Chemical ecology of seed dispersal : odors, taste and nutritional ecology

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Fruit and seed characteristics are of extreme importance for the diet of the dispersing animals. For the plants, a high investment to dispersal implies high investment into volative compounds and the nutritional values of the fruits and seeds, i.e. high amounts of carbohydrates, protein, fat, and/or various cations. The symposium aims at discussing the trade-offs of these investments for plants and animals. Although several groups of frugivores have well-developed olfactory perception, only few studies have addressed the roles of odours as signals in the ecological interactions between plants and seed-dispersing animals. The first focus of this symposium is plant volatile compounds in fruits and their olfactory perception by frugivores, presenting current results and framing questions for future research in this embryonic but promising area. The second focus is on the comparative analysis of chemical composition and nutrient contents of seeds and fruits, and its relation to animal nutrition and dispersal syndromes. (Photo: *Ficus capensis* in Kibale National Park, Uganda. © Alain Houle)

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Plenary 30'

When should fig fruit produce volatiles? Pattern in a ripening process

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The domesticated fig *Ficus carica* as well as some others, e.g. *Ficus religiosa*, are considered to have climacteric fruit wherein there is very rapid ripening following a burst of ethylene production. Such fruit may have very short retention time on the plant after ripening. However, not all fig species show such a ripening phenomenon. In this paper, we examine the differences in ripening, fruit presentation and fruit availability in some Asian fig species and also investigate whether these patterns relate to their dispersal agents, and when in the diel cycle the figs are dispersed. We examine variation in diel production of volatile organic compounds by ripe figs and attempt to relate these patterns to disperser identity and activity. We erect and test the hypothesis that volatile production for figs which attract their dispersers by olfactory processes should be most pronounced when dispersers are most active during the diel cycle.

Oral 15'

Nutritional importance of *Ficus* for the common fruit-eating bat *Artibeus jamaicensis*

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Figs (*Ficus sp.*) are frequently considered as keystone resources for many frugivorous mammals due to their abundance and year-round fruiting phenology. In addition, nutritional values and mineral composition may contribute to the importance of figs for frugivores. Particularly the very high calcium concentration found in many fig species has been proposed to be crucial for successful reproduction in frugivorous mammals, as calcium is the most important and often limited mineral for the development of the offspring. We will present and compare data about the mineral and nutritional composition of fruits from about 170 trees of 18 *Ficus* species present in the Gatún Lake area in Panama and of several non-fig fruit species eaten by the common fruit-eating bat *Artibeus jamaicensis* (Chiroptera, Phyllostomidae). Figs have a significantly higher calcium concentration (2,8 – 19,8 mg/g dry matter) than the other fruits analyzed (0,13 – 7,6 mg/g dry matter). To further elucidate the importance of figs as calcium source we also performed assimilation experiments with wild-caught *A. jamaicensis* at different reproductive stages. The bats were fed for several nights with one fruit type (either fig or non-fig fruits).We subsequently collected faeces and fruit pellets and analyzed these samples for their mineral composition. Based on these data we determined the calcium balance of the bats. Finally we discuss the importance of figs as keystone resource for calcium in frugivores.

Scent as a Component of Dispersal Syndromes: a Comparative Analysis in the Genus *Ficus*

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Many studies of plant/frugivore interactions have focused on identifying traits adapting plants to different seed-dispersing animals. Almost no work has examined the role of fruit scents in differential attraction. We focus on this neglected element of dispersal syndromes. The unique phenology of figs (*Ficus* spp.), with year-round fruiting, sometimes makes them keystone resources for frugivores. Figs of some species are eaten primarily by bats, others by birds, and others (in Madagascar) by lemurs. Little is known about how these frugivores are differentially attracted. Recent work has shown that mutualisms between figs and their specialized pollinating wasps are chemically mediated: emission of specific volatile signals by figs and their perception by the pollinator ensure encounter of the mutualists. To explore whether fig/frugivore interactions are also chemically mediated, we used adsorption/desorption methods to study scents emitted by mature fruits of several fig species from different tropical regions. We examined whether the identity of the main seed disperser (bats/birds/lemurs) was associated with the quality and quantity of the bouquet of scents emitted by figs at the seed-dispersal stage. We found consistent differences between scents emitted by mammal- and bird-dispersed fig species. Based on our results, we discuss the importance of scent in adaptations of figs to seed-dispersing vertebrates.

Bat fruits and fruit bats: chemical adaptations for seed dispersal by bats within the genus *Ficus* (Moraceae)

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Using the genus *Ficus* as a model, this study explored the fruit scents of nine species of fig, from the New and Old World tropics, in relation to the foraging behaviour of New and Old World fruit-eating bats, to test the following hypotheses: 1) variation in the chemical composition of fruit scent in the genus *Ficus* is adaptive, rather than phylogenetic in origin, 2) the composition of fruit scent, among bat-dispersed fig species, is convergent within geographically isolated and phylogenetically separate lineages. The fruit scents of bat and bird-dispersed figs were sampled in the field, using dynamic headspace adsorption techniques. Chemical analyses, using gas chromatography (GC) and GC/mass spectrometry (MS), revealed a broad overlap in scent class between bat-dispersed species from both biogeographic regions. The bouquets of these species were dominated by monoterpenes, which, contrary to phylogenetic predictions, were almost completely absent from bird-dispersed species from both regions. The scents of bird-dispersed figs were also unattractive to bats. Thus, variation in fruit scent, between bat and bird-dispersed figs, is almost certainly adaptive rather than phylogenetic in origin. However, a strong phylogenetic component to

fruit scent variation was revealed among fig species dispersed by bats. Behavioural experiments, on naïve bats, from the New and Old World tropics, suggest that interactions between bats and figs could be more specialized in the Neotropics.

Frugivory and digestive physiology in arboreal, tropical Carnivora (*Arctictis binturong, Potos flavus*)

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While most Carnivora species consume animal diets, *Arctictis binturong* (binturong) and *Potos flavus* (kinkajou) are – like many primates - flexible omnivores and frugivores. Our aim was to evaluate whether these species also exhibit convergence with primates in their digestive physiology. Data on digestive retention (MRT), carbohydrate fermentation, short-chain fatty acid (SCFA) production, and fiber digestion were collected at the Carnivore Preservation Trust, NC. Carbohydrate fermentation, SCFAs, and fiber digestibility data were measured on fecal samples assayed in the laboratory. Carbohydrate fermentation samples were incubated anaerobically and analyzed for methane, pH, and SCFA. Digestibility and fiber were assayed using standard NDF and ADF methods. Preliminary results indicate that both species digest food several orders of magnitude faster than comparably-sized frugivorous/omnivorous primates (binturong: 13-27kg; MRT = 38mins; kinkajou: 2–5kg; MRT: 27mins). Data on carbohydrate fermentation and fiber digestion are consistent with this pattern. NDF assays indicate fiber digestion at only 14.22% and ADF at 28.82%; only trace SCFAs were found. All data suggest that these species concentrate on extraction of simple sugars/disaccharides in the small intestine rather than fermentation of polysaccharides in the large intestine. Implications for interpreting adaptations to a fruit diet, seed dispersal, and competition with primates will be discussed.

A temperate diplochorous seed dispersal system? Interactions between herbs, slugs and ants

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Ants are the best-known dispersers of elaiosome-bearing seeds of early spring flowering plants in temperate ecosystems. In order to identify those seed properties that trigger the ants' choice for certain seeds, we correlated seed preferences in field experiments with structural and chemical analyses. We expected that certain fatty acids play a major role as cues for seed removal behaviour. However, bioassay-guided analyses of the chemical profile of preferred seeds revealed that the amount and composition of amino acids in elaiosome-bearing seeds is a better predictor of the ants' seed choice. In further field experiments, we identified slugs as a second important and highly effective group of seed dispersers with a strong preference for elaiosome-bearing seeds. Slugs swallow seeds and defecate them after several hours of ingestion. Surprisingly, seeds with their attached elaiosomes remain intact after the gut passage. Therefore one can expect that such defecated seeds attract secondary dispersers. We

tested if these defecated elaiosome-bearings seeds attract ants, but observed a diminished attraction. Analyses revealed strong differences in the amino acid profile between these slug-treated seeds and intact seeds. In conclusion, ants may act as secondary dispersers of seeds primarily transported by slugs, but since amino acids are key substances that render seeds attractive to ants, the altered chemical composition may be responsible for low transport rates.

Fruit and seed chemistry and dispersal modes in Amazonian floodplain forests

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In Amazonian floodplain trees, there is a large variety of morphological, nutritional and chemical traits of fruits and seeds. With a flooded period of up to 7 months, fruits and seeds are released into the water and may be submerged or floating for several days to months – a situation which normally makes most seeds unviable. Trees are adapted and seeds remain visually sound for >2 months when continuously submerged. This stands in contrast to the majority of land plants, whose seeds quickly lose viability if submerged for prolonged periods. On the contrary, seeds of floodplain species kept in air dry or decompose within few days or weeks. Many species have high nutrient contents as a function of the relation to fish dispersal, just as in upland forests diaspores of species dispersed by mammals are rich in fat and proteins. However, in Amazonian floodplain trees dispersal syndromes are closely linked to water, with all necessary adaptations enhancing floatation and attractiveness for fish. High nutrient contents are also advantageous for the seedling, because a high investment of the parent tree into seed reserves guarantees fast initial growth. This can be crucial in an environment with a flood amplitude exceeding 10m. Time for seedling establishment in the non flooded terrestrial period is reduced to few months or weeks. For a fast and well timed establishment, seeds must germinate fast and they need adequate nutrient reserves, especially in nutrient poor environments like black water floodplains.