antiinflammatory response to steroids awaits further investigation. Our suggestion that σ receptors may be involved in the antiinflammatory action of certain steroids cannot be ruled out at present. As to the possibility that exogenously administered steroids may induce psychiatric disturbances, several reports have already indicated such a finding (*8*).

We close with the following statement from a review article by Gorski and Gannon (*9*).

> It should be apparent to the reader that a wide variety of mechanisms have been suggested to explain steroid hormone action. One of the minority views mentioned here or perhaps not even referred to in this review may hold the key to understanding steroid hormone action. Until more substantial evidence clearly establishes the validity of one model, it is obviously prudent to maintain an open and critical mind when considering new data and their interpretation.

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Hydrolysis of Carbon Tetrachloride

The ocean water dating technique described by M. Krysell and D. W. R. Wallace (*1*) uses careful measurements of the ratios of concentrations of several anthropogenic halocarbons. Krysell and Wallace recognize that some of these compounds can hydrolyze, but our recent experiments (*2*) show that the standard literature reference for hydrolysis of carbon tetrachloride (CCl_4) (*3*) is wrong. That is, the reaction is reported as second-order in CCl_4, but we have found clear first-order kinetic behavior. It is only for a first-order reaction that the half-life is independent of concentration. In addition, hydrolysis reactions have significant activation energies, so half-lives vary over wide ranges as temperature changes. The 7000-year half-life cited by Krysell and Wallace is a calculated value for CCl_4 assuming a second-order reaction process at 25°C and an initial concentration of 1 ppm. For a first-order reaction, the half-life $\tau = 0.69/k$, where k is the rate constant. Specifically, we have found that, for CCl_4 $k(\text{hyd}) = 4.07 \times 10^{12} \exp(-13{,}790/T)$ min^{-1} and for methyl chloroform (CH_3CCl_3), $k(\text{hyd}) = 2.96 \times 10^{14} \exp(-13{,}970/T)$ min^{-1}, where T is temperature in degrees Kelvin. These rate constant expressions yield the values shown in Table 1:

Table 1.

	CCL_4		CH_3CCl_3	
T (°C)	k (min^{-1})	τ (year)	k (min^{-1})	τ (year)
25	3.25E-8	40.3	1.29E-6	1.0
10	2.80E-9	468	1.08E-7	12.2
0	4.70E-10	2790	1.77E-8	74.2

The results in Table 1 show that Krysell and Wallace correctly assumed negligible degradation of CCl_4 in seawater at 0°C, but for what appears to be the wrong reason. Clearly, CCL_4 does not have a 7000-year half-life under all conditions, but at 0°C is half-life is very long compared with the other ages of interest. Conversely, methylchloroform is also stable enough at 0°C that its concentration should provide valid and independent dating information. However, if this technique is used in significantly warmer water than those found in the Arctic Sea, then the hydrolysis rates of these compounds should be integrated into the age calculations. It should be reemphasized that both CCl_4 and CH_3CCl_3 hydrolyze by (pseudo) first-order reactions with no pH dependence and no significant contribution from other nucleophilic catalytic agents, so that the hydrolysis rate is determined strictly by the temperature.

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Response: The new measurements by Jeffers *et al.*, if applicable to seawater, have implications for the use of CCl_4 as an oceanographic tracer. Figure 1 shows that for a volume fraction of ~92% of oceanic waters, more than 95% of the initial CCl_4 level remains even after 70 years. The absolute amount of CCl_4 loss (not shown) in much of the older, colder water is almost undetectable with the use of current analytical techniques (for example, less than 0.025 pmol/liter). For the relatively small volume fraction of warm ocean waters, corrections for hydrolysis should be applied. Such corrections necessitate that temperature as well as the tracer be modeled. Fortunately the warmer, upper-ocean water masses tend to have sufficiently short renewal times with the ocean surface so that they are labeled with more recently introduced members of the "halocarbon tracer suite" [F-11 (CCl_3F), F-12 (CCl_2F_2), F-113 (CCl_2FCClF_2)]. Hence corrections will be both small and facilitated by supporting tracer data.

The unique CCl_4 input function (*1*) is ideally suited to studies of the circulation of the cold, deep waters that make up the bulk of the world's oceans. Hydrolysis corrections are almost negligible in these waters and in high-latitude seas (for time scales of less than 100 years). Even over 500 years [the average mixing time scale of the ocean deeper than 1500 m (*2*)], losses due to

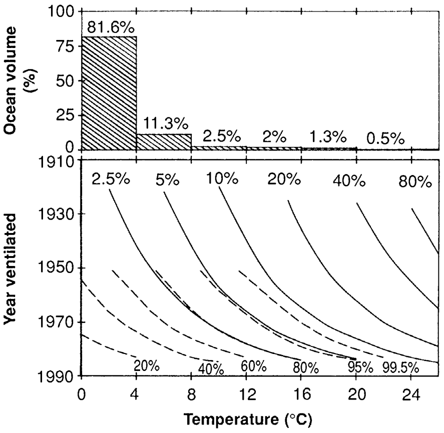

Fig. 1. Plot of the percentage concentration decrease by the year 1990 for CCl_4 (solid lines) and CH_3CCl_3 (dashed lines) for various water temperatures, based on the assumption that a water mass equilibrates with the atmosphere during a "ventilation year" and is subsequently isolated from exchange with the atmosphere and other water masses. Absolute concentration decreases were also calculated; for CCl_4, a preindustrial atmospheric CCl_4 mixing ratio of 6 ppt was assumed (*1*).

hydrolysis would be small, so it is still possible to estimate preindustrial CCl_4 levels accurately from measurements in slowly renewed deep waters (*1*).

In contrast, loss of CH_3CCl_3 would be considerable even in cold waters over a period of only 40 years (that is, since CH_3CCl_3 was introduced into the environment), and it has an input function that is not dramatically different in nature from those of F-11 and F-12 (*1*). We thus reiterate that no great advantage will be gained from its use as an additional tracer.

We recommend that CCl_4 be measured together with F-11, F-12, and F-113 during future oceanographic sampling expeditions. We also encourage our colleagues to perform hydrolysis rate measurements for these compounds and the chlorofluorocarbons in seawater: data concerning the latter class of compounds, and measurements in seawater in general, are notably lacking in the literature.

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Caterpillars and Polymorphisms

Greene reports (*1*) that two seasonal morphs of the herbivore *Nemoria arizonaria* are adapted for feeding and hiding on their respective substrates, oak catkins and leaves. While we do not dispute the occurrence of this polymorphism, the striking resemblance of each to its substrate, or its purported adaptiveness, we contend that the proposed mechanism for its induction, dietary tannin, is unlikely.

Greene's conclusion that the "developmental polymorphism is triggered by the dietary concentration of defensive compounds [tannins]" is based on two lines of evidence. First, he observed that caterpillars eating spring catkins remain as catkin morphs while those feeding on summer foliage of four Arizona oak species develop into twig-like morphs. He assumes that catkins are low in tannins relative to leaves on the basis of citations (*1*, note 16) that do not deal explicitly with catkin phytochemistry. We examined this assumption by analyzing tannin content of catkins of *Quercus emoryi*, one of the host plants of *N. arizonaria* (*2*). Condensed tannin content of catkins is relatively low [three trees, 0.59% (± 0.05), 0.39% (± 0.01), 0.29% (± 0.10)] but comparable to that of mature leaves (*2*). Hydrolyzable tannin content, however, is relatively high [three trees, 15.08% (± 2.28), 18.50% (± 0.82), 17.65% (± 2.66) (*2*)]. Clearly, low tannin content is not a common feature of catkins, weakening Greene's contention that dietary tannin level is the mechanism for the polymorphism.

Second, Greene found that diets of catkins plus the tannin quebracho, of catkins plus leaves, or of only leaves induced the twig morph. The latter two artificial diets included new, spring leaves (*3*), but in nature the twig morphs feed on mature, summer leaves. Something common to mature leaves and artificial diet plus new leaves or quebracho must induce the twig morph; Greene proposes it is either specific tannin compounds or tannin concentrations, but neither are likely to be shared among the three diets. *Quercus emoryi* and *Q. arizonica*, two hosts of *N. arizonaria*, vary seasonally in tannin types and concentrations (*4*). New and mature leaves differ in condensed tannin content (new, <1% dry mass; mature, ≈5% dry mass) and hydrolyzable tannin content (new, 25% dry mass; mature, 10 to 12% dry mass), as well as in other phenolic compounds (*4*). Quebracho is mostly condensed tannins, yet it triggers the same response as new leaves with little condensed tannin. Further, condensed tannins are unlikely to be the inducing factor since they are typically bound indissolubly to plant tissues (*5*) and are too large to pass through the peritrophic membrane of insects (*6*). Finally, Greene presents no evidence, and we are not aware of any, for the existence of tannin "receptors" in insects.

A more parsimonious explanation for Greene's results is that the twig morph is simply induced by a low protein diet. Low protein is a shared feature of the twig morph's natural and artificial diets. New and mature oak leaves are low in protein (for example, *Q. emoryi*, 2 to 5% dry mass; *Q. arizonica*, 2 to 6% dry mass). Adding quebracho or ground leaves that contain phenolic compounds to an artificial diet would lower relative protein, since tannins bind to plant proteins in agar media (*7*). Higher protein levels in catkins could inhibit development of twig morphs.

Low dietary protein triggers polymorphisms in other insects (*8*) and in vertebrates (*9*). Low protein is also consistent with slow development and decreased mass and fecundity of the twig morph (*10*). Toughness (fiber content) of leaves could also induce the twig morph. Consumption of hard tissues can induce morphological changes in insects (*11*) and in vertebrates (*9*). Greene's dietary experiments do not distinguish among increased tannins, reduced protein, or increased toughness as the inducing mechanism because tannins interfere with protein availability and fiber content was not controlled. Dietary experiments with varying levels of protein without tannins or fiber could resolve this issue.

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Response: Faeth and Hammon are correct in pointing out that the feeding experiments with *Nemoria arizonaria* (*1*) do not establish what differences between catkin and leaf diets are responsible for inducing the development of the two morphs. Polyphenolic compounds may trigger the development of