stressors produce higher levels of circulating corticosteroids than controllable stressors (*22*). However, since they used stress conditions very different from ours, it cannot be assumed that our groups differed in corticosterone levels. Another possibility concerns endogenous opioids. Opiate antagonists can inhibit tumor growth and prolong survival in animals implanted with tumors (*23*). As already noted, Shavit *et al.* (*14*) found conditions that produce opioid analgesia to be immunosuppressive, while conditions that produce nonopioid analgesia were not. Lymphocytes and neutrophils have been reported to possess opiate receptors (*24*), and our inescapable shock conditions produce opioid analgesia (*15*). Perhaps an endogenous opiate is released, causing immunosuppression. However, many other hormones and neuroregulators affect lymphocyte activity, and many are altered by stress (*25*).

Regardless of the mechanism involved, these findings suggest a link between psychological factors and disease. Psychosocial and environmental factors have long been recognized as affecting health and disease (*1*), and the immune system has often been thought to be the link. However, in experiments involving direct measures of immune functioning, the impact of simple physical stressors has typically been studied. By demonstrating the responsiveness of the cellular arm of the immune system to the dimension of controllability rather than to shock per se, our findings suggest that the immune system can be modulated by more complex psychological factors. These results also suggest that the immune system might be altered by the sorts of variables known to modulate previously studied consequences of uncontrollability, such as learned helplessness (*26*).

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Population Density of Tropical Forest Frogs: Relation to Retreat Sites

Abstract. *The forest frog* Eleutherodactylus coqui *defends specific sites for retreats and nests in the Luquillo Forest, Puerto Rico. The hypothesis that shortages of nest and retreat sites limit population size was tested by placing 100 bamboo frog houses in plots measuring 100 square meters in areas of high frog density. These new sites were readily adopted by adult frogs. After one year, experimental plots had significantly more nests and frogs of all sizes than did control plots.*

Shortages in retreat and nest sites are often cited as limits to population size (*1*), but few studies (most of them of birds) have shown the effects on population of an increase in the number of retreat and nest sites (*2*). In studies of reef fishes, critical experiments were either lacking or showed equivocal results (*3*). We now report that population density increases significantly when additional retreat and nest sites are provided for *Eleutherodactylus coqui* Thomas, a terrestrial-breeding frog that is abundant throughout Puerto Rico (*4*). We have studied the biology of *E. coqui* in the Luquillo Division, Caribbean National Forest, since 1978. The coqui is nocturnal, calling and foraging from ground to subcanopy heights, with most activity occurring within 3 m of the ground. Males are territorial and call from exposed sites on, for example, leaves, tree trunks, or human artifacts. Eggs, attended by males, are laid in specific kinds of sites, usually rolled leaves or leaf axils on or near the ground. Of 31 nests located in July 1978, 97 percent were within 1 m of the ground and 87 percent were in rolled leaves on the ground. Such sites also serve as diurnal retreats. At 350 m in mid-elevation forests at El Verde Field Station, where we conducted our study, the preferred nest and diurnal retreat sites are within fallen rolled leaves of *Cecropia peltata* or of the sierra palm, *Prestoea montana*. Frogs are discriminating in their selection of nests and retreat sites (*5*). Our knowledge is based on the location of hundreds of nests and retreats during numerous complete searches of possible off-ground sites as well as ground litter.

Population densities of coqui vary greatly; we have found 1 to 24 adults and 1 to 230 frogs of all size classes per 100 m^2. The highest densities occur in areas of high density of sierra palm. Palms provide axils of leaf bases and fallen fronds, which are favorable calling, foraging, retreat, and nest sites. High population densities, the rapid decay of dried leaves, and the behavior of the frogs suggest that the availability of retreat and nest sites is important in limiting population size. Adult males are territorial and actively defend eggs on which they sit. Intruding males attempt to eat eggs and if successful may usurp the nest sites (*6*). Only one individual occupies a retreat, and both sexes aggressively defend retreats against other frogs.

To test the hypothesis that shortages of appropriate retreat and nest sites limit population size, we established four pairs of plots in the forest; each pair consisted of an experimental and a control plot. Plots were 10 by 10 m. Four frog houses (see legend to Fig. 1) were hung on each of 25 trees in each experimental plot. The density of trees was similar for all plots. Plots were censused once each month, both day and night, in July, August (day only), and October 1979, then again from January to August 1980. Counts were made on the same days and in the same manner for each pair of plots. Any errors in counts are presumed to be similar for all plots. During diurnal searches, all appropriate retreat and nest sites, including frog houses, were examined. In experimental plots, during the day, most of the adults—and only adults—were found in houses. In both experimental and control plots, possible nest and retreat sites were well known and easily located so that each could be examined during searches. Nocturnal counts (at 2000 to 2300 hours) were made with a lantern along 2-m strips; in addition to retreats, we examined all surfaces from ground to the upper limits of visibility. Most of the population perch on understory vegetation, which seldom exceeds 3 m in height. Because of intolerance to desiccation, few frogs climb trees to forage in the canopy and then only on wet nights (*7*).

Results are shown in Table 1. Before the test, populations in pairs of plots did not differ significantly (initial points in Fig. 1) ($P > 0.4$, t-test). In all pairs of plots, the pattern of population changes was similar to that shown in Fig. 1. In addition to the effects of improved habitat, results from all plots showed seasonal effects on populations. Numbers increased rapidly during the summer as the year's young appeared after increased breeding during spring and summer. During winter months when little reproduction occurred, the number of preadults dropped markedly. Reproduction increased in April and May.

The numbers of egg clutches for one pair of plots are shown at the top of Fig. 1. In all pairs of plots, the numbers of clutches in experimental plots (Table 1) was significantly greater than the number of clutches in control plots, averaging 0 to 1 in control plots and 6.4 to 7.2 in experimental plots. The differences are highly significant ($P < 0.005$, Wilcoxon signed-ranks test; $N = 10$). The experimental plots contained a significantly greater number of both preadults and adults than did control plots ($P < 0.05$ and $P < 0.005$, respectively; Wilcoxon

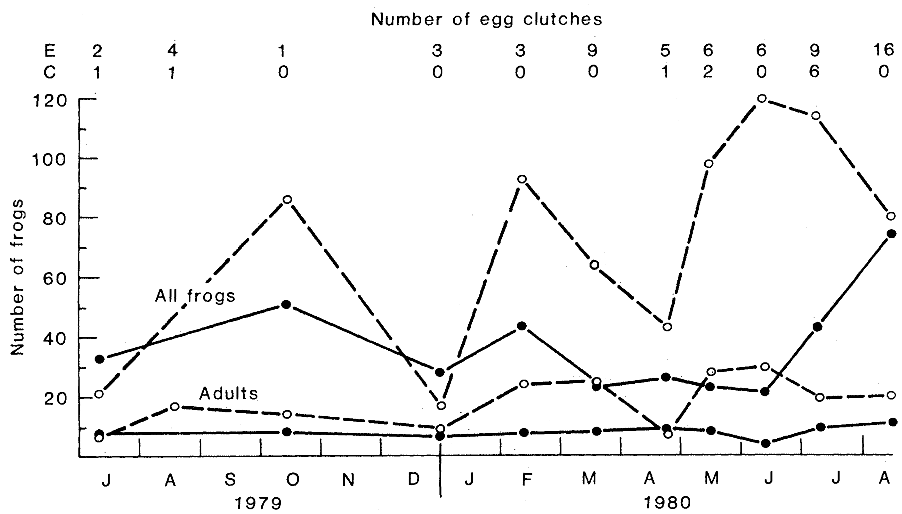

Fig. 1. Number of *E. coqui* and their egg clutches found in a pair of 10 by 10 m plots (River) over a 1-year period (experimental plot, *E* and dashed lines; control plot, *C* and solid lines). One hundred numbered bamboo frog houses were hung on tree trunks in the experimental plot. The houses were hung at 75 and 150 cm above ground level, two at each level (four on each trunk). Frog houses (*9*) were cylinders of bamboo canes, 15 to 18 cm long with a 3 to 4 cm interior diameter. Cylinders were cut below a node, which provided a floor. A small door was cut in the lower part of the cylinder, and the removable top was made of heavy polyethylene plastic and fiber tape. Frogs were counted at night once a month for the 10 months shown. They were classified as preadults (snout-vent length < 24 mm) and adults; size classes were based on our observations of development of secondary sex characters. Juveniles are sensitive to local environmental changes; few were active during heavy rains or extended dry periods. Although rain usually falls daily with a monthly mean of 37.6 cm, there were periods of up to 10 days without rain during the test period.

Table 1. Comparisons of numbers of *Eleutherodactylus coqui* and their egg clutches in four pairs of plots in October 1979 and January to August 1980. Range, mean, and standard deviation (S.D.) of nine monthly counts of frogs (nocturnal) and clutches (diurnal) in 10 by 10 m plots without (control) and with (experimental) 100 bamboo frog houses. Preadults have a snout-vent length of less than 24 mm.

Plots	Adults*			Preadults†			All frogs*			Clutches*		
	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
					Tower 1							
Control	1–8	4.2	2.5	26–71	46.6	16.6	27–73	50.8	16.0	0	0	0
Experimental	4–19	12.8	4.4	15–92	52.2	22.2	26–103	65.0	22.3	0–16	6.9	6.3
					Tower 2							
Control	3–9	6.9	2.1	18–75	36.7	19.7	26–83	43.6	20.5	0–1	0.1	0.3
Experimental	3–21	13.4	6.3	22–82	44.8	19.3	30–103	58.2	24.1	0–15	6.7	5.5
					Bridge							
Control	1–13	5.3	3.5	5–116	62.0	37.2	6–123	67.3	38.2	0–2	0.9	0.9
Experimental	8–26	17.5	6.8	7–123	57.5	41.0	15–145	75.0	43.2	0–12	7.2	5.1
					River							
Control	4–11	8.0	1.9	15–63	28.9	16.4	21–74	36.9	17.6	0–6	1.0	1.9
Experimental	7–29	19.1	7.9	7–96	58.1	29.0	16–120	77.2	34.1	1–16	6.4	4.3

*$P < 0.005$. †$P < 0.05$, for differences in experimental and control plots, based on Wilcoxon signed-ranks test.

signed-ranks test, $N = 9$) (Table 1). In the final census (August 1980), numbers of frogs in control and experimental plots differed significantly ($P < 0.005$ for adults; $P < 0.05$ for all frogs; *t*-test). Up to 46 percent of the houses were occupied during the day.

The significant increase in the number of preadult frogs supports the assumption that the increase is intrinsic and is not simply the result of a relocation of frogs from the surrounding forest. The increase in the number of adults in houses is an indicator of the growth of the previous year's young. Movements of ten marked frogs in the River experimental plot were observed throughout one night. The mean maximum distance moved from diurnal retreat sites was 200 cm [standard deviation, 95 cm], indicating that the frogs remained in the plot during their nocturnal activities.

Increasing the number of retreat and nest sites resulted in a significant increase in numbers of preadult and adult coqui and their nests. Most studies of population regulation have emphasized food, predation, or behavioral interactions as regulators of population density (*8*). We have shown experimentally that the number of appropriate retreats and nest sites limits population size of *E. coqui*, a terrestrial ectothermic vertebrate.

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Rate of Synaptic Replacement in Denervated Rat Hippocampus Declines Precipitously from the Juvenile Period to Adulthood

Abstract. *Synaptic contacts per unit area in the rat dentate gyrus reach adult numbers by the end of the first month after birth and remain constant thereafter. This experiment demonstrated that the rate at which synapses were replaced by sprouting after a lesion declined dramatically from 35 to 90 days of age. Thus, the juvenile period of the rat's life is marked by a considerable change in neuronal plasticity. This may be related to age-dependent effects in recovery from brain damage.*

Developing neural systems have great potential to reorganize, including forming aberrant fiber tracts, after lesions in the perinatal animal (*1*). With maturation, lesion-induced neural growth becomes more restricted and arises primarily from a limited formation of new synapses by intact axons in response to adjacent axonal and synaptic degeneration (*2*). Although the rate of synaptic restoration is known to undergo substantial changes during development (*3*), quantitative comparisons of this variable in juvenile and adult animals are lacking. Since sprouting is involved in the behavioral consequences of lesions in the central nervous system (*4*), changes in the speed at which synapses are replaced may help explain certain age-dependent behavioral effects of brain injury [such as acquired aphasia (*5*)]. We now report that reinnervation of the rat dentate gyrus after removal of a major input slows considerably during the juvenile period.

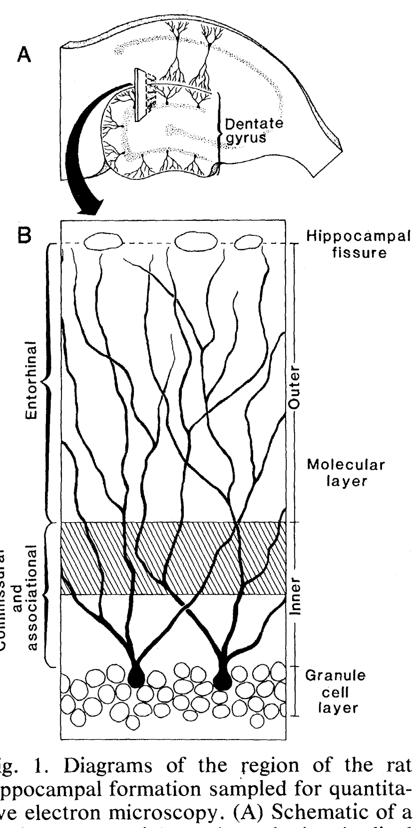

Fig. 1. Diagrams of the region of the rat hippocampal formation sampled for quantitative electron microscopy. (A) Schematic of a section cut at a right angle to the longitudinal axis of the hippocampus. Ultrathin sections were taken from the region of the dentate gyrus shown along the indicated plane. (B) The granule cells are located within a discrete layer, and their dendrites extend outward into a largely cell-free molecular layer. Quantification within the commissural projection to the outer half of the inner molecular layer (hatching) is consistent across animals (*6*); this subfield was used in this experiment.

The dentate gyrus of the rat hippocampal formation contains a population of granule cells organized in a horseshoe-shaped layer. The dendrites of these neurons extend outward and form a homogeneous molecular layer (Fig. 1). The major inputs to the granule cells arise from (i) the entorhinal cortex and (ii) the contralateral (commissural projection) and ipsilateral (associational projection) hippocampus. The hippocampal systems occupy the inner third of the dendritic field, and the entorhinal fibers the outer two-thirds of the molecular layer; the projections do not overlap. The simplicity of these anatomical arrangements has made the dentate gyrus a useful system for anatomical studies of neuronal plasticity.

Commissural axon degeneration, induced by either removal of the contralateral hippocampus (*6–8*) or contralateral cerebral ischemia (*9*), leads to a growth response within the inner molecular layer of the adult rat. Since the commissural