Cebus Monkeys: Effect on Branching of Gustavia Trees

Abstract. *One 50-tree site with monkeys and one without were similar with respect to tree height and tree diameter, but the site with monkeys had trees with significantly more branches than those on the site without monkeys. Possibly removal of terminal buds during feeding by the monkeys releases the lateral buds from apical dominance and allows increased branching.*

On Barro Colorado Island in the Canal Zone, the white-faced monkey, *Cebus capucinus* (Cebidae), feeds on the branch ends of "membrillo," *Gustavia superba* (HBK.) Berg, of the family Lecythidaceae. Most of this feeding occurs during the rainy season, August to December, although it may occur at other times of the year (*1*).

While eating ends of the branches a monkey removes the bark along with some of the leaves, which are concentrated at the distal end. One or more inches of meristematic tissue and soft wood are then removed from the tip of the branch and eaten. Sometimes the end of the branch, with all the leaves, is broken off during feeding and dropped to the ground.

Membrillo has been described as growing "to about 20 m tall, with stout straight trunks, branching infrequently . . ." (*2*). Initial observations suggested that at least some trees on Barro Colorado Island were highly branched in an irregular fashion, and the trunks were rarely straight. It was hypothesized that the high number of branches might be brought about by the removal of branch ends by the monkeys, in the same manner as it might be brought about by pruning (*3*).

Two tracts of similar forest were chosen for study in August 1968. One was on Barro Colorado Island (BCI), where the monkeys are protected and have been observed eating the branch ends of *Gustavia.* The second site was on the mainland along Pipe Line Road (PLR), about 11 km east of BCI. Here hunting occurs, and monkeys are generally less frequent. Visits were made to this site during 1968 and no monkeys were seen.

Both tracts are described as semi-evergreen, seasonal, tropical forest (*4*). Annual precipitation averages about 267 cm, with a distinct dry season occurring from January to April. Frijoles clay occurs on BCI, whereas Arraijan clay is present at PLR. Both clays are similar, although Frijoles clay dries out more slowly (*5*). Topography and species composition of both areas were similar. At both sites membrillo was a conspicuous member of the under story. Records suggest both tracts were undisturbed for at least 45 years.

Fifty trees at each site were measured for diameter at breast height (1.4 m), for height, and for number of branches. We selected the trees by walking through a section of forest and measuring the first fifty suitable individuals that were encountered. Suitable trees were those that had a single trunk up to breast height and arose from their own root system.

Tree diameter was measured to the nearest half-inch with a tape measure. Height was measured with an optical range finder. A measurement of branching was obtained by scoring one "fork" each time a branch divided. Division of a trunk, of a large branch, or sprouting of a twig from a branch, all qualified as single forks. Presence of a branch stub also counted as a fork, whereas branch scars were ignored.

Trees were divided into seven classes on the basis of diameter. In four of these the number of trees counted at each site was equal or nearly so (Fig. 1, top). The heights of the trees increased as the diameters increased, and did so at similar rates at both sites (Fig. 1). A *t*-test for the difference between means showed that the two samples were similar with respect to diameter ($t = 1.55$, $P > .05$) and height ($t = 1.83$, $P > .05$). The number of forks per tree at BCI was higher than at PLR (Fig. 2), and the difference was significant ($t = 3.79$, $P < .001$). A further test, Hotelling's T^2, which allows for high correlation between diameter and number of forks, also showed that the two samples were significantly different ($F = 7.63$, $P < .01$).

Apparently by removing the branch ends, the monkeys were removing the inhibitory effect of the terminal bud on the lateral buds, that is, removing apical dominance. Browsing animals, such as deer and elk, do the same thing (*6*), and several experiments have been done to duplicate the effect of browsers on vegetation. Although the effect of browsing, or removal of terminal buds, varies with the plant species involved, moderate browsing tends to increase branching and the amount of foliage available for future browsing (*7*). It also increases the number of sites available for flowers and fruits in later years. Conversely, increased production of branches and foliage occurs at the immediate expense of flower and fruit production, due to the limited supply of carbohydrates (*8*). At the present time the white-faced monkey appears to be increasing the supply of branch ends. Fruit production on Barro Colorado Island continues to occur during the months of April to August in the following year, though perhaps at a reduced rate. The monkeys eat the pulp of these large fruits. Under conditions of a higher monkey population, it is conceivable that feeding on branch ends would be extreme enough to eliminate membrillo fruit production in the following year. Under these circumstances the food potentially available

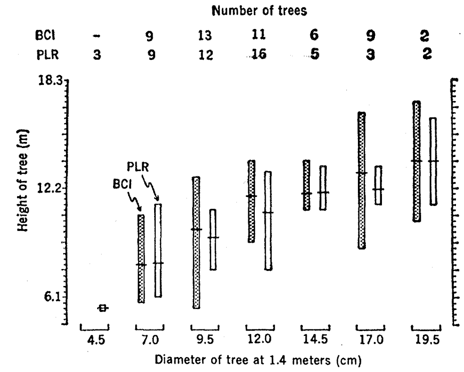

Fig. 1. Relation of height to diameter of *Gustavia* trees on which *Cebus* monkeys feed (BCI) and those on which *Cebus* monkeys do not feed (PLR). Number of trees at each site in each diameter class is at top. Trees of greater diameter were taller. Trees of the same class at Barro Colorado Island (stippled) and at Pipe Line Road (nonstippled) were equivalent in height. Horizontal lines represent the means. Columns represent the range.

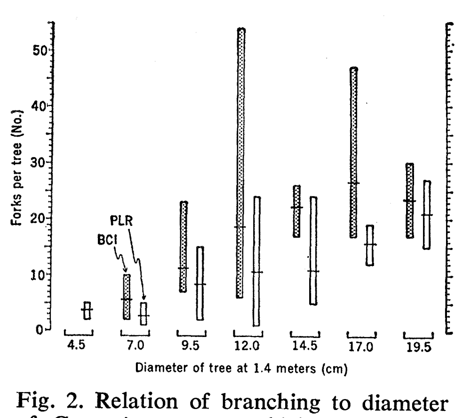

Fig. 2. Relation of branching to diameter of *Gustavia* trees on which *Cebus* monkeys feed (BCI) and those on which *Cebus* monkeys do not feed (PLR). Trees of greater diameter had a greater mean number of branches. Trees on Barro Colorado Island (stippled) had more branches than trees of the same class at Pipe Line Road (nonstippled). Horizontal lines represent the means. Columns represent the range.

to the monkeys would be reduced, when the demand for food is actually at its greatest.

Much attention has been focused on the ability of man to change and modify his environment, whereas the similar ability of nonhuman primates has gone unnoticed. The white-faced monkey, as an integral part of its environment, disperses plant seeds, pollinates flowers, limits the reproductive ability of plants, lowers the numbers of certain insects (*2*), and apparently changes the morphology of a few plant species in the surrounding forest.

JOHN R. OPPENHEIMER
Department of Pathobiology, Johns Hopkins University, Baltimore, Maryland 21205

GERALD E. LANG
Botany Department, University of Wyoming, Laramie 82070

References and Notes

1. J. Oppenheimer, thesis, University of Illinois, Urbana (1968).
2. R. Woodson, *Ann. Mo. Bot. Gard.* **45**, 115 (1958).
3. J. Oppenheimer, *Bull. Ecol. Soc. Amer.* **48**, 138 (1967); thesis, University of Illinois, Urbana (1968).
4. J. Beard, *Ecology* **36**, 89 (1955).
5. H. Bennett, *U.S. Dept. Agriculture Tech. Bull. No. 94* (Washington, D.C., 1929), pp. 1–47.
6. T. Bedell and H. Heady, *J. Range Manage.* **12**, 116 (1959); W. Gaffeny, *J. Wildlife Manage.* **5**, 427 (1941).
7. S. Aldous, *J. Wildlife Manage.* **16**, 401 (1952); T. Bedell and H. Heady, *J. Range Manage.* **12**, 116 (1959); G. Garrison, *ibid.* **6**, 309 (1953).
8. G. Garrison, *J. Range Manage.* **6**, 309 (1953).
9. J.R.O. was supported by a Smithsonian Institution predoctoral internship and PHS postdoctoral training grant 5 T01 MH 11110-01 to Johns Hopkins University. G.E.L. was supported by NSF grant GB-7778 to D. H. Knight. We thank W. Rand for his help and suggestions on statistical analysis, and D. Knight, S. Rand, M. Robinson, and C. Southwick for reading this manuscript.

27 February 1969; revised 21 April 1969

Luminescent Systems in Apogonid Fishes from the Philippines

Abstract. *Luminescence has been discovered in five apogonid fishes from the Philippine Islands. The luminescent organ systems, which are of two types, are morphologically different from the systems in the Japanese cardinal fish,* Apogon ellioti, *and in the apogonid genus* Siphamia. *Extracts of the organs all show a luciferin-luciferase type of reaction and cross-react with extracts of* Apogon ellioti, Parapriacanthus ransonneti, *and* Cypridina hilgendorfii.

The marine teleost family Apogonidae contains about a hundred small, shallow-water species widely distributed in the Pacific and Indian oceans, as well as a few widely distributed pelagic species. Before our study was undertaken six luminous species were known: *Apogon ellioti* and five species of *Siphamia* (*S. versicolor, S. majimai, S. elongata, S. cuneiceps,* and *S. roseigaster*). We obtained material from five additional luminous apogonids from Cebu in the Philippines during May and October 1968: *Archamia fucata* (Cantor), 58 specimens; *A. zosterophora* (Bleeker), 18 specimens; *A. lineolata* Cuvier and Valenciennes, 62 specimens; *Apogon striata* (Smith and Radcliffe), 23 specimens; *Rhabdamia cypselura* Weber, 624 specimens. We also obtained specimens of *Apogon elliott* (*1*) and of another luminous species, *Parapriacanthus ransonneti*, of the family Pempheridae (*2*).

Luminous organs are similarly constructed and arranged in *Archamia lineolata, A. fucata, A. zosterophora,* and *Apogon striata,* which have the luminous body located at the juncture of the pyloric ceca and the intestine. Light is also emitted from the proximal portion of the intestine and the pyloric ceca. In a specimen of *Archamia lineolata* 55 mm in length, the luminous organ is 1.6 mm in diameter. The luminescence is visible externally through the translucent thoracic muscle.

The luminous organ of *Rhabdamia cypselura* is different; the distal ends of a pair of pyloric ceca are transformed into luminous bodies or ducts (Fig. 1c, *PHOT*). A pair of transparent lens-like organs (*L*), encircled with black pigment lie in the ventral-lateral wall of the body cavity (Fig. 1b and 1d, *L*). The luminous ducts are attached to the lens-like organs and through them light is transmitted to the outside. In a specimen 44 mm in length, the diameters of the lens-like organs and luminous bodies (*PHOT*) are 1.0 mm and 0.6 mm, respectively.

These two distinct systems of luminous organs each differ markedly from the system of *Apogon ellioti,* and to an even greater degree from that of *Siphamia,* in the five species of which the luminescence is continuous and appears to be due to the presence of symbiotic luminous bacteria in the photogenic organs (*3*). Hence at least four types of luminescent organ systems are developed in apogonids.

The luminescent organ system of *Apogon ellioti* consists of an oval-shaped, lemon-yellow organ (1 to 2 mm in diameter) connected by a duct to the second bend of the intestine (*1*). This organ (the thoracic or anterior luminous duct) lies in the ventral, translucent keel muscle, through which the light passes to the exterior. Toward the posterior lie a pair of small organs (the anal or posterior luminous ducts) attached to either side of the rectum by a pair of ducts.

Light is produced in *Apogon ellioti* through a luciferase-luciferin (enzyme substrate) type of reaction, involving the oxidation of luciferin by molecular oxygen. When a dark, cold-water extract (luciferase) and a hot-water extract (luciferin) of an organ are mixed, light results (*4*). When luciferin and luciferase from two different organs are mixed, a light-emitting cross-reaction occurs.

Apogon luciferin will undergo a further light-emitting cross-reaction with the luciferase of both the luminous fish *Parapriacanthus ransonneti* and *Cypridina hilgendorfii,* a small marine ostracod crustacean (*4, 5*), two other species in which the luciferin-luciferase type of reaction has been demonstrated. Correspondingly, *Apogon* luciferase cross-reacts with *Parapriacanthus* and *Cypridina* luciferins. The luciferin and luciferase of *P. ransonneti* also give light-emitting cross-reactions with the luciferin and luciferase of *C. hilgendorfii* (*6*). Moreover, the chemical properties of the luciferins of *Cypridina, Apogon,* and *Parapriacanthus* are closely related or identical (*6, 7*).

The luminous organs of *Archamia fucata, A. lineolata,* and *Rhabdamia cypselura* were used in studies in vitro. Soon after the specimens were collected, the organs were removed, air-dried, and stored over $CaCl_2$. The organs were thoroughly dried under vacuum after they were returned from the Philippines. Crude luciferase was prepared from one to three organs ground in 3.5 ml of $0.1M$ sodium phosphate buffer, pH 6.8, in an all-glass homogenizer chilled in an ice bath. The homogenate was dialyzed overnight against $0.1M$ sodium phosphate buffer, pH 6.8, at 4°C and then centrifuged at $15,000g$ for 1 hour at 5°C; the supernatant was used at once. Crude luciferin was prepared from three luminous organs homogenized in 3.5 ml of boiling distilled water for 1 minute; the homogenate was then rapidly cooled in an ice bath and centrifuged at $15,000g$ for 5 minutes; the supernatant was used immediately.

When the organs were first ground in phosphate buffer, the extract exhibited a blue luminescence readily visible in the dark. The luminescence