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# Does frugivory by European starlings (*Sturnus vulgaris*) facilitate germination in invasive plants?<sup>1</sup>

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LAFLEUR, N., M. A. RUBEGA (Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269), AND J. PARENT (Department of Natural Resources Management and Engineering, University of Connecticut, Storrs, CT 06269). Does frugivory by European starlings (*Sturnus vulgaris*) facilitate germination in invasive plants? *J. Torrey Bot. Soc.* 136: 332–341. 2009.—Fleshy-fruited plants are an important component of the invasive flora of the northeastern United States, but few studies have examined how avian frugivory may benefit such plants. European starlings (*Sturnus vulgaris*) are one of the most abundant avian frugivores in New England, and if effective seed dispersers for fleshy-fruited invasive plants, starlings may participate in a mutualistic interaction which benefits both the invasive plants and birds involved. Here, we investigate the role of European starlings in facilitating the germination of three invasive, fleshy-fruited plants with which they co-occur: *Elaeagnus umbellata*, *Celastrus orbiculatus*, and *Rosa multiflora*. For each plant species examined, less than 20% of the seeds ingested by captive starlings were not voided, and assumed to be destroyed as the result of passage through the digestive system. Starlings retained the seeds of *E. umbellata* 29 (mean)  $\pm$  19 (SD) min, *C. orbiculatus* 43  $\pm$  20 min, and *R. multiflora* 27  $\pm$  9 min. We also examined whether ingestion of seeds by starlings affected the germination of *E. umbellata* and *C. orbiculatus* seeds. Seeds that were cleaned by hand or regurgitated by birds had the same likelihood of germinating, and were significantly more likely to germinate than were seeds contained in intact fruit. Defecated *C. orbiculatus* seeds germinated significantly less well than hand-cleaned or regurgitated seeds, but better than those that were contained in intact fruits. We also found that *C. orbiculatus* seeds ingested by starlings required significantly less time to germinate than those contained in intact fruits. This study shows ingestion by starlings improves germination for both *E. umbellata* and *C. orbiculatus* seeds, and that starlings retain seeds long enough for seed dispersal to occur. Studies to determine the extent to which starlings feed on these plants, and the distances which seeds are moved, are needed.

Key words: *Celastrus orbiculatus*, *Elaeagnus umbellata*, germination, invasive, invasive species, mutualism, passage rates, *Rosa multiflora*, seed dispersal.

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Fleshy-fruited plants are an important component of the invasive flora of the United States. In the northeastern United States, nearly all invasive shrubs and vines appear to rely on birds to move their seeds (Silander and Klepeis 1999). However, although the ability of fleshy-fruited plants to reproduce (Murray 1988, Stiles 2000) and colonize (Howe and Smallwood 1982, Richardson et al. 2000) depends on frugivore physiology and behavior, the relationship between frugivores and fleshy-fruited invasive plants remains relatively unexplored (Reichard et al. 2001).

Birds may facilitate the spread of fleshy-fruited plants by moving seeds, promoting germination, or both. Foraging birds handle seeds in a variety of ways, with differing outcomes for seed dispersal. For instance, seeds may be discarded without being swallowed, ingested and subsequently regurgitated,

or passed through the entire digestive system and ultimately either defecated or destroyed. Of the seeds that are ingested, regurgitated seeds are typically passed more quickly than those that are defecated (e.g., Sorensen 1984, Levey 1987), and large seeds are likely to be passed more quickly than small ones (e.g., Levey 1987, Stanley and Lill 2002). While faster passage rates may increase the ability of seeds to germinate (Charalambidou et al. 2003), slower passage rates may enhance the likelihood that seeds are moved away from parent plants, reducing intraspecific competition (Howe and Primack 1975, Chapman and Chapman 1996). Further, seeds may be moved to locations where exposure to predators and pathogens is less likely because of decreased seed density (e.g., Janzen 1969, Augspurger and Kelly 1984, Augspurger 1984, Herrera 2002). Finally, birds may move seeds to sites where seeds have a greater than random probability of survival (Buchanan 1989, Wenny and Levey 1998) or into a wider variety of microhabitat conditions than are found near the parent plant (Hoppes 1988).

Effective seed dispersers must also pass seeds that are able to germinate. In a literature review, Traveset (1998) found the effects of seed ingestion on germination depended on the combination of fruit and frugivore involved. Considering studies that examined 42 species of birds in 19 families, ingesting seeds of 80 plant species, seed germination increased after ingestion in 36% of studies, decreased in 16%, and remained unchanged in 48%. Similarly, Traveset found no consistent relationship between ingestion by birds and the amount of time required for seeds to germinate; time until germination was reduced in 41% of cases, increased in 14%, and unaffected in 45%. Thus, both the likelihood and rate of germination (the amount of time required for seeds to germinate) depend on the specific combination of fruit and frugivore (Traveset 1998). Additionally, the length of time seeds are retained in a bird's digestive system may also affect germination (Charalambidou et al. 2003, Fukui 1996, Murray et al. 1994).

Teasing apart the interactions between fruit-producing plants and frugivorous birds is further complicated by the fact that seed dispersal systems are typically broadly-based mutualisms (e.g., Janzen 1983), with both the frugivores and fruit-producers involved often having multiple partners. One way to untangle

the complex web of interactions in such systems is to start by focusing on the major participants. Here, we concentrate on three fruit-producing invasives that are abundant and aggressive in Connecticut: *Elaeagnus umbellata* (autumn olive), *Celastrus orbiculatus* (Asiatic bitter-sweet), and *Rosa multiflora* (multiflora rose), and the most abundant overwintering frugivore, the European starling (*Sturnus vulgaris*) (National Audubon Society 2002). Although starlings and these three plants do not co-occur in their native ranges, we expect starlings to be effective seed dispersers for these plants due to the broadly-based nature of most seed dispersal mutualisms. Further, fall and winter starling diets include large amounts of fruit (Fischl and Caccamise 1986, Lindsey 1939), giving starlings the potential to be important dispersers for the plants upon which they feed. In Connecticut, free-living starlings feed heavily on *C. orbiculatus* during the late fall and early winter (LaFleur 2006), and in choice tests captive starlings preferred *E. umbellata* and *R. multiflora* fruit to those of *Ilex verticillata* and *Rosa palustris*, respectively (LaFleur et al. 2007). Here, we expand on our earlier work investigating the potential for mutually beneficial interactions between starlings and fleshy-fruited invasive plants. We first estimate the ability of European starlings to move the seeds of selected invasive plants by asking how long such seeds are retained in starlings' digestive tracts, and then examine how passage through the digestive system of starlings affects the germination of *E. umbellata* and *C. orbiculatus* seeds.

**Materials and Methods.** **STUDY SPECIES.** We selected three of the most problematic woody invasives in the northeast for this study: *Elaeagnus umbellata* Thunb. (autumn olive), *Celastrus orbiculatus* Thunb. (Asiatic bitter-sweet), and *Rosa multiflora* Thunb. ex. Mur (multiflora rose). *Elaeagnus umbellata* is a nitrogen-fixing shrub (Catling et al. 1997), sold for use as wildlife food and cover (Henry 1980). It spreads aggressively (Catling et al. 1997) and concentrations of up to 5225 plants per ha have been reported (Ebinger 1992). *Celastrus orbiculatus*, imported into the United States in the 1860s as an ornamental (Patterson 1974), arrests the development of native forests after timber harvesting (Silveri et al. 2001) and halts old-field succession (Fike and

Niering 1999) in New England. *Rosa multiflora*, originally imported as rootstock for roses, is now widely distributed across the eastern United States, where it reduces pasture (Barbour and Meade 1980) and lowers crop yields (Labisky and Anderson 1965). All three of these species produce small fruits, which are less than 1 cm in diameter, and which are fed upon by a variety of frugivorous birds, including starlings, during the fall and winter months (LaFleur, unpubl. data).

**BIRD CAPTURE AND MAINTENANCE.** We captured starlings (7 males, 4 females) with mist nets and walk-in traps during the winter of 2000–2001, in Mansfield and Chaplin, Connecticut. After capture, birds were housed in groups of two to four in indoor aviaries (1.65 × 1.65 × 2.44 m) at the University of Connecticut's Avian Research Facility in Storrs, Connecticut. Birds were maintained under dark: light conditions that replicated natural photoperiod; lighting was provided by a large window supplemented with fluorescent lights. Birds were held at 21 °C during June–September, and 10 °C during November–April, to mimic seasonal temperature changes. Because the normal suite of behavioral and locomotory responses wild-living birds use to cope with temperature extremes was limited by the conditions of captivity, we did not expose captive birds to more extreme temperatures. In October and May, temperatures were gradually decreased or increased respectively. We maintained birds on an artificial fruit diet of mashed bananas and soy protein *ad libitum* (Denslow et al. 1987) between tests because some birds (e.g., robins) decrease the amount of time food is retained in the digestive system when switched from an insectivorous diet to a fruit diet (Levey and Karasov 1994). All birds were allowed to acclimate to captivity for at least 14 d before participating in experiments.

**SEED PASSAGE RATES.** We estimated the abilities of starlings ( $N = 9$ ) to move seeds by determining passage times through birds' digestive systems. The day prior to passage rate experiments, we fed starlings fruits of the species for which passage rates were to be determined. Birds were held overnight without food immediately prior to testing to minimize variation in passage rates caused by disparity in the amount of food in different bird's stomachs (French 1996), and to encourage

feeding. On the morning of testing, individual starlings were placed in large aviaries (1.65 × 1.65 × 2.44 m) which allowed visual and auditory contact with other birds. Each bird was offered 5 fruits of *Elaeagnus umbellata*, *Celastrus orbiculatus*, or *Rosa multiflora*, and water *ad libitum*. Birds were observed continuously until they began feeding, at which time measurement of passage rates began. Any uneaten fruits and uningested seeds were removed from aviaries one minute after feeding began; starlings always ingested *E. umbellata* and *C. orbiculatus* seeds with the fruits, but occasionally broke *R. multiflora* fruits apart while feeding and lost seeds to the aviary floor. Once uneaten fruits were removed, birds were provided with apple slices which they ate readily and were allowed to feed *ad libitum* for the remainder of the trial. Allowing birds to feed during passage rate trials is more reflective of natural bird foraging behavior than withholding food for the duration of the trials, as birds may be expected to have completely empty guts only prior to their first meal of the day. Our data provide conservative estimates of the length of time which starlings retain seeds, as birds in these passage rate trials began the experiments with empty guts, a state which may decrease seed retention times (French 1996). Aviaries were inspected for seeds every 5 min, once birds began to eat. We considered seeds we found in feces to have been defecated, and those clean of fecal material and pulp regurgitated. We calculated mean passage rates by first calculating an average time retained for all regurgitated, defecated, or total seeds passed by each bird. Mean passage rates for each category of seeds (regurgitated, defecated, and total) were then calculated by averaging across birds. *Elaeagnus umbellata* trials were concluded when all seeds had been passed. *Celastrus orbiculatus* and *R. multiflora* trials were terminated at 150 min, a period of time which studies on passage rates in starlings and comparable species suggest is long enough for most or all seeds to be passed (Barnea et al. 1991, Clergeau 1992, Levey and Karasov 1992, 1994, Sorensen 1984). Passage rate trials were conducted from December 2001 to January 2002. If a bird showed no interest in eating within the first 20 minutes, the trial was terminated and the bird was tested later in the day, or at a later date. All trials began between 0800 and 1300 hours, Daylight Sav-

ings Time, and each bird was tested only once with each fruit. Fruits used in these tests were collected as needed from field sites in Storrs, CT during December 2001 and January 2002, and frozen until use. Free-living starlings regularly consume *C. orbiculatus* and *R. multiflora* fruits throughout the winter, and after freezing conditions have occurred in our study area (LaFleur 2006), and thus ingest seeds which have been previously frozen.

**SEEDS DESTROYED AS THE RESULT OF INGESTION.** Seeds ingested by frugivores may occasionally be ground to bits as the result of the digestive process. We determined the percentage of seeds starlings destroyed in this manner as follows. *Elaeagnus umbellata* has only one seed per fruit, so we calculated the percentage of seeds destroyed (i.e., seeds either not visibly passed within 24 hours or seeds passed as fragments) by each starling during passage rate trials (described above). We then averaged these data over all birds to calculate the mean percentage of *E. umbellata* seeds destroyed. However, because the mean number of seeds contained in the fruits of *Celastrus orbiculatus* ( $5.1 \pm 1.4$  SD;  $n = 20$ ) and *Rosa multiflora* ( $4.7 \pm 1.8$  SD;  $n = 20$ , N. LaFleur, unpubl.) varies, we were unable to use this method for these species. Instead, we ensured the ingestion of a specific number of seeds for these two species by removing seeds from ripe fruits that had been frozen upon collection the previous winter. Each seed used was inspected to make sure it was fully-formed and did not show signs of insect or fungal damage. Seeds were then inserted into the pedicel ends of purchased blueberries, which starlings ate readily. Each blueberry received only one seed, and a maximum of two seeds were used from each *C. orbiculatus* or *R. multiflora* fruit. The number of seeds voided by each bird ( $n = 10$ ) was compared to the number of seeds ingested to determine the percentage of seeds destroyed as the result of passage through the digestive system.

We encouraged starlings to feed by withholding food from 08:00 EST on the morning of testing. Prior to testing, starlings were transferred to individual cages ( $0.65 \times 0.65 \times 0.65$  m) and each bird was offered 10 blueberries prepared with either *Celastrus orbiculatus* or *Rosa multiflora* seeds. We allowed birds to feed until all blueberries had been consumed (typically about 1.5 hours),

then provided birds with maintenance diet and examined cage floors for seeds. Although passage rates were not specifically measured in this experiment, starlings voided most seeds within 1.5 hours, a period of time consistent with passage rates of seeds contained in intact fruits. To be sure all seeds were collected, we held birds in individual cages overnight, and checked for seeds again the next morning. Trials began in mid-morning or early afternoon, and each bird was tested only once with each fruit. These tests were conducted from July–August 2002. Seeds from these trials were not used in either passage rate or germination studies.

**SEED GERMINATION.** We used germination tests to examine how ingestion by starlings ( $n = 11$ ) affects *Elaeagnus umbellata* and *Celastrus orbiculatus* seeds. We considered four treatments: 1) seeds contained in intact fruits, 2) seeds from which the fruit pulp had been cleaned by hand, 3) seeds which had been regurgitated by starlings, and 4) seeds which had been defecated by starlings. Eight replicates of 50 seeds were planted for each species and treatment combination, with two exceptions. As *C. orbiculatus* has a mean of  $5.1 \pm 1.4$  SD seeds per fruit (N. LaFleur, unpubl.), we chose to plant 50 intact fruits per replicate rather than manipulate the fruit to reduce the number of seeds each contained. Further, we omitted the defecated seed treatment for *E. umbellata* as birds defecated only seven seeds out of more than 800 ingested. We used two measures of germination success; the percentage of seeds germinating, and the time required for 50% of seeds to germinate. Although free-living European starlings feed upon *R. multiflora* fruits (LaFleur 2006), this species was omitted from germination tests because captive starlings are very reluctant to eat it (LaFleur 2007) and were unlikely to maintain body weight if fed exclusively on *Rosa multiflora* for periods long enough to produce adequate seeds for germination trials.

Fruits containing seeds to be used in all treatments were collected at the same time. We collected *Elaeagnus umbellata* fruits in October 2001 at two sites in Storrs, CT, one site in Mansfield, CT, and one site in Putnam, CT. *Celastrus orbiculatus* fruits were collected in November 2001 from four sites in Storrs, CT. At each site a minimum of 250 fruits were collected from each of two plants. Upon

collection, fruits were placed in sealed plastic bags and refrigerated at 4 °C until use; for all treatments 21 d elapsed between *E. umbellata* collection and planting, and 31 d passed between *C. orbiculatus* collection and planting.

We prepared seeds for the germination tests as follows. Seeds in the intact fruit treatment were left unmanipulated inside their respective fruits. Seeds in the hand-cleaned treatment were manually removed from fruits. *Elaeagnus umbellata* seeds were rinsed in tap water to remove any remaining pulp; but as *Celastrus orbiculatus* pulp did not stick to seeds, these seeds were not rinsed. Hand-cleaned seeds were air dried, wrapped in dry paper towels, placed in sealed plastic containers, and refrigerated at 4 °C until planting. Seeds in the regurgitated and defecated treatments were obtained by feeding fruits to captive starlings. We held birds in groups of 3–4 per aviary, and each group was offered the fruits of a single plant and water. For *E. umbellata*, fruit from another plant was offered when we had recovered 95% of the seeds ingested and birds had gone one-half hour without passing any more seeds. If these criteria were not met, we placed birds on maintenance diet until the next day to prevent mixing seeds from different individual plants. Unlike *E. umbellata*, *C. orbiculatus* has a variable number of seeds per fruit, so we could not use observation to determine when birds had passed all seeds. Therefore, we waited three hours after the consumption of the last *C. orbiculatus* fruit to collect seeds. Defecated and regurgitated seeds were stored in the same manner as hand-cleaned seeds until planting. All birds were offered fruits from all individual plants; *E. umbellata* seeds were planted within 15 d of processing by birds, and *C. orbiculatus* seeds within 20 d.

We planted seeds in trays of 288 2-cm cells filled with #2 potting soil. Seeds were planted just below the surface of the soil, and seed placement was randomized on the basis of individual plant, treatment (intact, hand-cleaned, regurgitated or defecated) and aviary. An error in assigning cells for *Celastrus orbiculatus* caused a disproportionate number of defecated seeds to be planted in trays 4, 5, and 6; however, since all trays were treated equally and tray positions were rotated during germination, we believe that our results were not affected. Seeds were planted at a depth approximately equal to seed diameter and

loosely covered with soil. Fruits were buried deeply enough to be nearly or completely covered with potting soil. Seed trays were thoroughly watered the day after planting, then cold stratified for 31 d at 4 °C (Patterson 1974, Wendel 1974). Heated propagation mats were used to maintain soil temperature at approximately 22 °C, under artificial lighting (16:8 light:dark cycle), for the first 10 d following cold stratification. Thereafter, seed trays were removed from propagation mats and maintained under natural light conditions in a different greenhouse to facilitate access for germination checks. Temperature in this greenhouse was not recorded.

We checked trays for newly emerged seedlings at least six days per week once germination began. The date of seedling emergence was recorded for each cell, and seedlings were removed from the tray. To determine the germination date of seedlings emerging between checks, we allowed some seedlings to grow for 3–4 d. These observations established that seedlings with fully upright cotyledons had germinated the previous day, while those with cotyledons less than fully upright had germinated the day of the germination check. Seeds and fruits of *Elaeagnus umbellata* were planted on November 1, 2001 and germination was monitored for 60 d. Seeds and fruits of *Celastrus orbiculatus* were planted on December 4, 2001, and germination was monitored for 50 d.

**STATISTICAL ANALYSIS.** For seed destruction and passage rate trials, data were first averaged by individual bird, and then averaged over all birds. The specific tests used for each analysis are reported with the results. We used SYSTAT 10.0 (SYSTAT Software Inc. 2002) for all analyses. Means are reported  $\pm$  1 SD. Results were considered significant if  $P$ -values  $<$  0.05.

**Results. SEED PASSAGE RATES.** Starlings passed most of the seeds they ingested in less than one hour. All the *Elaeagnus umbellata* seeds starlings passed were regurgitated, with a mean passage rate of 29 min ( $\pm$  19,  $N$  = 9 birds, 28 seeds; Fig. 1). *Celastrus orbiculatus* seeds were regurgitated slightly more often than they were defecated (54% vs. 45%); and the mean passage rate for all *C. orbiculatus* seeds was 43 min ( $\pm$  20,  $N$  = 9 birds, 108 seeds). Starlings regurgitated *C. orbiculatus*

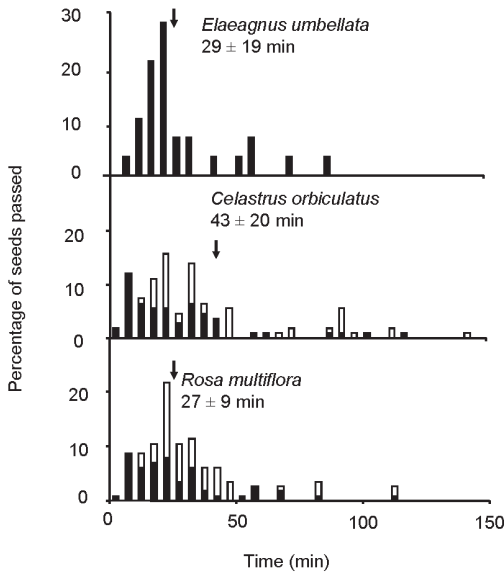


FIG. 1. Passage rates for the seeds of three invasive plants when ingested by captive starlings ( $N = 9$ ). Arrows denote means  $\pm$  SD; open bars, regurgitated seeds; filled bars, defecated seeds.

seeds significantly more quickly than those that were defecated ( $24 \pm 25$  min vs.  $47 \pm 27$  min; paired  $t$ -test,  $t = 2.3$ ,  $df = 5$ ,  $P = 0.0071$ ,  $N = 6$ ). Starlings were equally likely to regurgitate or defecate the seeds of *Rosa multiflora*. *R. multiflora* seeds were retained a mean of 27 min ( $\pm 9$ ,  $N = 9$  birds, 115 seeds), and there was no significant difference in passage rates for regurgitated or defecated seeds ( $33 \pm 24$  min vs.  $27 \pm 6$  min respectively; paired  $t$ -test:  $t = 0.53$ ,  $df = 5$ ,  $P = 0.62$ ,  $N = 6$ ).

We examined seed passage rates among species by pooling regurgitated and defecated seeds. Neither mean nor minimum retention times were found to vary by plant species when regurgitated and defecated seeds were pooled (one-way ANOVA, mean:  $F_{2,24} = 1.7$ ,  $P = 0.20$ ; minimum:  $F_{2,24} = 0.91$ ,  $P = 0.42$ ); however, maximum passage rates (i.e., the longest time required for a bird to pass a seed) for *Elaeagnus umbellata* seeds were significantly shorter than for *Celastrus orbiculatus* seeds (*E. umbellata*:  $31 \pm 19$  min,  $N = 9$ ; *C. orbiculatus*:  $82 \pm 41$  min,  $N = 9$ ; one-way ANOVA followed by Bonferroni correction for multiple comparisons,  $F_{2,24} = 5.8$ ,  $P = 0.009$ ). Maximum passage rates for *Rosa multiflora* seeds ( $67 \pm 31$  min,  $N = 9$ ) did not differ significantly from either *E. umbellata* or *C. orbiculatus*.

SEEDS DESTROYED AS THE RESULT OF INGESTION. Starlings passed 85% of the *Elaeagnus umbellata* ( $n = 11$  birds; 110 seeds) and *Celastrus orbiculatus* ( $N = 10$  birds, 100 seeds) seeds they ingested, and destroyed 15%. Starlings passed 82% of the *R. multiflora* ( $N = 10$  birds; 100 seeds), seeds, while 18% were destroyed.

SEED GERMINATION. Treatment method significantly affected the percentage of seeds germinating for both *Elaeagnus umbellata* (one-way ANOVA,  $F_{2,21} = 160$ ,  $P = 0.001$ ) and *Celastrus orbiculatus* (one-way ANOVA,  $F_{3,28} = 19$ ,  $P = 0.001$ ; Fig. 2). In both cases, significantly lower percentages of seeds contained in intact fruits germinated than did seeds in other treatments (*E. umbellata*: intact fruits  $13 \pm 6.7$ ,  $N = 8$ , hand-cleaned seeds:  $80 \pm 11$ ,  $N = 8$ ; regurgitated seeds =  $80 \pm 7.7$ ,  $N = 8$ ; *C. orbiculatus*: intact fruits  $44 \pm 12$ ; hand-cleaned seeds:  $82 \pm 9.1$ ,  $N = 8$ , regurgitated seeds:  $81 \pm 9.3$ ,  $N = 8$ , defecated seeds:  $62 \pm 17$ ,  $N = 8$ ). Germination percentages of hand-cleaned seeds did not differ from those of regurgitated seeds for either species. Significantly fewer defecated *C. orbiculatus* seeds germinated when compared to intact, hand-cleaned or regurgitated seeds.

The number of days until 50% of seeds germinated was not affected by treatment in *Elaeagnus umbellata* (intact:  $37 \pm 9.1$  d; hand-cleaned:  $32 \pm 4.4$  d; regurgitated:  $32 \pm 5.3$  d; one-way ANOVA,  $F_{2,21} = 1.4$ ,  $P = 0.27$ ; Figs. 2 and 3). In contrast, *Celastrus orbiculatus* seeds showed significant treatment effects ( $F_{3,28} = 4.9$ ,  $P = 0.007$ ). Seeds in intact fruits ( $23 \pm 5.7$  d) took significantly longer to germinate than either regurgitated ( $17 \pm 3.6$  d) or defecated ( $15 \pm 3.7$  d) *C. orbiculatus* seeds, which did not differ from each other. The number of days until 50% of the hand-cleaned *C. orbiculatus* seeds ( $18 \pm 3.9$  d) germinated did not differ significantly from any other treatment.

**Discussion.** SEED PASSAGE RATES AND DESTRUCTION OF SEEDS AS A RESULT OF INGESTION. For each of the three plant species examined, starlings voided over 80% of the seeds ingested. Furthermore, seeds of all species were retained approximately 30–45 min, long enough to be dispersed substantial distances. These passage rates are consistent with those reported for starlings and other similar-sized birds. Levey and Karasov (1994) found that European

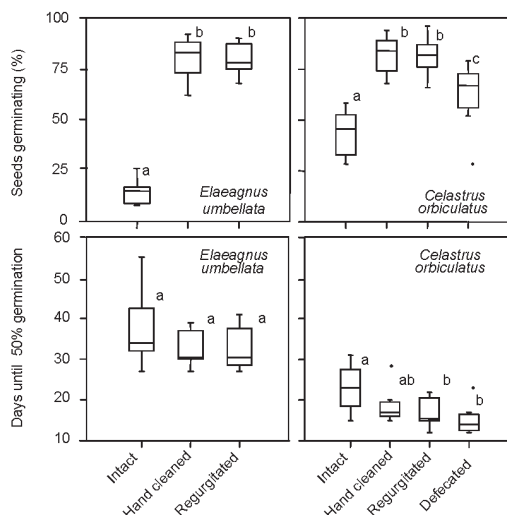


FIG. 2. The percentage of seeds germinating (top panels) and the number of days after planting on which 50% of seeds germinated (bottom panels) for autumn olive (*Elaeagnus umbellata*) and Asiatic bittersweet (*Celastrus orbiculatus*) seeds in four treatments: intact seeds sown in fruits, hand-cleaned seeds, and seeds regurgitated or defecated by captive European starlings. Medians are shown as horizontal lines within boxes, first and third quartiles as upper and lower horizontal box edges. Whiskers denote the most extreme values with inner fences, and outliers are asterisks. For each species, boxes marked with different letters are significantly different at the 0.05 level or greater, those marked with the same letter are not.

starlings fed a frugivorous diet passed fruit pulp 18 min after consumption. Johnson et al. (1985) found *Turdus migratorius* Linnaeus (American robins), on average, required 19 min to regurgitate, and 30 min to defecate the first seed from a meal. Sorensen (1984) and Barnea et al. (1991) reported that *Turdus merula* Linnaeus (Eurasian blackbirds) passed the seeds of a variety of plants in 6–73 min. Seed dispersal distances may be estimated by combining passage rate data with information on bird flight speeds. European starlings fly at speeds of up to 48 km hr<sup>-1</sup> (Hamilton and Gilbert 1969), giving them the potential to move seeds distances of up to 24 km in 30 min. Seeds that are passed through the digestive system more slowly may be transported further. Starlings in this study occasionally retained seeds for nearly two hours, but in contrast to Proctor (1968), we found no indication that starlings held viable seeds for more extended periods.

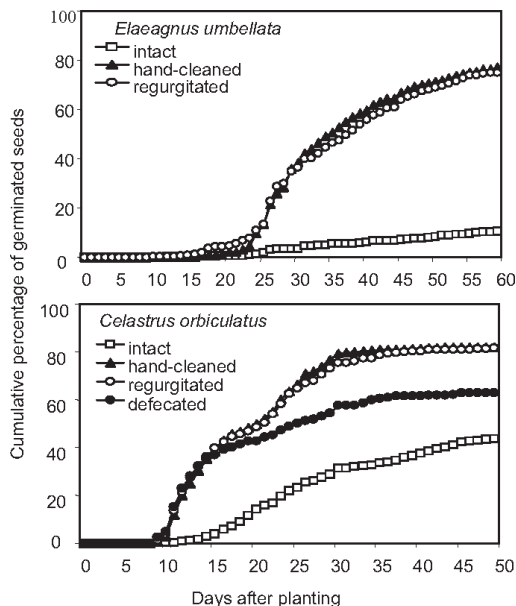


FIG. 3. The cumulative percentage of autumn olive (*Elaeagnus umbellata*) and Asiatic bittersweet (*Celastrus orbiculatus*) seeds germinating, over time, in four treatments: intact seeds sown in fruits, hand-cleaned seeds, and seeds regurgitated or defecated by captive European starlings.

**SEED GERMINATION.** Seed ingestion by starlings significantly increased the percentage of *Elaeagnus umbellata* and *Celastrus orbiculatus* seeds that germinated. Previous studies report germination percentages of 75–96% for *E. umbellata* seeds (Fowler and Fowler 1987, Heit 1968), results similar to ours. In the case of *C. orbiculatus*, Greenberg et al. (2001) found, as we did, that fewer seeds contained in intact *C. orbiculatus* fruits germinated when compared to seeds that were hand-cleaned or ingested by *Dendroica coronata* Linnaeus (Yellow-rumped warblers) (51% vs. 82% germination, respectively). They suggest that birds contribute to germination by removing pulp from seeds, rather than by scarifying seeds as they pass through the digestive tract. Other researchers (Dreyer et al. 1987, Ellsworth et al. 2004, Patterson 1974) have reported a wide range in the percentage of *C. orbiculatus* seeds germinating (30–95%); values at the higher end of this range, where ours fell, are most typical.

Seed ingestion did not influence the length of time required for germination in *Elaeagnus umbellata* seeds, but *Celastrus orbiculatus* seeds that had been either hand-cleaned or ingested by birds germinated significantly



earlier than those that were contained in intact fruits. Likewise, Greenberg et al. (2001) also found that *C. orbiculatus* seeds contained in intact fruits took significantly longer to germinate than those ingested by birds or that were hand-cleaned. While the benefits of increased germination percentages are readily apparent, there are also benefits to germinating earlier. For instance, seeds that germinate earlier may experience reduced exposure to seed predators (Traveset et al. 2001), have higher growth rates (Paulsen and Hogstedt 2004, Traveset et al. 2001), or may be able to increase the length of their first growing season (Paulsen and Hogstedt 2004). All of these are competitive advantages which may lead to increased seedling survival.

Although native birds have been observed to feed on the fruits of both *Elaeagnus umbellata* and *Celastrus orbiculatus* (e.g., White and Stiles 1992, Suthers et al. 2000), we know of no published studies which examine the contribution of native birds to the germination or dispersal of either species.

However, the seeds of many other invasive plants have been shown to benefit from ingestion by birds. In South Africa, Glyphis et al. (1991) found that bird ingestion of invasive *Acacia cyclops* G. Don (rooikrans) seeds increased germination from 2–18% to 22–36%. In the southeastern United States, Renne et al. (2001) found that ingestion by birds more than doubled the percentages of *Triadica sebifera* (L.) Small (Chinese tallow tree) seeds germinating (51% vs. 22.5%). Similarly Panetta and McKee (1997) found that removal of the exocarp, by birds or by hand, increased germination of *Schinus terebinthifolius* Raddi (Brazilian pepper-tree) seeds from only 10% to 87–100%. In contrast, LaRosa et al. (1985) examined the effects of ingestion by *Acridotheres tristis* Linnaeus (common mynas) and *Zosterops japonicus* Temminck & Schlegel (Japanese white-eyes) on the seeds of a variety of plants invasive in Hawaii. They found that for most, including, *S. terebinthifolius*, ingestion had no effect on the ability of the seeds to germinate. Ward and Labisky (2004) have also reported poor germination (7.5%) for seeds of *Cinnamomum camphora* (camphor tree) after ingestion by European starlings. Together, these findings are similar to those reviewed in Traveset (1998), who suggested that the effects of bird ingestion on the ability of seeds to germinate

depends on the specific combination of plant and bird.

**Conclusions.** European starlings are extremely abundant and widespread invasive frugivores, with a North American population estimated at over 200 million birds (Cabe 1993). In previous work (LaFleur et al. 2007), we have shown that captive starlings prefer the fruits of *Elaeagnus umbellata* and *Rosa multiflora* to those of native plants, a situation that may result in a lack of dispersal for the seeds of native plants (Knight 1986, Ferguson and Drake 1999). Work presented here suggests starlings retain seeds in their digestive systems long enough to move them substantial distances. In addition, ingestion of seeds by starlings resulted in the destruction of few seeds and significant increases in the percentage of both *E. umbellata* and *Celastrus orbiculatus* seeds germinating. Starling numbers, starling preferences for the fruits of certain invasive plants, and the potential of starlings to disperse seeds that germinate more readily than uningested seeds, all suggest that these invasive birds exert a strong, negative effect on native plant populations by promoting the spread of invasives. This negative effect may be compounded if the presence of extremely abundant fleshy-fruited invasives causes native frugivores to replace native fruits with invasive fruits in their diets (Oatley 1984, Knight 1986). Future work in this system should include measurement of starling movement patterns to better estimate distances starlings move seeds, and to determine if starlings direct seeds towards microhabitats where they are more likely to germinate than would be expected by chance (Wenny 2001).

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