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18. Annual censuses of demersal fishes were performed with stationary point counts (*34*). A 10-m tape was placed across the reef, and all fish observed within a 5-m radius of the center of the tape were counted for 15 min and their lengths estimated visually to the nearest centimeter. Two hundred and seventy-five counts were made annually by C.M.R. and J.P.H., split approximately equally between 5- and 15-m depths. Data were pooled across depths and observers before analyses. Fish biomass was calculated from length estimates for species from five commercially important families: Acanthuridae (surgeonfishes), Scaridae (parrot fishes), Serranidae (groupers), Haemulidae (grunts), and Lutjanidae (snappers) (*35*).
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Ecological Meltdown in Predator-Free Forest Fragments

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The manner in which terrestrial ecosystems are regulated is controversial. The "top-down" school holds that predators limit herbivores and thereby prevent them from overexploiting vegetation. "Bottom-up" proponents stress the role of plant chemical defenses in limiting plant depredation by herbivores. A set of predator-free islands created by a hydroelectric impoundment in Venezuela allows a test of these competing world views. Limited area restricts the fauna of small (0.25 to 0.9 hectare) islands to predators of invertebrates (birds, lizards, anurans, and spiders), seed predators (rodents), and herbivores (howler monkeys, iguanas, and leaf-cutter ants). Predators of vertebrates are absent, and densities of rodents, howler monkeys, iguanas, and leaf-cutter ants are 10 to 100 times greater than on the nearby mainland, suggesting that predators normally limit their populations. The densities of seedlings and saplings of canopy trees are severely reduced on herbivore-affected islands, providing evidence of a trophic cascade unleashed in the absence of top-down regulation.

Ecosystems are structured by the amount of energy flowing through them and by how much primary productivity reaches consumers (primarily herbivores), predators, and decomposers. Plant growth is enhanced through bottom-up effects exerted by light, warmth, and the availability of moisture and nutrients. However, plants are subject to top-down forces when they are eaten by consumers.

The degree to which top-down versus bottom-up forces regulate terrestrial ecosystems has not been resolved (*1, 2*). Proponents of the top-down view argue that the world is green because predators regulate the numbers of herbivores, thereby limiting the damage herbivores do to vegetation (*3, 4*). Advocates of a bottom-up view argue that herbivores are limited by low forage quality and/or by constitutive and inducible plant defenses, which render much foliage unpalatable or indigestible (*5, 6*).

A naïve test of the top-down versus bottom-up models is simple in principle but difficult in practice because vertebrate predators and their prey operate on spatial scales lying beyond the practical reach of direct experimentation (*7*). However, if all relevant predators could be excluded from a sufficiently large experimental area, the top-down model would predict that consumer populations would expand, whereas the bottom-up model would predict little change in consumer numbers. The prediction is naïve, because many ecosystems have both top-down and bottom-up components and because prey behavior can vary greatly in response to the perceived risk of predation (*8*). Nevertheless, simple qualitative predictions are the best that ecological theory can muster at present.

A second test of the top-down model is based on the concept of a trophic cascade, in which a perturbation at one trophic level propagates through lower levels with alternating positive and negative effects. Thus, removal or absence of predators would be expected to lead to increased densities of consumers, which, in turn, would be predicted to have negative consequences for producers (*9, 10*).

Here we report on the strength of top-down forces unleashed in a set of forest fragments through the fortuitous exclusion of predators. The fragments are islands in Lago Guri, a 4300-km^2 hydroelectric impoundment in the Caroni valley of the state of Bolivar, Venezuela (*11, 12*). Isolated by rising water in 1986, these islands range from 0.2 to 4.9 km from the nearest point on the mainland, and all are situated at least 100 m across open water from any other landmass. The vegetation is semideciduous, tropical dry forest.

In 1993 and 1994, we conducted faunal inventories of six "small" islands (0.25 to 0.9 ha), four "medium" islands (4 to 12 ha), two "large" islands ($\geq$150 ha), and two sites on the mainland (*13, 14*). Through these inventories, we measured the abundance at each site of all vertebrates and selected invertebrates. The inventories revealed that small and medium islands already lacked $\geq$75% of the vertebrate species known to occur on the nearby mainland, whereas the two large islands retained nearly all species (*13*). We thus designated the two large islands along with two stations on the mainland as control sites.

Animals persisting on small islands fall into three trophic categories: predators of invertebrates (spiders, anurans, lizards, and birds), seed predators (small rodents), and herbivores (howler monkeys, common iguanas, and leaf-cutter ants) (*15*). Medium islands harbor, in addition, armadillos, agoutis, and, in one case, capuchin monkeys (*16*). Apart from the island with capuchins, frugivores (the principal seed dispersers of tropical forests) and predators of vertebrates are largely to entirely absent from both small and medium islands (*17, 18*). The resulting communities are thus highly aberrant, consisting of a suite of consumers without predators.

Consumers able to persist on small and medium islands are typically hyperabundant in relation to their number in control sites. The mean number of rodents captured per 100 station-nights on three medium and six small islands was 35 times greater than at three sites on a large island and one on the mainland (*19*). Transect counts of iguana dung indicated a 10-fold increase in abundance relative to counts on the mainland (*13*). Beyond these density estimates, we have little information about iguanas because they live in the canopy where they are almost invisible. Howler monkeys on some small islands persist at densities equivalent to 1000 per square kilometer (20 to 40 per square kilometer is normal for the mainland), and the density of mature leaf-cutter ant colonies is roughly two orders of magnitude higher than that on large landmasses (Table 1 and Table 2) (*20*).

Reproduction of howler monkeys appears to be suppressed where they are hyperabundant, suggesting strong density dependence and bottom-up regulation. On one 0.6-ha island, a group of howlers containing two adult females produced only one young in 4 years (0.125 birth per female-year), whereas on a 350-ha island, 10 adult females belonging to two groups produced five infants in 2001 (0.5 birth per female-year).

On medium islands, rodents were as abundant as on small islands, but densities were less for common iguanas, howler monkeys, and, especially, leaf-cutter ants (Tables 1 and 2) (*20, 21*). The difference in the density of leaf-cutter colonies on small and medium islands was investigated by placing wire cages over entrances to young colonies. On medium islands, cages resulted in substantially increased colony survivorship by excluding armadillos. Cages had no effect on small islands where armadillos were not present (*20*).

The truncated animal communities of small and medium Lago Guri islands are ideal for revealing the strength of top-down regulation because the principal herbivores (howlers, iguanas, and leaf-cutter ants) all feed mainly or exclusively on the foliage of canopy trees and lianas. Moreover, none of these animals has a juvenile stage that feeds at a lower trophic level, a factor that frequently complicates the interpretation of food web interactions in aquatic systems (*22*).

Table 1. Tree species diversity and densities of saplings, howler monkeys, and mature leaf-cutter ant colonies on six small Lago Guri islands (1996–97).

Parameter	Island					
	Baya	Cola	Colón	Iguana	Perímetro	Palizada
Area (ha)	0.25	0.7	0.3	0.6	0.5	0.9
No. trees $\geq$ 10 cm DBH	203	490	290	381	301	403
No. tree species	32	40	33	47	54	55
No. stems $\geq$ 1 m tall, $<$1 cm DBH/500 m^2	39	84	147	90	156	301
No. howler monkeys	2	6	3	6	–	–
Howler monkeys per ha	4.0	8.6	10.0	10.0	–	–
No. leaf-cutter colonies	1	3	2	4	2	1
No. leaf-cutter colonies/ha	4.0	4.3	6.7	6.7	4.0	1.1

Table 2. Tree species diversity and density of saplings and mature leaf-cutter ant colonies on medium and large Lago Guri landmasses.

Parameter	Landmass								
	Medium				Large				
	Ambar	Chota	Lomo	Pano	DM-15	DM-12	Grande	TF-1	TF-2
Area (ha)	8	5	11	12	350	350	150	∞	∞
No. tree species per 300 stems $\geq$ 10 cm DBH	63	42	49	51	50	55	46	51	50
No. stems $\geq$ 1 m tall, $<$1 cm DBH/500 m^2	214	311	375	236	304	–	379	340	–
No. leaf-cutter colonies	2	1	2	2	=4	$\geq$4	$\geq$2	–	–
No. leaf-cutter colonies/ha	0.25	0.20	0.18	0.17	=0.01	$\geq$0.01	$\geq$0.01	$\leq$0.04	$\leq$0.04

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The presence of hyperabundant consumers on predator-free islands supports the naïve prediction of the top-down hypothesis and could signal the operation of a trophic cascade. To investigate this possibility, we established plots for monitoring vegetation change on each of the six small and four medium islands and at five sites on large landmasses (*23*). Concurrently, we tested a second hypothesis proposed to account for the rapid loss of tree species on small islands in Lake Gatun, Panama, namely, that plant recruitment had been suppressed by desiccating dry-season winds (*24*). Accordingly, the small-stem subplots were situated within each site so that half had a windward exposure and half a leeward exposure.

Counts of small [≥1 m tall, <1-cm diameter at breast height (DBH)] and large (≥1 cm DBH, <10 cm DBH) saplings in exposed and sheltered subplots on small, medium, and large landmasses were analyzed by analysis of variance (ANOVA), with orientation (exposed versus sheltered) nested within landmass. There proved to be a highly significant effect of landmass size on the number of small saplings in 225 m^2 [$F(2, 21) = 8.0$, $P = 0.003$], and a marginally significant effect on the number of large saplings [$F(2,21) = 3.7$, $P = 0.046$]. Small saplings were less than half as dense on small islands than on larger landmasses (compare Table 1 and Table 2). There was no difference in the effect of windward versus leeward exposure on either stem size class [$F(1) = 0.57$, $P = 0.64$]. These stem counts probably do not accurately reflect current rates of plant recruitment, because it is likely that many of the stems became established before isolation of the islands in 1986 (*25*).

A better representation of recruitment under current conditions is provided by the smallest class of plants, those <1 m tall. Small islands proved to have low numbers of stems in this class [4.7/m^2 versus 13.1 stems/m^2 on a large landmass, $F(1) = 41.5$, $P < 10^{-6}$]. Numbers of stems representing species of canopy trees were only 20% of the control value [0.86/m^2 versus 4.25/m^2, $F(1) = 14.7$, $P < 0.001$]. More than half the stems on the small islands were of lianas (especially Bignoniaceae, Leguminosae, and Malpighiaceae), and most of the rest were understory shrubs and bambusoid grasses. Recruitment of canopy trees appears to be severely depressed, providing further evidence of a trophic cascade on these small islands.

We expect that processes set in motion at the time of isolation will run their course on most small islands in another few decades. Hyperabundant folivores threaten to reduce species-rich forests to an odd collection of herbivore-resistant plants (*26*). Along the way, much plant and animal diversity will probably be lost. The endpoint is likely to be a biologically impoverished system, much like that found today on 85-year-old islands in Lake Gatun, Panama (*24*).

In a parallel situation, long-term overgrazing of semiarid range is well known to convert grassland to thornscrub or shrub steppe (*27, 28*). Intense grazing predictably reduces the ratio of palatable to unpalatable species, thereby increasing the resistance of the vegetation and reducing the carrying capacity for grazers. Our results show that these processes can operate in forests, with similar implications for reduced diversity, increased plant defenses, and lowered carrying capacity for consumers. Similar, if less extreme, processes have been unleashed in parts of the United States where hyperabundant ungulates have massively affected natural vegetation (*29, 30*). Wild pigs (*Sus scrofa*) are severely reducing plant recruitment in a remnant forest in Malaysia where they lack predators (*31*). These observations are warnings, because the large predators that impose top-down regulation have been extirpated from most of the continental United States and, indeed, much of Earth's terrestrial realm.

It has long been known that herbivore populations explode on predator-free islands, to the detriment of natural vegetation (*32*). But in the absence of controlled experiments, many ecologists have passed off accounts of such population explosions as unreliable anecdotes, rather than as convincing evidence of top-down regulation. By taking advantage of a fortuitous natural experiment, we have shown that the absence of predators consistently frees certain consumers to increase many times above "normal," unleashing a trophic cascade.

The extreme hyperabundance of herbivores on small Lago Guri islands demonstrates that food availability (and by implication, plant defenses) does not limit these consumers in the presence of predators (*33*). Where predators depress herbivore populations, plant species with relatively low investments in chemical and mechanical defenses can attain high densities, because such plants grow faster and compete better than species that invest heavily in antiherbivore defenses (*34*). Herbivore populations explode in the absence of predators, but only as a transient phenomenon, until the species composition of the vegetation adjusts to impose regulation from the bottom up (*35*). Herbivore pressure has been weak over much of Earth since the eradication of megafauna by Stone Age hunters, so bottom-up regulation has become widespread, creating aberrations that have spawned the top-down versus bottom-up controversy (*36*).

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Matching Spiracle Opening to Metabolic Need During Flight in *Drosophila*

Fritz-Olaf Lehmann

The respiratory exchange system of insects must maximize the flux of respiratory gases through the spiracles of the tracheal system while minimizing water loss. This trade-off between gas exchange and water loss becomes crucial when locomotor activity is increased during flight and metabolic needs are greatest. Insects that keep their spiracles mostly closed during flight reduce water loss but limit the flux of oxygen and carbon dioxide into and out of the tracheal system and thus attenuate locomotor performance. Insects that keep their spiracles completely open allow maximum gas exchange but face desiccation stress more quickly. Experiments in which water vapor was used as a tracer gas to track changes in the conductance of the respiratory system indicated that flying fruit flies minimize potential water loss by matching the area of the open spiracles to their gas exchange required for metabolic needs. This behavior maintained approximately constant pressure for carbon dioxide (1.35 kilopascals) and oxygen (19.9 kilopascals) within the tracheal system while reducing respirometric water loss by up to 23% compared with a strategy in which the spiracles are held wide open during flight. The adaptive spiracle-closing behavior in fruit flies has general implications for the ecology of flying insects because it shows how these animals may cope with environmental challenges during high locomotor performance.

The increased power output required for flapping flight places special demands and constraints on the respiratory system of flying insects (*1*). On the one hand, the respiratory system must permit the flux of oxygen (O_2) and carbon dioxide (CO_2) to and from flight muscles. On the other hand, the structures that permit respiratory exchange leave an animal susceptible to the loss of water vapor, thus increasing the danger of desiccation. The spiracles that occlude the outer openings of the insect tracheal system function as barriers that control the gas exchange between the network of air sacs, tracheas, and tracheoles and the outer environment. The terminal internal endings of the tracheal system, the tracheoles, are thought to be water filled, establishing a pressure that continuously drives water vapor out of the insect body when spiracles open for gas exchange (*2–5*). The potential threat of desiccation is greatest during flight, when the spiracles must remain open to sustain increased metabolic activity of the wing muscles. The metabolic cost of flight is not constant, however, but varies as an animal alters force production to carry loads or perform flight maneuvers (*6–8*).

In a diffusion-based respiratory system (*9*), the rate with which a gas is exchanged depends on two factors: the partial-pressure gradient between ambient and tracheal gas, and the cross-sectional area for diffusive flux (the area of the spiracle opening). The driving force on water vapor is assumed to be constant, so the flux of water depends only on the size of spiracle opening (*10*). The situation for the respiratory gases (CO_2 and O_2) is more complex, because the internal tracheal partial pressures might vary with metabolic rate. To limit water loss, an insect ought to match spiracle opening with its instantaneous metabolic demands. To test this hypothesis, I developed a method for indirectly measuring spiracle-opening area in tethered fruit flies, *Drosophila melanogaster*, flying within a respirometric chamber of a virtual-reality flight arena and estimated the concomitant changes in partial pressure of tracheal gases from simultaneous measurements of total flight force production, CO_2 release, and water-loss rate (*11*, *12*). The experiments were performed under visual closed-loop feedback conditions, in which the fly itself controls the angular velocity of a vertical dark stripe displayed in the arena by changing the stroke amplitude of its two wings during flight. Under these conditions, a fruit fly attempts to stabilize the azimuth position of the dark stripe in the frontal region of its visual field. While the animal actively controlled the dark bar, a superimposed background pattern of diagonal stripes was oscillated vertically around the animal.

In the fruit fly, 4 thoracic and 14 abdominal spiracles control the diffusive flux into

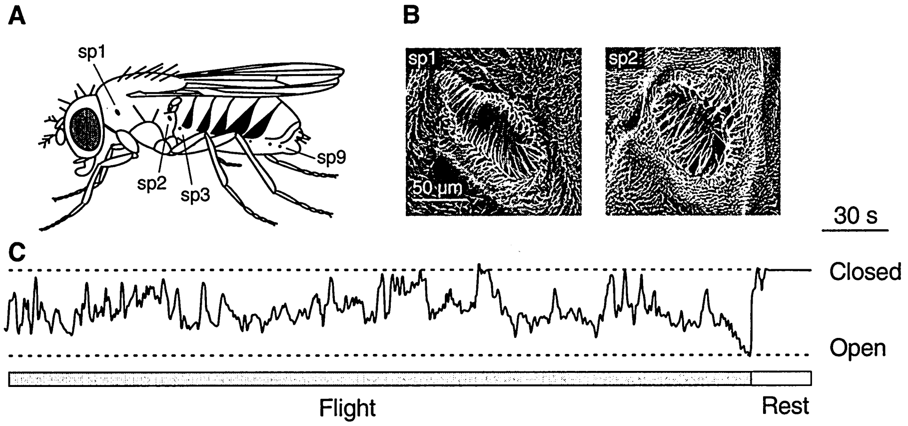

Fig. 1. Location of spiracle openings, and spiracle closing and opening behavior during flight, in the fruit fly *Drosophila*. (**A**) sp1, mesothoracic spiracle; sp2, metathoracic spiracle; sp3 to sp9, abdominal spiracles. (**B**) The oval thoracic spiracular openings are bordered by a thick sclerite and protected with hairs. Narrow flexible spiracular lids cover the tracheal entrance. Spiracles open by the elasticity of their cuticular structures and are held actively closed by the spiracle-closing muscle (*32*). Images are taken from *D. virilis*. (**C**) Closing and opening behavior of the right mesothoracic spiracle in *D. mimica* Hardy (3.06 mg wet body mass) during tethered flight and rest (*33*).

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