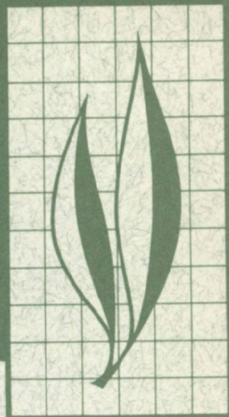


# HILGARDIA

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**Competitive Displacement: Extinction of the  
Yellow Scale, *Aonidiella citrina* (Coq.)  
(Homoptera: Diaspididae), by Its Ecological  
Homologue, the California Red Scale,  
*Aonidiella aurantii* (Mask.) in Southern  
California**

**Paul DeBach, Robert M. Hendrickson, Jr., and Mike Rose**





Discussion, historical data, and laboratory experiments are used to show that competitive displacement may occur even when there are no apparent shortages of requisites or direct aggression between ecological homologues. The final determinant is a relative difference in effective progeny production,  $R$  (as modified or even reversed by other environmental factors—such as natural enemies). These concepts are opposed to those of Huffaker and Laing (1972) who consider "escape from natural enemies" or the effects of other extrinsic factors as resources or requisites.

The decline of yellow scale, *Aonidiella citrina*, on citrus in southern California was documented with changes in distribution and abundance mapped from earliest records until its extinction sometime in the 1960s. Possible explanations—such as natural enemies, insecticides, and climate, were examined and found untenable. Extinction took place only where California red scale, *A. aurantii*, was present with yellow scale for a number of years. This led to the hypothesis that the California red scale was an ecological homologue of the yellow scale and that competitive displacement was responsible for extinction.

Results of laboratory tests all favored California red scale: (1) Gross fecundity, sex ratio, minimum and average time per generation were better, and more crawlers of California red scale than yellow scale survived to reproduce. (2) Computer calculation of the compound effective progeny production of a female scale and that part of her progeny which were themselves producing crawlers showed the "compound-interest" effect (California red

*(continued inside back cover)*

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INTRODUCTION

THE PRINCIPLE of competitive displacement has been the subject of considerable review and controversy over the years, beginning with its implicit statement by Darwin (1859) to the more recent reviews by Hardin (1960), Cole (1960), DeBach (1966), and Huffaker and Laing (1972) among others. Very briefly, our concept of competitive displacement is that it occurs when one species displaces another ecologically homologous species in the same habitat where both species are capable of surviving independently. Our views of this principle along with necessary pertinent definitions are given in DeBach (1966) and DeBach and Sundby (1963). Hardin's (1959, pp. 84-85) theoretical model helps clarify the basis of competitive displacement as used in this paper:

"Let us imagine a very odd savings bank which has only two depositors. For some obscure reason, the bank pays one of the depositors 2 percent compound interest, while

paying the other 2.01 percent. Let us suppose further (and here the analogy is really strained) that whenever the sum [author's underlining] of the combined funds of the two depositors reaches two million dollars, the bank arbitrarily appropriates one million dollars of it, taking from each depositor in proportion to his holdings at that time. Then both accounts are allowed to grow until their sum [author's underlining] again equals two million dollars, at which time the appropriation process is repeated."

A little intuition (supported by mathematics) shows that the depositor with the greater rate of interest will eventually have all the funds, while the individual with the lower rate of interest will be penniless. Hardin (1959) continues:

"Translated into evolutionary terms, this is what competition in nature amounts to. The fluctuat-

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ing limit of one to two million represents the finite available wealth (food, shelter, etc.) of any natural environment, and the difference in interest rates represents the difference between the competing species in their efficiency in producing offspring. No matter how small this difference may be, one species will eventually displace the other. In the scale of geological time, even a small competitive difference will result in a rapid extermination of the less successful species. Competitive differences that are so small as to be unmeasurable by direct means will, by virtue of the compound-interest effect, ultimately result in the extinction of one competing species by another."

Hardin's model is very simple, because entities representing environmental and biological variables are given known values. While the conditions existing in nature are complex due to the diversity and variability of factors influencing organisms in a given habitat, the principle itself remains truly simple. A combined population ceiling dictated by the effect of the total environment on the joint populations assures that increase is regulated and limited. Resources (Hardin's \$1 million to \$2 million range of wealth) in any system are finite and although they may be relatively abundant, their acquisition by ecological homologues (Hardin's depositors) as requisites for life entails competition. Different rates of effective progeny production,  $R$ , (Hardin's 2.00 versus 2.01 percent rates of compound interest) are assured by the axiom of inequality between species, and because in each generation (or time period) there are new individuals whose relative proportion is determined by the difference in their  $R$  values. All causes of immature mortality are merely factors that may influence the  $R$  values of two homologues, but in

themselves never directly cause displacement. Therefore, all that is really necessary for displacement to occur between sympatric ecological homologues is a limit to combined population increase and differential effective progeny production,  $R$ .

As noted previously, definitions of the major terms used in the preceding discussion are given in DeBach (1966) and DeBach and Sundby (1963). The interpretation of these definitions by others has resulted in some semantic confusion; to facilitate our views of the principle of competitive displacement, our definitions are included here.

**Ecological homologues** are species having the same ecological niche. An ecological niche "refers to the role played by an animal based upon its precise food, spatial, or habitudinal requirements in a particular habitat" (DeBach, 1966, p. 185). It is important to avoid confusing ecological niche, which has to do with function, with the concept of spatial niche, which has to do with location.

**Role** is what an organism does to obtain its particular requisites for survival and reproduction in a particular habitat; its inherent biophysiological characteristics as modified by the environment.

**Effective progeny production,  $R$** , was defined by DeBach (1966) as the number of female progeny produced per parental female which are themselves capable of producing progeny, thus excluding males and sterile females. In Hardin's model, different rates of effective progeny production are analogous to different rates of compound interest. Most importantly, with each successive generation (time), old individuals are replaced by new ones with the relative proportion of each being dependent on the difference in  $R$  of the two species. It is also important to stress that these different rates of effective progeny production do not refer to a maximum rate



of reproduction established by rearing individuals under ideal conditions or the  $r_m$  (intrinsic rate of natural increase of Andrewartha and Birch, 1954). Competitive displacement can take place only if conditions causing a population ceiling exist, but this, of course, is always true in nature (no species increases without limit).  $R$  should be considered the net reproductive *response* of an organism to its environment. Factors which modify  $R$  such as natural enemies or climate are then *expressed* in differential  $R$  values.

As in Hardin's model, the composition of the joint (combined) population level (sum) is dependent on  $R$  values (2.0 percent versus 2.01 percent). The displacement is dependent on the relative differential between the  $R$ s of the two species. In the voluminous literature of actual cases of competitive displacement, particularly in the laboratory, generally far fewer than 100 generations are required for complete displacement to take place. However, in cases where ecological homologues have similar  $R$  rates, the time required could be very lengthy. As an example, in southern California, the California red scale took about 100 years or approximately 300 generations to completely displace the yellow scale, but various factors modified the outcome to lengthen it. The most important probable factor was that both scales were invading species that did not become sympatric in all districts until as recently as 20 to 30 years ago.

In nature, population levels are maintained by various environmental limiting factors. Populations of sympatric ecological homologues that can occur only temporarily except where ranges overlap (see p. 28) or where spatial refuges or differences in microhabitats occur, are essentially acting as one species and have a combined population ceiling or combined upper population limit resulting from the action of the aforementioned environmental

factors—including the effects of natural enemies, climate, and other abiotic factors. The population ceiling or, better, the equilibrium position may be high or very low. Obviously, environmental factors do not have equal effect on the  $R$  of both populations (for example, more efficient natural enemies may attack one species), and the relative effect may differ in different habitats. One species therefore, may have the greater  $R$  in one habitat, and the other species the greater  $R$  in a different habitat. Thus, the species with the greatest  $R$  value after moderation by environmental conditions will increase at the expense of the competing species, regardless of the relative abundance or scarcity of food and space.

As an example, California red scale is controlled by natural enemies in certain citrus groves in various parts of California at roughly 0.001 of what its population would be if limited only by available food and shelter. Yellow scale likewise is controlled by natural enemies in certain groves in the San Joaquin Valley at a similarly low density. The same held true for yellow scale in Ventura County before its displacement by red scale there. Parasites effectively regulate the scale populations because of their inherent searching abilities (efficacy), but in nature over large areas *all* hosts are *never* found as shown by Nicholson's (1933) competition curve. A resource is not involved in this, rather the level of host population regulation is dependent on the searching ability of the parasite(s).

Thus, when the two scales occur together in a habitat where either occurring alone would remain scarce due to regulatory factors, food and space are *not* in short supply. Displacement will occur regardless, because there is necessarily a naturally regulated upper combined population limit, and the scale with the greatest  $R$  value will gain a larger proportion of each successive generation.

If individual organisms of two species are homologous, that is, share the same requirements for food or space, and are present together, then ultimate success for one organism occurs at precisely that time when that individual utilizes food or space which was mutually sought by an ecologically homologous individual. One can visualize this process, because homology essentially dictates that individuals of the two species are behaving in the same manner as far as requisites are concerned (or, in effect, acting as one species), so that interaction and, therefore, displacement eventually must occur so long as there is any difference in  $R$ , regardless of a seemingly great excess of requisites.

Combined population ceilings, (that is, natural control), finite resources, and differences in  $R$  are truisms; they exist as part of the nature of physical, organic, and ecological systems and are determined by inherent biophysiological characteristics and species response to the environment.

The theory of competitive displacement depends on the existence of true ecological homologues—the only element in the competitive displacement principle that is not obviously true or factual and requires experimental proof.

Establishing the identity of ecological homologues requires a clear separation between the type of competition that results in displacement and the kind of competition or “coexistence” which is reflected by organisms that occur superficially together while utilizing non-identical food and space or other requirements. One or more essential requisites must be identical for two species to be ecological homologues. Living on the same tree or even on the same leaf may not be enough. A species living only on the upper leaf surface and another species only on the lower surface of the same leaf would not be ecological homologues, although they might compete through adverse effects caused to the food source.

However, two species can be “partial” ecological homologues as, for example, the California red scale and the yellow scale, in which case one species can displace the other, but not vice versa (see p. 13). In theory, ecological homologues can share the same habitat (appear to coexist) under certain conditions, for example, if various microhabitats within the larger habitat provide differences in temperature which moderated  $R$  of each species so that the  $R$  of species A would be greater in one microhabitat and that of species B greater in another microhabitat. Furthermore, if the reproductively inferior homologue in a given habitat had an alternate host or a spatial refuge suitable only to itself, then it would survive and apparently “coexist” because of these differences.

To demonstrate whether two organisms (A and B) are ecological homologues, they first must be able to exist alone indefinitely under given test or natural conditions within defined average upper and lower population limits and require at least one mutual identical requisite. The determination that the mutual requisite is truly *identical* is the key. *Similar* needs or roles do not make ecological homologues. However, when both homologous organisms, A and B, come together under these same conditions, one eventually will become extinct. Sexual isolation of the two organisms assures that requisites will not be shared equally, so resource utilization will be progressively greater for one species in each successive generation depending on the relative  $R$  value of each species. The changes with time of the number of organisms of population A or B is dependent on  $R$ , and the winner in competitive displacement will be the organism (A or B) with the higher  $R$  value. For example, if  $AR$  is always more than  $BR$  under  $X$  conditions, but mortality of A is subsequently increased by the introduction of a more efficient specific natural enemy of A, then B would displace A if the value of



AR became less than the value of BR.

It is stressed that the changes in relative proportions of populations A or B with time as mediated by R, determines displacement. The average population level or density is not the determining factor. As stated earlier, low numbers do not halt competition or meetings between individuals of competing ecological homologues, only the frequency of attempted joint usage of requisites is reduced. Even when requisites are abundant, competition does not stop; only occasional interaction between individuals of ecological homologues assures that identical requisites will, over time, be utilized more completely by the organism with the greater R value however slowly the process occurs.

Food and space are the two major essential terms which are used to define the requisites of ecological homologues. Although food and space usually are separate entities in nature, they may be considered to be the same in the case discussed in this paper. Similarly ecological homologues may be functionally viewed as one "species" as far as their *role* is concerned. With the two scale insects studied by us, food and space are essentially identical, because the space they occupy as sessile organisms is also the source of their food.

To us, competitive displacement is an important part in the evolutionary processes of adaptation and speciation. Just as there are expressed differences in environmentally modified R values between ecological homologues, there is expressed genetic variability within specific populations. Certain genetic variations can be enhanced (or depressed) by the selective action of the environment. This process could be termed intraspecific competition as envisioned by Darwin (1859). A continuum from intraspecific competition to general interspecific competition would include, at a point very close to intraspecific competition, direct competition between ecological homologues. Such homologues are usually closely re-

lated species. This intense and probably accelerated form of competition results in eventual displacement. In the case discussed in this paper, extinction over a large area was the fate of yellow scale, the ultimate failure of any species.

The key to understanding competitive displacement between ecological homologues is that R is relative to environmental impact. As previously noted, R can be modified, for example by natural enemies, so that the R of species A is lower than R of species B even though individuals of A may have an inherently higher reproductive capacity ( $r_m$ ). Thus, the competitive advantage of either homologue will be determined on average by R of the species which is the *population's* expression in response to modifiers of inherent  $r_m$  values. Of course, all factors which modify R are important in understanding competition between specific ecological homologues. However, the final determinant of success in a given "habitat" will be expressed by the differential R values of the competing organisms.

### Another view

In a review of DeBach's (1966) and DeBach and Sundby's (1963) approach to competitive displacement, Huffaker and Laing (1972) disagreed with these authors on certain points. It is our view now that the "disagreement" is based on Huffaker and Laing's misinterpretation of DeBach's term *resource*, which they define as including parameters other than physical or organic requisites or resources such as food and space. Huffaker and Laing also failed to recognize that DeBach definitely holds that competition must occur, even though there is an abundance of food or other essential resources (see DeBach, 1966, p. 186). Furthermore, implicit in DeBach's idea of competitive displacement is the requirement for population limitation by regulating mechanisms (such as natural enemies

or others) acting on the competing species.

The postulation by Huffaker and Laing that species compete for space or sites protected from natural enemies is incidental to the effectiveness of the natural enemies in host population regulation and, we feel, to competitive displacement. The inherent searching ability of the natural enemy, combined with "random searching" in the sense of Nicholson (1933) is what determines the limits within which the host is maintained, other things being equal. The idea of competition for enemy-free space merely confuses the main point of competitive displacement between ecological homologues—that differences in effective progeny production, *R*, is what counts. Parasites merely operate

to modify *R* of one or both competing homologues. In so doing, they may influence which species wins or the rate of displacement, but they are not a *direct* part of the displacement process.

In our opinion, and all in all, the views of DeBach, and Huffaker and Laing, are more similar than they are contradictory. However, the latter two authors, as do many others, emphasize that a shortage of some essential resource such as food or space concomitant with crowding and intense competition is required for displacement to occur. We disagree, and point to our experimentally-based conclusion that competitive displacement between ecological homologues can occur in the presence of a relative abundance of mutually needed requisites.

## HISTORY AND DOCUMENTATION OF EXTINCTION

Early literature indicates that before 1910, yellow scale, *Aonidiella citrina* (Coquillet), was present throughout southern California except for the Coachella and Imperial valley areas. However, it was then a pest only in a few places within this major citrus-growing area (Coquillet, 1891; Quayle, 1911a). These reports also noted that California red scale, *Aonidiella aurantii* (Maskell), was a serious pest, especially along the coast, although it was not reported from several major citrus-producing districts. DeBach and Sundby (1963) suggested that the yellow scale had become extinct in most of southern California as a result of competition with the California red scale.

### Methods

The necessary information regarding the chronological changes in distribution and abundance of yellow and California red scales in California was compiled from an examination of scale identification records or interviews with representatives of the county commissioners of agriculture of San Diego,

Orange, Los Angeles, Riverside, San Bernardino, Kern, Tulare, Fresno, Sacramento, Yuba, Butte, and Glenn counties; interviews with University of California farm and home advisors in San Diego, Tulare, Kern, and Fresno counties; interviews with entomologists and examination of scale identification records at the California State Department of Food and Agriculture, Sacramento; and interviews with University of California entomologists. Use was also made of the extensive correspondence of the first author with entomologists regarding records of yellow scale in southern California. Furthermore, examination was made of each issue of the Bulletin of the California Department of Agriculture (1911–1967), California Citrograph (1915–1968), Citrograph (1969–1972), Exchange Pest Control Circular (1935–1952), Sunkist Pest Control Circular (1952–1967), Pest Control (1968–1973), and Pest Control Circular (1973), as well as the reports of Coquillet (1891), Quayle (1911a, 1938), Woglum (1932), Dick-



son and Lindgren (1947), and Compere (1961).

Although some of the early taxonomic morphological identification of individual scales is doubtful, the record becomes more reliable following McKenzie's (1937) description of the morphological characters that distinguish between the two closely related species. However, even with these characters, it has been our experience as well as that of the coccidologist for the California State Department of Food and Agriculture (Raymond Gill, personal communication) that about 5 percent of the scales cannot be confidently separated. So there remains a small margin of error in identification.

On the other hand, a number of characters make identification of these species in the field fairly easy, and this was the basis for most early records. A living yellow scale has a definite yellow color, while California red scale is brownish-red. Yellow scale is found only on fruit and leaves, while California red scale inhabits all parts of the tree. Yellow scale produces chlorotic spots or streaks on leaves, which are more pronounced than those associated with California red scale and are typically distinctive.

In spite of the usable field characters, early systematists were unable to find morphological differences, so that *citrina* was described as a variety of *aurantii* by Coquillett (1891). Their specific status was argued for years. Later, a series of crossing experiments showing reproductive isolation between the two and the discovery of slight, but difficult to use, morphological differences led Nel (1933) to raise *citrina* to species status. Finally, McKenzie (1937) showed the California red scale to have sclerotized areas on the ventral side of the pygidium anterior to the vulva which are lacking in yellow scale.

A further proof of the species status of the two scales has recently been obtained in negative bioassays of cross at-

traction to female sex pheromones in a wheel olfactometer (Moreno *et al.*, 1972).

Today the parasite species or races associated with the two scales also are generally different, and this enhances our ability to distinguish between the two species.

The ability to distinguish one of these scale species from the other is essential to the determination of whether or not extinction has occurred. It has been indicated that taxonomic identification is not always easy. In spite of difficulties encountered in identification, we feel that no error is inherent in the broad results presented or in the fact of actual extinction in southern California.

## Results

**Southern California.**—California red scale was probably introduced into southern California from Australia and had become a serious citrus pest in certain groves by 1877 (Compere, 1961). Early efforts to control the scale were ineffective. Coquillett developed a practical method of California red scale control using cyanide gas fumigation before 1893 (Compere, 1961).

Early records indicate that California red scale was a severe pest throughout the Los Angeles and Orange county areas, except for the San Gabriel Valley (Los Angeles County). Here Coquillett (1891) reported that the scale was absent. In the interior districts, it was absent or was only a minor pest in most areas until the 1930s and 1940s. It continued to increase its range steadily and by 1950 was reported as a serious pest from nearly all districts.

Red scale protective districts were formed for the detection and eradication of the pest where it did not occur or was just getting started. The first of the districts was formed in Ventura County in 1922 by growers alarmed at the increasing severity of infestations in nearby San Fernando Valley. This was followed by formation of a second

district in the Redlands-Highlands area (San Bernardino County) in 1936, two additional districts in Ventura County in the early 1940s, and additional districts in Fontana (San Bernardino County), Moreno, Hemet, and Coachella valleys (all of Riverside County) in the middle 1940s.

In the Coachella Valley, California red scale was first reported infesting ornamentals in the early 1930s. A survey in 1938 showed 30 infested residential properties. The first orchard infestation was found in Indio in 1944, and a second in 1945. The Coachella Valley Citrus Pest Control District was formed in 1946 to combat the pest and remains the only major eradication district in California which is still in operation. Its effectiveness has been enhanced by the adoption in 1971 of an improved detection method, sex pheromone traps (Daniel Moreno, personal communication).

Yellow scale was reported in the San Gabriel district (Los Angeles County) in the 1880s where California red scale was not reported. It became a serious pest there. In 1910, yellow scale was reported from all southern California citrus areas, apparently including San

Diego County (Quayle, 1911a). It was reported in 1913 as a major pest in the Redlands-Highlands, Highgrove, Rialto, and Cucamonga districts (all of San Bernardino County) and remained so at least in the first two districts through the 1940s. By 1950, however, yellow scale distribution was reduced. It was only reported from Ventura and western San Bernardino counties as occasionally moderate to heavy infestations in the former and as very light infestations in the latter. An occasional report of the scale was recorded in counties south of Ventura County during the 1950s, but these were largely found on dooryard citrus, ornamentals, or imported nursery material in quarantine. With the exception of a few localities in Ventura County, it was not considered a pest during this period on commercial citrus. By 1970, yellow scale had become extinct in southern California, including Ventura County. To our knowledge, this is the first authenticated case of a diaspidid scale (in this instance a numerous and widely distributed one) becoming naturally extinct in a relatively short period of time, i.e., about 100 years.

The historical changes in distribution

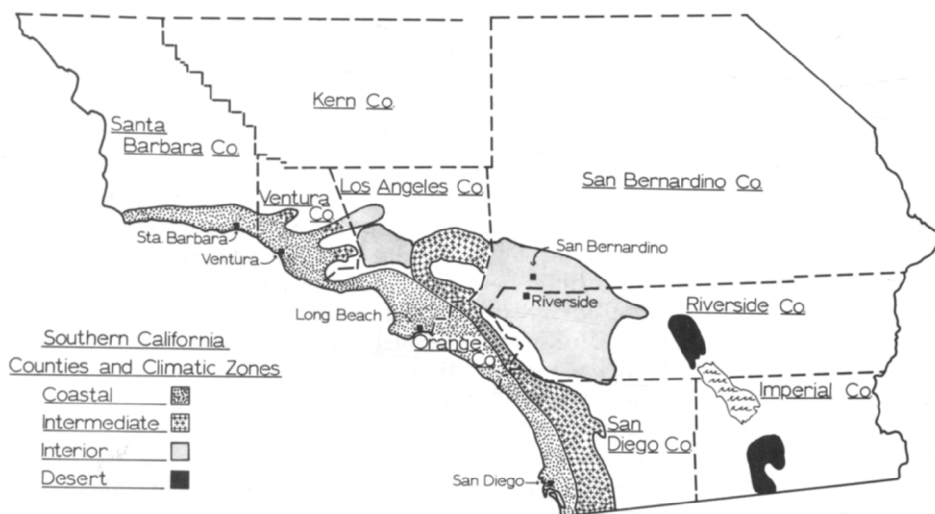


Fig. 1. The counties and climatic zones of southern California citrus areas.



and relative abundance of yellow and California red scales in southern California are given in Figure 2, *a* to *f*. The maps tell their own story and should be compared in sequence. In order to better interpret the maps, the counties and climatic zones of southern California are shown in Figure 1.

The general period 1890 to 1920 is represented by the map for 1910 (Fig. 2*a*). During this time, the yellow scale was more widely distributed in southern California than the California red scale. It was the only species of the two present in all of Ventura County and in most of the interior citrus areas of San Bernardino County. It was present in varying degrees of abundance in most other citrus districts, although the California red scale was dominant in most coastal and intermediate climatic zones and in the interior climatic zone of the San Fernando Valley. The yellow scale apparently occurred in San Diego County at this time, but this is not depicted on the maps because interim data are insufficient.

By 1930 (Figure 2*b*), the California red scale had been found in one coastal district of Ventura County and was beginning to be found somewhat more in the interior area of San Bernardino County, although the yellow scale remained vastly predominant in these areas. In Orange County, the yellow scale had disappeared and in Los Angeles County, it had become rather restricted both in distribution and abundance. In Riverside County, the status of the two scales remained about the same as in 1910.

The situation by 1940 (Figure 2*c*) in Ventura County showed the California red scale to be a little more common, but still scarce with yellow scale remaining strongly predominant. The

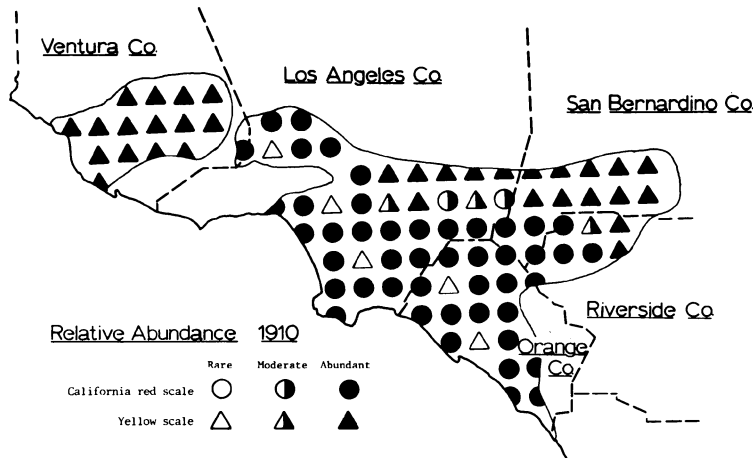
relative status was little changed in San Bernardino or Riverside counties since 1930. Orange County remained all California red scale and Los Angeles County showed an increasing scarcity of yellow scale.

By 1950 (Figure 2*d*), the picture changed rather dramatically. California red scale went from scarcity and limited distribution in 1940 to general distribution and equal abundance with yellow scale in Ventura County. Yellow scale disappeared completely from Los Angeles County, while California red scale became generally distributed and abundant. Yellow scale remained absent from Orange County with California red scale abundant everywhere. Yellow scale decreased from general distribution and high abundance in San Bernardino County to a restricted distribution and real scarcity, whereas the California red scale became strongly predominant and generally distributed. In Riverside County, the yellow scale became very rare. Thus, by 1950, the yellow scale had disappeared from all but the easternmost and the westernmost parts of the range for the two species.

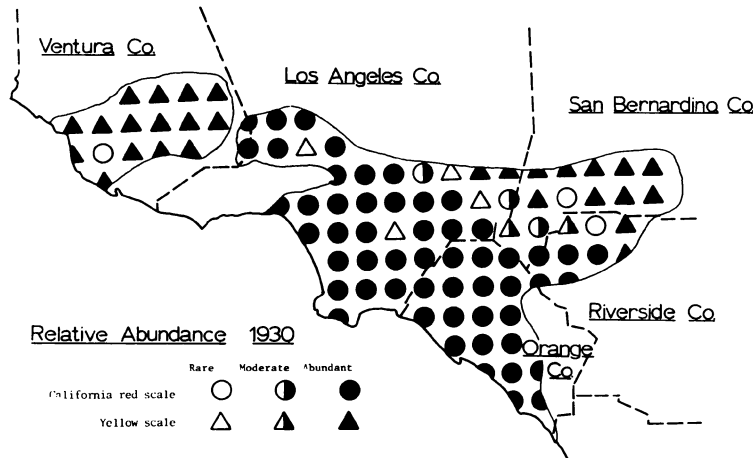
During the next decade (Figure 2*e*), the yellow scale became extinct in the eastern part of the range, i.e., San Bernardino and Riverside counties and survived until 1960 only in the non-coastal portions of Ventura County.

By 1970 (Figure 2*f*), the yellow scale had disappeared from Ventura County and was extinct throughout all of southern California. It was replaced completely by California red scale. This was true also in San Diego County, but the replacement apparently occurred before adequate records were kept. We have no knowledge of the existence of yellow scale in San Diego County after 1930.

2a



2b



2c

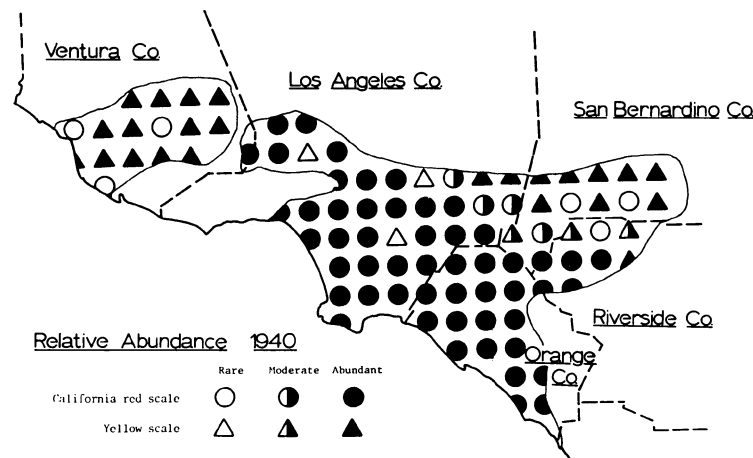
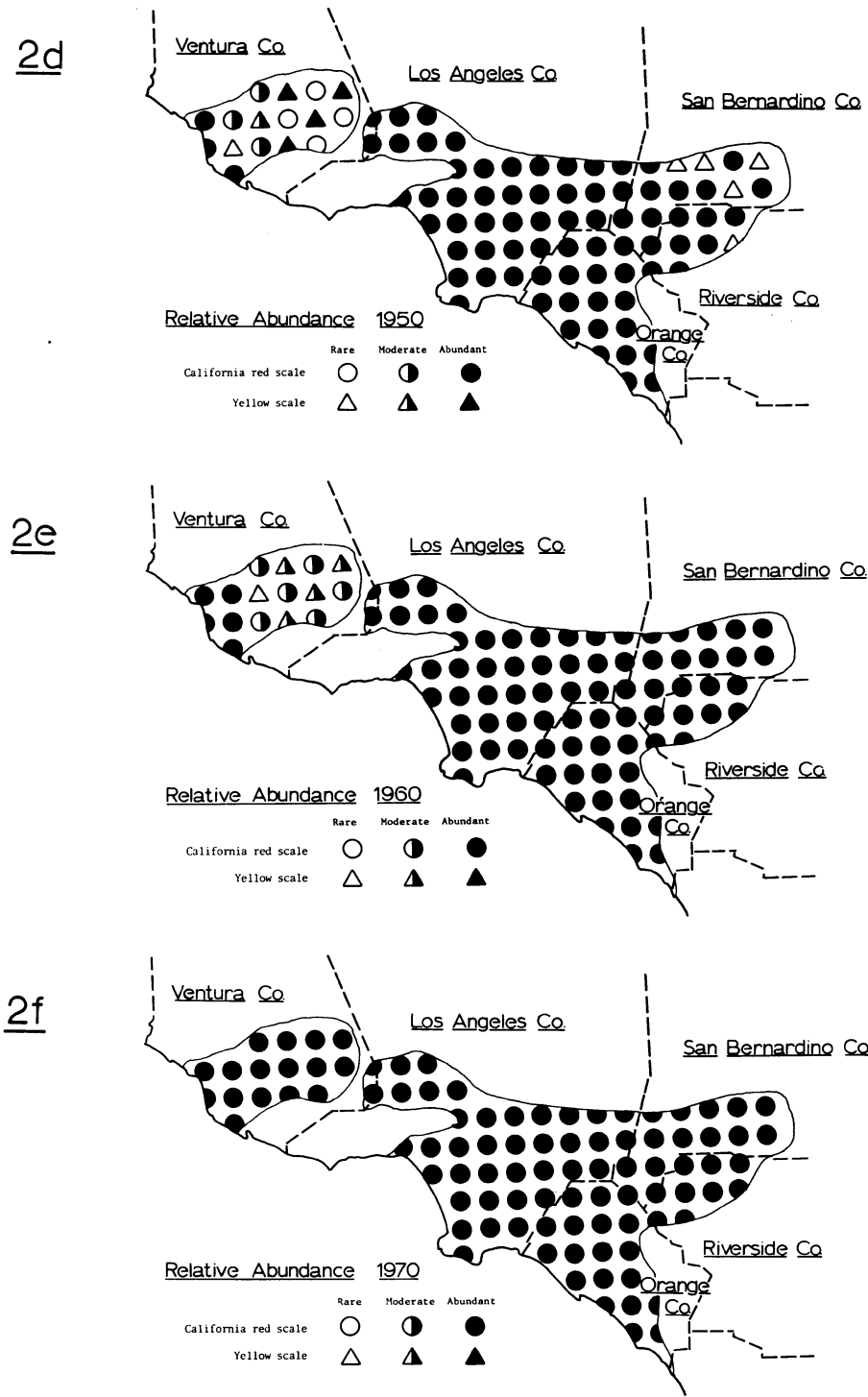


Fig. 2 a-f. Chronological changes in distribution and relative abundance of California red and yellow scales in southern California 1910-1970.





(Fig. 2 continued.)

### Possible Explanations for the Extinction of Yellow Scale in Southern California

Between 1960 and 1970, the last yellow scale in southern California disappeared. Surprisingly this took place essentially unnoticed except for the single reference to its presumed occurrence over a major part of southern California (i.e., except Ventura County) by DeBach and Sundby (1963). How could this be explained when this species was for years a serious pest, broadly distributed and occurring in uncounted hundreds of millions?

Food and space did not seem to be resources normally in short supply for yellow or California red scale. These scales were found together in hundreds if not thousands of acres of citrus in southern California for years, generally at the low densities maintained by natural enemies or pesticides. Rarely did either species build up sufficiently to cause defoliation or branch death.

Natural enemies can be dismissed as a possible cause of the extinction of yellow scale on several grounds. Natural enemies seldom if ever cause the extinction of their prey or hosts except perhaps in isolated microhabitats. Population declines of yellow scale in southern California were ascribed to biological control by the parasites, *Aspidiotiphagus citrinus* (Crawford) (Quayle, 1911b) and *Comperiella bifasciata* Howard (Japanese race) (Flanders, 1948). Before the extinction of yellow scale populations in Ventura County, recoveries of *Aphytis melinus* DeBach were also common from that species (unpublished data). Today, even with these and other yellow scale parasites present in the San Joaquin Valley of central California since 1930, the yellow scale is still common and occasionally a serious pest. This is further evidence that parasites did not *directly* cause its extinction in southern California.

Insecticides did not cause the extinction either. The yellow scale has never been eradicated chemically over a significant area by any of the various rigorous and costly campaigns conducted against it. The development of cyanide resistance by California red scale may have been responsible for the reduction of yellow scale populations to low levels in areas of sympatric distribution. Cyanide resistance by California red scale was first noted in 1914 in the Corona district of Riverside County. These resistant populations spread and others developed independently in almost all the major citrus-growing districts of California (Quayle, 1938). Field fumigation with cyanide killed 98 to 99 per cent of yellow scale, but only 89 to 96 percent of resistant California red scale. However, this is not to suggest that frequent fumigation was responsible for the extinction of yellow scale, because intensive eradication efforts with cyanide fumigation failed to eradicate yellow scale from the Central Valley and elsewhere, and, more to the point, yellow scale became extinct in Ventura County about 15 to 20 years after cyanide fumigation was abandoned.

Yellow scale was able to invade, increase to major pest status in various districts and to survive for 50 to 60 more years in southern California before it disappeared about 1965. The period is sufficiently long, and the scale's distribution in different habitats in California sufficiently extensive, to eliminate the adverse effects of climate as a possible explanation for its extinction.

One climatic factor which may occasionally have reduced, but not eliminated, yellow scale populations was defoliation due to freezing (Woglum, 1932). Even the great freeze of 1913 which caused extensive defoliation of citrus

trees in the Redlands-Highlands, Highgrove, Rialto and Cucamonga districts did not cause the extinction of yellow scale, since it again became abundant and remained a pest in the Redlands-Highlands area until the late 1940s.

The more obvious explanations for extinction of yellow scale have been found untenable. The chronological distribution maps (Figure 2, *a* to *f*) have indicated that the decline and extinction of yellow scale always occurred where California red scale shared the range of yellow scale for any substantial number of years. The two scale species appear to be ecological homologues, sharing the essential attributes of an ecological niche, i.e., the same food and space. More precisely, the California red scale is an ecological homologue of the yellow scale, but only partially vice versa. Both occur on the leaves and fruit, which furnish the sole space and food for the yellow scale. However, the California red scale also occurs on the twigs, branches and trunk where it is free from competition by yellow scale. Thus, yellow scale could not under any circumstances displace California red scale from an entire citrus tree, but California red scale could displace yellow scale from a citrus tree.

DeBach and Sundby (1963) suggested yellow scale may have become extinct in southern California (except then for Ventura County) due to competitive displacement by California red scale. The data and discussion presented here support their earlier hypothesis—as do the experimental laboratory tests which will be described later.

Although extinction of the yellow scale in the Central Valley (including the San Joaquin and Sacramento valleys) has not occurred yet, we consider that it is underway and therefore think it valuable to document the broad changes that have occurred there thus far in the population density and distribution of the two scale species. The Central Valley citrus is so geographic-

ally separated from southern California citrus that they can be considered as ecological islands with little interaction, except that one may serve on occasion as a locus for invasion of the other by a pest species not common to both (see Fig. 3). The yellow scale initially started in the Central Valley just before 1900, about 30 years before the California red scale did. It remained the dominant scale pest until the 1960s, but in that decade the California red scale became much more generally distributed and dominant in at least some groves or districts. More details follow for the two subdivisions of the Central Valley, the San Joaquin Valley, and the Sacramento Valley.

**San Joaquin Valley.**—Yellow scale was first reported from Visalia (Tulare County) in 1897. An eradication attempt started in 1908 was unsuccessful. The first commercial infestations were reported around Merryman and Venice Cove in 1915. These infestations gradually spread, and along with later independent infestations at Exeter (1921), Lindsay (1927), Sultana (1940), and Success (1941), the infested area included almost all of the central Tulare County citrus-growing areas by 1944.

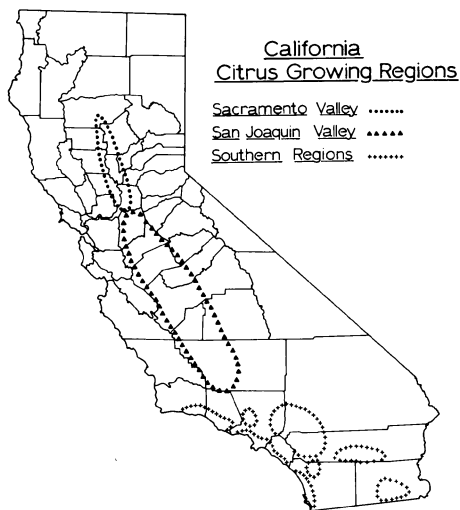


Fig. 3. The major citrus growing regions of California.

Isolated infestations also occurred in the southern and northern sections of Tulare County, and a number of small infestations were noted near Selma and Reedley in Fresno County.

In 1939, Porterville district growers became concerned by the increasing yellow scale populations and formed a protective district encompassing about 10,000 acres in an attempt to eradicate it. Their efforts reduced yellow scale populations throughout the 1940s, but did not achieve eradication.

By 1960, the scale had spread to include the area from the Richgrove-Jasmine district of southern Tulare County to Sanger in Fresno County, although there were localized areas in which the pest was absent or very rare. Recently (1973) yellow scale has increased its range slightly and is still spotty in distribution.

In Kern County, the only report of yellow scale has been from Delano, near the county's northern border.

California red scale was reported from a few localities in the San Joaquin Valley in the early 1930s. Mackie (1941) reported that before 1941, California red scale had been recorded from 37 locations in Fresno, 51 in Kern, and 31 in Tulare counties. Hartford Keifer (personal communication), former Chief of Insect Identification, California State Bureau of Entomology and Plant Quarantine, has indicated all state taxonomic records of California red scale before 1937 are suspect. However, as indicated previously, field identification of either scale was and is rather accurate.

During the period 1938 to 1941, the county commissioner of agriculture's office, Tulare County, carried out a program of inspection and eradication of California red scale around residences in towns. The scale was first discovered in the county's commercial citrus in 1947. Within a year of this discovery, an eradication district was formed for northern Tulare County and included

30,000 acres of citrus. An eradication district for the southern section of the county had been formed in 1939 for yellow scale; about 1948, the program of detection and eradication was expanded to include California red scale. Thus, by 1948, the entire county was covered by the two eradication districts.

By 1948, commercial citrus plantings in Fresno County remained uninfested with California red scale. However, ornamentals or dooryard citrus infestations of this species were common in urban areas, and some half-dozen semi-commercial orchards around the Selma-Reedley-Sanger area were also infested.

In the early 1950s, California red scale was found in the Edison district of Kern County and another eradication district was formed. Thus, by the middle 1950s, five eradication districts were operating in the three Central Valley counties. They merged in 1960 to form the Central California Citrus Pest Control Agency, which at that time covered about 80,000 acres of citrus. In the first year of its operation, only 1,226 acres of citrus were treated for California red scale. At that time, the major areas of infestation were the Sanger-Centerville district of Fresno County, the Orange Cove-Dinuba districts of both Fresno and Tulare counties, and the Jasmine-Delano and Edison areas of Kern County. Eradication efforts were hampered by the large number of scale-infested host plants around residences. Although many of these infestations were eliminated, they were difficult to control and were one probable source of frequent presumed reinfestations of "eradicated" commercial groves. Infestations of California red scale became so general throughout the San Joaquin Valley by the late 1960s that eradication efforts appeared fruitless, and many growers decided to handle scale control for themselves. The eradication district has since confined its activity chiefly to testing for citrus diseases. A few localized protective dis-



tricts are still functioning. California red scale is now a serious general pest in Kern County. It is abundant in Tulare County but, as yet, not every grove is infested. Commercial citrus in Fresno County is generally free of the pest, although the Sanger-Centerville district requires extensive control work.

Various records and our observations indicate, especially in Tulare County, that coincident to the development of heavy California red scale infestations in recent years, yellow scale populations have declined to levels that are no longer of concern or, in fact, have disappeared. Substantiating this, recent information indicates that substantial reductions or perhaps near extinction of the yellow scale has in fact occurred in parts of Tulare County where California red scale has become abundant (Karl Opitz, Chuck Kennett, personal communication, 1976).

Citrus is of minor importance in the

Sacramento Valley, hence, records there are sparse. We note the following mainly to serve as background for possible future changes in scale populations. Yellow scale was first noted on citrus in the Sacramento Valley in the 1910s. These infestations were scattered and light, seldom requiring chemical treatment. A similar condition prevails today.

California red scale was found around residences in the early 1940s, and efforts were taken in a few areas to eradicate the pest. In 1945, growers in Oroville (Butte County) undertook its eradication on six commercial properties. The scale was also found on one 20-acre grove in Orland in Glenn County. Although the present range of the California red scale has spread, its populations are usually light and there remain sections of the valley from which it has never been reported.

## LABORATORY TESTS OF YELLOW AND CALIFORNIA RED SCALES RELATIVE TO COMPETITIVE DISPLACEMENT

The outcome of competitive displacement between ecological homologues hinges on which of the competing species has the greatest effective progeny production under given conditions. The effective progeny production, i.e., the relative rate of production per parental female of female progeny that survive to reproduce, or  $R$  of DeBach (1966), is based on total fecundity, sex ratio, survival to reproduction, and time required for development to reproductive maturity. These parameters were ascertained for the two scale species in a series of tests in a controlled environment. All of the preceding parameters may be modified by a variety of environmental conditions, such as temperature, humidity, food quality or quantity, intraspecific competition, and the like, so that many factors act to de-

termine  $R$  in any particular "habitat" and thus modify the rate of displacement or even reverse the outcome.

### Fecundities and times for development

**Materials and methods.** The total and daily fecundities and time for development to reproductive maturity of both scale species individually were determined from the daily crawler (first instar mobile nymph) production over a 100-day period on lemon fruits. From other experiments, it was known approximately how long a time was required for both a crawler to reach maturity and for the adult scale to begin producing new crawlers under laboratory conditions of  $26.7 \pm 1^\circ \text{C}$  and  $60 \pm 10$  percent R.H. (relative humidity) on green lemons. To determine daily

crawler production, a thin ring of tree tanglefoot was placed around each mated maternal female scale a few days before crawlers were expected to emerge. As the crawlers emerged, they either settled within the circle or were trapped in the tanglefoot. Each day of the test, the crawlers were counted and removed from the encircled area and tanglefoot.

Fifty female California red scales and 40 female yellow scales, maintained separately—five to a lemon—were examined daily for 100 days. Fewer yellow scales were used because of a shortage in the culture. The experiment was terminated at 100 days because the host fruits, if maintained for much longer periods, begin to desiccate and this might bias fecundity figures.

**Results.** The data (Table 3, Fig. 4) show an average reproductive superiority of about 3:1 in total progeny, as well as a greater daily rate of fecundity for California red scale compared to yellow scale for the 100 days of the test. Peak production of crawlers occurred within two or three days of the minimum time for a generation, and thereafter showed a gradual decline for both species.

California red scale has been the subject of many studies of crawler production under laboratory conditions, and there is great variation depending on conditions. Quayle (1911*b*) checked 14 females during September and October in an open insectary. They produced an average of 55 crawlers per female over a reproductive period of 24 days. Under similar conditions, Bliss *et al.* (1931) obtained an average value of 72.6. Under controlled conditions at 25° C on lemons, average fecundity was 263.2 with a maximum of 576 crawlers (Yust, 1943), whereas, on lemons at 25° C and 65 percent R.H., Munger (1948) reported 326 crawlers per female. Again, Tashiro and Beavers (1968) recorded 352 crawlers per female on lemons at 25° C and 70 percent R.H. with a re-

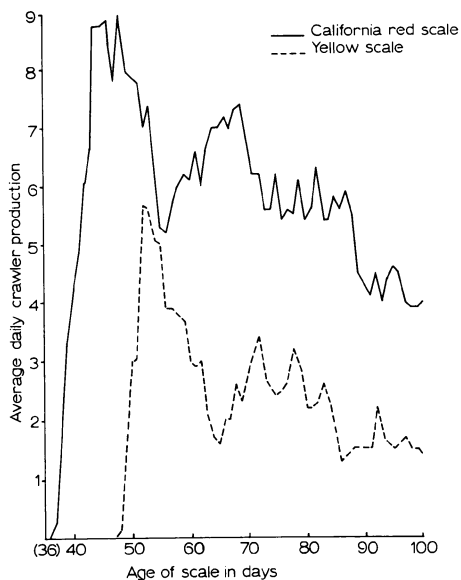


Fig. 4. Daily crawler production by California red and yellow scales at  $26.7 \pm 1^\circ \text{C}$  and  $60 \pm 10$  percent relative humidity (R.H.) for a 100-day period commencing when the parental scales were crawlers.

productive period of 70 to 175 days.

The data obtained by the authors under controlled conditions differed from those obtained in the earlier studies, probably because of improvements in maintaining host fruits and plants. The temperature we used was about 1.6° C higher than that used in any of the other studies, and may account for our somewhat higher reproduction figures.

No published information is known to us regarding total progeny production by yellow scale under laboratory conditions.

In comparison to the high fecundity values for California red scale obtained in laboratory studies, a field study by Quayle (1938) reported a production of only two to three crawlers per female per day until a total of about 150 was reached on citrus in Riverside. Similarly, Yust (1943) reported a production of 169.5 crawlers per parental female from the time the first crawlers appeared in June. In other cooler

months, the average was as low as 55.0 per female.

The minimum and average generation time at 26.7° C (crawler to first F<sub>1</sub> crawler) was 37 and 66.8 days for California red scale and 48 and 70.3 days, for yellow scale.

These generation times at 26.7° C were generally shorter than those of other previous studies. According to Tashiro and Beavers (1968), under laboratory conditions at 25° C and 70 percent R.H., California red scale averaged 43 days for a minimum complete life cycle (crawler to first F<sub>1</sub> crawler). On exposed citrus in Riverside during summer, a minimum of 42 days with an average of 65 days was required for development (Quayle, 1938). During summer months in Corona, California, the minimum time needed was 49 days, but records of 56 days were common (Yust, 1943). On field citrus, it was possible for three generations of scales to simultaneously produce crawlers (Yust, 1943). A minimum of 56 and a maximum of 262 days were required for maturation to reproduction in various California citrus districts (Dickson and Lindgren, 1947). In Southeast China, the life cycle of the scale varied from 40 days in summer to 120 days in winter (Flanders and Gressitt, 1958). The maximum rate of development, approximately 36.3 days, occurred at a steady temperature of 30° C (Munger and Cressman, 1948). In an exposed lath house in summer and in the laboratory during cooler months in Riverside, 60 days were required for California red scale and 65 days for yellow scale (Nel, 1933).

### Sex ratios

**Materials and methods.** The sex ratios for both scales were determined by examining laboratory-reared (26.7 ± 1° C, 60 ± 10 percent R.H.) similarly-aged scales when females were early third instars. At this point in female development, the great majority of

males have completed development and emerged leaving empty scale coverings which can be easily distinguished from the female scales.

**Results.** The male:female sex ratio for California red scale was 1.27:1 (507 examined) and for yellow scale was 1.64:1 (516 examined).

Competitive displacement based on effective progeny production, R, involves the number of reproducing female progeny, and the California red scale has an advantage in sex ratio over yellow scale.

Studies of male:female sex ratio by others have produced diverse results. Quayle (1911b) noted a change in sex ratio for California red scale from 1.75:1 to 1:1 from the first to the second half of the year. In a study of 645 California red scale crawlers, a sex ratio of 0.38:1 was obtained on Valencia oranges and Eureka lemons (Ebeling, 1950). Yust (1943) found the sex ratio of 1:1 for California red scale under field conditions. Nel's (1933) study indicated a sex ratio of 0.63:1 for California red scale and 1.31:1 for yellow scale. We will use our values for comparison and evaluation of our results.

### Survivorship

**Materials and methods.** Twenty crawlers from each species were placed on each of 10 waxed green lemons. The crawlers were transferred one at a time with a single strand camel's-hair brush. Since the crawlers are phototactic and tend to settle quickly and at random in darkness, the infested fruit were immediately placed in the dark at 26.7 ± 1° C and 60 ± 10 percent R.H. to reduce wandering and loss of the crawlers. The scales on each fruit were examined daily for 60 days.

Scales suspected of having died were marked and checked for growth. If they failed to grow and fell well behind the normal life history of their species, they were examined under the microscope

with a probe. In this manner, no live scales were killed.

**Results.** Sixty-four percent of the California red scale and 53.5 percent of the yellow scale crawlers reached reproductive maturity.

Other studies of survivorship have produced varying results. Ebeling (1950) reported a maximum of 59.3 percent of California red scale crawlers reached maturity on lemons. In an open insectary during summer, 67 percent of the crawlers reached maturity on lemon fruits and 57 percent on citrus seedlings (Bliss *et al.*, 1931). In a laboratory at 25° C and 70 percent R.H., 85.6 percent of the crawlers survived to maturity (Tashiro and Beavers, 1968). Nel (1933) found 57.5 percent of California red scale crawlers reached maturity in an open lath house during summer. Under identical conditions, he reported 26.9 percent survival for yellow scale crawlers.

In each aspect of reproductive ecology examined, i.e., gross fecundity, minimum and average time for a generation (crawler to F<sub>1</sub> crawler), percentage female offspring and survival to reproductive maturity, California red scale tended to be superior to yellow

scale under the laboratory conditions tested.

An exception to our results was the Australian report by McLaren (1971) that the intrinsic rate of natural increase ( $r_m$ ) was greater for yellow scale than for California red scale over the temperature range 23.9° C to 29.4° C at 34 to 40 percent R.H. and at 75 percent R.H. The apparent contradiction might be explained on the basis of ecotypes. However, to oppose this, we learn (various personal communications) from South Australia and Victoria that California red scale is becoming more dominant at the expense of yellow scale and so presumably has a higher  $R$  in the field. Possibly yellow scale in Australia, studied by McLaren, is biologically distinct from yellow scale in California. We have some evidence for biotypes of yellow scale existing in California. Yellow scale was readily parasitized by *Aphytis melinus* in Ventura County following its introduction, but we never obtained successful parasitization by this same parasite in Tulare County even during the most favorable periods of the year and in spite of releases with many thousands of parasites.

## EXPERIMENTAL TESTING OF THE HYPOTHESIS OF EXTINCTION OF YELLOW SCALE BY COMPETITIVE DISPLACEMENT

Yellow scale has become extinct, and has very likely been displaced, in southern California by competition from its ecological homologue, the California red scale.

The theoretical basis of displacement requires that two competing species share the essential elements of an ecological niche, i.e., food and space. Each must be able to survive and maintain their numbers in a given habitat when the other species is absent. Therefore, it is important to compare the competing species on the basis of mutual host

plant species and parts of plants infested. Also, the potential ability of natural enemies, insecticides, or unfavorable climate to cause extinction should be examined as possible alternative explanations.

Both scale species occur on a wide variety of host plants. Quayle (1938) listed 81 plants acceptable to California red scale and 12 suitable for yellow scale. The California Department of Food and Agriculture has records of several hundred hosts for California red scale and 54 for yellow scale. Some of



the plants acceptable to yellow scale are not recorded for California red scale, but a "refuge-plant" for yellow scale, one upon which California red scale could survive poorly if at all, is not known in southern California. Citrus trees have been and are the major host plants for both scales in California.

The California red scale can use all parts of a citrus tree, i.e., fruits, leaves, twigs, and branches. Yellow scale is limited almost entirely to fruits and leaves. Thus, once California red scale infests a tree, it cannot be displaced on twigs and branches by yellow scale, even assuming reproductive superiority of yellow scale on the other parts of the trees. The broader ecological niche of California red scale gives it a competition-free preserve from the yellow scale on citrus.

The history of the interactions of several species of natural enemies on California red scale in California furnishes one of the best examples of recorded competitive displacement in the field (DeBach and Sundby, 1963). The first well-established parasite was *Aphytis chrysomphali* (Mercet), accidentally introduced around 1900. It was followed by the purposeful introduction of *Comperiella bifasciata* Howard (Chinese race) in 1941, *Prospaltella perniciosi* Tower (California red scale race) and *A. lingnanensis* Compere in 1948, and *A. melinus* DeBach in 1957 (DeBach and Sundby, 1963). All these species are presently found in southern California citrus, although competition between *A. lingnanensis* and *A. melinus* limits the former to coastal areas and the latter to interior areas. *Aphytis chrysomphali* now (1976) is a competitively displaced rarity, confined to the small climatically favorable coastal Encinitas area of San Diego County. The present case of the two scale species is a further example of competitive displacement.

One condition for testing competitive displacement is that each homologue

must be able to maintain its population in the absence of the other. Obviously California red scale is well able to survive in southern California, since it is common and generally distributed today. Evidence has been presented to argue that yellow scale did not become extinct in southern California because of climatic variations, control attempts, or natural enemies.

The effect of natural enemies on competition between the scales has been a subject of varying opinions. Flanders (1956) explained the coexistence of yellow and California red scales in Southeast China by the evenly balanced regulating action of natural enemies. But the senior author (from observations in the same area—unpublished data) considers that different host plant preferences are responsible for this apparent coexistence.

In California, the larger number of host plant species and the wider exploitation of the citrus tree by California red scale shows it has a broader ecological niche that overlaps that of yellow scale. However, in the laboratory, all tests were performed on the same host plants thus avoiding any complications due to breadth of niche. Thus, in our laboratory tests, the species were true ecological homologues.

### Interspecific aggression

**Materials and methods.** An approximation of the maximum number of female scales that could survive under crowded conditions was obtained by counting the number of third-instar crawler-producing female yellow scales that occurred in a 1 cm<sup>2</sup> area on each of 10 heavily-infested lemon fruits. The average number of mature females was 28.9 with a range of 20 to 38.

With this information, three plastic cells of one centimeter-square area were placed on each of four lemons. A given number of yellow scale crawlers were placed in one of the cells on each lemon, in another, the same number of Califor-

TABLE 1

NUMBER OF CRAWLERS OF CALIFORNIA RED SCALE (CRS), YELLOW SCALE (YS) AND EQUALLY MIXED SCALE SPECIES DEVELOPING TO REPRODUCTIVE MATURITY (THIRD INSTAR FEMALES) ON 1 CM<sup>2</sup>-AREAS OF LEMON FRUITS AT  $26.7 \pm 1^\circ \text{C}$ ,  $60 \pm 10$  PERCENT RELATIVE HUMIDITY

Initial no. crawlers	No. third instars developed				
	CRS	YS	Equally mixed		Totals
			YS	CRS	
40	5	7	2	5	7
60	7	10	6	3	9
80	5	4	3	3	6
100	12	19	4	6	10
	—	—	—	—	—
Total	29	40	15	17	32

$\chi^2 = 4.85$ ,  $P < 0.75$ , 6 d.f.

nia red scale crawlers and in the third cell, one-half the given number for each species. The number of scales/cell tested were 40, 60, 80, and 100. The cells were sealed with fine nylon parachute cloth to prevent the crawlers from escaping.

**Results.** The results (table 1) indicate there were no substantial or significant differences in the total numbers of female scales developed in the mixed-species cells when compared with single-species cells. There was no indication of interference of one scale species by the other. However, a possible adverse effect of increasing density on survival is indicated.

The results confirm field and other laboratory observations of mixed-scale populations in which *individuals* of the two scale species appear to coexist in very close proximity without obvious harmful effect.

This experiment was designed to test the possibility that the competing scale species were able to "harm" each other when reared in close proximity, perhaps by toxic secretions, or some "territorial" feeding behavior.

### Competition at spatially saturated densities

The object of this experiment was to determine the outcome of competition between yellow scale and California red scale under different relative initial pop-

ulation densities when allowed to increase to saturation densities. Under such crowded conditions, the scales virtually cover the substrate. Competition should become maximal under these conditions and displacement, if it occurs, should take place rapidly. It should be noted that saturation densities rarely occur under natural conditions in southern California and then usually only on a portion of a given tree or branch. If competitive displacement has taken place in the field as we hypothesize, it has occurred at actual densities *very* much less than those attained in this experiment. As mentioned previously, this is because either natural enemies or insecticidal control have effectively maintained both scales at fairly low densities in virtually the entire commercial citrus acreage as well as on most dooryard citrus.

**Materials and methods.** A total of 100 crawlers composed of both scale species was placed on individual, partially paraffined, green lemons in one of the following ratios: 3:1, 1:1 and 1:3. The paraffin coating helped to preserve the fruit and to confine the scales to an area of about one-third of the fruit surface. The fruit were maintained at  $26.7 \pm 1^\circ \text{C}$  and  $60 \pm 10$  percent R.H. in about 1-liter ice cream containers with muslin-covered ventilation holes in the lid. Ten replicates in sep-

TABLE 2  
COMPETITIVE DISPLACEMENT OF YELLOW SCALE (YS) BY CALIFORNIA RED SCALE (CRS) AT SATURATION DENSITIES FOLLOWING INITIAL INFESTATION OF LEMON FRUIT WITH THREE RATIOS OF SCALE CRAWLERS AT  $26.7 \pm 1^\circ \text{C}$  AND  $60 \pm 10$  PERCENT RELATIVE HUMIDITY

Days after start	Percentage California red scale resulting from initial crawler ratios (YS:CRS):		
	3:1	1:1	1:3
105	85.1	90.1	90.1
145	88.6	89.1	95.2
223	90.2	97.9	100.0
251	97.3	98.8	100.0
292	99.3	100.0	100.0

arate containers were used at each initial ratio.

At intervals of approximately 75 days, a fresh host fruit was placed in the containers with the unwaxed surface directly contacting the scales on the fruit below. Crawlers moved to the new fruit and thus insured a continuous viable culture. Each fruit was allowed to remain in the containers for 150 days, its maximum useful life. It was then replaced with a fresh lemon. In each container, beginning at about 100 days and thereafter at approximately 50-day intervals, the scales from a randomly selected 1 cm<sup>2</sup> area on each of the two fruits in each replicate were removed, counted, and identified to species under the microscope. A substantial minority of scales were unidentifiable due to alterations in morphology caused by intense crowding or to damage at the time of removal, but this applied equally to the species.

**Results.** Regardless of the relative initial density, California red scale quickly dominated and by the end of the experiment, at 292 days, only one identifiable yellow scale was found in the one centimeter-square areas removed from two fruit in one of the 30 replicates (table 2). The maximum number of generations in the period was 7.89 for California red scale and 6.08 for yellow scale. Considerable overlapping of generations would occur if the fruits remained in a firm, undesiccated condition for the entire 150 days

in the containers. If this condition prevailed, it is probable that crawlers would be produced by three to four generations simultaneously.

The results demonstrated the ability of California red scale to displace yellow scale under conditions of intense crowding on green lemons in the laboratory where they are true ecological homologues.

### Computer simulation

The object of the computer simulation experiment was to establish the compound effective progeny production of a single female scale and its first generation progeny which were themselves producing crawlers, while living in pure cultures, assuming they had available an abundant supply of food and space for 100 days.

Computer simulation provides the only practical way of exploring the compound-interest aspect of competitive displacement when overlapping generations and variable daily fecundities are involved.

The first step was to determine with the hand calculator the effective progeny production of single female scales for 100 days from the equation:

$$EPP = DF \times S \times F$$

where *EPP* = effective progeny production

*DF* = daily fecundity based on age in days

*S* = survival to reproduction

*F* = proportion female

TABLE 3  
EFFECTIVE PROGENY PRODUCTION OF SINGLE FEMALE SCALES AND  
COMPUTER-DETERMINED COMPOUND EFFECTIVE PROGENY PRODUCTION  
FOR 100 DAYS BASED ON DATA FROM TEST 1 AND FIGURE 4

Scale sp.	Gross fecundity		Proportion surviving to reproduction		Proportion female		EPP* or CEPP†
California red							
Parental ♀ only	371.7	×	0.64	×	0.44	=	104.7*
Parental ♀ and crawler producing first generation progeny	2991.1	×	0.64	×	0.44	=	842.3†
Yellow							
Parental ♀ only	131.5	×	0.535	×	0.378	=	26.6*
Parental ♀ and crawler producing first generation progeny	479.2	×	0.535	×	0.378	=	96.9†

\* EPP = effective progeny production.  
† CEPP = compound effective progeny production.

The compound effective progeny production (*CEPP*) is the summation of effective progeny production (*EPP*) for the parental female scale and each of her first generation progeny which have begun to produce crawlers within the 100-day period. Expressed mathematically it is:

$$CEPP = \sum EPP$$

The data used for the terms of the equation and the results are presented in table 3. The theoretical outcome of compound effective progeny production at four initial scale ratios was calculated and is presented in table 4.

The effective progeny production of a single female California red scale was about four times that of a single yellow scale for 100 days. When the compounding effect of overlapping generations, modified by fecundities based on age in days was calculated, the advantage of California red scale was 8.7 times that of yellow scale for a similar period.

A more striking result would have been obtained had the results for three generations been calculated and we know from Yust (1943) that three generations do simultaneously produce crawlers on field citrus.

The similarity in displacement re-

TABLE 4  
THEORETICAL PERCENTAGES OF CALIFORNIA RED SCALE (CRS) AND  
YELLOW SCALE (YS) AFTER 100 DAYS COMPOUND EFFECTIVE PROGENY  
PRODUCTION BEGINNING WITH FOUR DIFFERENT INITIAL CRAWLER  
RATIOS BASED ON DATA FROM TEST 1 AND FIGURE 4

Initial crawler ratio		Percent total ♀ scales after 100 days	
CRS	YS	CRS	YS
<i>Number</i>		<i>Percent</i>	
1	10	46.5	53.5
1	5	63.5	36.5
1	2	81.3	18.7
1	1	89.7	11.3



sults obtained after 100 days in the experiment (table 2) and in the computer run (table 4) was striking, when the initial densities were common to both, i.e., one to one ratio, yellow to California red scale. After 100 days, 90.1 percent and 89.7 percent were California red scale in the experimental and computer runs, respectively.

### Parasite moderation of results of competitive displacement

Flanders (1956) believed the presumed long term coexistence between California red scale and yellow scale observed in Southeast China was achieved through the evenly balanced regulating action of their natural enemies. The reason given for the yellow scale being reduced in southern California was that this scale suffered from the depredations of the parasites *Aphytis citrinus*, *Aspidiotiphagus citrinus*, and *Prospaltella aurantii*, believed to have been accidentally introduced into California before 1900. Up to 1948, the only parasite attacking California red scale was *Aphytis chrysomphali* and this parasite was effective only in coastal areas (DeBach and Sundby, 1963). The natural enemies attacking yellow scale were further augmented by the importation of *Comperiella bifasciata* (Japanese race) in 1931 and 1932 which reproduces on yellow scale, but not on California red scale. About 10 years later, the introduced Chinese race of *C. bifasciata* slowly became established and distributed in the field on California red scale. However, later on in 1948 and 1957, more effective parasites of the California red scale also became established (DeBach, 1969). Reduction of yellow scale populations by parasites, especially *C. bifasciata*, has been demonstrated in the field (DeBach, 1969), but reduction is not extinction. Flanders (1956), however, did not consider the possibility that competitive displacement was involved, nor did he realize that yellow scale had be-

come extinct in commercial citrus in most of southern California by 1955.

The present experiment was designed to ascertain the outcome of competitive displacement between equal initial populations of California red scale and yellow scale in the presence of various parasites species.

The parasites used were *Aphytis lingnanensis*, *A. melinus*, *Comperiella bifasciata* (Chinese race), *C. bifasciata* (Japanese race), and *Habrolepis rouxi* Compere. Of these, only the two *Comperiella* races figured in Flanders's account of declining yellow scale populations. The other species referred to by Flanders were not available in culture, and only rarely have they been found by the authors in thorough field surveys of natural enemies of the scales in recent years. They are no longer considered to be of any consequence in effective population regulation of the yellow scale in the San Joaquin Valley of California where yellow scale is still prevalent. *Habrolepis rouxi* has become permanently established only on California red scale in very restricted coastal localities in San Diego County and was tested because it was available in laboratory culture. It is of no practical significance in biological control in the field.

*Aphytis lingnanensis* attacks California red scale and yellow scale, although in the field, it is confined almost entirely to California red scale. This holds true for *A. melinus* as well. The Chinese race of *Comperiella bifasciata* is capable of using either scale as a host under laboratory conditions, but in the field, is found only in areas of pure California red scale or where the two host species occur on a single tree or in a single orchard in the San Joaquin Valley. The Japanese race of the same species is incapable of developing in California red scales, although it readily oviposits in them in the laboratory. It is found in areas where yellow scale alone occurs or where the ranges of both

scales overlap. *Habrolepis rouxi* successfully attacks both scale species in the laboratory, but is found in the field at present only on California red scale. To our knowledge, it was never colonized in areas where yellow scale occurred.

**Materials and methods.** Small sleeve cages were prepared containing 20 lemons, 10 infested with California red scale and 10 with yellow scale in nearly equal densities and with developmental stages about equally represented. Twenty fresh uninfested lemons were placed on top of these fruit to provide sites for crawlers to settle and thus maintain the scale colony on a continuous, dynamic basis. Fifty pairs of a given parasite species, derived from insectary cultures, were then introduced into a scale colony in a sleeve cage and this was repeated for each parasite species. The cages were inspected weekly and fresh lemons added when any of the original 40 became desiccated or reached 100 days of age. The cages were maintained at  $26.7 \pm 1^\circ$  C and  $60 \pm 10$  percent R.H.

The progress of displacement was monitored by removing scales from a one centimeter-square area from each of five randomly selected fruits per sleeve cage. The scales were slide mounted for microscope identification to species at intervals beginning on the ninety-first day.

**Results.** A control run in the absence

TABLE 5  
COMPETITIVE DISPLACEMENT  
BETWEEN CALIFORNIA RED SCALE  
(CRS) AND YELLOW SCALE IN THE  
ABSENCE OF PARASITES ON LEMON  
FRUIT HOSTS AT  $26.7 \pm 1^\circ$  C,  $60 \pm 10$   
PERCENT RELATIVE HUMIDITY

Days	Percent CRS
0	50.0
91	78.1
106	73.4
138	87.5
203	94.1
290	93.9
374	95.5
433	98.2
468	100.0

of parasites showed that it took about 468 days for California red scale to completely eliminate yellow scale (table 5).

When parasites were present in the mixed cultures (table 6) in every case, with the exception of *Habrolepis rouxi*, the California red scale, after 173 days, made up a higher proportion of the population than did yellow scale as compared to the control and much more rapidly displaced it. This was presumably because the parasites, other than *Habrolepis rouxi*, caused more mortality to the yellow scale than to the California red scale.

The results obtained were similar with both *Aphytis* species. They attack both scale species when exposed to them simultaneously, but apparently pre-

TABLE 6  
MODIFYING EFFECT OF DIFFERENT PARASITE SPECIES ON COMPETITIVE  
DISPLACEMENT BETWEEN CALIFORNIA RED SCALE AND YELLOW SCALE  
ON LEMON FRUIT HOSTS AT  $26.7 \pm 1^\circ$  C,  $60 \pm 10$  PERCENT  
RELATIVE HUMIDITY

Parasite species	Percent California red scale at day				
	91	131	173	209	293
<i>Aphytis lingnanensis</i>	37.5	67.9	100.0	100.0	100.0
<i>Aphytis melinus</i>	40.8	73.4	95.6	100.0	100.0
<i>Comperiella bifasciata</i>					
Japanese race	72.0*	72.3	100.0	100.0	100.0
Chinese race	62.0*	67.6	100.0	100.0	100.0
<i>Habrolepis rouxi</i>	91.1*	92.3	86.8	48.0	0.0

\* Initial scale ratio favored California red scale over yellow scale due to greater crawler production by California red scale during the initial infestation period.

ferred yellow scale. However, theoretically even if they show *exactly* the same preference for each scale species or perhaps some preference for California red scale, the superior effective progeny production of California red scale should still result in the displacement of yellow scale.

The Japanese race of *Comperiella* represents a case in which the parasite acted almost entirely against yellow scale. The parasite oviposits in either species but is capable of developing only in yellow scale. It could diminish the numbers of California red scale only in rarely observed cases of over-stinging. Of all the parasites tested, the data suggest (table 6) that slightly more rapid displacement of yellow scale occurred with this race of *Comperiella* than with any other race or species. This would be expected on theoretical grounds.

The Chinese race of *Comperiella*, capable of developing in either scale host, as expected, caused displacement slightly slower than its conspecific race (table 6) but still caused displacement of yellow scale to proceed more rapidly than occurred in the absence of parasites (table 5).

The outcome of competitive displacement was reversed by *Habrolepis rouxi*. This species, capable of developing on either host, shows a marked preference for California red scale. In another test with this parasite using pure California red scale and pure yellow scale cultures, the former culture was exterminated, while the latter culture sustained both the parasite and the scale at low populations for 243 days when the experiment was terminated.

In these laboratory experiments, most scales were available for parasitism, because the limited size of the universe reduced the area of search. Even so, some scales usually escape to reproduce. The extermination of the pure culture of California red scale by *Habrolepis* may represent a random accident, such

as occasionally occurs in small isolated sites in nature due to the action of natural enemies. This parasite caused a decline in populations of scales in all other tests, but not extermination. Thus, it is especially significant that displacement occurred in these tests in spite of a gradual decrease in scale populations. This means that competition and competitive displacement can occur, while food and physical space for the competing scales are abundant in relation to the animals' immediate needs (DeBach, 1966).

Twice as much time was needed in the control (table 5) as in the test culture for displacement to occur (table 6), probably because the control scale populations were relatively more similar in their effective progeny production. The parasites made the differences in R values comparatively greater between the scale species, and thereby accelerated displacement. These results are indicative of what has occurred in the field in Israel between the Florida red scale, *Chrysomphalus aonidum* (L.) and the California red scale.

The observations of Schweig and Grunberg (1936) of Florida red scale and California red scale on citrus in Israel indicate the two species are biologically and ecologically similar requiring approximately the same time for a developmental cycle and producing the same number of generations per year in the field. The maximum reproductive periods of the species do not coincide. California red scale has a higher fecundity in spring and early summer, while Florida red scale dominates in the warmest times of summer. At the time of the report by Schweig and Grunberg, the species still were occasionally spatially isolated, but when they shared a common range, one or the other species was always reduced to an inferior status.

The spatial niches on citrus of the competing species do not exactly coincide. California red scale is found on all

parts of the tree, while Florida red scale is found on all parts except woody branches. Thus, once California red scale becomes established on a tree, apparently it cannot be displaced from the woody branches.

Both species are found on Israeli citrus at the present time. In the early 1950s, the Florida red scale was the dominant pest. Since then, it has been reduced to the status of a minor pest by the action of the imported parasite, *Aphytis holoxanthus* DeBach. California red scale, under only partial biological control by *A. coheni* DeBach and *A. melinus* in the interior areas and by *A. chrysomphali* along the coast, has now gained the ascendancy as the major scale pest on Israeli citrus (David Rosen, personal communication).

The case presents several interesting aspects. The spatial niches of the scales on citrus do not completely overlap and this theoretically would prevent the entire displacement of California red scale. Nor do the scales share the same dominant natural enemy. However, it appears definite that the effectiveness of *Aphytis holoxanthus* against Florida red scale has already drastically reduced its relative rate of effective progeny production, and that ultimate extinction of this scale by competitive displacement is probable in most, if not all, of Israel.

Our experiment shows that parasites, like many other factors, may alter the effective progeny production of ecological homologues and therefore modify or reverse the result of competitive displacement, but that displacement always takes place between true homologues. The suggestion of Flanders (1956) that California red scale and yellow scale had coexisted for a long period in Southeast China due to the action of natural enemies appears unfounded. On theoretical ground, it is highly unlikely that natural enemies would influence effective progeny production to precisely equal values for the

two scale species. The first author during several trips (unpublished data) rarely observed yellow scale on citrus in the Hong Kong area investigated by Flanders, but commonly found it on wampei, a native ornamental and fruit tree which is not a preferred host for California red scale. Thus, yellow scale has a refuge or alternate host where it has the advantage over California red scale, hence, cannot be displaced from the "Hong Kong habitat." From wampei and perhaps other preferred alternate hosts, it can reinvade citrus, hence apparently "coexists" in the competitive displacement sense.

Flanders's (1956) view that the more numerous and more effective species of parasites attacking yellow scale than California red scale were responsible for the declining populations of the former species in southern California may have been correct as far as it went. Introduced parasites do cause decreases, but they result in attainment of a balance between host and parasite. Parasites are by themselves considered incapable of causing extermination, except perhaps in microhabitats, certainly never over an area as large as southern California. Competitive displacement appears to be the only logical answer.

### Competitive displacement on banana squash

An experiment involving competitive displacement between California red scale and yellow scale was carried out using banana squash as host material rather than green lemons. The purpose of the experiment was to ascertain if a difference in host plant would affect the results of displacement when scale populations were allowed to increase to saturation densities.

**Materials and methods.** An elongate area of approximately 38 cm-square on each squash was enclosed with a narrow band of sticky tree tanglefoot to provide an experimental area of uniform size. The tests were performed in the

TABLE 7  
COMPETITIVE DISPLACEMENT BETWEEN CALIFORNIA RED SCALE (CRS)  
AND YELLOW SCALE (YS) ON BANANA SQUASH WITH THREE INITIAL  
CRAWLER RATIOS AT  $26.7 \pm 1^\circ$  C AND  $60 \pm 10$  PERCENT RELATIVE HUMIDITY

Initial scale ratios (YS:CRS)	No. days	No. adult scales examined	Percent CRS
1:1	0	0	50.0
	77	77	76.1
	116	74	87.7
	164	45	100.0
2:1	0	0	33.3
	77	51	60.9
	116	73	88.1
	164	54	100.0
5:1	0	0	16.7
	77	64	28.1
	116	52	75.0
	164	57	100.0

laboratory at  $26.7 \pm 1^\circ$  C and  $60 \pm 10$  percent R.H.

Crawlers were transferred to the squash by placing crawler-producing infested lemons of each scale species with approximately equal numbers of similarly-aged scales against the target area on the squash. The fruit were held in place by a wooden framework taped to the squash. The infested lemons were left in contact with the banana squash for two days during which the crawlers transferred. Three initial ratios of yellow scale to California red scale crawlers were used, i.e., 1:1, 2:1, and 5:1.

The resulting dense scale infestations resulted in the production of a watery brown exudate and a gradual dying of the scales after about 75 days. Fresh banana squash then were placed in contact with the earlier infested areas for the days 75 through 100, and crawlers transferred from the first to the second squash. The area of contact on the new squash was limited to 38 cm-square by a border of tree tanglefoot.

Scales taken from five randomly selected one centimeter-square areas on each squash at 77, 116, and 164 days after initiation of the tests, were slide-mounted for microscope identification. Some scales were unidentifiable using

this method, especially at high scale densities, but this is not thought to have introduced any significant error.

**Results.** The results (table 7) indicate the clear superiority of California red scale over yellow scale in competitive displacement on banana squash under laboratory conditions. At 77 days, 60 percent or more of the scales at the 1:1 and 2:1 yellow to red initial ratios were California red scale, compared to about 30 percent of California red scale at the 5:1 ratio. At 116 days, the proportion of California red scales in the 5:1 ratio test had increased to 75 percent. By this time, three generations of California red scale would have been produced on green lemons, but only two from yellow scale. At the concluding count, 164 days, all squash were covered by a dense infestation of California red scale.

Replacing lemon with banana squash as a host had little effect on competitive displacement of yellow scale by California red scale. Apparently the effective progeny production of the scales on squash closely parallels that obtained on green lemons. It is also apparent that the initial ratios of the two competing species did not affect the final result.



### Possible substrate poisoning on squash

The object of this experiment was to test the hypothesis that differential toxic substances, produced by the two scale species when feeding on squash, moderate the rate of competitive displacement.

In our previous experiments with squash, the longer the squash was infested, the fewer newly produced crawlers settled and reached maturity near older scales even when there appeared to be adequate space for them. The effect might be caused by the injection of toxic materials by feeding scales or by the normal physiological changes of the aging host.

**Materials and methods.** Twenty-five to 50 third instar female scales (60–70 days old) were removed from an area of infested squash and a 2-cm I.D. plastic cell was glued over the area. Fifty crawlers were individually transferred into the cell using a single strand camel's-hair brush. The cell was then sealed with fine muslin. The host surface area enclosed was 3.14 cm<sup>2</sup>. The crawlers were allowed 50 days to reach third instar, and then all scales were counted. California red scale crawlers were placed on areas from which either pure cultures of California red scale or yellow scale had been removed, and yellow scale crawlers were placed on areas from which either pure cultures of yellow scale or California red scale had been removed. Two controls were set up using 50 crawlers of each species on the same squashes as above, but on a previously uninfested area. The six treatments were replicated twice.

**Results.** No significant evidence was obtained that previous feeding by one species decreased the suitability of the substrate for the other species. In general, more of the California red scales survived to maturity, in comparison to yellow scale, suggesting a greater fitness of California red scale to the sub-

optimum conditions used. It is well known that California red scale has a broader nutritional base than does yellow scale.

### Temperature gradient test

In nature, many apparent examples of competitive displacement occur in which one ecological homologue is the exclusive winner at one end of the distributional range and the other species the winner at the other end with apparent coexistence occurring in the middle zone of overlap.

For example, the range of the cottony-cushion scale, *Icerya purchasi* Maskell, extends throughout the citrus-growing areas of southern California. However, its two natural enemies occur together essentially only in the middle of the range. Contrary to popular belief, the parasitic fly, *Cryptochaetum iceryae* (Williston), is dominant on this host in the coastal areas, while the predatory vedalia beetle, *Rodolia cardinalis* (Muls.), formerly generally given sole credit for controlling the cottony-cushion scale in California, is dominant in the desert areas. Both the parasite and the predator coexist in the interior and intermediate parts of the range, probably because both migrate from their respective areas of dominance (Quezada and DeBach, 1973).

A similar case is found in San Diego County where the California red scale parasite, *Aphytis melinus*, dominates in interior areas of the county, while its congener, *A. lingnanensis*, dominates in coastal areas. In the intermediate regions, both species are found, again probably because of dispersal from areas of dominance (DeBach and Sundby, 1963).

Scale insects would seem to offer an ideal means of testing such field observations experimentally in the laboratory, because a "geographical" range could be reduced to a matter of centimeters or meters in a controlled environment cabinet and dispersal would

TABLE 8

SURVIVAL TO MATURE THIRD INSTAR OF CALIFORNIA RED SCALE (CRS) AND YELLOW SCALE (YS) CRAWLERS PLACED ON VARIOUSLY CONDITIONED BANANA SQUASH SUBSTRATES AT  $26.7 \pm 1^\circ \text{C}$  AND  $60 \pm 10$  PERCENT RELATIVE HUMIDITY

Treatment (two replicates, 50 crawlers each)	Total no. surviving to maturity (replicates combined)	5% statistical reliability
CRS on aged unfed surface	71	a
CRS on CRS-removed area	69	ab
CRS on YS-removed area	58	ab
YS on aged unfed surface	49	bc
YS on CRS-removed area	37	bc
YS on YS-removed area	22	c

be of little or no consequence because the first instar "crawlers" tend to settle rapidly and within millimeters of the mother scale. Thus, an experiment was planned to ascertain the results of competition between California red scale and oleander scale, *Aspidiotus nerii* Bouche, when the competing scales were cultured along a temperature gradient. The temperature gradient would represent a microgeographical distribution. The uniparental oleander scale was chosen because previous work indicated this scale to be suitable for the test (DeBach and Fisher, 1956). One-hundred percent crawler mortality occurred at  $26.7^\circ \text{C}$  (DeBach and Fisher, 1956), a temperature still within the optimal reproduction range of the California red scale. To avoid a lethal extreme for either scale,  $26.1^\circ \text{C}$  was chosen as the upper temperature limit at the high end of the temperature gradient box and  $22.8^\circ \text{C}$  as the lower temperature limit. A comparison of re-

production data for California red scale and uniparental oleander scale at two temperatures is found in table 9.

The final outcome of the test was uncertain *a priori* on the basis of available laboratory data on reproduction. Our hypothesis was that California red scale would displace oleander scale at the upper temperature limit of the test ( $26.1^\circ \text{C}$ ) which was the upper temperature limit tolerable to uniparental oleander scale, and that uniparental oleander scale might be the winner at the lower temperature limit ( $22.8^\circ \text{C}$ ). Both species should "coexist" in the middle if displacement of one by the other occurred at each end.

**Materials and methods.** The temperature gradient box was constructed of 0.95 cm clear plexiglass in the shape of a square-based "U." It was placed in a constant temperature chamber maintained at a base temperature of  $22.8 \pm .25^\circ \text{C}$ . Thermostatically controlled heating within the "U" gradient re-

TABLE 9

COMPARISON OF REPRODUCTION DATA FOR CALIFORNIA RED SCALE AT  $26.7 \pm 1^\circ \text{C}$ ,  $60 \pm 10$  PERCENT RELATIVE HUMIDITY AND UNIPARENTAL OLEANDER SCALE AT  $23.9^\circ \text{C}$

Item	California red scale	Oleander scale*
Age (days) at first crawler production	37.0	49.0
Age (days) at first peak of crawler production	48.0	60.0
Number days in production	>63.0	38.0
Daily progeny production	5.8	2.8
Total progeny produced	371.7	94.0
Percentage ♀	44.0	100.0

\* Data from DeBach and Fisher (1956, p. 238).

TABLE 10  
CHANGE WITH TIME IN PERCENTAGES OF MIXED POPULATIONS OF  
CALIFORNIA RED SCALE AND UNIPARENTAL OLEANDER SCALE AT  
22.8° C AND 26.1° C ON WHITE ROSE POTATOES IN A CONTROLLED  
TEMPERATURE GRADIENT BOX SIMULATING A NATURAL  
GEOGRAPHICAL RANGE

Days after infestation	22.8° C		26.1° C	
	California red scale	Oleander scale	California red scale	Oleander scale
	<i>Percent</i>		<i>Percent</i>	
60	36.1	63.9	32.8	67.2
90	43.6	56.4	66.5	33.5
120	58.8	41.2	95.1	4.9
150	63.7	32.3	100.0	0.0
180	77.6	22.4	100.0	0.0

sulted in the temperature grading gradually between 26.1° and 22.8° C. Light was not a factor in the competition.

Each end of the temperature gradient box was ventilated by a ca. 7.6 cm diameter electric fan very gently moving air directly onto the thermometers and the thermostat sensing element (Thermoswitch® Control, catalogue number 17100-0). The humidity produced by the potatoe food source was controlled by sulfuric acid baths.

Potatoes (cultivar White Rose), heavily infested either with crawler-producing uniparental oleander or California red scales, were removed from insectary cultures and laid alternately over fresh uninfested potatoes placed along the bottom of the entire temperature gradient box. Sixteen days later, the original infested potatoes were removed. Abundant settled crawlers were evident on the previously scale-free potatoes. This provided for an initial mixed infestation of both scales along the entire temperature gradient or micro-range.

Sixty days after the crawlers were initially added to the box and at 30-day intervals thereafter, the scale proportions were sampled by removing a 1 cm<sup>2</sup>-area from five randomly selected potato tubers in each arm. The scales were slide-mounted for identification.

**Results.** During the first sampling of the scales it was found that oleander

scale dominated by approximately three to one. However, as previously shown, unequal initial numbers do not alter the final outcome of competitive displacement so long as each competing species has a sufficiently large breeding stock so that random extinction due to small numbers does not occur.

The results, given in Table 10, showed a more rapid decline of oleander scale in the 26.1° C end than in the 22.8° C end of the gradient. Unfortunately, the experiment was accidentally terminated at 189 days due to a malfunction with the large constant temperature chamber.

The California red scale had a higher rate of effective progeny production than uniparental oleander scale even at the lowest temperature tested and presumably would have eventually completely displaced the oleander scale throughout the temperature gradient.

Although the hypothesis was not confirmed, the data (table 10) indicate that had the cool end of the temperature gradient been lower, say 21° C, then the oleander scale could have been the winner with both species "coexisting" in the middle of the gradient. Such "coexistence" would have simulated the case of apparent "coexistence" of the two natural enemies of cottony-cushion scale discussed by Quezada and DeBach (1973).

## CONCLUSIONS AND SUMMATION

Based on all evidence we have concluded that the yellow scale has become extinct in southern California due to competitive displacement by its ecological homologue, the California red scale. This has happened in spite of a continuous surplus of food and space for both species which are the only requisites or resources being competed for and in spite of no aggression occurring between the species. These results are in opposition to those authors who claim that essential resources or requisites must be in short supply. Thus, considerable controversy surrounds the theory of competitive displacement between ecological homologues.

In order to establish whether species are true ecological homologues in a given environmental context, it is necessary to experimentally show that each species is able to maintain its numbers sufficiently for population continuity when the other is absent; and that when the two competitors share the same experimental universe and have the same requisites (are homologous), one ultimately becomes extinct. In some situations, particularly in complicated field environments, classical experimentation may be impossible so that painstaking observations may be necessary to show the overwhelming probability that two species—one of which has displaced or excludes another—share the essential attributes of an ecological niche (at least with respect to major requisites such as food and space) and are homologues. However, the displacement of an established species by an invading species in the field essentially constitutes an “experiment” in time and should be so considered. The establishment of the fact that they are ecological homologues is the major remaining necessity.

If the species satisfy the tests for ecological homologues, then on the basis

of the axiom of inequality by which no two things in the real world are exactly the same, it is assumed they will differ in their relative rates of effective progeny production no matter how slight the difference may be. Many factors other than innate reproductive capacity influence effective progeny production, such as natural enemies and climate. When the competitors first share a habitat or experimental universe, each species will increase in numbers at its own rate until a combined population limit level is attained.

Differential R values, which result in changing relative species proportions, inevitably gives the competitor with the highest R a larger and larger proportion of the combined total population as time goes on until ultimate displacement occurs.

Essential to this concept is that the same resource(s) is necessary for both competitors. It may or may not ultimately come into *obvious* short supply, but nonetheless, there will be competition for the resource if the two species share the same habitat regardless of how low their equilibrium populations may be. We consider that the case of the yellow scale being displaced by the California red scale as reported herein, constitutes a “natural” experiment which was replicated many fold in time and space.

Field records show that the yellow scale became established in southern California about 100 years ago. Populations of yellow scale in some southern California citrus regions had been observed declining as long ago as the 1910s, but were attributed to the action of parasites which doubtless did exert considerable biological control over the years. While California red scale continued to disperse and became dominant, the decline of yellow scale continued and reached final extinction

throughout the area including Ventura County, sometime in the 1960s. This is documented for the first time in a series of time sequential maps (Figure 2 *a-f*) showing the changing distribution and relative abundance of California red scale and yellow scale from 1910 to 1970.

Parasites could not be the cause of this phenomenon because they are incapable of causing the extinction of a host species in the field except perhaps in microhabitats. Current field evidence shows that yellow scale and its parasites continue to survive in those parts of the state still without California red scale and also did so for years in other areas where California red scale did not invade for lengthy periods.

Nor can extinction be attributed to pesticides. Intensive chemical eradication was attempted at various times, but never resulted in more than reducing scale populations to very low levels. Conventional pest control methods used in the southern California areas were the same as those used in the Central Valley where yellow scale is still found.

Climate cannot be the cause of extinction because yellow scale has shown the ability to prosper in many different climatic localities over long periods of time. Its decrease in a given area always depended on whether or not California red scale also had been present for some substantial period. The most severe freezes in California history were observed to greatly reduce yellow scale populations because of defoliation, but the scale rebounded to again become a pest. Similarly, hot extremes did not eliminate the scale. Actually, yellow scale remained a pest longest in the more climatically severe California citrus areas.

Throughout its range, yellow scale has become extinct only where it was originally, or later became, sympatric with California red scale for any appreciable number of years. The hypothesis was examined that the two species were

ecological homologues and competitive displacement was responsible for the decline and extinction of yellow scale.

The scales were observed to be close ecological homologues in the field on citrus except that California red scale was able to survive and reproduce on the woody portions of the host, where yellow scale is rarely found. Thus, California red scale in the field on citrus has a competition-free reserve from which it cannot be displaced by yellow scale. However, California red scale is a true ecological homologue of yellow scale.

This broader spatial-niche advantage of California red scale is lost when the scales are reared on lemon fruit or other hosts in the laboratory. Here the scales are true ecological homologues since on a given fruit, they share the same food, space, and feed in the same manner. They differ only in their relative rates of effective progeny production,  $R$ , and they are ideally simple organisms for the basic study of the competitive displacement process.

Laboratory experiments helped illustrate why and how California red scale had displaced yellow scale in the field. Basic reproduction data such as fecundity per female, minimum and average time per generation and sex ratio all favored California red scale in the laboratory. In addition to these advantages, this scale was superior in survival from the mobile crawler stage to the adult stage. Calculation of the effective progeny production of single female scales from the time they were crawlers (nymph one) for a 100-day period, showed California red scale had a superiority of about four to one. Computer calculation of the *compound* effective progeny production for a similar 100-day period showed that California red scale had a reproductive superiority of about eight to one.

No evidence was found that the scales were involved in any kind of direct interference or "aggression." The possi-

bility of differential substrate poisoning because of scale feeding was examined and it was found that feeding does cause a decline in the suitability of squash substrates for scale maturation. However, there was almost no statistically significant difference in response of either scale to previously fed-upon substrates.

A series of experiments in which mixed species scale populations were allowed to increase to a maximum density and persist for long periods (simulating nature) on lemon fruits or squash inevitably ended in displacement of yellow scale. Initial crawler ratios giving a decided edge to yellow scale (five to one) slightly slowed, but did not otherwise affect the final outcome of displacement.

In order to determine the effect, if any, of different natural enemies on displacement, five species of parasites were each introduced individually into mixed scale cultures. The parasites in each of the five mixed cultures considerably reduced the density of scales as compared to controls over time, producing a situation which closely parallels actual field conditions in some orchards that have a low scale population density regulated by parasites. As a consequence, food and space for potential scale increase becomes abundant.

Competitive displacement always occurred under these low density conditions and, significantly, the parasites in every case caused displacement to take place in about half the time required for the control without parasites. This is because they caused differential mortality to the two scale species, hence, increased the difference between them in effective progeny production. Natural enemies in the field may be expected to generally speed up displacement as well, even though the expected winner may be reversed. However, should a parasite species attack only the superior ecological homologue (A) and, thus, reduce its effective progeny production

relative to the other scale species (B), but still leave the effective progeny production of A greater than B, then A will still be the winner, but displacement will take a longer period.

An interesting case of reversal did occur in our tests. When mixed cultures were exposed to the parasite, *Habrolepis rouxi*, yellow scale displaced the usual winner. California red scale is strongly preferred as a host, although the parasite will oviposit in and reduce populations of yellow scale. This singular exception demonstrates the potential of natural enemies (or other environmental factors) to modify or reverse the usual outcome of displacement, even when one competitor, in this case California red scale, has a markedly superior effective progeny production—at least under the parasite-free optimal laboratory conditions originally tested.

Obviously, there is a certain risk in extrapolating laboratory data obtained at constant temperature and humidity to a variable, much more complicated field situation. However, it appears overwhelmingly probable that the cause of extinction of yellow scale in southern California was competitive displacement. On the basis of field observations, it appears that this process is now being repeated in the San Joaquin Valley of central California, and we predict that yellow scale will become extinct there probably within 10 to 20 years.

The presumed long term "coexistence" of mixed populations of yellow and California red scales on citrus in Southeast China based on the effect of evenly balanced natural enemy activity as postulated by Flanders (1956), conflicts with our field observations in California and our laboratory experiments. In the first author's opinion (unpublished data), "coexistence" is due to the marked reproductive superiority of yellow scale over California red scale on a few species of host plants in China of which wampei is a notable example. These serve as refuges from which yel-

low scale cannot be displaced by California red scale and from which yellow scale can continually reinfest citrus on a limited basis. He has observed that yellow scale is extremely rare on citrus in southeast Asia.

California red scale may itself be susceptible to competitive displacement by some other scale species. Since the other species would ordinarily more successfully exploit citrus, it appears risky to pursue the matter as a practical means of eliminating California red scale. However, a possibility exists that an economically less harmful scale species could effect displacement if a complex of natural enemies reduced the progeny production of California red scale somewhat while having little or no effect on the invader. This would appear somewhat more feasible if the invader was known to be under excellent biological control in other countries having similar climates and could itself be brought under biological control after California red scale had been displaced.

In general, yellow scale survives on citrus in invaded areas throughout the

world only where California red scale also has not invaded. Perhaps yellow scale will ultimately become extinct on citrus in invaded countries over the entire globe, but again it may persist at low levels depending on the presence of alternate host plants more favorable to yellow scale.

Yellow scale is able to survive on a number of host plant species in various countries on which California red scale has not been recorded, so ultimate worldwide extinction by competitive displacement outside the native range is probably impossible. Yellow scale has not been identified by entomologists of the California Department of Food and Agriculture from southern California on any of the 54 hosts on which it has been found in California except for plants imported into nurseries since the early 1960s, indicating it has been displaced throughout its entire range of hosts in southern California. We have noted its disappearance also on alternate hosts such as English ivy which we knew to be infested with yellow scale at one time.

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