imal and a novel opponent were placed in the wooden arena and allowed to interact until the test animal submitted. We used two measures to assess submissiveness during this test. The first, the latency to submit minus the latency to attack, was defined as the duration of the interval between the opponent's initial attack and the subsequent submission by the test animal. According to this measure, the shorter the interval, the more submissive the test animal. The second measure was the number of aggressions or attacks by the opponent needed to induce submission in the test animal; here, the fewer attacks required, the more submissive the test animal.

Administration of ACTH immediately after the initial defeat led to increased submissiveness in the mice tested at 24 or 48 hours, but not in those tested at 168 hours (Fig. 1). This effect was apparent in both measures of submissiveness used, the latency to submit minus the latency to attack ($P < .06$, by analysis of variance) and the number of aggressions to submission ($P < .01$). Thus, increasing ACTH levels after an initial defeat leads to increased submissiveness in future competitive encounters, and this effect lasts for at least 48 hours but not for 7 days.

The second experiment examined the effects of postdefeat treatments with lysine vasopressin on future submissiveness. The design of this experiment was identical to that of the first, except that the mice (8 to 11 per group) in the three experimental groups were treated with a single subcutaneous injection of synthetic lysine vasopressin (Nutritional Biochemicals Corp.), which was administered at a dosage of 0.08 I.U. in 0.05 ml of saline. This dosage was selected because it has marked effects on avoidance responding in mice (*3*).

In this second experiment, postdefeat treatment with lysine vasopressin led to increased submissiveness in those mice tested at 48 or 168 hours, but not in those tested at 24 hours (Fig. 2). Again, this effect was reflected in both measures of submissiveness used ($P < .01$ for both). However, the control mice tested at 24 hours were quite submissive, and thus a "ceiling effect" may have precluded seeing any effects of vasopressin at this testing time. Therefore, this study shows that increasing vasopressin levels immediately after an initial defeat leads to increased submissiveness in future encounters, and that this effect, once evident, persists until at least 7 days after the initial experience.

These two studies show that increasing the levels of the pituitary peptides ACTH and vasopressin immediately after an initial defeat leads to increased submissiveness in future competitive situations. Because submissive responses can be viewed as naturally occurring avoidance reactions (*11*), these findings are consistent with earlier studies of laboratory-specific avoidance responses in showing that raising the levels of these hormones after initial stressful experiences enhances later adaptive responding (*6*). Furthermore, the time courses of the effects of ACTH and vasopressin observed here are similar to those observed in earlier studies of avoidance behavior: ACTH exerts relatively short-lived effects, whereas those of vasopressin last much longer (*3, 12*). Thus, although ACTH and vasopressin have similar facilitative effects on adaptive responding, the time courses of their effects are different.

Because both ACTH and vasopressin levels normally increase following exposure to stressful stimuli (*13*), it seems likely that the techniques used in these studies produced a functional exaggeration of those normal peptide responses to stress. Therefore, we interpret the results of these two studies as supporting the suggestion (*1, 2, 4*) that the normal peptide hormone responses to initial stressful experiences in some way can facilitate the memory of those experiences, as reflected in future adaptive behavioral responses.

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Intermediate-Disturbance Hypothesis

There is a tropical island ideally suited for testing Connell's (*1*) intermediate-disturbance hypothesis for tropical forest species diversity, upon which there are contrasting disturbed and undisturbed areas. Whitmore's (*2*) monograph on the forests of the Solomon Islands is an essay on disturbance by cyclones and the adaptation of tree species for different roles in the regeneration process. The cyclone-disturbed north coast forests of Kolombangara Island are dominated by relatively light-demanding tree species that are not reproducing themselves in the understory; shade-tolerant species are also present in lesser numbers. The relatively undisturbed west coast forests are dominated by fewer, more shade-tolerant species that are well represented in the understory. The number of tree species scarcely differs between the north and the west coasts (129 versus 122, respectively), but species diversity is greater in the cyclone-disturbed north coast forests (.898 as against .715 on the west coast) (*3*). The noticeably greater evenness of representation of species in the disturbed forests accounts for this. This comparison is especially suitable because it demonstrates the effect of disturbance in ecological time on an island where the species pool is the same for both sample areas (evolutionary changes are discussed below). In this instance, the difference in number of species is disappointingly small, but this might be related to the position of these communities on a scale of disturbance relative to dynamic stability (*4*).

Connell's (*1*) dated reference to the

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importance of disturbance to mid-latitude plant species diversity gives the impression that this subject has been neglected. To the contrary, the relation between species diversity and disturbance is currently the subject of much theoretical and empirical study (*4-9*). I will not discuss similar work on mid-latitude marine intertidal communities (*10*). Grime (*7*) presented much direct evidence that plant species richness in British pastures is greatest at intermediate levels of either disturbance or physiological stress. The intermediate-disturbance hypothesis illustrated in Connell's figure 1 was also inferred by Grime and is illustrated in his figure 4, a transect from undisturbed pasture to a heavily trampled path. Grubb's (*8*) recent account of the regeneration niche in relation to plant species diversity is an important synthesis for both mid-latitudes and tropics, complementing Connell's paper. Connell deals more with levels of species richness and frequency of disturbance, while Grubb examines the variety and ubiquity of plant species' adaptations for occupying different niches appearing during the process of regeneration which follows disturbance. Both conclude that diversification in the regeneration niche accounts for a large part of plant species diversity.

Horn (*4*) deduced the intermediate-disturbance hypothesis from a Markov-chain model of forest succession, finding that diversity is greatest at an intermediate level of the ratio of disturbance to dynamic stability. That is, the effect of disturbance upon diversity is relative to the rate of compositional recovery [see also (*5*)]. Horn's result lends insight into observations that species diversity is often greatest midway along gradients in physiological stress instead of where there is least stress (*7*). A gradient in physiological stress is ipso facto a gradient in dynamic stability (that is, rate of plant growth, plant replacement, and compositional change). If there were an approximately constant level of disturbance across the gradient (*11*), then we might observe the same effect as along a gradient in disturbance, because it is the ratio of disturbance to recovery that is important.

Both Connell and Grime compare the intermediate-disturbance hypothesis to the paradigm that competition limits diversity. Disturbance is seen as a way of continually forestalling competitive elimination of a great many species. This explanation represents only one aspect of a broader theoretical synthesis which has recently emerged. Temporally variable events that are uncorrelated in space, like tree blowdowns, desert rainstorms, badger disturbances, or fires, create spatial heterogeneity that can serve as a basis for niche diversification (*5, 8, 9*). This particular sort of spatio-temporal heterogeneity ("disturbance" in a broad sense) and dispersal among patches are keys to the maintenance of species diversity by disturbance (*5*). Many of what Connell calls nonequilibrium hypotheses are now understood in the context of macroscopic equilibrium (*5*).

There are geographical and evolutionary corollaries to the intermediate-disturbance hypothesis. Latitudinal gradients in forest tree species diversity may be owed in part to the increase in thunderstorm frequency (and by inference the frequency of windthrow) from the poles to the equator (*12*). Horn's (*4*) result on the ratio of disturbance to dynamic stability provides an attractive partial explanation for the evolution of plant species diversity in a wide range of vegetation types. This ratio is probably characteristic of a vegetation type, inasmuch as the factors determining it (climate, soils, physiographic processes, and variability caused by fire, wind, landslide, solifluction, ice action, herbivory, and variable rainfall) have probably been associated with a vegetation type over evolutionary time, during large fluctuations in its areal extent, degree of geographical isolation, and geographical location. A characteristic level of disturbance or spatio-temporal heterogeneity may thus have been more constantly associated with a flora or a vegetation type through evolutionary time than have area or geographical subdivision, two factors invoked as alternative explanations for the evolution of plant species diversity (*13*).

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Fox (*1*) is correct in pointing out that I did not refer to the large amount of theoretical and empirical study on the importance of disturbance to the diversity of mid-latitude communities of plants and marine intertidal organisms. As stated (*2*, p. 1302) I intentionally restricted my attention to only two communities, tropical rain forests and coral reefs, and further limited it to the trees and corals themselves. I did not intend to give the impression that this subject has been neglected in theoretical or empirical studies at mid-latitudes; I have read and benefited from many of these studies, including Fox's present comment.

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Where Has All the Carbon Gone?

Woodwell *et al.* (*1*), in discussing biota and the world carbon budget, conclude that terrestrial vegetation, mainly forest, is a major source of release of carbon to the atmosphere. They find that "the most probable range for the total world release from the biota annually is 4 to 8×10^{15} g of carbon." They also mention that if these appraisals are correct, carbon released from the biota approximately equals that released from burning fossil fuels. Since only 2.3×10^{15} g of

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