and tetrahydrobiopterin are converted to pterin (2-amino-4-hydroxypteridine) and nonfluorescent material. The ratio of biopterin content after oxidation at *p*H 13 to that after oxidation at *p*H 1 is therefore an indication of the relative amount of biopterin originally present in the sample as quinonoid dihydro- or tetrahydrobiopterin (*5*). Since it is unlikely that substantial amounts of quinonoid dihydrobiopterin exist in vivo, the results of this analysis indicate that more than 85 percent of the biopterin was in the tetrahydro form in both control and treated glands. The rest was either 7,8-dihydro- or oxidized biopterin.

The mechanism and physiological importance of adrenergic cyclic AMP–dependent regulation of pineal tetrahydrobiopterin biosynthesis are unknown. The possibility that a decrease in pineal content of reduced biopterin would decrease hydroxylation is not supported by the available data (*10*), which indicate that tryptophan hydroxylation within pineal glands in the presence of physiological concentrations of tryptophan is not decreased by adrenergic cyclic AMP stimulation in organ culture. Adrenergic cyclic AMP stimulation increases the activity of *N*-acetyltransferase by an induction-activation mechanism. The gradual nature of the decline in biopterin levels in response to adrenergic stimulation is similar to the gradual nature of the increase in the activity of *N*-acetyltransferase (*11*). The inhibition of biopterin biosynthesis and the resulting decline in biopterin content could be related to this increase in enzyme activity. Such a possibility is of particular interest because tetrahydrobiopterin is a reducing agent and because of indications that redox changes may play a role in the rapid neurally controlled turn-off of pineal *N*-acetyltransferase activity (*4, 12*).

Further study of the adrenergic cyclic AMP–induced inhibition of pineal biopterin biosynthesis may lead not only to an increased understanding of the regulation of biopterin synthesis, but also to the discovery of a new function of biopterin in the pineal gland and possibly a new role for the compound in other tissues.

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Carotenoids Function in Photoperiodic Induction of Diapause in a Predacious Mite

Abstract. *Predacious mites fed for two generations solely on the eggs of wild-type spider mites responded normally to short day lengths by entering diapause. However, predacious mites fed for two generations on eggs of albino spider mites, which are completely devoid of carotenoids, did not respond to short-day photoperiods. Apparently carotenoids are essential for photoperiodic induction; possibly a carotenoid or carotenoid derivative functions as the photopigment concerned in photoperiodic light reception in these mites.*

The reception of photoperiod in terrestrial arthropods presupposes the presence of a photoreceptor pigment, which is probably located in the central nervous system (*1*). Various techniques have been used in attempts to identify the pigment (or pigments) involved in photoperiodic light reception in insects and mites, such as action spectra studies, isolation and characterization of pigments from insect heads, and rearing of insects on artificial diets deficient in certain colored compounds (*2*). However, convincing evidence regarding the class of pigments involved in insect photoperiodism has not been produced. Evidence for the participation of carotenoids or derivatives of carotenoids in the photoperiodic induction of diapause has now been obtained for spider mites, by means of a genetic approach (*3*). Diapause induction appeared to be disturbed in albino spider mites, which lack all pigmentation due to a block in the uptake of carotenoids from the food plant (*4*). However, photoperiodic induction was normal in albino spider mites originating from hybrid mothers, which possess the wild pigmentation. Apparently minimal amounts of carotenoids of maternal origin suffice to restore the capability to diapause in albino mites. Using a technique based on the feeding of predacious mites with eggs of normally pigmented (wild-type) and albino spider mites, we demonstrate here that carotenoids are essential for the photoperiodic induction of diapause in these predacious mites also.

The predacious mite, *Amblyseius potentillae*, exhibits a facultative reproductive diapause, induced by short-day

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photoperiods experienced during the immature stages (*5*). The photoperiodic response curve (*6*) of the Dutch strain of *A. potentillae* which we used in our experiments is of the long-day type with a sharply defined critical day length of 14 hours. Photoperiods with photophases of from 4 to 13 hours result in 100 percent diapause; photophases of 15 hours and longer completely prevent diapause. A sharp drop in the incidence of diapause occurs at ultrashort day lengths, resulting in 0 percent diapause in continuous darkness. Similar results have been obtained with related species of predacious mites and with spider mites (*7*).

Under the test conditions of 8 hours light and 16 hours dark (LD 8:16) and 18°C, sustained throughout the development of the mites, all females entered diapause provided that they had been fed on a wild-type strain of the spider mite *Tetranychus urticae*. Under the same rearing conditions no diapause was observed in a long-day regime of LD 16:8. Complete reproductive arrest of individual female mites was taken as the criterion for diapause. All females mated during the first few days of adult life. About 25 females of *A. potentillae* were used in each of the following tests (*8*).

Predacious mites were fed solely on a diet of spider mite eggs since preliminary experiments had shown that carotenoids present in the intestinal tract of the moving stages of their prey suffice for a normal photoperiodic reaction in the predator. Moreover, the tests for photoperiodic responsiveness were restricted to the second generation of predacious mites reared on spider mite eggs because previous studies had shown that diapause induction is not affected in the first generation of *A. potentillae* fed on albino eggs. These results are in accordance with the findings for spider mites, for which even small amounts of maternally derived carotenoids proved to be sufficient for a normal operation of the photoperiodic mechanism (*3*).

Under the test regime used (LD 8:16, 18°C), *A. potentillae* females fed on the eggs of wild-type spider mites showed 100 percent diapause. In contrast, *A. potentillae* females fed on albino eggs produced eggs when reared under the short-day regime mentioned above and thus responded with 0 percent diapause. Under a long-day regime of LD 16:8 and 18°C, all females fed on the eggs of either wild-type or albino spider mites produced eggs. The number of eggs laid was about equal in both cases, namely, approximately one egg per female per day. Therefore, under long-day conditions, diapause incidence was 0 percent in predacious mites fed on either type of spider mite eggs. Repeating these experiments yielded identical results. Since the only difference in the diets fed to the predacious mites is to be found in the absence of carotenoids in the eggs of albino spider mites, we conclude from the complete lack of photoperiodic response of *A. potentillae* females fed on albino eggs that carotenoids or derivatives of carotenoids are essential for the photoperiodic mechanism to be functional in these predacious mites.

Further evidence for the involvement of carotenoids or carotenoid derivatives in mite photoperiodism was obtained in feeding experiments in which the diet of albino spider mite eggs was supplemented with a 1 percent (weight to volume) solution of β-carotene in olive oil, administered as small droplets spread evenly along the margins of the plastic arenas the mites were maintained upon. Three sides of the rectangular arenas were treated this way; the fourth side was left untreated to allow the mites access to the drinking water supply. Other arenas were prepared likewise with olive oil only. In these tests, mites were used which originated from parents fed solely on albino spider mite eggs. When placed under the test regime (LD 8:16, 18°C) the mites fed on albino eggs supplemented with β-carotene showed a 100 percent diapause response (13 mites) whereas all 17 females in the control group (fed on albino eggs with olive oil) produced eggs. Under a long-day regime of LD 16:8 and 18°C both groups (12 and 15 mites, respectively) produced eggs. Repeating these experiments yielded 96 percent diapause incidence in a group of 24 mites fed on the β-carotene–supplemented diet, and 4 percent diapause in the controls (23 mites) under the short-day conditions. Apparently the chance encounters of the mites with the oil droplets occurred frequently enough to allow some β-carotene to be taken up by the mites during the cleaning behavior shown after contact with the oil. The absence of diapause in the controls shows that the olive oil itself did not contain any diapause-promoting compounds. The results of these experiments confirm the conclusion we arrived at above, namely that carotenoids or carotenoid derivatives are essential for photoperiodic induction in these mites.

The all-or-none response found in the above experiments demonstrates a complete inability of the predacious mites to perceive the short day lengths when fed on albino eggs. Apparently the photoperiodic photoreceptor is not functioning in carotenoid-depleted mites, and consequently photoperiodic time measurement is not executed. The reaction of mites that have become functionally blind to photoperiod by lack of carotenoids may be comparable to that of normally fed mites reared in continuous darkness, which also results in a complete absence of diapause. The results therefore permit the conclusion that diapause induction is an actively controlled process in these mites, demanding a functional photoreceptor and clock. On the other hand, for reproduction to proceed no photoperiodic time measurement seems to be required.

In insects, photoperiodic control of development is mediated through extraretinal photoreceptors, while extraretinal pathways are also prominent in mediating the interactions between light and circadian rhythms (*9*). In mites photoreceptors that mediate photoperiodism and circadian rhythms have not been localized. However, since eyes or ocellilike structures are absent in the predacious mite *A. potentillae* (*10*), it follows that photoperiodic photoreception in these mites must occur extraretinally. Whether the photoreceptor and other elements of the photoperiodic mechanism are located in the central nervous system of these mites remains to be investigated.

In view of the widespread occurrence of photoperiodic phenomena and circadian rhythms in both plants and animals, the question whether basic features of the underlying mechanisms are common to various groups of organisms is of interest. As regards the photoreceptor pigments involved in these light-controlled processes, various pigments have been implicated, and the long-standing controversy whether carotenoids or flavins, flavoproteins, or a combination of flavin and cytochrome are the primary photoreceptors for many blue light–controlled physiological processes has not yet been solved (*11*). In insects, studies with carotenoid-depleted diets did not yield any indications of carotenoids being involved in photoperiodism or entrainment of circadian rhythms (*12, 13*), but further consideration of these results is required since in insects also it may take one or more generations to dilute out all carotenoids of maternal origin (*12, 14*). In higher plants phytochrome appears to be involved in photoperiodism and circadian rhythmicity (*15*), whereas in vertebrates it is not certain whether rhodopsin acts as the primary photoreceptor even in the case of retinal photoreception (*16*). From our results it is apparent that very different pigment systems are involved as primary photo-

receptors in the great variety of animals and plants in which photoperiodism or circadian rhythmicity (or both) have evolved.

Our results indicate that carotenoids or derivatives of carotenoids such as retinoids may function as the photoreceptor pigments in photoperiodic light reception in these predacious mites. However, the conclusion that the photopigment is a carotenoid will have to await confirmation from studies of action spectra.

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Allelopathy Between Zooplankton: A Mechanism for Interference Competition

Abstract. *The filtering rate of the copepod* Diaptomus tyrrelli *is reduced in the presence of its potential competitor and predator,* Epischura nevadensis, *by as much as 60 percent. This effect is caused by a chemical released into the water by* Epischura. *The chemical does not pass through dialysis tubing with a pore size of 10^4 angstroms, indicating that it is a large molecular weight compound. The reduction in filtering rate is the result of interference competition between two species and may be linked to the evolution of a mechanism for avoiding predation.*

The effect of physical interactions between zooplankton on their ability to feed has not been well documented (*1*), and the effect of chemical interactions on feeding is less well known. Physical encounters between animals may result in either a change in swimming movements (speed, direction, pattern) or an adjustment of feeding time related to time spent avoiding predators (*2*). Such behavioral changes in one species of zooplankton, elicited by the physical presence or chemical effect of a second, could result in a change in the filtering, or feeding, rate of both species. Although chemically induced inhibiton of feeding has not been demonstrated for these animals, several studies provide evidence of the ability of pelagic zooplankton to respond to chemical stimuli. For example, Gilbert (*3*) showed that a chemical released by the predator stimulated a morphological change in the prey that made it less vulnerable to predation. It has also been shown that zooplankton can modify their feeding behavior in response to chemical differences among food types (*4*).

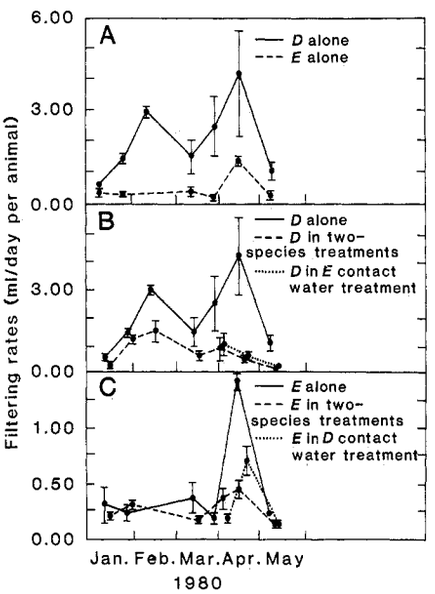

Fig. 1. Filtering rates for *Diaptomus* (*D*) and *Epischura* (*E*) in water from Lake Tahoe. (A) The filtering rates were measured for each species in single-species experiments on seven dates. (B) The filtering rates of *Diaptomus* in three experiments. (C) The filtering rates of *Epischura* in three experiments. Data points are means ± standard errors of the mean.

When the ability of one species to use resources is reduced by the chemical or physical intervention of a second species, it is termed interference competition. We present evidence that this phenomenon occurs between some species of herbivorous zooplankton. We found that a change in the filtering rates of one species of zooplankton occurred when it was placed with a second species in experimental containers. The second species released a chemical that caused a reduction in the filtering rate of the first, thus providing evidence for chemical allelopathy as a mechanism for interference competition between species of zooplankton.

The animals studied were taken from Lake Tahoe on the California-Nevada border. The pelagic zooplankton fauna of the lake consists of the mysid shrimp *Mysis relicta*; two species of calanoid copepods, *Diaptomus tyrrelli* and *Epischura nevadensis*; the rotifer *Kellicotia longispina*; and extremely low numbers of the cladoceran *Bosmina longirostris* (*5*). *Diaptomus*, *Epischura*, *Kellicotia*, and possibly early instars of *Mysis* make up the entire pelagic community of grazers most of the year. We studied the two species of copepod, which interact in several ways: as predator (*Epischura*)

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