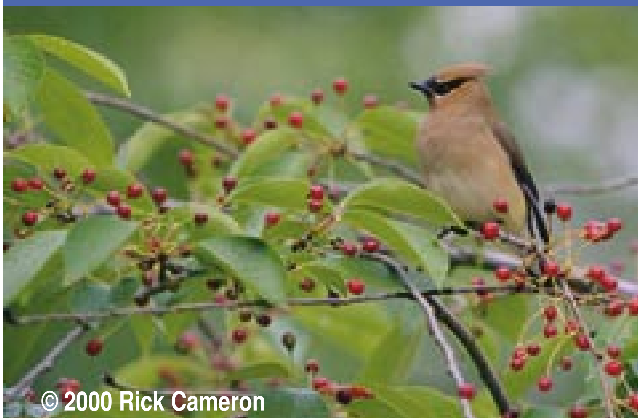
What role do birds play in dispersal of invasive plants?



"Look, that bird is eating a fruit! But is it dispersing the seed?"

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Introduction

Plants use various strategies for dispersing seeds and a thorough understanding of how dispersal occurs for invasive, exotic species is essential if we want to understand and control their spread. There may be several reasons why a particular species is designated as a FLEPPC Category I plant, but without a reliable dispersal mechanism, a species will not become a problem beyond a local scale.

We have examined the literature to see what is known about vertebrate-assisted seed dispersal of FLEPPC Category I species, and were surprised to find how few dispersers have been adequately verified. Identification of dispersal agents seems to lean heavily on assumptions and little on testing. Moreover, while there is a basic understanding of this type of dispersal, there often seems to be a lack of knowledge of important subtleties. Consequently, the purpose of this article is to provide a basic explanation of vertebrate-assisted seed dispersal and, using examples from literature involving exotic species, to illustrate when the process has been misapplied or not fully understood.

Vertebrate-assisted seed dispersal

Ecologists recognize several reasons why seed dispersal is important to plants. First, because sites suitable for growth vary in space and time, plants must be able to colonize new areas as conditions change. Second, dispersal beyond the parental canopy is a means of avoiding competition with the parent and siblings. Finally, dispersal from the parent is important because some predators of seeds (e.g., rodents, insects, or microbes) often concentrate their efforts under parent plants where food density is highest.

For most plants, mechanisms have evolved for their seeds to be dispersed beyond the range of their branches. Usually these are fairly straightforward processes, such as by wind or water. Two strategies involve animals carrying seeds either externally or internally, termed ectozoochory and endozoochory, respectively. Ectozoochoric fruits or seeds attach to animals with hooks, barbs, or sticky secretions, while endozoochoric fruits usually entice animals with a meal of some sort. In the simplest example of endozoochory, an animal eats a fleshy fruit and later expels an undamaged seed away from the parent plant.

Simple, yet confusing, terminology

It is important to remember that the terms *fruit* and *seed* are not synonymous, and that it is confusing when they are used interchangeably in the literature. Also, fruit consumption does not guarantee seed dispersal. Granivorous birds consume seeds, and this is referred to as predation because the seeds are rendered non-viable. Frugivorous birds consume fruit, which can include the skin, pulp and seed(s). The seeds can be expelled in a viable state and this activity is referred to as seed dispersal if the seed has been carried away from the parent plant.

A loosely coevolved mutualism

Endozoochory is an example of a loosely coevolved mutualism. In this example, loosely coevolved means that most frugivores will eat many different fruits. Tight relationships between a specific fruit and frugivore are unusual, and are not known to occur for invasive plants. Indeed, widespread dispersal is successful for many exotic plant species because endozoochory is loose. Species that are dependent upon a specific disperser probably would not become a problem when introduced beyond their natural range. This type of seed dispersal represents a mutualism because both participants benefit; the frugivore with a meal and the plant with its seeds dispersed.

Following fruit consumption, seeds may be carried away from or dropped near the parent plant, with the latter resulting in no dispersal. Furthermore, studies have found that ingestion may increase (e.g. Braun and Brooks 1987), decrease (e.g. Smith 1975), or have no effect on (e.g. Panetta and McKee 1997) seed germination rates. In all of these instances the frugivore benefits, but for the relationship to be mutualistic, ingestion and seed passage must not have any negative consequences on germination. These two events, seeds either not being moved away from the parent plant or being damaged during consumption, may account for the majority of instances where seed dispersal is not successful.

Why fleshy fruit?

Endozoochoric fruits consist of a digestible outer layer surrounding at least one seed, and in the majority of cases this is a fleshy pericarp consisting of pulp and skin. Alternatively, some fruits possess an aril, a fleshy protruding appendage (e.g., earleaf acacia [*Acacia auriculiformis*]) that in some species completely surrounds the seed (e.g., carrotwood [*Cupaniopsis anacardioides*]).

An exceptional plant.

Chinese tallow (*Sapium sebiferum*) has fruit that seems to be quite unique. The fruits are capsules that at maturity split open to expose three large seeds covered in a white waxy coating. This substance is high in lipids (very energy-rich), and is a fairly good source of protein as well. Birds use the sides of their bills to scrape the wax from the seeds, often using a foot to hold the fruit against a branch. While this is usually done on the parent tree, fruits are occasionally carried to adjacent trees for scraping. The seed is dropped once the nutritious wax has been removed. This dispersal system means that many seeds are not dispersed, and those that are dispersed may not make it very far. This could be a consideration if one were to attempt to model the speed at which Chinese tallow expands its range. Moreover, because this is a novel dispersal system, the naive native birds may have taken some time to learn how to utilize this new resource, and therefore contributed to a time lag before the tree became invasive.

Photo by Ken Langeland

Deceptive appearances

Seeds of rosary pea (*Abrus precatorius*) are unusual in that they are mimetic, a trait shared with the native coral bean (*Erythrina herbacea*). The glossy, hard seeds are bright red, and not surrounded by pulp or skin. Instead, they mimic fleshy-pulped fruits in a game of deception, taking advantage of frugivorous birds to disperse their seeds with no compensatory reward.

Seeds of rosary pea (*Abrus precatorius*)

Arillate fruits have their seeds dispersed in the same way as the more typical types (e.g. berries), so the difference may be of most importance to those working with plant anatomy or taxonomy.

The digestible material of a fruit has three main nutritional components: lipids, carbohydrates, and protein. Summer/early fall fruits tend to be higher in carbohydrates and water, while fall/winter fruits generally contain higher levels of lipids. Protein levels are usually low (perhaps nitrogen, a component of protein, is too important to the plant). Both birds and mammals feed on summer and early fall fruits, which are often sweet-tasting, while the lipid-rich fruits of fall and winter are mostly utilized by birds.

Many species of temperate fruiting plants in the Eastern U.S. set fruit in the fall, presumably to take advantage of migrating birds. These birds need energy to fuel migration, and fruits provide an easily assimilable and visible source. However, Florida's natural communities may operate a bit differently because they are subject to the selective pressure of a large overwintering bird population rather than the passage of fall migrants (Skeate 1987). Much of the state has a temperate flora and hence most plant species produce fruit in the early fall. However, greater fruit biomass may be produced in the late fall and winter months (albeit by fewer plant species) when birds such as American robins (*Turdus migratorius*), cedar waxwings (*Bombycilla cedrorum*), gray catbirds (*Dumetella carolinensis*), and yellow-rumped warblers (*Dendroica coronata*) overwinter in Florida.

The time of the year that ripe fruits are on the plant could influence the direction of seed dispersal. For example, an invading plant that fruits in the spring may be most likely to experience a gradual northward population shift due to the spring migration of millions of birds. It should be remembered that each bird carries seeds a small distance at a time (depending upon flight speed and duration of seed retention), not for the thousands of miles of the whole migration route.

The dispersal process

Seed ingestion. For efficient flight it is essential that birds try to minimize unnecessary weight, for example, by eliminating heavy, indigestible seeds as quickly as possible. There are various mechanisms to get rid of seeds, and frugivorous birds can be divided into two groups: gulpers and mashers (Levey 1987). Gulpers are species that tend to swallow fruits whole, separate the seeds from the pulp internally, and then void the seeds at some distance from the parent plant (e.g., northern mockingbird [*Mimus polyglottos*]). Mashers tend to crush fruits in their bills, separating the seeds from the pulp and swallowing just the pulp (e.g., northern cardinal [*Cardinalis cardinalis*] and boat-tailed grackle [*Quiscalis major*]). Generally, birds with heavier conical bills are mashers while those with thinner bills are gulpers.

Where a masher removes the seed is important. Birds usually stay in the parent plant to accomplish this task (personal observation), thus seed dispersal has not occurred. But if the bird flies to another perch to remove the seed, seed dispersal will have occurred.

Seed deposition. How a gulper rids itself of seeds is also important relative to plant dispersal. The seed may be separated from the pulp in the stomach with the seed regurgitated, or separation can occur further along the digestive tract with the seed defecated. Birds are adept at this task and can regurgitate seeds that are cleaned of even the most adherent pulp. Since there is great variation among plant species in the adhesion of pulp to the seed, it is possible that the ease of this separation could influence fruit choice by frugivorous birds.

Murray et al. (1994) showed that there is a positive correlation between the distance over which a seed is dispersed and the length of time that a bird carries the seed. Thus, the mechanism of voidance can influence rates of expansion of plant populations because regurgitation is usually much quicker than defecation. Meyer and Witmer (1998) found that after fruit consumption by American robins, the mean seed defecation time of the

Pokeweed (*Phytolacca americana*) seeds left on the parent plant by a masher, the northern cardinal (*Cardinalis cardinalis*) Photo by Michael Meisenburg native shrub *Viburnum dentatum* was 58 minutes versus a mean regurgitation time of 19 minutes. Although these authors studied both voidance methods for one type of seed using a single bird species, it is more typical that each bird species will exclusively either regurgitate or defecate seeds of a particular size. It is likely that birds preferentially regurgitate seeds, so as to eliminate unnecessary weight as quickly as possible. However, smaller seeds are more likely to be defecated because they are not as easily separated from the pulp in the bird's crop.

In our own feeding trials with the fruit of *Ardisia crenata* (containing seeds of approximately 5mm diameter), northern mockingbirds typically regurgitate the seeds, while cedar waxwings will defecate them. Recognizing that many factors in addition to size influence which bird species feed on which fruits (e.g., fruit color, exposure on the plant), it can be hypothesized that as a result of different voidance methods, the rates of expansion of a plant species could be influenced by which bird species tend to feed on its fruits.

Discouraging predation

Ecologists have long tried to determine why fruits of some plant species are chosen in preference to others. The nutrient content of fruit flesh has an important influence on selection (lipids are particularly important for migrating birds), but many plants also produce distasteful secondary compounds (e.g., tannins, saponins). It seems contradictory that a plant with fleshy fruit that appears to be attractive for frugivores, would contain compounds that deter consumption. However, this deterrence may be intended for another type of organism. Moist fruit pulp is an ideal habitat for a variety of microorganisms which, if unrestrained, may cause seed mortality or make fruits distasteful to potential dispersers. Researchers at the University of Florida (Cipollini & Levey 1997a, 1997b) isolated secondary compounds from different *Solanum* species and tested them on microbes and frugivores. While these distasteful compounds significantly slowed fungal growth, they also discouraged consumption by frugivorous animals.

Although these interactions initially appear detrimental to the dispersal of a plant, there may be important consequences in the whole plant community. Fruit with secondary compounds may be retained on the plants for many weeks, due to resistance to microbes and distaste to frugivores. Since few plants produce fruit in the spring, those with fruit that persists until then may provide the only food source for birds on their spring migration. Similarly, for non-migratory birds such as northern mockingbirds, these persistent, least-preferred fruits may be crucial for surviving a cold, or extended, north Florida winter.

Other compounds may influence seed dispersal without reducing the consumption of fruit. It has been proposed by Murray et al. (1994) that some fruit may contain laxative compounds that hasten the defecation of seeds before they are damaged in the bird's gut. Also, many plants produce distasteful or toxic chemicals in the seeds themselves, to encourage seed ejection and deter seed predation (e.g., the bitter taste in apple seeds is due to cyanide compounds).

Added complexities

Although we tend to classify vertebrates as frugivores or granivores and assume that they may be responsible for seed dispersal and predation, respectively, this often oversimplifies the situation. Species such as squirrels that store certain seeds for later consumption often fail to recover all their cache. Surviving seeds that are able to germinate will have been successfully dispersed, even though the disperser is usually regarded as a seed predator. In an even more complicated relationship, acorns of the red oak group are high in tannins, but the tannins are concentrated in the lower half of the acorn. Squirrels often will eat only the top half of the nut and drop the bottom half. However, the lower half contains the embryo and will germinate, thereby establishing a mutualism in what would otherwise be interpreted as a predatory event.

Seed viability. The mutualism is only complete if an undamaged, viable seed is dispersed. Seeds may be damaged either in the bill or digestive tract. Such damage may improve germination for hard-coated seeds that need scarification before they can germinate, or it can cause seed mortality. The severity of damage may increase with the length of time a seed is retained in the bird's digestive tract (Murray et al. 1994). Thus, there may be a trade-off for the plant between the distance seeds are carried prior to defecation (improving seed dispersal), and the proportion of seed remaining viable (reducing seed dispersal).

In addition to frugivorous birds feeding on fruit pulp, granivorous birds may feed on the seeds of fruits. The house finch (*Carpodacus mexicanus*) is historically a western U.S. species that, following introduction into New York City in the 1940's, expanded its range into Florida. These finches are granivorous, and as such are seed predators. While they are commonly observed feeding on fruits, often they are actually cracking the seeds and feeding on the entire fruit (skin, pulp, and seeds). Similarly, with a gizzard that is capable of crushing pecans and acorns, wild turkeys (*Meleagris gallopavo*) and other members of the order Galliformes often digest the seeds, rendering them non-viable. An observation of these species feeding on fruits can easily be misinterpreted as seed dispersal rather than seed predation.

Seed dispersal verification

Thus, a conclusive determination of endozoochoric seed dispersal by birds requires verification that the seeds are 1) ingested, 2) carried away from the parent plant, and 3) voided in a viable condition. Observation of fruit consumption does not distinguish between seed dispersal and

Table 1.

Predominant dispersal mechanism for FL EPPC Category I plants described in the literature (not including ferns). (Other mechanisms may predominate as a method of reproductive increase.)

Dispersal mechanism		
Wind	*{Casuarina* spp.*}*	*Imperata cylindrica*
	Macfadyena unguis-cati	*Melaleuca quinquenervia*
	Neyraudia reynaudiana	
Water	*Colubrina asiatica*	*(Eichhornia crassipes)*
	(Hydrilla verticillata)	*(Hygrophila polysperma)*
	Hymenachne amplexicaulis	*Ipomea aquatica*
	Mimosa pigra	*(Pistia stratiotes)*
	Solanum tampicense	*Thespesia populnea*
Vertebrate: Verified	*Ardisia crenata*	*Jasminum* spp.
	Ligustrum spp.	*Sapium sebiferum*
	Schinus terebinthifolius	*Solanum viarum*
Vertebrate: Observations only	*Abrus precatorius*	*Acacia auriculiformis*
	Ardisia elliptica	*Asparagus densiflorus*
	Bischofia javanica	*Cestrum diurnum*
	Cinnamomum camphora	*Cupaniopsis anacardioides*
	Eugenia uniflora	*Ficus microcarpa*
	Lantana camara	*Lonicera japonica*
	Melia azedarach	*Nandina domestica*
	Paederia spp.	*Psidium* spp.
	Rhodomyrtus tomentosa	*Scaevola sericea*
	Schefflera actinophylla	*Solanum torvum*
	Syzygium cumini	
Vegetative expansion	*Colocasia esculenta*	*Dioscorea* spp.
	Panicum repens	*Pennisetum purpureum*
	Pueraria montana	*Urochloa mutica*
Other / unknown	*Albizia* spp.	*Bauhinia variegata*
	Calophyllum antillanum	*Senna pendula*
	Tradescantia spp.	

Parentheses indicate dispersal of vegetative propagules or fragments rather than seeds.
{Reported in error as vertebrate dispersed}; For citations, contact authors, or review Langeland and Burks (1998). Please let the authors know of literature or unpublished data that support a different category for a particular species.

seed predation (van der Pijl 1972). However, documentation of seedlings distant from the rest of the plant population and in sites frequented by birds (e.g., under tree roosts; along fence lines) is an indication that bird dispersal is likely (McDonnell and Stiles 1983).

Categories of verification

In an attempt to determine how many vectors of vertebrate-assisted seed dispersal for FLEPPC Category I plants have been verified, we searched the literature but were disappointed to find the evidence somewhat limited. Literature searches were aided by using Langeland and Craddock Burks *Identification & Biology of Non-Native Plants in Florida's Natural Areas* (1998). We used their species accounts to find citations pertaining to seed dispersal, and performed our own searches for additional references. Though by no means complete, we believe our list is a representative sample of what exists in the literature. These accounts were then assigned to categories based on the dispersal mechanism and extent of verification. Of the 62 species covered by Langeland and Craddock Burks, 30 produce fruits that appear to be (mostly) endozoochoric, making this dispersal mechanism the most utilized by Category I species (Table 1). For seeds thought to be dispersed by birds or mammals, our categories were based on whether: 1) seed viability was assessed for voided seeds, 2) claims of dispersal agents were based only on observations of fruit consumption, or 3) they contained probable erroneous information.

Dispersal and viability confirmed

Dispersal vectors have been studied in detail for species such as Brazilian pepper (*Schinus terebinthifolius*)(Panetta and McKee 1997, Ewel et al. 1982), tropical soda apple (*Solanum viarum*)(Akanda et al. 1995), and Chinese ligustrum (*Ligustrum sinense*)(Montaldo 1993). Panetta and McKee (1997) fed Brazilian pepper fruits to captive birds and compared germination rates of defecated seeds to those that were manually depulped, finding no difference. Ewel et al. (1982) observed Brazilian pepper seedlings sprouting in mammal scat but, while verifying mammals as dispersal agents, such reports often fail to distinguish the mammalian species. Mammal scat, whether from raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), red fox (*Vulpes vulpes*), or gray fox (*Urocyon cinereoargenteus*), is difficult to key out to species, especially when consisting of seeds.

Observations of fruit consumption

Another category is of simple reports of fruit consumption. For example, Martin et al. (1951) and Handley (1945) report consumers for Japanese honeysuckle (*Lonicera japonica*) fruits, Kellum (1997) for nandina (*Nandina domestica*), and Nelson (1994) for Chinaberry (*Melia azederach*) fruits. However, of these reports, not one mentions subsequent seed dispersal. Reports such as these should be interpreted with caution, because consumption does not necessarily imply seed dispersal. As a case in point, Langeland and Burks (1998) cited Morton (1980) as reporting that Australian pine (*Casuarina equisetifolia*) is dispersed by birds (especially exotic parrots and parakeets). However, what Morton wrote is that the birds feed on the seeds of these trees, and this is the correct statement. Australian pine seeds are winged samaras (like maple fruit) that implies wind dispersal, and as such these seeds lack a fleshy coating. Parrots or any other birds feeding on these seeds would be responsible for seed predation rather than dispersal.

Missing or erroneous evidence

There are also authors that report birds as seed dispersers, but with no mention of any direct evidence, as Morton (1982) did for day jessamine (*Cestrum diurnum*), and Cronk and Fuller (1995) for strawberry guava (*Psidium cattleianum*). What information such statements are based upon is unclear, but they may rely on uncited or unpublished material, untested assumptions, or lack of knowledge of the complexities of bird - plant interactions.

Finally, there are reports that are likely in error. Cronk and Fuller (1995) reported that kudzu (*Pueraria lobata*) is dispersed by birds and mammals, but it is likely that neither disperses the seeds. As many legumes do, kudzu produces fruits in the form of a pod that splits open when dry to release its seeds. While it is possible that seeds could be dispersed by mammals grazing on the plant, there is no reason for birds to eat the pods. Conversely, rooting at the nodes along the creeping branches and intentional planting by humans are the primary modes of dispersal in the U.S. (D. Orr, North Carolina State University, 2001 personal communication). Any seed dispersal occurring may be accomplished by the plant alone: with branches up to sixty feet long, the plant is capable of delivering seeds at a significant distance from its own roots. However, it is considered that nearly the entire seed crop produced by kudzu falls prey to beetles. Consequently, in the U.S. seed production in the field is insignificant (D. Orr, pers. comm.).

Conclusion

How a plant disperses its propagules beyond the reach of its branches is a problem that most species must solve. Animals are dispersal vectors for many plant species, ferrying seeds either internally or externally. Unlike the species-specific relationships that are sometimes seen with plants and their pollinators, dispersal relationships are usually general in nature. Thus, when a plant that relies upon endozoochory for seed dispersal is introduced outside it's native range, it is likely that suitable vertebrate dispersers will be available. However, it should be remembered that not all occurrences of fruit-eating result in seed dispersal. A better understanding of the process may lead to greater objectivity in the conclusions that we draw from our observations.

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