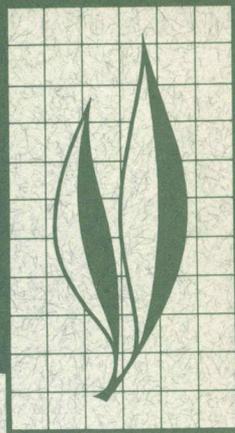


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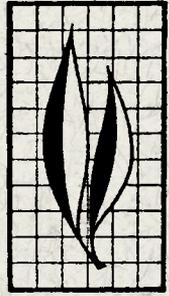
Ecology of Tetranychid Mites and Their Natural Enemies: A Review

I. Tetranychid Enemies: Their Biological Characters and the Impact of Spray Practices

J. A. McMurtry, C. B. Huffaker, and M. van de Vrie

II. Tetranychid Populations and Their Possible Control by Predators: An Evaluation

C. B. Huffaker, M. van de Vrie, and J. A. McMurtry



The two papers presented here were prepared at the request of the Special Committee of the International Biological Program, as part of a broad program on the ecology and natural control of spider mites (Tetranychidae) on a worldwide basis.

Part I is a review of the pertinent literature and a discussion of the biology and ecology of various spider mite enemies, their potential as biological control agents, and the effects of pesticides on their populations.

Part II reviews the literature pertaining to tetranychid abundance, and the evidence supporting various hypotheses concerned with their populations. It evaluates the action of various predators and discusses possible ways of implementing biological control.

A third paper in this series (Part III), by the same authors, will review the literature and discuss the problem of spider mites from the standpoint of their biology, ecology, pest status, and their relationship to host plants. This paper is expected to be published shortly.

THE AUTHORS:

C. B. Huffaker is Professor of Entomology and Entomologist in the Experiment Station, Berkeley.

J. A. McMurtry is Associate Entomologist in the Experiment Station and Lecturer in Biological Control, Riverside.

M. van de Vrie is with the Institute for Phytopathological Research, Wageningen, The Netherlands. He was a Research Associate in the Experiment Station, Riverside, for six months in 1970.

I. Tetranychid Enemies: Their Biological Characters and the Impact of Spray Practices^{1,2}

INTRODUCTION

NATURAL ENEMIES of tetranychids are many and varied. In a world review of the literature on the European red mite, *Panonychus ulmi* (Koch), Groves (1951) stated that on *P. ulmi* alone, over 65 species of predators had been reported. Berker (1958) reported 59 species of tetranychid predators on fruit trees alone, during a three-year study in central Germany. The predatory mites of the family Phytoseiidae have received the most recent and widespread attention, and certain groups of insectan predators have been fairly

widely studied. Other forms, such as spiders, have been investigated very little. Disease-producing pathogens of spider mites have been known for a long time, but only in recent years has there been intensive effort to determine their etiology or to explore their potential in control of spider mites.

A brief synopsis of the kinds of spider mite enemies is here presented, followed by a comparison of some of their biological properties. Additional recent reviews are those of H. Mori (1967) and Muma (1969).

PATHOGENS

Baker (1936) reported that an undetermined disease caused high mortality of *Tetranychus telarius* (L.), especially during hibernation. Collyer (1964c) observed a sudden collapse in *Panonychus ulmi* populations on apple in New Zealand, and also of *Tetranychus* sp. on native vegetation, which seemed to be the result of disease, "probably fungal."

Charles (1940, 1941) observed a fungus disease in *Oligonychus yothersi* (McGregor) from Florida and *Tetranychus telarius* from Kansas. An *Entomophthora* sp. was found infesting citrus red mite, *Panonychus citri* (McGregor), in Florida (Fisher, 1951). Ac-

cording to Muma (1955a, 1958), infestations of *P. citri* were controlled by this fungus during periods of high humidity or heavy rainfall, and the mortality ranged from 30 to over 90 per cent. Apparently sprays of copper or sulfur reduce the effectiveness of this fungus (Thompson, 1939, 1944; Griffiths and Fisher, 1949). Citrus red mite has also been found infected with *Hirsutella* sp. in Florida (Fisher, 1955; Muma, 1958; Muma, Selhime, and Denmark, 1961).

Eutetranychus banksi (McGregor) is known to become infected by species of *Hirsutella* and *Entomophthora* (Fisher, 1954; Muma, Selhime, and Denmark,

¹ Submitted for publication March 5, 1969.

² See "Literature Cited" for citations referred to in text by author and date.

1961). The latter was described by Weiser and Muma (1966) as *Entomophthora floridana* Weiser and Muma, and is considered an important pathogen of *Eutetranychus banksi* in Florida (Muma, Selhime, and Denmark, 1961; Selhime and Muma, 1966). Selhime and Muma studied the life cycle and epizootiology of *Entomophthora floridana*. A *Hirsutella* sp. has also been found in the six-spotted mite, *Eotetranychus sexmaculatus* (Riley) (Fisher, 1954; Muma, Selhime, and Denmark, 1961).

Fungus infections have not been found in either citrus red mite or six-spotted mite in California, possibly because of the drier climate. H. Mori (unpublished data) found an unidentified fungus attacking *Tetranychus urticae* on beans in Hokkaido, Japan.

Carner and Canerday (1968) observed a high percentage of infection in populations of *Tetranychus urticae* and *T. cinnabarinus* (Boisduval) by the fungus *Entomophthora fresenii* Nowakowski in some cotton fields in Alabama. Up to 88 per cent of live mites collected from fields where epizootics were occurring succumbed to mycosis after two days in the laboratory. The authors concluded that the fungus may play an important role in regulation of some spider mites on cotton.

Munger, Gilmore, and Davis (1959) reported a disease that greatly reduced citrus red mite populations in the laboratory in California. Evidence indicated the pathogen to be a virus (K. M. Smith *et al.*, 1959). Many of the diseased mites contained characteristic birefringent crystals (K. M. Smith and Cressman, 1962). Some of the properties and the transmissibility of the virus were studied by Gilmore and

Munger (1963, 1965). Gilmore (1965) confirmed the presence of a naturally-occurring epizootic in the field. Tashiro and Beavers (1966) indicated that under certain conditions, the virus exerts definite suppressive action against high populations of *Panonychus citri*. More extensive surveys by Shaw, Tashiro, and Dietrick (1968) indicated that the virus was also present in low populations and was found in 82 per cent of the sample groves in southern and central California.

Attempts have been made in California to induce or enhance field epizootics by spraying virus suspensions or disseminating diseased mites. Gilmore (1965) reported that reductions in mite populations were correlated with virus treatments, although the results were not entirely conclusive. Shaw, Chambers, and Tashiro (1968) showed that suspensions of triturated diseased mites or introductions of diseased mites enhanced the progress of natural epizootics of citrus red mite. These workers also studied the effects of various concentrations and of buffering the suspensions, and compared effectiveness of releasing naturally-infected or laboratory-infected mites. They concluded that this general approach showed sufficient promise to justify further work toward a practical application.

A possible virus disease was also reported in *Panonychus ulmi* from California (Steinhaus, 1959). Rod-shaped virus particles were found in fat cells of *P. ulmi* in a sample from Vineland Station, Ontario, Canada (Bird, 1967). Previously, Putman and Herne (1966) noted an apparent epizootic of *P. ulmi* on peach from the same region, but no pathogen was discovered at that time.

PHYTOSEIIDAE

Mites of the family Phytoseiidae, a diverse and widespread group, occur throughout the world from the Arctic through the tropics. The number of de-

scribed species has increased from fewer than 20 in 1951 (Nesbitt, 1951) to over 450 in 1965 (Chant, personal communication). Opinion differs among taxon-

omists on the generic classification of the Phytoseiidae. Extreme positions are held by Hirschmann (1962), who placed all of the species usually considered as Phytoseiidae in a single genus, *Typhlodromus*, which he included in the family Gamasidae, and Muma (1961b), who recognized 43 genera of Phytoseiidae. Other important works on classification of genera and subfamilies include those of Chant (1959, 1965), Chant and Baker (1965), Pritchard and Baker (1962), Wainstein (1962), Schuster and Pritchard (1963), and Stammer (1963).

Information on the geographic distribution and host plants of phytoseiids, types of habitats, and prey species with which they have been associated can be found in various systematic papers or annotated lists from various parts of the world: *northern Africa*, Athias-Henriot (1958); *central Africa*, Pritchard and Baker (1962); *South Africa*, van der Merwe (1965, 1968); *Asia* (in general), Ehara (1966a); *Australia and New Zealand*, Womersly (1954), Collyer (1964d); *Caribbean area*, DeLeon (1965a, b); *Europe*, Nesbitt (1951), Collyer (1956), Chant (1956a), Günthart (1957), Berker (1958), Dosse (1958a), Wainstein (1962), Stammer (1963), Carmona (1964), Boezek and Kropczyńska (1965); *Far East*, Evans (1953), Chant (1960), Narayanan, Kaur, and Ghai (1960), Swirski and Shechter (1961), Ehara (1964, 1967a, b), Rao and Rao (1964), Corpuz and Rimando (1966), Muma (1967a); *Mexico and Central America*, DeLeon (1959a, b, 1961), Chant and Baker (1965); *Middle East*, Swirski and Amitai (1961), Zaher and El Badry (1962), Porath and Swirski (1965), El Badry (1967a); *North America*, Garman (1948, 1958), Nesbitt (1951), Cunliffe and Baker (1953), Muma (1955c, 1961a, 1962, 1964a, b, 1965a), Chant (1957b), Anderson, Morgan, and Chant (1958), Fleschner (1958b), Kennett (1958), Oatman (1963),

Schuster and Pritchard (1963), Denmark and Muma (1967), Specht (1968); *South America*, Gonzalez and Schuster (1962), DeLeon (1965b, 1966), Ehara (1966b); *worldwide*, Chant (1959).

The first published remarks regarding the possible value of phytoseiids in the control of phytophagous mites were apparently those of Parrott, Hodgkiss, and Schoene (1906), who noted "*Seius pomi*" preying on the pear blister mite, *Eriophyes pyri* (Pgst.). Quayle (1912), Ewing (1914), Newcomer and Yothers (1929), Gilliatt (1935), Garman and Townsend (1938), Bailey (1939), Kuenen (1947), Garman (1948), L. M. Smith and Summers (1949), and Nesbitt (1951) were among the earlier workers who considered the group to be important predators of tetranychid mites. Two species were shown to be efficient predators of the tarsonemid mite, *Steneotarsonemus pallidus* (Banks), on strawberry in central California (Huffaker and Spitzer, 1951; Huffaker and Kennett, 1953b, 1956), and several species were considered important mortality agents of spider mites on citrus and avocados (Fleschner and Ricker, 1954). Since the mid-1950's, publications on the Phytoseiidae have appeared in rapid succession.

On the basis of either field observation or population studies, many workers have considered certain phytoseiids to be of some or of major importance in the control of spider mites on various crops. This information is summarized in table 1.

As might be expected, many of these reports were based only on limited observations or routine population counts. An experimental approach, in which predators have been added or removed, has been used in the field in some cases, including the work of Collyer (1964b) and Dosse (1960) for *Typhlodromus pyri* (Scheuten); Fleschner, Hall, and Ricker (1955) for *Amblyseius hibisci* (Chant) and *A. limonicus* (Garman

TABLE 1
PHYTOSEIID MITES CONSIDERED TO BE IMPORTANT PREDATORS OF TETRANYCHIDS ON VARIOUS CROPS

Phytoseiid	Tetranychid	Crop	Location	Reference
<i>Amblyseius</i> species:				
<i>aberrans</i> (Ouds.)	<i>Panonychus ulmi</i> (Koch)	Grape	Switzerland	Mathys, 1958
	<i>Eotetranychus carpini</i> (Ouds.)	Grape	France	Rambier, 1964
<i>cucumeris</i> (Ouds.)	<i>Tetranychus urticae</i> Koch	Alfalfa	Washington, U.S.A.	Cone, 1963
	<i>T. cinnabarinus</i> (Bois.)	Cotton, fruit	Egypt	Zaher & El Badry, 1962
	<i>P. ulmi</i> (Koch)	Apple	Wisconsin, U.S.A.	Oatman, 1965a
<i>fallacis</i> (Garman)			W. Virginia, U.S.A.	Clancy & McAlister, 1958
	<i>T. urticae</i> Koch	Apple	Wisconsin, U.S.A.	Oatman, 1965a
<i>finlandicus</i> (Ouds.)	<i>P. ulmi</i> (Koch)	Apple	Poland	Kroczynska, unpublished data
	<i>Oligonychus punicae</i> (Hirst)	Avocado	California, U.S.A.	Fleschner & Ricker, 1954; Fleschner, 1958b; McMurtry & Johnson, 1966
<i>hibiscii</i> (Chant)			California, U.S.A.	Fleschner & Ricker, 1954; Fleschner, 1958b
	<i>P. citri</i> (McGregor)	Citrus	California, U.S.A.	Fleschner, 1958b
<i>largensis</i> Muma	<i>E. sermaculatus</i> (Riley)	Avocado	California, U.S.A.	S. Mori, 1964
<i>libanesi</i> Dosse	<i>P. citri</i> (McGregor)	Citrus	Japan	Dosse, 1967
<i>limonicus</i> (Garman & McGregor)	" <i>Tetranychus cinnabarinus</i> complex"	Citrus, castor bean	Lebanon	Fleschner, Hall, & Ricker, 1955
	<i>E. sermaculatus</i> (Riley)	Avocado	California, U.S.A.	McMurtry & Johnson, 1966
	<i>O. punicae</i> (Hirst)	Avocado	California, U.S.A.	H. Mori, 1969
<i>longispinosus</i> (Evans)	<i>T. urticae</i> Koch	Clover	Japan	van de Vrie & Kroczynska, 1965;
<i>potentillae</i> (Garman)	<i>P. ulmi</i> (Koch)	Apple	Netherlands	Kroczynska & van de Vrie, 1965
			Japan	Ehara, 1964
<i>rademacheri</i> Dosse	<i>T. urticae</i> Koch	Soybean	Japan	Kuenen, 1947
<i>similis</i> (Koch)*	<i>P. ulmi</i> (Koch)	Plum	Netherlands	Ehara, 1964
<i>tsugawatai</i> Ehara	<i>T. urticae</i> Koch	Soybean	Japan	
Phytoseiulus species:				
<i>macropilis</i> (Banks)	<i>T. urticae</i> Koch	Strawberry	California, U.S.A.	L. M. Smith & Summers, 1949
<i>perstans</i> Athias-Henriot (= <i>P. ritegati</i>)	<i>T. urticae</i> Koch	Bean	Canada (indoors)	Chant, 1961a
			Germany (indoors)	Dosse, 1958a
		Cucumber	Netherlands (indoors)	Bravenboer, 1963; Bravenboer & Dosse, 1962
			England (indoors)	Hussey & Parr, 1965
			U.S.R. (indoors)	Begjarov, 1967
		Peach	Netherlands (indoors)	Bravenboer & Dosse, 1962
		Roses	United States (indoors)	Smith, Henneberry, & Boswell, 1963
		Strawberry	California, U.S.A. (indoors)	Laing & Huffaker, 1969
			California, U.S.A. (outdoors)	Oatman, 1965b; Oatman, McMurtry, & Voth, 1968
		Vegetables	Lebanon	Dosse, 1967

*"*Tetranychus cinnabarinus* complex"

TABLE 1—Continued

Phytoseiid	Tetranychid	Crop	Location	Reference
<i>Phytoseius macropilis</i> (Banks)	<i>P. ulmi</i> (Koch)	Plum	Poland	Niemczyk & Wiackowski, 1965
<i>Typlothromus</i> species:				
<i>caudiglanis</i> Schuster	<i>P. ulmi</i> (Koch)	Peach	Ontario, Canada	Putman & Herne, 1964, 1966
		Apple	Wisconsin, U.S.A.	Oatman, 1965a
	<i>T. urticae</i> Koch	Apple	Wisconsin, U.S.A.	Oatman, 1965a
<i>floridanus</i> Muma	<i>E. sermaculatus</i> (Riley)	Citrus	Florida, U.S.A.	Muma, 1958, 1964a
<i>longipilus</i> Nesbitt†	<i>T. urticae</i> Koch	Fruit	Netherlands (indoors)	Bravenboer, 1959
	<i>T. species</i>	"Orchards"	Washington, U.S.A.	Hantsbarger & O'Neill, 1954
<i>occidentalis</i> Nesbitt	<i>E. willamettei</i> McGregor	Grape	California, U.S.A.	Huffaker & Flaherty, 1966; Flaherty, 1967
	<i>T. species</i>	Cotton	California, U.S.A.	Leigh (in Huffaker & Flaherty, 1966)
	<i>T. medaniensis</i> McGregor	Apple	Washington, U.S.A.	Hoyt, 1969a, b
	<i>T. pacificus</i> McGregor	Grape	California, U.S.A.	Huffaker & Flaherty, 1966; Flaherty, 1967
<i>pomi</i> (Parrott)	<i>T. urticae</i> Koch	Strawberry	California, U.S.A.	Laing & Huffaker, 1969; Allen, 1959a
	<i>P. ulmi</i> (Koch)	Apple	W. Virginia, U.S.A.	Clancy & McAlister, 1956, 1958
<i>pyri</i> Scheuten (= <i>T. tiltae</i>)	<i>P. ulmi</i> (Koch)	Apple	England	Collyer, 1958, 1964b; Collyer & Kirby, 1959
			Netherlands	van de Vrie, 1964; van de Vrie & Kropeczyńska, 1965
			Germany	Dosse, 1960; Berker, 1956, 1958
			Nova Scotia, Canada	Lord, Herbert, & MacPhee, 1958; Lord, 1949
		Apple & other deciduous fruits	New Zealand	Collyer, 1964c
<i>rhenanus</i> (Ouds.)	<i>Bryobia arborea</i> Morgan & Anderson	Apple	Canada	Nesbitt, 1951
	<i>T. urticae</i> Koch	Apple	Switzerland	Günthart, 1957; Mathys, 1956, 1958
			Nova Scotia, Canada	Herbert, 1962b
			Quebec, Canada	Parent, 1967
<i>soleiger</i> Ribaga	<i>T. viennensis</i> Zacher	Fruit trees	Illinois, U.S.A.	Snetsinger, 1959
Species not indicated	"Red spider"	Fruit trees	Tambow, U.S.S.R.	Rymasevskaja, 1964
Species not indicated	<i>P. ulmi</i> (Koch)	Apple	U.S.S.R.	Rymasevskaja, 1964
			Ohio, U.S.A.	Suncova, 1963
			W. Virginia, U.S.A.	Cutright, 1944
			Connecticut, U.S.A.	Clancy & Pollard, 1952; Clancy & McAlister, 1958
				Garman & Townsend, 1938

* This may represent a misidentification; the author was probably working with *A. pendentillae* (van de Vrie, unpublished).

† Recent research (Kennett and Huffaker, unpublished) has indicated that *T. longipilus* from Europe may be conspecific with *T. occidentalis*.

and McGregor); Huffaker and Spitzer (1951), and Huffaker and Kennett (1953b, 1956) for *A. cucumeris* (Ouds.) and *A. aurescens* (Athias-Henriot); Oatman and McMurtry (1966) and Oatman, McMurtry, and Voth (1968) for *Phytoseiulus persimilis* (Athias-Henriot); van de Vrie and Kropczynska (1965) for *A. potentillae* Garman on apple; and Flaherty (1967) for *T. occidentalis* Nesbitt. Each of these studies showed that the species concerned were effective predators. Other detailed studies covering several consecutive seasons and strongly indicating importance of certain species include those of Hoyt (1969a, b) on *T. occidentalis*; Muma (1958) for *T. floridanus* Muma; McMurtry and Johnson (1966) for *A. limonicus*; and Putman and Herne (1964, 1966) for *T. caudiglans* Schuster.

On the other hand, studies in England and Canada led Chant (1958, 1959, 1963) and Anderson and Morgan (1958a) to conclude that certain species were of little value in the control of tetranychids. This question is discussed by Huffaker, van de Vrie, and McMurtry (see second paper herein).

Various controlled population experi-

ments in greenhouses, laboratories, or growth chambers have demonstrated the ability of several species to overtake and suppress rapidly increasing tetranychid populations, e.g., Collyer (1958, 1964a), Herbert (1962b), and van de Vrie and Kropczynska (1965) for *Typhlodromus pyri*; Bravenboer and Dosse (1962), Chant (1961a), Force (1967), Gould, Hussey, and Parr (1969), Hussey and Parr (1965), Laing and Huffaker (1969) for *Phytoseiulus persimilis* (= *P. riegei*; Huffaker (1958), Huffaker, Shea, and Herman (1963), Laing (1968), Laing and Huffaker (1969) for *T. occidentalis*; McMurtry and Scriven (1966c, 1968) for *Amblyseius hibisci*; McMurtry and Scriven (1971) for *A. limonicus*; Collyer (1964a) for *A. finlandicus* (Ouds.); Hessein (1967) for *Iphiseius degenerans* (Berl.). However, such studies have also indicated that some species under certain conditions were unable to effectively suppress particular spider mite populations, e.g., *T. umbraticus* Chant, *T. tiliarum* (Ouds.), and *Phytoseius macropilis* (Banks) (Collyer, 1964a), and *A. hibisci* (Chant) (McMurtry and Scriven, 1966c).

Some Features of the Biology of Phytoseiids

Development

Phytoseiidae have four developmental stages: the egg, the six-legged larva, the protonymph, and the deutonymph. The last two stages have eight legs. One exception to this sequence has been reported by Ballard (1954), who observed that males of *Amblyseius fallacis* (Garman) have no deutonymph stage. The quiescent period between stages is apparently quite short (Ballard, 1954; Bravenboer, 1959; Lee and Davis, 1968).

The larvae of many species apparently require food in order to transform to the protonymph, but some do

not. Larvae of *Typhlodromus occidentalis* have been observed to feed in some cases, and not to feed in others (Waters, 1955; Laing, 1968a; Lee and Davis, 1968). Nonfeeding larvae have been reported for *T. pyri* (Chant, 1959); *Amblyseius cucumeris* (Dosse, 1955); *A. chilensis* Dosse, *A. rademacheri* Chant, *Phytoseiulus persimilis* (Dosse, 1958b); *P. macropilis* (Prasad, 1967); and *T. rickeri* Chant (McMurtry and Scriven, 1964a). In some of these cases, it is possible that the larvae could have obtained some nourishment from the foliage, although *T. rickeri* larvae transformed even in empty cells. Swirski, Amitai, and Dorzia (1967a) found that

TABLE 2
SOME REPORTED RATES OF DEVELOPMENT OF PHYTOSEIIDAE
UNDER LABORATORY CONDITIONS

Species	Temperature	Time	Reference
	° C	days	
<i>Phytoseiulus persimilis</i> Athias-Henriot (= <i>P. riegeli</i>)..	30	3.8	Dosse, 1958b
	30	4.9*	Begljarov, 1967
	28	4.7*	McClanahan, 1968
	23	6.9*	McClanahan, 1968
	25	4.6	Dosse, 1958b
	25.5	4 to 5	Böhm, 1966
	23	8.2*	Begljarov, 1967
	20†	7.4	Laing, 1968a, b
<i>P. macropilis</i> (Banks).....	26	4.2	Prasad, 1967
<i>Amblyseius cucumeris</i> (Ouds.).....	25 to 26	6.7	Dosse, 1955
	20 to 21	10.5	Dosse, 1955
	15 to 16	23.5	Dosse, 1955
<i>A. chilensis</i> (Dosse).....	30	5.5	El Badry and Zaher, 1961
	30	5	Dosse, 1958b
	25	6	Dosse, 1958b
<i>A. fallacis</i> (Garman).....	26	5	Ballard, 1954
	26	5.8*	McClanahan, 1968
	21	5 to 6†	Herbert, 1953
	20	11.6*	McClanahan, 1968
	23	8	McMurtry & Scriven, 1964b
<i>A. limonicus</i> Garman and McGregor.....	22.2	6	McMurtry & Scriven, 1965
<i>Typhlodromus caudiglans</i> Schuster.....	25	6.7	Putman, 1962
	21	7.0	Putman, 1962
	20	10.4	Putman, 1962
	22	7	Bravenboer, 1959
<i>T. longipilus</i> Nesbitt.....	18.3	10‡	Herbert, 1961
<i>T. pyri</i> Scheuten (= <i>T. tiliae</i>).....	20	16	Böhm, 1960
	25	8	Böhm, 1960
	25 to 26	7.2	Dosse, 1956
	15 to 16	23.4	Dosse, 1956
	22.2	6	McMurtry & Scriven, 1964a
<i>T. rickeri</i> Chant.....	24	6.3	Lee and Davis, 1968
<i>T. occidentalis</i> Nesbitt.....	20†	8.5	Laing, 1968a

* Also includes preoviposition.

† Mean of programmed fluctuating temperatures.

‡ Excluding the egg stage.

although larvae of *A. rubini* Swirski and Amitai were predaceous, some reached the deutonymphal stage on leaves alone. The ecological significance of these differences is not known, but if it can be assumed that the eight-legged protonymphs have a greater searching ability than the six-legged larvae, it might be advantageous if the larva does not have to find food.

The period of development in phyto-seiids is generally shorter than that of the tetranychids under comparable conditions. Some data, from various sources, on development time are shown in table 2.

In a few studies, rate of development

of the spider mite prey as well as that of the predators has been determined under the same conditions at several constant or patterned temperatures. Bravenboer and Dosse (1962) and Begljarov (1967) found that *Phytoseiulus persimilis* (= *P. riegeli*) developed markedly faster than did *T. urticae* at a number of temperatures ranging from 10° to 35°C, and Laing (1968) found that both *P. persimilis* and *Typhlodromus occidentalis* developed markedly faster than *T. urticae* under programmed fluctuating temperatures.

Although the minimum developmental time for most phyto-seiid species seems to be about six to seven days, the

Phytoseiulus species appear to develop somewhat more rapidly. It is obvious that development is prolonged at low temperatures. The quantity and quality of food also markedly affect speed of development. If few prey are available, development is prolonged (Herbert, 1956, 1961; Dosse, 1958b; Chant, 1959; Putman, 1962). A diet of tetranychid mites alone may not be optimum for rapid development in some species. Chant (1959) found that *Typhlodromus pyri* developed faster on the eriophyid *Aculus* (= *Vasates*) *schlectendali* (Nalepa) than on *Panonychus ulmi*, and Burrell and McCormick (1964) reported that *T. occidentalis* developed faster on the same eriophyid than on tetranychids. *Amblyseius hibisci* developed faster on various kinds of pollen than on tetranychids (McMurtry and Scriven, 1964b).

Mating and Sex Ratios

For the Mesostigmata, to which phytoseiids belong, early indications were that reproduction is not arrhenotokous (Whiting, 1945), but recently arrhenotoky in this group has been indicated both from genetic studies (Skaliy and Hayes, 1949; Camin, 1953; and Filipponi, 1955, 1957) and cytological studies (Oliver, Camin, and Jackson, 1963). In the Phytoseiidae, one species, *Amblyseius elongatus* (Garman), has been observed to be thelytokous (Kennett, 1958). All others studied have been found to oviposit only after insemination, and some require repeated insemination for continued oviposition (Smith and Summers, 1949; Ballard, 1954; Dosse, 1955, 1957b; Herbert, 1956; Huffaker, 1958; Chant, 1959; El Badry and Zaher, 1961; Putman, 1962; McMurtry and Scriven, 1964a; Böhm, 1966). Hansell, Mollison, and Putman (1964) and Wysocki and Swirski (1968) conducted cytological studies, and present evidence that sex may be determined, not by segregation of sex chro-

mosomes, but by a haploid-diploid mechanism (arrhenotoky). All this suggests that ovigenesis requires some stimulus associated with mating or presence of sperm in arrhenotokous forms, even though the developing, unfertilized ova produce males; otherwise, the female would presumably continue to produce male (haploid) offspring after the sperm were exhausted, and there would be no cessation of egg laying. Study on this point is needed.

Ballard (1954), Dosse (1959b), El Badry and Elbenhawy (1968a) and Lee and Davis (1968) describe the mating process in phytoseiids. According to Dosse, the males use their chelicerae to place the spermatophores into the "coxal glands" or spermathecae between coxae III and IV of the female. Dosse also claimed that the number of successful copulations could be determined by the number of spermatophores in the spermathecae.

Putman (1962) found that the initial egg laid by *Typhlodromus caudiglans* was nearly always a male, but that in a random sample, only 15 per cent were males. The sex ratio in *T. rickeri* Chant was observed to be about two females to one male (McMurtry and Scriven, 1964a). Dosse (1957a) reported males of *T. pyri* to be most numerous in the first generation.

Preoviposition and Oviposition

The preoviposition period in some phytoseiids may be quite short at warm temperatures. For example, Prasad (1967) reported an average of 30.7 hours for *Phytoseiulus macropilus* (Banks), Ballard (1954) reported 24 hours for *Amblyseius fallacis*, and Lee and Davis (1968) found an average of 1.3 days for *Typhlodromus occidentalis*. However, two to three days seems to be common for many species, such as *A. cucumeris* (El Badry and Zaher, 1961), *A. limonicus* (McMurtry and Scriven, 1965), *T. caudiglans* (Putman, 1962),

and *T. rickeri* (McMurtry and Scriven, 1964a). Furthermore, it may be considerably longer at lower temperatures. Herbert (1961) reported a period of five days for *T. pyri* at 65°F, while under controlled temperatures simulating those in the field, this period averaged from 5.2 days for the first generation to 11.6 for the third (Herbert, 1962a). Putman (1962) obtained a mean preoviposition period for *T. caudiglans* of 9.2 and 16.3 days at 63.2° and 58.6°F, respectively. Dosse (1957a) reported a 15-day mean preoviposition period for females of *T. pyri* when held at 25° to 26°C, after being collected in the field in March. Van de Vrie (1963, 1964) found that the preoviposition period of field-collected females of *T. pyri* decreased as the winter progressed (i.e., mites collected in January had a longer period than did those collected in April). Kennett (unpublished data) found that *T. occidentalis* collected in November and December under bud scales of grape varied greatly in the time required before egg deposition began when supplied prey in the laboratory. Such cases may be related to diapause (see section "Overwintering and Diapause").

Table 3 presents examples of egg-production rates and total eggs, as reported by various authors. About two to two and one-half eggs per female per day seems to be maximum production for many species at warm temperatures and with abundant prey, although some, especially the *Phytoseiulus* species, appear to have a rather higher rate. On the other hand, the maximum rate of oviposition of some species fed tetranychids was found to be little more than one per day at warm temperatures (e.g., *Typhlodromus pyri*, *Amblyseius hibisci*, *A. rubini*, and *A. swirskii* Athias-Henriot). The reason for this, for the last three species at least, is that spider mites apparently are not the most favorable food and do not induce the high

rate of oviposition that results with certain other foods (McMurtry and Scriven, 1964b; Swirski, Amitai, and Dorzica, 1967a).

Mean total eggs per female seems to vary considerably, depending on the species and the testing conditions. The values obtained from *Phytoseiulus* species were mostly in the range of 50 to 60 (Dosse, 1958b; Böhm, 1966; Prasad, 1967; Laing, 1968; McClanahan, 1968). Reports show considerable variation for other species, but the number commonly seems to be around 30 to 50. The rate of egg production is typically greatest during the early part of adult life, and then gradually drops off (Waters, 1955; McMurtry and Scriven, 1964a; Kuchlein, 1966a; Laing, 1968a, b; McClanahan, 1968). The oviposition period may be over 30 days at moderate to warm temperatures (Waters, 1955; Herbert, 1956, 1961; Putman, 1962; McMurtry and Scriven, 1964a) and probably much longer under cool conditions.

The rate of egg production was shown to be affected by the number of prey consumed. Chant (1961b) found that *Typhlodromus occidentalis* could lay eggs at a low rate (one every two or three days) when given only one spider mite protonymph per day, and that as the number of prey was increased to as many as 20 per day, the rate increased to a maximum of two eggs per day. Herbert (1956), Dosse (1958b), Bravenboer (1959), Bravenboer and Dosse (1962), Kuchlein (1965), and McMurtry and Scriven (1966a) also noted an increased rate of egg production, up to a maximum, as more prey were provided. It is of interest that Kuchlein (1966b) reported an increase in fecundity of *T. longipilus* and *Phytoseiulus persimilis* with increasing prey density up to a plateau, after which a decrease occurred (see the second paper in this series).

Overwintering and Diapause

In temperate climates, the overwinter-

TABLE 3
SOME REPORTED RATES OF OVIPOSITION OF PHYTOSEIIDAE FEEDING
ON TETRANYCHIDS UNDER LABORATORY CONDITIONS

Species	Temperature	Eggs per ♀ per day	Total eggs per ♀	Reference
	° C			
<i>Phytoseiulus persimilis</i> Athias-Henriot (= <i>P. riegei</i>)	35	5.2	64*	Dosse, 1958b
	30	3.6	..	Begjarov, 1967
	30	4.2	..	Dosse, 1958b
	27	4.1	..	Begjarov, 1967
	25	4	104*	Begjarov, 1967
	25 to 26	..	58 to 60	Böhm, 1966
	18	0.8	..	Begjarov, 1967
	20†	2.4	53.5	Laing, 1968a, b
	26	3 to 5	53.5	McClanahan, 1968
<i>P. macropilis</i> (Banks)	26	4	52	Prasad, 1967
	..	2 to 3	..	Smith and Summers, 1949
<i>Amblyseius cucumeris</i> (Ouds.)	25 to 26	1.4	54*	Dosse, 1955
<i>A. chilensis</i> (Dosse)	35	2.7	24*	Dosse, 1958b
	30	3.3	28*	Dosse, 1958b
	25	2.7	68*	Dosse, 1958b
<i>A. fallacis</i> (Garman)	26	2.2	..	Ballard, 1954
<i>A. gossipi</i> El Badry	26.5 to 28.5	3.1	49	El Badry <i>et al.</i> , 1968
	21	2.7	37.5	Herbert, 1953
	26	2 to 4	37.6	McClanahan, 1968
<i>A. hibisci</i> (Chant)	23	1.3	..	McMurtry and Scriven, 1964b
<i>A. limonicus</i> Garman and McGregor	26.7	2.7	..	McMurtry and Scriven, 1965
	22.2	2.2	..	McMurtry and Scriven, 1965
	21.1	1.8	..	McMurtry and Scriven, 1965
	25 to 27	0.86	..	Swirski and Dorzia, 1968
<i>A. rubini</i> Swirski and Amitai	25 to 27	1.2	..	Swirski, Amitai, and Dorzia, 1967a
<i>A. swirski</i> Athias-Henriot	25 to 27	1.2	..	Swirski, Amitai, and Dorzia, 1967a
<i>Typhlodromus athiasae</i> Porath and Swirski	25 to 27	0.8	..	Swirski, Amitai, and Dorzia, 1967b
<i>T. caudiglans</i> Schuster	20	1	..	Putman, 1962
<i>T. occidentalis</i> Nesbitt	23	2	..	Chant, 1961b
	20†	2.2	35	Laing, 1968a
<i>T. longipilus</i> Nesbitt†	20	2	38	Bravenboer, 1959
	15.6 to 26.7	1.9	40	Burrell and McCormick, 1964
<i>T. pyri</i> Scheuten (= <i>T. tiliae</i>)	25 to 26	1.3	58*	Dosse, 1956
	32*	Collyer, 1956
	18	1	25	Herbert, 1961
<i>T. rickeri</i> Chant	24	1.9	..	McMurtry and Scriven, 1964a
	21	1.3	..	McMurtry and Scriven, 1964a
	15.6	0.7	..	McMurtry and Scriven, 1964a

* Maximum.

† Mean of programmed fluctuating temperatures.

‡ See footnote †, table 1, regarding taxonomic status of *T. longipilus*.

ing stage of all phytoseiids studied appears to be the mated female (Dosse, 1955; Chant, 1959; Putman, 1959, 1962; Böhm, 1960; Herbert, 1962a). The overwintering females seek out protected places; the arboreal species, for example, are encountered in deep crevices, canker wounds, beneath leaf or bud scales and bark (Chant, 1959; Putman, 1959, 1962; van de Vrie, 1964). Mac-

Phee (1963) found that extremely low temperatures were necessary to freeze the body fluids of four species of phytoseiids occurring in Nova Scotia. The mean freezing points varied from about -20° to -24° F.

Winter mortality of some species is thought to be 80 per cent or more in severely cold years in deciduous orchards in Germany (Dosse, 1957a),

Austria (Böhm, 1960), England (Chant, 1959), and Canada (Anderson and Morgan, 1958a; Herbert, 1962a; Chant, 1963; and Putman and Herne, 1964). Chant (1963) considered this high mortality a major limiting factor in the effectiveness of such species. Moreover, he felt that the catastrophic nature of the winter mortality, coupled with the lack of continuity enforced by the dormant season, was actually responsible for regulating the abundance of the phytoseiids. This infers that a higher percentage of winter mortality would occur when overwintering phytoseiid populations are high. No evidence for this was presented. Collyer (1964b) considered winter mortality merely a feature of the biology of the phytoseiids rather than a factor hindering their potential for control. Van de Vrie (1964) also considered that in normal years, and in situations where there is no severe shortage of sheltering crevices in bark, bud scales, etc., the level of mortality in the Netherlands is not very high.

Winter mortality is usually rated by comparing numbers of mites present in autumn with numbers found the next spring. Because only the adult females overwinter, only that stage should be used in calculating percentage mortality. This fact, however, is seldom considered. Furthermore, the period in the spring during which phytoseiid numbers are estimated is important because their emergence from hibernation sites can take place over a considerable period of time. Moreover, the mites may spend considerable time on the branches and twigs, so that a leaf sample in the spring may give a spurious estimate of winter mortality.

While apparently little phytoseiid mortality on subtropical crops and grapes in southern California results from cold, a high fall and winter mortality may often occur—possibly as a result of food shortage (McMurtry and Johnson, 1966; Flaherty, 1967). Phy-

toseiids are present on the foliage of evergreen citrus and avocado trees throughout the winter, and all stages can often be found.

Evidence for an imaginal female diapause has been given by Putman (1962) and Sapožnikova (1964a, b). Sapožnikova found that at 18°C, all adult females of *Amblyseius similis* (Koch) entered diapause when exposed to photoperiods of nine, 10, and 11 hours, whereas none entered diapause under 15-, 18-, and 24-hour light periods. The critical photoperiod at which 50 per cent entered diapause was 11.5 hours. At 25°C, no individuals entered diapause, regardless of the photoperiod. It was also found that diapausing or non-diapausing prey mites were equally favorable as food, and that the diapause of *A. similis* was well synchronized with that of its prey. Putman (1962) obtained data indicating that photoperiod was the major factor affecting reproductive diapause of *Typhlodromus caudiglans*. A 12-hour photoperiod induced diapause and a 14-hour one either broke or failed to induce it. Exposure to the 12-hour photoperiod during at least the last three days of development was needed to induce diapause.

The absence of reproduction under otherwise favorable conditions was apparently the only reliable criterion that could be used for detecting diapause in the above-mentioned studies. Dosse (1957a) reported that overwintering females feed during warm winter days.

Foods and Feeding Habits

The Phytoseiidae contain many diverse forms with respect to feeding habits, ranging from strict carnivores to some which apparently prefer non-animal foods, such as pollen.

Feeding as predators. Some species seem to be specialized predators of tetranychids, and show no tendency to reproduce on other types of food. *Phytoseiulus persimilis* is apparently dependent on tetranychids (Dosse, 1958b;

Chant, 1961a) and serves as an example of this type of predator. Several types of nonprey foods had no effect on survival of this species (H. Mori and Chant, 1966b). *Typhlodromus occidentalis* in parts of California seems to thrive only in the presence of tetranychids, although it has been observed to feed on tarsonemids and other prey species (Huffaker and Kennett, 1956; Flaherty, 1967).

Some tetranychids may be more favorable as prey than others, even for phytoseiids that accept many different kinds of animal prey. For example, *Amblyseius fallacis* fed and reproduced readily on *Tetranychus urticae* and *T. mcdanieli* McGregor, but did poorly on *Panonychus ulmi* and *Bryobia* spp. (Herbert, 1959; Burrell and McCormick, 1964). *Typhlodromus occidentalis* preys more readily on *Tetranychus pacificus* McGregor than on *Eotetranychus willamettei* (McGregor) on grape (L. M. Smith and Stafford, 1955; Flaherty, 1967). This appears to be related to the pattern of distribution of the two species of prey, *T. occidentalis* thriving in the strongly aggregated and heavily webbed colonies of *T. pacificus* rather than the more diffuse or scattered colonies of *E. willamettei*. (See further, Flaherty, 1967; and the second paper in this series.) A somewhat similar example is found in *T. occidentalis* on apples in Washington. There, according to Hoyt (1969a, b), this phytoseiid is an effective predator of *T. mcdanieli*, an aggregating, strongly webbing species, but is not effective on *P. ulmi*, which webs lightly and has a different type of distribution. *T. floridanus* Muma and *Phytoseiulus persimilis* are also examples of predators associated with prey that form strongly aggregated colonies (*E. sexmaculatus* and *T. urticae* complex, respectively) (Muma, 1955a, 1958; Dosse, 1958b, 1967). On the other hand, *T. caudiglans* and *A. hibisci* apparently are not adapted to such situations, as they are hindered by

the webbing in colonies of the *T. urticae* complex, but prey readily on such species as *P. ulmi* and *P. citri*, which web little (Putman, 1962; McMurtry and Scriven, 1964b). In laboratory experiments, *T. pyri* is often found caught in webbing of *T. urticae* (van de Vrie, unpublished).

Many other characteristics of predators and of the prey may also affect the degree of prey specificity. Burrell and McCormick (1964) reported that *Amblyseius cucumeris*, which readily develops on *Bryobia*, seizes the latter by the leg, apparently piercing it and paralyzing the mite. But this predator attacked other species of tetranychids in the more usual manner of piercing the body cavity. The fact that *Bryobia* is large and has long legs may be a factor in the different mode of attack.

Some examples of rates of consumption of tetranychid prey by phytoseiids are shown in table 4. The daily capacity of ovipositing female phytoseiids seems generally to be fewer than 5 adult female spider mites or fewer than 20 larvae. Comparatively high rates were those by *Amblyseius limonicus* on *Panonychus citri* protonymphs (McMurtry and Scriven, 1965) and *Phytoseiulus persimilis* (= *P. riegeli*) on *Tetranychus dianthica* immature stages (Bravenboer and Dosse, 1962) and on *T. urticae* (stages unspecified) (Begljarov, 1967). Both of these predators are relatively large phytoseiids. Non-ovipositing females have been shown to consume considerably fewer prey than ovipositing ones (Putman, 1962; McMurtry and Scriven, 1964a).

It is significant that minimum numbers of prey required to sustain oviposition are much lower than those shown in table 4. *Typhlodromus occidentalis* was able to lay one egg every two or three days when consuming only one protonymph per day (Chant, 1961b), and *Amblyseius hibisci* laid an average of 0.5 egg per female per day when consuming an average of less than

TABLE 4
SOME REPORTED RATES OF PREY CONSUMPTION OF
TETRANYCHIDS BY PHYTOSEIID MITES

Species	Av. no. prey consumed	Prey species and stage	Reference
Ovipositing females:*			
<i>Amblyseius fallacis</i> (Garman).....	8	<i>Tetranychus urticae</i> ♂	Ballard, 1954
<i>A. hibisci</i> (Chant).....	3.8	<i>Oligonychus punicae</i> ♀	McMurtry and Scriven, 1965
	9	<i>Panonychus citri</i> protonymphs	McMurtry and Scriven, 1965
<i>A. limonicus</i> Garman and McGregor....	5.7	<i>O. punicae</i> ♀	McMurtry and Scriven, 1965
	22	<i>P. citri</i> protonymphs	McMurtry and Scriven, 1965
<i>Phytoseiulus persimilis</i> A. H. (= <i>P. riegeli</i>).....	4.8	<i>T. urticae</i> ♀	H. Mori and Chant, 1966a
	34	<i>T. urticae</i> eggs	Bravenboer and Dosse, 1962
	26.5	<i>T. dianthica</i> immature stages	Bravenboer and Dosse, 1962
	23.2	<i>T. urticae</i> (stage unspecified)	Begljarov, 1967
<i>P. macropilus</i> (Banks).....	3.0	<i>T. tumidus</i> ♀	Prasad, 1967
	15.6	<i>T. tumidus</i> larvae	Prasad, 1967
	6.4	<i>T. tumidus</i> nymphs	Prasad, 1967
<i>Typhlodromus caudiglans</i> Schuster.....	12.8	<i>P. ulmi</i> larvae	Putman, 1962
	6.9	<i>P. ulmi</i> deutonymphs	Putman, 1962
<i>T. occidentalis</i> Nesbitt.....	11.3	<i>T. urticae</i> protonymphs	Chant, 1961b
	1.97	<i>T. urticae</i> (stage unspecified)	Lee and Davis, 1968
<i>T. pyri</i> Scheuten.....	14.6	<i>P. ulmi</i> larvae	Herbert, 1961
<i>T. rickeri</i> Chant.....	4.3	<i>T. pacificus</i> ♀	McMurtry and Scriven, 1964a
	13.4	<i>T. pacificus</i> protonymphs	McMurtry and Scriven, 1964a
Immature stages:†			
<i>A. fallacis</i>	11.4	<i>T. urticae</i> ♂	Ballard, 1954
<i>A. cucumeris</i> (Ouds.).....	114	<i>T. cinnabarinus</i> eggs	El Badry and Zaher, 1961
<i>A. finlandicus</i> (Ouds.).....	27	<i>P. ulmi</i> larvae	Chant, 1959
<i>P. macropilus</i>	10.3	<i>T. tumidus</i> eggs	Prasad, 1967
	11.6	<i>T. tumidus</i> larvae	Prasad, 1967
	5.1	<i>T. tumidus</i> nymphs	Prasad, 1967
<i>T. caudiglans</i>	20.1	<i>P. ulmi</i> larvae	Putman, 1962
	17.3	<i>P. ulmi</i> protonymphs	Putman, 1962
	13.0	<i>P. ulmi</i> deutonymphs	Putman, 1962
<i>T. pyri</i>	119	<i>P. ulmi</i> larvae	Herbert, 1961
	17.8	<i>P. ulmi</i> larvae	Chant, 1959
<i>T. occidentalis</i>	16 to 17	<i>E. sezmaculatus</i> eggs	Waters, 1955

* Consumption rates represent average number of prey per day.

† Consumption rates represent average total prey consumed during development.

one *Oligonychus punicae* adult female per day (McMurtry and Scriven, 1966a). *T. pyri* laid seven eggs in 39 days when consuming 0.9 *Panonychus ulmi* larva per day, and laid 11 eggs in 35 days when consuming 2.1 larvae per day (Herbert, 1961).

The average number of prey consumed during full development generally seems to be fewer than 20 (table 4). The values of 119 prey eggs reported for *Amblyseius cucumeris* (El Badry and Zaher, 1961), and 114 larvae for *Typhlodromus pyri* (Herbert, 1961) appear to be exceptionally high. In the latter case, however, it was shown that development could be completed on

considerably fewer prey. A high percentage of predators completed development when given only two larvae. The developmental period was prolonged, averaging 12 days, during which an average of 22 larvae per predator was consumed. When predators were given only one prey larva per day, an average of 19 larvae per predator was consumed over a 21-day developmental period, 44 per cent of the predators reaching the adult stage (Herbert, 1961). The data thus indicate that the maximum capacity of the immature stages was about seven times greater than the minimum requirement. Chant (1959) found that *Typhlodromus pyri*

could complete its development on as few as three *Panonychus ulmi* larvae when confined on apple leaves, but it required more in the absence of leaf material.

The number of the various stages of prey consumed is probably at best only a rough indication of the quantity of food consumed, as some species of predators may extract the contents of the prey more completely than do other species. Moreover, the amount of fluids extracted from a prey may be influenced by the level of hunger of the predator.

Eriophid mites may also be commonly utilized as prey. Some phytoseiids, such as *Amblyseius hibisci* (McMurtry and Scriven, 1964b), *A. limonicus* (McMurtry and Scriven, 1965; Swirski and Dorzia, 1968), and *A. rubini* (Swirski, Amitai, and Dorzia, 1967a), feed on them but do not readily reproduce or develop. Others are reported to feed and reproduce equally well on tetranychids and eriophyids. These include *Typhlodromus caudiglans* (Putman, 1962), *T. longipilus*, *A. fallacis* (Burrell and McCormick, 1964), and *T. rickeri* (McMurtry and Scriven, 1964a). For still others, eriophyids may be a more favorable diet than tetranychids. For example, Chant (1959) showed that *T. pyri* developed faster on eriophyids than on *Panonychus ulmi*, possibly because they show more tendency to engorge themselves with the eriophyids. Burrell and McCormick (1964) observed that *T. rhenanus* Ouds. and *T. occidentalis* developed more readily on eriophyids than on tetranychids. However, the latter species is widely known to be closely associated with tetranychids in the field. Such obviously conflicting reports indicate that different workers may have been working with different species or different biotypes. (See second paper in this series.)

The presence of eriophyids as alternate food for the phytoseiids may result

in the phytoseiids being more effective in preventing increases of tetranychids (Collyer, 1964a; Hoyt, 1969a, b).

Several other groups of acarina may be utilized as food. Huffaker and Kennett (1956) found that both *Amblyseius cucumeris* and *A. aurescens* on strawberry in central California are essentially specific predators on tarsonemids, especially *Steneotarsonemus pallidus* (Banks), and do not feed to any extent on *Typhlodromus urticae*.

Brevipalpus species are accepted as food by *Amblyseius rubini*, *A. swirskii* (Swirski, Amitai, and Dorzia, 1967a), *A. chilensis* (Gonzalez, 1961), *Typhlodromus athiasae* (Swirski, Amitai, and Dorzia, 1967b), and *T. pyri* (Chant, 1959), all known to be tetranychid feeders. Tydeid mites seem to be the preferred food of two species studied. Dosse (1956) and Fleschner and Ricker (1954) found that *T. soleiger* (Ribaga) and *T. conspicuus* (Garman), respectively, developed and reproduced on tydeids, but not on other groups of mites tested. Böhm (1960) also reported that *T. soleiger* definitely preferred tydeids. *A. cucumeris*, in Germany, attacked the acarid *Czenspinksia lordi* Nesbitt, as well as tetranychids, but not species of *Brevipalpus* or *Brachytydeus* (Dosse, 1955). *C. lordi* was reported to be a favorable food for *Phytoseius macropilus* (Banks) (Dosse, 1956).

Eggs or immature stages of certain groups of insects can be utilized by some phytoseiids, but none has been reported to be the preferred prey. Scale crawlers are present in many orchard situations and it is not surprising that they may be attacked. Muma (1955c) observed that *Amblyseius* (= *Iphiseius*) *quadripilis* (Banks) and *A. peregrinus* Muma fed on scale crawlers, and McMurtry (1963) found that *A. hibisci* and *A. limonicus* laid eggs, and a few individuals completed development, on crawlers, while Swirski, Amitai, and Dorzia (1967a, b) also obtained development and reproduction of *A. rubini*,

A. swirskii, and *Typhlodromus athiasae* on armored-scale crawlers. The latter three species also developed and reproduced on certain species of moth eggs, whiteflies, and thrips (Swirski, Amitai, and Dorzia, 1967a, b; Teich, 1966). MacGill (1939) and El Badry (1967b) also found that certain phytoseiids could utilize thrips. *A. aleyrodii* El Badry had a higher rate of reproduction on whitefly nymphs than on tetranychid mites (El Badry, 1968).

An unusual and interesting relationship is that involving a species described as *Macroseius biscutatus* Chant, Denmark, and Baker, which has been found only in leaf cups of the pitcher plant, *Sarracenia minor* Walt., and which apparently prefers nematodes (Muma and Denmark, 1967a).

No high degree of cannibalism in phytoseiids has been reported, although larger stages may feed on the smaller ones in the absence of other food. This has been observed in *Typhlodromus longipilus* (Bravenboer, 1959), *T. occidentalis* (Waters, 1955; Laing, 1968), *A. fallacis* (Ballard, 1954), *T. rickeri* (McMurtry and Scriven, 1964a), *T. caudiglans* (Putman, 1962), and *Phytoseiulus persimilis* (Dosse, 1958b).

Feeding as herbivores or scavengers.

Some phytoseiids apparently extract juices from the host plant (Mathys, 1958; Chant, 1959). This was demonstrated by Chant for *Typhlodromus pyri*, *T. rhenanus*, and *Amblyseius finlandicus* by using systemic dyes, and, as previously stated, *T. pyri* required fewer prey to mature when confined on apple leaves than when confined without plant material but with available water.

Pollen-feeding in the Phytoseiidae was first reported by Chant (1959), and it has since been found that many species can utilize pollen to varying degrees. *Typhlodromus rickeri* could develop and reproduce on avocado pollen, but not nearly so rapidly as on tetranychid mites (McMurtry and Scriven,

1964a). An interesting situation was reported by Dosse (1961) in which overwintering females of *T. pyri* reproduced on pollen, but the F₁ females apparently did not reproduce unless they consumed some animal prey. Putman (1962) observed that pollen was a satisfactory food for *T. caudiglans*, but its development was somewhat slower than when fed on prey mites. The rates of development and oviposition of *Amblyseius limonicus* were about the same when this species fed on either pollen or spider mites (McMurtry and Scriven, 1965). *A. gossipi* apparently had a comparable reproductive rate and slightly faster developmental time on pollen as compared with spider mite prey (El Badry and Elbenhawy, 1968b). Pollen was found actually to induce a higher rate of reproduction than did spider mites in four species of phytoseiids: *Amblyseius rubini*, *A. swirskii* (Swirski, Amitai, and Dorzia, 1967a); *Typhlodromus athiasae* (Swirski, Amitai, and Dorzia, 1967b); and *A. hibisci* (McMurtry and Scriven, 1964b). The latter species also develops faster, with less mortality, when fed on pollen than on various species of tetranychids (McMurtry and Scriven, 1964b), and marked increases of *A. hibisci* in the spring, on avocados, in the virtual absence of prey mites were shown to result from the presence of pollen (McMurtry and Johnson, 1965).

Various kinds of fungi seem to be potential sources of food. Chant (1959) found that *Typhlodromus pyri*, *Amblyseius aberrans* Ouds., and *A. umbraticus* (Chant) completed development on leaves infected with powdery mildew, *Podosphaera leucotricha*; and Kropczyńska (unpublished data) observed that *A. finlandicus* also laid eggs when offered this fungus as food, but lived a shorter time than when provided with animal prey foods. Dosse (1959a) obtained negative results testing *Fusicladium dentriticum*, *Penicillium* sp., and *Aspergillus* sp. as food for several spe-

cies of phytoseiids. Since fungi of various types are present in most environments, further investigations should be conducted on this subject.

Certain carbohydrate-rich substances, such as nectar and honeydew, can also serve as food. Honeydews from aphids, soft scales, whiteflies, and mealybugs have been shown to promote survival but little reproduction (Huffaker and Kennett, 1956; Chant and Fleschner, 1960; McMurtry and Scriven, 1964*a, b*, 1965). Huffaker and Kennett believed that honeydew and other sugary excreta of homoptera served as important foods to maintain *Amblyseius cucumeris* and *A. aurescens* in strawberries during periods when their prey, the cyclamen mite, was very scarce. When honeydew was provided to *A. hibisci* in combination with tetranychid mites, there was less mortality during development, the preoviposition period was reduced, and the rate of reproduction was increased as compared with that when only prey mites were provided (McMurtry and Scriven, 1964*b*). Nectar from orange blossoms prolonged survival of some individuals of *A. limonicus* for as long as 60 days, as compared with only a few days' survival without food (McMurtry and Scriven, 1965).

Certain phytoseiids are able to develop and reproduce to some extent on artificial foods containing yeast and a carbohydrate (McMurtry and Scriven, 1966*b*). The more general feeders, *Amblyseius limonicus* and *A. hibisci*, benefited more from this diet than did the more specialized mite feeders tested, i.e., *Typhlodromus occidentalis*, and *T. rickeri*.

Summarizing the food habits of phytoseiids, it is evident that not all species are predators of tetranychids, and some that are do not reach their maximum rate of reproduction when restricted to such prey. Therefore, the presence of various alternate or supplemental foods may have an important

bearing on the predator-prey interactions of many species under field conditions. In some cases it may be unrealistic to determine rates of increase of certain species when feeding them mite prey only, when under natural conditions they may readily obtain certain food supplements that increase their productivity and survival. (See second paper in this series.)

Some Aspects of Phytoseiid Behavior

Phytoseiids generally spend much of their time on the undersurfaces of leaves. Experiments on *Typhlodromus caudiglans* indicate that this behavior is related to low photokinesis, thigmokinesis, and a tendency to remain on the lower side of horizontal surfaces (Putman, 1962). Many phytoseiids tend to lie close to the physical junctions or protective angles formed by the leaf midribs and major veins.

Anderson and Morgan (1958*a*) and Chant (1959) considered such behavior a disadvantage to effective predation on *Panonychus ulmi* on apple, since a large percentage of the latter species is found on the upper surfaces of leaves. However, some phytoseiids have been observed to roam over the upper surfaces of the leaves on all parts of the tree, especially at night or under shady conditions (Fleschner, Hall, and Ricker, 1955; Clancy and McAlister, 1958; McMurtry and Johnson, 1966). They may be expected to do so even more when their prey on the lower surfaces have become scarce.

Putman and Herne (1964) found that *Typhlodromus caudiglans* occurred more frequently on bark than on leaves. This would appear to be a disadvantage, since *Panonychus ulmi* occurs mainly on the leaves, except as winter eggs. Putman and Herne (1966) concluded, however, that this phytoseiid is the principal factor maintaining *P. ulmi* at low endemic densities on peach

in Ontario. (See second paper in this series.)

Some phytoseiids are widely found in low herbaceous vegetation, in intermediate shrubby growth, and in arboreal situations as well. *Typhlodromus occidentalis* in California is a good example (Schuster and Pritchard, 1963). Anderson and Morgan (1958b) found *Amblyseius cucumeris* mainly on low-growing plants, where it was a voracious predator of eggs of the clover mite, but unimportant as a predator of *Bryobia rubrioculus* (= *B. arborea*) on trees.

An effective predator obviously needs to be well adapted to the type of habitat in which a preferred species thrives. Unpublished data (Chant in Canada, McMurtry in California, and van de Vrie in the Netherlands) indicate that the use of *Phytoseiulus persimilis* on trees has been unsuccessful, apparently because it would not colonize the arboreal habitat in those environments. Flaherty and Kennett (unpublished data) also found that it would not colonize grapevines in the San Joaquin Valley of California. However, Athias-Henriot (1958) collected it from pear trees in Algeria, and Gonzalez and Schuster (1962) reported it (= *P. riegei* Dosse) from apples in Chile. Dosse (1967) and Rambier (personal communication to van de Vrie) also report finding it on trees in Lebanon and southern France, respectively. This suggests either the existence of strains or that this species cannot thrive on trees in certain environments.

Certain behavioral tendencies may even result in one variety of host plant being more successfully colonized than another. Downing and Moilliet (1967) found that in British Columbia, Canada, *Typhlodromus caudiglans* was more numerous on Spartan and McIntosh varieties of apple than on Delicious. The reason suggested was that the first two varieties have more highly

pubescent leaves with more pronounced veins, which provide more sheltered areas for the phytoseiids, and rough fruit spurs, for good overwintering sites. Collyer (1958) observed that *Phytoseiulus macropilis* preferred hairy leaves. Putman (1962) and Putman and Herne (1964) observed greater movement of *T. caudiglans* between bark and leaves on peach trees, which have glabrous leaves, than on apple trees, which have hairier leaves. Such differences may affect predator-prey interactions.

Phytoseiids may alter their pattern of "preferred sites," depending upon season of the year and the coincident availability of preferred prey populations. Collyer (1956), Günthart (1957), Chant (1959), and van de Vrie (1963) found that some species, such as *Typhlodromus massei* (Nesbitt) and *T. bakeri* (Garman), seem to be entirely bark-inhabiting; they were seldom found either on the twigs and spurs in winter or on the leaves in summer. Other species are associated more with the foliage, and hibernate mostly on the spurs and twigs.

In a study in apple orchards in England, Niemczyk (1965) found that during the first few weeks after emergence from their hibernation sites in the spring, *Typhlodromus pyri* showed a marked preference for sites affording shelter. They were observed to utilize loose bud scales and bark or other crevices between flower buds, while the buds were expanding, then enter flower buds at pink-bud stage, and finally occupy the undersides of leaves by the blossom period. Niemczyk considered this behavior to be related to the species' preference for protected places, rather than attraction to a particular food source, such as pollen in the flowers; in fact, many were present in flower buds before the petals opened and the anthers had dehisced, but these sites were rapidly vacated at petal opening. The

smaller number observed in exposed situations had a high percentage of individuals with red gut contents, suggesting that they had gone in search of prey.

Mathys (1958) indicated that phytoseiids were more effective against *Panonychus ulmi* on grape in the spring before the leaves have opened, since the prey are then confined to a smaller area.

Hoyt (1969a) observed a rapid response by *Typhlodromus occidentalis* to increasing densities of *Tetranychus mcdanieli*, and indicated that distribution was one of the major factors, the predator being found in all areas of the tree where this prey was located. Chant (1961b) and Oatman and McMurtry (1966) found that *Phytoseiulus persimilis* was rarely found on leaves not infested with *T. urticae*. This association in distribution between predator and prey probably results from the high mobility of *P. persimilis*, combined with its dependence on tetranychids for food. McMurtry and Johnson (1966) reported that the distribution of *Amblyseius hibisci*, a more general feeder, was essentially random on avocado, but that of the prey, *Oligonychus punicae*, was more clumped. In experiments with *T. pyri* and *A. potentillae*, van de Vrie and Backels (1968) found no close correlation between the presence of prey and the occurrence of predators, on an individual leaf basis, although the predators suppressed the prey populations (see also Kropeczyńska and van de Vrie, 1965).

Certain conditions may be sought for oviposition sites. In some cases, as with *Typhlodromus occidentalis* and *Phytoseiulus persimilis*, the preferred site seems to be in the midst of the prey colony itself, which seems ideal since the immature stages would not have to travel far to find prey. On the other hand, *Amblyseius hibisci* seems to prefer to lay its eggs on the undersides of leaves affording maximum shading and

protection, such as those that are somewhat curled downward (McMurtry and Johnson, 1966). These progeny may be wasted because such leaves often contain no prey. Thus a numerical response may not begin until the prey density is quite high. Intraleaf and intratree distribution of phytoseiids in relation to predation potential is further discussed in the second paper of this series.

It is not surprising that behavior may be different under different physical conditions, such as temperature and humidity. Mori and Chant (1966b) found that *Phytoseiulus persimilis* as well as the prey, *Tetranychus urticae*, was more active at low than at high humidities. The prey tended to avoid high humidities, but the predator did not. The increased activity at the lower humidities resulted in a higher rate of prey consumption than occurred at the high humidity. Begljarov (1967) also found a higher rate of consumption by *P. persimilis* at low humidity, but a lower rate of oviposition. This may be related to water balance. On excised leaves, *Amblyseius limonicus* was observed to lay eggs in close proximity to the water-saturated, cellulocotton barriers placed around the periphery of the leaves. A high humidity is necessary for hatching of this species (McMurtry and Scriven, 1965).

Natural Enemies of Phytoseiids

Published reports on the enemies of phytoseiids have for the most part been based on only limited observations. The staphylinid beetle *Oligota pygmaea* Sol. and the coccinellid *Stethorus punctillum* Weise were observed to attack phytoseiids (Bravenboer, 1959; Gonzalez, 1961). Chant (1956b) reported that several species of spiders would feed on phytoseiids in apple orchards in England. Phytoseiids were also observed to be attacked by the mirids *Blepharidopterus angulatus* (Fall.), in England (Collyer, 1952), and *Diaphnidia pelucida* Uhl. in Canada (Herbert, 1962a).

Adults of the six-spotted thrips, *Scolothrips sexmaculatus* (Pergande), were observed feeding on eggs of *Phytoseiulus persimilis* (Oatman, personal communication).

The most extensive study on natural enemies of phytoseiids was conducted in Germany by Krämer (1961) who found that 38 species of arthropods on apples would feed on the predaceous mites. *Orius minutus* L. was considered the most important, followed by *Chrysopa vulgaris* Schneid. and *Anthocoris nemorum* L. In a field experiment, trees were artificially infested with either *Typhlodromus pyri* or both *T. pyri* and *O. minutus*. The data indicated that *T. pyri* was markedly reduced by *O. minutus*, but in the second year, densities of *Panonychus ulmi* were lower on the trees stocked with both predators than on those stocked with the phytoseiid only. This suggests that the combined action of the two predators, in

spite of the predation of *O. minutus* on *T. pyri*, was more efficient than that by *T. pyri* alone. Nevertheless, Krämer concluded, perhaps erroneously, that the reduction of *T. pyri* by *O. minutus* was of such importance that it could prevent control of spider mite populations by *T. pyri*. He also believed that reductions in numbers of phytoseiids on fruit trees, such as reported by Collyer (1956), Berker (1958), Chant (1959), Redenz-Rüsh (1959), and Dosse (1960) are related to the activity of insect predators rather than to the reasons mentioned by some of these authors, e.g., "natural mortality" and dispersal onto newly developing leaves. Dosse (1962) discussed the work of Krämer (1961) and Berker (1958), stated that *O. minutus* is an important predator of *T. pyri* on apple, and claimed that it prefers phytoseiids to other kinds of prey, such as spider mites and aphids.

OTHER ACARINA

A number of other predatory Acarina that commonly feed on tetranychids are found in the Bdellidae, Trombidiidae, Anystidae, Stigmaeidae, and probably also in the Cheyletidae.

Anderson and Morgan (1958b) stated that an unidentified bdellid was the most important predator of clover mite, *Bryobia praetiosa* Koch, on orchard covercrops and the trunks of trees in British Columbia, but never on tree foliage. Snetsinger (1956) considered *Bdella depressa* Ewing an important enemy of clover mite in grassy areas in the midwestern United States. Gonzalez (1961) reported that *Cyta* sp. attacked overwintering *Tetranychus urticae* at the bases of tree trunks in Chile.

Among the Trombidiidae, a species of *Allothrombium* was reported to be predatory on *Eutetranychus banksi* in the southwestern United States (Dean,

1952). *A. fuliginosum* Herm. has been collected in orchards in Europe, but actual feeding on spider mites was not reported (Redenz-Rüsh, 1959; Post, 1962).

The Anystidae were listed as probable mite predators by Ewing (1914) and Gilliatt (1935) in North America, and by Berker (1958), Redenz-Rüsh (1959), and Post (1962) in Europe. They apparently have a wide range of prey, however, and are seldom abundant in tetranychid infestations. Garman and Townsend (1938), Lord (1949), and Putman and Herne (1966) report *Anystis* spp. feeding on *Panonychus ulmi*. Lord considered their value in control of any one species to depend on the numerical relationships of all the species on which they feed. Putman and Herne also observed *Balaustium* sp. to attack all stages of *P. ulmi* and also eggs of some insects. They were

quite abundant in some orchards, but had a slow rate of increase, with only two generations per year.

Various species of predatory mites of the family Stigmaeidae prey on tetranychids. Because there was considerable confusion in the generic categories until recently, the literature is rather difficult to appraise. Taxonomic revisions by Summers (1960) and Gonzalez (1965) have considerably clarified the situation, and their nomenclature is used here. Accordingly, *Zetzellia* is used for certain species formerly referred to under *Mediolata*.

Zetzellia mali (Ouds.) has been reported as a predator of tetranychids in both North America and Europe. Lord (1949) called this species *Mediolata nova-scotiae* Nesbitt (see Gonzalez, 1965), and considered it an important predator of the clover mite in Nova Scotia, but stated that it could not by itself keep the pest in check. Parent and LeRoux (1956) and Parent (1967) concluded from studies in Quebec that it preyed on both *Tetranychus urticae* and *Panonychus ulmi* on apples, but had a more important controlling effect on the latter. Studies in the northwestern United States by Hoyt (1969a) indicated that *Z. mali* was sometimes responsible for maintaining the apple rust mite, *Aculus schlechtendali*, at low densities. *Z. mali* also occurs in orchards in Europe, sometimes in high numbers (Berker, 1958; Redenz-Rüsh, 1959; Böhm, 1960; Post, 1962). Its biology was studied in Germany by Berker (1958). He found that a wide range of food was acceptable, including various tetranychids, eriophyids, the acarid *Czenspenskia lordi*, and pollen. Two generations per year occur, and when food becomes scarce on the foliage in the fall, they may consume aphid eggs and winter eggs of tetranychids. Böhm (1960) also observed two generations per year in Austria. At 25°C, with *Panonychus ulmi* as food, females laid an average of 26 eggs during their life

span. Dosse (1967) lists both *Z. mali* and *Z. talhouki* Dosse as predators of spider mites in Lebanon.

The genus *Agistemus* also includes species known to feed on spider mites. These include *A. fleschneri* Summers on *Panonychus ulmi* in Wisconsin (Oatman, 1963), on *Tetranychus cinnabarinus* (Boisd.) on cotton in Egypt (Zaher and El Badry, 1962), and *T. kanzawai* Kishida on tea in Japan (Osakabe, 1963); *A. floridanus* Gonzalez on *Eotetranychus sexmaculatus* on citrus in Florida (Muma, 1961a, 1965b); *A. exsertus* Gonzalez (see Gonzalez, 1965) on *P. citri* in Japan (Tanaka, 1966); *A. fanari* Dosse on tetranychids in Lebanon (Dosse, 1967); *A. longisetus* Gonzalez on *P. ulmi* and *Bryobia rubrioculus* in New Zealand (Collyer, 1964c). Collyer found *A. longisetus* to reproduce very rapidly and at times, in late summer, to outnumber the phytoseiid predator *Typhlodromus pyri* in some locations. Collyer observed that *A. longisetus* is not self-limiting at relatively low densities, as she had suggested is the case for some *Typhlodromus* species (see also Putman and Herne, 1964). In the laboratory during the summer, *A. longisetus* laid an average of five eggs per day and required 23 days to develop from oviposition to the adult stage. Muma (1965b) observed a "weak lag effect" between *Agistemus* spp. and *Eutetranychus banksi* (McGregor) on Florida citrus.

Agistemus species may also be associated with other groups of mites. Muma (1961a) found *A. floridanus* to feed on tarsonemids and tydeids. Collyer (1964c) observed *A. longisetus* to lay eggs when fed *Brevipalpus* sp. or certain tydeids, and McMurtry (unpublished data) found *A. terminalis* (Quayle) on avocado to be more closely associated with tydeids than tetranychids and he observed no increase in this species when the tetranychid *Oligonychus punicae* became abundant.

On the basis of our present knowl-

edge of the Stigmaeidae, these mites are apparently rather general feeders, of questionable importance in the control of tetranychids. More detailed studies are needed to determine if they have a potential for the control or regulation of tetranychid populations.

Mites in the family Cheyletidae have

also been seen feeding on spider mites. *Paracheyletia bakeri* Ehara fed and reproduced on three species of spider mites and also on scale crawlers in the laboratory, but this predator was considered a negligible factor in the biological control of mites on citrus in Florida (Kanavel and Selhime, 1967).

ARANEIDA

Although spiders are predaceous and almost ubiquitous, very few studies have been made of their potential as mite predators. Chant (1956b, 1957a) recorded more than 30 species predatory on phytophagous mites in English apple orchards, of which three families were most important: Argiopidae, Theridiidae, and Linyphiidae. Only the small species and immature forms fed readily on orchard mites. Dondale (1956, 1958) reported on the spider fauna of deciduous fruit orchards in Nova Scotia and in the Australian Capital Territory, Australia. Legner and Oatman (1964) surveyed the spider populations in Wisconsin apple orchards, and Specht and Dondale (1960) presented records from New Jersey orchards.

In his studies on the fauna of apples in Japan, Hukusima (1961) reported 36 species of spiders, and Hukusima and Kondo (1962) placed considerable emphasis on their presence. The evidence from these studies, however, can be considered only as an incentive to further research. Lord (1949) observed spiders

feeding on *Panonychus ulmi* in Nova Scotia. McMurtry and Johnson (1966) observed a species of Micyrphantidae feeding on *Oligonychus punicae* on avocado, but predator numbers did not increase with increases in mite density. Putman and Herne (1966) found, by paper chromatography, that most small spiders collected in peach orchards in Ontario, Canada, had fed on *P. ulmi* when the latter's density was high. They noted a functional response but no numerical response to increasing density of *P. ulmi* or *Bryobia rubrioculus* (= *B. arborea*). Putman (1967) found that *Philodromus* spp., and sometimes *Theridion murarium* Emerton, were the only abundant spiders in peach orchards in Ontario, and that the percentage that had fed on spider mites increased with density. He concluded, however, that the spiders formed only a part of the minor complex of enemies that aid the major predators in controlling spider mites (see second paper in this series). Evidence that spiders have any major importance in the control of tetranychids is thus lacking.

COLEOPTERA

The order Coleoptera contains a number of important mite predators that

occur mainly in two families, the Coccinellidae and Staphylinidae.

Coccinellidae

Stethorus

This genus apparently contains only predators of mites. There are no reports of their reproduction on any foods other than mites. They are worldwide

in distribution, being commonly found in situations where tetranychids are abundant. References to their effects on mite populations are too numerous to cite and only representative references

are given here. Many *Stethorus* are relatively small and remarkably well adapted to live and search for prey in the microenvironments of tetranychids. They require much less food than many of the larger insectan predators of spider mites, and thus should be effective at lower prey densities (see second paper in this series).

Occurrence on crops. *Stethorus picipes* Casey has been reported as a common predator of tetranychids in the United States: in California, on citrus (Quayle, 1912; Fleschner, 1958*b*), avocado (Fleschner, Hall, and Ricker, 1955; Fleschner, 1958*b*; McMurtry and Johnson, 1966); walnuts (Michelbacher, 1959), and melons (Michelbacher, Middlekauff, and Bacon, 1952); and in the Pacific Northwest on apples (Newcomer and Yothers, 1929).

Stethorus punctum Leconte is a common predator of tetranychids on deciduous fruits in North America (Gilliatt, 1935; Garman and Townsend, 1938; Robinson, 1952; Clancy and McAlister, 1956; Anderson and Morgan, 1958*b*; and Cutright, 1963).

Stethorus punctillum Weise (= *Scymnus punctillum* = *Scymnus minimus* = *Stethorus minimus*) is an Old World species that has long been considered an important predator of *Panonychus ulmi* in Europe, e.g., in such countries as Austria (Böhm, 1960), England (Collyer, 1953*a*), Finland (Listo, Listo, and Kanervo, 1939), Germany (Andersen, 1947; Berker, 1958), Netherlands (Geijskes, 1938; Kuenen, 1947), Switzerland (Günthart, 1945), U.S.S.R. (von Vitzthum, 1943), and also in New Zealand (Cottier, 1934). It has also been reported to have become dominant over *S. punctum* in a relatively short time in certain areas of Ontario, Canada (Brown, 1950; Putman, 1955). *S. punctillum*, as well as the phytoseiid *Typhlodromus longipilus*, persists naturally as a predator of *Tetranychus urticae* in greenhouses in the Netherlands (Bravenboer, 1959). Bravenboer con-

sidered *Stethorus* to be of more value than the phytoseiid in suppressing *T. urticae* on fruit in greenhouses. *S. punctillum* was also considered capable of quick reduction of spider mites on citrus in Anaseuli, U.S.S.R. (Siharulidze, 1962). Plaut (1965) considered the same species an important predator of *T. cinnabarinus* (= *telarius*) on beets in Israel. Absence of *S. punctillum* was correlated with high densities of the pest mite.

Stethorus utilis Horn is considered a major predator of the six-spotted mite, *Eotetranychus sexmaculatus*, in Florida (Muma, 1958), and *S. atomus* Casey feeds on *Eutetranychus banksi* and *Oligonychus pratensis* in Texas (Dean, 1957).

Stethorus japonicus Kamiya was reported by Tanaka (1966) to be the most efficient of all the predators on *Panonychus citri* in citrus groves in Kyushu, Japan, although Nakao (1964) considered the endomychid beetle *Saula japonica* Gohrman the most important on that species in Fukuoka (p. 357).

Rymasevskaja (1964) found, but did not identify, a species of *Stethorus* to be important in control of mites on fruit trees in Tambow, U.S.S.R.

Cottier (1934) reported *Scymnus minutulus* Brown, thought by Kapur (1948) to be *Stethorus bifidus* Kapur, predatory on *Panonychus ulmi* in New Zealand. Collyer (1964*c*) found *S. bifidus* to be the most abundant insect predator of tetranychids in and around orchards there.

Stethorus gilvifrons Muls. in Lebanon was considered by Dosse (1967) and Kaylani (1967) to be an important predator of spider mites on a variety of crops.

Biology and ecology. Biological studies have been conducted on a few species of *Stethorus*. Development proceeds from the egg, through four larval instars and a pupal stage, to the adult (Fleschner, 1950; Robinson, 1953; Putman, 1955; Bravenboer, 1959; Collyer,

TABLE 5
SOME OBSERVED DEVELOPMENTAL RATES OF *STETHORUS* SPECIES

Species	Temperature	Time from egg to adult	Reference
	° C	days	
<i>S. punctillum</i> Weise.....	19	29.2	Berker, 1958
	25	19.3	Berker, 1958
	35.6	12.8	Berker, 1958
	21	21.1	Putman, 1955
	26 to 28	15.2	Putman, 1955
	22 to 24	19.4	Putman, 1955
	20	20	Bravenboer, 1959
<i>S. punctum</i> LeConte.....	26.7	14.5	Robinson, 1953
<i>S. gilvifrons</i> Muls.....	20	28.3	Kaylani, 1967
	25	18.2	Kaylani, 1967
	29.7	14.5	Kaylani, 1967

1964c; Kaylani, 1967). Some data on rates of development are shown in table 5. It is evident that development may be completed in less than two weeks, at high temperatures (Berker, 1958), while at moderate temperatures the average time appears to be about three weeks. Under comparable conditions, spider mites generally complete development in a shorter time. Bravenboer (1959) compared development of *S. punctillum* and the prey *Tetranychus urticae* at 20°C and found that the latter developed in 14 days, or about six days faster than the predator.

The *Stethorus* species have a relatively long oviposition period, lay large numbers of eggs per female, and have a potentially high daily oviposition rate when food is abundant (table 6).

Sex ratios of the species of *Stethorus* studied appear to be about 1:1, and periodic matings are required for continued production of fertile eggs (Putman, 1955; Kaylani, 1967).

The manner in which *Stethorus* consumes mites has been described by Fleschner (1950), Robinson (1953), Collyer (1953a), Putman (1955), and Kaylani (1967). The consumption capacity is high (table 7). The daily rate of prey consumption of ovipositing females may exceed 40 adult or large, immature spider mites, and that of fourth-instar larvae may be even higher, with the total consumption during larval development being in excess of 200 mites in most cases. If only eggs or small, immature stages of the prey are given, much larger numbers are

TABLE 6
SOME DATA ON FECUNDITY OF *STETHORUS* SPECIES

Species	Temperature	Oviposition period	Eggs per ♀ per day	Total eggs per ♀	Reference
	° C	days			
<i>S. punctillum</i> Weise....	21.1	..	11.7	..	Putman, 1955
<i>S. punctillum</i> Weise....	Insectary, July	45 to 123	..	743 to 1,290	Putman, 1955
<i>S. punctum</i> LeConte....	26.7	..	4 to 10	..	Robinson, 1953
<i>S. bifidus</i> Kapur.....	..	61 to 69	6*	308 to 438	Collyer, 1964c
<i>S. bifidus</i> Kapur.....	..	17 to 28	2†	24 to 67	Collyer, 1964c
<i>S. gilvifrons</i> Muls.....	25	..	5.6	..	Kaylani, 1967
<i>S. gilvifrons</i> Muls.....	..	32 to 42	8.4	250+	Dosse, 1967
<i>S. picipes</i> Casey.....	23	..	6	..	McMurtry and Sandness (unpublished)

* Fed 40 mites/♀/day.

† Fed 20 mites/♀/day.

TABLE 7
SOME RECORDS OF PREY CONSUMPTION CAPACITY OF *STETHORUS*

Species	Temperature	Prey consumed	Prey species*	Reference
Adults:				
	° C			
<i>S. punctillum</i> Weise ♀	16 to 21	40/day	<i>Tetranychus urticae</i>	Putman, 1955
<i>S. punctillum</i> ♂	16 to 24	20/day	<i>T. urticae</i>	Putman, 1955
<i>S. punctillum</i>	..	20/day	<i>Panonychus ulmi</i>	Collyer, 1953a
<i>S. bifidus</i> Kapur ♀	..	40 to 60/day	<i>P. ulmi</i>	Collyer, 1964c
<i>S. gilvifrons</i> Muls. ♀	25	38.7/day	<i>T. cinnabarinus</i>	Kaylani, 1967
<i>S. gilvifrons</i> ♂	25	18.5/day	<i>T. cinnabarinus</i>	Kaylani, 1967
Larvae:				
<i>S. punctillum</i>	..	238.6	<i>T. urticae</i>	Putman, 1955
<i>S. punctillum</i>	22	250	<i>T. urticae</i>	Bravenboer, 1959
<i>S. punctillum</i>	..	640	<i>T. urticae</i> eggs	Radzievskaja, 1931
<i>S. punctillum</i>	..	160	<i>T. urticae</i> adults	Radzievskaja, 1931
<i>S. punctillum</i>	..	24/day	<i>P. ulmi</i>	Collyer, 1953a
<i>S. japonicus</i> Kamiya	..	771	<i>P. citri</i> eggs	Tanaka, 1966
<i>S. gilvifrons</i>	25	161 to 221	<i>T. cinnabarinus</i>	Kaylani, 1967
<i>S. gilvifrons</i>	25	27 to 47/day†	<i>T. cinnabarinus</i>	Kaylani, 1967
<i>S. picipes</i> Casey	26.7	247 to 486	<i>P. citri</i>	Fleschner, 1950
<i>S. picipes</i>	26.7	94 to 190†	<i>P. citri</i>	Fleschner, 1950
<i>S. picipes</i>	26.7	47 to 95/day†	<i>P. citri</i>	Fleschner, 1950
<i>S. picipes</i>	..	291 to 372	<i>P. ulmi</i>	Newcomer and Yothers, 1929

* Adults and/or deutonymphs unless otherwise specified.

† Fourth instar only.

required. Tanaka (1966) found that *S. japonicus* needed at least 50 to 100 eggs or 15 to 17 adults of *Panonychus citri* per day for oviposition.

Prey preferences within the tetranychids have not been adequately studied although Putman (1955) found that *Stethorus punctillum* did not readily feed on *Bryobia*, and Kaylani (1967) found that oviposition of *S. gilvifrons* ceased when they were given *Bryobia* for food. Various species have been observed to attack other kinds of prey in the laboratory when spider mites were not available, including phyto-seiids (Putman, 1955; Kaylani, 1967), and aphids (Putman, 1955). But neither oviposition nor development on any food other than mites has been reported. Cannibalism has been observed when mites are scarce (Collyer, 1953a; Putman, 1955; Kaylani, 1967). Putman found that raisins, nectar, and honeydew were utilized by *S. punctillum*, thus prolonging survival in the absence of other food.

The seasonal life history of *Stethorus* species is affected by climate. *S. punctil-*

lum has been studied by several workers in temperate climates. This species hibernates as an adult and has two or three generations per year (Collyer, 1953a; Putman, 1955; Berker, 1958). Putman found that some females live longer than one year. Species with a range that includes both temperate and subtropical climates may hibernate in the colder area but not in the warmer. For example, *S. gilvifrons* was observed to enter hibernation in the higher elevations in Lebanon, but in the mild coastal area it was active all year (Dosse, 1967; Kaylani, 1967). *S. picipes* can be found in all stages and in high numbers on certain plants, such as *Ricinus communis* L., in midwinter in coastal southern California (McMurtry, unpublished), although its range reportedly extends into Washington where it presumably enters hibernation (Newcomer and Yothers, 1929). A similar phenomenon seems to occur with *S. bifidus* in New Zealand (Collyer, 1964c).

Behavioral studies have been conducted by Fleschner (1950) for *Ste-*

thorus picipes and by Putman (1955) for *S. punctillum*. *S. picipes* larvae were found to have an essentially random pattern of searching on universes of uniform light and topography. After encountering and consuming a prey, both species were observed to search more intently in the immediate vicinity, but the prey was detected only by actual contact. *S. picipes* exhibited a positive phototropism, in this respect corresponding closely to the behavior of its prey, *Panonychus citri*.

The eggs of *Stethorus* are generally deposited in the midst of the mite colonies (Putman, 1955; Berker, 1958; Bravenboer, 1959; Böhm, 1960; Dosse, 1967). Some host plants may not be favorable even if infested by a suitable prey species. Some varieties of beans may support adults, but because of the hooked trichomes, the larvae may be killed or greatly impeded in their movement (Günthart, 1945; Putman, 1955; Berker, 1958; Bravenboer, 1959; Plaut, 1965). This has also been observed for other coccinellids (de Fluiter and Ankersmit, 1948).

Research has shown that *Stethorus* species are specialized predators of spider mites, commonly associated with high populations on many crops. In many cases, however, they probably do not exert a suppressive effect on the population before the economic level is exceeded. This can be attributed largely to the fact that high densities of prey are generally required before the predators begin to increase in numbers (Kuenen, 1947; Clancy and Pollard, 1952; Putman, 1955). (See second paper in this series.) Another factor may also be important. Since *Stethorus* will not remain in an environment when mites are extremely scarce, a subsequent response to increasing mite densities will depend partly on migration from other reservoirs. If such reservoirs are scarce because of intensive cultivation and/or use of pesticides, the chances of large numbers of immigrants reaching an in-

creasing tetranychid population at an early stage become remote (Putman, 1955; Herne and Putman, 1966).

Stethorus species may be important controlling factors in certain cases, however. McMurtry and Johnson (1966) rated *S. picipes* as the "key predator" in suppressing infestations of *Oligonychus punicae* on avocados in southern California. There was a consistent correlation between numbers of *Stethorus* in the early part of the increase cycle of the prey and the peak density of the latter. When *S. picipes* showed a marked numerical response to increases of *O. punicae* while populations of the latter were still at low to moderate densities, control resulted before severe leaf bronzing occurred. Conversely, when severe bronzing occurred, *S. picipes* had been slow to increase in response to increases of the mite population. McMurtry and Johnson suggested that properly timed mass releases of *S. picipes* might result in better control of *O. punicae* in situations where the natural build-up of *Stethorus* populations was slow. McMurtry, Johnson, and Seriven (1969) conducted replicated field experiments in avocado orchards having a history of heavy infestations of *O. punicae*, and found that mass releases of *S. picipes* did result in an earlier build-up of the coccinellid population and lower peaks of *O. punicae* as compared with "check" plots where no releases were made.

McMurtry and Johnson (1966) pointed out that *Stethorus picipes* could be an effective predator of *Oligonychus punicae* on avocados, since its "high density" control was sufficient to prevent excessive damage to the trees, which can tolerate relatively high densities of this mite. The same level of control might be insufficient to prevent serious damage with other species of mites on other crops. Also, there are indications that *Stethorus* species may be important if the spider mite prey are either concentrated on certain parts of

a tree or even dispersed, but in substantial colonies. Thus, the predators have access to high local densities of prey even though the average density is still quite low (Putman, 1955; Putman and Herne, 1966). Hand-removal experiments by Fleschner (1952, 1958a) in California have also demonstrated the importance of *S. picipes* in suppressing *Panonychus citri* on citrus in some instances.

Other Coccinellids

Some of the larger coccinellids, although not primary predators of mites, may occasionally exert a suppressive effect. *Hippodamia convergens* Guér. and *Olla abdominalis* (Say) have been observed feeding on heavy populations of spider mites (Dean, 1957). Gravid females moving in from other plants may lay eggs, and the resulting larvae may be numerous enough to affect the

density of the mite population (Fleschner, 1958b). Gonzalez (1961) lists three species of *Adalia*, and single species each of *Eriopis*, *Psyllobora*, and *Scymnus* as predatory on *Bryobia rubrioculus* (= *B. arborea*) in Chile.

Several workers have reported a number of species of larger coccinellids preying on tetranychids on deciduous fruits in Europe and North America (Ross and Robinson, 1922; Lord, 1949; Collyer, 1953a; Berker, 1958; Redenz-Rüsh, 1959; Post, 1962; Niemczyk, 1966), but none was considered important. Anderson and Morgan (1958b) list six species seen feeding on *Bryobia*. Citrus red mite is preyed on by certain species (Selhime, 1956; Fleschner, 1958b). Kamiya (see H. Mori, 1967) and Muma (1955b) report the feeding of several species on tetranychids under laboratory conditions.

Staphylinidae

In this family, members of the genus *Oligota* (= *Somatium*) (= *Holobus*) are predators of spider mites. Observations or studies have been made on only a few species, and these seem to be specialized mite feeders. *Oligota flavicornis* Boisd. is a predator of tetranychids in deciduous fruit orchards in Europe (Listo, Listo, and Kanervo, 1939; Collyer, 1953a; Berker, 1958). Günthart (1945) reported *O. pusillima* (Grav.) predaceous on tetranychids in Switzerland. In his review, H. Mori (1967) cites reports of *O. oviformis* (Casey) and *O. flavicornis* preying on *Panonychus citri*, and *Oligota* sp. feeding on *P. ulmi* in Japan. *O. oviformis* is a common predator of spider mites on subtropical crops in California (Quayle, 1912; Ewing, 1914; Badgley and Fleschner, 1956; Fleschner, 1958b). *Oligota* (= *Holobus*) *pygmaea* Sol. is considered a major predator of spider mites on apples and other crops in Chile (Gonzalez, 1961).

The biology of *Oligota flavicornis* was studied by Collyer (1953a). Larval development requires eight to 15 days, after which the insect drops from the tree to pupate just below the surface of the ground. Females in the laboratory lived up to five weeks and laid from 40 to 50 eggs. Eggs hatched in four to seven days, and the life cycle from egg to adult averaged 28 days. Both adults and larvae preferred active stages of spider mites to eggs. Only one complete, and a partial second, generation occurred in England. Overwintering takes place in the adult stage. Collyer indicated that *O. flavicornis* was of little value in the control of spider mites in orchards in England. Berker (1958) reached similar conclusions about its value in orchards in Germany.

Badgley and Fleschner (1956) studied the biology of *Oligota oviformis*. At 80°F, the incubation period was four days. The larva, after feeding for a

minimum of four days, seeks a pupation site in the soil and spins a cocoon in which it remains in a prepupal state for several days. The total time in the larval and prepupal stage ranged from eight to 13 days, and the pupal stage lasted nine to 13 days. The oviposition period was about 30 days, and a single female was capable of producing more than 300 eggs, with as many as 16 being deposited in a 24-hour period. Quayle (1912) found that larvae consumed an

average of 20 spider mites per day, for a total of 200 to 300, while the adults averaged about 10 per day. Because this species is quite erratic in abundance, its value on citrus and avocado is rather limited (Fleschner, 1958*b*; McMurtry and Johnson, 1966). Badgley and Fleschner (1956) indicated that it was of less value on citrus than on avocado, because in the former crop, clean cultivation is practiced, which tends to destroy many of the pupae in the soil.

Endomychidae

Nakao (1964) reported that *Savila japonica* Gorham was the most important among the predators of *Panonychus citri* in an orchard in Fukuoka,

Japan. Its potential for suppressing the mite populations was apparently greatest in the autumn.

NEUROPTERA

Chrysopidae

As a rule, the chrysopids are considered to be mainly aphid predators (R. C. Smith, 1922), but many are general feeders and they will consume spider mites.

Chrysopa carnea Stephens (= *C. californica* = *C. plorabunda*) is a general predator which has been observed to prey on spider mites in both North America and Europe. It is listed as a predator of *Panonychus ulmi* in deciduous fruit orchards in Canada (Putman and Herne, 1958, 1966), the United States (Huffaker and Spitzer, 1950), England (Collyer, 1953*b*), and Finland (Listo, Listo, and Kanervo, 1939), and has been collected in orchards in Poland (Niemyzyk, 1966), Netherlands (Post, 1962), and Germany (Redenz-Rüsh, 1959). Spider mites are not its preferred prey, and it is usually not considered important in suppressing them. Mass releases of *C. carnea* eggs on pears in California resulted in a significant reduction of *Panonychus ulmi* but failed to prevent economic loss (Huffaker and Spitzer, 1950). However, Putman and Herne (1966) believed

that this species may be an important member of the complex of predators that apparently maintains *P. ulmi* at low densities on peaches in Ontario, Canada.

Chrysopa carnea is also found commonly on citrus and avocado in southern California. Its effect on mites appears to be greatest when it has been attracted to other prey and the larvae linger on after those prey have declined to low numbers (Fleschner, 1958*b*).

Several other chrysopids, including *Chrysopa perla* L., *C. vulgaris* Schneider, *C. humili* L., and *C. septempunctata* Wesm. were reported to feed occasionally on tetranychids in Germany (Berker, 1958) and Austria (Böhm, 1960). H. Mori (1967) cites references to two *Chrysopa* species feeding on *Panonychus ulmi* and *P. citri* in Japan. *C. lateralis* Guér. is a trash-carrying species found on citrus in Florida. It readily develops when feeding on the six-spotted mite, *Eotetranychus sexmaculatus* (Muma, 1957). Lord (1949) found that chrysopids are often the first predators to reappear in Nova

Scotia apple orchards treated with DDT, and he rated them important in the fall, at which time they fed on overwintering eggs of *P. ulmi*.

Detailed biologies of the Chrysopidae were published by R. C. Smith (1922) and Killington (1936). Several species studied in relation to spider mites were observed to complete development on mites alone. These include *Chrysopa carnea* (Fleschner, 1950; Putman and Herne, 1966), *C. vulgaris* (Berker, 1958), *C. rufilabris* Burm. (Putman and Herne, 1966), and *C. lateralis* (Muma, 1957). In the latter case, six-spotted mites were more favorable than other prey tested, and the developmental time from egg to adult at 80° F averaged 30 days. On the other hand, Huffaker and Spitzer (unpublished data) found that when released as eggs in pear orchards, very few *C. carnea* completed development in the field on *Panonychus ulmi* alone. Chrysopid larvae are voracious feeders. Last-instar larvae of *C. carnea* consumed an average of 1,000 to 1,500 citrus red mites daily, and completed larval development in 13 to 19 days at 26.7°C (Fleschner, 1950). *C. vulgaris* larvae consumed an average of 30 to 50 *P. ulmi* per hour, and required 18 and 31 days to complete development at 35.6° and 25°C, respectively (Berker, 1958). Fleschner (1950) showed that *C. carnea* larvae had a considerably greater searching

capacity than either *Stethorus picipes* or a coniopterygid studied. Using paper chromatography, Putman and Herne (1966) confirmed that *C. carnea* larvae may attack *P. ulmi* in orchards at extremely low mite densities.

The adults of some chrysopids are carnivorous, but others seem to feed only on free liquid nutrient (R. C. Smith, 1922). The latter habit is generally assumed to be true of *Chrysopa carnea*, although Collyer (1953b) reports that this species will feed on winter eggs of *Panonychus ulmi*. Longevity and egg production of *C. carnea* are high when only honeydews (Hagen, 1950) or a combination of honeydew and pollen (El Badry and Fleschner, 1965) are fed. *C. carnea* thrives on synthetic diets, on which the females are highly fecund. Hagen (1950) obtained 18,000 eggs from 30 females in 46 days, when they were fed a diet of protein hydrolysate and honey.

Larvae of *Chrysopa carnea* have also been reared on a synthetic diet (Hagen and Tassan, 1965).

The chrysopids are attacked by parasites, most of which emerge from the pupa (R. C. Smith, 1922; Clancy, 1946; Muma, 1959). Clancy indicated that in California, parasitism generally had little effect on the average density, although McGregor (1914) reported a high parasitization.

Hemerobiidae

This is another group of general predators that have been observed feeding on tetranychids, but to no significant extent.

Collyer (1953b) observed adults and larvae of *Hemerobius humulinus* L. and *H. lutescens* Fab. feeding on *Panonychus ulmi* in England, and Putman and Herne (1966) made similar observations for *H. humulinus* and *H. stigmatarius* Fitch in Ontario, Canada. Several species were also observed in deciduous

fruit orchards in Europe by Berker (1958), Redenz-Rüsh (1959), and Post (1962), but no observations were reported on their feeding habits. *H. pacificus* Banks was found to feed on the two-spotted mite and citrus red mite in California (Quayle, 1912; Ewing, 1914; Moznette, 1915). Quayle included some information on the biology of this species. The biology of the Hemerobiidae was covered, in general, by Killington (1936).

Coniopterygidae

The coniopterygids also apparently have rather general feeding habits, but some seem to utilize spider mites to a considerable degree. Three species commonly occur on citrus in California: *Parasemidalis flaviceps* Banks; *Conwentzia nigrans* Carpenter; and *Coniopteryx angustus* Banks (Fleschner and Ricker, 1953b; Fleschner, 1958b). Under certain conditions, these species appear to be important enemies of citrus red mite (DeBach, Fleschner, and Dietrick, 1950; Fleschner, 1958b). *Coniopteryx vicina* Hagen feeds on the citrus rust mite, *Phyllocoptera oleivora* (Ashmead), and the six-spotted mite, *Eotetranychus sexmaculatus*, on citrus in Florida (Muma, 1955a, 1967b).

Putman and Herne (1966) found that both *Coniopteryx vicina* and *Conwentzia hageni* Banks showed some numerical response to increases of *Panonychus ulmi* on peaches in Ontario, Canada, but never occurred in large numbers. Withycombe (1924) liberated pupae of *Conwentzia psociformis* (Curt.) on fruit trees and reported success in reducing red spider mite populations until the following year, when a parasite, *Lygocerus* sp., reduced their numbers.

Collyer (1951) observed that *Conwentzia pineticola* End. and *C. psociformis* preyed mainly on *Panonychus ulmi* in orchards in England, but were associated only with outbreaks of the pest. In one orchard, *C. pineticola* was observed to be active until the end of December, and greatly reduced the winter egg population of *P. ulmi* (Collyer, 1953c). Listo, Listo, and Kanervo (1939) also mentioned the irregular occurrence of this predator in orchards in Finland. Agekyan (1965) reported that *C. psociformis* fed on all stages of *P. citri* in Georgia, U.S.S.R., but that it was highly polyphagous. He believed, however, that it was a significant member of the complex of predators. Two

additional species, *Coniopteryx tineiformis* Curt. and *Semidalis aleyrodiiformis* (Steph.) were also mentioned by Collyer (1951) as predators of *P. ulmi* in severe infestations.

H. Mori (1967) lists *Semidalis albata* End. as a predator of *Panonychus ulmi* and *P. citri* in Japan.

The food habits of the three commonest coniopterygids on California citrus were studied by Fleschner and Ricker (1953b). Attempts to rear the larvae on spider mites alone were unsuccessful, but all three species developed readily on scale crawlers or eggs of the potato tuberworm moth, *Pthorimaea operculella* (Zeller). Adults failed to reproduce on spider mites or scales alone, but oviposited readily if either of these prey species was offered in combination with honey. Field observations indicated that feeding occurred on armored- or soft-scale crawlers, nectar, and honeydew, as well as on tetranychid and eriophyid mites. The coniopterygids appeared to be important as spider mite predators mainly in orchards with low populations of honeydew-secreting insects.

Collyer (1951) successfully reared *Conwentzia pineticola* on *Panonychus ulmi* in England. She found that the life cycle could be completed in a minimum of 16 days in midsummer, and that females laid an average of five eggs per day, with the observed maximum total egg production being 107. Consumption by adults and third-instar larvae averaged 30 to 40 mites per day. Two complete generations, and a partial third, occurred.

Muma (1967b) found that *Coniopteryx vicina* fed readily on tetranychids and eriophyids, and on whitefly eggs and crawlers. The whiteflies were the most favorable prey for development, an average of 34.3 days being required from egg to adult at 80°F. On the six-spotted mite, *Eotetranychus sexmacu-*

latus, development was completed in an average of 36.4 days, but mortality was high as many larvae became trapped in the webbing. On citrus rust mite, *Phyllocoptruta oleivora* (Ashmead), developmental time averaged 43.5 days at 80°F, and again mortality was high. When fed citrus red mite, *Panonychus citri*, larvae consumed 29 to 83 eggs, larvae, or nymphs during development.

Egg production ranged from two to five per day, with an oviposition period of 16 to 26 days and a maximum fecundity level of 266 eggs. Field data indicated a correlation between abundance in this predator and that of whiteflies, on Florida citrus (Simanton, 1960). General field observations by Muma indicated that the larvae preferred whiteflies and six-spotted mites.

HEMIPTERA

Some crops harbor a large fauna of predaceous bugs, many species of which are known or suspected to feed on spider mites. The majority belongs to two families, the Anthocoridae and Miridae. Rather complete faunistic surveys of this group have been made in apple orchards in Europe and North America, including those of Collyer (1952, 1953*a, b*) in England; Berker (1958) and Redenz-Rüsh (1959) in Germany; Post (1962) in the Netherlands; Niemezyk (1966) in Poland; Listo, Listo, and Kanervo (1939) in Finland; Lord (1949) in Canada; and

Garman and Townsend (1938) in the United States. Few, if any, of these species appear to be specialized predators of mites. In unsprayed orchards where a variety of prey is present, mites may form only a small part of their diets. In sprayed orchards, however, where fewer species of prey occur, the main diet may be mites, because in such orchards the mite populations usually reach high numbers. No complete listing of recorded species is attempted here; only selected examples from various parts of the world are considered.

Anthocoridae

Anthocoris species are known to prey on spider mites. *A. musculus* Say is active throughout the growing season in Nova Scotia, and can reportedly act as a "density-dependent factor" on *Panonychus ulmi*, increasing in response to mite density by reproduction as well as by movement into the orchard (Lord, 1956; Lord, Herbert, and MacPhee, 1958). *A. nemorum* (L.) is reported to feed on *P. ulmi* in orchards in many parts of Europe (Masse and Steer, 1929; Geijske, 1938; Listo, Listo, and Kanervo, 1939; Kuenen, 1942; von Vitzthum, 1943; Günthart, 1945; Andersen, 1947; Berker, 1958; Böhm, 1960; Post, 1962; Niemezyk, 1966). Niemezyk (1966) considered this species especially important in Poland because of its abundance and continued presence

throughout the season. Fritzsche (1958) found *A. nemorum* predatory on *Tetranychus urticae* on beans. It has two complete generations and a partial third per year in England, and the adults overwinter (Collyer, 1953*a*, 1967). Berker (1958) obtained development from egg to adult in 34 and 23 days at temperatures of 20° and 25°C, respectively, whereas Böhm (1960) reported only 16 days at 25°C. Berker (1958) observed that adults destroyed 10 to 20 *Panonychus ulmi* per hour, but Collyer (1953*a*) found that the average was about 50 per day. Collyer also found that the female laid an average of two eggs per day and a total of up to 200. *A. nemorum* is apparently quite polyphagous, and preys on aphids and scale insects as well as spider mites

(Böhm, 1960; Collyer, 1967). Van de Vrie (unpublished) observed that young instars of this species feed readily on *P. ulmi*, whereas the later instars prefer larger prey species, and adults rarely feed on the spider mites.

Orius (= *Triphleps*) species are known to prey on spider mites as well as other small insects, such as thrips and aphids. *O. minutus* L. is listed as a predator of *Panonychus ulmi* by several workers in Europe (Günthart, 1945; Andersen, 1947; Collyer, 1953a; Berker, 1958; Redenz-Rüsh, 1959; Post, 1962). Collyer (1953a) and Berker (1958) indicated that the life history and habits were similar to those of *Anthocoris nemorum*. Collyer observed adults to consume as many as 32 mites in one hour, and Berker obtained an average of 10 to 20 per hour. H. Mori (1967) lists *Orius* sp. as well as *Anthocoris* sp. feeding on *P. ulmi* and *Tetranychus kanzawai* in Japan.

Orius insidiosus (Say) and/or *O. tristicolor* (White) are well known predators in North America. For example, they have been observed feeding on *Tetranychus urticae* on such crops as melons (Michelbacher, Middlekauff, and Bacon, 1952), hops (Ewing, 1914),

strawberries (Allen, 1959a; Oatman and McMurtry, 1966); on *Panonychus ulmi* on deciduous fruits (Newcomer and Yothers, 1929; Putman and Herne, 1966); on *P. citri* on citrus (Quayle, 1912); and on *Tetranychus* sp. on cotton (McGregor and McDonough, 1917; Iglinsky and Rainwater, 1950; Leigh, 1963). Iglinsky and Rainwater considered *O. insidiosus* (Say) the most important natural enemy of tetranychids, in their studies in Texas. Van den Bosch and Hagen (1966) found that *O. tristicolor* (White) occurred most commonly in the buds and flowers in cotton, where it was associated with thrips, but sometimes it was also abundant in spider mite colonies. Observations on the biology of *O. tristicolor* were conducted by Newcomer and Yothers (1929) and Iglinsky and Rainwater (1950).

Putman and Herne (1966) found that *Orius* sp. characteristically showed a numerical response to increasing densities of *Panonychus ulmi* in peach orchards in Canada, but attributed little influence to them because of the low numbers. This is consistent with the opinion of Lord (1949) in reference to apple orchards in Nova Scotia.

Miridae

Blepharidopterus angulatus (Fall.) has received considerable study as a predator of *Panonychus ulmi* in Europe. Collyer (1949, 1960, 1965) and Muir (1965a, b, 1966) conducted detailed studies of its effect on *P. ulmi* populations in commercial apple orchards in England. These papers have been reviewed by Huffaker, van de Vrie, and McMurtry (see second paper in this series). This species has also been reported as occurring in orchards in Germany (Berker, 1958; Redenz-Rüsh, 1959) and the Netherlands (Post, 1962). The biology was studied in some detail by Collyer (1952) and Muir (1965a, b). Eggs are laid in the wood

of the trees from July to October, where they remain imbedded until the following spring. Muir (1965a, b) found that *B. angulatus* eggs hatch four to five weeks later than those of *P. ulmi*; consequently, when the predator does suppress *P. ulmi*, it is not until the second *P. ulmi* generation. The total time required to complete development of the nymphal stages averaged from 35 to 39 days. The average fecundity was 43 eggs over a period of 51 days. During their lifetime, female bugs consumed as many as 4,000 adult mites, averaging up to 50 per day during the adult stage. Collyer observed that *B. angulatus* feeds mainly on *P. ulmi* in commercial

orchards although it will also consume many other mites and small insects, including other predators of mites. It also apparently extracts juices from plant tissue, but no injury was noted.

The biologies of some other common mirids in European orchards have been studied by Collyer (1953*b*) and Berker (1958).

Campylomma verbasei (Mey.-D.) occurs in orchards in both Europe and North America (Garman and Townsend, 1938; Lord, 1949; Collyer, 1953*a*; Berker, 1958). Lord found that its feeding caused damage to apples, but indicated that this was probably balanced by its predation on *Panonychus ulmi*. Anderson and Morgan observed it to feed voraciously on *Bryobia* larvae in the spring, in British Columbia.

Hyaloides harti Knight (= *H. vitripennis*) is a common mirid in apple orchards in parts of North America

(Gilliatt, 1935; Garman and Townsend, 1938; Lord, 1949; Lord, Herbert, and MacPhee, 1958). Lord considered it one of the three important mirids preying on *Panonychus ulmi* in Nova Scotia (along with *Diaphnidia pellucida* Uhl. and *Campylomma verbasei*). Since *H. harti* has only a single generation per year, its numerical response to high mite populations is delayed (Lord, 1956). This permits large fluctuations of the prey where other factors do not intervene (Sanford and Lord, 1962). Sanford and Lord found that this species became the dominant predator in plots receiving perthane treatments, and that it controlled *P. ulmi* in the third and fourth seasons of such treatments. Gilliatt (1935) observed that *H. harti* was quite voracious, a fourth-instar larva consuming 73 mites and eggs in two hours.

Nabidae

There is little information on this group in relation to mites. Several species are recorded from apple orchards in Europe (Collyer, 1953*b*; Berker, 1958; Redenz-Rüsh, 1959; Krämer, 1961; Post, 1962; Niemczyk, 1966).

Berker (1958) and Collyer (1953*b*) studied the feeding habits of *Nabis apterus* Fab., and both authors concluded that although spider mites are eaten, larger prey are preferred.

Lygaeidae

Geocoris species are common in certain field crops in the United States (Essig, 1926). They are known to feed on various kinds of small insects, and

there are some indications that they may have a significant predatory effect on *Tetranychus* on cotton (McGregor and McDonough, 1917; Leigh, 1963).

THYSANOPTERA

Thripidae

The six-spotted thrips, *Scolothrips sexmaculatus* (Pergande), occurs commonly in North America. It appears to be a specialized predator of spider mites, preying on such species as *Panonychus ulmi* on apple (Newcomer and Yothers, 1929; Garman and Townsend,

1938; Lord, 1949); and *Tetranychus* sp. on melons (Michelbacher, Middlekauff, and Bacon, 1952), walnuts (Michelbacher, 1959), and cotton (Lincoln, Williams, and Barnes, 1953; Leigh, 1963; Whitcomb and Bell, 1964; van den Bosch and Hagen, 1966). Lincoln

et al. credited it with preventing a serious outbreak of mites on cotton in Arkansas. This species was the most important of the native predators on *T. urticae* on annual plantings of strawberries in Orange County, California, where it appeared when mite populations were still low, and increased with increases in the pest mite population (Oatman and McMurtry, 1966; Oatman *et al.*, 1967). It is commonly found developing in colonies of *T. cinnabarinus* and *T. urticae* on various wild host plants, such as *Ricinus communis* L., *Malva*, and *Nicotiana*, in southern California (McMurtry, unpublished). It has been observed to feed on citrus red mite, *Panonychus citri*, and avocado brown mite, *Oligonychus punicae*, in California (Quayle, 1912; Fleschner, 1958b), but apparently is not significant in their control (Fleschner, 1958b; McMurtry and Johnson, 1966). According to Muma (1955a, 1958), *S. sexmaculatus* preys on the six-spotted mite but not on the citrus red mite or the Texas citrus mite, *Eutetranychus banksi*, in Florida. There are also several reports of *S. sexmaculatus* preying on *T. kanzawai* in Japan (H. Mori, 1967).

The biology of the six-spotted thrips was studied by Bailey (1939). In the

laboratory, the egg stage lasted six to 10 days, the larva as few as five days, the prepupa one day, and the pupa five days. The adult lived two to three weeks. Bailey concluded that the rate of increase in relation to that of spider mites was too slow for the thrips to be an effective controlling agent. In this, Bailey may not have considered its powers of prey consumption (see Huffaker and Flaherty, 1966).

Scolothrips longicornis Priesner was found to prey on *Tetranychus urticae* in East Germany, on beans, on which predatory mites occur only occasionally (Fritzsche, 1958). Adult thrips were found to consume five mites or eight eggs per day, while the last larval instar consumed nine mites per day. However, the species did not occur in the field in large numbers. *S. longicornis* occurs frequently on fruit trees in Austria, where it apparently prefers species of spider mites that do not form webbing (Böhm, 1960).

Thrips tabaci Lind., a species generally assumed to be strictly phytophagous, has been observed feeding on *Panonychus ulmi* in England (Collyer, 1953b) and Canada (Putman, 1942; Putman and Herne, 1966).

Aeolothripidae

Putman and Herne (1966) noted occasional occurrence of larvae of *Aeolothrips melaleucus* Haliday feeding on *Tetranychus urticae* and, more rarely, *Panonychus ulmi*, in peach orchards in Ontario, Canada, but they indicated

the thrips was of no practical importance. Another species, *A. fasciatus*, was also detected, but the larvae were not distinguished from those of *A. melaleucus*.

Phlaeothripidae

Cryptothrips nigripes Reuter (= *C. latus* = *C. major*) was found only in hibernation sites of *Tetranychus urticae* in East Germany (Fritzsche, 1958). The larvae were very active even at 0° C, causing high mortality of hibernating mites. Their distribution, however, was irregular. No information was given on their summer behavior.

Haplothrips faurei Hood was considered one of the most important predators of *Panonychus ulmi* on apple in Nova Scotia (Lord, 1949; Lord, Herbert, and MacPhee, 1958). MacPhee (1953) stated that evidence indicated it to be a density-dependent factor in the regulation of *P. ulmi* populations. Putman (1965) concluded that its most im-

portant effect on peach in Ontario, Canada, occurs in the fall, when it preys on winter egg populations of *P. ulmi* and *Bryobia arborea*.

In a study of the biology of *H. faurei*, Putman (1965) found that the prey are not grasped with the legs, and the thrips are therefore limited mainly to the nonmotile forms of mites. Larvae ate an average of 143 eggs of *Panonychus ulmi* during a developmental period of eight to 10 days at 24°C. Adult females at the same temperature ate an average of 43.6 *P. ulmi* eggs per day and laid 3.3 eggs per day. Reproduction was higher on eggs of the oriental fruit moth, *Grapholitha molesta* (Busk.). Eriophyids, phytoseiids, and pollen

could also serve as food. Studies by MacPhee (1953), under insectary conditions, indicated that an average of 33 days was required to complete the life cycle from egg to adult, 15 of which were spent in the larval stage. There were two or three generations a year in Nova Scotia. Besides feeding on *P. ulmi* and *Bryobia*, the thrips was seen feeding on a tyroglyphid mite, on a cecidomyid larva, moth eggs, and phytoseiid eggs.

Leptothrips mali (Fitch) was observed by Bailey (1940) to have very general feeding habits although on peach trees in California it appeared to seek out and prey chiefly on eriophyids, spider mite eggs, and thrips.

DIPTERA

Cecidomyiidae

Arthrocnodax occidentalis Felt occurs in citrus and avocado orchards in California (Quayle, 1912; Fleschner, 1958b). It is not an effective predator of the citrus red mite or avocado brown mite (Fleschner, 1958b; McMurtry and Johnson, 1966), apparently being better adapted to feeding on the six-spotted mite, which develops in aggregated colonies. It may sometimes be important against that species (Fleschner, 1958b). Quayle (1912) observed that a larva consumed 380 mites in 17 days. Ewing (1914) considered this species important in the control of *Tetranychus*

urticae, and McGregor (1914) rated *Arthrocnodax* sp. the most important predator of red spiders on cotton, but gave little supportive evidence.

Several other spider mite-feeding species of *Arthrocnodax* were described by Felt (1913, 1914a, b).

Collyer (1953a) lists an undetermined cecidomyid larva as a predator of *Panonychus ulmi* in England. Barnes (1933) mentioned that *Arthrocnodax carolina* Felt fed on eggs of many species of red spiders in England. A few other citations are also listed in Groves's (1951) review.

Syrphidae

Syrphid larvae have been observed feeding on such mites as *Tetranychus urticae* (Ewing, 1914; Garlick, 1929), *Tetranychus* sp. (McGregor, 1914; Robinson, 1952), *Panonychus ulmi*

(Geijskes, 1938; Collyer, 1953b; Putman and Herne, 1966), and *P. citri* (Quayle, 1912). Almost nothing is known about the species involved or their prey preferences.

Dolichopodidae

Boyce and Le Roux (1951) reported adults of three species in three different genera of Dolichopodidae feeding on

adults of *Panonychus ulmi* in Ontario, Canada. No statements were made on their abundance or importance.

Empididae

Adults of *Drapetis microphyga* Mel. were observed feeding on citrus red mites in California, sometimes in rather large numbers (Fleschner and Ricker, 1953a). The feeding habits of the larvae are unknown.

COMPARATIVE CHARACTERISTICS OF VARIOUS KINDS OF PREDATORS

Speed of Development

The short development time in the egg and immature stages gives the Phytoseiidae the potential ability to complete a generation in a shorter time than do their tetranychid prey. The life cycles of all the other groups of predators seem to be rather longer than that

of the tetranychids, being longest with some of the large forms, such as chrysopids and some mirids, and among the shortest in the *Stethorus* species. Only scant data are available on developmental rates for some groups.

Egg-laying Potential

The Phytoseiidae seem to have a lower maximum daily egg deposition rate than do the tetranychids, but the oviposition period is generally longer. Under conditions of abundant food, *Stethorus* species have a maximum daily rate at least as high as that of tetranychids, and a considerably longer ovi-

position period; their total fecundity is thus greater. The same may be true for *Oligota* and the coniopterygids, but too few species have been studied. While the chrysopids have a relatively long period of development, they have an extremely high egg-laying potential.

Prey-consumption Capacity

The Phytoseiidae, and probably the Stigmaeidae as well, have the lowest prey-consumption capacity among the predators of tetranychids. Consequently, they also have the lowest minimum food requirements for development and reproduction, this being an obvious advantage for potential effectiveness at low prey densities. A few prey eggs or small, immature stages per day are sufficient for most species to develop and lay eggs. Some of the smaller thrips, such as *Scolothrips*, although requiring more prey than phytoseiids, seem to have a fairly low capacity as compared with most of the insectan predators. *Oligota* and *Stethorus* species have progressively higher

capacities and minimum requirements, but they still have considerably lower requirements than do some of the larger forms, such as the chrysopids. A high food requirement is presumably a limiting factor in the ability of a predator to hold populations at low levels. However, the high capacity for destroying prey is probably one of the main factors enabling some predators, such as *Stethorus picipes* and *Blepharidopterus angulatus*, to overcome great numerical odds in overtaking and suppressing very much higher prey populations (Muir, 1965b; McMurtry and Johnson, 1966). (See also the second paper in this series.)

Host Specificity

Although there are no documented cases of mite predators preying on only a single species of tetranychid, some obviously thrive best on certain species that have a particular type of distribution, webbing characteristics, or colony formation, while some have a broader spectrum, but are essentially confined to the Tetranychidae. All *Stethorus* species thus far studied, and *Scolothrips sexmaculatus*, *Oligota oviformis*, and some phytoseiids, such as *Phytoseiulus persimilis*, are examples of tetranychid specialists. On the other hand, some predaceous thrips and phytoseiids are very general feeders, utilizing both plant and animal foods. The coniopterygids studied readily consume

tetranychids and are associated with spider mites in the field, but there is no evidence that these are actually preferred to other prey, such as scale crawlers or whiteflies. Most chrysopids and predaceous Hemiptera accept a wide range of prey, although some appear to respond both functionally and numerically to changes in density of tetranychid populations.

The attractiveness or suitability of the host plant to predators may also be of great importance. Although it is known that certain species of predators may colonize some types of plants but not others, there is almost no information about the factors involved.

Searching Ability

There is little information on the searching capacities that can be used for comparative purposes. Since prey are apparently perceived only by direct contact, the predators that cover more area per unit time should theoretically be the best searchers. Fleschner (1950) demonstrated that larvae of *Chrysopa* moved more rapidly and covered considerably more area than did *Stethorus* or *Conwentzia*, and they were also more successful in holding and subduing the prey once a contact was made. The Phytoseiidae, being among the smallest of the predators of mites, probably have a correspondingly lower searching capacity, but they may compensate or more than compensate for this by their low food requirements (see second paper in this series).

The searching capacity of a population on an area-wide basis is also affected by the power of dispersal, which in effect is a form of searching efficiency. Thus the flying species should have better chances of locating new in-

festations when a local shortage of food develops, and it might be expected that flying species would be predominant on short-term crops where there is a discontinuous habitat. Information on dispersal powers of various mite predators is almost entirely lacking.

The Phytoseiidae, being small and wingless, cannot be expected to colonize a new planting, or recolonize an area in which previous extermination has occurred, as rapidly as do either the more mobile insects or the spider mite prey, which are more readily dispersed by wind or air currents. The Phytoseiidae may depend on such means as crawling, or on transport either by wind, on detached leaves, or by chance association with flying animals. On the other hand, the persistence of such predators should be greater than that of the more mobile forms in a continuous environment, such as an orchard, the winged forms having a greater tendency to leave the environment if the prey density becomes low.

Distribution in Relation to the Prey

The patterns of occurrence of predators in relation to those of their prey can be affected by a complex of tropisms and behavioral responses. Few comparative generalities among groups are possible. Probably the lower the specificity, the less likely would the predator's occupancy of the habitat tend to be closely correlated with that of the prey. For example, *Chrysopa carnea* will generally be most abundant on the part of the tree containing the most aphids, and will show no relationship to the distribution of spider mites. *Amblyseius hibisci* may be as abundant on

uninfested leaves as on mite-infested ones (McMurtry and Johnson, 1966). On the other hand, the distribution of *Phytoseiulus persimilis* is closely associated with that of its spider mite prey (Chant, 1961a; Oatman and McMurtry, 1966). However, an effective predator may not necessarily have a distribution pattern that is perfectly correlated with that of its prey (van de Vrie and Backels, 1968; Kropczyńska and van de Vrie, 1965). These questions are discussed in detail in the second paper of this series.

Seasonal Synchrony

Some phytoseiids, such as *Typhlodromus pyri* and *T. caudiglans*, seem to be quite well synchronized with *Panonychus ulmi* in deciduous orchards. Both species hibernate on the trees, *P. ulmi* as eggs, and the predators as adults. The latter emerge from hibernation before *P. ulmi* eggs begin hatching, and are active until the leaves start to fall in the autumn (Dosse, 1961; Putman, 1962; Collyer, 1964b; Putman and Herne, 1964). *Stethorus* species usually are not seen in large numbers until later in the population cycle of the prey, probably because they require relatively high numbers of prey in order to reproduce. On the other

hand, when *S. punctillum*, emerges from hibernation in the spring, in Canada, it may have a significant effect on the first generation of *P. ulmi* on peach while the prey is still concentrated on the small, young leaves (Putman, 1955).

Some forms, such as some of the predaceous Hemiptera, may be active only during a part of the season. As expected, the univoltine forms are not ideally synchronized with the multivoltine tetranychids. For example, the overwintering eggs of the mirid *Blepharidopterus angulatus* do not start hatching until several weeks after the *P. ulmi* hatch (Collyer, 1952; Muir, 1965a, b).

EFFECTS OF SPRAY PRACTICES ON MITE PREDATORS

Only the effects on predators are considered here. The effects of sprays on diseases are almost entirely unknown as yet.

We have known for a long time that agricultural sprays, especially the fungicides, insecticides, and acaricides, can have drastic effects on the natural enemies of insect and mite pests (e.g., Masee and Steer, 1929; Thompson, 1939). Among others, Ripper (1956),

Masee (1958), Steiner (1956, 1959, 1962, 1965a, b, c), Boudreaux (1963), Bartlett (1963, 1964), and Patterson (1966) present useful accounts of important work on this subject. In Steiner's (1959) extensive work, all material tested, except nicotine and lead arsenate, had noticeable detrimental effects. Most of the commonly used pesticides have a more or less broad-spectrum toxicity, yet some are rela-

tively innocuous in particular situations.

Adverse effects can arise either from direct mortality or, less obviously, reduced natality, or in various indirect ways. Sanford and Herbert (1966) emphasized that the long-term effects of a pesticide may be detrimental to predator complexes even at low dosages and when no immediate adverse effects are apparent. Some materials that have no immediate effect may, however, reduce egg production, as has been shown in some species of phytoseiids (Ristich, 1956; van de Vrie, 1962; Daneschwar, 1963).

A specific pest may be so effectively annihilated as to cause the predator species to die out from lack of food, even if the chemical has little direct effect on it. Or elimination may result

from severe reduction of some other food species critical for the predator at times when the given pest species is unavailable. Possibly, the sprays may inhibit development of fungi, mosses, or lichens, which serve as food for alternate prey or as abode for the predators. (See p. 372.)

Some of the effects of spray chemicals on the predators are considered here, and the resulting effects in terms of spider mite abundance are discussed by Huffaker, van de Vrie, and McMurtry in the second paper in this series. For this review, we have attempted to include a relatively large number of examples, rather than to compile a complete list of observed effects. A compilation of effects of pesticides on phytoseiid mites was published by Bartlett (1964).

Direct Effects

Dust or Inert Carriers

Deposits of road and field dust or inert carriers for pesticide dusts are known to be toxic or to impair movements or reproduction of certain mite predators (Fleschner, 1958c; Fisher and Fleschner, unpublished data). Fleschner (1958c) found that larvae of *Stethorus picipes* were greatly handicapped in searching behavior and were eventually killed when confined on papers with deposits of dry particles of field dust.

Fungicides

The fungicides consist of a variety of compounds that are here considered together.

The sulfur preparations, although used in some cases as insecticides or acaricides, have their widest use as fungicides. They seem to have a rather general detrimental effect on predaceous mites (Cutright, 1944; Lord, 1949; MacPhee and Sanford, 1954, 1956; Collyer and Kirby, 1955, 1959; Clancy and McAlister, 1956; Braven-

boer, 1959; Thill, 1959; Günthart and Clausen, 1959; Böhm, 1960; van de Vrie, 1962; Sanford and Lord, 1962; Bartlett, 1964; Sanford, 1967). In some cases, the insect predators may also be affected. Reed (1959) studied the influence of lime-sulfur on the mirid *Psallus ambiguus* in the laboratory and found that wet and recently dried deposits were highly toxic to nymphal stages. The toxicity of the dry deposits decreased rapidly, suggesting that it was the result of fumigant action. Muir (1962) also obtained a detrimental effect with lime-sulfur on *P. ambiguus* and *Blepharidopterus angulatus* in the laboratory, whereas dispersible sulfur and colloidal sulfur preparations caused only a low mortality. Lord (1949) observed that elemental sulfur was also detrimental to predaceous thrips and some mirids on apple. Apparent exceptions are known in a few cases, in which wettable sulfur showed little evidence of toxicity to phytoseiids (Mathys, 1956, 1958; Müller, 1960; Daneschwar, 1963).

Studies involving a number of species under a variety of conditions indicate that Captan is generally not harmful to phytoseiid mites (Collyer and Kirby, 1955; Mathys, 1958; Günthart and Clausen, 1959; Müller, 1960; MacPhee and Sanford, 1961; Sanford and Lord, 1962; van de Vrie, 1962, 1963; F. F. Smith, Hanneberry, and Boswell, 1963; Bartlett, 1964; Sanford, 1967). This generally low toxicity seems to hold true for other groups of predators as well (MacPhee and Sanford, 1961; Bartlett, 1963), but few data are available.

Glyodin is another compound that has shown low toxicity to mite predators in several cases (Collyer and Kirby, 1955, 1959; Clancy and McAlister, 1956; MacPhee and Sanford, 1956, 1961; Collyer, 1964c). Some of the other fungicides, however, have shown indications of being detrimental to phytoseiid mites. These include: Zineb (Mathys, 1958); Maneb and Ziram (Morgan, Anderson, and Swales, 1958; Swirski *et al.*, 1968); Karathane (Morgan, Anderson, and Swales, 1958; van de Vrie, 1962); Ferbam (MacPhee and Sanford, 1961); and Selbar (Daneschwar, 1963). Evidence on some of these compounds is conflicting, however, so that generalizations cannot be made. For example, Smith, Hanneberry, and Boswell (1963) found that residues of Zineb and Maneb had no effect on two species of phytoseiids in the laboratory.

Chlorinated Aryl Hydrocarbons and DDT Relatives

This group of compounds, notably DDT, are known to be highly toxic to many mite predators (e.g., Newcomer and Dean, 1946; MacPhee and Sanford, 1954, 1956, 1961; Clancy and McAlister, 1956, 1958; Lord, 1956; Ristich, 1956; Bravenboer, 1959; Putman and Herne, 1959; Thill, 1959; Böhm, 1960; Iacob, 1961; van de Vrie, 1962; Bartlett,

1963, 1964; Cone, 1963; Cutright, 1963; Daneschwar, 1963; Gratwick, 1965; Sanford and Herbert, 1966).

However, the chlorinated hydrocarbons, even DDT, also present some examples of rather limited direct effect on certain mite predators. Tolerance to DDT has been observed in larvae of *Chrysopa* (Doutt and Hagen, 1949; Putman, 1956) and *Anthocoris musculus* (Lord, 1956) as well as in several species of phytoseiids, including *Typhlodromus tiliae* on grapes in Switzerland (Mathys, 1958), *Amblyseius fallacis* on beans in the greenhouse in the United States (F. F. Smith, Hanneberry, and Boswell, 1963), and *T. caudiglans* on apple in Canada (Herne and Putman, 1966). The latter two were considered the result of development of resistant strains. Collyer (1964c) found that under certain conditions, in New Zealand orchards, *T. pyri* and *A. cucumeris* survived DDT sprays, and Niemezyk (1965) in England observed an immediate reduction of *T. pyri* by DDT and BHC, but within a week they were again increasing. The field studies of MacPhee and Sanford (1961), Collyer (1964c), and Sanford (1961) indicate that stigmatheids on apple trees are not greatly reduced by DDT. Other related compounds, such as dieldrin, may be only moderately or slightly toxic to phytoseiids, as was found in the laboratory by Ristich (1956), F. F. Smith, Hanneberry, and Boswell (1963), and Bartlett (1964), and in the field by Clancy and McAlister (1958) and Cone (1963). Endosulfan has been shown to be similarly safe for several species of phytoseiids (Allen, 1959b; Hukusima, 1960, 1963a, b; van de Vrie, 1962), although Bartlett (1964) found it to be toxic to *Amblyseius hibisci* in the laboratory, and van de Vrie (1962) found some evidence that it temporarily inhibited egg production of phytoseiids on apple in the Netherlands.

Some of the compounds in this group

that are used specifically as acaricides show some selectivity, being relatively nontoxic to phytoseiids. Hukusima (1960, 1963a, b), Daneschwar (1963), and Herne and Chant (1965) reported that dicofol has little effect on various species of phytoseiids, although in some cases, moderate or even high toxicity was evident (Günthart and Clausen 1959; van de Vrie, 1962; Bartlett, 1964; Sanford, 1967; Sanford and Herbert, 1967). In still other cases, however, more subtle effects were apparent. Downing (1966) noted low initial toxicity but a long residual effect, and Daneschwar (1963) reported an inhibitory effect on reproduction. Chlorobenzilate has shown generally light toxicity to phytoseiids in the laboratory (Ristich, 1956; F. F. Smith, Henneberry, and Boswell, 1963; Bartlett, 1964), and also in the field in orchards in Quebec (Parent, 1961) and eastern United States (Clancy and McAlister, 1958). Little information is available on the effects of these acaricides on other mite predators, but indications are that they are not very detrimental to *Stethorus* (Bravenboer, 1959; Bartlett, 1964) or predaceous hemiptera or thrips (MacPhee and Sanford, 1961).

Organophosphorus Materials

The organic phosphorus compounds have generally been severely toxic to mite predators. Many records show the high toxicity to phytoseiids of such compounds as parathion, malathion, azinphosmethyl, and demeton (MacPhee and Sanford, 1954, 1956, 1961; Ristich, 1956; Günthart and Clausen, 1959; Böhm, 1960; Parent, 1961; F. F. Smith, Henneberry, and Boswell, 1963; Bartlett, 1964; Herne and Chant, 1965; Downing, 1966) and to certain insect predators of mites as well (MacPhee and Sanford, 1954, 1956, 1961; Thill 1959; Günthart and Clausen, 1959; Böhm, 1960; Hukusima, 1960, 1963a, b; Steiner, 1962; van de Vrie, 1962; Bartlett, 1963; Gratwick, 1965). Huf-

faker and Spitzer (1951) and Huffaker and Kennett (1953b, 1956) used parathion to eliminate two species of phytoseiids in strawberry plants as a "check-method" to evaluate their ability to control cyclamen mite. However, one phytoseiid, *Typhlodromus occidentalis*, exhibits (some degree of) tolerance or resistance to normally highly toxic organophosphates in western North America (Huffaker and Kennett, 1953a; Morgan and Anderson, 1958; Hoyt, 1969b). Parent (1961), in Quebec, reported that the stigmatid *Zetzellia* (= *Mediolata*) *mali* was not greatly reduced by sprays of organic phosphates, including azinphosmethyl, malathion, demeton, and phosdrin, while the phytoseiid *T. rhenanus* was almost completely destroyed by these compounds. In studies on plums in Germany, Thill (1959, 1964) found that trichlorfon reduced the number of *T. tiliarum* Ouds. but that the remaining population was able to keep *Panonychus ulmi* under control.

Carbamates

Carbaryl seems generally to be quite detrimental. Most of the available information on this compound concerns its effect on phytoseiids, to which it is highly toxic (Putman and Herne, 1960; MacPhee and Sanford, 1961; F. F. Smith, Henneberry, and Boswell, 1963; Bartlett, 1964; and Sanford, 1967). However, van de Vrie (1962) noted only a small direct effect, but a lower egg production by the surviving population. Detrimental effects of carbaryl have also been observed on *Stethorus* in the laboratory by Bartlett (1963) and in the field as well as on *Chrysopa* by Putman and Herne (1960). Gratwick (1965) found it toxic in the laboratory to a mirid, an anthocorid, and two coccinellids. MacPhee and Sanford (1961) reported at least partial reduction of predaceous thrips and Hemiptera. Zectran is another compound that appears to be highly toxic to predators (Bart-

lett, 1963, 1964). Not all compounds in this group, however, show such a high degree of toxicity. For example, Isolan has been reported to be low in toxicity to phytoseiids (van de Vrie, 1962) as have some of the fungicides (see p. 369).

Sulfonates, Sulfides, Sulfonamides, and Sulfites

Some of the acaricides in this group have been observed to be relatively nontoxic to predaceous mites. They include tetradifon, ovex, aramite, tetrasul, and chlorobenside (Ristich, 1956; Günthart and Clausen, 1959; Müller, 1960; MacPhee and Sanford, 1961; Parent, 1961; Suski, 1961; van de Vrie, 1962; Daneschwar, 1963; F. F. Smith, Henneberry, and Boswell, 1963; Bartlett, 1964; Sanford, 1967). However, van de Vrie reported a lower egg production of phytoseiids on apple tree plots treated with chlorobenside. Only a limited amount of data exists on the effects of these materials on insect predators of mites, but indications are that they are generally not harmful (Bravenboer, 1959; MacPhee and Sanford, 1961; Bartlett, 1963).

Nitrophenols and Derivatives

A number of these materials seem to be detrimental to mite predators. Niemyzyk and Wiackowski (1965) found that dinitroresol nearly annihilated the phytoseiids *Phytoseius macropilis*, *Typhlodromus tiliarum*, and *Amblyseius finlandicus* on plum in Poland, and Collyer and Kirby (1959) observed similar effects on *T. pyri* on apple in England. The acaricide binapaeryl was observed to reduce numbers of *T. caudiglans* (Downing, 1966) and *T. pyri* (Sanford, 1967) on apples in Canada. Dinocap, which is also used as a fungicide, was reported nontoxic to *P. persimilis* (= *P. riegeli*) in the Netherlands (Bravenboer, 1963). On the other hand, Morgan, Anderson, and Swales (1958) and Downing (1966) found the same compound highly toxic

to *Typhlodromus* sp. and *T. caudiglans*, respectively, in British Columbia. Also Collyer (1964c) in New Zealand and van de Vrie (1962) in the Netherlands found it highly toxic to *T. pyri*.

Miscellaneous Materials

The heterocyclic acaricide moristan seems to be notably toxic to predaceous mites. Reports confirming this include those of Bravenboer (1965) for *Phytoseiulus persimilis* in the Netherlands, Downing (1966) for *Typhlodromus caudiglans* in Canada, and Sanford (1967) for five species of phytoseiids and a stigmatid in Canada. *Stethorus punctillum* was also susceptible to this compound but not to eradex, which was, however, toxic to *P. persimilis* (Bravenboer, 1965).

The oils appear to have little detrimental effect under certain conditions. Clancy and McAlister (1958) and Downing (1966) report little or no effect on phytoseiids when these materials were used on apples in the delayed-dormant and green-bud stages, respectively. Bartlett (1964) obtained no effect from oil deposits on *Amblyseius hibisci* in the laboratory. However, Lord (1949) observed a summer oil spray to be very detrimental to *Typhlodromus* sp. in Nova Scotia, and Böhm (1960) reported that oil sprays caused reduction, but not elimination, of *T. tiliae* and *Zetzellia mali* in Austria.

Of the botanicals, several references indicate that ryania is not harmful to phytoseiids (Clancy and McAlister, 1956, 1958; Ristich, 1956; MacPhee and Sanford, 1961; Bartlett, 1964; Collyer, 1964c; Sanford, 1967). Ryania also appears to have little effect on *Stethorus* species (Bartlett, 1963; Collyer, 1964c). In some laboratory tests, on the other hand, rotenone showed high toxicity, and sabadilla showed medium toxicity to *Amblyseius hibisci* (Bartlett, 1964). Rotenone was also toxic to larvae of *Stethorus picipes* (Bartlett, 1963).

Lead arsenate, in general, seems to cause little or only partial reduction of mite predators (Lord, 1949; Clancy and McAlister, 1958; MacPhee and Sanford, 1961; Bartlett, 1963, 1964; Gratwick,

1965). It is noteworthy, however, that Ristich (1956) found that lead arsenate affected egg production of *Typhlodromus fallacis* in the laboratory.

Indirect Effects on Predators

Klostermeyer (1959) concluded that the role of chemicals in causing mite increases may be complex and varied, involving direct mortality effects and various biotic interactions. The basic changes in plant physiology attributed to treatments with agricultural chemicals (see second paper in this series) may conceivably affect the predators of phytophagous mites as well as their prey. No one has tested whether the power of increase of a predator is changed by feeding indirectly on the altered plant food. An unusual phenomenon was reported by Fleschner and Scriven (1957) who observed that adult *Chrysopa* laid more eggs on small trees treated with DDT than on untreated trees even when all prey were removed.

Systemic compounds, generally assumed to be safe for the natural enemies because they do not feed on the plant material, may be indirectly harmful since they can be ingested when a predator feeds on prey. McClanahan (1967) has shown that systemic root drenches of dimethoate and thionazin were more toxic to *Phytoseiulus persimilis* feeding on the two-spotted spider mite than they were to the mite itself, thus illustrating the principle of food-chain accumulation.

Predators may be decimated (or increased) by materials that do not kill

them directly, or affect their fecundity. Cone (1963) found that dieldrin used in alfalfa caused no change in the tetranychid populations but did result in an increase in the phytoseiids. He suggested that this resulted from the great reduction of other predators of the mites, which presumably left a greater proportion of the prey to the phytoseiids, and in turn resulted in reduced interspecific competition. Lord (1956) found that *Anthocoris musculus* became very abundant following use of DDT sprays. This predator and the phytophagous mites were tolerant to DDT, but the other predators were very susceptible. Dominance of phytoseiid species has been reversed by spray practices, e.g., in sprayed and unsprayed apple orchards (Snetsinger, 1959; Oatman, 1963).

As has been suggested by Cutright (1963) and Oatman (1965a), a very high kill of phytophagous mites on apple may cause the predator population to die out from lack of food. A necessary supplemental food in the form of aphids or other prey or their products, as well as the prey mites themselves, might also be involved in some cases.

Furthermore, certain sprays are known to kill mosses and lichens, which may provide necessary shelter for some predaceous species (Collyer, 1953c).

Summary of Effects

Thus we see that the agricultural chemicals exert a wide variety of influences on mite predators. The fungicides, acaricides, and insecticides are notably detrimental in particular situations, but they also vary within a class

with respect to degree of influence—those hazardous to certain kinds of enemies are sometimes much less harmful to others. Most of the work, especially in the laboratory, has dealt with the effects of chemicals on phytoseiid

mites. Considerable evidence also suggests that important insect predators of mites may be quite adversely affected (e.g., Günthart, 1945; DeBach, Fleschner, and Dietrick, 1950; Collyer, 1953*c*, 1964*c*; MacPhee and Sanford, 1954, 1961; Kuenen and Post, 1958; Bravenboer, 1959; Hukusima, 1960, 1963*a, b*; Sanford and Lord, 1962; Muir, 1962, 1965*a, b, c*; Bartlett, 1963; Gratwick, 1965; Patterson, 1966). It cannot be said that those chemicals used primarily as insecticides are harmful only to insectan predators nor that those used primarily as acaricides are harmful only to acarine predators, although the latter may be more nearly true than the former. Results in the laboratory are not always consistent with those obtained in the field, and since field trials were conducted under a variety of conditions, e.g., different crops, climatic areas, species of arthropods, dosages, and the like, it is not surprising that

reports are conflicting. A substantial number of materials, however, are obviously mild enough in their effects on certain kinds of mite predators to offer possibilities for use in integrated control programs, while others are so severe as to be avoided in such programs.

The indirect influences from use of agricultural chemicals are less obvious, but may be equally detrimental to effective predator action. Long-term balance disturbances may arise from use of such materials, even though they result in only mild direct toxicity. Furthermore, the results obtained from replicated single-tree treatments or small plots may not reflect the severity of treatments covering large areas, since in the former case, re-migration into the treated area would be relatively easy for many species. A spray program on an entire crop which dominates a large area was termed the "blanket effect" by Herne and Putman (1966).

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