# Frugivory and Seed Dispersal: 'La Coevolución ha Muerto – ¡Viva la Coevolución!'

Nathaniel T. Wheelwright

SIX YEARS AGO, a group of ecologists interested in interactions between fruiting plants and animal seed dispersers met for a four-day conference at the Los Tuxtlas Biological Station in Veracruz, México. Their aim was to share the results of their research in a relatively young field and, by highlighting its unanswered questions, chart its future course. In June 1991, an expanded group convened in Veracruz for the second symposium-workshop on frugivory and seed dispersal, organized once again by Alejandro Estrada (Universidad Nacional Autónoma de México, México City, México) and Ted Fleming (University of Miami, Florida, USA). The 28 invited papers and 46 posters described current studies in 11 countries and will be published next year by Kluwer Academic Publishers and the journal *Vegetatio*.

Since the first symposium, the focus of research on frugivory and seed dispersal has shifted. Preoccupation with determining the role of coevolution has abated, despite the fact that many essential questions about the evolutionary origin and consequences of plant–disperser interactions remain unresolved. Coevolution, now viewed by many as a reasonable but essentially untestable concept, has faded as the paradigm directing the study of seed dispersal by animals. Nonetheless, although few participants in this year's symposium were willing to attribute the existence of specific plant–animal syndromes to coevolution, few were ready to throw out the concept altogether. Their ambivalence was expressed by Mexican biologist Ellen Gryj (Duke University, North Carolina, USA), who noted, 'La coevolución ha muerto – ¡Viva la coevolución!' ('Coevolution is dead – Long live coevolution!')

An intriguing case for diffuse coevolution and parallel adaptive radiation in interacting plant and animal taxa was made by Gary Stiles and Loreta Rosselli (Universidad Javeriana, Bogotá, Colombia). They pointed out that manakins (Pipridae), small birds with broad gapes and the habit of regurgitating rather than defecating seeds, abound in lowland habitats in the neotropics, where plants with large-seeded fruits predominate. Tanagers (Thraupinae), which are proficient at separating large seeds from the pulp and spitting them out without dispersing them, apparently originated in highland habitats, where small-seeded fruits, such as melastomes, are most diverse.

Gene Schupp (Savannah River Ecology Laboratory, South Carolina, USA) emphasized that the effectiveness of a particular seed disperser – and the evolutionary outcome of an interaction – depend upon the quality of dispersal (seed treatment, deposition patterns, etc.) as well as on the quantity of seeds it removes. Most dispersers seem to have a mixture of good and bad traits with respect to their impact on plant fitness, but it is their overall effectiveness that determines the nature of evolutionary interactions. If birds do in fact discriminate among plants on the basis of fruit form, there is the potential for rapid evolutionary responses in at least one tree species, *Ocotea tenera* (Lauraceae), whose reproductive traits have been shown to be highly heritable (based on parent–offspring regressions using trees that I grew in common gardens in Costa Rica).

The 'black box' of avian fruit processing has been opened at last and serious attention has been paid to fruit preferences by animals. Taking to heart a former professor's admonition that 'ecology is nice, behavior is good, but first you have to know the anatomy and physiology', Carlos Martínez del Rio (Princeton University, New Jersey, USA) and Carla Restrepo (University of Florida, Gainesville, USA) argued that it is time to abandon the 'cow paradigm' of vertebrate digestion and proximate nutrient analysis, and instead to measure the postingestinal component of profitability. Gut morphology varies extensively among fruit-eating birds. In certain species of tanagers and mistletoe birds, for example, the gizzard has been reduced to a tiny diverticulum or eliminated

Nathaniel Wheelwright is at the Dept of Biology, Bowdoin College, Brunswick, ME 04011, USA.

altogether, speeding the processing of nondigestible seeds. Certain taxa of birds apparently lack sucrase and the ability to digest sucrose-rich fruits. Martínez del Rio and Restrepo maintained that interactions between physiological features of animals and chemical characteristics of fruits determine the profitability of feeding on different fruits. It is these interactions rather than traits intrinsic to fruits that influence animals' choices among fruiting plants, and potentially mediate reciprocal evolution between plants and their seed dispersers. In support of the explanatory power of proximate nutrient analysis, Ted Stiles (Rutgers University, New Jersey, USA) found consistent preferences for high-lipid fruits in several temperate-zone bird species in the field and in captivity.

Greg Murray and his colleagues (Hope College, Michigan, USA) examined how seed packaging affects the profitability of fruits for several species of temperate-zone birds. Using artificial fruits in which fruit diameter, nutrient concentration and seed load (the ratio of edible pulp to the total volume of seeds) were held constant, they varied seed number and size and discovered that seed retention times were shorter and pulp consumption rates higher when birds fed on fruits with few large seeds rather than those with many small seeds. Consequently, birds generally favored large-seeded fruits, although closely related bird species and even individuals within the same species showed marked differences in preferences. Such individual 'prejudices' may make the search for simple fruit-preference-decision rules elusive.

Several contributors emphasized the importance of viewing the interaction between plants and seed dispersers in a broader context by considering the impact of pre- and postdispersal seed predators or following the demography of seeds through the seedling and sapling stages. Anna Traveset (Estación Biológica de Doñana, Seville, Spain) demonstrated that parasitic wasps arrest color changes that normally signal ripening in a Mediterranean shrub, *Pistacia terebinthus*, discouraging birds from removing fruits and ultimately destroying more seeds than are dispersed by birds. Margaret Byrne and Doug Levey (University of Florida, Gainesville, USA) documented that ants visit the droppings of fruit-eating birds in Costa Rica, removing the seeds they contain and secondarily dispersing many of them. Not all seed predators respond similarly to factors such as distance from parent plants, as pointed out by Hank Howe (University of Illinois–Chicago Circle, USA). Insects on Barro Colorado Island in Panama, for instance, show distance-dependent predation on *Virola* seeds, whereas mammals do not.

Complex interactions between plants and animals are challenging to characterize in any one system, but it may be even more difficult to make generalizations between one region and another. Mark Leighton (Harvard University, Cambridge, USA) in Borneo and Pierre Charles-Dominique (Museum National D'Histoire Naturelle, Brundy, France) in French Guiana, for example, found extreme dietary specialization among fruit-eating animals and predictable morphological syndromes among rainforest plants. The importance of a comparative perspective was illustrated by Annie Gautier-Hion's (Station Biologique de Paimpont, Paimpont, France) work on four closely related monkey species (*Cercopithecus* spp.) in Africa. In Gabon, where most plant species produce fleshy fruits, the monkeys feed on fruits and are important seed dispersers. In Zaire's legume-dominated forest, fleshy fruits are relatively uncommon. There, monkeys mainly eat leaves and immature fruits, destroying 40% of the seeds they consume. Because many vertebrates can respond opportunistically to local fruit availability, distant relatives in sympatry may be more similar in diet than closely related species in allopatry. Even at extremely local scales in Costa Rican lowland forest, fruit resources and avian populations vary substantially, according to Bette Loiselle and John Blake (University of Missouri, St Louis, USA). A species list unfortunately reveals very little about the nature of interactions between plants and their seed dispersers.

The evolutionary potential of species interactions depends upon the extent to which they overlap in space and time. Pedro Jordano (Estación Biológica de Doñana, Seville, Spain) compared the geographical ranges, habitat preferences and local abundances of six European thrush species (*Turdus*) and five juniper species (*Juniperus*) whose fruits the birds eat. Birds range more widely than plants; the abundance of both birds and fruits varies between seasons and years. Yet there was no correlation between biogeographic congruence of a pair of plant and bird species and the degree to which the plant depended upon the bird for seed dispersal or the bird relied on the plant for fruit.

Veracruz has been an appropriate site for the two symposia on seed dispersal by animals. Most trees and shrubs in México's Atlantic lowland forests produce fleshy fruits, as in other tropical regions, and a third to a half of the native species of birds and mammals consume fruits and disseminate or prey upon seeds. México also starkly showcases the worldwide dilemma of tropical habitats: more than a third of the country's forests have been converted to pasture. Preserves like Los Tuxtlas, shrunken and isolated pieces of a magnificent forest, have already lost a number of species of fruit-eating animals. Various papers and posters dealt with plant reproductive biology in isolated forest patches in México, Brazil and Australia, but none clearly demonstrated an impact on plant populations of a diminished seed-disperser fauna. Indirect evidence for population-level impacts of seed dispersal came from Jim Hamrick and co-workers' (University of Georgia, Athens, USA) study of the population-genetic structure of Panamanian tree species with distinct seed-dispersal mechanisms. Dispersal by gravity, wind or bats tends to be local or clumped, leading to fine-scale genetic structure that is less apparent in plants with more mobile dispersers. Sergio Guevara (Instituto de Ecología, Xalapa, México) suggested that pasture trees such as figs (*Ficus* spp.) might sustain forest fruit-eaters for a while in altered landscapes and forestall the expected negative consequences of their local extinction. Working in Peru, David Gorchov (Miami University, Ohio, USA) concluded that, following strip-cutting, seed dispersal by animals may be less important in forest regeneration than growth from stump sprouts and pre-existing seedlings and saplings.

The relationship between fruiting plants and their seed dispersers is widely cited as an example of a mutualism, an interaction in which each species positively affects the fitness of the other. Nonetheless, the degree to which animals depend on fruits for food remains poorly quantified, although during years in which fruits are scarce in tropical forests, famine or emigration has occasionally been documented in fruit-eating animals. Even less well-understood is the fate of plants that have lost their coterie of seed dispersers. Park managers and politicians can be assured that forest fragmentation and isolation will lead to the elimination of many fruit-eating animals, but will animal-dispersed plants follow? We may have to wait until the third symposium to know the answer.