

# Crafoord Prize 1984



Mrs Anna-Greta Crafoord congratulates Professor Daniel H. Janzen on the award of 1984 Crafoord Prize.

The Crafoord Prize for 1984 was awarded in biosciences with particular emphasis on ecology. The field selected was "coevolution - the mutual adaptation of organism populations in the natural environment". The prizewinner, Professor **Daniel H. Janzen**, Philadelphia, USA was chosen "for his imaginative and stimulating research into coevolutionary connections and processes, through which numerous researchers have been inspired to further work in this field".

At a ceremony on October 3, 1984, the rewarded work was presented and Professor Janzen received his prize and the Crafoord medal in gold from the hands of the donor, Mrs Anna-Greta Crafoord. Before the ceremony, Daniel Janzen delivered his Crafoord lecture "The most coevolutional animal of them all". The text is printed on the following pages.

The Crafoord Prize was first awarded in 1982. The discipline was mathematics and the field nonlinear differential equations. Joint prizewinners were Professors **Vladimir I. Arnold** of the USSR and **Louis Nirenberg** of the USA for their valuable work in this field.

In the following year the geoscience prize was awarded to Professors **Edward N. Lorenz** and **Henry Stommel**, both from the USA, for their unique contributions to a deeper understanding of the large-scale movements of the atmosphere and the sea respectively.

# The most coevolutionary animal of them all

Daniel H. Janzen

Department of Biology, University of Pennsylvania, Philadelphia, USA

Coevolution is an unfamiliar word to most, though evolution is a long-time resident in our vocabulary. Why the 'co' on the front of "evolution"? Let us agree that evolution is the genetic change of a population. Let us also assume that it usually occurs as a consequence of selection by some environmental process, be that environment inside or outside of the organism. Now imagine that a particular genetic change is produced by a selective pressure by some other organism that in turn has its environment changed by the evolutionary event. Then assume that the second organism evolves in response to the selection wrought by the environmental change. This pair of reciprocal evolutionary changes is termed "coevolution". One organism has changed in response to another, which in turn has changed in response to the first. It is commonplace for biologists to think of such a process as capable of going on and on through many reciprocal steps in evolutionary time. Likewise, it is commonplace for us to think of one or even both sides of the coevolutionary interaction as being represented by a set of organisms with similar traits. In this situation, one may speak of diffuse coevolution, such as when a large number of species of solitary bees are diffusely coevolved with the array of species of flowers that they pollinate. This is another way of saying that while bees and flowers as a group have clearly had a strong evolutionary effect on each other, no one species of either group has been the primary selective pressure that produced the other group. The same may be said of birds and the fruits they eat (and seeds that they thereby disperse), and of herbivores and the foliage that they consume as a group.

There are very few examples of one-on-one coevolution that you are already familiar with in your own habitat. On the other hand, if we lived in Costa Rica, Nigeria, or elsewhere in the tropics, I could describe a coevolutionary example that lives within a few kilometers of you. Examples of one-on-one coevolution are very few and far between outside of the tropics, if indeed they can be found at all. And the example of coevolution that I am about to describe in detail is in fact a tropical example (but the tropics are not really so foreign - we tend to forget our tropical ancestry).

Diffusely coevolved systems are a bit easier to describe and certainly more widespread than are one-on-one systems; there is even a diffusely coevolved system inside of all of you. Inside every person is a six meter tube that is occupied by several hundred species of organisms all busy digesting the last

meal. These microbes, highly mutualistic as a group, have clearly been evolutionarily molded as a response to the kind of environment that you represent: your body, temperature, pattern of eating, food types, weaning age, starvation capabilities, internal oxygen-free habitat, food passage rates, secretions into the gut, etc. Each species of gut microbe has evolved in response to *Homo sapiens* and to other microbes, and I assure you that over a long time you have evolved a wide range of traits to keep them happy. If they get unhappy, you get unhappy. Each of them has evolved with you and you have diffusely coevolved with them as a group. Many diffusely coevolved systems are mutualisms (Janzen 1985a).

I now turn to my tropical example of one-on-one coevolution. The ant-acacias (*Acacia* spp.) and the *Pseudomyrmex* ants that protect them have been known to western science since at least 1874, when an astute mining engineer in tropical Nicaragua told us quite clearly (Belt 1985:219) what numerous authorities on ant biology then chose to ignore (e.g., Wheeler 1942). Belt told us unambiguously that the ants protected the acacias from various leaf-eaters, and in more ponderous and 'scientifically proper' experiments I showed the same thing (Janzen 1966,1967). Here I would like to reconstruct a bare outline of what I suspect was the coevolutionary process that produced the ant and the acacia that it protects.

The story began in the northern Neotropics tens of millions of years ago, at a time when this land was richly populated with a species-rich fauna of large herbivorous mammals. Among these were many that lived in somewhat arid regions and browsed on shrubs. Among these shrubs were many species in the genus *Acacia*, shrubs that have a long tradition of long thin thorns as defenses against large browsing mammals (Janzen 1986, Janzen and Martin 1982). If we may infer from modern reactions of large herbivores to thorny plants (including *Acacia*) in Africa and in the New World, these thorns were moderate to thorough deterrents to large browsers but were of no significance in defense against small herbivores such as insects. Ant-attracting nectaries on the leaves were one of the many defenses against small herbivores that the acacia possessed (along with toxic and/or distasteful chemicals in the leaves).

In the same habitats were many species of twig-inhabiting ants of the genus *Pseudomyrmex*. These ants had a well-developed sting and were agile diurnal hunters of insects on vegetation. Somewhere a species of this ant genus appeared that found the thorns of a species of *Acacia* to serve as high quality "hollow twigs". Such an ant colony also found that the sugar-producing nectaries on the acacia foliage were a high quality source of food. Because the colony lived in the acacia crown (Figure 1) and because the ant colony concentrated its foraging on the acacia crown, we had the elements for a true one-on-one coevolutionary interaction. A mutant acacia that made larger and more easily hollowed thorns (Figures 2,3) became occupied by a larger and healthier ant colony. The same was true of a mutant with more productive nectaries on the foliage (Figure 4). Any mutant ant colony that made better use of these resources and protected them against strangers (whether they were large browsing mammals, leaf-eating insects, or nectar robbers) not only became a larger ant colony but also occupied a healthier acacia. Furthermore, somewhere in this coevolutionary spiral of increasing fitness of the ant and

the acacia, a mutant acacia appeared that made modified leaflet tips that contain the proteins, oils and vitamins needed by the ant larvae (Figure 5). The modified leaf tips were christened "Beltian bodies" after the man who first described them to the world of science.

At this point, the ants were no longer dependent on insect prey for food and the colony could grow as large as the resources of the acacia permitted. A healthy acacia-ant colony may have 10-50 thousand worker ants (Janzen 1967, 1975) that spend their entire lives within a couple of cubic meters of habitat. The ant responded to selection for doing all of its foraging in the crown of the acacia. In the highly seasonal environment of tropical Mesoamerica, mutant acacias were also favored that retained their leaves during most or all of the dry season, even though other species become deciduous. Such an ant-acacia has a large and healthy ant colony at the time the rains begin and the world becomes flooded with insect herbivores; during the food-poor dry season, its green leaves are also well protected from herbivores by the ants. The system was also ripe for response to selection for thorough and round-the-clock



Figure 1. Crown of an adult 4-m-tall adult ant-acacia (*Acacia collinsii*) in Santa Rosa National Park, Costa Rica.

foraging by the ants, extreme aggressiveness by the ants (they no longer even take insects as prey), very large and concentrated colony size, aggressiveness to any foreign object (including vines and other plants), a very severe sting, group attacks organized through alarm pheromones, and year-round production of reproductives (seedlings are always present) (Janzen 1967). In areas where the climate is so severe that colonies founded by a single queen have little chance of establishment but established ant-acacias can live essentially forever, the colonies even accept their own daughters as new queens and thereby accumulate millions of egg-laying queens and become essentially immortal (Janzen 1973).

So now we have a species of ant and a species of acacia that have truly coevolved. Many of the traits of importance to the coevolved interaction were present prior to the interaction (e.g., thorns, foliar nectaries, well-developed sting by the ant, attack behavior). Only the Beltian bodies are clearly novel to the interaction, but in a certain sense even they are just modifications of pre-existing structures - the leaflet tips. The acacia now has a set of defenses

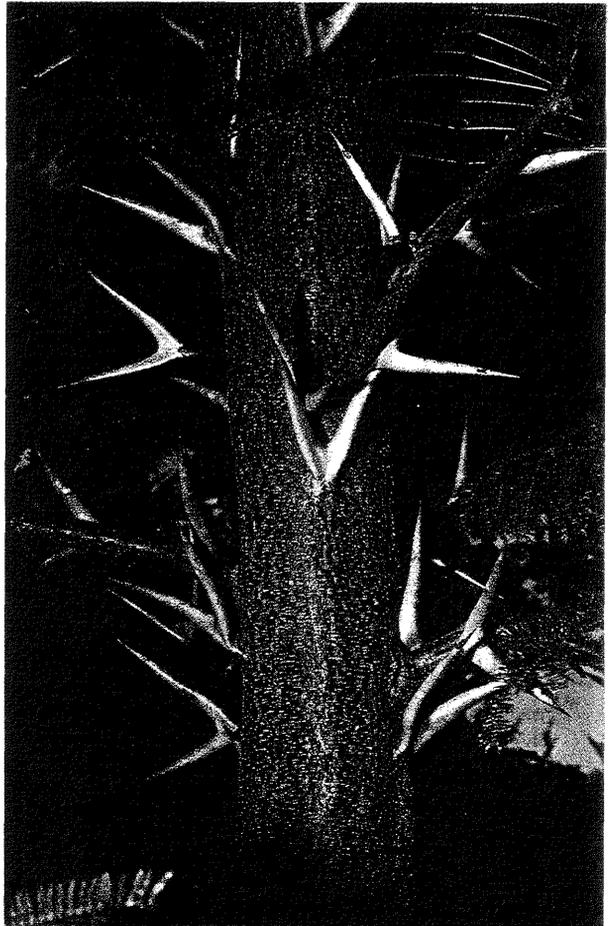


Figure 2. Swollen thorns of an ant-acacia (*Acacia cornigera*) in Palo Verde National Wildlife Refuge, Costa Rica. Several ant entrance holes are visible near the thorn tips.

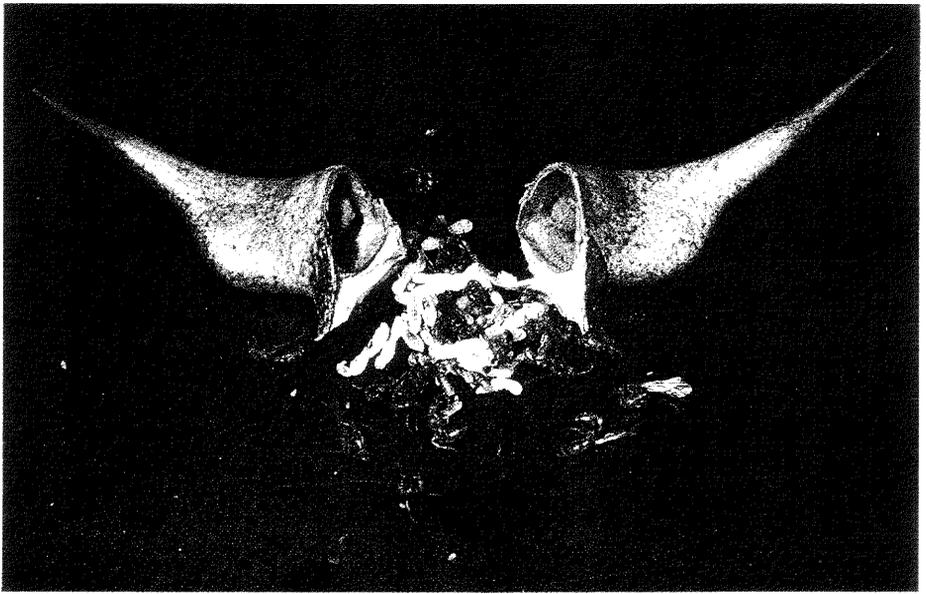


Figure 3. Swollen thorn split open and ants and brood dumped out. Winged forms are virgin reproductives (*Acacia collinsii*, Palo Verde National Wildlife Refuge, Costa Rica).

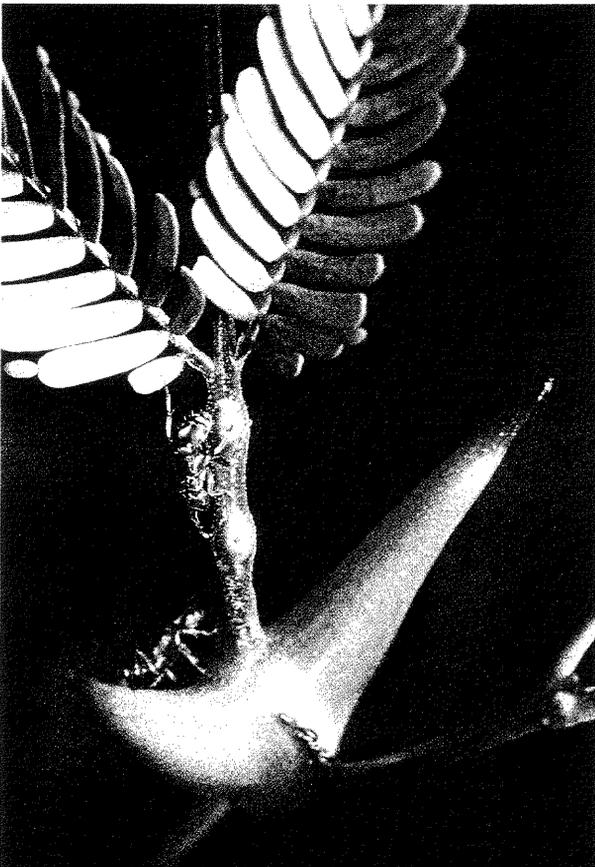


Figure 4. Two dome-shaped green sugar-producing nectaries on the petiole of an ant-acacia leaf. The ant is *Pseudomyrmex ferruginea*, a widespread acacia-ant (same plant as in figure 3).

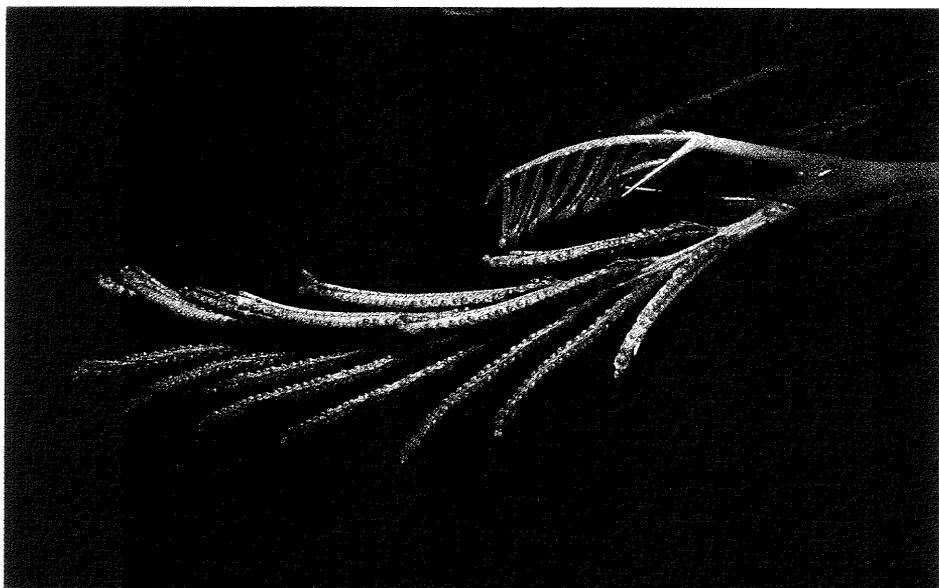


Figure 5. Two newly expanding leaves with orange oval Beltian bodies on their tips. The Beltian bodies on the leaflets are not yet ready to be harvested, while the large ones on the tips of major leaf segments are mature (*Acacia collinsii*, Santa Rosa National Park, Costa Rica).



Figure 6. A worker ant of *Pseudomyrmex nigropilosa*, a parasite of the ant and acacia mutualism (Palo Verde National Wildlife Refuge, Costa Rica).

against the challenge of browsing mammals, insects, vines and fungi. These defenses are directly analogous to the combination of chemical and morphological defenses against these same challenges that are possessed by more ordinary plants. The ant-acacias have even lost many of their conventional chemical defenses (Rehr *et al.* 1973). The ant colony now has a large and reliable food source and nest site. Likewise, it has lost its ability to forage and live in the habitat at large.

There are numerous instructive complications. At the present time in the northern Neotropics there are some 12 species of ant-acacias (Janzen 1974) and about as many species of acacia-ants. So why would one think that the system evolved as a one-on-one coevolved relationship, rather than as a diffusely coevolved system between many species of *Pseudomyrmex* and many *Acacia*? There are two simple and likely non-coevolutionary ways to add more species of *Acacia* to the system, once we have our coevolved ant-acacia-ant interaction; these two ways are far more likely than would be the independent evolution of this complex event on a minimum of 12 different occasions.

First, our new ant-acacia may simply form more species through ordinary geographic isolation, followed by sufficient evolution that the different populations are now recognized as different species. The new ant-acacias will belong to the same sub-group of the genus *Acacia*. Indeed a number of species of ant-acacias are unambiguously closely related to each other as suggested by floral, fruit and vegetative similarities (Janzen 1974). However, there are also several conspicuous sub-groups among the species of ant-acacias and these sub-groups are sufficiently different in traditional taxonomic characters that it seems unlikely that they have close common ancestors. This suggests a second way of producing a new species of ant-acacia. I think that these new lineages of ant-acacias came about through introgressive hybridization. In short, when an ant-acacia hybridizes with a non-ant-acacia (and they do so frequently in nature), the offspring tend to have either large thorns, Beltian bodies and large foliar nectaries, or none of these traits. The traits of most direct importance to the ant-acacia interaction appear to act as though they are controlled by a supergene (in reality they probably are just very well linked). Furthermore, if you get the ant-acacia traits, you also get an ant colony. This means that in certain ecological circumstances, if a non-ant-acacia is occupying a habitat next to a habitat occupied by an ant-acacia, the non-ant-acacia may well pick up the ant-acacia habit (and the ants) by introgression. If the non-ant-acacia was from a different sub-group of *Acacia*, we now have a new lineage of ant-acacias. This appears to have occurred at least three times within the Mesoamerican acacias; there is the *Acacia cornigera-sphaerocephala-mayana* group, the *Acacia hindsii-collinsii* group, and the *Acacia melanoceras-ullenii* group (Janzen 1974). One can easily argue that "ant-acacianess" is a trait that strongly enhances fitness in at least certain habitats (if you have the rest of the traits needed to support it - one can imagine that it might not suit, for example, a rainforest avocado tree).

However, if the ant-acacias are speciating and evolving through geographic isolation, and through introgression and invasion of new habitats, it seems unlikely that our original species of acacia-ant will remain unresponsive to these same circumstances. It is clear that there has been at least one large and

multi-branched radiation of acacia-ants (containing such species as *Pseudomyrmex belti*, *ferruginea*, *nigrocincta* and *satanica*). It is also clear that other lineages have been added, not through introgression but through ordinary evolution. The ant-acacia, with its copious food supply and reliable nest sites is a resource that is exceptionally available and of high value to other groups of twig-inhabiting ants, including other members of the genus *Pseudomyrmex*. Quite ordinary evolutionary change in a twig-inhabiting *Pseudomyrmex* may turn it into an acacia-ant, since the other half of the interaction is already set up, so to speak. This has clearly occurred once in the acacia-ants (there are at least two distinct lineages). In addition it is clear that in one case the evolutionarily incoming species of *Pseudomyrmex* (Figure 6) became simply a parasite of the ant-acacia mutualism; it harvests the resources and lives only on (dying) ant-acacias, but does not protect the acacia (Janzen 1975).

The ant-acacia interaction is spectacular, and it is a clear example of both one-on-one coevolution and how such a two-species interaction can then become multi-specific on both sides. However, its significance is much broader in two respects. First, as simply an example of evolution it is unambiguous. There is no reason to suspect that the ant-acacia interaction is simply the consequence of fortuitous ecological fitting of two or more species of organisms - the mechanism by which it is becoming clear that many complex interactions come about (Janzen 1985b). Second, it is an exceptionally clean example of the importance of the defenses of plants against the herbivores that surround them. This point is worth some elaboration.

Leaving the question of coevolution quite to one side, how does one show that in fact the acacia raises the fitness of the occupant *Pseudomyrmex* ant colony and vice versa? It is easy to determine what the ant-acacia means to the ant colony. The acacia-ants are so specialized that if the colony is removed from the acacia, the colony gradually dies. It dies of starvation (no Beltian bodies to feed the brood) and attrition as workers are lost in their incessant wandering in search of an ant-acacia to colonize. A newly mated founding queen can live for a month or more on her food reserves while she searches for a young ant-acacia to colonize, but she will not even attempt to establish a young colony in any other kind of substrate. But the dependency of the acacia-ants on ant-acacias has never been questioned since in nature it is obvious that the acacia-ants are obligatory seekers and occupiers of ant-acacias.

It is also easy to determine what the acacia-ant colony means to the ant-acacia, but it takes a little more physical labor. Conceptually, it is identical to demonstrating that the chemical defenses of any plant protect it; however, you cannot remove the tannins from an oak, the nicotine from a tobacco plant, or the latex from a rubber tree and then see how severely the plant is attacked by herbivores. Just think how much more we would understand of the function of secondary chemicals in plant defenses if such removals were easy or even possible. However, one can remove the ant colony from an ant-acacia (or prevent its arrival in the first place in the form of colonizing queens). The acacia-ant colony may be removed by two easy methods. A pesticide, such as parathion, thoroughly removes the ant colony; if the pesticide is one with a short half-life, within a few weeks the ant-free leaves are safe for consumption

by herbivores. Alternatively, the tree may be cut off at its base. In the experimental plots, the acacia crowns (with their ant colonies) are removed; in the control plots, the crown is left at the base of the acacia. In both plots, the acacia stumps rapidly produce new sucker shoots (coppice), but in the experimental plots there are no protective ant colonies (and colonizing acacia-ant queens use a minimum of nine months to produce even the smallest standing army of protective ants).

In experiments such as these, the results are most conspicuous and dramatic (Figures 7, 8). Many species of insects (and sometimes small rodents) arrive and feed heavily on the ant-free acacias. Many are species that commonly feed on or even specialize on other species of mimosoid legumes (as is *Acacia*). In most habitats, the majority of the ant-free ant-acacias are dead within a year. Their death is hastened by the shade from vines that find the ant-free acacias to be excellent trellises, much better trellises than are the ordinary woody plants that grow in vine-rich early successional habitats (where ant-acacias are often a conspicuous part of the flora).



Figure 7. Nine months of sucker shoot regeneration of an ant-acacia (*Acacia cornigera*) after the tree was cut back to a 65 cm stump, but the colony of acacia-ants (*Pseudomyrmex ferruginea*) was left at the site to immediately occupy the new sucker shoots – compare with figure 8 (Veracruz, Mexico).

There are, however, a few habitats where the ant-free ant-acacia<sup>5</sup> survive somewhat longer, such as in open pastures, where herbivorous insects are at a relatively low density and where competing plants are scarce. Furthermore, if the experiments are started in the dry season, when herbivorous insect density is very low and plant growth rates are minimal, the ant-less ant-acacias may survive quite well until the rainy season begins. Finally, if the experiments are done in a habitat where acacias have few relatives (and therefore the fauna of herbivores that feed on *Acacia* and their relatives is relatively small), a year or more may be required for the ant-free acacia to receive a lethal dose of herbivory and shade. Rainforest understory is such a habitat (e.g., *Acacia allenii*, Janzen 1974).

It is clear that the ant-acacia interaction coevolved and then became species-rich through ordinary evolutionary processes. However, there are two spectacular and instructive aspects of the interaction that are not coevolved, and one of these is not even evolved. First, there are a number of species of insects that specialize at feeding on thoroughly occupied (defended) ant-acacia-

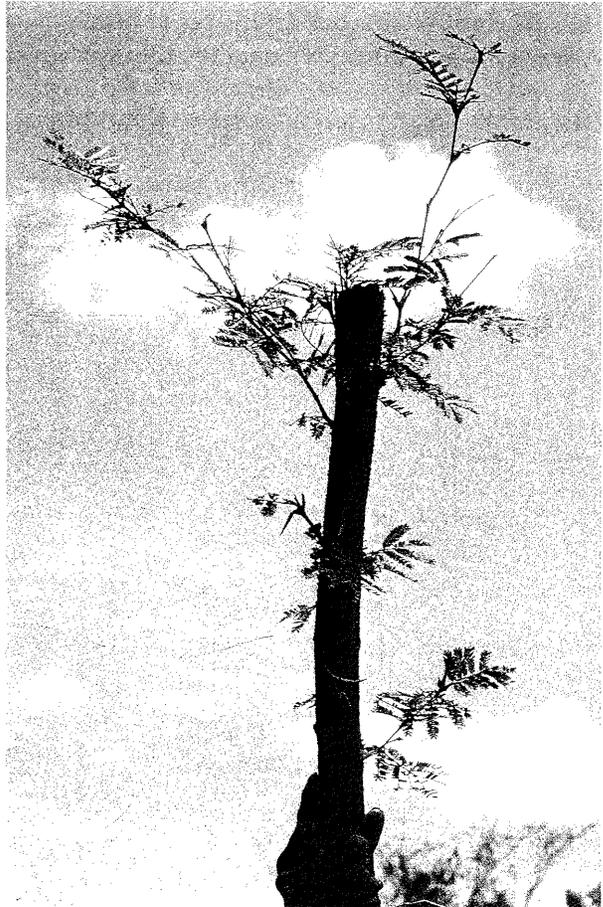


Figure 8. Nine months of sucker shoot regeneration of an ant-acacia after the tree was cut back to a 65 cm stump, but the colony of acacia-ants was removed – compare with figure 7.

cias. Each of these insects has evolved some distinctive way of dealing with the ants. *Pelidnota punctulata* is a large scarab beetle that is simply an animated tank that eats only young leaves of ant-acacias; the ants attack (Figure 9) but they cannot penetrate the beetle's defenses. Its special defense is simply to ignore the ants; this is successful with acacia-ants, but it would be fatal if the beetle were to behave in this manner in the presence of the diverse array of ants and other beetle predators in the world at large (Janzen 1967). *Syssphinx mexicana* is a large moth caterpillar that acquires the odor of the ant colony and feeds on the ant-acacia leaves among the worker ants, ants that viscerously attack other (foreign) herbivores; from the viewpoint of the ants, *S.mexicana* caterpillars are simply part of the acacia. From the viewpoint of the caterpillars, the occupied ant-acacia is both food and a violently urticating defense against the vertebrates that normally eat caterpillars (Janzen 1984). *Coxina hadenoides* is a small noctuid moth caterpillar that walks up to an ant-acacia, runs rapidly to the very tip of a growing branch, turns around, and faces a small army of pursuing ants. It then grabs each ant with its forelegs and with a quick flip of the body, throws the ant off the acacia. It can remove more than one ant per second; when the young growing branch end has been cleaned of ants, the caterpillar then eats the shoot tip and later walks off (or runs off) the acacia in search of another acacia with new foliage to consume. If there are too many ants and one succeeds in grabbing the caterpillar, the caterpillar has a second line of defense; it deposits a small drop of saliva on the ant, which kills the ant virtually instantly (Janzen 1967).

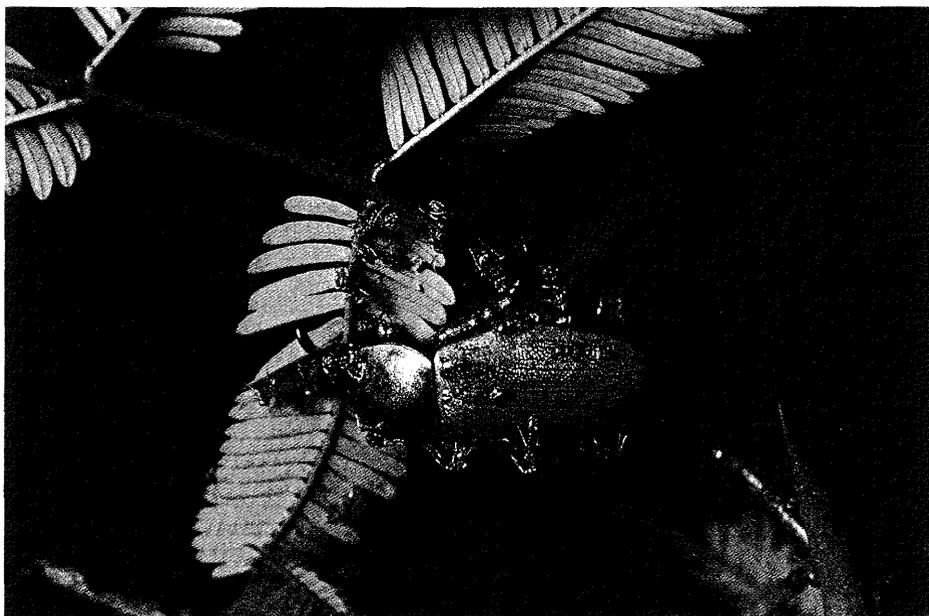


Figure 9. An adult *Pelidnota punctulata* beetle eating an ant-acacia (*Acacia collinsii*) and being ineffectively attacked by acacia-ants (*Pseudomyrmex ferruginea*) (Santa Rosa National Park, Costa Rica).

These animals, and some others with equally effective means of bypassing or countering the defenses of the ant-acacia, are directly analogous to the small and distinctive suite of somewhat specialized herbivores that can penetrate the chemical defenses of each species of plant. Every species of plant is fed on by at least one species of herbivore, even though each species of plant is well-defended against the vast majority of the species of herbivores on Earth. The beetle and caterpillars mentioned above clearly evolved with respect to the ant-acacia interaction. However, there is no reason to postulate that the acacia-ants or the ant-acacia interaction evolutionarily changed in response to these small herbivores.

In other words, there is no reason to apply the word coevolution to these herbivores. It was certainly not these herbivores that were the selective pressure for the ant-acacia interaction to coevolve in the first place. Rather, it was (and still is) those herbivores that the ants are successful in keeping off the acacia that selected for the coevolution. Unfortunately for **most** attempts to study coevolution, the herbivores with which a plant and its defenses evolved (or coevolved) are invisible. If these herbivores are even present in the habitat, they are likely to be feeding on some other species of plants, those that did not coevolve with them or those that have **not** yet made the next coevolutionary step and kicked them off. They will only appear at the plant with which they coevolved, or at least they only have a chance of appearing at that plant, if the defenses of the plant are relaxed (as when the ants are removed from the ant-acacias). However, even in this case they need not appear. This becomes evident when you consider that by removing the ants from the acacias, you do not bring back the now extinct Mexican and Central American herbivorous megafauna. Likewise you do not attract an insect that long ago evolutionarily left the acacia and has now evolved a set of very specific attractions to the plants that did not evolve a successful defense against it.

The second spectacular trait of the ant-acacia interaction is that in present-day Neotropical habitats that are rich in ant-acacias, the ant-acacias often grow on a disc of vegetation-free soil that is 1-2 m in diameter. When these habitats are burned, as cattle pastures and other kinds of young secondary succession often are during the dry season, this bare area makes a high-quality fire-break. The fire is often hot enough to kill the above-ground part of the ant-acacia, but not to kill the roots and the ant colony in the thorns. As the new sucker shoots appear with the first rains (or even before), they are immediately occupied by the large colony of acacia-ants that survived the fire. This rapid and protective occupation would not have occurred if the ant colony had been destroyed by the fire and the new sucker shoots were then dependent on newly colonizing queens for protection.

If one thinks only in the context of the modern tropics, it is easy to view the bare disc of ground as being the consequence of selection for vegetation removal by the **ants**, with its fitness-enhancement coming about through the ant colony surviving fires. However, ground fires in the dry season have been a conspicuous part of ant-acacia habitats only during the past 300 years or so (post-conquest European-style agriculture). It is much more likely that the bare basal circle below ant-acacias is simply the basal portion of the cylinder of vegetation-free space that the ants create by attacking foreign seedlings and

branch tips (and by carrying off seeds). This cleaning activity is in turn functional to the ant-acacia in minimizing its shading by intruding vines and adjacent shrubs. Yes, today the bare basal disc is a trait of importance in the interaction, but its evolution had nothing to do with fire.

Now I wish to leave this highly esoteric area of evolutionary biology, with a deeply felt note of regret that even as you read this, these magical mystery machines are being converted to hamburger, rice, boards and people. It won't be long before we can theorize all we wish, but there will be no non-anthropomorphic reality against which we can measure the relevance and accuracy of our thoughts, and stimulate our relatively dull mental abilities. I turn to a very human reason why we should understand evolution and especially coevolutionary biology

Humans are without doubt the most coevolved of any animal or plant that has ever walked the face of this planet. It is simply incorrect to think that when humans put shoes on their feet and coats on their backs they stopped evolving, and from there on its just cultural change. Allow me to redefine *Homo sapiens*. *H. sapiens* is an ordinary species of animal except that a very large portion of the individual's program is carried by the environment, an environment rich in conspecifics. This portion of the individual's program is fed into the computer after birth (Figure 10) rather than hard-wired at birth. That is to say, a new-born human is a very large stack of computer tapes, most of which are blank. The hard-wired programs are basic and general ones, such as physical traits, physiological traits, vocal capacity, mating drives, gathering drives, mental and physical dexterity, information storage capacity, memory reorganization and regurgitation ability, etc. Many of these traits and skills are



Figure 10. A group of juvenile *Homo sapiens* having their programs written by a *H. sapiens* adult and the environment of the Philadelphia Zoo.

the same whether, for example, dexterity is applied to picking seeds off the ground, catching fleas in your hair, fashioning stone arrowheads, typing, or playing a violin. A sample of 5 000 humans 5 000 years ago contained as many potential Nobel laureates as would the same size sample today. All these human activities require personalized development of subroutines for time, speed, accuracy, and appropriateness of execution. But the evolution of the capability to perform them came about through human harvest and use of resources, resources that by and large have not changed evolutionarily in response to this interaction. Yes, on occasion humans as hunters and gatherers may have coevolved with their unhuman living resources, but I suspect that it was usually diffuse coevolution if it occurred at all. In other words, humans, just like all other organisms, have a huge set of traits that took on their ancient and contemporary significance through ordinary evolution and serendipity.

What is exceptional about humans is not their average traits so much as the enormous superficial variability displayed among the members of the human population(s) for the details of these traits, a variation that comes about largely through programming of children by a highly variable human and inhuman environment. Humans are incredibly plastic. There is every reason to believe that the biological trait special to humans is the ability to fine tune a set of individuals to a local set of environmental circumstances through the ways that the software of the children is written, and through the flexible information storage, retrieval and alteration programs that are carried by the children and adults.

So where is the coevolution? Humans have two unique traits. One we have



Figure 11. A population of **wheat (*Triticum*)** plants whose DNA has been coevolutionarily captured by *Homo sapiens* (Saskatchewan, Canada).

just discussed. The second is that they do not simply use the world as it is. Recall the ant-acacia interaction. What is the acacia-ant colony from the viewpoint of the ant-acacia? It is simply a phenotypic trait that appears when the ant-acacia is programmed to make big thorns, Beltian bodies, foliar nectaries and stay green in the dry season. But what a trait!

The ant-acacia gets a whole genome-worth in return for a few lousy genes. It appears that humans discovered that one very early on. No, they don't get something for nothing, but they nearly do. What they discovered was that when commerce is conducted in the coinage of fitness, some very unequal exchanges may occur. In short, if I capture the fitness of a wheat plant (Figure 11) by protecting its seeds from granivorous rodents all winter in a clay jar and by planting a few of the seeds in soil that is relatively competition-free and nutrient- and water-rich, then I have the entire DNA of that plant working for me; to hell with the rodents and little birds that used eat wheat seeds and live in the habitats that have now become wheat fields. What does it matter if 200 species of prairie herbs and grasses once grew where a wheat monoculture now stands?

Humans are like an ant-acacia with a very large number of species of ants spliced onto the plant's genome. We have quite literally captured the genomes of hundreds of species of plants and animals, cleared the world of many of their competitors and consumers, and put them to work making products harvestable by humans. We have evolutionarily reshaped their genomes to where they make products for us. With contemporary genetic engineering, our capacity for this trick is even greater. We are generating enormous amounts of evolutionary change in a small select subset of the organisms around us.

But then, that is just evolution. Since we have obviously had about the same hard-wiring for millenia, perhaps then there has been no coevolution to speak of? Not so. The programming of each of us from birth onward is, or ought to be, finely tuned to match or complement the traits of the environment we live in - both that environment of the organisms whose DNA we largely control (including ourselves) and the portion we do not (as yet) control or find cause to attempt to control. The programs in that software make our interaction with much of the rest of the world a coevolutionary one. And I would argue that we have proven ourselves rather grossly incompetent at getting the programming right. This is not the place for a general evaluation of human progress at matching up the individual's software with its habitat - but if it were, we would mostly get failing grades. As I see it, the basic problem is that the programming feedback links between small clusters of family units and their immediate environment, and between individuals and their immediate environments, don't work worth a damn in today's world. Those links worked well until we got to where a human has potential daily contact with, or anonymity in the ocean of, tens of thousands of unknown humans.

I want to close with a mention of two areas of conspicuous failure. First, there are humans who look with pride at the huge suite of agricultural organisms whose genomes we now manipulate with a certain class of success in the production of resources for human harvest. Let me name a few. Cows, corn, eggs, chickens, cotton, citrus, vanilla, potatoes, coffee, tea, chocolate, milk,



Figure 12. The first steps in removal of wild organisms that compete with consume maize (*Zea*), a plant that is strongly coevolved with *Homo sapiens* (mountainous central Costa Rica). Compare with figure 13.



Figure 13. The final steps in removal of most of the wild organisms that compete with and consume pasture grasses, the food of large animals that are strongly coevolved with *Homo sapiens* (mountainous central Costa Rica). Compare with figure 12.

rubber, pepper, tomatoes, peppers, avocados, beans, rice, sorghum, tobacco, honey bees, manihot, squash, melons, sugar cane, and bananas. Oops, I left out humans. Recognize that list? Those are all tropical organisms (despite where some may be grown at the present). The human genome is, at this very moment, extinguishing easily 80 percent of the terrestrial species that were present during most of human evolution and long before as well. Within your childrens' lifetimes, this mass extinction will be complete. How could the great organizers, planners and controllers of our societies be so incredibly stupid as to imagine that our clutzy and desperate ancestors even began to scratch the surface of the pool of usable species when they extracted that list of 28 species from the millions available?

Our coevolution with our agricultural animals and plants has two basic parts - twist the genome (traditional crop and animal breeding), and clean away the organisms that interfere (Figures 12,13). The latter process is running full speed amuck. The tragedy of the commons (Hardin 1968) is here, and the commons is the entire tropical world. Traditional human software programs have core programs that say "when you can convert resources to people or to sequesterable resources, do so". For most of human evolution and coevolution, such programs were highly functional. They had nature with all its fine-scale opposition to the *Homo sapiens* working against them. If humans got too successful, they locally overshot the habitat's carrying capacity and paid a severe price. But humans persevered and humans won, at least by the rules of certain games. The simple question is, do we come up with a new program, or do we follow tradition and let a consequence select for a new program? That is to say, do you turn off the nuclear winter or do you put on a coat when it appears on the horizon?

But a certain part of the world is already screaming what I am saying here, and many are saying it better and more clearly. Maybe someone will realize it is to their advantage to listen. However, there is yet a second area in which we get very low marks in our recognition and development of our coevolved understanding and pragmatics.

We are very proud of our brains, and we know quite well what complicated things they can do if competently programmed. I might note, however, that if the software is incompetently programmed, the human brain functions much less well than do the brains of most other animals - it lacks high quality hard-wiring and there is interference from messed up software. However, I would argue that not only do you not know of what your brain is capable, but in the steady homogenization of the natural habitat you are rapidly destroying a major mechanism by which your brain's abilities are realized. Allow me an analogy. You are all aware of the complexity that color gives to your world (Figure 14). It allows the expression of variation and pattern far greater than is possible with black, white and shades of gray. Well, there are two ways that I can deprive you of the complexity that color vision adds to your world. I can make you colorblind. Or, I can leave you your color vision and turn the sun's rays into monochromatic light (try deciding on a color print shirt under very bright moonlight, if you want a feel for what I refer to).

The wholesale, and final, destruction of the last parts of the biologically complex portions of the earth's surface is monochromatizing the earth's sur-

face, depriving you quite thoroughly of the opportunity to ever know the capacity of major parts of your brain. I do not exaggerate; all of New York city is to a square miie of lowland tropical rainforest as a mouse's squeak is to all the music that has ever been produced by humanity. Europe was totally trashed and has remained so. North America is the same, minus a couple of percent. What is unique about the tropics is not just its rampant complexity and beauty, but the fact that a portion of it is still there. Illinois with its passenger pigeons, forest bison, mammoths, oak forests and prairies was also complex, beautiful and mentally stimulating. And I might add that if you think an Iowa cornfield is boring, you ain't seen nothing til you have stood in 100 square kilometers of Brazilian sugar cane or Costa Rican cattle pasture.

But you counter with the statement that many humans seem to do just fine without ever being exposed to the complexity and pattern that nature can offer, tropical or otherwise. That is drivel. Most humans have always been raised to be animate machines, beasts of burden and cannon fodder. Their brain capacity is never realized. Is that the pinnacle of success to which we strive? Is it really human destiny to lionize the production of more humans, more crops and more monotony? You may have a fine brain, and you may pass it on to your grandchildren; but they won't even know they have it, much less use it for anything, if the only thing to which they can apply it is the trivial boredom of a world made by other humans. Study nature, not books? No, study both of them (but hurry with the nature, last chance, folks).



Figure 14. Adult female silk moth, *Rothschildia erycina*. Imagine trying to understand and react to the messages on its wings without the use of color vision (Santa Rosa National Park, Costa Rica).

# Crafoord Lectures

1982 **Vladimir I. Arnold:** On some nonlinear problems.

**Louis Nirenberg:** Mathematical methods in nonlinear problems.

1983 **Edward N. Lorenz:** Irregularity: a fundamental property of the atmosphere.

**Henry Stommel:** The delicate interplay between wind-stress and buoyancy input in ocean circulation: the Goldsbrough variations.

1984 **Daniel H. Janzen:** The most coevolutionary animal of them all.