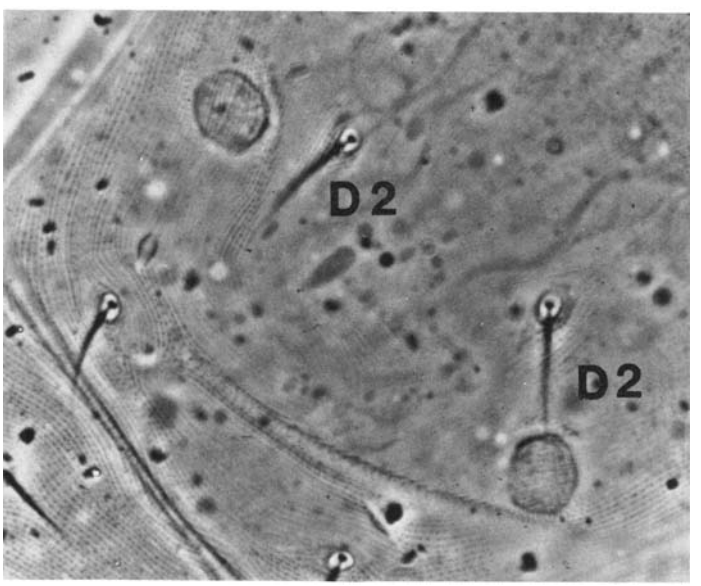

Fig. 4. Dorsal view of male *H. anconai* opisthosoma. Phase contrast micrograph, 1420x. Dark disks are visible behind the D2 setae at the sites of attenuated striations described in Fig. 3.

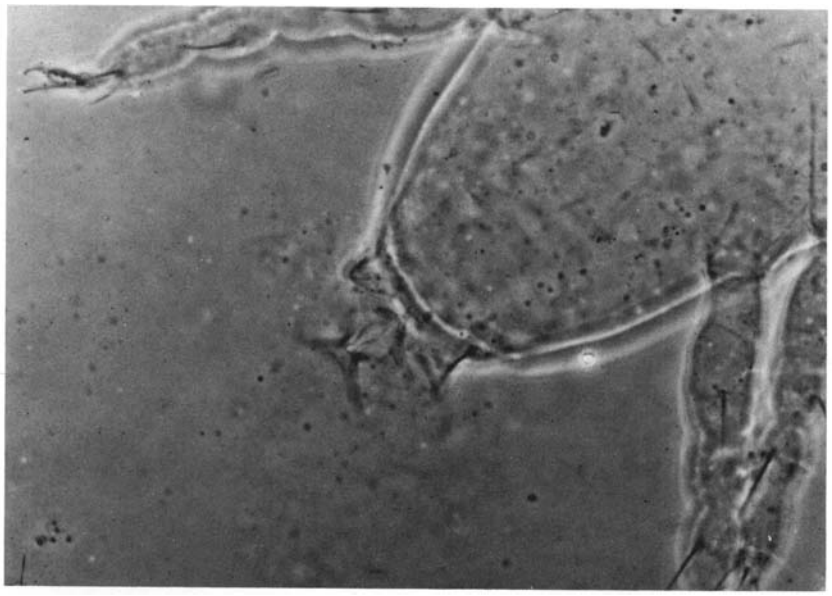

Fig. 5. Opisthosoma of male *H. anconai* with extruded aedeagus. Phase contrast micrograph, 530x.

striae in *staerki*. Examination of the literature and of a long series of *anconai* specimens suggests that there is size variation within *anconai*. The females on the Baker slide are smaller than most of the laboratory-reared *anconai* females in our colonies. Since size-related characters appear to be all that separate *anconai* and *staerki*, they may not be distinct species.

Material examined. Mexico: 2 females on a single slide labeled "Type" ex *Buddleia verticillata* Sesse and Moc, Mexico-Cuerna Vaca Highway, 22.i.1941 (E. W. Baker). **United States:** 75 females, 15 males collected from 27 vineyards (*Vitis vinifera* L.) in the San Joaquin Valley of California 1968-81 (M. A. Hoy, R. T. Roush, K. B. Smith, N. F. Knop); 18 females, 2 quiescent nymphs from 3 almond orchards (*Prunus amygdalus* Batsch.) in the San Joaquin Valley of California, 1979 (R. T. Roush, K.B. Smith); 1 male ex blackberry (*Rubus vitifolia* Cham & Schlecht) (N. F. Knop); 13 females, 10 males ex lab colony, Berkeley, 1978-81 (N. F. Knop).

In addition to the preceding localities and plants, *H. anconai* occurs on strawberry in California (Oatman 1971), pecan in Georgia (Boethel 1978), apple in Missouri (Childers and Enns 1975) and North Carolina (Farrier, Rock, and Yeargan 1980), grape (*V. vinifera*) in north coast vineyards of California (Kinn and Doutt 1972), muscadine grape (*V. rotundifolia*) in Mississippi (A. Chandrapatya, personal communication), a variety of plants in the United States and Argentina (Baker 1968) and a variety of trees, shrubs, and herbaceous plants on the southern coast and in the steppe portion of the Crimea, USSR (Kuznetzov 1972).

The type specimens are in the collection of E. W. Baker. Voucher specimens of *H. anconai* from laboratory colonies established from San Joaquin Valley, California, vineyards and used for this research have been placed in the United States National Museum of Natural History (USNMNH), Washingon, D.C.; the

Canadian National Collection (CNC), Biosystematics Research Institute, Ottawa, Canada; the Acarology Laboratory, Ohio State University, Columbus, Ohio; and the Essig Museum, University of California, Berkeley, California.

METHODS AND MATERIALS

Maintenance of laboratory colonies

Laboratory colonies of *H. anconai* were established from mites collected on grapes (*Vitis vinifera* L. var. Thompson Seedless) in the San Joaquin Valley of California during 1979-81. The Parlier (P) colony was established from mites collected at the Kearney Field Station, Parlier, during May 1979, December 1979, and April 1980. Mites from these collections were pooled. Unless otherwise noted, the P colony was studied. Sufficient numbers were not always available from this colony, and it was occasionally necessary to supplement with mites from WSFS, collected at the West Side Field Station, near Five Points, in September 1979; VG, Van Gundy vineyard, American and Peach Avenues, Fresno, in April 1980 and June 1980; B, Boeger vineyard, near Placerville, in June 1981; SJV, a mixture from the central San Joaquin Valley, in April 1980; and several laboratory colonies of mixed origin.

Each colony was maintained in the laboratory in a series of 6.5 x 8 cm plastic culture boxes without lids. The mites were reared on the undersides of California blackberry leaves (*Rubus vitifolia* Cham and Schlecht) laid on wet cotton in the culture boxes. Young but hardened blackberry leaves, hairy but not felty on the underside, were chosen because of their durability and because the many leaf hairs provided ideal resting and oviposition sites. Blackberry leaves were collected in Berkeley, washed with Alconox, rinsed, dried, and examined under a dissecting microscope to eliminate any resident mites or insects. Trimming all edges of the leaves before placing them on the wet cotton ensured that water entered the leaf tissue.

The principal food supplied was cattail pollen (*Typha* sp.), which was dusted on the leaves with an artist's brush two or three times a week. Cattail pollen was collected July 1980 and stored at −40 °C in small lots in 4-dram screw-cap vials. About once a month, a vial was transferred to a freezer (−18 °C) for short term storage. Condensation resulted when pollen was moved frequently from the freezer to room temperature and encouraged fungal growth and spoilage. For that reason, amounts sufficient for a week or two of feeding were held at room temperature in a closed, dry container. Fresh pollen from iceplant (*Carpobrotus* spp.) and bottlebrush (*Callistemon citrinus* Stapf) was used until cattail pollen was collected but only occasionally thereafter.

Colonies were kept at ambient temperatures (16° to 26 °C) and 18 hours of light. We were able to maintain the colonies on blackberry leaves in this manner for two months or more. When the leaves began to senesce, we transferred the mites by picking up the old leaf and turning it over onto a fresh leaf in a culture box. The mites moved to the new leaf as the old leaf dried out.

Observation and handling of individual mites

Living mites were observed under a dissecting microscope at 20 to 40x, with a fluorescent light source to reduce the effects of heat. These mites are fast-moving and run backward as rapidly as forward. They were more likely to run off the leaf surface onto the wet cotton if observed at high temperature, and heat also increased the difficulty of handling them. We picked up individual mites by touching the tip of a damp sable brush to the dorsum, and transferred the mite by gently brushing it onto the new substrate. Choice of brushes size 00 to 00000 was based on the fineness of the hairs rather than on the manufacturer's size code. Two dissecting microscopes were used while transferring mites, one for the stock culture box, and one for the recipient leaf disks.

Developmental time, longevity, and fecundity

Mites were reared individually or in small groups on 1-cm-diameter blackberry leaf disks placed on squares of wet cotton in 13-cm^2 plastic trays and surrounded by a sheet of Parafilm in which 20 to 30 holes had been cut with a 1.4-cm-diameter cork borer. The Parafilm reduced moisture loss from the wet cotton and lowered the humidity in the temperature cabinets. Cattail pollen was added to the disks and replenished two to three times a week throughout the experiment. All development, longevity, and fecundity experiments were conducted under an 18-hour photoperiod.

Developmental time at 24 °C. Developmental time was determined for mites reared individually and in groups in two replicates started one month apart. For individual rearing, a single female was transferred from the laboratory colony to each of 60 leaf disks. For group rearing, 5 to 10 females were transferred to each of 20 leaf disks. In replicate 1, mites from the P, WSFS, VG, and SJV colonies were used; only mites from the P colony were used for replicate 2. The trays of females were placed in a Percival temperature cabinet (Model I-30B) set at 24 °C and 18 hours of light. Trays were checked every 8 hours. The grouped females were removed from the disks after 8 hours when they had deposited four to eight eggs on each of these disks. The females placed on disks individually were removed as soon as each laid an egg, and if more than one egg was laid in the 8-hour interval, all but one were squashed. To facilitate finding the transparent hatched eggs later, the location of each egg was marked with a dot from a fine-point felt-tip pen (water-soluble ink). Disks were examined every 8 hours until the mites reached adulthood and females produced at least one egg. Temperature and humidity were monitored throughout the experiment with a hygrothermograph placed inside the cabinet. The hygrothermograph indicated that temperature was within 1 ° of 24 °C, and that relative humidity (RH) ranged from 30 to 60 percent in replicate 1 and from 40 to 90 percent in replicate 2.

Longevity and fecundity at 24 °C. Females reared in replicate 2 of the developmental study were used to determine longevity and fecundity at 24 ± 1 °C. Within a day of adult ecdysis, 41 females were individually moved to new disks. Females on 20 disks were not provided males; two or three males were added to each of the other 21 disks. Young males from replicate 2, 1 to 2 days

old, were used if available, otherwise males of unknown age from the laboratory colony were used. Egg production was recorded daily. When 5 to 10 eggs had been laid on a disk, females and males were moved to an adjacent fresh disk. These transfers were continued throughout the life of the female, and the eggs were reared to adulthood to determine whether female offspring were produced. The relative humidity was 60 to 90 percent during the time these these studies were conducted.

Development, longevity, and fecundity at 30 °C. Individual mites (59) were reared at 30 ± 2 °C using the procedures just described. Fecundity and longevity were measured for 25 females; 14 of these were provided males. Humidity was not monitored continuously; however, a hygrothermograph placed in the cabinet during one week indicated that RH ranged from 40 to 75 percent.

Development at 18 °C. Preliminary experiments demonstrated the difficulty of rearing *H. anconai* at 18 °C, probably because of the high RH (>90 percent) in the cabinets at the cool temperature. For that reason we abandoned attempts at individual rearing. In one instance, mites were reared in groups in the temperature cabinet beginning with 76 eggs ($\bar{x}$ eggs/leaf = 2.5). The procedures were the same as at 24 °C, except that data were taken once a day rather than every 8 hours.

Data analysis: developmental, longevity, and fecundity studies. Mean total developmental times at 24 °C were compared by replicate, sex, and rearing method. Means and standard deviations were determined for the time individually reared *H. anconai* spent in each stage at 24 ° and 30 °C. When the mites were group-reared, only the length of the egg stage and total developmental time (egg to active adult) could be individually determined. Life table statistics were determined and graphed using computer programs (RCALCM, PLOTIT) developed by A. P. Gutierrez and colleagues at the Division of Biological Control, University of California, Albany.

Effect of relative humidity on egg hatch

Egg hatch was determined at low (32 percent), medium (74 percent), and high (97 percent) relative humidities using saturated salt solutions (calcium chloride, sodium nitrate, and potassium phosphate, respectively) prepared as described by Winston and Bates (1960) and placed in plastic dishes in the bottom of 3.75-liter stainless steel and glass desiccator cabinets. The desiccators were placed in a Percival temperature cabinet set at 20 °C and allowed to stabilize. Females were isolated on blackberry leaf disks and allowed to deposit eggs. After 48 hours, eggs were transferred to paraffin-coated paper squares by removing with jeweler's forceps the leaf hairs to which the stalked eggs were fastened. Eggs from each of 40 females were transferred to squares of paraffin so that eggs from the same female were distributed among three sets of squares. One set was placed in each desiccator. After 10 days, the chambers were opened and the number of eggs that had hatched was determined.

Temperature threshold for egg hatch

To see if eggs would hatch at 6° and 12 °C, we transferred eggs of unknown age (but not within a day of hatch according to appearance) from the laboratory colony to fresh blackberry leaf culture boxes. Boxes with a total of about 80 eggs from the same cultures were placed in each temperature. Hatch was determined after one month. Because humidity is a factor in hatch, we expanded the study to evaluate hatch in desiccators at 6°, 12°, and 15 °C, and at ambient temperatures (16° to 26 °C) with humidity held constant at 75 to 76 percent RH using sodium chloride, which maintains these humidities over the range of temperatures tested (Winston and Bates 1960). Eggs were transferred directly from the laboratory colony to paraffin-coated paper squares. Squares holding a total of 20 eggs each were placed in each of the four desiccators. Hatch was determined after one month.

Tests for hibernal diapause

These mites overwinter as adult females under the scales of grape buds (Flaherty and Hoy 1971). We followed three lines of investigation to determine whether *H. anconai* females have a hibernal reproductive diapause: (1) placing laboratory cultures in a field cage to see if oviposition continued into the winter, (2) bringing field-collected overwintering *H. anconai* into the laboratory from Parlier, California, to see if and when females began oviposition, and (3) rearing eggs from laboratory colonies under several controlled temperature and photoperiod regimes to see if diapause was induced.

Diapause induction in a field cage. Twelve blackberry leaf culture boxes, each with about 150 mites of all ages including gravid females, were placed in a field cage in Berkeley, California, on September 1, 1981. Cattail pollen was added twice weekly. Females (15 to 20) were sampled every two weeks until January 5, 1982, and brought into the laboratory, where they were held at ambient temperatures (16° to 26 °C) and 18 hours of light on individual blackberry leaf disks supplied with pollen. The disks were checked daily until eggs were laid or death occurred.

Reproductive status of females overwintering in grape buds. Cane sections were cut from Thompson Seedless grapevines in each of five experimental plots at the Kearney Field Station, Parlier, and at Road 80 and Avenue 88 near Dinuba, California, on December 18, 1979. Twenty-eight buds from each plot were dissected, and the stage and sex of overwintering tydeids were noted. Female *H. anconai* found overwintering under the bud scales were placed individually on Thompson Seedless grape leaf disks and supplied with bottlebrush or iceplant pollen. One group of 37 females was placed in a Percival cabinet at 19 °C and 8 hours light, and the other group of 40 females was placed in 27 °C and 16 hours of light. Pollen was added and disks were examined for eggs two to four times a week for 35 days.

Experimental induction of diapause. Using eggs from the laboratory colonies (two cultures from the P colony and three mixed cultures) we reared the mites at 18 °C and 8 or 18 hours of light to see if oviposition would occur soon after females reached adulthood in both cases. To collect large numbers of eggs

of known age, we transferred females to grape leaf squares with few leaf hairs, and provided cotton strands as oviposition sites. After 48 hours, when 25 to 30 eggs had been laid on the strands, eggs and strands were transferred to fresh blackberry leaf culture boxes. Two boxes were held under 8-hour and three boxes under 18-hour photophase. Another batch of eggs collected during the next 48 hours was placed in the temperature cabinets in reverse order so that eggs from the same females were tested in both cabinets. A third batch was reared in four boxes at room temperature (16° to 20°C) and 18 hours of light. Pollen was added two to three times a week, and cultures were checked for eggs at least every other day. The experiment was terminated after 100 days. The experiment was replicated beginning two months later, using four culture boxes with mites from the P colony for each set of conditions.

A second experiment tested the effects of an 8-hour photoperiod at 24°C using the procedures described for collecting eggs and rearing. In the first replicate of this experiment, cultures from five laboratory colonies were used: SJV, WSFS, B, and two mixed colonies. In the second replicate, two cultures from the P colony were used.

In all the diapause induction experiments, cultures were maintained until adults were reared and eggs were produced or until the females died. Temperatures in the rearing cabinets were checked with a thermometer. In the cabinet set at 18°C, temperatures ranged from 17.2° to 20.5°C. The cabinet set at 24°C ranged from 23.8° to 24.2°C. Humidity was not monitored. The data compared were the days from the time the eggs were placed in temperature cabinets until the first production of eggs on the cultures.

Feeding studies

Flaherty and Hoy (1971) reported that *H. anconai* could be successfully reared on pollens of bottlebrush (*Melaleuca hypericifolia* Smith), grape (*Vitis vinifera* L.), and cattail (*Typha* sp.), but not on bee-collected pollens. They found that this tydeid fed on conidia of powdery mildew (*Uncinula necator* [Schw.]), but very poor colonies developed. They were unable to rear the mite on synthetic honeydew, the fungus *Cladosporium* sp., or grape leaf tissue alone, although leaf probing was observed. They also noted that female *H. anconai* would readily cannibalize their eggs when ovipositional sites were limited.

In an attempt to expand these studies, we transferred gravid *H. anconai* females from laboratory colonies to new blackberry or grape leaf squares and supplied them with one of several other pollens to see if colonies could be established. Pollens tested were another bottlebrush, *Callistemon citrinus* Stapf., iceplant (*Carpobrotus* sp.), *Cosmos* sp., *Dahlia* sp., California poppy (*Eschscholzia* sp.), *Magnolia* sp., and *Pinus* sp.

Attempts to rear *H. anconai* on grape leaf alone failed, confirming the results of Flaherty and Hoy (1971). Preliminary attempts to rear *H. anconai* on artificial substrates with pollen alone were equally unsuccessful. To quantify the productivity of females on artificial versus natural substrates, we isolated gravid females on disks cut from washed grape leaves, cork, or plastic, with or without cattail pollen added as food. Survival, productivity, and cannibalism (egg stalks

with drained, shriveled eggs) were recorded for 6 days. The first test compared plastic and grape leaf, and the second compared cork and grape leaf.

Because adult female *H. anconai* cannibalize their own eggs, it is perhaps not too surprising that they will puncture and feed on spider mite eggs as well. In preliminary tests, starved *H. anconai* females were observed puncturing and draining the contents of tetranychid eggs. There was no doubt that they fed on the spider mite eggs, since the females increased visibly in size as they fed. Several experiments were designed to determine the extent of this egg predation. To estimate the effect of length of starvation and the maximum amount of predation, we starved 63 new adult *H. anconai* females for 2 to 12 days and then placed them individually on grape leaf disks with an ample supply of 0- to 2-day-old Pacific (*Tetranychus pacificus* McGregor) or Willamette (*Eotetranychus willamettei* Ewing) spider mite eggs. After 72 hours, the number of punctured, shriveled spider mite eggs was scored.

To evaluate long-term survival and productivity of *H. anconai* on Pacific mite eggs, we put new adult females singly on grape leaf disks: 10 with 0- to 2-day-old Pacific mite eggs only, 10 with Pacific mite eggs plus cattail pollen, and 10 with cattail pollen only. The mites were maintained at 16° to 26°C and were transferred to disks with fresh eggs or pollen, or both, every other day until death. Predation on Pacific mite eggs, productivity, and longevity were scored. The experiment was replicated three times.

To learn whether spider mite webbing interfered with egg production, we transferred gravid females from laboratory colonies to disks with pollen, pollen and Willamette mite eggs (and webbing), or pollen and Pacific mite eggs (and webbing) for 48 hours. We compared the number of eggs laid in each regime.

Preference of females for washed versus previously inhabited leaves

Quiescent and active stages and exuviae are commonly observed in aggregations (Fig. 6), even in sparse laboratory colonies, and are often, but not always, associated with some structural feature of the leaf. Exuviae, egg stalks, and fecal deposits may provide tactile or chemical cues for aggregation. Both exuviae and egg stalks adhere to the leaf surface, and waste material is deposited on the substrate as an opaque white liquid. This fecal deposit dries, leaving a white residue that is imperceptible on the leaf surface but clearly visible on glass cover slips. Schuster (1972) reported silk production by another tydeid, *Tydeus schusteri* André and Naudo, but we never saw any evidence of silk production by *H. anconai*.

Because female *H. anconai* cannibalize eggs, hungry females seemed most likely to respond to the residues left by other *H. anconai*. The behavior of both hungry and well-fed females was tested by adapting the method of Hoy and Smilanick (1981). Grape leaves were cut into 2.2-cm-diameter disks and put on moist cotton. Ten females each were placed on one set of disks, while another set of disks was left with no mites. After 48 hours, the mites were removed. Pollen food had not been provided, and all the eggs that were laid were cannibalized. The leaf disks were then cut in half and clean disk halves were paired with halves with tydeid residues to make a test disk. The clean and residue

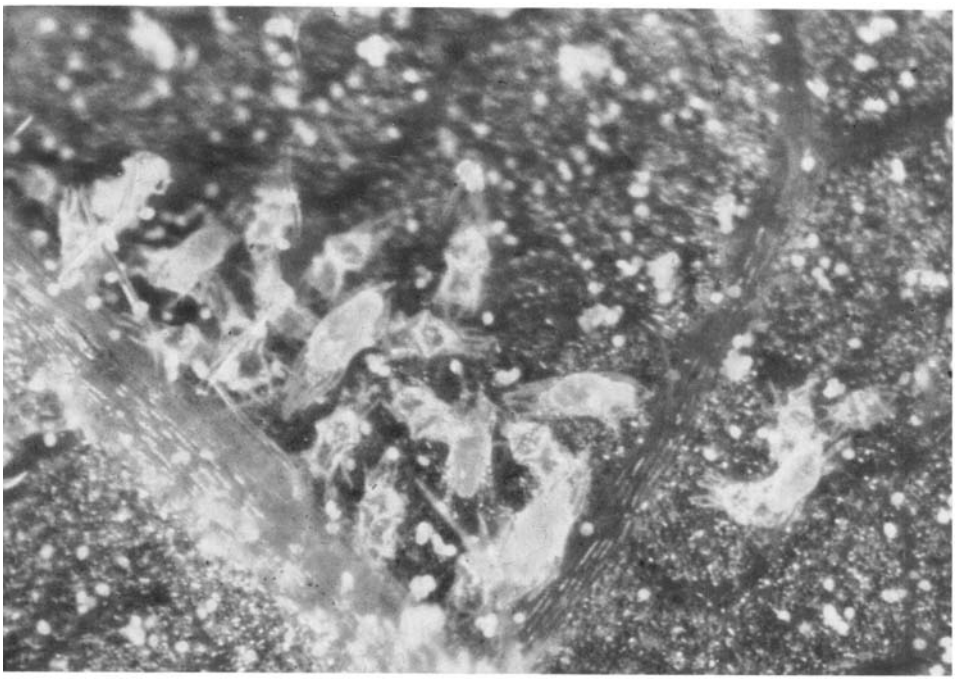

Fig. 6. Aggregation of quiescent and active stages and exuviae of *H. anconai* along the vein of a Thompson Seedless variety grape leaf. Granular material is cattail pollen. 67x.

halves always came from the same grape leaf, and the clean side was placed on the left as often as on the right. The halves were sealed together with melted paraffin applied rapidly over the seam with a sable brush. A single female was placed on the paraffin midrib of each disk. One group consisted of hungry test females, starved on leaf disks without pollen for 48 hours, the other of well-fed females from a laboratory colony. The location of each female was scored every 5 minutes for 2 hours. The sum of the observations on each half was compared with the expected (equal numbers on each half) using chi-square analysis. Preliminary tests demonstrated that females could travel the diameter of these disks in approximately 20 seconds. When we observed them continuously, females crossed the test disk midline numerous times in 5 minutes, hence we made the assumption that their locations at 5-minute intervals were independent. Since females observed on one side only during the 2-hour observation period might have been injured in handling, those sets of observations were discarded.

RESULTS AND DISCUSSION

Life history

There are six stages in the life history of *H. anconai*: egg, hexapod larva, three octopod nymphal stages (protonymph, deutonymph, tritonymph), and adult. Schruft (1972) described only two nymphal stages, protonymph and deutonymph, in the closely related species *H. staerki*; however, he may have overlooked the tritonymph. Schruft (1972) described three nymphal stages for *T. goetzi*. There are contradictory reports about the number of life stages in *T. californicus*. Soliman, Zaher, and El-Safi (1974) individually reared *T. californicus* and described three nymphal stages. Zaher and Shehata (1963) and Wahab, Yousef, and Hemada (1974) followed similar rearing procedures but observed only two nymphal stages. Since there are also differences in the feeding and oviposition behavior they described, "*T. californicus*" as used by these authors may be more than one species. Kuznetzov (1980) stated that a nymphal stage may be omitted in some tydeid species. The three nymphal stages in *H. anconai* represent the primitive condition in the family Tydeidae.

We did not see a prelarva (Kuznetov 1980) inside the egg of *H. anconai*. However, further study may reveal a prelarva in this species. The egg is a transparent oblong spheroid on a fine stalk, which is often attached to the tip of a leaf hair. A gravid female climbs to the top of a leaf hair, then turns, backs up to the tip again and presses the genital opening to the tip of the hair. The stalk is attached and drawn out, the hind feet climbing out on the stalk in the process, and the large egg is extruded (about 125 μm in length, half as long as the female). The stalk attachment is on the side of the egg near one end. Once the egg is laid, the female climbs down the stalk and the leaf hair and moves away. As the egg nears hatch, the dorsal stripe (excretory duct) characteristic of these mites can be seen in the larva inside, and the egg loses its shape and conforms to the shape of the larva. At hatch, the egg splits open across the end away from the stalk, and the larva moves partially out of the egg, gnathosoma first. It rests for ½ hour or more with the back legs still inside the shell before emerging completely and moving away. Larvae were frequently observed feeding on pollen. During its active phases, *H. anconai* runs on legs II-IV, tapping the substrate rapidly with the first pair of legs, which lack pretarsi in all postlarval stages but are supplied with numerous sensory setae (Fig. 1).

Each postlarval stage begins with a period of quiescence. Larvae and nymphs preparing to become quiescent exhibit a different behavior—running a few steps and then raising the first pair of legs alternately, usually until a leaf hair, cotton strand, or leaf vein is encountered by the forelegs. If exuviae or other quiescent *H. anconai* are present, these are favored sites for molting. Aggregations of exuviae and pharate *H. anconai* are characteristic and usually, but not always, form along leaf veins or other structural features (Fig. 6). Once a resting site has been located, the larva or nymph stretches its legs I and II forward, and its legs III and IV backward along the body on the substrate. After a short period (<1 hour), the mite becomes immobilized and does not respond to probing. Apolysis occurs during the first part of quiescence, after which the nymph or adult is pharate inside the old cuticle. If pharate individuals are mounted in Hoyer's

medium and examined with a phase contrast microscope, the new cuticle and its characteristic setation are clearly visible inside the old cuticle. The new legs are visible inside the old leg cuticle (type B apolysis, Woodring 1969). When quiescence ends, the cuticle splits across the prodorsum and the mite emerges dorsum first, drawing out the forelegs and then the hindlegs.

A distinct quiescent phase between active phases is characteristic of mites in the Acariformes (Woodring 1969). Nevertheless, the term ecdysis rather than apolysis has been used as the stage-defining event in this order (i.e., Woodring 1969, Hazan, Gerson, and Tahori 1973, Penman and Cone 1974). Potter (1981) recognized the problem when he referred to the quiescent phase preceding the active adult female *Tetranychus urticae* Koch (Tetranychidae) as both "quiescent deutonymph female" (early in quiescence) and "pharate adult female" (late in quiescence). According to Woodring (1969), apolysis begins as quiescence begins. If one follows the thinking that the new stage begins with apolysis (Hinton 1976, but c.f. Whitten 1976), it is more accurate to consider the quiescent phase the beginning of the new stage rather than the end of the preceding stage. In this paper the beginning of quiescence is defined as the beginning of the nymphal and adult stages.

Development, longevity, and fecundity

Laboratory survival and sex ratio. The success of laboratory rearing under various temperature regimes is compared in Table 1. Overall, 86.4 percent of the eggs hatched, and 64 percent were reared to adulthood. There was no consistent pattern to survival of eggs, but the survival of immatures was related to temperature in these experiments. The low survival of immatures at 18 °C may be due to the generally higher relative humidity in the cabinet at this temperature. Most immatures died because they ran off the leaf disk and got stuck in the wet cotton or in leaf sap and bacterial growth at the leaf edge. Food quality was reduced in higher humidity since fungus grew on the pollen, causing more immatures to leave the disk where the damp bacterial growth was more likely to ensnare them.

TABLE 1. SURVIVAL AND ADULT SEX RATIO OF *H. ANCONAI* IN VARIOUS LABORATORY REARING REGIMES

Temperature °C	% RH	Rearing method	No. eggs	% hatch	%reared to adult	No. reared to adult ♀♀	No. reared to adult ♂♂	Adult sex ratio ♀♀ :1♂
18	60-95*	grouped	76	92.1	38.2	18	11	1.6
24	30-60	single	58	89.7	62.1	31	5	6.2
24	40-90	single	56	78.6	71.4	26	14	1.9
24	30-60	grouped	117	83.8	66.7	53	25	2.1
24	40-90	grouped	120	75.8	65.0	50	28	1.8
30	40-75*	single	59	94.9	84.7	36	14	2.6
Overall rearing success and sex ratio			486	86.4	64.0	214	97	2.2

*Range estimated from hygrothermograph data taken during one week of the experiment.

TABLE 2. DEVELOPMENT OF GROUP- AND INDIVIDUALLY-REARED *H. ANCONAI* MALES AND FEMALES COMPARED FOR TWO REPLICATES AT 24 °C

Rearing method (1$\bar{x}$ eggs reared/ 1 cm leaf disk)	Replicate	Development (days) from egg to active adult					
		♀♀			♂♂		
		n	$\bar{x}$	(SD)	n	$\bar{x}$	(SD)
Group (5.9)	1	53	12.9	(1.3)	25	12.5	(0.7)
Group (6.0)	2	50	15.4	(1.8)	28	14.8	(1.5)
Single (1)	1	31	12.3	(0.8)	5	12.7	(0.5)
Single (1)	2	26	13.8	(1.0)	14	13.0	(0.6)

The adult sex ratio varied between experiments but was always female-biased. The lack of relationship between sex ratio and survival (Table 1) suggests that differential mortality cannot account for the adult sex ratio. The sex ratio of this species may vary with time and environmental conditions, but since no pattern emerged in these studies, the overall sex ratio of 2.2 females to 1 male (69 percent females) was used for the life table statistics.

Development. The mean time from egg to active adult was 37.9 days at 18 °C, 13.6 days at 24 °C, and 8.1 days at 30 °C. In two replicates *H. anconai* was reared both grouped and singly at 24 °C. As stated, the grand mean time from egg to active adult was 13.6 days at 24 °C; however, there were differences between means for males and females, between means for mites reared in groups and individually, and between means for replicates 1 and 2 (Table 2).[3] In general, males developed faster than females, and individuals reared singly developed faster than those reared in groups. The difference between means for replicates was unanticipated: developmental time was longer in replicate 2 than in replicate 1. Temperature variation recorded during these replicates was within the error range of the hygrothermograph measuring it. The pollen used as food was taken from the same frozen batch, and rearing techniques were identical. The only variable that could not be controlled was humidity; RH was higher in the second replicate. High humidity may have direct detrimental effects on *H. anconai*, or may have indirect adverse effects because the pollen food deteriorates more rapidly. The slower development of group-reared than individually reared mites in both humidity regimes may also have been due to reduced food availability, but in this case as a result of competition.

Table 3 compares the times individually reared *H. anconai* spent in each stage at 24 ° and 30 °C. Because total developmental times were different between replicates at 24 °C (Table 2), suggesting that humidity as well as temperature affects developmental time, the data for each replicate are given separately. The decrease in total developmental time at 30 °C is not due to shortening of any one stage; each stage is proportionately shorter (Table 3). In all cases, about half the time between the egg stage and active adulthood is spent in a pharate condition.

Longevity and fecundity. Reproduction is arrhenotokous in *H. anconai*.

[3] Analysis of variance suggested that each of these differences was significant, but assumptions for this statistical analysis were not fully met. Sample sizes were unequal, and correction of unequal variance by a $\log_{10}$ transformation was only marginally successful. Thus, we have not assigned a level of significance to the differences.

TABLE 3. DEVELOPMENT OF INDIVIDUALLY REARED MALE AND FEMALE *H. ANCONAI* AT 30° AND UNDER TWO HUMIDITY REGIMES AT 24 °C

Temp. °C ± 2	Range in % RH	No. reared to adult	Sex	Mean (standard deviation) days											
				Egg	Larva	Protonymph		Deutonymph		Tritonymph		Quiescent adult	Total egg to active adult	Active adult to 1st egg	Total egg to first egg
						Quiescent	Active	Quiescent	Active	Quiescent	Active				
24	30-60	31	♀	5.0 (0.2)	1.1 (0.3)	0.8 (0.2)	0.8 (0.2)	0.9 (0.2)	0.7 (0.3)	0.9 (0.2)	1.0 (0.4)	1.1 (0.2)	12.3 (0.8)	2.3 (0.5)	14.2 (1.1)
24	40-90	26	♀	5.3 (0.3)	1.4 (0.2)	0.9 (0.2)	1.0 (0.2)	0.8 (0.2)	1.0 (0.2)	0.9 (0.2)	1.3 (0.5)	1.1 (0.2)	13.8 (1.0)	1.8 (0.3)	15.4 (1.0)
24	30-60	5	♂	5.4 (0.1)	1.0 (0.0)	1.0 (0.0)	0.9 (0.2)	0.8 (0.2)	0.7 (0.2)	0.9 (0.2)	0.9 (0.3)	1.0 (0.2)	12.7 (0.6)	--	--
24	40-90	14	♂	5.3 (0.2)	1.3 (0.3)	1.0 (0.2)	0.8 (0.2)	0.8 (0.2)	0.8 (0.3)	0.8 (0.2)	0.9 (0.1)	1.2 (0.2)	13.0 (0.2)	--	--
30	(40-75)*	36	♀	3.2 (0.2)	1.0 (0.3)	0.6 (0.1)	0.5 (0.2)	0.6 (0.2)	0.5 (0.3)	0.5 (0.3)	0.6 (0.3)	0.8 (0.1)	8.2 (0.7)	0.9 (0.4)	9.1 (0.6)
30	(40-75)*	14	♂	3.2 (0.2)	0.8 (0.2)	0.5 (0.2)	0.7 (0.1)	0.4 (0.2)	0.5 (0.2)	0.5 (0.2)	0.5 (0.3)	0.7 (0.1)	7.9 (0.5)	--	--

*Range estimated from hygrothermograph data taken during one week of the experiment.

Virgin *H. anconai* females laid eggs that developed into males. Of 302 eggs laid by individually reared unmated females, all 115 progeny that developed to adulthood were male. "Mated" females were provided males at any time up to 24 hours after adult ecdysis. Since subsequent work demonstrated that mating is successful for only a short interval after adult ecdysis (8 hours or less at 24 °C for most females) (Knop 1982), females that were provided males but produced only male offspring were assumed to be virgin. Fecundity and longevity data from

TABLE 4. FECUNDITY AND LONGEVITY OF VIRGIN AND MATED *H. ANCONAI* FEMALES AT 24 °C and 30 °C

Temperature °C ± 2	♀♀	No.	Eggs $\bar{x}$ (S.D.)	Lifespan (egg-death) $\bar{x}$ (S.D.) days
24	Virgin	24	15.9 (4.8)†	39.5 (15.4)†
	Mated	17	15.2 (7.4)	41.9 (16.5)
		41	15.6 (5.9)	40.5 (15.7)
30	Virgin	18	44.8 (21.9)†	22.4 (9.7)†
	Mated	7	46.0 (21.8)	21.4 (5.4)
		25	45.2 (21.5)	22.2 (8.6)

†Virgin not significantly different from mated, t-test, $\alpha = .10$.

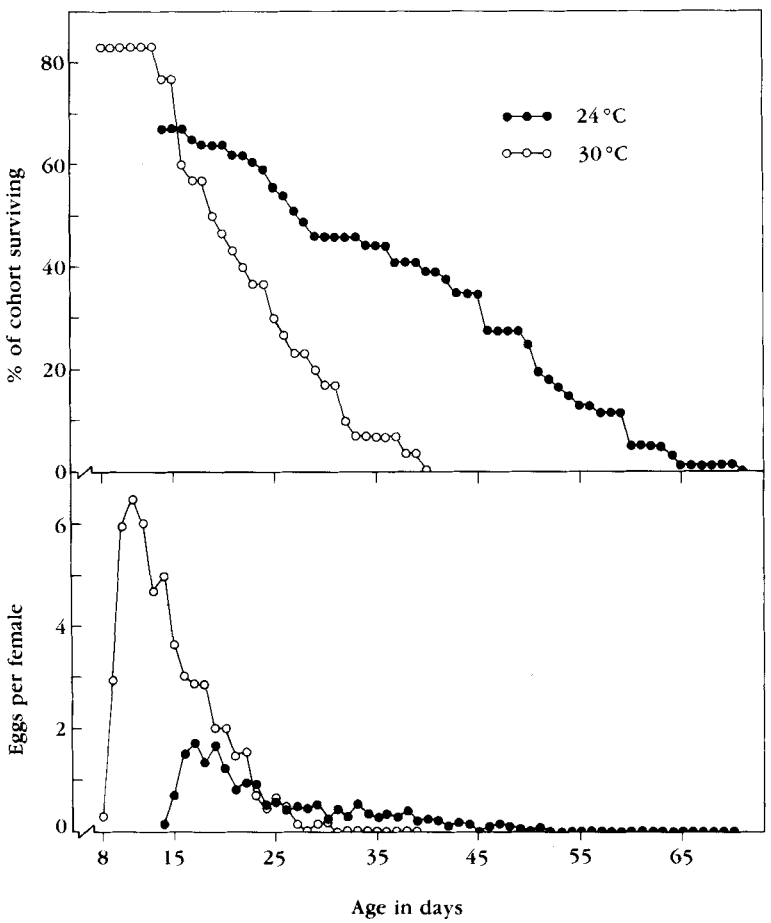

Fig. 7. Survival and productivity of *H. anconai* females at 24° and 30 °C. The calculated initial cohort of eggs was 30 females at 30 °C, 61 females at 24 °C.

these females (4 of 21 females provided males at 24 °C and 7 of 14 at 30 °C) were included with those for isolated virgin females in the longevity and fecundity statistics.

Fecundity at 30 °C was nearly triple that at 24 °C, although the lifespan was about half as long (Table 4). Neither mean total productivity nor mean lifespan (egg to death) was significantly different between virgin and mated females (t-test, $\alpha = 0.10$) (Table 4). The patterns of egg production and survival of virgin and mated females combined are shown in Figure 7. The survivorship curves are similar in shape, but the slope is steeper at 30 °C. At both temperatures, peak egg production occurs early in the active adult stage and there is a long postreproductive period. The long postoviposition period observed in well-fed *H. anconai* may be an adaptation to fluctuation in the availability of wind-blown pollens or other foods. In laboratory studies, starved *H. anconai* females resumed oviposition after periods of starvation ended (Knop and Hoy, unpublished data). Blommers and Arendonk (1979) showed that *Amblyseius bibens* Blommers females (Phytoseiidae) had a long postreproductive period when food was ample but could postpone egg production when food was limited, suggesting that the long postoviposition period observed in some predatory phytoseiids is an adaptation to fluctuating prey density.

Survivorship (l_x) and age-specific fecundity (female offspring per female, m_x) data at 24 °C and 30 °C, and the resulting life table summary statistics, are given in Tables 5 and 6. Because there was no difference in productivity or survivorship between mated and virgin females (Table 4) they were combined, and a frequency of 0.69 female (the overall sex ratio, Table 1) was assumed for all eggs in the calculation of r_m. Pollen deteriorated rapidly in high humidity; thus, food may have been limiting due to high RH in replicate 2 when the life table data were taken, leading to an underestimate of r_m and R_0 and an overestimate of T at 24 °C.

Most life table studies of Actinedida have been done in the family Tetranychidae. Values of r_m for three tetranychid mite species ranged from 0.097 to 0.259 at various temperatures and relative humidities (reviewed in Saito 1979). Feldman (1981) reported r_m values of 0.273 and 0.286 for strains of *Tetranychus urticae* at 28 °C and 70 percent RH, and Watson (1964) reported an r_m of 0.202 to 0.254 (depending on host plant conditions) in fluctuating temperatures averaging 25 °C in 36 to 65 percent RH. In contrast, Laing (1969) reported an r_m of only 0.143 for *T. urticae* in fluctuating temperatures averaging 20.3 °C and 55 to 98 percent RH, suggesting that high RH lowers r_m in *T. urticae*. There may be a similar relationship between low temperatures, high humidity, and low r_m in *H. anconai*. The r_m of 0.278 at 30 °C and 40 to 75 percent RH for *H. anconai* is comparable to that reported by Feldman (0.273 and 0.286 at 28 °C and 70 percent RH) for *T. urticae*.

Effect of relative humidity on egg hatch

Egg hatch was low in both the high and low relative humidities tested. At 74 percent RH, 92.5 percent of the eggs hatched, but only 28.6 percent and 22 percent of the eggs from the same females hatched at 32 percent and 97 percent RH, respectively. The humidity may never drop as low as 32 percent in the leaf sur-

TABLE 5. LIFE TABLE OF *H. ANCONAI* AT CONSTANT 24°C. 60 TO 90 PERCENT RH*

Age in days (midpoint of interval)	Proportion of females alive at age x	Number of female progeny per female†
x	l_x	m_x
0.5	1.000	0.000
13.5	0.672	0.118
14.5	0.672	0.471
15.5	0.672	1.043
16.5	0.656	1.173
17.5	0.639	0.938
18.5	0.639	1.150
19.5	0.639	0.867
20.5	0.623	0.563
21.5	0.623	0.654
22.5	0.607	0.653
23.5	0.590	0.345
24.5	0.557	0.406
25.5	0.541	0.293
26.5	0.508	0.334
27.5	0.492	0.299
28.5	0.459	0.370
29.5	0.459	0.172
30.5	0.459	0.296
31.5	0.459	0.197
32.5	0.459	0.394
33.5	0.443	0.256
34.5	0.443	0.204
35.5	0.443	0.230
36.5	0.410	0.193
37.5	0.410	0.276
38.5	0.410	0.138
39.5	0.393	0.144
40.5	0.393	0.144
41.5	0.377	0.090
42.5	0.344	0.131
43.5	0.344	0.099
44.5	0.344	0.000
45.5	0.279	0.081
46.5	0.279	0.122
47.5	0.279	0.081
48.5	0.279	0.041
49.5	0.246	0.000
50.5	0.197	0.057
51.5	0.180	0.000
52.5	0.164	0.000
53.5	0.148	0.000
54.5	0.131	0.000
55.5	0.131	0.000
56.5	0.115	0.000
57.5	0.115	0.000
58.5	0.115	0.000
59.5	0.049	0.000
60.5	0.049	0.000
61.5	0.049	0.000
62.5	0.049	0.000
63.5	0.033	0.000
64.5	0.016	0.000
65.5	0.016	0.000
66.5	0.016	0.000
67.5	0.000	0.000

Summary statistics, TABLE 5
intrinsic rate of increase, $r_m = 0.097$
net reproductive rate, $R_o = \Sigma l_x m_x = 7.35$
generation time, $T = \log_e R_o / r_m = 20.56$

*Fecundity and longevity data were taken for 41 females. Using immature mortality and adult sex ratio data, and assuming no differential mortality, we calculated the initial cohort to be 61 females.
†The overall sex ratio, 0.699♀ (Table 1), was used in the calculation of m_x.

TABLE 6. LIFE TABLE OF *H. ANCONAI* AT 30°C. CONSTANT TEMPERATURE, 40 TO 75 PERCENT RH*

Age in days (midpoint of interval)	Proportion of females alive at age x	Number of female progeny per female†
x	l_x	m_x
0.5	1.000	0.000
7.5	0.833	0.221
8.5	0.833	2.042
9.5	0.833	4.112
10.5	0.833	4.471
11.5	0.833	4.195
12.5	0.833	3.257
13.5	0.767	3.450
14.5	0.767	2.520
15.5	0.600	2.147
16.5	0.567	1.989
17.5	0.567	1.989
18.5	0.500	1.472
19.5	0.467	1.429
20.5	0.433	1.062
21.5	0.400	1.092
22.5	0.367	0.502
23.5	0.367	0.314
24.5	0.300	0.460
25.5	0.267	0.345
26.5	0.233	0.099
27.5	0.233	0.000
28.5	0.200	0.115
29.5	0.167	0.138
30.5	0.167	0.000
31.5	0.100	0.000
32.5	0.067	0.000
33.5	0.067	0.000
34.5	0.067	0.000
35.5	0.067	0.000
36.5	0.067	0.000
37.5	0.033	0.000
38.5	0.033	0.000
39.5	0.000	0.000

Summary statistics
intrinsic rate of increase, $r_m = 0.278$
net reproductive rate, $R_o = \Sigma l_x m_x = 26.27$
generation time, $T = \log_e R_o / r_m = 11.76$

*Fecundity and longevity data were taken for 25 females. Using immature mortality and adult sex ratio data, and assuming no differential mortality, we calculated the initial cohort to be 30 females.
†The overall sex ratio, 0.699♀ (Table 1), was used in the calculation of m_x.

face microclimate,and the deposition of stalked eggs on the tips of leaf hairs by *H. anconai* may place the eggs outside the area nearest the leaf, where humidity might be expected to be highest, so the two extremes tested may seldom occur under natural conditions.

Temperature threshold for egg hatch

In the first test, no eggs hatched on leaves at 6 °C, and 16.5 percent hatched at 12 °C. However, relative humidity was uncontrolled in this test, and percent hatch must have been affected by high humidity. When the humidity was controlled at 75 to 76 percent RH, 80 percent of the eggs hatched on paraffin disks at room temperature (16° to 26 °C), 85 percent hatched at 15 °C, 75 percent hatched at 12 °C, and none hatched at 6 °C. These data suggest that the threshold for egg development and hatch is between 6° and 12 °C. There is no information to allow comparison with other tydeid mites. In the family Tetranychidae, Putman (1970) reported that *Panonychus ulmi* (Koch) eggs hatched at 10.8 °C, but suggested that the threshold was a few degrees below that, and Nickel (1960) reported an egg hatch threshold near 10 °C for *Tetranychus desertorum* (Banks). The threshold for completion of the life cycle is below 18 °C for *H. anconai*, since it successfully developed and reproduced at that temperature.

Hibernal diapause

Evidence from three lines of research demonstrated that *H. anconai* undergoes a photoperiodically induced, temperature-sensitive, hibernal reproductive diapause.

Diapause induction in a field cage. *H. anconai* females transferred from the Berkeley field cage to the laboratory during September laid eggs within 24 hours, indicating they were not in diapause. In contrast, less than half of the females brought into the laboratory during October and none of those brought in during November, or later, laid eggs within 24 hours (Table 7). Females that did not oviposit in 24 hours did not become gravid and begin to produce eggs until 11 to 32 days later (Table 7), indicating that they were in reproductive diapause, and that the diapause was stable, even at 16° to 26 °C under an 18 hour daylength.

Diapausing females in the field cage colonies were nongravid, and were very tightly aggregated, usually near a leaf vein or under cotton strands. These aggregations were larger and more compact than the clumps of quiescent and active mites observed in laboratory colonies under 18 hours of light. The tight aggregations of diapausing females were not a result of low temperatures, because they were observed on warm October days as well as on colder days. When fresh pollen was added, mites did feed on it. They moved if disturbed but, in general, moved less than nondiapausing females. At least a few males (<10 percent) were observed in each field cage culture every time samples were taken. These males were probably survivors of the last fall generations. We do not have any evidence that males diapause.

TABLE 7. DAYS UNTIL OVIPOSITION BY FEMALE *H. ANCONAI* PERIODICALLY TRANSFERRED FROM A BERKELEY, CALIFORNIA, FIELD CAGE TO A LABORATORY (16-26°C, 18 HOURS LIGHT)*

Date transferred	% females that oviposited within 24 h	% females that oviposited after 24 h	Mean (range) days to first egg if after 24 h
September 15	100	0	--
September 28	100	0	--
October 12	40	60	14.9 (11 - 19)
October 26	14	86	19.1 (14 - 28)
November 9	0	100	18.9 (14 - 24)
November 23	0	100	19.3 (15 - 23)
December 8	0	100	20.8 (11 - 32)
December 21	0	100	19.4 (14 - 26)
January 5	0	100	16.6 (8 - 24)

*On each date, 15 to 20 females were transferred; 8 to 16 ($\bar{x}$ = 14) survived and oviposited.

TABLE 8. DAYS UNTIL OVIPOSITION BY *H. ANCONAI* FEMALES REMOVED FROM VINEYARD-COLLECTED (DECEMBER 18, 1979) GRAPE BUDS

Temperature °C	Photoperiod hours	No. (%) females that oviposited	Mean (range) days to first egg	No. (%) surviving females that did not oviposit within 35 days
27	16	20 (100.0)	11.2 (7-20)	0 (0.0)
19	8	3 (8.3)	25.3 (21-34)	21 (87.5)

TABLE 9. EFFECT OF TEMPERATURE AND DAYLENGTH ON DIAPAUSE INDUCTION IN *H. ANCONAI* FEMALES REARED FROM EGG TO ADULT UNDER CONTROLLED CONDITIONS

Rearing conditions			
Temperature °C	Photoperiod hours	No. cultures*	Mean days (range) from egg to first egg
18	8	9	94.2 (90-100)†
18	18	9	32.9 (29-37)
16-26	18	8	19.1 (17.5-21)
24	8	10	22.0 (16.3-37.5)

*Each culture began with 25 to 30 eggs.
†Females on three of nine cultures did not produce eggs before the experiment was terminated at 100 days.

Reproductive status of females overwintering in grape buds. Ninety-three females and seven males or immatures were dissected from grape buds collected in the San Joaquin Valley during December, confirming that the adult female is the primary overwintering stage. Of 77 females placed in temperature cabinets, 44 survived to oviposit or until the end of the test (35 days). Females transferred from grape buds to 27°C and 16 hours of light laid eggs after an average of 11.2 days (range 7 to 20 days) (Table 8). These data are comparable to the data obtained for females reared in Berkeley in field cages and sampled during November or later (Table 7). Only 3 of 24 field-collected females transferred to 19°C and 8 hours of light laid eggs during the 35 days of the test (Table 8). Both females and males were reared from the eggs laid by the field-collected females, demonstrating that the diapausing females had been mated.

Experimental induction of diapause. Diapause was induced in the laboratory by rearing males and females under a short photoperiod and cool temperature. Males were not given particular attention in these tests; however, their behavior and survival appeared similar to males in non-diapause-inducing conditions. Females in three of nine cultures reared from eggs and maintained at 8 hours of light and 18 °C did not oviposit within 100 days, and the first egg was observed in the other six cultures only after an average of 94.2 days (Table 9).

Cool temperature alone, without an accompanying short daylength, was not sufficient to induce diapause. Thus, when another batch of eggs from the same females was reared at 18 °C but was provided 18 hours of light, new eggs were observed in the cultures within a few days of the time adults were first observed. The first eggs were deposited after a mean of 32.9 days (Table 9). The control cultures were reared at room temperature and 18 hours of light and produced eggs in 19.1 days, as expected (Table 9).

Diapause was prevented in most of the cultures when mites were reared under warm temperature and short photoperiod. When cultures were reared at 24 °C in 8 hours of light, the first new eggs were observed an average of 22 days after the parental eggs were placed in the temperature cabinet (Table 9). In eight of these ten cultures, eggs were observed after 16 to 18.5 days. This is close to the egg-to-egg time of 14.2 to 15.4 days expected from the rearing data at 24 °C and 18 hours of light (Table 2). However, two of the cultures reared at 24 °C and 8 hours of light did not produce eggs until 25.5 and 37.5 days, suggesting that the females in these cultures did experience a short reproductive diapause. One of the two colonies was a mixed colony of uncertain origin. The other one was from the Boeger colony. The Boeger vineyard is on the east side of the San Joaquin Valley in the Sierra foothills, where winter conditions are more severe than in the San Joaquin Valley and diapause attributes might be intensified. The suggestion that diapause response varies between populations of *H. anconai* is preliminary but indicates an area for future research.

Lobes of the body striae of certain tetranychids and eriophyids are absent on diapausing forms of the same species (Jeppson, Keifer, and Baker 1975). In contrast, diapausing *H. anconai* females taken from aggregations of nongravid females in Berkeley field cage cultures during late October, mounted in Hoyer's medium, and examined with a phase contrast microscope had clearly lobed body striations that appeared identical to those of reproducing females.

Feeding studies

Healthy, reproducing colonies of *H. anconai* were established on leaf disks supplied with pollen of *Callistemon* bottlebrush, iceplant, *Magnolia*, and California poppy, but not with *Cosmos*, *Dahlia*, or pine pollens. Subsequently, laboratory colonies were maintained on bottlebrush and iceplant pollen as well as on cattail pollen. Tydeids reared on poppy pollen were noticeably more golden in color than those reared on cattail, bottlebrush, or iceplant pollens.

In the test comparing cork or plastic with grape leaf substrates, *H. anconai* females did not continue to produce eggs when transferred to one of the artificial substrates, even if pollen was supplied (Table 10). Only when pollen was

supplied on the grape leaf substrate did egg production continue. Females survived for 6 days on grape leaf alone as well as on grape leaf with pollen, perhaps because on leaves they were able to find and cannibalize eggs laid during the first few days. Pollen was necessary on all substrates for continued egg production (during days 4 to 6), but not sufficient in the absence of some other unknown factor(s), perhaps an essential nutrient, moisture, or other microhabitat requirement, or ovipositional cue provided by the leaf tissue.

Predation by *H. anconai* on spider mite eggs is incidental and would have little impact on spider mite populations in vineyards. In the 72-hour feeding test, limited predation by starved *H. anconai* females occurred on spider mite eggs, and the females did not produce eggs on a diet consisting solely of spider mite eggs (Table 11). A third of the tydeids that were offered young Pacific mite eggs preyed on them, puncturing about 1.5 each.

In the test evaluating long-term survival and productivity of *H. anconai* on Pacific mite eggs, females preyed on spider mite eggs whether pollen was available or not (Table 12). They ate more eggs if pollen was not available, but in either case predation was low. It is interesting that the tydeids laid more eggs and lived longer on pollen only than on pollen plus spider mite eggs. The reason may be that the spider mite eggs are laid in a network of fine webbing that interfered with the tydeid's movements. Tydeid females fed Pacific mite eggs and pollen laid an average of 22.6 eggs. This is significantly lower than the 34.3 eggs laid by those fed pollen alone. Table 13 shows that productivity of gravid females from laboratory colonies was significantly less during 48 hours on leaf disks with spider mite eggs and pollen than on leaf disks with pollen only, demonstrating that the reduced productivity is independent of longevity. These data suggest that high spider mite populations might interfere with *H. anconai*.

Generally, this work confirms Flaherty and Hoy's (1971) conclusion that *H. anconai* feeds primarily on pollen. There are some difficulties in interpreting the feeding data, because bacteria and fungi, including powdery mildew, appeared around the edges and on the surfaces of many of the grape leaf disks in the tests, even though the leaves were previously washed. Although the microflora and leaf tissue may provide sufficient nourishment for survival, *H. anconai* cannot reproduce on these food sources alone. The predation rate on spider mite eggs was low, and *H. anconai* could not reproduce on leaves having only spider mite eggs. However, these alternate foods may enable *H. anconai* to survive in vineyards when pollens are scarce.

Preference of females for previously inhabited leaf surfaces

In the tests using paired leaf halves, hungry *H. anconai* females spent significantly more time ($p < 0.005$) on leaf disk halves previously occupied by other *H. anconai* females than on clean leaf disk halves (Table 14). All the hungry females observed crossed the midline at least once and were included in the analysis. Well-fed females did not show a preference. Three of 12 females did not cross the midline and were excluded from the analysis. The fecal residues and egg stalks on the previously inhabited disk half may provide tactile and/or chemical cues that *H. anconai* perceives with its forelegs. These are not walking legs, but are well supplied with sensory setae and pegs (Fig. 1) and

TABLE 10. SURVIVAL AND PRODUCTIVITY OF GRAVID FEMALE *H. ANCONAI* FROM LABORATORY COLONIES DURING SIX DAYS ON PLASTIC OR CORK SUBSTRATES OR GRAPE LEAF SUBSTRATE

Substrate	Food	No. ♀♀	% survival over 6 days	Total no. eggs laid in 6 days	Total no. eggs laid days 4-6	Total no. eggs cannibalized in 6 days*
Plastic	none	20	30	10	0	3
	pollen	20	50	17	6	3
Grape leaf	none	20	75	26	2	11
	pollen	20	80	118	36	17
Cork	none	25	52	29	1	3
	pollen	25	28	22	0	0
Grape leaf	none	25	72	33	2	16
	pollen	25	72	91	20	9

*Egg stalks with drained, shriveled egg shells.

TABLE 11. PREDATION BY STARVED *H. ANCONAI* FEMALES OFFERED SPIDER MITE EGGS FOR 72 HOURS

Prey offered*	No.♀♀ tested	No. ♀♀ that preyed on eggs	No. of eggs punctured†
Pacific mite eggs	33	11	16
Willamette mite eggs	32	15	38

*Initially 0 to 2 days old.

†Punctured eggs were shriveled and completely drained of their contents.

TABLE 12. LONG-TERM SURVIVAL AND PRODUCTIVITY OF *H. ANCONAI* ADULT FEMALES TRANSFERRED FROM LABORATORY COLONIES TO GRAPE LEAF DISKS PROVIDED WITH VARIOUS TYPES OF FOOD

Food offered	No. ♀♀ tested	$\bar{x}$ Pacific mite eggs punctured	$\bar{x}$ total productivity	$\bar{x}$ days adult longevity
Pacific mite eggs only	24	3.9	1.6	15.6
Pacific mite eggs and cattail pollen	23	1.4	22.6*	16.7
Cattail pollen only	37	-	34.3	21.9

*p = cattail pollen only <0.01, one-tailed T-test.

TABLE 13. PRODUCTIVITY DURING 48 HOURS OF GRAVID *H. ANCONAI* FEMALES OF UNKNOWN AGE TRANSFERRED FROM LABORATORY COLONIES TO LEAF DISKS WITH VARIOUS TYPES OF FOOD

Food offered	No. ♀♀ tested	$\bar{x}$ eggs/ in 48 h
Pacific mite eggs and cattail pollen	91	4.1*
Willamette mite eggs and cattail pollen	34	3.9*
Cattail pollen only	58	5.1

*p = cattail pollen only <0.01, one-tailed Wilcoxon non-parametric, $\alpha/2$ for two comparisons.

rapidly tap the substrate as the mite moves.

The test reported here is only a preliminary step toward understanding the aggregating behavior in this species, but it is of interest because the tendency to aggregate is also reported for other species in the family Tydeidae. Fleschner and

TABLE 14. PREFERENCE OF HUNGRY AND WELL-FED *H. ANCONAI* FEMALES FOR LEAF HALVES WITH *H. ANCONAI* FEMALE RESIDUES*

Condition of female	No. observed	No. that crossed midline	No. of times observed (expected) on		Chi square
			Clean half	Half with residues	
Hungry	14	14	112 (155)	198 (155)	23.8†
Well-fed	12	9	101 (104.5)	108 (104.5)	0.2

*Location of each female was scored every 5 minutes for 2 hours. Only those that crossed the midline one or more times were included in the analysis.
†p observed = expected <0.005.

Arakawa (1953) and Gerson (1968) reported large aggregations of *Tydeus californicus* on the leaves, branches, and bark of citrus and avocado, forming particularly at midrib-vein junctions on the undersides of leaves. Nachev and Simova (1978) found several tydeid species occurring commonly at the base of the central vein on plum leaves. Smirnoff (1957) described spots 2 to 3 cm in diameter on citrus twigs and branches that were aggregations of *Lorryia formosa* adults, immatures, and their shed exuviae. Inserra (1967) included photographs of light patches on citrus fruits that are aggregations of *L. formosa* and their exuviae. This behavior provides an intriguing area for future research. Although tactile stimuli are clearly important, it would not be surprising to learn that pheromones are also involved in tydeid aggregation behavior.

CONCLUSIONS

Our understanding of the biology and ecology of *H. anconai* has increased substantially. As a result, we can better predict how pest management practices in vineyards will affect not only the tydeids, but also the Pacific and Willamette spider mites and the predator *M. occidentalis*. Knop and Hoy (1983) found that *H. anconai* occurs in all the grape-growing areas of the San Joaquin Valley of California. They examined high temperatures and the pesticides used in vineyards as factors that might explain why *H. anconai* populations are low in commercial vineyards during the summer. Cyclic high temperatures and long days were not detrimental to egg hatch, development, or reproduction of *H. anconai*, but sulfur, acaricides and most insecticides commonly used in California vineyards were toxic at field rates. These toxicity data allow consideration of the selectivity of pesticides in designing integrated pest management programs for grapes. If pollen is available and selective pesticides and/or selective application rates are used, *H. anconai* is likely to be available to *M. occidentalis* as an alternate prey during the growing season as well as in overwintering sites under bud scales. Incorporation of *H. anconai* life table data into a grape pest management model may refine predictions of predator-prey interactions between predatory mites and spider mites.

The importance of alternate prey for predatory mites in vineyards and in orchard crops is well established (Flaherty 1969, Hoyt 1969, Flaherty and Huffaker 1970, Kinn and Doutt 1972, Calvert and Huffaker 1974, Flaherty, Hoy and Lynn 1981). Laing and Knop (1983) review the widely scattered literature on the

beneficial roles of tydeid mites as predators and fungus feeders in addition to their role as alternate prey. It is clear that these tiny mites deserve and will receive increasing attention in the development of pest management programs.

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appearance from nondiapausing females only because they are nongravid. The primary differences are behavioral: aggregating behavior is marked in diapausing females, and they are less active and feed less than nondiapausing females.

The mites are primarily pollen-feeding, and females continue to oviposit only on leaves supplied with pollen. Colonies are easily maintained with pollen provided as food on both blackberry and grape leaves, but not on leaf tissue alone. Attempts to rear *H. anconai* on pollen on artificial substrates were also unsuccessful. Leaf tissue, while not sufficient for development and reproduction, may provide a necessary nutrient, microhabitat requirement, or ovipositional cue. Other foods utilized include spider mite eggs and fungi.

These data allow predictions about field populations of *H. anconai.* Life table analysis suggests that, during the summer months, populations in the San Joaquin Valley are made up of many (about 10) overlapping generations during April-October. Field populations should increase rapidly when wind-blown pollens are abundant and temperatures are warm. Populations probably survive periods of low pollen availability by using alternate food sources, including spider mite eggs, and by delaying their own egg production. Clumped distributions are expected on grape leaves, and this may result in inbreeding when populations are low. Females that develop in the fall when daylengths are sufficiently short enter a reproductive diapause. Behavioral shifts observed in these females in field cage cultures are probably related to finding, and remaining in, their common overwintering sites under the grape bud scales in vineyards.

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