6. This refers to magnets or battery-powered coils attached directly to a bird.
7. This refers to the production of an artificial ambient field over a relatively large area, in which the bird is subjected to orientation problems.
8. The facility is located in the Chequamegon National Forest near Clam Lake, Ashland County, Wis. The proposed system will employ two 88-km-long antennas with an interconnecting grid. There has been concern about the environmental impact of the electric and magnetic fields emitted by the operational system. Because of public concern in states proposed as possible sites for Sanguine, construction has been delayed, Congress has been critical of budget matters, and the scientific feasibility of the system has been questioned [see N. Gruchow, *Science* **166**, 850 (1969)]. This study and others have been conducted to determine if any detrimental effects are evident. Most studies have shown Sanguine test fields to have no undesirable effects. But, in most cases, the organisms tested or the methods used were not known indicators of electromagnetic field effects.
9. For further details see *Sanguine System Final Environmental Impact Statement, Technical Annexes* (Department of the Navy, Electronic Systems Command, Washington, D.C., April 1972).
10. Field measurements at WTF were arranged for by the Navy and performed by Illinois Institute of Technology Research Institute (IITRI) personnel. The magnetic field intensities listed in Table 1 are for the a-c field produced by the energized antenna. I measured the d-c geomagnetic field separately with a Radio Frequency Laboratories model 101 magnetometer. I requested information from the Navy and IITRI to show the interaction of the two fields, but the necessary data were not provided.
11. For details of orientation cage design and trial procedure see W. E. Southern, *Wilson Bull.* **86**, 256 (1974). The structure was made of nonmagnetic materials but formed a closed conductor when exposed to a-c fields. This is why the test fields (Table 1) were reduced when the cage was present. The resultant field was still within the range proposed for the operational Sanguine system.
12. Data on *K*-indices of magnetic activity were received from the World Data Center, Denver, Colo.
13. Results obtained on overcast days are inconsistent with those obtained on clear days. On overcast days the experimental and control groups showed statistically significant mean angles of 138° and 146°, respectively. Because there were fewer overcast days, these data are not comparable with the data for clear days. Only portions of 2 days were completely overcast, and during this time 491 trials were conducted. This necessitated scheduling the same group of 60 gull chicks for more individual trials per unit time than were scheduled for any other test situation. The chance of habituation or some other phenomenon biasing the results seemed likely. However, when the data for overcast days are combined with those for clear days (N = 1133) there is a statistically significant mean angle of 146° (P = .0005). Further fieldwork is necessary to resolve the causes of this inconsistency.
14. The Rayleigh test indicates whether a significant mean bearing exists in the distribution; the V test determines whether there is a significant grouping of headings about a hypothesized bearing, in this case 165°. See E. Batschelet, in *Animal Orientation and Navigation*, S. R. Galler, L. Schmidt-Koenig, G. J. Jacobs, R. E. Belleville, Eds. (NASA SP-262, National Aeronautics and Space Administration, Washington, D.C., 1970), pp. 61–91.
15. The data were divided into several subsets that could be considered as replicate experiments. Each subset was used to evaluate the possible effects of various aspects of the operational Sanguine system, such as mode of transmission, frequency of signal, and antenna type. The results for each subset are consistent with those for the main data set for clear days.
16. Supported by the Naval Electronic Systems Command through ONR contract N00014-72-A-0050-0002. Field assistance was provided by F. J. Cuthbert, F. Loomis, C. Lovekin, F. Moore, and J. O'Brien.

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Behavior of *Hymenaea courbaril* When Its Predispersal Seed Predator Is Absent

Abstract. *Members of lowland Costa Rican forest populations of* Hymenaea courbaril *(Leguminosae) have longer intervals between seed crops, a later age at first reproduction, larger seed crops, and more resin in the pod walls than do the* H. courbaril *native to Puerto Rico. The primary predispersal seed predators of* H. courbaril *in Costa Rica,* Rhinochenus *spp., are absent from Puerto Rico, and it is postulated that this is a major cause of the interpopulation differences.*

The hypothesis that supra-annual fruiting periodicity in individual trees is adaptive primarily in satiating seed predators with a large seed crop has anecdotal and theoretical support (*1–3*) but has not been subject to direct tests. One kind of test would be to record predispersal seed predation on individual conspecific and sympatric seed crops that are (i) out of phase with other conspecifics' crops, (ii) exceptionally many years apart (and therefore exceptionally large), or (iii) of different sizes in an asynchronously fruiting population (*4*). A second kind of test would be to compare the behavior of the tree in an area where the seed predators have been absent over evolutionary time with its behavior in habitats rich in seed predators and fruit parasites. Such a comparison is generally difficult, with one exception: tree species with both mainland and island populations. Here, I contrast a Costa Rican deciduous forest population of *Hymenaea courbaril* (a caesalpinaceous legume known as "guapinol" in Central America) with that on Puerto Rico, with respect to four traits that I expect have been influenced by selective pressures exerted by Costa Rican *Rhinochenus* weevils (Curculionidae), the only severe predispersal seed predators of *H. courbaril* in Costa Rica (*5*).

Hymenaea courbaril is the only member of its genus in Central America. In Costa Rica, it occurs as scattered large trees in the forests of the Pacific coastal plain and foothills of the provinces of Guanacaste and Puntarenas [as well as from lowland tropical Mexico to much of lowland tropical South America (*6*)]. Here, in this highly seasonal habitat, most adults flower in March or April (the last half of the dry season), but in a given year about 10 percent or less of individuals in relatively undisturbed sites (*7*) produce fruit crops of 100 to 500 pods and do so at 3- to 5-year intervals. This fruit production is annually asynchronous among members of the population (*8*) but synchronous within the year (*9*). When growing in a forest (*7*), only trees whose diameter at breast height (DBH) is more than about 20 inches (0.5 m) produce these large pod crops (*10*). Smaller and sick trees reproduce only by pollen production (*11*). By counting annual rings, I have determined that a 20-inch-DBH tree is usually 80 to 150 years old (*12*).

Hymenaea courbaril pods are immature, green, and full-sized for about 8 to 11 months, and then drop after maturing in the middle of the dry season (*9*). They are 10 to 20 cm long and may weigh 25 to 125 g. Indehiscent and extremely hard, they must be opened by a dispersal agent. During the last third of the fruit maturation period (October to December), 10 to 50 female *Rhinochenus* weevils begin to oviposit in the pod crop of a single tree (*13*). It appears that the female can oviposit in the pod wall for only about a month. During this short period, the copious resin in the pod wall is beginning to dry, and it does not well out when she cuts an oviposition hole with her mouthparts nor when the first instar larva bores further through the pod wall. This susceptible period is terminated when the pod wall becomes so hard with solidified resin that it is impenetrable (*14*). The total seed predation by *Rhinochenus* weevils in the seed crops of specific trees ranges from less than 5 to more than 90 percent, and the absolute number of pods whose contents are destroyed is usually between 30 and 100 in forest situations (*15*). On emerging from the pods, the adult weevils disperse from the tree. This dispersal is expected, since in a forest situation there will be no pods on that tree the next year (*16*). After they disperse, I have not been able to locate adult *Rhinochenus* until they appear at a new pod crop on a different tree in the next fruiting season. Thorough collection of seeds of other potential hosts has shown that a second generation does not occur on other plant species (*5*).

According to seed predator satiation theory (*1–3*), the production of large seed crops at intervals of n years rather than a crop $1/n$ times as large every year is selected for because (i) it causes the seed crop to be attacked only by weevils that can "colonize" the crown anew each time it fruits rather than weevils that might wait at the tree from crop to crop if it fruited annually, and (ii) it gives a tree time to accumulate enough reserves to make a crop large enough to satiate the oviposition abilities of beetles that do arrive at its crop. For example, if the beetles arriving at a crop can kill the seeds in 100 pods, then the

tree that produces 400 pods every 4 years has half as much seed mortality overall as one that produces 200 pods every 2 years. However, it should be noted that waiting many years between crops maximizes this process but at the same time results in long periods when a tree is contributing only pollen to future generations. The other costs are those of storing reserves and of the timing mechanisms.

In Puerto Rico the situation is quite different from that described for Costa Rica. There is no hint that *H. courbaril* is other than indigenous to Puerto Rico (*17, 18*), although it is conceivable that it is an ancient introduction by Amerindians moving among Caribbean islands, since the pulp around the seeds is eaten by people and sold in markets in Colombia and Costa Rica. There are no *Rhinochenus* weevils in Puerto Rico or other Caribbean islands (*19*), nor are there other insects preying on the seeds of *H. courbaril* which behave in a manner such as to select for supra-annual production of a large seed crop by individual trees (*20*). In 1969, at the end of the fruit maturation season (February), I examined every wild *H. courbaril* tree that I could find in Puerto Rico (*21*). I located 63 individual trees between 3 to 30 inches in DBH, and all but 4 had moderate to heavy pod crops on them; for the smallest trees, this was 10 to 30 pods and for the largest, 200 to 300. If there is supra-annual fruiting by *H. courbaril* in Puerto Rico, it therefore must be synchronized over the entire island. However, there was no hint of this being the case since rotting pods of one to many years of age were on the ground beneath many of the larger trees. Furthermore, following this finding, F. H. Wadsworth of the Institute of Tropical Forestry in Puerto Rico informed me that "trees of *Hymenaea courbaril* on our Institute grounds and at my home . . . have born fruit every year for at least the past 10 or 15 years" (*18*).

The second expected trait of the Puerto Rican populations of *H. courbaril* is that they will begin to bear fruit at a small size. This is expected since in the absence of the weevil there should be no selection against small seed crops. In the sample of 63 trees mentioned above, there were 16 less than 8 inches in DBH and all of these had large fruit crops for their size (10 to 30 pods on the smallest trees, up to 100 pods on the largest trees). Comparable behavior has never been observed for trees of this size in Costa Rica; on very rare occasions a small tree growing for many years in full sunlight will produce 1 to 15 pods but small trees in forest never do. The Puerto Rican trees ranged from trees in open roadsides to dense stands of *H. courbaril* and other species. There was no hint that the early age of reproduction was due to reduced competition. Wadsworth says that "trees of *Hymenaea courbaril* on our Institute grounds and at my home started to fruit in about their fourth or fifth year" (*18*).

The third expected trait of *H. courbaril* on Puerto Rico is that the pods will have a much lower resin content than do the Costa Rican pods. This prediction is based on the observation that not only is the weevil absent, but also other potential seed predators are generally missing in Puerto Rico (*22*). The walls of newly fallen pods of *H. courbaril* in Costa Rica are extremely hard, because of their impregnation with hardened resin. A hammer is required to break them open. The newly fallen pods in Puerto Rico can be broken by squeezing them between the hands and have conspicuously less resin in the pod walls than do those from Costa Rica. The resin in a mix of pulverized dried pod walls from 12 trees in Guanacaste Province were extracted with *n*-pentane, diethyl ether, and acetone and found to contain 15.4 percent (dry weight) of resin (*23*). A mix of ten trees' pulverized pod walls from Puerto Rico had 5.2 percent (dry weight) of resin (*23*). Resins are of noticeably higher caloric value than the woody tissue normally making up legume pod walls. When analyzed by bomb calorimetry, the Costa Rican sample produced two subsamples of 4868.5 and 4817.3 cal/g, while the Puerto Rican sample produced two subsamples of only 4578.9 and 4534.7 cal/g (dry weights) (t = 8.459, significant at P = .05; d.f. = 2) (*24*). It is of interest here that in the Puerto Rican habitats, which lack dispersal agents that will open the indehiscent woody pods, a soft pod wall is adaptive in that the pod will rot rapidly and the germinating seeds can push their way out. The reduced resin content in Puerto Rico may therefore be viewed as actively selected for by both increased economy in the face of a reduced herbivore challenge and the need for a self-opening pod.

The above natural history suggests that in Costa Rica, *Rhinochenus* is probably selecting for longer intervals between seed crops, greater age at first reproduction, greater size of seed crops, and greater resin content of pod walls than in Puerto Rican habitats relatively free of seed predators. Studies on an array of seed-eating insects in Costa Rican lowland forests suggest that this type of selection is a general phenomenon and influences the reproductive behavior of many species of large tropical trees (*25*).

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References and Notes

1. D. H. Janzen, *Annu. Rev. Ecol. Syst.* **2**, 465 (1971).
2. ———, *Ecology* **53**, 258 (1972); *ibid.*, p. 954.
3. ———, *Biotropica* **6**, 69 (1974).
4. Which test is relevant depends on the natural histories of the tree species and, most importantly, on whether the fruiting members of the tree population are usually in synchrony.
5. Throughout the range of Costa Rican *H. courbaril*, the larvae of *Rhinochenus stigma* L. and *R. transversalis* Chevrolat (determined by D. Whitehead), and sometimes a third *Rhinochenus* species, regularly attack its seeds. They occur only on *H. courbaril*, a degree of host-specificity that is usual for Costa Rican seed predators that live within the fruit or seed [D. H. Janzen, in *Taxonomy and Ecology*, V. H. Heywood, Ed. (Academic Press, London, 1973), pp. 201–211]. In Costa Rica, the immature pods are very rarely chewed open by parrots and squirrels; if dispersal agents have been eliminated, with the consequence that the unopened pods lie on the ground for many months, the seeds may be attacked by *Stephanoderes buscki* Hopkins (determined by S. Wood), a generalist, seed-eating scolytid beetle. In South America, *H. courbaril* and congeners are attacked by the three species of *Rhinochenus* listed above and others.
6. S. S. Martin, J. H. Langenheim, E. Zavarin, *Biochem. Syst. Ecol.* **2**, 75 (1974).
7. Trees growing in pastures, roadsides, and other competition-free habitats also flower annually, but may bear crops as large as 2000 pods and may do it annually for as long as three consecutive years before halting seed production for a year or two. Such trees require separate analysis and obviously cannot be used directly in comparing Costa Rican and Puerto Rican populations with respect to behavioral parameters. These valuable lumber trees are left standing as a cash resource when the forest is cleared. Their human-influenced biology is the subject of a study in progress.
8. In Guanacaste Province there are some years when more *H. courbaril* make large pod crops than in other years. However, there is no hint of regular supra-annual intrapopulation seeding synchrony as is standard with tropical Dipterocarpaceae (*3*) or conifers and hardwoods in northern latitudes (*1*).
9. Almost all pods mature and fall from the tree during a 2-month period that varies with locality by as much as a month in either direction. While the need for cross-pollination may require such intra-annual synchrony of flowering, such synchrony in seed fall may be solely under the constraints of external environmental factors such as the rainy season, seed predators, dispersal agents, and so forth.
10. This statement and those in (*7*) are based on 3 to 7 years of individual fruiting and flowering records for more than 600 *H. courbaril* ranging from Santa Rosa National Park in coastal northwestern Costa Rica, to Alajuela (elevation, 1000 m) in the central foothills, to near Palmar Sur in southwestern Costa Rica.
11. The population of *H. courbaril* in any year contains many pollen donors (effectively males) that are too young or too weak to produce a large pod crop or are accumulating reserves between pod crops, and hermaphrodites that are pollen donors and pollen receivers. The flowers of all of these plants are identical morphologically. In effect, the males are competing among themselves for the services of the pollinating bats to carry pollen to the few trees that are acting in a female capacity in that year.
12. In this highly seasonal habitat, many of the deciduous tree species display annual growth rings (examples are *Tabebuia* spp., *Bursera simarouba, Guazuma ulmifolia, Acacia* spp., and *Cedrela odorata*). While *H. courbaril* is essentially evergreen, it drops its leaves for a period of a week or two in the middle of the dry season and the wood shows very distinct annual rings.
13. The number of weevils arriving and the time of their arrival varies strongly from tree to tree and is still a subject of study. However, I can state with certainty that the usual 10 to 80 percent seed destruction of a 100- to 400-pod crop is achieved by as few as 10 weevils and probably never more than about 50 weevils.
14. The great differences in chemical composition between *H. courbaril* pod and leaf resins (*6*) are likely to be in part related to this requirement for a change from a liquid to a solid defense system by the pod resins, a change not required of the leaf resins. The walls of mature Costa Rican *H. courbaril* pods are so hard that adult *Rhinochenus stigma* weevils cannot cut their way through them and therefore must rely on dispersal agents to open the pods. *Rhinochenus transversalis* adults likewise cannot cut through the pod wall, but the larva cuts an exit hole for the adult before pupating [these two species' names were reversed in the only

other description available of their biology, in D. H. Janzen, *Nat. Hist.* **83**, 48 (1974)].
15. This is based on more than 400 pod collections from more than 600 trees between 1968 and 1975.
16. They also disperse from pasture trees that will have a pod crop the following year (there is no way the beetle can know this); the result is that the same absolute number of pods are killed in successive seed crops rather than an increasing number, as would be expected if the weevils could respond to this newly displayed behavior by the trees.
17. E. L. Little and F. H. Wadsworth, *U.S. Dep. Agric. Agric. Handb. No. 249* (1964).
18. F. H. Wadsworth, personal communication.
19. This is based on information in G. N. Wolcott, *J. Agric. Univ. P.R.* **20**, 1 (1936) and on field collections of several thousand pods during February 1969. Furthermore, J. H. Frank writes from Jamaica that he has found no *Rhinochenus* there, although *H. courbaril* is common (13 May 1971). There are no specimens of *Rhinochenus* from any Caribbean island, except Trinidad, in either the British Museum of Natural History or the U.S. National Museum of Natural History.
20. The only predispersal seed predator of *H. courbaril* in Puerto Rico is the generalist scolytid, *Stephanoderes buscki* Hopkins (determined by S. Wood) which may kill some of the seeds if the pods lie intact on the ground for many months.
21. Most passable roads on the island were driven; all trees encountered were below an elevation of 400 m and in the moister, eastern half of the island. They were in pastures, roadsides, and forest.
22. Thus in the more northern Mexican populations of *H. courbaril*, where *Rhinochenus* has never been recorded, a high resin content in the pod walls is still expected since there are numerous other potential seed predators (parrots, squirrels, Hemiptera, and so forth) in these habitats.
23. R. Cates and D. Rhoades, Department of Zoology, University of Washington, Seattle, 12 January 1973.
24. C. Smith, Division of Biology, Kansas State University, Manhattan, 13 January 1973. The methods used were those of R. T. Paine [*Ecology* **45**, 384 (1964)] for a Parr semimicro oxygen bomb calorimeter.
25. D. H. Janzen, in preparation.
26. Supported by NSF grant GB-35032X and the teaching program of the Organization for Tropical Studies. Numerous persons aided in fieldwork, as will be documented in a longer report on the interactions of *Rhinochenus* and *Hymenaea* (*25*). Constructive criticism of the manuscript was offered by H. G. Baker, K. S. Bawa, G. W. Frankie, J. H. Langenheim, P. A. Opler, C. M. Pond, A. K. Sakai, C. C. Smith, R. L. Trivers, and D. R. Whitehead.

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Sexual Behavior: Extreme Reduction of Postejaculatory Refractory Period by Midbrain Lesions in Male Rats

Abstract. *The refractory period that characteristically follows ejaculation was abolished or significantly reduced by rostral midbrain lesions in male rats. The postejaculatory vocalization was also abolished or reduced, but other aspects of copulatory performance were unaffected. The results were attributed to disruption of biogenic amine pathways that pass from the ventral part of the rostral midbrain into the posterior hypothalamus.*

A period of sexual incapacity characteristically follows ejaculation in male mammals. In the rat this phase, the postejaculatory refractory period, is highly stable and only drastic experimental procedures are capable of greatly reducing or abolishing it. In a few instances electrical stimulation of preoptic and hypothalamic regions has had this effect (*1*), and, in one study, massive lesions at the midbrain-diencephalic junction reduced the refractory period to about 25 percent of normal (*2*).

Exogenous stimulation such as handling, electrical shock to the skin, or electrical stimulation of the brain normally does not reduce the refractory period to less than about 75 percent of normal (*3*). The resistance of the refractory period to abbreviation is due to a preeminent inhibitory state that prevails during the first three-fourths of the refractory period (*4*). This phase, designated as the absolute refractory period, is characterized by a high-amplitude, slow-wave electroencephalogram (EEG), the emission of 22-khz vocalizations (*5*), and a lack of spontaneous resumption of sexual activity (*6*).

The postejaculatory vocalization begins about 30 to 40 seconds after ejaculation, and shortly thereafter the animal shows a predominance of sleeplike EEG. The mechanism that underlies this behavior is not known; however, it is possible that the ejaculatory reflex triggers the postejaculatory refractory period and its concomitant vocalization by a neurohumoral link. Serotonergic, noradrenergic, and dopaminergic pathways run via the medial forebrain bundle from cell bodies in the midbrain to the hypothalamus (*7*). The biogenic amines have been implicated in the regulation of sleep and arousal (*8*), and are theoretically capable of regulating both the refractory period and endogenous sexual arousal (*9*).

Ejaculation occurs after a cerebral disinhibition of spinal reflexes (*10*). The refractory period could be triggered by events that underlie the disinhibition that allows ejaculation or in response to messages emanating in the spinal cord. In either case the mediation of the refractory period could involve transmission in specific neurohumoral pathways. We predicted that if a mechanism of this sort were involved, destruction of one or more of these pathways would result in a diminished refractory period and, possibly, altered sexual arousal.

We can now take a fresh look at earlier studies on the destruction of posterior hypothalamic and midbrain loci. Heimer and Larsson (*2*) reported dramatic reduction of the refractory period with massive lesions that might have destroyed the critical pathways. Subsequent attempts to achieve the same effect with smaller lesions in the mammillary region were unsuccessful (*11*). In similar experiments discrete lesions in the mammillary area of the brain of male rats resulted in an increased production of copulatory plugs (*12*); however, the effect was due to a reduction in the time to ejaculation and not to a decreased refractory period (*13*). Other studies have shown that posterior hypothalamic and rostral midbrain destruction is generally disruptive to male copulatory behavior (*14*). Thus the findings of Heimer and Larsson remained an enigma.

We report here that destruction of the focal point of the biogenic amine pathways in the anterior midbrain abolishes or severely curtails the postejaculatory refractory period and its concomitant postejaculatory vocalization and, in general, leaves other aspects of copulatory behavior unaltered.

Selection of male Wistar rats for the experiment was based on their ability to execute the complete pattern of male copulatory behavior on two baseline tests. These subjects received bilateral electrolytic lesions in either the area through which the biogenic amine pathways course [an area about the ventral portion of the medial lemniscus (VML)] or in other hypothalamic and midbrain loci (*15*). Postoperatively, animals were tested two or three times weekly for 1 to 4 weeks, depending on the time required for them to achieve a stable and repeatable level of sexual performance (*16*). Standard measures of male copulatory behavior were recorded through two ejaculatory series as follows: intromission frequency, the number of intromissions to ejaculation; ejaculation latency, the time from the first intromission until ejaculation (a rate measure of copulatory activity, the intercopulatory interval, is obtained by dividing ejaculation latency by intromission frequency); and postejaculatory interval, the time from ejaculation until the next intromission (the time from ejaculation to the next mount was also noted). The occurrence and timing of the postejaculatory vocalization was recorded in terms of vocalization latency and vocalization termination; respectively, these are the times from ejaculation until the beginning of the vocalization and its termination. The ultrasound was monitored with a capacitance microphone, the output of which was displayed on an oscilloscope screen (*17*).

Twenty-three of the animals regained good postoperative health and all exhibited complete mating behavior. The remaining six did not survive. The animals were divided into four main groups based on the location of their lesions. Those animals