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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References and Notes

1. A. D. Lees, *J. Exp. Biol.* **41**, 119 (1964); C. M. Williams and P. L. Adkisson, *Biol. Bull. (Woods Hole, Mass.)* **127**, 511 (1964); J. Claret, *Ann. Endocrinol.* **27**, 311 (1966); J. Seugé and K. Veith, *J. Insect Physiol.* **22**, 1229 (1976); C. G. H. Steel and A. D. Lees, *J. Exp. Biol.* **67**, 117 (1977).
2. A. D. Lees, *Ann. Appl. Biol.* **40**, 449 (1953); A. D. Lees, *Nature (London)* **210**, 986 (1966); A. M. Ajami and L. M. Riddiford, *Biochemistry* **10**, 1455 (1971); D. K. Hayes, M. S. Schechter, H. R. Moffitt, *Isr. J. Entomol.* **11**, 125 (1971); M. Rothschild, in *Biochemical Aspects of Plant and Animal Coevolution*, J. B. Harborne, Ed. (Academic Press, New York, 1978), 259; I. Shimizu, S. Kitabatake, M. Kato, *Abstr. 16th Int. Congr. Entomol. Kyoto* (1980), p. 86.
3. A. Veerman and W. Helle, *Nature (London)* **275**, 234 (1978); A. Veerman, *Physiol. Entomol.* **5**, 291 (1980).
4. A. Veerman, *Comp. Biochem. Physiol.* **47B**, 101 (1974).
5. J. A. McMurtry, D. L. Mahr, H. G. Johnson, *Int. J. Acarol.* **2**, 23 (1976).
6. W. P. J. Overmeer and A. Q. Van Zon, unpublished results.
7. W. L. Putman, *Can. Entomol.* **94**, 163 (1962); M. A. Hoy, *J. Insect Physiol.* **21**, 605 (1975); A. Veerman, *ibid.* **23**, 703 (1977).
8. The experiments with *A. potentillae* were performed on the inert surface of rectangles of black plastic, measuring 8 × 15 cm, surrounded by a barrier of moist filter paper. Cultures of the predacious mites were regularly supplied with all developmental stages of the spider mite *T. urticae* as prey. For the experiments eggs deposited by female spider mites on bean leaves were transferred daily with a fine brush to the plastic arenas the predacious mites lived on, attention being paid that no excrements of spider mites were carried with the eggs. Care was taken to ascertain that no shortage of food ever occurred. The method used is a modification from the one described in more detail by J. A. McMurtry and G. T. Scriven [*J. Econ. Entomol.* **68**, 319 (1975)]. Once adult females of the predator had emerged, the arenas were examined daily over a period of 8 days. The average preoviposition period of nondiapausing females of *A. potentillae* at 18°C is 3 days.
9. J. W. Truman, *Photochem. Photobiol.* **23**, 215 (1976).
10. G. W. Krantz, *A Manual of Acarology* (Oregon State University Book Stores, Corvallis, 1978), p. 115.
11. V. Munoz and W. L. Butler, *Plant. Physiol.* **55**, 421 (1975); E. Klemm and H. Ninnemann, *Photochem. Photobiol.* **24**, 369 (1976); R. D. Brain, D. O. Woodward, W. R. Briggs, *Carnegie Inst. Washington Yearb.* **76**, 295 (1977); R. D. Brain, J. A. Freeberg, C. V. Weiss, W. R. Briggs, *Plant Physiol.* **59**, 948 (1977); E. Klemm and H. Ninnemann, *Photochem. Photobiol.* **28**, 227 (1978); L. N. Edmunds, Jr., R. I. Apter, P. J. Rosenthal, W.-K. Shen, J. R. Woodward, *ibid.* **30**, 595 (1979); H. Ninnemann, *BioScience* **30**, 166 (1980); W. Shropshire, Jr., in *The Blue Light Syndrome*, H. Senger, Ed. (Springer-Verlag, Berlin, 1980), p. 172.
12. W. F. Zimmerman and T. H. Goldsmith, *Science* **171**, 1167 (1971).
13. M. Rothschild, in (2); I. Shimizu, S. Kitabatake, M. Kato, in (2).
14. R. H. Dadd, *Bull. Entomol. Res.* **52**, 63 (1961).
15. M. B. Wilkins and P. J. C. Harris, in *Light and Plant Development*, H. Smith, Ed. (Butterworth, London, 1976), p. 399; O. M. Heide, *Physiol. Plant.* **39**, 25 (1977); S. Kaihara and A. Takimoto, *Plant Cell Physiol.* **21**, 21 (1980).
16. M. Menaker, in *The Neurosciences Third Study Program*, F. O. Schmitt and F. G. Worden, Eds. (MIT Press, Cambridge, Mass., 1974), p. 479; J. S. Takahashi and M. Menaker, in *Biological Rhythms and Their Central Mechanism*, M. Suda, O. Hayaishi, H. Nakagawa, Eds. (North-Holland, Amsterdam, 1979). p. 95.

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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*).

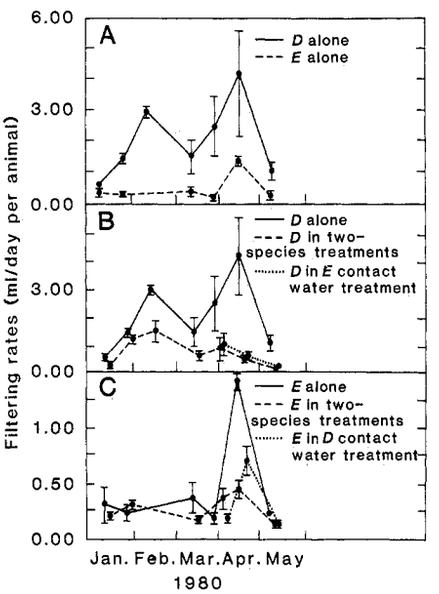

Fig. 1. Filtering rates for *Diaptomus* (*D*) and *Epischura* (*E*) in water from Lake Tahoe. (A) The filtering rates were measured for each species in single-species experiments on seven dates. (B) The filtering rates of *Diaptomus* in three experiments. (C) The filtering rates of *Epischura* in three 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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and prey (*Diaptomus*), as competing herbivores, or as a combination of these two. When adults of *Epischura* were given nauplii, copepodids, and adults of *Diaptomus* in laboratory and field experiments, *Epischura* preyed heavily only on the nauplii and small copepodids of *Diaptomus* (*6*). Although we saw adult *Epischura* eat adult *Diaptomus* in the laboratory at extremely high densities, we were unable to measure a significant predation rate on the adults in feeding experiments at in situ densities. Therefore, the predation of adult *Diaptomus* by *Epischura* is likely to be low. *Epischura* also grazes on algae, and the filtering rates of *Diaptomus* are always greater than those of *Epischura* (Fig. 1A). Since *Diaptomus* and *Epischura* overlap spatially and temporally, attain the same size as adults, depend on filter feeding for a portion of their food, and are thought to graze on a similar size range of particles, they are probably competitors on at least some occasions. When we measured the filtering rate of animals in experiments with both species, the filtering rates of *Diaptomus* were 60 percent lower than the rates measured in experiments with a single species (Fig. 2).

All copepods were collected at the same location with an 80-μm mesh net and towed vertically from 100 m to the surface. The experiments were conducted with a composite sample of lake water drawn from four depths. A radioactively labeled food suspension was prepared by adding 350 μCi of the radionuclide phosphorus-32 (as $H_3{}^{32}PO_4$) to 450 ml of the composite sample of lake water and incubated for 24 hours under low light. Adult copepods were placed into 125-ml glass jars containing 120 ml of fresh lake water (*7*). After acclimation (30 to 45 minutes), 5 ml of the labeled food was added to each jar, and the animals fed for 10 to 15 minutes. All of the experiments were run at 8°C in the dark. Filtering rates were calculated from measurements of ^{32}P uptake estimated from scintillation counts (*8*).

The filtering rate of *Diaptomus* was significantly lower in experiments with *Epischura* ($P < .005$) (*9*). The observed temporal differences in the filtering rates of *Diaptomus* (significant at $P < .005$) (Fig. 1B) were probably due to seasonal changes in the composition of the in situ food and in the physiology of the animals.

Experiments were performed at four different times to demonstrate that the cause of the reduction in the filtering rate of *Diaptomus* was a chemical released by *Epischura*. The filtering rates of *Diaptomus* were measured in three types of treatments with (i) only *Diaptomus*, (ii) both species, (iii) *Diaptomus* and lake water that had contained *Epischura*. The water for the third treatment, described as contact water (Fig 1, B and C), was prepared by leaving 25 adult *Epischura* in a 1-liter jar of lake water for 12 to 24 hours. After the *Epischura* were removed, 25 ml of the remaining *Epischura* contact water was added to the experimental containers. The filtering rate of *Diaptomus* in the treatments with *Epischura* and *Epischura* contact water was significantly lower than in the treatment with only *Diaptomus* (Fig. 1B) ($P < .01$). We concluded that a chemical allelopathic agent released by *Epischura* caused the reduction in filtering by *Diaptomus*. The release of this chemical is not actively generated by the presence of *Diaptomus* because the *Epischura* contact water was produced by *Epischura* in the absence of *Diaptomus*.

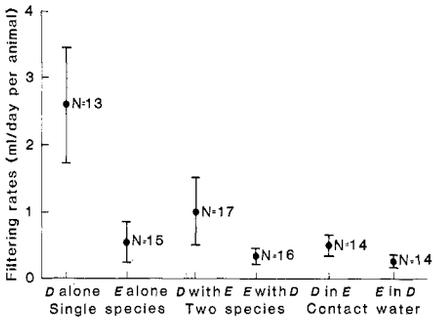

Fig. 2. Comparison of three experiments: single species, two species, and contact water. Mean filtering rates and 95 percent confidence intervals are shown for pooled data of experiments on the 4 days; *N*, number of values pooled; *D*, *Diaptomus*, and *E*, *Epischura*.

The following experiment was conducted to characterize the allelopathic agent as either a low molecular weight compound (for example, ammonia) or a high one. *Epischura* contact water (250 ml) was placed into dialysis tubing (pore size, 10^4 Å) and allowed to equilibrate with 2 liters of quartz distilled water for 24 hours. The water remaining inside the dialysis tubing after 24 hours (termed dialysis water), contained the algae from the composite sample of lake water and any materials produced by *Epischura* that were too large to pass through the tubing (*10*). The filtering rates of *Diaptomus* were then measured in six types of treatments with (i) only *Diaptomus*, (ii) both species, (iii) *Diaptomus* and 25 ml of *Epischura* contact water, (iv) *Diaptomus* and 25 ml of *Diaptomus* contact water (*11*), (v) *Diaptomus* and 25 ml of *Epischura* dialysis water, and (vi) *Diaptomus* and 25 ml of *Diaptomus* dialysis water. The filtering rate of *Diaptomus* showed a statistically significant depression by exposure to both the *Epischura* contact and the dialysis water ($P < .001$) (*12*). These results suggest that the chemical causing the depression in the filtering rate of *Diaptomus* was either a large molecular weight compound that remained inside the dialysis bag or a compound effective at extremely low concentrations. Finally, the filtering rate of *Diaptomus* was not depressed by exposure to *Diaptomus* contact water ($P > .5$). This result provided further evidence that the allelopathic agent was not ammonia, but a product directly linked to *Epischura*.

The effect of *Diaptomus* on the filtering behavior of *Epischura* was also examined by measuring the filtering rate of *Epischura* in treatments similar to all those described for *Diaptomus* (Fig. 1C). The data for these experiments were pooled and did not show a statistically significant difference between the filtering rate of *Epischura* in the presence or absence of *Diaptomus* ($P > .1$) (*13*). Although the filtering rate of *Epischura* was depressed significantly in two of the eight experiments (*14*), *Diaptomus* did not have a direct effect on the filtering rate of *Epischura*.

Thus, in laboratory experiments, a chemical released by *Epischura* causes a depression in the filtering rates of *Diaptomus*. In experiments with both species, the filtering rate of *Diaptomus* is reduced by 60 percent, from five times the filtering rate of *Epischura*, when rates in the single-species treatments of both species are compared, to less than three times the filtering rate of *Epischura* in two-species treatments (Fig. 2). This reduction in filtering rate by *Diaptomus* is evidence of interference competition whereby the weaker filter feeder has a negative impact on the feeding of the stronger grazer.

In order to estimate the importance of this allelopathy in the field, measurements of the time the animals spend in patches of one or both species at specific densities are needed, along with estimates of the density of competitors required to elicit a response and of the correlation between filtering rate and individual fitness. Most of these data are not available, or cannot be gathered, for Lake Tahoe populations; however, we have data on high density patches of both species that overlap spatially and temporally (*15*). The effect of allelopathy between *Epischura* and *Diaptomus* is likely to be episodic in situ, occurring at the specific depths and times of the year when both species are most abundant,

and inshore where large swarms of both species form in the late summer and fall (*16*).

Although the presence of *Epischura* can cause a substantial decrease in the filtering rate of *Diaptomus*, the ultimate effect on the fitness of *Diaptomus* may not be negative. For example, upon sensing the chemical released by *Epischura*, *Diaptomus* may stop feeding and attempt to avoid predation by ceasing to move or by spiraling away (*17*). The reduction in filtering rate could thus be the result of a mechanism for escaping predation that may have evolved because of predation pressure on early instars.

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References and Notes

1. J. L. Li and H. W. Li, *Limnol. Oceanogr.* **24**, 613 (1979); W. C. Kerfoot, *ibid.* **23**, 1089 (1978).
2. A. Sih, *Science* **210**, 1041 (1980).
3. J. J. Gilbert, *ibid.* **181**, 63 (1973).
4. S. A. Poulet and P. Marsot, *ibid.* **200**, 1403 (1978).
5. S. J. Threlkeld, *Limnol. Oceanogr.* **26**, 433 (1981).
6. C. L. Folt, E. Byron, C. Sims, S. Boddy, C. R. Goldman, in preparation.
7. The density of animals in the single-species treatments varied from four to six adults per 125 ml. For the two-species experiments the total density equaled the single-species density, and equal numbers of both species were used. In contact water and dialysis experiments the number of animals was equal to the number in the single-species experiment. There were three to six replicates of each experiment. The densities of animals used in these experiments represent the upper range of in situ densities that we have measured.
8. The animals were heat-killed, rinsed, soaked in a mild phosphate buffer for 2 hours, and solubilized in 0.5-ml Soluene-350 (Packard) for 24 hours at 50°C. Then 10 ml of Dimilume (Packard) was added, and the radioactivity in the animals was counted in a Beckman LS-100 scintillation counter. The food suspension (1 ml) was filtered onto 0.45-μm HA Millipore filters (three replicates). Filters were dissolved in Bray's scintillation fluid and counted. The filtering rates were calculated as milliliters per animal per day = counts per minute in the animal/counts per minute in the food divided by length of feeding period (hours)/24 hours.
9. The data were analyzed two ways with the same statistical result. The difference between filtering rates of animals in all single- versus all two-species experiments was tested by the Mann-Whitney U test ($P < .01$). Filtering rates from experiments at seven different times were pooled for single- and two-species treatments. Analysis of variance resulted in a significant difference between treatments at $P < .005$.
10. The water in the dialysis tubes was stirred several times during the 24-hour incubation period. If the equilibrium was complete for ammonia and other low molecular weight compounds, the result would have been a decrease in concentration to 12.5 percent of the concentration in the contact water. Since the filtering rates were significantly depressed in the presence of dialysis water, we hypothesized that the chemical involved was either equally effective at very low concentrations or was a large molecular weight compound unable to pass through the tubing.
11. As a control for the effect of the manipulation, *Diaptomus* was tested for an effect on itself. The water was prepared in the same way as *Epischura* contact water and dialysis water.
12. Each species was also examined for an effect on the filtering rate that might be due to the physical or chemical presence of the other. The results of the three experiments with *Diaptomus* (alone, in *Diaptomus* contact water, and in *Diaptomus* dialysis water) were pooled and tested for differences from two-species experiments (both species together, *Diaptomus* in *Epischura* contact, and *Diaptomus* in *Epischura* dialysis). The difference was statistically significant ($P < .005$).
13. Although the effect of *Diaptomus* contact water on *Epischura* filtering rates was significant ($P < .05$) with data pooled from experiments on four dates, the effect was not significant for three of four experiments. The overall significance was due to the highly significant depression measured on 14 April 1980.
14. Our data indicate that a depression in *Epischura* filtering rates resulting from exposure to *Diaptomus* occurred only when *Epischura* filtering rates in single-species experiments were above 1 ml per animal per day. On the other dates *Epischura* filtering rates were so low that it may have been impossible to reduce them further without killing the animals. We suggest that *Epischura* may only be affected by *Diaptomus* when its filtering rate is above some threshold value.
15. J. T. Rybock, thesis, University of California, Davis (1979).
16. E. Byron, in preparation.
17. C. L. Folt, personal observation.
18. We thank R. Gersberg, E. Byron, R. Folt, K. Hopper, D. Peart, R. Richards, and an anonymous reviewer for suggestions and assistance and M. Smith for manuscript preparation. Supported by NSF grant DEB79-16221.

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Central Norepinephrine Metabolism During Alcohol Intoxication in Addicts and Healthy Volunteers

Abstract. *The concentrations of the major norepinephrine metabolite, 3-methoxy-4-hydroxyphenylethylene glycol (MOPEG), in lumbar cerebrospinal fluid of alcoholic patients were markedly elevated during intoxication and successively declined during 1 and 3 weeks of abstinence. During intoxication the MOPEG concentration in cerebrospinal fluid showed a statistically significant correlation with the blood alcohol concentration. In healthy volunteers who received 80 grams of ethanol, the MOPEG concentration in cerebrospinal fluid increased significantly. Healthy subjects sampled during intoxication had significantly higher concentrations of MOPEG in the cerebrospinal fluid than did subjects sampled after the end of intoxication. The results indicate that alcohol administration markedly stimulates norepinephrine metabolism in the central nervous system in human subjects, possibly by increasing unit impulse activity of central noradrenergic neurons.*

In spite of extensive research, the mechanisms for the euphoriant effect of alcohol are still unknown. Nor have the psychiatric symptoms dominating the withdrawal reaction in alcohol addicts been definitely correlated to specific alterations of brain biochemistry. In patients with delirium tremens (*1*), elevated concentrations of MOPEG (3-methoxy-4-hydroxyphenylethylene glycol), the major norepinephrine metabolite, have been observed in the cerebrospinal fluid (CSF). This effect has been assumed to reflect an increased release of norepinephrine in the central nervous system in connection with the development of the delirious symptoms. Some animal experiments support this assumption, since a stimulating effect of acute alcohol intake on norepinephrine synthesis and metabolism in the brain has been reported (*2*), but other studies could not verify these results (*3*). The demonstration of a role of the noradrenergic system in the reinforcing effect of ethanol on self-administration of the compound in rats also supports a critical interference of ethanol with noradrenergic mechanisms in the central nervous system (*4*). This view is further supported by the findings that the catecholamine synthesis inhibitor α-methyltyrosine counteracts the stimulating effects of alcohol in rats and healthy volunteers (*5*).

We have reported the presence of elevated concentrations of MOPEG in the CSF of patients during alcohol withdrawal (*6*). This effect was selective, since concentrations of two other major transmitter metabolites, homovanillic acid and 5-hydroxyindoleacetic acid, in the CSF were not elevated or correlated with the MOPEG concentrations (*7*). The stimulation of central norepinephrine metabolism during alcohol withdrawal may be related to direct or indirect effects of alcohol on the noradrenergic system. If the MOPEG elevation in the CSF is related to direct effects of ethanol, it might be correlated with the blood alcohol concentration during intoxication. A MOPEG elevation in the CSF might also be produced during alcohol administration in healthy volunteers.

We analyzed concentrations of MOPEG in the lumbar CSF of alcohol addicts and healthy volunteers and found that in both groups MOPEG concentrations were markedly elevated during intoxication. In the addicts, where very high concentrations of alcohol were found, there was a statistically significant correlation between the alcohol concentration in the blood and the MOPEG concentration in the CSF.

In one group of alcoholic patients ($N = 18$), CSF samples were taken when the patients were intoxicated and immediately after admission to the hospital (day 1). Samples were taken again after

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