are repellents. All of the attractants discovered so far are compounds such as amino acids and sugars capable of sustaining rapid cell growth, while repellents can all be associated with some deleterious effect. Phenol and indole are toxic at high concentrations, and are excretion products of tyrosine phenol lyase and tryptophanase reactions of organisms in soil and fecal matter (*13*). The inhibition of isoleucine biosynthesis by valine and hence inhibition of cell growth is well known (*14*). Acetate and other carboxylic acids are excretion products of fermentative metabolism and may be warning signals of crowded conditions. It was interesting that attractants act at considerably lower thresholds than repellents, but that the magnitudes of the responses above threshold are similar. These facts are in keeping with the respective significance of attractants and repellents to the organism. If highly toxic repellents are found, their taxis thresholds should be correspondingly low.

The relationship between chemotaxis and transport is still not clear. Chemotaxis toward an attractant is, however, a futile event if the compound is not subsequently transported and utilized, whereas chemotaxis away from a harmful repellent is a successful event in itself. Substances such as phenol and indole cannot be utilized as carbon sources by *Salmonella* (*15*), suggesting that the taxis binding protein may function solely as a sensory receptor devoid of any function in transport.

Our conclusions from this initial survey of repellents are the following. First, the response of bacteria to gradients of repellents is essentially the inverse of the response to attractants. In each case the favorable direction, whether a positive gradient of attractant or a negative gradient of repellent, causes decreased tumbling and hence a prolongation of travel in that direction. Second, competition experiments support the notion of discrete chemoreceptors with restricted specificity, as has already been found for attractants (*2, 9, 10*). Third, the additive nature of attractants and repellents suggests they may operate through a common mechanism. As has been discussed for attractants (*6*) this involves a biochemical "memory" which allows a past environment to be compared with a present one. Assuming that the initial event in chemotaxis is the binding of the chemical to a receptor protein, it is possible that the attractant-receptor complex of an attractant system is equivalent to the uncombined receptor of a repellent system and vice versa, but that subsequent elements of the two systems are identical and may in fact be shared with other tactic stimuli such as *p*H, oxygen, and (for photosynthetic organisms) light.

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Induction and Ecological Significance of Gigantism in the Rotifer Asplanchna sieboldi

Abstract. *Dietary α-tocopherol and cannibalism together induce the giant, campanulate morphotype. Campanulates, unlike the two smaller female morphotypes, do not respond to α-tocopherol by forming male-producing offspring. Campanulate production probably is very significant ecologically, allowing a rapid, adaptive response to increased prey size and a rapid reproductive rate uninterrupted by sexuality and consequent dormancy.*

Asplanchna sieboldi is a large, planktonic, usually predatory, ovoviviparous rotifer that can reproduce both sexually and parthenogenetically (*1*) and which may exhibit extensive nongenetic polymorphism in female body size and shape (*2–7*). The mode of reproduction depends on whether mictic or only amictic females are present. Amictic females usually predominate and always produce diploid females parthenogenetically. The morphologically similar, mictic females produce haploid eggs which develop into males parthenogenetically or into thick-walled resting eggs if fertilized. The phenotypic plasticity of females is extraordinary and involves three basic morphotypes with intermediates: (i) a relatively small, saccate type; (ii) an intermediate-sized, humped or cruciform type (*8*); and (iii) a very large, campanulate type (Figs. 1 and 2). Each transformation from one morphotype to another occurs between two or more generations, the phenotype of a given female being fixed shortly before birth (*9*).

Dietary α-tocopherol (vitamin E) induces amictic saccates to produce cruciform and some mictic offspring (*6, 10*). Resting eggs always develop into amictic saccates (*3, 4*), and this type of female continues to reproduce itself as long as the diet contains subthreshold levels of tocopherol. The factors necessary for the induction of campanulates have not been determined, although their presence is associated with the previous existence of cruciforms and with cannibalism or the ingestion of large prey (*4, 5, 7*). In this study the effects of α-tocopherol and cannibalism on the induction and mode of reproduction of campanulates are examined.

Cultures of two clones of *A. sieboldi* were kept at 25°C in the dark and fed a diet of either *Paramecium aurelia* (*11*) or conspecifics. Stock and experimental cultures were transferred daily. Generation times of the rotifers under these conditions were about 30 hours. When the rotifers became adults bearing late-stage embryos, they were killed and fixed in 30 percent and then 70 percent ethanol; they were measured from a dorsoventral aspect with an ocular micrometer in a Wild M-5 stereomicroscope at 37 or 50 magnifications (*12*). The standard errors of the means of these measurements were calculated for all sample populations. In order to prevent excessive bacterial growth penicillin G (300 μg/ml) was added to all cultures in experiments with tocopherol, including the controls.

The size distributions of clone 1 rotifers in two typical cultures with abundant paramecia (Fig. 3) show that adults were 400 to 720 μm long (means were 576 ± 5 and 529 ± 5 μm). If the supply of paramecia in such cultures became exhausted, some of the individuals ate the very small, newborn offspring of starving adults and grew larger than normal. The comparable size distributions of clone 1 adults in two cultures in which such starvation and cannibalism had progressed for about a day (Fig. 3) illustrate the presence of these larger animals, several being longer than 900 μm (means were 630 ± 8 and 657 ± 14 μm). Increasing the duration of paramecia deprivation and cannibalism resulted in a decrease in the size of the starving adults and in no further increase in the size of the cannibals. All rotifers in these cultures were amictic saccates. The significant increase in body size caused in some of these saccates by cannibalism is analogous to situations found in some ciliated protozoa (*13*). However, cannibalism alone cannot induce the larger, campanulate morphotype.

When cultured for several days on paramecia with emulsified 2×10^{-7} to $5 \times 10^{-7}M$ *d*-α-tocopherol (*14*), populations initiated with saccates were composed almost entirely of the larger cruciforms. The mean size of adults in one such clone 1 population was 831 ± 17 μm. Culturing amictic cruciforms on newborn saccates with α-tocopherol induced them to produce offspring of the campanulate morphotype. Well-fed campanulates from both clones were always larger than 1 mm and often attained lengths of 1250 μm. The body shape was similar to that of both paramecia-fed and cannibal saccates except that the body widths and especially the corona widths were disproportionately greater. Mean ratios of body and corona widths to lengths were as follows: campanulates, 0.55 and 0.53 for clone 1 and 0.57 and 0.57 for clone 2; paramecia-fed saccates, 0.51 and 0.41 for clone 1 and 0.50 and 0.41 for clone 2; and cannibal saccates, 0.53 and 0.43 for clone 1 and 0.52 and 0.44 for clone 2 (the standard error was ≤ 0.01 for all means). The campanulates in these two clones were similar in size to some found in natural populations (*7*) but were considerably smaller and less bell-shaped than others (*4*).

Three separate experiments with two clones show that both α-tocopherol and cannibalism, as opposed to a diet of paramecia, were required for the maintenance as well as the induction of the campanulate morphotype. In one experiment clone 1 campanulates were subdivided into three groups. Two groups were given a surplus of newborn saccates as food (30 to 100 newborns per campanulate), but only one of these groups was cultured with α-tocopherol. The third group was cultured on paramecia with α-tocopherol. Two groups of saccates were cultured in parallel on paramecia, one with and one without α-tocopherol. Cultures were maintained in plastic petri dishes (35 by 10 mm) containing 3 ml of culture fluid. Tocopherol was added to a concentration of $2 \times 10^{-7}M$ by injecting, for each milliliter of culture fluid, 2 μl of a $10^{-4}M$ aqueous emulsion prepared daily from a $10^{-2}M$ ethanolic solution. Adult rotifers from each culture were fixed after 5 days. The results from this and two other experiments, one of which lasted for 30 days, were very consistent and showed that (i) campanulates fed on young saccates with α-tocopherol continually reproduce themselves and never produce cruciforms (mean lengths of clone 1 and clone 2 campanulates after 5 days were 1137 ± 18 and 1224 ± 36 μm, respectively); (ii) campanulates deprived of α-tocopherol, whether fed on paramecia or young saccates, revert to the saccate morphotype after several generations without producing cruciform intermediates; and (iii) the offspring of both campanulates and saccates cultured on paramecia with α-tocopherol become more or less cruciform after one or two generations. The cruciform morphotype is maintained under these conditions, although a small but variable proportion of the individuals are campanulate in the apparent absence of cannibalism. These cam-

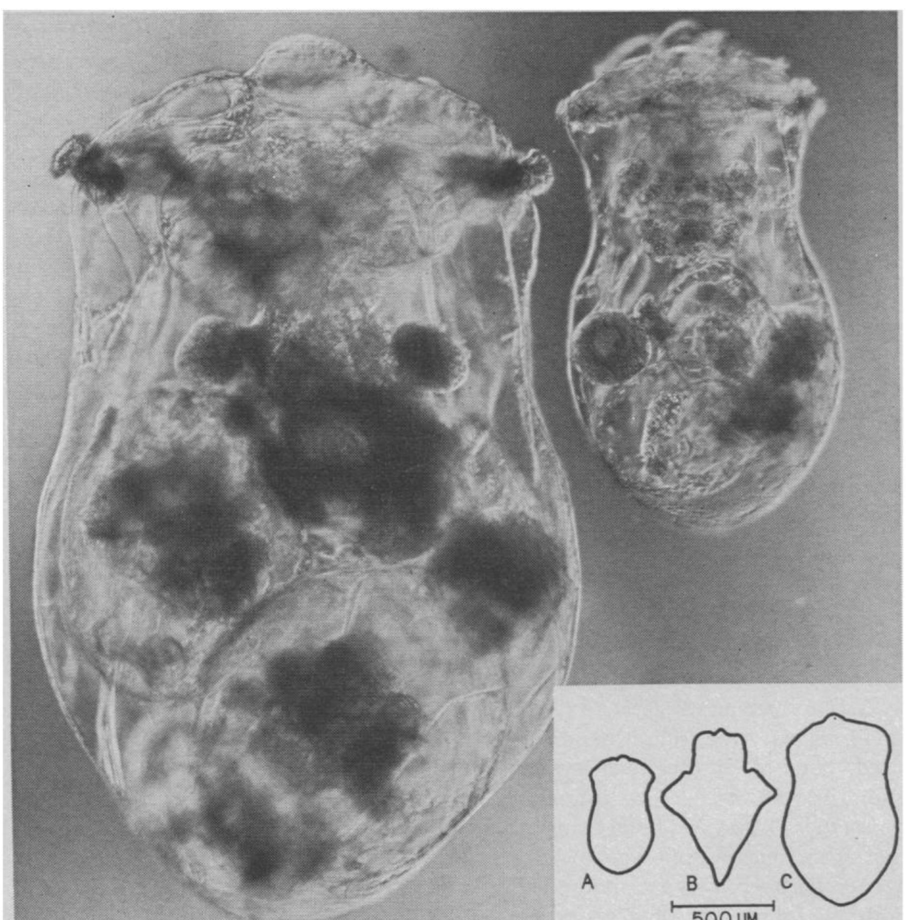


Fig. 1. Adults of the large campanulate and the small saccate morphotypes of the rotifer *Asplanchna sieboldi* (ethanol fixed; interference contrast optics, $\times$ 110). Fig. 2. Diagram of the three basic morphotypes of *A. sieboldi* females: (A) saccate, (B) cruciform, and (C) campanulate.

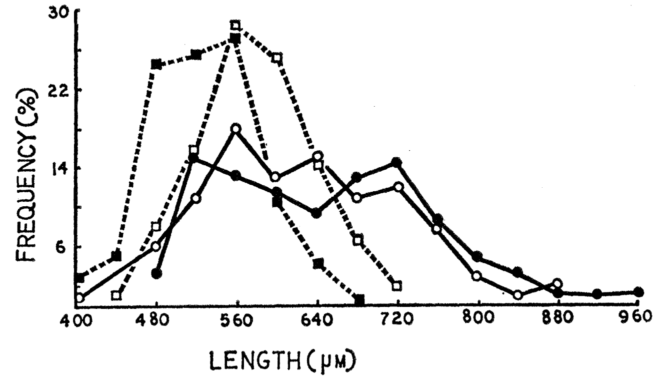
panulates are small (no more than about 1 mm in length) and reproduce slowly—probably because of their inability to capture enough of the relatively very small paramecia.

The marked increase in body size caused by α-tocopherol is the effect of both cytoplasmic growth and nuclear division. Cruciforms, in comparison with saccates, have the same number of nuclei in the syncytial hypodermis but have more nuclei in the syncytial gastric glands and vitellarium (*15*). Nuclear numbers in campanulates have not been examined in detail, but tentative nuclear maps indicate that campanulates have about the same number of nuclei in the hypodermis as saccates (*16*).

Although cannibalism is required for the induction and maintenance of campanulates in these experiments, its effect probably can be replaced by the ingestion of any relatively large prey species. The small size and low reproductive rate of the campanulates occurring infrequently in populations cultured on paramecia with α-tocopherol suggest that only the lack of large prey prevents attainment of full size and potential reproductive rate. Also, campanulates have been maintained on a diet of the crustacean *Moina* (*4*), and analyses of stomach contents show that natural populations of campanulates eat a variety of rotifer and crustacean prey, the latter, especially copepods, sometimes being dominant (*7*).

One of the most striking aspects of cannibal campanulates cultured with $2 \times 10^{-7}M$ α-tocopherol is their consistent failure to produce mictic offspring. Populations of paramecia-fed saccates invariably produce mictic offspring in response to this dose (*6, 10*). The α-tocopherol definitely is being incorporated by these campanulates and is mediating the body growth response, for without it the offspring revert to the saccate morphotype. Because there may be significant differences in the sensitivities of individuals in a clone of *Asplanchna* to a mictic female inducing stimulus (*11*), it is possible that campanulates are derived from individuals having the potentiality to undergo only the body growth response. However, when continually cultured with α-tocopherol, campanulates fed on saccates for many generations without producing mictics or cruciforms do produce them as soon as their diet is changed to paramecia. The following experiment was one of several which demonstrate that cannibalism inhibits the mictic female response in campanulates.

Fig. 3. Size distributions of *A. sieboldi* saccates from two cultures with abundant paramecia (dashed lines) and two cultures after about 1 day of paramecia deprivation and cannibalism (solid lines).



Campanulates were induced and maintained on saccates with $5 \times 10^{-7}M$ *d*-α-tocopheryl polyethylene glycol succinate (TPGS) (*14*). The water-soluble TPGS, introduced by injecting 0.5 μl of a $10^{-3}M$ ethanolic solution per milliliter of culture fluid, was expected to enhance the penetration of α-tocopherol into the cannibal campanulates (*17*). Forty-eight campanulates were subdivided randomly into three equal groups, and each rotifer was cultured individually in a 1-ml volume for 4 days. Individuals from one group, cultured on saccates with TPGS, produced a total of 203 offspring, all amictic. Individuals from a second group of campanulates, cultured on paramecia with TPGS, produced 155 offspring, 10.3 percent being mictic. The offspring from 10 of the 16 isolated campanulates in this group contained mictic individuals, many appearing after one or two generations. These mictics were about the same size as the cannibal campanulates; some were more or less cruciform, and others possessed no detectable humps. Individuals from the third group of campanulates, cultured on paramecia without TPGS, produced a total of 131 offspring. All of these were amictic and of increasingly small size; none were cruciform.

Although campanulates maintained on large prey other than conspecifics have not been investigated, it is likely that the campanulate morphotype will have the characteristic feature of producing neither mictic nor cruciform offspring, except when transforming from or into the cruciform morphotype. Thus, the ingestion of conspecifics, or probably large prey in general, modifies the response of *A. sieboldi* to α-tocopherol in several very significant ways. The size or perhaps the quality of the prey determines whether α-tocopherol will (i) stimulate the hypodermis to enlarge primarily in certain specific regions, as in cruciforms, or in a more generalized way, as in campanulates; and (ii) induce some oocytes to undergo two maturation divisions and become haploid, as in cruciforms, or be unable to elicit this response, as in campanulates.

My finding that cannibal campanulates do not produce mictic females is in apparent conflict with reports that campanulates produce males and resting eggs (*4, 5, 7*). The most extensive and best documented of these reports (*7*), however, shows that on almost every sample date the percentage of campanulates with resting eggs is either zero or very much lower than that for cruciforms. These mictic campanulates may be recently formed from cruciforms or in the initial stages of reverting to cruciforms, just as in my experiments.

The adaptive significance of the large size of the campanulate morphotype has been considered (*7, 18*). The production of campanulates by cruciforms may allow the population to utilize large prey species in the absence of smaller ones and, through cannibalism, to exist for at least short periods in the absence of other prey species. What has not been mentioned before, however, is the striking fact that this gigantism can be a direct, adaptive response to an increase in the size of available prey. Such direct adaptation in metazoa is very rare and reminiscent of the defensive, phenotypic response of the rotifer *Brachionus calyciflorus* to its predator *Asplanchna* (*19*).

To a more limited extent, gigantism is also possible within the saccate morphotype, which is maintained when the rotifers contain subthreshold amounts of tocopherol. Some saccates, for example, can become significantly larger in response to an increase in prey size —such as when they become cannibalistic (Fig. 3). Attainment of maximum potential size in the species, however, appears to be impossible without tocopherol. The adaptive significance, if any, of the α-tocopherol requirement for the extreme size of campanulates is enigmatic.

The inhibition of mictic female production in campanulates may be extremely adaptive, for it would allow continuous, rapid, parthenogenetic reproduction at times when the diet contains large, as well as tocopherol-rich, prey. Otherwise, production of males and resting eggs, which may be dormant for a long time, would decrease the reproductive rate when such food was abundant. Since α-tocopherol is found in most algae (*20*) and hence in algivorous zooplankters, the diet available to this species often must be tocopherol-rich. Inhibition of sexuality in campanulates would not endanger the long-term survival of the population by resting eggs, because natural populations are not composed entirely of campanulates (*4, 5, 7*) and because sexual cruciforms would be produced before, and possibly after, campanulate production.

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Fire and the Nitrogen Cycle in California Chaparral

Abstract. *Analysis of soils from burned and unburned chaparral indicates that high nitrate concentrations following fire are due to the addition of ammonium and organic nitrogen in the ash. Inhibition of mineralization in unburned chaparral results in low nitrate concentrations. Fluctuations in the amount of soil nitrate in unburned chaparral are the direct result of foliar leaching.*

Fire is a frequent occurrence in chaparral, a shrubby vegetation common in areas subject to prolonged summer drought. Many recent studies have emphasized the beneficial aspects of such brush fires in the maintenance of a healthy plant cover (*1*). One such benefit is the addition to the soil of ash which has high concentrations of nutrients that were previously held in the standing crop. Nitrate has been of particular interest in this regard because of its apparent deficiency in many chaparral soils (*2*) and comparatively high concentrations after burning (*3*). Although speculation is plentiful, the questions of why chaparral soils are low in nitrate and why nitrate concentrations increase after fire have largely been left unanswered.

The data presented here are part of a study undertaken to investigate changes in various essential plant nutrients after fire and to evaluate their importance in revegetation after fire. In September 1971 a 30-ha plot of dense chaparral, dominated by *Adenostoma fasciculatum* (chamise), burned in the Santa Ynez Mountains near Santa Barbara, California. Because of its close proximity to unburned chaparral growing on the same soil type and slope, this area was ideal for study. Soil samples were collected immediately after the burn and at nine other times through the next 14 months. On each date six 1-kg samples of the upper 2 cm of mineral soil were taken from each of the burned and unburned chaparral. After being passed through a 2-mm screen, each sample was analyzed for organic matter content, total nitrogen, exchangeable ammonium, and exchangeable nitrate (*4*). The *p*H of each sample in water was also determined (*4*). Soil samples were also collected in the field in airtight tins for moisture analysis. To evaluate the effects of shrub removal without the addition of ash, clearings were made in mature chaparral in the late summer of 1971 and of 1972. Soil from these clearings was analyzed in the same manner as that from the burned and mature chaparral areas. Statistical comparisons were made with the use of Student's *t*-test. In this report all soil nutrient values are expressed relative to soil oven-dry weight.

To assess the importance of foliar leaching of nutrients in unburned chaparral, several rain-collection vessels were placed under the shrub cover and in the cleared areas in the fall of 1972. These vessels were fitted with a float valve allowing the collection of a maximum of 0.6 cm (0.25 inch) of rainwater from any single storm. As materials washed from plant leaves would be concentrated in the first few milliliters of rain drip, this valve arrangement prevented dilution and aided quantification. Collected rainwater was returned to the laboratory as quickly as possible for analysis.

The total content of organic matter in unburned chaparral soil varied between 12 and 24 percent, but constituted only 6 to 8 percent of the burned-over soil. The total nitrogen content was also lower in the burned soil than in the unburned soil (2.7 versus 3.0 mg of nitrogen per gram of soil), but this apparent loss was not proportional to the loss in total organic matter.

The aboveground parts of several *Adenostoma* shrubs were incinerated, and the ash was analyzed in the same manner as the soil. The nitrate content was comparatively low in the ash (1.3 μg of nitrogen per gram), whereas the ammonium content was high (127 μg of nitrogen per gram). The total nitrogen content was 7100 μg/g. Ignition of this ash at 700°C resulted in a 38 percent loss, indicating a high content of organic matter. It is clear that ash not only supplies mineral nitrogen to the soil but may also provide a reservoir of organic nitrogen.

Soil nitrate concentrations were nearly equal in the burned and unburned chaparral soil immediately after the fire (Fig. 1). Ammonium concen-