



## Ecology and evolution of frugivory and seed dispersal (Part II)

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(Dung of *Ursus americanus*,  
 Photo © [Phil Myers](#))



**Black bears (*Ursus americanus*) are effective seed dispersers, with a little help from their friends**

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Black bears (*Ursus americanus*) are generally considered effective seed dispersal agents for fleshy-fruited plants because they can consume hundreds of fruits at once and have large home ranges. Seedlings can emerge from fecal piles, but if any seeds are removed from feces by rodents, it is often considered seed predation. In theory, removal of seeds from bear feces by seed-caching rodents could represent a second phase of dispersal that benefits fleshy-fruited plants, yet this idea has never been tested. I tested four hypotheses regarding the idea that a second phase of seed dispersal by seed-caching rodents is beneficial to fleshy-fruited plants that are initially dispersed by black bears in the Sierra Nevada. We determined that deer mice (*Peromyscus maniculatus*) removed seeds from bear feces and cached them in soil. These seeds escaped several sources of mortality by being moved to relatively safe locations. A field germination study confirmed that caching can benefit seedling emergence. In addition, rodents discovered seeds in bear feces more quickly than those in bird feces, suggesting that a bear-rodent tandem could be the most effective seed dispersal syndrome for some fleshy-fruited plants. With further study, the two-phase seed dispersal syndrome presented here could help elucidate patterns of species diversity and distribution of fleshy-fruited plants.

**Microsatellite analysis of seed dispersal of *Myrica rubra* by the Yakushima macaque (*Macaca fuscata yakui*) on Yakushima Island, Japan.**

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Primates are considered to be efficient seed dispersers. It is impossible to directly track seed movement once an animal has ingested seeds, and also little information exists regarding the spatial pattern of seed dispersal by primates using maternity analysis based on genetic methods. The objective of this study was to describe the spatial pattern of seed dispersal of *Myrica rubra* by the Yakushima macaque (*Macaca fuscata yakui*) by genotyping seed maternal tissues in the forest of the Japanese island of Yakushima. Macaques are habituated to observers without provisioning and their social and feeding habits have been under constant study since 1976 at our study site. The fruits of *M. rubra*, a tree widely distributed in evergreen forests, are an important source of food for macaques in early summer. Conversely, macaques are major seed dispersers for *M. rubra* because the fruit and seeds of *M. rubra* are large (fruit: 13.2 mm in diameter, seeds: 7.7 mm in diameter). Here, we conducted direct observation of macaque's feeding behavior, collected *M. rubra* seeds dispersed by macaques, and analyzed the maternal origin of seeds dispersed by macaques. We showed by field survey that macaques selected more profitable patches according to ripe fruit availability. By genetic methods, we detected a high level of diversity among the dispersed seeds in each feces with



long dispersal distance. We discuss the spatial pattern of seed dispersal of *M. rubra* by macaques in relation to their behavior.

### **"Liaisons dangereuses" in the Mediterranean dwarf palm: the defensive role of fresh pulp against seed predators**

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We chose the interaction between the Mediterranean dwarf palm (*Chamaerops humilis*) and its major seed disperser, the Eurasian badger (*Meles meles*) to evaluate the hypothesis that endozoochory is characterized by a mixture of conflicting and overlapping interests, with the capacity of being positive or negative for the palm fitness. Our experimental results from field sowing monitored over two years revealed the multifunctionality of *C. humilis* fruit pulp and that pulp consumption by badgers had conflicting outcomes for the palm. Seed survival was much lower and seed predation by bruchids much higher for badger-ingested than for control seeds, supporting a defensive role of *C. humilis* ripe fruit pulp. All seedlings emerging during the first months after sowing came out from badger-ingested seeds, suggesting an early inhibitory function of fruit pulp. Badgers imposed a sizeable short-term fitness cost to *C. humilis* and therefore could be categorized as a 'dangerous liaison'. Nonetheless, because of badger high mobility, their dispersal service appears paramount given the severe fragmentation and isolation of most *C. humilis* populations across the highly humanized Mediterranean basin. Our study, thus, illustrates the necessity of integrative analyses in which focal plant-animal interactions (e.g., fruit-frugivore systems) are accounted in conjunction with other species interacting with the plant at different stages of the life cycle and recruitment process.

### **Establishment of novel dispersal mutualisms between introduced plants and resident birds in California, USA**

Clare Aslan<sup>1</sup>

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Vertebrate dispersal may promote plant invasiveness. I examined the role of bird-plant dispersal mutualisms in invasion potential of three non-native plant species: *Triadica sebifera*, *Ligustrum lucidum*, and *Olea europaea*. I paired foraging observations in California, USA, with aviary experiments to quantify dispersal, assess bird preferences, and compare mutualism features between the non-natives and a native species, *Heteromeles arbutifolia*. Fruit removal was highest for *H. arbutifolia* (94%) and lowest for *T. sebifera* (24%). Most foraging was done by dispersers (vs. seed predators) and by "pulse feeders" with potential for long-distance dispersal (vs. "background feeders"). The number of conspecific plants per stand was significantly related to bird visitation; larger source stands may promote bird-mediated invasions. Disperser-defined niches were narrow, indicating that a few bird species did most dispersal, but niche overlap between *H. arbutifolia* and *L. lucidum* highlighted the diffuse nature of these mutualisms and suggested that *L. lucidum* may compete for dispersers



with *H. arbutifolia*. In aviaries, native birds (*Turdus migratorius* and *Catharus guttatus*) preferred native fruits but switched to non-natives when native fruits were withheld. Accustomization to non-native fruits did not alter preference. Non-native European starlings (*Sturnus vulgaris*) preferred *O. europaea*. No case study species appear dispersal limited and all have established mutualisms with local birds.

### **Fruit choice and seed size selection in an eclectic primate omnivore and implications for plant community dynamics in West Africa**

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Olive baboons (*Papio anubis*) in West Africa are highly frugivorous and disperse seeds of 26% of the regional pool of woody plant species. They are characterised as eclectic feeders yet the role of morphological fruit and seed traits in baboon fruit choice remains largely unexplored. We investigated a) if baboons prefer particular traits relative to the availability among plant species and b) which suites of traits best predict fruit choice and seed handling (dispersal vs. predation). Seed size is an important plant fitness trait and often varies considerably also within plant species. We thus tested for c) intra-specific seed size selection, expecting baboons to choose fruits with smaller than average seeds in species the seeds of which they swallow with pulp and larger seeds when they predate on the seeds. Among plant species, baboons seemed to consume whatever fruit type, colour, and size of fruit and seeds available, though they especially included larger fruit into their diet. Fruit type and colour best predicted whether a species was part of baboon diet whereas fruit type and seed size best predicted seed predation. Within species, baboons were seed-size selective in 9 out of 11 plant species which can impact dispersal distance and plant reproductive success. As most plant species in the savanna-forest mosaic of West Africa have medium-sized to large fruits and seeds, large frugivores like baboons seem particularly important for plant community dynamics in this ecosystem.

### **Testing the Janzen-Connell hypothesis at the community level with functional traits**

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We conducted a novel test of the Janzen-Connell hypothesis (J-C), which proposes that seedling mortality increases with increasing proximity to (or density of) conspecific adults. Though this hypothesis has been extensively tested, and by and large supported, we still lack interpretations at the community level, in large part because many species are too rare to permit rigorous tests of their spatial distribution. Previous tests of J-C at the community level have been limited by the difficulty of acquiring data on the survival of seedlings of rare species. Thus, previous studies have focused upon one or few common studies, making it difficult to infer the generality of distance-dependent mortality patterns. We make a general test of J-C at the community level by using functional traits. Essentially, we recast J-C to ask



whether seedling survival is affected by the proximity of adults with similar functional trait values. In a pristine tropical rain forest in French Guiana, we observed the survival of 8600 seedlings over seven years, and identified all adult trees within 15 m of seedling plots. We integrated these datasets with data on adult traits and phylogenetic distances collected as part of the BRIDGE project. We report on the increase in seedling mortality resulting from the proximity of functionally similar adult trees. Our results should have important implications for the extent to which J-C mechanisms contribute to the maintenance of diversity in species-rich tropical forests.