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Russian Olive (*Elaeagnus angustifolia*) Dispersal by European Starlings (*Sturnus vulgaris*)

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Studies were conducted to document that European starlings consume Russian olive fruits and determine subsequent effects on seed germination. In the first study, avian feeding patterns at Russian olive trees were monitored over a 1-yr period using motion activated digital photography. Starlings fed on Russian olive fruits with highest activity occurring in November and December. In a second study, 20 captive European starlings were fed Russian olive fruits and seed germination rates were determined for three categories: consumed by starlings, hulled fruits (pericarp removed), and whole fruits. Starlings readily consumed Russian olive fruits and most seeds were regurgitated 30 min after consumption. Germination rates of ingested/regurgitated seeds (57%) and pericarp-removed seeds (40%) were greater than whole fruits (0%). Viability tests confirmed that 85% of starling ingested seeds remained viable after consumption. Our data suggest that Russian olive dispersal may be dependent upon animals for effective spread.

Nomenclature: Russian olive, *Elaeagnus angustifolia* L.; European starlings, *Sturnus vulgaris*.

Key words: Animal dispersal, digestion, feeding study, increased germinability, invasive species interactions.

Since its introduction to the United States in the early 1900s, Russian olive (*Elaeagnus angustifolia* L.) has escaped from its ornamental and wind-break plantings and spread across many western habitats. Within 100 yr of its arrival, Russian olive has become the fifth most dominant woody riparian species in the western United States (Friedman et al. 2005). Russian olive is currently found throughout most of the country except 13 states in the southeast (Katz and Shafroth 2003). Much of the debate over the invasiveness and impacts of Russian olive on native vegetation and water management is derived from western states (Brock 1998; Christensen 1963; Stannard et al. 2002). Russian olive planting was promoted in the western U.S. in the 1930s because of the species drought tolerance and ability to grow in a wide range of soils. These characteristics probably contributed to its ability to escape cultivation, and it began to naturalize by 1948 (Christensen 1963; Knopf and Olson 1984; Stannard et al 2002).

Russian olive trees produce hard-coated seeds that are surrounded by fleshy pericarp (Jinks and Ciccarese 1997; Zouhar 2005). This attribute makes them attractive as food sources for birds which could complicate control efforts. Our study focuses on elucidating the potential risk birds may have on Russian olive seed dispersal. Specifically, we set out to document the attractiveness of Russian olive fruits to European starlings, and the potential for starlings to enhance germination and viability of Russian olive seeds.

Russian olive seeds require a period of after-ripening to successfully germinate (Belcher and Karrfalt 1979; Hogue and LaCroix 1970). Under natural conditions, Russian olive seeds require exposure to 41 F (5 C) or below for 2 to 3 mo (stratification) to break dormancy (Hogue and LaCroix 1970; Taylor 1941; Williams and Hanks 1976). Scarification may improve Russian olive germination rate (Brock 1998; DiTomaso and Healy 2003) and Zouhar (2005) suggested digestion of fruits may break dormancy.

The scientific literature cites many instances of Russian olive spreading through avian vectors primarily driven by ample production of nutritious and palatable fruits (Borell 1951; Kindschy 1998; Knopf and Olson 1984; Olson and Knopf 1986; Van Dersal 1939). Olson and Knopf (1986) hypothesized that seeds are ingested along with the fruits, pass through the bird digestive tract, and are deposited in

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Management Implications

Our research clearly demonstrates that European starlings will consume Russian olive fruits. Most consumed seeds would be regurgitated and left on the soil surface in a more germinable state than whole fruits. This strongly suggests that Russian olive is dependent upon animals to disperse seeds and cause spread of this invasive species. Russian olive fruits are palatable to European starlings and many other bird and several mammal species that contribute to its effective spread. The change in germinability in fruits consumed by European starlings provides impetus for managing Russian olive particularly if passage through other animals' GI tracts has a similar effect. This interaction between two invasive species likely will change our collective impressions of their management importance.

new areas where they can quickly germinate. Van Dersal (1939) and Borell (1951) described 37 bird and three mammal species that fed on Russian olive fruits, indicating their highly palatable nature and the potential for these animal species to disperse the seed. Many citations, however, report eyewitness accounts of birds simply perching upon Russian olive trees (Borell 1951; Knopf and Olson 1984; Olson and Knopf 1986; Stoleson and Finch 2001; Van Dersal 1939). A controlled study would be of value to document consumption of fruits by birds and subsequent effects on seed germination.

European starlings (*Sturnus vulgaris*) are invasive birds that were introduced into North America in 1890 to 1891 (Cabe 1993). European starlings' native range stretches throughout much of Eurasia from Scandinavia in the north to Italy in the south with an eastern edge somewhere east of Lake Baikal in Russia (Cabe 1993). Coincidentally, this range overlaps with the native range of Russian olive.

Our primary objective was to document that European starlings will consume Russian olive fruits and will do so preferentially when other food is offered. Our second objective was to determine the effects of consumption on Russian olive seeds. We addressed these objectives by: (1) examining the natural feeding behaviors of European starlings using wildlife photography cameras; and (2) conducting controlled feeding experiments of Russian olive fruits by captured European starlings and determining their subsequent effects on seeds.

Materials and Methods

Game Camera Study. Observations were carried out at two field sites (Nunn, CO and Wellington CO). At both sites, cameras were affixed to 2.7 m (9 ft) U-posts 1.2 m from the trunks of trees. Cameras were positioned at two heights; 2.4 m and 0.3 m. The top camera was a motion activated WSCA01 Wing-Scapes Birdcam (Wingscapes, 3280 Highway 31 Suite B Calera, AL 35040; available from http://www.wingscapes.com/birdcameras?cn=3000192&att=3000192). This camera was designed to capture the feeding habits of any birds that flew into the upper portions of the Russian olive trees. The camera was set to capture 8 mega pixel high resolution still life images set for three image bursts when movement was detected. Photos were captured only during the day as this camera did not operate at night. The lower camera was a Moultrie MFH-DGS-I60 (Moultrie Feeders, 3280 Highway 31 Suite B Calera, AL 35040; available from http://www.moultriefeeders.com/?cn=3000003&att=3000003) game spy digital camera set 30 cm above the soil to capture small mammals and birds that foraged at ground level. This camera was set to operate in both the day and night to capture 6 mega pixel high resolution photos of any mammal or bird that was detected in a 7.6 m arc from the camera. Both cameras were powered by batteries and supplemented with solar panels. All images were stored on removable 4GB SD media cards.

Photos were analyzed for any bird or mammal species. Data were collected on species identification and any other visual observations pertaining to feeding that could be discerned from the photos. The experiment was carried out over a 1-yr period with cameras checked weekly for photos and maintenance. Cameras were moved after a 4-wk period to a new location on the site and re-setup following the same methods. A total of 12 trees were monitored for 720 hr each over a period of 1 yr.

Fruit Collections. Russian olive fruits were collected from four sites across northern Colorado; Nunn, Greeley, Wellington, and Ft. Collins. During August to September 2010, 1000 fruits were hand collected from 50 different trees at each site (4,000 fruits total). Collected fruits all were within the researcher's standing reach on each tree. Fruits were stored in four separate plastic totes and stored at 40 F for 4 mo until used in experiments. Seeds were removed from cold storage as needed over the 1-wk long bird feeding study.

Bird Feeding Study. Starlings were captured using a modified crow trap (JWB Marketing LLC, 230 Raven Trail, West Columbia, SC 29169; http://www.birdtraps.com.au) under federal (MB019065) and state (10TRb2006) permits and all studies were approved by the institutional animal care and use committee. Starlings were transported by vehicle in well-ventilated transport boxes to the NWRC outdoor aviary research facility where they were housed in individual cages (0.9 m by 1.8 m by 0.9 m). Starlings were provided an *ad libitum* pelletized food (Layena pelletized feed from Purina,Northern Feed and Bean, 33278 Hwy 85, Lucerne, CO 80646: http://purinapoultry.com/what-to-feed/products/layena/)and water diet throughout the study.

After a 5-hr period of adaptation of ad libitum feeding, 25 Russian olive fruits were presented to the birds in a small clay dishes and left for 24 h. Russian olive fruits were presented to birds for 4 consecutive days, which allowed birds to consume 50 fruits each. This free choice testing was carried out over a 1-wk period and water, maintenance diet, and test fruits were checked daily at 0700 hours.

Feeding was monitored using a camcorder mounted on a tripod facing the cages for further analysis on feeding behaviors. Video cameras were positioned either on tripods on top of the cage or were attached to the sides of the cage. Video was recorded over an 11-hr time period just after fruits were introduced to the birds in the morning. Videos were screened after the testing to determine feeding behaviors.

Paper tray liners were removed from the cages every other day for seed collections from the fecal matter and those that were regurgitated. Seeds were considered scarified if they were defecated or regurgitated based upon their morphology associated with the digestive processes that occurred.

On completion of the study, all Starlings were euthanized by CO_2 asphyxiation in accordance with American Veterinary Medicine Association (AVMA) standards.

Seed Testing. The effects of starling digestion on seed germination and viability were determined separately. The three seed treatments included: (1) Control: entire fruits with pericarp intact and untreated; (2) Hulled: whole fruits soaked in 250 ml of deionized water (DI) for 24 h then pericarp removed; and (3) Consumed: fruits ingested by starlings and seeds regurgitated and fruits ingested and passed in feces by starlings. All seeds were surface sterilized before germination procedures with a 10% household bleach (sodium hypochlorite or NaClO) solution. Seeds were positioned on DI-soaked germination paper sheets, 40 to a sheet, then covered with another DI-soaked germination paper, rolled up and placed into plastic sealable bags and put into a 22 C (72 F) growth chamber. Seeds were checked weekly over 6 wk for emergence of the hypocotyls, which indicated germination. Germinated seeds were removed from the germination paper to prevent double counts. Data for percent germination were checked for normality and transformed by square root then subjected to an analysis of variance using SAS version 9.2 PROC GLM procedure. Transformed means were separated by Fishers Protected LSD ($\alpha = 0.05$) but are presented in their original scale.

Total seed viability was determined separately using a tetrazolium (TZ) test (Colorado Seed Laboratory, Dept. of Soil & Crop Science, Colorado State University, Ft. Collins, CO 80523). Lots of 60 seeds were replicated three times for all three test groups. Pericarp was removed from intact fruits and seed coats of all three test groups were nicked. Seeds were then soaked in DI water for 24 h. After soaking, a small slice of the embryo was removed and placed in a TZ solution for 24 h. Embryos were examined under a microscope and viability was determined visually (live embryos stained red whereas dead embryos showed no red color). Data for percent viability were checked for normality and transformed by square root then subjected to an analysis of variance using SAS version 9.2 PROC GLM procedure. Transformed means were separated by Fishers Protected LSD ($\alpha = 0.05$) but are presented in their original scale.

Results and Discussion

Game Camera Study. European starlings were readily observed feeding upon Russian olive fruits in late November/early December (http://bspm.agsci.colostate.edu/people-button/faculty-new/beck-george/ Figures 1 and 2). Birds exhibited a flocking feeding behavior and fed upon fruits en masse. From the Bird Cam photos, birds seemed to flock on trees with visible fruit and fed continuously over a 4-wk period from December 11 through January 7. Observations of the photos also indicated that some birds picked the fruit and appeared to disperse it away from the parent plant. During the observation periods, starlings typically fed upon fruits from 1500 h to 1645 h (3:00 pm to 4:45 pm). Other birds observed in the Russian olive trees, but not observed feeding upon the fruits included American robins, northern flickers (*Colaptes auratus*), American crows (*Corvus brachyrhynchos*) and a house finch (*Carpodacus mexicanus*).

The ground camera photographed European starlings feeding on the ground, but no documented consumption of fruit. From January 7 onward, birds were detected by the ground-based camera more frequently feeding on the soil surface and searching through the snow for feed. Birds appeared to have cued in on the availability of the Russian olive fruits on the soil surface and were continually attracted to those fruits even after snow had covered the ground. A high proportion of photos taken were, however, of cottontail rabbits (*Sylvilagus* spp.). Other animals seen searching under Russian olive trees included coyotes (*Canis latrans*), mule deer (*Odocoileus hemionus*), magpies (*Pica hudsonia*), and skunks (*Mephitis mephitis)*.

Bird Feeding Study. Starlings consumed seven to nine fruits within 3 to 5 min of fruit introduction. Birds were immediately attracted to the Russian olive fruits and quickly consumed them. Within 2 d of testing, 17 starlings had consumed 850 fruits. Video analysis indicated that seeds were regurgitated approximately 30 min after consumption and starlings exhausted their daily Russian olive fruit allotment (25 fruits/bird/day) within 4 h. Videos of European starling feeding were examined and two video clips were selected and posted on YouTube for public observation (http://www.youtube.com/watch?v=7Q5Ybic-UhU; and http://www.youtube.com/watch?v=bCZos7I8L-s).

Seed Testing. Germination rates differed among seed treatment groups ($F = 58.76$, $P < 0.05$, $df = 2$).

Figure 1. A flock of European starlings feeding on Russian olive fruits. Note the bird in the circle with a fruit in its beak.

Germination of Russian olive seeds consumed by European starlings (57%) was higher than hulled seeds (40%) and none of the control seeds germinated (Figure 3). Viability of among seed treatment groups also differed ($F = 12.6$, $P < 0.05$, $df = 2$). Viability of seeds was highest for the consumed (85%) and control (76%) seeds and both were greater than hulled (31%) seeds (Figure 3).

It is clear that European starlings consume Russian olive fruits and that ingestion and subsequent regurgitation has a positive effect on seed germination. Interestingly, germination was enhanced by a limited time in the starling's digestive system (30 min). Our findings stand in contrast to a previous study where Kindschy (1998) detected no difference in seed germination between those fruits digested by European starlings (10.4%) and whole Russian olive fruits (9.8%). One possible difference from our study was that Kindschy apparently did not include a cold storage component in his germination study. Nonetheless, we have shown that European starlings may act as a potential dispersal vector.

Russian olive fruits are palatable and contain high amounts of carbohydrates (83.8% N-free extract; National Research Council 1971), which makes them attractive feed for European starlings and many other bird species. Indeed, Van Dersal (1939) observed American robins (*Turdus migratorius*), ring-necked pheasants (*Phasianus colchicus*), sharp-tailed grouse (*Tympanuchus phasianellus*), cedar waxwings (*Bombycilla cedrorum*), Hungarian partridge (*Perdix perdix*), northern bobwhite (*Colinus virginianus*), western evening grosbeak (*Coccothraustes vespertinus*), valley quail (*Callipepla californica*), and Bohemian waxwings (*Bombycilla garrulus*) feeding upon Russian olive fruits and Borell (1951) documented 28 additional bird species that too feed on Russian olive fruits. Our research clearly showed that European starlings readily consumed Russian olive fruits under controlled conditions and in the wild. Under controlled conditions, European starlings regurgitated Russian olive seeds about 30 min following consumption suggesting that they could be a dispersal vector if they took flight after consuming fruits, which is unlikely because entirely or partially frugivorous birds often remain in trees after feeding bouts (Pratt and Stiles 1983). If, however, European starlings took flight before regurgitating seeds, we calculated the maximum distance they may

Figure 2. A flock of European starlings feeding on Russian olive fruits. Note the bird in the circle flying off with a fruit in its beak.

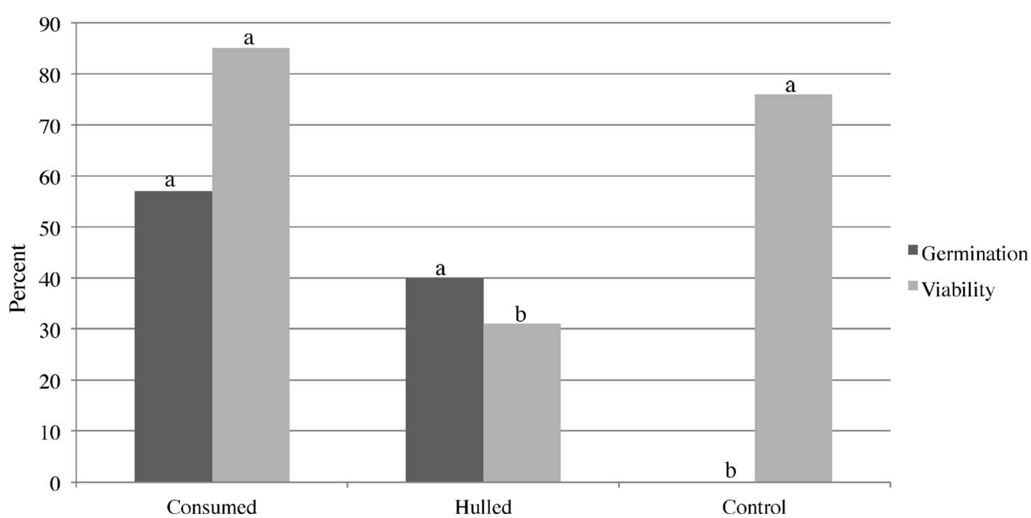

Figure 3. Percent germination and viability of Russian olive seeds consumed by European starlings compared to hulled (pericarp manually removed) and control (whole fruits); means were square root transformed but presented in their original scale. Compare means only within a category (germination or viability); means followed by the same letter are not different, Fishers Protected LSD ($\alpha = 0.05$).

disperse a Russian olive seed after consumption. European starlings' average flight speed is 60 to 80 km/h (37 to 50 mph) (Cabe 1993); thus if a bird takes flight shortly after consumption, it may disperse Russian olive seeds up to 30 to 40 km 0.5 hr^{-1} or 19 to 25 radial miles from the origin.

Several key observations were made from our experiments on the behavior of European starling feeding. It became obvious in the late fall/early winter that European starlings seemed to congregate in Russian olive trees readily feeding upon fruits still on the branches. Our original intent was to document that starlings would feed upon Russian olive fruits and then defecate the digested seeds. Some seeds exhibited a darkened exterior, indicating that, indeed they had been digested and passed through the whole digestive tract of the birds. However, these seeds were rare and accounted for a small portion of the whole. Video analysis of the controlled feeding study showed that the majority of fruits fed upon by European starlings were regurgitated within 30 min of feeding. Birds consumed between seven to nine seeds within the first few minutes of fruit/seed introduction in the morning. After 30 min, birds were observed regurgitating Russian olive seeds, followed by consumption of one or two more seeds. Birds typically consumed the 25 seeds allotted to them within 4 h. When fed seeds were collected, the pericarp had been completely removed leaving the stripped hard seed. This lack of fleshy pulp suggests that the birds were digesting off the easy to remove pericarp and then expelling the hard seed. This digestive process likely occurred in the bird's proventriculus, or glandular stomach, where acid and digestive enzymes breakdown food before it is passed to the gizzard, or muscular stomach, where physical abrasion of food occurs. Viability testing from TZ analysis indicated that seeds that had been ingested by European starlings were still viable and scarification by the bird had not damaged the embryo (Figure 3). The birds' digestive tract simply removed the pericarp and left seeds in a more germinable state (Figure 3).

Hamilton and Carpenter (1976) found that Russian olive seed dormancy was related to a coumarin-like inhibiting substance found throughout the seed. Jinks and Ciccarese (1997) removed the seed from the pericarp and observed an increase of 50 to 60% in Russian olive seed germination. This germination inhibitor may act as a natural dispersal mechanism where fruits must be consumed by animals to digest off the pulp and in turn transported to a new location away from the parent thus avoiding intraspecific competition from adults and as a consequence, spread to new areas.

Our data clearly show that European starlings will consume Russian olive fruits and removal of the pericarp by ingestion increases germination compared to whole fruits. Our data and the many published observations that other birds and mammals feed on Russian olive indicate that it is dependent upon animals for effective spread.

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